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Leen Depauw

Global-change effects on understorey community trajectories in European temperate deciduous forests: the mediating role of land-use history and forest management

Thesis submitted in fulfilment of the requirements for the degree of Doctor (PhD) of Bioscience Engineering: Natural Resources

Dutch translation of the title:

Effecten van globale milieuveranderingen op veranderingen in kruidlaaggemeenschappen in gematigd loofbos in Europa: het belang van landgebruiksgeschiedenis en bosbeheer

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3 februari 2020



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SUMMARY

Summary

Temperate forests are considered as one of the most important ecosystems in the world, since they constitute an important source of biodiversity and provide a wide range of ecosystem services that are important to human well-being. Yet, their composition and functioning is being altered by several human-induced global environmental changes, most importantly climate change, atmospheric deposition of acidifying and fertilizing compounds, and land-use changes. Research on the impact of global environmental changes on forests has expanded over the last decades, but the majority of studies focused on the effect of single drivers over short time periods. Moreover, studies that do consider multiple drivers often do not account for land-use legacies, despite its demonstrated importance for explaining the contemporary structure and function of forests. This limits our ability to make accurate and robust predictions about the effects of global change on the future composition and functioning of forests.

Here, we aimed to disentangle the impact and importance of different environmental changes that are simultaneously affecting forests: (i) climate change (temperature and precipitation), (ii) nitrogen deposition and (iii) land-use changes (comprising forest management and land cover changes). We zoom in on a very important but often overlooked part of the forest: the herb layer (also called 'the understorey'), which contains the majority of plant biodiversity in temperate forests and plays a crucial role in forest functioning. In this PhD, we addressed the following main research question: **are impacts of multiple global-change drivers on forest understorey community changes over time dependent on the land-use history?** Specifically, we asked whether there were different responses to environmental change in ancient and recent forests. Ancient forests are forest sites without any known agricultural use, since at least 1810, while recent forests are forest sites on abandoned agricultural land. Furthermore, we addressed methodological questions related to the quantification of two of the major drivers of herb layer dynamics, i.e. canopy characteristics (reflecting light availability at the forest floor) and land-use history.

We performed vegetation resurveys in 192 plots spread across nineteen regions within the European temperate deciduous forest biome. This spatio-temporal study design allowed us to determine long-term temporal shifts in community composition across multiple regions spanning gradients in environmental change factors. Within each region, we aimed at maximizing differences in land-use history between plots by sampling in ancient vs. recent forest. We assessed both biodiversity-related and functional aspects of the herb layer composition, including species richness, Shannon diversity, species evenness, beta diversity, mean indicator values for the light-and nutrient requirements of the community, herb layer productivity, and the community weighted mean values of plant height and specific leaf area.

Summary

Our findings clearly demonstrated that responses in herb layer composition to changes in climate, nitrogen deposition and light availability depend on the land-use history of the forests. In general, light availability was the most important driver for compositional changes in the herb layer, suggesting that forest management – a rather straightforward tool to control light levels at the forest floor – could be used for forest adaptation to (future) consequences of global change. Importantly, time lags should be taken into account, meaning that the present-day herb layer composition might be more related to past (e.g. a few decades ago), rather than current, light levels at the forest floor. Moreover, herb layers in recent forests were less responsive to altered light levels than herb layers in ancient forests. Similarly, the sensitivity of the herb layer to increased temperatures and nitrogen deposition depended on the land-use history, as increased temperatures caused decreases in the total cover of the herb layer in recent forests, but not in ancient forests, while increased nitrogen deposition only caused herb cover decreases in ancient forests. These findings clearly demonstrated the importance of land-use legacies from former agricultural use. Importantly, legacies were not only reflected by expected differences in soil nutrient contents, but also by unexpected differences in canopy composition.

In addition, we addressed one of the main challenges associated with land-use history related research: the quantification of past land-use changes. We proposed a generally applicable modelling framework, which could assist future forest research to go beyond simplistic land-use history classification (such as ancient vs. recent forests) and include all available details on the past land use when predicting herb layer changes. Our framework is based on the idea that past land use affects current (and future) ecological properties through altering past resources and conditions that are the driving variables of ecosystem and community responses.

In sum, this PhD showed the complexity of forest dynamics in response to different local and regional environmental drivers. We specifically highlighted the importance of considering the landuse history of forests in order to make robust and accurate predictions for the future development of forests, their biodiversity and functional role, under global change.

> ... 111

SAMENVATTING

Samenvatting

Gematigde bossen behoren tot één van de belangrijkste natuurlijke ecosystemen ter wereld. Ze zijn een belangrijke bron van biodiversiteit en voorzien de mens van een waaier aan cruciale ecosysteemdiensten. De samenstelling en het functioneren van deze bosecosystemen is momenteel echter in verandering door menselijk veroorzaakte globale milieuveranderingen (*global change*), zoals klimaatverandering, atmosferische depositie van verzurende en bemestende stoffen, en veranderingen in landgebruik. Onderzoek naar de impact van globale milieuveranderingen op bossen is de afgelopen decennia enorm toegenomen, maar de meerderheid van deze studies focuste op de effecten van alleenstaande *global-change drivers* ("oorzaken") over korte tijdsintervallen. Bovendien houden studies die wel rekening houden met het simultaan optreden van meerdere *global-change drivers* vaak geen rekening met de geschiedenis van het landgebruik, ondanks het bewezen belang ervan voor het verklaren van de huidige structuur en functie van bossen. Dit beperkt ons vermogen om nauwkeurige en robuuste voorspellingen te doen over de effecten van globale milieuveranderingen op de toekomstige samenstelling en het functioneren van bossen.

De doelstelling van deze thesis was om de impact en het belang van verschillende milieuveranderingen die tegelijkertijd bossen beïnvloeden, te ontrafelen: (i) klimaatverandering (temperatuur en neerslag), (ii) stikstofdepositie en (iii) veranderingen in landgebruik (bosbeheer en verandering van landbedekking). We zoomen in op een zeer belangrijk, maar vaak over het hoofd gezien deel van het bos: de kruidlaag, die de meeste plantenbiodiversiteit in gematigde bossen bevat en een cruciale rol speelt in het functioneren van bossen. In dit doctoraat hebben we de volgende hoofdonderzoeksvraag behandeld: zijn de effecten van meerdere global-change drivers op temporele veranderingen in de samenstelling van de kruidlaag afhankelijk van de geschiedenis van het landgebruik? We vroegen specifiek of de kruidlaag verschillend reageert op milieuveranderingen in oude en recente bossen. Oude bossen zijn bosgebieden zonder enig bekend landbouwgebruik, sinds minstens 1810, terwijl recente bossen bosgebieden zijn op verlaten landbouwgrond. Verder hebben we methodologische vragen behandeld met betrekking tot de kwantificering van twee van de belangrijkste factoren voor de dynamiek van de kruidlaag, zijnde de karakteristieken van de boom- en struiklaag (representatief voor de lichtbeschikbaarheid op de bosbodem) en de geschiedenis van het landgebruik.

We deden vegetatie heropnames in 192 proefvlakken verspreid over negentien regio's binnen het bioom van Europees gematigd bladverliezend bos. Deze combinatie van het ruimtelijk en temporeel aspect stelde ons in staat om veranderingen over de tijd in de kruidlaaggemeenschap op lange termijn te bepalen langsheen een ruimtelijke gradiënt in omgevingsfactoren. Binnen elke regio streefden we naar het maximaliseren van verschillen in landgebruik geschiedenis tussen percelen door bemonstering in oud versus recent bos. We analyseerden zowel

Samenvatting

biodiversiteitsgerelateerde als functionele aspecten van de kruidlaagsamenstelling, waaronder soortenrijkdom, Shannon diversiteit, *species evenness* (de mate waarin elke soort een gelijkaardige abundantie heeft), bètadiversiteit, gemiddelde indicatorwaarden voor de licht- en nutriëntenbehoefte van de gemeenschap, kruidlaagproductiviteit en de gemiddelde planthoogte en specifiek bladoppervlak.

Onze bevindingen hebben duidelijk aangetoond dat veranderingen in de kruidlaag samenstelling veroorzaakt door veranderingen in het klimaat, de stikstofdepositie en de lichtbeschikbaarheid afhankelijk zijn van de geschiedenis van het landgebruik. Over het algemeen was lichtbeschikbaarheid de belangrijkste driver voor veranderingen in de samenstelling van de kruidlaag, wat suggereert dat bosbeheer - waarbij lichtniveaus op de bosbodem kunnen gemanipuleerd worden - kan worden gebruikt om bossen aan te passen aan de (toekomstige) gevolgen van global change. Daarbij is het belangrijk om rekening te houden met de typisch trage dynamiek van de kruidlaag, waardoor deze als het ware 'achter komt' in de tijd, wat betekent dat de samenstelling van de huidige kruidlaag mogelijk meer bepaald wordt door lichtniveaus in het verleden (bijvoorbeeld enkele decennia geleden), dan door de huidige lichtniveaus op de bosbodem. Bovendien was de kruidlaag in recente bossen minder gevoelig voor veranderende lichtniveaus dan de kruidlaag in oude bossen. Ook was de gevoeligheid van de kruidlaag voor verhoogde temperaturen en stikstofdepositie afhankelijk van de geschiedenis van het landgebruik, aangezien verhoogde temperaturen leidden tot een afname in de totale bedekking van de kruidlaag in recente bossen, maar niet in oude bossen, terwijl een verhoogde stikstofdepositie enkel leidde tot een afname in de totale bedekking van de kruidlaag in oude bossen. Deze bevindingen toonden duidelijk aan dat het belangrijk is om de voorgeschiedenis van het landgebruik van bossen in rekening te brengen. We vonden immers dat deze voorgeschiedenis niet alleen - zoals verwacht een effect had op de nutriëntenbeschikbaarheid in de bodem, maar ook een - minder verwacht effect op de samenstelling van de boom- en struiklaag.

Daarnaast hebben we een van de belangrijkste uitdagingen aangepakt die gepaard gaan met onderzoek naar landgebruik geschiedenis: de kwantificering van voormalige veranderingen in landgebruik. We ontwikkelden een algemeen toepasbaar modelleringskader, dat toekomstig bosonderzoek kan helpen om verder te gaan dan de simplistische landgebruiksclassificaties (zoals oude versus recente bossen) en alle beschikbare details over het voormalige landgebruik in rekening te brengen bij het voorspellen van veranderingen in de vegetatiesamenstelling. Het voorgestelde modelleringskader is gebaseerd op het idee dat landgebruik in het verleden de huidige (en toekomstige) eigenschappen van ecosystemen beïnvloedt door het veranderen van de *resources* en condities in het verleden. Kortom, dit doctoraat toonde de complexiteit van bosdynamiek aan als reactie op verschillende lokale en regionale milieufactoren. We benadrukten specifiek het belang van het in rekening brengen van de geschiedenis van het landgebruik van bossen om robuuste en nauwkeurige voorspellingen te doen voor de toekomstige ontwikkeling van bossen, hun biodiversiteit en hun functioneren, onder *global change*.



ABBREVIATIONS

| °C | degrees Celsius |
|--------------------|---|
| AF | ancient forest |
| AIC | Akaike Information Criterion |
| Al^{3+} | toxic aluminium (3+) cation |
| С | carbon |
| C(WS) | coppice(-with-standards) |
| C/N-ratio | carbon/nitrogen-ratio |
| CC | canopy cover |
| CC | clear-cut (in Chapter 5) |
| CH ₄ | methane |
| CI | 95% confidence interval |
| CO_2 | carbon dioxide |
| CWM | community-weighted mean |
| DBH | diameter-at-breast-height |
| df | degrees of freedom |
| DIV | Shannon diversity |
| EIV | Ellenberg indicator value |
| EIV_{F} | Ellenberg indicator value for soil moisture content |
| EIV_{L} | Ellenberg indicator value for light |
| EIV _N | Ellenberg indicator value for nutrients |
| EMEP | European Monitoring and Evaluation Programme (www.emep.int) |
| Est. | estimate |
| EVEN | species evenness |
| FS | forest specialists |
| GRAM | graminoids |
| HF | high forest |
| HNO3 | nitric acid |
| IPCC | Intergovernmental Panel on Climate Change |
| k | extinction coefficient |
| LAI | leaf area index |
| LQ | litter quality |
| LT | light transmittance |
| LU | land use |
| LUH | land-use history |
| MAT | mean annual temperature |
| ML | moderate light |
| MS | moderate shade |
| N | nitrogen |
| N_2O | nitrous oxide |
| Ndep | nitrogen deposition |
| $\rm NH_3$ | ammonia |
| | |

| $\mathrm{NH_4}^+$ | ammonium |
|-----------------------|--|
| NMDS | non-metric multidimensional scaling |
| NO ₃ - | nitrate |
| NO _x | nitrogen oxide |
| Nr | biologically reactive nitrogen |
| ns | non-significant |
| Р | phosphorus |
| Р | probability (in Chapter 5) |
| Permanova | permutational multivariate analysis of variance |
| pН | measure of acidity |
| PLU | past land use |
| ppm | parts per million |
| Prec | precipitation |
| p-value or p | significance of statistical test |
| R ² | R squared or proportion of explained variance |
| R ² c | conditional R squared, i.e. explained by fixed and random factors |
| R ² m | marginal R squared, i.e. explained by fixed factors only |
| RCP | Representative Concentration Pathways (IPCC future emission scenarios) |
| REML | restricted maximum likelihood |
| RF | recent forest |
| RM | recent management |
| RR | response ratio |
| r _s | Pearson correlation coefficient |
| SC | shelter cut |
| SCA | shade-casting ability |
| sd | standard deviation |
| se | standard error |
| SL | strong light |
| SLA | specific leaf area |
| SR | species richness |
| SS | strong shade |
| Т | thinning (in Chapter 5) |
| Т | canopy transmittance (in Chapter 4) |
| TPM | Transition Probability Matrix |
| VIF | variance inflation factors |
| WP | wood pasture |
| ZC | zero cut |
| ZM | zero management |



CHAPTER 1

General introduction

1.1. HUMAN-INDUCED GLOBAL CHANGE

Human-induced global change drivers are causing ecosystem changes across the globe. The most important direct drivers of change in ecosystems are habitat change (land-use change), overexploitation, invasive alien species, pollution and climate change (Millennium Ecosystem Assessment, 2005). Warming of the climate system is unequivocal, and since the 1950s, many of the observed changes are unprecedented over decades to millennia. The atmosphere and ocean have warmed, the amounts of snow and ice have diminished, sea level has risen, and the frequency of extreme weather and climate events (such as heat waves and heavy precipitation events) has increased. The atmospheric concentrations of air pollutants such as carbon dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O) have increased to the highest levels recorded during the past 800,000 years. The heat-trapping effects of these greenhouse gases have been the main cause of the observed warming since the mid-20th century (IPCC, 2014).

It is extremely likely (at least 95 % probable) that human influence has been the dominant cause of the observed warming since the 1950s (IPCC, 2014). In fact, evidence that human activities are causing climate change has reached a 'gold standard' level of certainty, meaning that scientists are 99.999 % sure (Santer et al., 2019). Fossil fuel combustion and land-use changes (mainly deforestation) are the main drivers of increased CO_2 concentrations. Sectors that emit large amounts of CH_4 include animal husbandry, waste/landfills and agriculture. Agriculture (soil and animal manure management) is also the main anthropogenic source of N_2O (IPCC, 2014). Despite the overwhelming evidence of the potentially irreversible human impact on our environment (e.g. 'World scientist's warning to humanity: a second notice' - Ripple et al. (2017)), economic systems as well as political decisions are lagging behind in their efforts to avoid major global environmental change (Hulme, 2016; International Energy Agency, 2017; Lockwood, 2013; Rogelj et al., 2016).

1.2. FORESTS AND GLOBAL CHANGE

Forests cover roughly 40 million km², which is 30.6 % of the global land area (FAO, 2016), and are considered as one of the most important ecosystems in the world, since they constitute an important source of biodiversity and provide a wide range of ecosystem services that are important to human wellbeing (Brockerhoff et al., 2017). Importantly, forests have the ability to mitigate global change. They can reduce greenhouse gas concentrations as they absorb roughly 2 billion tonnes of CO₂ equivalent each year (FAO, 2018). Moreover, forests sustain the hydrological cycle through evapotranspiration, which cools climate through feedbacks with clouds and precipitation (Bonan, 2008). Forests can further contribute to global change protection through offering environmental (e.g. erosion protection, biodiversity conservation) and socio-economic (e.g. sustainable wood production, recreation) benefits (Canadell & Raupach, 2008; Nabuurs et al., 2007). While having great potential to mitigate climate change, forests are also threatened by anthropogenic activities and the associated environmental changes. Below, we discuss how the three most important anthropogenic threats to temperate forests, i.e. climate change (2.1), increased atmospheric deposition of nitrogen (2.2), and land-use change (2.3) (Bonan, 2008), and possible interactions between past land use and environmental changes (2.4) can affect forests and their functioning. In this PhD, we zoom in on a very important but often overlooked part of the forest: the herb layer (also called 'the understorey'). Although trees are the dominant feature of forests, the herbaceous layer typically contains a much higher number of species. For example, in temperate forests in Europe, the ratio between the species richness of the herb layer and that of the overstorey tree layer varies between 2.0 and 10.0 (median, 5.1) (Hermy, 2015). Similarly, the herbaceous layer contains the majority of plant biodiversity in North American temperate forests (Gilliam, 2007). Furthermore, the herb layer plays a crucial role in several aspects of forest functioning, such as litter production, nutrient cycling, evapotranspiration, tree regeneration, pollination and pathogen dynamics (Landuyt et al., 2019).

1.2.1. Climate change

Human activities are estimated to have caused approximately 1.0° C (± 0.2° C) of global warming above pre-industrial levels (1850-1900) (IPCC, 2018). Under the best-case scenario¹, future temperature increases for Central and Western Europe are projected between 1-1.5°C for 2081-2100 relative to 1986-2005; for the worst-case scenario², this would be 4-5°C (IPCC, 2014). Besides global warming, climatic changes are also reflected in altered precipitation levels, but here, future projections for Central and Western Europe are more uncertain and depend on the assumed scenario (e.g. +0-10% for the best-case scenario, -10 to +30% for the worst-case scenario, for 2081-2100 relative to 1986-2005) (IPCC, 2014). In general, precipitation is likely to increase in winter but decrease in summer in Central Europe (Christensen et al., 2007). Finally, an increase in the frequency of extreme weather events, such as heat waves, droughts, cyclones and heavy precipitation events can be expected (IPCC, 2014).

Climate change is driving latitudinal and altitudinal shifts in species distribution worldwide, leading to novel species assemblages (Bertrand et al., 2011; Parmesan & Yohe, 2003). Such shifts have been demonstrated to occur in the forest understorey, among other ecosystems. For example, with increased temperatures, cold-tolerant plants are replaced by warmth-preferring species, a process described as thermophilization (De Frenne, Rodriguez-Sanchez, et al., 2013). Similarly, more frequent heat waves and droughts may favour drought-tolerant species (Helm et al., 2017). Climate change can also affect the herb

¹ The best-case scenario (RCP2.6) is a stringent mitigation scenario that aims to keep global warming likely below 2°C above pre-industrial temperatures, and is characterized by substantial net negative emissions by 2100, with CO₂-equivalent concentrations of 425 ppm (IPCC, 2014).

² The worst-case scenario (RCP8.5) is a scenario without additional efforts to constrain emissions, resulting in CO_2 -equivalent levels of more than 1200 ppm by 2100 (IPCC, 2014).

layer composition indirectly, through altering canopy characteristics. For example, tree mortality because of disturbances such as extreme summer droughts (Archaux & Wolters, 2006; Peterken & Mountford, 1996) and storms (Seidl et al., 2017) result in canopy gaps and increased light availability at the forest floor. Such disturbances pave the way for immigration of new herb layer species that are better adapted to higher light levels (Helm et al., 2017). Moreover, alterations in the canopy structure and composition can reduce microclimatic buffering effects, as was shown by De Frenne et al. (2015), who found that increased light availability accelerated the thermophilization of understorey communities in forests. All this reshuffling in herb layer communities due to these direct and indirect effects of climate change will strongly influence herb layer biodiversity and functioning. In general, forest plant species are likely to be vulnerable to changing environmental conditions, as they are adapted to the stable environmental conditions of forests (Hermy, Honnay, Firbank, Grashof-Bokdam, & Lawesson, 1999; Verheyen, Honnay, Motzkin, Hermy, & Foster, 2003). They usually have low migration rates, which may prevent them following the current rate of climate change, making them vulnerable to (local) extinction (Van Der Veken et al., 2004).

1.2.2. Atmospheric nitrogen deposition

Since the agricultural and industrial revolutions, atmospheric concentrations of reactive nitrogen (N_r) have increased tremendously. N_r includes all biologically active, chemically reactive and radiatively active N compounds in the atmosphere and biosphere of the Earth, thus comprising inorganic reduced forms (e.g. NH_3 , NH_4^+), inorganic oxidized forms (e.g. NO_x , HNO_3 , N_2O , NO_3^-), and organic compounds (e.g. urea, amines, proteins) (Bobbink et al., 2010). Major anthropogenic sources of N_r are combustion of fossil fuels and biomass and emissions from fertilizer and manure (Dentener et al., 2006). Several studies indicate substantial further increases of N_r emissions toward 2050 and 2100, with increasing food and energy requirements of a growing human population (Dentener et al., 2006; Galloway et al., 2004; Lamarque et al., 2005).

The majority of the Nr emitted to the atmosphere is deposited to the Earth's surface following transport through the atmosphere, causing multiple impacts on the biodiversity of the receiving ecosystems (Bobbink et al., 2010). Accumulation of N compounds, resulting in higher N availabilities and changes of plant species interactions ultimately leads to changes in species composition, plant diversity, and N cycling. Furthermore, inputs of nitrogen compounds can lead to soil acidification, increased leaching of base cations, increased concentrations of potentially toxic metals (e.g. Al³⁺), a decrease in nitrification, and an accumulation of litter (Bobbink et al., 2010; de Vries, Reinds, & Vel, 2003; Ulrich, 1991). Levels of N deposition received by the understorey may be higher compared with other vegetation types due to the high filtering effect of the canopy, with its high aerodynamic roughness and large intercepting surface (Fowler et al., 1999). In general, we would expect increased N deposition to cause drastic shifts in species

composition and reduce herb layer biodiversity, as N-efficient species will disappear in favour of a few dominant nitrophilic species (Gilliam, 2006). While several studies, both experimental and observational, confirm these expectations (see Bobbink et al. (2010) for a review), other studies did not find clear evidence of diversity losses and community restructuring driven by N deposition (e.g. a meta-analysis by De Schrijver et al. (2011)). Understanding the impact of increased N deposition on the forest herb layer is complicated by interactions with other system properties, such as light availability and background soil nutrient availability (Perring, Diekmann, et al., 2018). In forest ecosystems that are nitrogen-limited, small increases in nitrogen availability may cause large changes in community composition (Hedwall & Brunet, 2016). Moreover, P-limitations may hamper plant growth responses to increased nitrogen availability (Hedwall & Brunet, 2012) observed an apparent resistance of forest understorey communities to species losses with chronic N additions, due to simultaneous chronic decreases of light availability, but warn that opening up the forest canopies may change this resistance as light becomes a less limiting resource. In general, several studies have highlighted that other limiting factors, such as soil phosphorus and light availability, can mediate vegetation responses to N deposition.

1.2.3. Land-use changes

Land-use changes involve land cover and management intensity changes (Foley et al., 2005). On a global scale, a net deforestation took place between 1990 and 2015 (-1.29 million km²; FAO, 2015). The largest forest area losses occurred in the tropics, while forest area increased in the temperate zone (FAO, 2016). Temperate forests, particularly in Europe, have a very long history of human use (Bengtsson et al., 2000; Gossner et al., 2014; Rackham, 2003). An increasing proportion of today's European forests has developed on land that has been cleared for other, mainly agricultural, land uses in the past (Flinn & Vellend, 2005). In addition, during recent decades, management intensity has generally decreased in European temperate forests due to (i) a more protected status (e.g. under the EU Habitat Directive) for many semi-natural deciduous forests because of their conservation values, and (ii) large-scale abandonment of coppice or coppice-with-standards management in favour of high forest management (Kirby & Watkins, 1998; McGrath et al., 2015). A common feature of many forest plants is their long life span (Ehrlén & Lehtilä, 2002), and therefore, impacts of past land-use changes may be delayed and are still to come (Hermy, 2015).

1.2.3.1. Impact of management changes on the herb layer

Forest management affects herb layer composition mainly though altering light availability at the forest floor, which is a key resource for the growth and survival of forest understorey plant species (Plue et al., 2013). Compared to other environmental drivers of the forest understorey, such as climate change and atmospheric depositions, light availability acts on a very local scale, and can vary strongly within a single

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stand (Perot et al., 2017). Coppicing (i.e. a management system in which (some) trees and shrubs are regularly cut (2-30 years) (den Ouden et al., 2010)) leads to cyclic light variations at the forest floor (Ash & Barkham, 1976). The abandonment of this management practice reduces long-term average light availability, favouring shade-tolerant herbaceous species (Baeten, Bauwens, et al., 2009). Several studies have demonstrated that the abandonment of coppicing reduces species richness, as light demanding species characteristic for cyclic coppicing regimes disappear (Baeten, Bauwens, et al., 2009; Kopecký, Hédl, & Szabó, 2013; Müllerová, Hédl, & Szabó, 2015; Van Calster et al., 2007). Next to light availability, forest management activities can affect the forest understorey composition by altering the soil conditions through compaction of the soil or changing nutrient cycles (Ampoorter et al., 2011; Brunet et al., 2010; Godefroid & Koedam, 2004; Wagner et al., 2011).

1.2.3.2. Impact of past agricultural use on the herb layer

A history of agricultural use can have long-term consequences on plant species assemblages up to 2000 years after afforestation (Dupouey et al., 2002). Former agricultural use potentially affects vegetation both directly, by locally eliminating plants and propagules of forest species, and indirectly, by altering environmental conditions (Flinn & Vellend, 2005). Soils of post-agricultural forests (in this PhD referred to as 'recent forests') generally have higher pH and nutrient concentrations and lower organic matter content than soils of ancient forests (i.e. forest sites without a history of agricultural use since at least 1810; Hermy et al., 1999) (Flinn & Vellend, 2005; Koerner, Dupouey, Dambrine, & Benoit, 1997; Verheyen, Bossuyt, Hermy, & Tack, 1999). These altered soil conditions might hamper community recovery through recruitment limitations of ancient forest species (Hermy & Verheyen, 2007). In addition, dispersal limitations might be present, as ancient forest species are typically slow colonizers (Verheyen et al., 2003). Ancient forest plots are not necessarily richer in herb species than recent forests, but Peterken (1974) showed that ancient forest species are quality indicators and their diversity is a means to estimate the nature conservation value of forests (Hermy & Verheyen, 2007), because many of these ancient forest species' existence depends on the continuity of ancient forests on particular sites.

1.2.3.3. The challenge of quantifying past land use

Simple classifications, such as the ancient vs. recent forest distinction, can be used to characterize clear changes in land cover. However, if we want to account for more subtle land-use changes, such as shifts in management regime or intensity, more complex classification schemes or indices are needed. Again, qualitative, categorical definitions can be used, such as unmanaged vs. managed, or coppice (with standards) vs. high forest (e.g. da Silva et al., 2008; Müller et al., 2007; Paillet et al., 2010). Different quantitative approaches for assessing land-use and specifically forest management intensity have also been suggested, based on different aspects, such as the output of the system (e.g. yield or harvests), the
invested input (e.g. human efforts, materials), and the deviation of the system from a natural reference state (primary forests) (see Schall and Ammer (2013) for a review). For example, Kahl and Bauhus (2014) propose a Forest Management Intensity index (ForMI) based on inventory data of the living stand, stumps and dead wood. While their index was found to be applicable to a wide range of forest management types, it has the disadvantage that it can only assess management intensity for the last 30 to 40 years, depending on decay rates of stumps and dead wood. In general, most indices or classification schemes only consider contemporary land-use intensity, and do not capture past land-use changes (Luyssaert, Hessenmöller, Von Lüpke, Kaiser, & Schulze, 2011; Schall & Ammer, 2013). Hence, despite the growing awareness that past land use should be taken into account when predicting current and future herb layer composition (Perring et al., 2016), a quantitative measure of (changes in) *past* land-use intensity is currently lacking.

1.2.4. Interactions between land-use legacies and other environmental changes

Several recent studies have highlighted the importance of land-use legacies (i.e. the system properties resulting from past land use) in determining future ecosystem properties (Foster et al., 2003; Perring et al., 2016). Past land use has steered plant communities onto trajectories of change, through altering the resource availability and growing conditions that determine the community composition (Landuyt et al., 2019; Perring et al., 2016). These trajectories may be modulated by contemporary environmental changes such as climate change, nitrogen deposition and management changes (Perring et al., 2016). Therefore, this PhD focusses on potential interactions between the former agricultural land use of the forest and the ongoing environmental changes on the herb layer community dynamics.

Although specific studies that consider land-use legacies when projecting the effects of multiple environmental changes on future forest herb layer properties are rare, the literature provides insights in the interactive effects of resource alterations as key agents of ecological change. In general, the availability of water, nutrients and light will mainly determine the structure and functioning of plant communities (Craine et al., 2012). Understanding the combined role of these resources, and how land-use history and environmental changes simultaneously alter their availability, can help to predict how plant communities will evolve under global change. For instance, increased nitrogen (N) availability may promote plant growth in systems that have sufficient phosphorus (P) (such as many recent forests), while it may not enhance plant growth in P-limited systems (such as many ancient forests) (Hedwall et al., 2017, although note Treseder et al., 2001). Additionally, the availability of water for plants might be altered with climate change and changing light levels affecting evapotranspiration (Rind et al., 1990), but the droughtsensitivity of the system might depend on the land-use history: ancient forests typically have better developed organic soil layers than recent forests, improving their water storage capacity, and thus their

ability to mitigate the effects of a severe drought (Greiffenhagen et al., 2006; Von Oheimb et al., 2014). Another mechanism where interactions can occur is soil acidification: as ancient forests typically have a lower pH than recent forests, it can be expected that these soils enter the toxic aluminium buffer range $(pH_{H2O} < 4.2 \text{ sensu Ulrich}, 1991)$ sooner than recent forests in response to acidification. Furthermore, differences in nutrient availability between ancient and recent forest can lead to different responses to changing light levels, as the shade-tolerance spectrum of plants is wider on nutrient-rich sites than on nutrient-poor sites (Coomes, Kunstler, Canham, & Wright, 2009; Ellenberg, 1939; Heinken, 1995). This is consistent with the hypothesis that species cannot be simultaneously tolerant to multiple environmental stress factors (Niinemets & Valladares, 2006b).

1.3. RESURVEY STUDIES TO ASSESS TEMPORAL CHANGES IN THE HERB LAYER

To predict future plant responses to global-change drivers, many studies apply a so-called space-for-time substitution, using contemporary data on plant communities across spatial gradients in environmental drivers (Blois et al., 2013; De Frenne, Graae, et al., 2013). However, "time-for-time substitutions" (sensu De Palma et al., 2018), i.e. forecasting ecological changes based on past temporal changes may provide more realistic insights of ecosystem dynamics under global change (De Lombaerde et al., 2018). Therefore, the scientific value of long-term historical vegetation records is being increasingly recognized (Dornelas et al., 2013). Relocating and resurveying previously surveyed vegetation plots can provide valuable insights in temporal vegetation changes, particularly in systems that exhibit slower dynamics, such as plant communities in temperate forests (Kapfer et al., 2017; Verheyen et al., 2017).

The foundation of this PhD is a large dataset of vegetation resurveys, allowing us to assess actual *temporal* changes in both compositional and functional properties of the forest herb layer, such as different biodiversity metrics and community weighted mean indicator values and functional traits.

1.4. STUDY DESIGN

We selected 19 regions along spatial environmental gradients of atmospheric nitrogen deposition and climatic conditions (temperature, precipitation) within the European temperate deciduous forest biome (**Table 1.1, Fig. 1.1**). We then selected on average 10 forest plots per region, with a few exceptions (see **Table 1.1** and **Box 1.1**), resulting in a dataset of 192 study plots. The orthogonality of the study design (**Fig. 1.1**) allowed us to try and disentangle the separate effects of multiple environmental drivers on the response variables under study, using multilevel analyses with 'region' as a grouping variable. In multilevel modelling, a trade-off between sample sizes at different levels is often necessary, but in general, a large number of groups (here 'regions') is more important than a large number of individuals (here 'plots') per

group for accuracy and high power (Gelman & Hill, 2007; Hox et al., 2018). Therefore, our choice of selecting 19 regions, and 10 plots within each region, seems defendable.

The main plot selection criteria were the existence of prior understorey vegetation surveys (preferably at least 20 years ago, but we included one region with 17-19 year old vegetation data) and information on land-use history. Within the constraints of plot selection, we tried to minimize differences in parent material and topography among plots and regions. We aimed at maximizing differences in land-use history between plots within regions by sampling in ancient vs. recent forest, although this was not possible for all regions (**Table 1.1**). We define ancient forests as continuously forested since at least 1810, whereas recent forests have been afforested after 1810 (Hermy et al., 1999). Within the 57 recent forest plots, 31 plots were on former arable land, while 26 plots were on former grassland, but they were grouped to obtain a more balanced study design, given there were 135 plots located in ancient forests.

In May/June 2015/2016, we revisited all 192 plots. Local researchers (which were in some cases the original surveyor of the vegetation plot) assisted us on the field, mainly with plot relocation and determination of local plant species. Plots were either rectangular or circular, and varied in size between 50 and 2500 m² (**Table 1.1**). With a minimum of two people, to minimize observer errors (cf. Verheyen et al., 2018), we performed a vegetation survey, i.e. for each structural layer (tree, shrub and herb) we visually estimated the cover (%) of each species. To assure comparability between our survey and the original survey, we followed the original definitions of the vegetation layers, which differed among regions. Next to the vegetation resurvey, where temporal comparability was the main objective, we collected additional samples and data in a standardized way across all plots, to assure spatial comparability of (i) general plot characteristics, (ii) soil structure and chemical properties, (iii) litter quality and quantity, (iv) stand structure and composition, and (v) individual tree growth using tree increment cores. We followed a detailed field protocol, provided in **Appendix A1.1**. To characterize the land-use history across all plots in a standardized way, we asked the regional contact persons to investigate the plot history through maps and literature (e.g. management plans), oral interviews, and expert knowledge, and to report their findings in a questionnaire.



Figure 1.1. Study design. Geographical distribution of the 19 forest regions where we collected data (A) and the environmental gradients covered by these regions (B). Mean annual temperature (°C), averaged over the 10 years prior to our sampling (in 2015/2016) and nitrogen (N) deposition in the year 2000 (kg ha⁻¹ yr¹) are plotted, with the symbol size reflecting the mean annual precipitation (mm) averaged over the 10 years prior to our sampling. Pearson correlation coefficients between N deposition and temperature, precipitation and temperature, and precipitation and N deposition are respectively 0.42 (p = 0.075), 0.01 (p = 0.968) and -0.24 (p = 0.320), demonstrating the orthogonality of the design. The labels refer to **Table 1.1**.

Table 1.1. Overview of the 19 forest regions where we collected data. The first column shows the abbreviation of each region, which will be used consistently throughout this PhD. Δt indicates the number of years between the original vegetation survey, and our resurvey (in 2015/2016). LUH (land-use history) shows the number of plots on ancient forest (AF) and recent forest (RF) in each region.

| ID | Region, Country | Δt (yr) | LUH | Plot size (m ²) |
|-----|------------------------|-----------------|------------|-----------------------------|
| BI | Bialowieza, PL | 31-50 | 15 AF | 50-400 |
| BS | Braunschweig, GE | 24-25 | 5 AF, 5 RF | 625 |
| BV | Binnen-Vlaanderen, BE | 35 | 4 AF, 5 RF | 150 |
| CO | Compiègne, FR | 47 | 10 AF | 200-2000 |
| DE | Devin, CZ | 52-62 | 3 AF, 7 RF | 100-600 |
| GO | Göttingen, GE | 48-60 | 10 AF | 100-400 |
| KO | Koda, CZ | 58 | 10 AF | 400 |
| LF | Lyons-la-forêt, FR | 43 | 10 AF | 300-1000 |
| MO | Moricsala, LV | 88 | 5 AF, 3 RF | 1250-2500 |
| PR | Prignitz, GE | 17-19 | 5 AF, 5 RF | 120-300 |
| SH | Schleswig-Holstein, GE | 29-31 | 5 AF, 5 RF | 64-400 |
| SK | Slovak Karst, SK | 32-40 | 10 AF | 500 |
| SKA | Skåne, SW | 31 | 8 AF, 2 RF | 500 |
| SP | Speulderbos, NL | 57-59 | 5 AF, 5 RF | 100 |
| ТВ | Tournibus, BE | 48 | 5 AF, 5 RF | 100 |
| W | Wales, UK | 45 | 5 AF, 5 RF | 200 |
| WR | Warburg Reserve, UK | 41 | 5 AF, 5 RF | 100 |
| WW | Wytham Woods, UK | 41 | 5 AF, 5 RF | 100 |
| ZV | Zvolen, SK | 51-52 | 10 AF | 500 |
| | | | | |

All plots comprised closed-canopy deciduous forests (mean canopy closure of 82 %, Fig. 1.2) with a variable tree and shrub layer composition, but we focused on plots predominantly composed of broadleaved species, although a higher occurrence of coniferous species in the easternmost regions with a hemiboreal climate (Moricsala (MO) and Bialowieza (BI)) was unavoidable. The canopies at the time of our survey consisted mainly of *Quercus robur/petraea* (110/192 plots), *Fagus sylvatica* (78/192 plots), *Fraxinus excelsior* (69/192 plots), *Carpinus betulus* (64/192 plots) in the tree layer and *Corylus avellana* (71/192 plots) in the shrub layer (see **Appendix A1.2** for an overview of the shrub and tree layer composition of all plots). Overall, the plots covered rather mesic site conditions, i.e. habitats with a moderate supply of moisture when compared with the full range encountered in temperate European forests (mean Ellenberg Indicator Value (EIV) of soil moisture of 5.4) (Leuschner & Ellenberg, 2017).



Figure 1.2. (adapted from Maes, 2019) Distribution of the main environmental change drivers excluding land-use history (mean annual temperature and precipitation, and nitrogen deposition), and several important local resources and conditions in the study plots (canopy closure, mean Ellenberg Indicator Value (EIV) of soil moisture, pH(KCl), and C/N-ratio). The axis limits of each variable are the full ranges encountered in temperate European forests, according to the following studies: Bobbink, Ashmore, Braun, Flückiger, & Den (2017); Dreiss & Volin (2014); FAO (2000); Leuschner & Ellenberg (2017); Weil & Brady (2017).

Box 1.1. Skåne – a unique dataset within the PASTFORWARD project

For Skåne (Southern Sweden), one of the 19 regions from our main dataset, we collected data following our standard protocol (Appendix A1.1) from 35 plots instead of only 10. For an additional 27 plots, vegetation resurvey data, chemical soil properties and land-use history and management information were available from another study. This resulted in a unique dataset containing three vegetation surveys (in 1983, 1993/94 and 2014), extensive soil data (1983 and 2014) and notes on forest management and past land use for 62 permanent plots in oak forest in Southern Sweden. In the early medieval period, a socalled infield-outland agricultural system emerged in the region, resulting in a distinction between plots on former outland, managed for grazing, and plots on former infields, intensively manured for crop production and hay (Emanuelsson, 2009; Emanuelsson et al., 2002). Hence, in this region, past land-use changes are defined as the distinction between former infields (nutrient-enriched) and former outland (nutrient-depleted), rather than the classical ancient/recent forest distinction. Chapter 2 of this PhD is entirely based on the Skåne dataset, as regional environmental change drivers are not yet assessed in this chapter. In the following chapters, a selection of 10 plots from the Skåne dataset is included in the larger dataset of 192 plots across 19 regions, to obtain a balanced design. For this subset, we selected 10 plots with similar site conditions (soil texture) with a good spatial distribution across the region, for which detailed historical maps were available to allow reconstruction of the past land use.

1.5. MAIN OBJECTIVES AND OUTLINE

This PhD was built upon the main postulate of the PASTFORWARD project, i.e. changes in herb layer communities are driven primarily by past land use, but can be modulated by atmospheric deposition, climate warming and forest management. Hence, the main objective of this PhD was to assess the interactive effects between former agricultural land use and climate change, nitrogen deposition and forest management intensity on temporal changes in the herb layer composition. In Chapter 2 and 3, we focus on this objective through assessing both biodiversity-related and functional aspects of the herb layer composition, which is important to obtain a complete understanding of the impact of future global change on plant communities, especially as several studies report a disconnect between biodiversity and functional changes (Li & Waller, 2017; Perring, Bernhardt-Römermann, et al., 2018). Biodiversity measures included species richness, Shannon diversity, species evenness, and beta diversity. Measures of functional change in the herb layer included (i) mean indicator values for the light- and nutrient requirements of the community - because we expect that the considered environmental drivers will mainly act on the availability of light and nutrients - (ii) herb layer productivity (reflected as the total cover of the herb layer) - for its overall importance for several functions of the herb layer (Landuyt et al., 2019) - and (iii) the community weighted mean values of plant height and specific leaf area - which are both related to resource acquisition and expected to respond strongly to environmental changes (De Frenne et al., 2015; Dubuis et al., 2013). Then, the following two chapters (Chapter 4 and 5) are methodological studies that are not directly focussed on investigating the impact of multiple globalchange drivers on the understorey composition, but address methodological questions related to the quantification of two of the major drivers of herb layer dynamics, i.e. canopy characteristics (reflecting light availability at the forest floor) and past land use.

Specifically, in **Chapter 2**, we focus on only one forest region (Skåne, Southern Sweden; see **box 1.1**), and assess the interactive effects of past agricultural land use and forest management intensity on the herb layer composition. In this region, forest plots on former infields (nutrient-enriched) can be distinguished from former outlands (nutrient-depleted), and plots across both past land-use types also differed in the level of management intensity they experienced since the original vegetation survey. This crossing of past land use with a two-level management intensity factor allowed us to investigate both their main and interactive effects on the composition and diversity of the forest understorey community over a period of three decades.

In **Chapter 3**, we expand our dataset to the full range of 19 regions and 192 plots across Europe, allowing us to also exploit a gradient in climate change and nitrogen deposition. Here, we can assess the interactive effects of land-use history (ancient vs. recent forest) with both local scale drivers of change (i.e. canopy

characteristics, controlling light availability at the forest floor) and regional scale drivers of change (i.e. climate change and nitrogen deposition) on compositional changes in the herb layer.

In **Chapter 4**, we zoom in on what we found to be one of the main factors controlling the herb layer composition, i.e. light availability. We investigate how well both structural and compositional attributes of the canopy can predict the herb layer light signature. This can be of particular interest with regard to vegetation resurvey studies, as it can provide insights in past light levels when shrub and tree layer data were also recorded during the original vegetation survey.

In **Chapter 5**, we address one of the main challenges associated with land-use history related research: the quantification of past land-use changes. We propose a generally applicable modelling framework, which could assist future forest research to go beyond simplistic land-use history classification (e.g. ancient versus recent forests) and include all available details on the past land use when predicting herb layer changes. Our framework is based on the idea that past land use affects current (and future) ecological properties through altering past resources and conditions that are the driving variables of ecosystem and community responses. We illustrate the application of the framework with a case study on a subset of 29 plots in three regions from our larger dataset. With this case study, we assess the importance of past forest management practices, affecting past light levels, for the contemporary herb layer composition.

In **Chapter 6**, we summarize and integrate the main findings of this PhD, highlighting the key environmental driver(s) affecting understorey community changes over time and the dependency of these effects on past land use. Furthermore, we will discuss how our findings can contribute to management recommendations to mitigate potential negative effects of future global change, and we will provide suggestions for future research avenues.







CHAPTER 2

Interactive effects of past land use and recent forest management on the understorey community in temperate oak forests in South Sweden

After:

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2.1. ABSTRACT

Past agricultural land use and forest management have shaped and influenced the understorey composition in European forests for centuries. We investigated whether understorey vegetation assemblages are affected by (i) legacies from a historical infield/outland agricultural system (i.e. a system with nutrient-enriched vs. nutrient-depleted areas), (ii) recent management intensity (i.e. thinning/felling activities), and (iii) the interaction of recent management and potential legacies. We use three vegetation surveys (1983, 1993/94 and 2014) and notes on management and land-use history, available for 62 permanent 500 m² plots in oak forests in Skåne, south Sweden. We conducted linear mixed effect modelling to detect both main and interactive effects of past land use and recent management on understorey diversity measures and vegetation indicator values for light and fertility. We combined nonmetric multidimensional scaling (NMDS) with permutational multivariate analysis of variance (PERMANOVA) and indicator species analysis to detect compositional differences caused by past land use and/or recent management. We found that understorey diversity was mainly affected by management activities, but the former infield/outland agricultural system was an important determinant of understorey composition. Understorey composition of former infields reflected higher nutrient availability and lower light availability compared to former outland. Past land use and recent management had interactive effects on light-related understorey variables: for the less intensively managed plots, the outland plots contained more light-demanding species than the infield plots, while for the more intensively managed plots, the light-demanding signature³ of the understorey was similar for infield and outland plots. We concluded that different intensities of past land use as well as recent forest management influenced the composition of the forest understorey, and interactions were present. Therefore, careful consideration of both the long-term land-use history and the more recent disturbances due to forest management are necessary when making future predictions of understorey composition and diversity.

2.2. INTRODUCTION

Forests worldwide, as well as most other ecosystems, have been dominated, shaped and influenced by human activities for centuries and more (Bürgi & Gimmi, 2007; Williams, 1993). Hence, the European forests that we know today were created by a long history of human land-use changes, and only very few forests exist free of legacies from former human influence (Bengtsson et al., 2000; Gossner et al., 2014). Human activities affecting forests are very diverse (Foster et al., 2003), comprising episodes of deforestation and agricultural use (Foster et al., 1998), wood harvesting with different levels of intensity

³ The term 'light-demanding signature' is used throughout this PhD-thesis as an overarching term representing one or more measures (e.g. Ellenberg indicator value for light) to indicate whether a community of plant species has high or low light requirements.

(Gossner et al., 2014), manipulation of animal populations (Foster et al., 2003), litter collecting (Bürgi & Gimmi, 2007), and grazing by domestic animals (Bengtsson et al., 2000). Understanding how both past and present anthropogenic disturbances influence biodiversity and species assemblages is essential for conservation. Here, we focus on two aspects of anthropogenic disturbances that are common in European forests, but which rarely have been studied in combination, namely different intensities of both past agricultural land use and current forest management practices for wood harvesting. We assess their effects on the forest understorey layer, which represents the majority of plant species richness in temperate forests (Gilliam, 2007). This layer is most likely to reflect land-use legacies because it exhibits slow dynamics and is less easily manipulated (by e.g. plantation) compared to the overstorey.

Most present-day European forests occur on lands that at some point in history were used for agriculture, and many studies have demonstrated that these forests still bear imprints of their past land use, which we call land-use legacies (Blondeel et al., 2019; Emanuelsson, 2009; Flinn & Marks, 2007; Hermy & Verheyen, 2007; Perring et al., 2016; Vellend, 2003). Land-use legacies are often found in forest understoreys, due to a limited dispersal and recruitment capacity of typical forest species (De Frenne, Baeten, et al., 2011; Verheyen et al., 2003). As a result, forest understorey compositions may depend on environmental conditions that no longer occur in a forest stand (Jonason et al., 2014). Land-use legacies affect the understorey directly, by past elimination of plants and their diaspores, as well as indirectly, by altering environmental conditions such as soil pH, soil nutrient concentrations, soil organic matter content and light availability (Flinn & Marks, 2007; Hermy & Verheyen, 2007). Several studies found that forest soils on former arable land are still richer in nutrients and hence more productive as a result of past fertilization practices, compared to so-called ancient forests without a history of agricultural use (Falkengren-Grerup, Ten Brink, & Brunet, 2006; Koerner et al., 1997; Naaf & Kolk, 2015; Verheyen et al., 1999). These higher nutrient contents in post-agricultural forests can influence the composition of the established vegetation after abandonment of cultivation, due to a dominance of competitive species which hamper the establishment of slow-colonizing herbs (Baeten, Hermy, & Verheyen, 2009; Koerner et al., 1997).

In addition, most European temperate forests are or have been managed for timber production, fire wood production and/or grazing, with varying levels of intensity (e.g. clear-cuts, shelterwood systems, coppicing, single tree selection) (Gossner et al., 2014; McGrath et al., 2015). Extracting timber changes the tree age structure, composition of tree species and vertical stratification, causing changes in the soil, litter and microclimatic conditions. This results in the alteration or disappearance of microhabitats (e.g. dead wood, cavities, root plates or mature trees) that host forest biodiversity (Chaudhary et al., 2016). According to a meta-analysis by Chaudhary et al. (2016), forest management generally induces an overall decrease in local species richness (i.e. alpha diversity), but the effect of forest management differs between taxonomic groups (such as vascular plants, birds, fungi, beetles), and depends on the management type

and intensity. For understorey vascular plants in particular, forest management can affect their diversity and composition through altering the light regime by creating canopy gaps at variable points in time, as well as the soil conditions, through compaction of the soil or changing nutrient cycles (Brunet et al., 2010; Godefroid et al., 2005; Godefroid & Koedam, 2004; Vangansbeke et al., 2015; Wagner et al., 2011). Importantly, one has to consider that the impact of forest management on biodiversity at a larger scale and within the context of heterogeneous landscapes may be different than plot-scale effects (Chaudhary et al., 2016). For example, Schall et al. (2018) showed that landscape-scale biodiversity responds positively to forest management, if silviculture creates a variety of environmental conditions at the regional scale. In general, we should keep in mind that the impact of forest management on plant biodiversity is a complex matter, depending on a range of biodiversity measures (e.g. local-scale vs. landscape-scale) and a range of management strategies (Schulze et al., 2016).

Here, we are interested in how both recent forest management and past land-use intensity differences may have interactive effects on understorey assemblages and their trajectories over time. Reasons to believe such interactions are present arise from a study by Huston (2004), pointing out the importance of the disturbance-productivity interaction as a determinant of species richness. Within this framework, we consider the intensity of forest management as the disturbance factor, and different intensities of past agricultural land use as a proxy for the productivity factor. Several other studies argue that diversity may be a function of the interaction between disturbance and productivity, and therefore the productivity effects on diversity can only be assessed when they are stratified by disturbance regimes (e.g. Kondoh, 2001; Huston, 2014). For example, Proulx and Mazumder (1998) demonstrated that plant species richness increases with increasing disturbance (in this case grazing pressure) in a nutrient-rich environment, but decreases in a nutrient-poor environment. Furthermore, several studies highlight the occurrence of interactions between legacies of past land use with natural disturbance processes such as forest fires, hurricanes and droughts (Chazdon, 2003; Comita et al., 2010; Foster et al., 2003; Hogan, Zimmerman, Thompson, Nytch, & Uriarte, 2016). We believe that forest management actions can have similar effects on the forest vegetation as natural disturbances, and hence can interact with land-use legacies as well. Several studies indeed showed possible interactions between past land-use changes and alterations in present conditions through management practices on species richness and composition (e.g. Janssen et al., 2018; Kelemen, Kriván, & Standovár, 2014).

In this study, we use a unique dataset containing three vegetation surveys (in 1983, 1993/94 and 2014), extensive soil data (1983 and 2014) and notes on forest management and past land use for 62 permanent plots in oak forest in Southern Sweden. Our aim is to assess the combined effects of both past land use and recent disturbances due to management on understorey composition and diversity. In the early medieval period, a so-called infield-outland agricultural system emerged in the region, resulting in a distinction between plots on former outland, managed for grazing, and plots on former infields,

intensively manured for crop production and hay (Emanuelsson, 2009; Emanuelsson et al., 2002). In addition, plots across both past land use types also differed in the level of management intensity they experienced since the first survey in 1983. This crossing of past land use with a two-level management intensity factor allowed us to investigate both their main and interactive effects on the composition and diversity of the forest understorey community over a period of three decades. In contrast to previous studies on interactions between past land use and recent management (e.g. Janssen et al., 2017; Kelemen et al., 2014; Kolb & Diekmann, 2004), we are defining past land-use change as a distinction between former infields (nutrient-enriched) and former outland (nutrient-depleted), rather than the classical ancient/recent forest distinction. Furthermore, we have the opportunity to investigate trajectories of change in the understorey communities, thanks to the availability of three vegetation surveys over a time span of three decades.

Specifically, we investigated the following research questions:

- (i) Are legacies from the former infield/outland agricultural system reflected in the community composition and diversity of the understorey? Have these land-used legacies changed over time?
- (ii) Does recent forest management intensity affect the community composition and diversity of the understorey?
- (iii) Have recent disturbances due to forest management interacted with land-use legacies, causing changes in the dynamics of the understorey composition and diversity between 1983 and 2014?

2.3. MATERIAL AND METHODS

2.3.1. Study area: past land use and recent management

The study area comprises the south Swedish province of Skåne, an area of ca 11 000 km² and ca 1.3 million inhabitants. The border between the central-European sedimentary bedrock area (here mainly limestones and clay shales) and the Fennoscandian shield of Precambrian crystalline rocks (granite and gneiss) crosses the province from southeast to northwest, resulting in a gradient from the more densely populated southwest with fertile agricultural soils to the northeastern part dominated by forests on less productive soils (**Fig. 2.1**, including forest distribution). Most soils have not developed directly upon bedrock but originate from Quaternary deposits formed during and after the latest (Weichselian) glaciation which completely covered Skåne with its icesheet.

We sampled 62 permanent forest plots, situated in forests dominated by oak (*Quercus robur* and in some cases *Quercus petraea*) and hornbeam (*Carpinus betulus*) in the tree layer. Distances between study plots varied strongly, ranging from 15 m to 111 km, with a median value of all distances between plots of 41 km.

To characterize the past land use of each plot, we distinguished between former infields and outland (Emanuelsson, 2009). A permanent infield-outland system emerged in the early medieval period when villages became sedentary. Infields were located close to settlements or farm-houses, and were intensively manured. The infields were either used for crop production or managed as semi-open wooded meadows which produced hay, small-dimension wood products from coppice, as well as some timber trees. The outland was situated further from villages, and was managed jointly by the village for grazing, timber and other wood-based products. The manure from grazers was then applied on the infield lands. The infieldoutland system was functional until ca. 1800-1850 (Emanuelsson et al., 2002). Outland area gradually reduced in extent with the increasing demand for arable land due to continuous population increase since the 1700s. Based on cadastral maps (mainly spanning the period 1730-1870) at the final phase of this land use system, (https://historiskakartor.lantmateriet.se/historiskakartor/search.html), we classified 23 plots as 'Outland' (i.e. plots on former outland), and 39 plots as 'Infields' (i.e. plots on former infields) (Appendix A2.1). According to the cadastral maps, none of the infield plots has been used as arable field since at least ca. 1800. The majority of the stands are semi-natural, and developed from semi-open conditions to closed stands when livestock grazing (outland) or wooded meadow/coppice management (infield) ceased. In some sites (both infield and outland), oak was planted after felling of the previous stand. The evidence of continuous presence of trees on the historical maps varies, but all plots have been wooded since at least 1900. In this region, 43 plots would be classified as ancient forest, according to our definition of being continuously forested since at least 1810, and 12 plots as recent forest. For 7 plots in the region, there was insufficient historical data to determine the land-use history in terms of the ancient/recent classification.



Figure 2.1. (a) Geographical location and distribution of the 62 study plots. The number of plots in each land use category, which is the combination of past land use and recent management intensity, is shown in the legend. (b) Mean cover (%) of the three most dominant tree species, as well as the total tree layer in each survey year. (c) Mean cover of the dominant tree species in 1983 for infield and outland plots. (d) Mean cover of the dominant tree species in 1983 for plots with high and low recent management intensity.

In the area, forests are or have been managed for timber production, comprising felling practices with different levels of intensity. In this study, we made a rough distinction between 31 plots that were more intensively managed over the period 1983-2014 (referred to as 'High' management), and 31 plots that were less intensively managed (referred to as 'Low' management). We combined the different management classification approaches applied during the three surveys to reach this final management category (**Appendix A2.2**). We gave the most weight to the 1993 classification, because (i) it had a higher level of detail as the surveyors were explicitly interested in vegetation responses to management, and (ii) management intensity in the area was at its highest level around 1993, so differences between more and less intensively managed plots should have been most clear during this survey. Counts of the number of stumps, available in a subset of 35 plots in 2014, confirmed our management classification, as we found significantly (p=0.005) more stumps in the more intensively managed plots (6.17 stumps on average) (see **Appendix A2.1** and **A2.2**).

2.3.2. Soil and overstorey characterization

During the 1983 and 2014 surveys, samples were taken from the upper 5 cm of the mineral soil (i.e. after removal of the litter layer). For 1983, we have data on clay content and pH_{KCl} (see previous studies, such as Brunet et al., 1996, Diekmann et al., 1999) for details on soil sampling and chemical analyses). For 2014, we have data on soil total carbon (C), nitrogen (N) and phosphorus (P) (see Appendix A2.3 for details on soil sampling and chemical analyses in 2014). Plots on former infields had a higher clay and total P content in the soil, compared to former outland. Since texture is an intrinsic property of the soil, the differences in clay content suggest that when the infield-outland agricultural system was established, richer and more clayey soils were often chosen deliberately for infield use, given their potential for higher yields. The higher total P concentrations in former infields are likely a result of their fertilization history, which can leave imprints for at least a few thousand years after abandonment of agricultural use (Compton & Boone, 2000; Dupouey et al., 2002; Fraterrigo et al., 2005; Koerner et al., 1997). Overall, the differences in soil chemistry between infield and outland plots are probably partly related to an initial preference for richer clay soils for infield use (Flinn et al., 2005), after which the more intensive land use on infields has probably reinforced the higher fertility and productivity that these soils exhibit. Plots with a lower recent management intensity had significantly higher soil pH values and total P content, likely caused by a higher degree of protection of richer oak forests, which are therefore less intensively managed. There were no significant differences in total C and N content between either the recent management or the past land-use categories (see Appendix A2.4 for soil data).

Regarding the overstorey characterization, plots with high and low intensity management had similar tree cover values in 1983 and 2014, while more intensively managed plots had a significantly lower tree cover during the intermediate survey in 1993, reflecting the peak in forest management activity in the region at the time of the intermediate survey. Dominant tree species were *Quercus robur* (or *Quercus petraea* in a few cases), *Carpinus betulus* and *Corylus avellana* (Fig. 2.1b). At the time of the first survey (1983), both former infield plots and less intensively managed plots were characterized by more *Carpinus betulus* and *Corylus avellana* (Fig. 2.1c/d). The shade-casting ability (SCA) of the tree layer (i.e. a cover weighted average of the SCA scores per species, listed in Appendix A2.5, adapted from Ellenberg (1996) and complemented with expert knowledge of prof. Kris Verheyen) was similar between infield and outland plots within the more intensively managed plots, but clearly higher for infield than outland plots within the less intensively managed plots (see Appendix A2.6). We keep these soil and overstorey characteristics in mind when interpreting the results.

2.3.3. Vegetation surveys

In July-August 1983, 135 permanent plots were established by Professor em. Germund Tyler to study the relationships between soil, macrofungi and tree and herb layer species (e.g. Tyler, 1989). All these plots were resurveyed a first time in July-August 1993/1994 (further referred to as 1993) and a second time in August 2014, although only 62 of the plots were relocated at that time. All plots were 500 m² (20 m x 25 m). Criteria for the original plot selection in 1983 included no current livestock grazing and no thinning during approximately the five years prior to surveying (Brunet et al., 1996; Diekmann et al., 1999). Vegetation data were expressed as an estimated cover percentage for each individual species present. Two vegetation layers were distinguished: the *understorey* and the *tree layer*, respectively comprising all vascular plants below 5 m and above 5 m height (see **Appendix A2.7** for details on the vegetation data).

2.3.4. Response variables

For each plot at each survey time, we characterized the understorey diversity by calculating the **Shannon diversity** (i.e. plot-level diversity), and the **Bray-Curtis dissimilarity** (Bray & Curtis, 1957) (i.e. diversity among plots). We quantified the Bray-Curtis dissimilarity of each plot by creating a pairwise dissimilarity matrix and calculating for each plot the mean of the dissimilarities to all other plots. To further enhance our understanding of the processes and mechanisms behind possible changes in understorey composition and diversity due to differences in past land use and recent management intensity levels, we investigated plot characteristics related to the soil and light conditions. As a proxy of the prevailing plot-specific soil properties and light conditions, we calculated **mean Ellenberg indicator values for soil fertility (N) and light (L)**, based on presence/absence using the individual species' indicator values (Ellenberg & Leuschner, 2010). We based our calculations of indicator values on species' presence/absence rather than abundances, because this is the recommended approach when vegetation surveys are done by different observers, as inter-observer differences in cover estimation may distort the analysis (Diekmann, 2003).

2.3.5. Statistical analyses

To test how contemporary management intensities interact with past land use to alter the plot characteristics over time, we conducted linear mixed effect modelling with four response variables related to the understorey (and described above): Shannon diversity, Bray-Curtis dissimilarity, Ellenberg N, and L mean values. We confirmed that each response variable is normally distributed, using histograms.

We found the optimal model for each response variable according to the approach described by Zuur, Ieno, Walker, Saveliev, and Smith (2009), starting from the *beyond optimal model* (**Equation 2.1**).

Response variable ~ PastLandUse + Management + Year + PastLandUse:Management + PastLandUse:Year + Management:Year + (1 | PLOT ID) Equation 2.1

We added the variable Year to the model as a fixed effect, because we are interested in how each response variable has changed over time. We modelled Year as a factor with three levels (i.e. 1983, 1993 and 2014), rather than a continuous variable, to detect possible shifts in trends between the first period (1983-1993) and the second period (1993-2014). Management (High or Low) and Past Land Use (Infield or Outland) were both factors with two levels. To account for temporal pseudoreplication, given the fact that each plot was surveyed three times, we added PLOT ID to the model as a random intercept. We added the interaction between past land use and management to the model, to investigate whether the effect of recent management practices on the response variables is dependent on the past land use category. For both past land use and management, we also added the interaction with Year to the model; to study whether the response variables exhibit different temporal trends for different past land use or recent management categories. To detect possible multicollinearity among the explanatory variables, we calculated variance inflation factors (VIF) according to Zuur et al. (2009). VIF values were very low (<1.1), indicating low collinearity.

Next, we performed backwards elimination of the explanatory variables using maximum likelihood-fitted models at a 5% level of significance (Zuur et al., 2009), leading to the optimal model. For each response variable, we refitted the optimal model with restricted maximum likelihood (REML). For the final (optimal) model of each response variable, we inspected model diagnostic plots to check validity; all were satisfactory. For each model, we calculated the marginal and conditional R², representing the variance explained by fixed factors and the variance explained by both fixed and random factors, respectively (*MuMIn* package; (Nakagawa & Schielzeth, 2013)). Given the high number of parameters in the *beyond optimal model*, compared to a sample size of 62 plots, there is a possibility of overfitting. Therefore, we also performed a model comparison based on information criteria (AIC), which resulted in the same final (optimal) model for each response variable (**Appendix A2.8**). Additionally, we repeated the backwards elimination procedure for separate models for each year, which reduces the number of explanatory variables and thus the risk of overfitting. This additional analysis led to identical qualitative findings for all response variables except Ellenberg N, where an effect of recent management was identified in 2014 that was absent in other analysis approaches (**Appendix A2.9**).

To evaluate differences in understorey community composition in each survey year, between former infield plots and former outland plots, and between plots with high and low levels of management intensity, we conducted a permutational multivariate analysis of variance (PERMANOVA; *vegan* package; Anderson, 2001) using Bray-Curtis dissimilarities with 999 permutations (based on abundance data; Bray & Curtis, 1957). A significant PERMANOVA can result from differences among groups in their mean (centroid) values or the dispersion (i.e. spread) of values around the centroid of each group (Anderson et

al., 2006; Brudvig et al., 2013). The Bray-Curtis dissimilarity as described above (and used in the linear mixed effect modelling) on the other hand, only contains information on the dispersion. Hence, a PERMANOVA analysis can reveal compositional differences among groups resulting from differences in their mean (centroid) values, which would be overlooked when only focussing on the Bray-Curtis dissimilarity. We followed the PERMANOVA with a test for homogeneity of multivariate dispersion (PERMDISP), which evaluates the mean distance of each plot to the group centroid (Brudvig et al., 2013). We used nonmetric multidimensional scaling (NMDS) to visualize the compositional differences in the understorey vegetation. To identify species that typified the different plot groups (i.e. former infields vs. outland, and high vs. low intensity management), we also conducted an indicator species analysis (Dufrêne & Legendre, 1997) for the understorey data in each survey year, with the infield/outland and the high/low management distinction as classification variables (function *multipatt; indicspecies* package; Ampoorter et al., 2015; De Cáceres & Legendre, 2009). We performed t-tests to compare the mean Ellenberg N and L values of the indicator species.

To visualize changes in the understorey composition over time, for the different land-use and management categories, we made a NMDS plot showing the mean and standard error of the NMDS coordinates of the plots for each of the 12 plot groups, i.e. all possible combinations of survey year, past land use and recent management. To facilitate interpretation, we added the following variables to the NMDS-plot: Ellenberg N and L, tree cover, shade-casting ability, soil total P and clay content, and soil pH. All data analyses were performed in R version 3.4.3 (R Core Team, 2017).

2.4. RESULTS

For all four models, marginal R^2 (R^2m) was quite low (between 0.06 and 0.17) (**Fig 2.2; Appendix A2.10**), suggesting that the fixed effects *Year*, *Past Land Use* and *Disturbance* only explained a small part of the variance. Values for conditional R^2 (R^2c) were higher (between 0.48 and 0.86), indicating that a high proportion of the variance can be explained by the random effect *PLOT ID*. This suggests that other (unmeasured or unmodelled) variables could be important. We did not investigate such variables as the focus of our study was to detect main and interactive effects of past land use intensity and recent management.



Figure 2.2. Temporal changes in mean values (and standard errors) of the four response variables representing understorey diversity and composition. The level of recent disturbance by forest management is indicated by the line color (red = high; blue = low), while the past land use category is indicated by the line type (continuous = infield; dotted = outland). Below each graph, the significant predictors that were retained in the final model of the response variable are shown, with their level of significance ('***' for p<0.001; '**' for p<0.01; '*' for p<0.0.5). Interactions between predictors are indicated with ':'. The marginal and conditional R^2 (R^2m and R^2c respectively) for the final model of each response variable are also given. See **Appendix A2.10** for the full model results.

For both the Bray-Curtis dissimilarity (beta diversity) and the Shannon diversity (alpha diversity), the only significant predictor that was retained after model selection was the factor *Year* (**Fig. 2.2**; **Appendix A2.10**). Hence, these diversity measures changed significantly over time, but the changes were not related to either the past land use or recent management category. The Shannon diversity index increased significantly between 1983 and 1993 (+0.27 on average), but then decreased again to a level not significantly different from the original 1983 level. Bray-Curtis dissimilarity only started to increase significantly after the second survey, but the increases were minor (+0.042 on average between 1993 and 2014).

Ellenberg N values were significantly affected by past land use, with values being 0.46 units higher in former infield plots compared to former outland plots. In addition, during 1983-2014, we observed a small (+0.16) but significant increase in Ellenberg N values (**Fig. 2.2; Appendix A2.10**); there was no evidence for interactions.

We observed a small but significant increase in Ellenberg L values (+0.14) between 1983 and 1993. After 1993, Ellenberg L values decreased again to a level not significantly different from the original 1983 level. Over the entire period, we found a significant interactive effect between past land use and recent management disturbances on Ellenberg L values. For the plots with low recent management, Ellenberg L values were on average 0.48 units higher in outland compared to infields. For the plots with more intensive recent management, Ellenberg L values of infield and outland plots were closer to each other (**Fig. 2.2; Appendix A2.10**).

With PERMANOVA, we found a significant difference in the understorey composition between infield and outland plots in each survey year (**Fig. 2.3**). The permutational test for homogeneity of multivariate dispersion (PERMDISP) indicated that this difference was driven by different mean multivariate composition between infield and outland plots, and not the degree of multivariate dispersion (**Fig. 2.3**). This explains why no significant effects of past land use on the Bray-Curtis dissimilarity were found with the linear mixed effect modelling approach. Differences in the understorey composition between plots with high and low levels of management intensity were also significant in each survey year, although significance was often marginal and R^2 values were lower compared to the infield/outland PERMANOVA tests (**Fig. 2.3**). Differences in community composition between infield and outland plots can be related to the richer clay soils and the higher tree cover and SCA found in infield plots, compared to the outland plots (**Fig. 2.3**). Compositional differences between less and more intensively managed plots can also be related to the richer clay soils and the higher tree cover and SCA, which occur in the plots with lower management intensity.



Figure 2.3. NMDS of understorey composition for each survey year. In the upper row, red dots represent former infield plots and the species in red are the indicator species of infield plots; blue dots represent former outland plots and the species in blue are the indicator species of outland plots. In the lower row, red dots represent plots with high levels of management intensity and their respective indicator species are shown in red; blue dots represent plots with low levels of management intensity and their respective indicator species are shown in blue. The arrows indicate the variables characterizing the soil and overstorey of the plots, i.e. soil pH, soil clay and total P content, tree cover, and shade-casting ability. Species are abbreviated with the first four characters of the genus and species name. The following species occur on the figure: Acer platanoides, Acer pseudoplatanus, Aegopodium podagraria, Agrostis capillaris, Anthriscus sylvestris, Athyrium filix-femina, Avenella flexuosa, Betula pendula, Betula pubescens, Carex pilulifera, Convallaria majalis, Dryopteris carthusiana, Fagus sylvatica, Festuca ovina, Fraxinus excelsior, Hepatica nutans, Mercurialis perennis, Picea abies, Poa nemoralis, Polygonatum multiflorum, Ribes uva-crispa, Prunus padus, Rubus idaeus, Rubus saxatilis, Salix caprea, Scrophularia nodosa, Silene dioica, Stellaria holostea, Stellaria media, Taraxacum vulgare, Tilia cordata, Ulmus glabra, Veronica officinalis (see **Appendix A2.11**).

Typical species on former infields were *Convallaria majalis* and *Poa nemoralis*, while typical former outland species included *Dryopteris carthusiana, Juncus effusus* and *Carex pilulifera* (but these species were not indicators in 2014). *Mercurialis perennis, Melica nutans* and *Hepatica nobilis* (not in 2014) were indicative of a less intensive management, while *Betula pubescens/pendula* was indicative of a higher management intensity (**Fig. 2.3, Appendix A2.11**). The following commonly prevailing herbaceous species seemed indifferent for both past land use and recent management intensities, and were found in all plot groups: *Oxalis acetosella, Maianthemum bifolium, Viola spp., Rubus idaeus,* and *Galeopsis spp.*. Comparison of mean Ellenberg

N and L values between indicator species groups only revealed significant differences in Ellenberg N values in 1983 (infield indicators: 6.14; outland indicators: 3.71; $t_{9.98} = 2.69$; p = 0.023).



Figure 2.4. (a) Mean and standard error of the NMDS-coordinates for each survey year and for each plot category (resulting in 12 possible combinations of year, past land use and recent management level). The level of recent disturbance by forest management is indicated by the line colour (red = high; blue = low), while the past land use category is indicated by the line type (continuous = infield; dotted = outland). The black arrows visualize the trajectories of the understorey compositions over time. (b) Correlation of relevant plot characteristics (orange arrows: soil clay and total P content, soil pH, cover and shade-casting ability (SCA) of the tree layer) and community descriptors (green arrows: mean Ellenberg N and L values) with the plot positions on the NMDS ordination figure. The length of the arrows indicates the degree of correlation.

For all outland plots, and for the infield plots with high management intensity, the direction of compositional change indicated by the mean NMDS (**Fig. 2.4**) showed similar patterns, first going down along the second axis, and then going up along the same axis. For the infield plots with low management intensity, we observed an initial small upwards shift along the second axis between 1983 and 1993, followed by a bigger shift in the same direction between 1993 and 2014. The understorey compositions of more intensively managed infield and outland plots are converging over time, compared to the less intensively managed plots. As Ellenberg L values are negatively related to the second axis of variation, it seems that the compositional shift over time is partly related to an initial increase in light-demanding species between 1983 and 1993, followed by a decrease in these species after 1993. All former outland plots had negative means along the first axis of variation, while means for former infields were centred around zero or had positive values. This shows that compositional differences between former infields and outland the first axis. Also, the first axis of variation was strongly correlated

with Ellenberg N and to a lesser extent shade-casting ability and tree cover, which indicates that more nutrient-demanding understorey species and more shade casting overstorey species have a higher affinity for infields compared to outland.

2.5. DISCUSSION

This is the first study, to our knowledge, investigating both the main and interactive effects from legacies of a historical infield/outland system and recent management intensity levels on contemporary understorey compositions and their trajectories over time. We found that plot-level understorey diversity (i.e. alpha diversity) depended mainly on recent management intensities, and not on past land use. Higher levels of disturbance due to management positively affected alpha diversity. We found dissimilarities in species composition (i.e. beta diversity) among plots with different past land uses, and (to a lesser extent) different recent management intensities. Legacies from the former infield/outland agricultural system clearly persisted in the nutrient-demanding signature of the understorey. Interestingly, we also found an indirect effect of past land use on the light levels at the forest floor, through its effect on the soil nutrient availability. The more nutrient-rich soils of former infields seemed to result in forest canopies casting a deeper shade. However, recent management activities overruled this effect of past land use on the light-demanding signature of the understorey for light regardless of past land use when plots were intensively managed.

2.5.1. Research question 1: Land-use legacies in the understorey

We found clear compositional differences in the understorey between former infields and former outland (**Fig. 2.3**). Compositional differences in the forest understorey due to past land use have been consistently reported in the literature (e.g. Brudvig et al., 2013; Hermy & Verheyen, 2007), and can be related to fragmentation, dispersal limitations, and recruitment limitations due to differences in soil properties (Baeten et al., 2009). While fragmentation and dispersal limitations are outside the scope of this study, we present evidence that at least part of the compositional differences in our study plots are related to differences in soil characteristics due to past land use. Both the direction of the environmental variables on the NMDS-plots (**Fig. 2.3**) and the significantly higher amount of nutrient-demanding species in the understorey of former infields suggest that not only the higher clay content (resulting from an initial preference for clayey soils for infield use), but also the higher nutrient availability in infield plots drives compositional differences between infield and outland plots. Similar findings have been noted where more extreme land use comparisons (i.e. ancient vs. recent forest) have been made (e.g. Dupouey et al., 2002; Koerner et al., 1997).

2.5.2. Research question 2: impact of recent management on the understorey

We found that different levels of recent management intensity affected the community composition of our study plots, in terms of their mean position in the ordination figures. We also observed an increase in plot-level diversity between 1983 and 1993, followed by an overall decrease between 1993 and 2014 across all past land use/management combinations. These changes are probably related to the overall management intensity trajectory for the entire region. Overall management intensity in the region increased after the ratification of the Swedish Broadleaves Act in 1984, which prescribed that oak/hornbeam stands larger than 0.5 ha must not be converted to coniferous plantations, but regenerated with oak or other temperate hardwoods, and which stimulated interest in active management of hardwood forests. After 1993, management intensity decreased again due to changes in the Swedish forest policy that now gave more importance to the environmental goal of forests whereby biodiversity was to be secured and ecosystems conserved (Simonsson et al., 2015). This suggests that management intensity and alpha diversity are positively correlated. Several other studies reported similar findings, where forest management has a positive effect on species richness of the understorey vegetation (e.g. Brunet, Falkengren-Grerup, & Tyler, 1997). The dissimilarity in species composition among plots increased slightly between 1993 and 2014, and displayed the opposite trend to alpha diversity. This result can be explained by the dependence of the Bray-Curtis index on alpha diversity, where both measures are inversely correlated due to the multiplicative definition (alpha x beta = gamma) (Jost, 2007). Hence, a decrease in alpha diversity due to the disappearance of some species can result in plots becoming more dissimilar and thus an increase in beta diversity.

Studies on conversion of coppice-with-standards forests to high forest systems with less frequent disturbances, have often shown an overall increase in plot-level diversity, and an associated decrease in dissimilarity in species composition (beta diversity), suggesting biotic homogenization across stands (Hermy, 2015; Van Calster et al., 2007, 2008). These findings seem to contradict our results, as we found a decrease in alpha diversity and increase in beta diversity when management intensity decreased again after 1993. Of course, this decrease in management intensity in our study region was merely a decrease in harvesting frequency/intensity, and might therefore not be comparable to an actual change in management regime from coppicing to high forest.

The level of recent management intensity, according to our classification, did not affect the nutrientdemanding signature of the understorey. However, we observed an overall eutrophication signal over time since 1983 over all plot groups. This can be attributed to the closing of the canopy related to an overall decrease in management activities after 1993 as well as (but probably to a lesser extent) increased atmospheric N depositions (Verheyen et al., 2012). The light-demanding signature of the understorey was affected by both the overall change in management intensity over time due to the Swedish forest policy and the more subtle management differences between plots. The overall increase in light-demanding species during 1983-1993 is likely the result of the increased management activity, creating more canopy openings (see **Fig. 2.1b**), followed by an overall decrease in light-demanding species once management activity started decreasing again. Additionally, the significant main positive effect of management intensity on the light requirement of the understorey reflects our distinction between plots with high and low management intensity. This effect can be related to the higher share of *Carpinus betulus* and *Corylus avellana* in the less intensively managed plots, which cause higher shade levels at the forest floor (see '2.3.2. Soil and overstorey characterization').

2.5.3. Research question 3: interactive effects of past land use and recent management on the understorey

We found a clear interactive effect between past land use and recent management levels on the light requirement of the understorey. Within the less intensively managed plots, infield plots had fewer lightdemanding species than outland plots. This decline is likely associated with the higher soil nutrient content in infield plots, resulting in a denser (sub)canopy and lower light availability at the forest floor compared to the less nutrient-rich outland plots. Indeed, when characterizing the overstorey of the study plots (see '2.3.2. Soil and overstorey characterization') we found that former infield plots had a higher share of Corylus avellana and Carpinus betulus in their (sub)canopy, which can cause high shade levels. Similar examples of lower light transmission on richer soils, potentially due to a denser layer of subcanopy trees, have been reported in other parts of the world (e.g. Coomes & Grubb, 1996; Coomes et al., 2009; Tilman, 1988). Within the more intensively managed plots however, the understorey light requirements of infield and outland plots were similar, indicating that recent disturbances in the tree and shrub layer due to management practices have caused similar light levels at the forest floor, regardless of soil fertility, and thus regardless of the past land use. In other words: recent management disturbances might have 'overruled' differences in light availability due to past land use. We also observed an overruling effect of recent management disturbances for compositional differences among plot groups. Across both landuse intensities, the intensively managed plots have become more similar over time, while this was not the case for the group of less intensively managed plots, where communities on former infield and outland are still very distinct from each other in 2014. These findings contrast with Jonason et al. (2016), who observed that clear-cutting sustained legacies from former use as meadowland. However, they observed only small differences in soil nutrients between land-use types (i.e. forest history vs. meadow history), while soil nutrient content was an important driver behind land-use legacies (resulting from infield vs. outland use) in our study.

2.6. CONCLUSION

Recent forest management intensity had a positive effect on plot-level diversity. The former infield/outland agricultural system was an important determinant of both the nutrient- and light-demanding signature of the understorey composition. The level of disturbance intensity due to recent management practices interacted with this past land-use effect, but only on the light-demanding signature of the understorey, where differences resulting from past land use had disappeared in the more intensively managed plots. Our results differ from previous studies, where disturbances were found to preserve legacies from past land use (e.g. Hogan et al., 2016; Jonason et al., 2016).

Our findings suggest that while increasing the management intensity could increase plot-level diversity, it might reduce diversity in community composition. Especially with regard to light-demanding species, understoreys in infield and outland plots will become more similar when management intensity increases.







Light availability and land-use history drive biodiversity and functional changes in forest herb layer communities

After:

Depauw, L., Perring, M.P., Landuyt, D., Maes, S.L., Blondeel, H., De Lombaerde, E., Brūmelis, G., Brunet, J., Closset-Kopp, D., Czerepko, J., Decocq, G., Den Ouden, J., Gawryś, R., Härdtle, W., Hédl, R., Heinken, T., Heinrichs, S., Jaroszewicz, B., Kopecký, M., Liepiņa, I., Macek, M., Máliš, F., Schmidt, W., Smart, S.M., Ujházy, K., Wulf, M., Verheyen, K., 2020. Light availability and land-use history drive biodiversity and functional changes in forest herb layer communities. *Journal of Ecology*, 00, 1-15.

3.1. ABSTRACT

A central challenge of today's ecological research is predicting how ecosystems will develop under future global change. Accurate predictions are complicated by (i) simultaneous effects of different drivers, such as climate change, nitrogen deposition, and management changes; and (ii) legacy effects from previous land use. We tested whether herb layer biodiversity (i.e. richness, Shannon diversity and evenness) and functional (i.e. herb cover, specific leaf area (SLA) and plant height) responses to environmental change drivers depended on land-use history. We used resurvey data from 192 plots across nineteen European temperate forest regions, with large spatial variability in environmental change factors. We tested for interactions between land-use history, distinguishing ancient and recent (i.e. post-agricultural) forests, and four drivers: temperature, nitrogen deposition and aridity at the regional scale, and light dynamics at the plot-scale. Land-use history significantly modulated global-change effects on the functional signature of the herb layer (i.e. cover, SLA and plant height). Light availability was the main environmental driver of change interacting with land-use history. We found greater herb cover and plant height decreases and SLA increases with decreasing light availability in ancient than in recent forests. Furthermore, we found greater decreases in herb cover with increased nitrogen deposition in ancient forests, while warming had the strongest decreasing effect on the herb cover in recent forests. Interactive effects between land-use history and global change on biodiversity were not found, but species evenness increased more in ancient than in recent forests.

Synthesis: Our results demonstrate that land-use history should not be overlooked when predicting forest herb layer responses to global change. Moreover, we found that herb layer composition in semi-natural deciduous forests is mainly controlled by local canopy characteristics, regulating light levels at the forest floor, and much less by environmental changes at the regional scale (here: warming, nitrogen deposition and aridity). The observed disconnect between biodiversity and functional herb layer responses to environmental changes the importance of assessing both types of responses to increase our understanding of the possible impact of global change on the herb layer.

3.2. INTRODUCTION

Global environmental changes can strongly modify forest ecosystems and their plant communities (Gilliam et al., 2016; Hedwall & Brunet, 2016; Perring et al., 2016). While there is already a good understanding of variation in plant community properties across spatial environmental gradients, knowledge of long-term temporal changes in ecosystems across environmental gradients remains limited (Amatangelo et al., 2014; Bjorkman et al., 2018; Dwyer et al., 2014). Understanding temporal changes in plant communities, and the role of global change, is complicated by the simultaneous effects of different drivers, such as climate change, atmospheric deposition of eutrophying and/or acidifying compounds,
and management changes (Bernhardt-Römermann et al., 2015; Hedwall & Brunet, 2016; Perring, Bernhardt-Römermann, et al., 2018). In addition, legacy effects of past land use are often present in plant communities with slow dynamics (Bürgi et al., 2017; Perring et al., 2016). Hence, disentangling the combined and possibly interactive effects of land-use history and different environmental drivers on temporal community dynamics is key to predict how plant communities will be altered under future global change.

Plant communities can exhibit both biodiversity and functional changes in response to environmental change (Closset-Kopp et al., 2019; Mayfield et al., 2010). Assessing both types of changes is important to obtain a complete understanding of the impact of future global change on plant communities, especially as several studies report a disconnect between biodiversity and functional changes (Li & Waller, 2017; Perring, Bernhardt-Römermann, et al., 2018). We focus our study on herb layer communities in temperate forests. The forest herb layer contains the majority of plant diversity (Gilliam, 2007) and plays a key role in forest functioning (Landuyt et al., 2019). Understanding how future environmental changes will affect the herb layer is key to make informed management decisions for sustaining forest biodiversity and functioning. In this study, biodiversity changes refer strictly to the 'compositional component' of biodiversity (Maes, Fontaine, Rongé, Hermy, & Muys, 2011). We measured biodiversity changes as changes in species richness, Shannon diversity and species evenness. We define functional changes as changes in the functional signature of the herb layer, which represents a combination of functional ecological features at the community level. We assessed functional changes through evaluating changes in the total herb layer cover, which can be considered a measure for herb layer productivity. Several functions of the herb layer largely depend on this productivity, including nutrient and carbon cycling, evapotranspiration and tree regeneration (Landuyt et al., 2019). In addition, we assessed functional changes through evaluating changes in two important functional traits (those properties that characterize the ecological strategies of species), i.e. plant height and specific leaf area (SLA), which are both related to resource acquisition and expected to respond strongly to environmental changes (De Frenne et al., 2015; Dubuis et al., 2013).

Global-change drivers have the potential to alter herb layer communities by altering resource availability and growing conditions at the forest floor that control herb layer community composition (Landuyt et al., 2019). The simultaneous occurrence of different drivers, potentially causing interactions, complicates understanding the magnitude and direction of shifts in resources and conditions, and the consequent response of the herb layer community to these shifts. Here, we focus on interactions between land-use history on the one hand, and ongoing environmental changes (i.e. climate change, enhanced nitrogen deposition, and changing canopy cover and composition) on the other hand. To account for land-use history, we compared post-agricultural forests (further on referred to as 'recent forests') with ancient forests (i.e. forest sites without any known agricultural use, since at least 1810). We expect that alterations

in resources and conditions engendered by previous land use have steered communities and their constituent traits onto trajectories of change, which may then be modulated by contemporary environmental changes (Perring et al., 2016).

Although specific studies that consider land-use legacies when projecting the effects of multiple environmental changes on future forest herb layer properties are rare, the literature provides insights in the (interactive) effects of resource alterations as key agents of ecological change. In general, the availability of water, nutrients and light will mainly determine the structure and functioning of plant communities (Craine et al., 2012). Understanding the combined role of these resources, and how landuse history and environmental changes simultaneously alter their availability, can help to predict how plant communities will evolve under global change. For instance, increased nitrogen (N) availability may promote plant growth in systems that have sufficient phosphorus (P) (such as many post-agricultural forests), while it may not enhance plant growth in P-limited systems (such as many temperate ancient forests (e.g. Gress et al., 2007)) (Hedwall et al., 2017, although note Treseder et al., 2001). N deposition rates have a direct effect on N availability, but warming and changes in light regimes can also affect N availability, as higher temperatures and light levels can increase mineralization rates (Koch et al., 2007; Van Calster et al., 2007). Additionally, climate change and altering light levels can affect the water availability through altering evapotranspiration (Rind et al., 1990). Moreover, the drought-sensitivity of the system might depend on the land-use history: forest sites without previous agricultural use (e.g. ancient forests) typically have better developed organic soil layers than post-agricultural forest sites, improving their water storage capacity, and thus their ability to mitigate the effects of a severe drought (Greiffenhagen et al., 2006; Von Oheimb et al., 2014).

Resurvey data with a long time period (typically multiple decades) between surveys are ideally suited to assess changes in systems that exhibit slower dynamics, such as plant communities in temperate forests (Dornelas et al., 2013; Kapfer et al., 2017). In the present study, we use a combined temporal and spatial approach to test for interactions between land-use history (i.e. former agricultural use) and environmental changes (i.e. climate change, enhanced nitrogen deposition, and changing canopy cover and composition) on biodiversity and functional changes in temperate forest herb layer communities. We use herb layer resurvey data from 192 plots across nineteen European temperate forest regions, where we can exploit large spatial variability in environmental change factors (Verheyen et al., 2017). The timing of afforestation of the recent forest sites ranged from 1810 to 1970, but with the majority (47/57) afforested before 1930. We complement our resurvey study with direct characterisation of soil and canopy properties through *in situ* measurements, which allows us to account for differences in soil type and canopy structure and composition at the plot-scale in our analyses.

We tested the following hypothesis:

The herb layer's biodiversity and functional signature will respond to environmental changes, but these responses depend on land-use history. When assuming that herb layer communities are mainly shaped by resource availability, we expect to see stronger herb layer responses to environmental changes in the recent forests, which are typically less P-limited due to former fertilization practices.

This hypothesis was based on two expectations, which we checked prior to testing our main hypothesis: (i) we expect that several decades after afforestation, legacies from former agricultural land use are mainly reflected in the soil nutrient levels, with higher phosphorus levels in recent forests due to former fertilization practices. This expectation was based on previous analyses by Maes et al. (2019) on the same set of study plots, which showed that soil P content was the only soil variable significantly affected by past land use; (ii) we expect that differences in species pools due to dispersal limitations will be less important than nutrient availability in shaping herb layer communities, as the land-use change happened in the distant past and species already had time to colonize the recent forests.

3.3. MATERIAL AND METHODS

3.3.1. Study sites

We selected 19 regions along spatial environmental gradients of atmospheric nitrogen deposition and climatic conditions (temperature, precipitation) within the European temperate deciduous forest biome (**Fig. 1.1A**). The main selection criteria were the existence of prior understorey vegetation surveys (preferably at least 20 years ago, but we included one region with 17-19 year old vegetation data) and information on land-use history. In addition, we tried to minimize differences in parent material and topography between plots and regions. We aimed at maximizing differences in land-use history between plots within regions by sampling in ancient vs. recent forest, although this was not possible for all regions (**Table 3.1**). We define ancient forests as continuously forested since at least 1810, whereas recent forests have been afforested after 1810 (Hermy et al., 1999). Within the 57 recent forest plots, 31 plots were on former arable land, while 26 plots were on former grassland. Within fifteen out of nineteen regions, all, or all but one, plots were on the same soil type (**Table 3.1**). In addition, all plots are situated in 'mesic' forests, with a moderate supply of moisture (**Table 3.1**).

All plots comprised closed-canopy forests with a variable tree and shrub layer composition, but we focused on plots predominantly composed of broadleaved species, although a higher occurrence of coniferous species in the easternmost regions with a hemiboreal climate was unavoidable. The canopies at the original survey consisted mainly of *Quercus robur/petraea* (104/192 plots), *Fraxinus excelsior* (67/192 plots), *Fagus sylvatica* (65/192 plots), *Carpinus betulus* (64/192 plots) in the tree layer and *Corylus avellana* (76/192 plots) in the shrub layer.

Table 3.1. Ecological details of the 19 regions where we did vegetation resurveys. Δt = time interval between original and new survey (in years); LUH = land-use history; AF = ancient forest; RF = recent forest; EIV-F = Ellenberg indicator value for soil moisture; S = Sand; ClayC = Clay with carbonates; ClayNC = Clay with no carbonates; ΔMAT = rate of change of mean annual temperature; Δ Aridity = rate of change of De Martonne aridity index; Ndep = average annual rate of nitrogen deposition; se = standard error. Δ Management indicates in how many plots management intensity has decreased (1), increased (1) or stayed the same (=) over time (Appendix I). See text for a detailed description of the variables. For Δ MAT, Δ Aridity and Ndep, mean values ± standard error across all regions are shown at the bottom of the table, as well as a p-value to indicate whether the mean value is significantly different from zero.

| | | | | Plot size | Mean Olsen P | Mean EIV-F | | | | | |
|----|-----------------------|--------|-----------------|-----------|---------------------|---------------|---------------------|--------|---------------------------------------|-------------------------------------|------------------|
| | | | LUH | (range) | (range) | (range) | | ΔΜΑΤ | ΔAridity | Ndep | ΔManagement |
| ID | Region, Country | ∆t (y) | (135 AF, 57 RF) | m² | mg kg ⁻¹ | | Soil type | °C y-1 | mm °C ⁻¹⁻ yr ⁻¹ | kg ha ⁻¹ y ⁻¹ | (112↓, 65=, 15个) |
| BI | Bialowieza, PL | 31-50 | 15 AF | 50-400 | 36 (10.4-100.5) | 5.4 (5.1-6.0) | S | +0.029 | -0.028 | 13.75 | 10 =, 5 🗸 |
| BS | Braunschweig, GE | 24-25 | 5 AF, 5 RF | 625 | 33.3 (5.7-82.8) | 5.1 (4.7-5.6) | S | +0.035 | -0.101 | 17.22 | 4 =, 6 ↓ |
| BV | Binnen-Vlaanderen, BE | 35 | 4 AF, 5 RF | 150 | 34.1 (10.8-53.3) | 6.0 (5.5-6.4) | S(8), ClayC(1) | +0.033 | +0.069 | 22.12 | 5 =, 4 🗸 |
| СО | Compiègne, FR | 47 | 10 AF | 200-2000 | 17.6 (6-40.6) | 5.1 (4.5-6.0) | S | +0.026 | -0.015 | 15.66 | 5 =, 5 🗸 |
| DE | Devin, CZ | 52-62 | 3 AF, 7 RF | 100-600 | 34.4 (10.2-75.3) | 4.6 (3.7-6.2) | ClayC(5), ClayNC(5) | +0.024 | -0.028 | 16.45 | 10↓ |
| GO | Göttingen, GE | 48-60 | 10 AF | 100-400 | 14.3 (6.6-53.4) | 5.5 (5.1-5.9) | ClayC(6), ClayNC(4) | +0.017 | -0.010 | 17.75 | 7 =, 3 🗸 |
| KO | Koda, CZ | 58 | 10 AF | 400 | 28.7 (7.7-58.6) | 4.6 (4.3-4.9) | ClayC(1), ClayNC(9) | +0.021 | +0.003 | 16.32 | 3 =, 7 ↓ |
| LF | Lyons-la-forêt, FR | 43 | 10 AF | 300-1000 | 15.5 (10.2-26.9) | 5.3 (5.0-5.7) | ClayNC(9), S(1) | +0.030 | -0.030 | 16.23 | 10 个 |
| MO | Moricsala, LV | 88 | 5 AF, 3 RF | 1250-2500 | 11.4 (6.4-26.4) | 5.0 (4.6-5.4) | ClayNC(1), S(7) | +0.013 | +0.008 | 5.2 | 7 =, 1 ↓ |
| | | | | | | | | | | | |

| PR | Prignitz, GE | 17-19 | 5 AF, 5 RF | 120-300 | 19.3 (7.3-32.8) | 5.6 (5.1-6.0) | S | +0.030 | -0.042 | 16.33 | 5 =, 5 🗸 |
|-----|------------------------|-------|------------|---------|------------------|---------------|---------------------|---------------------------|------------|-----------|----------|
| SH | Schleswig-Holstein, GE | 29-31 | 5 AF, 5 RF | 64-400 | 37.9 (9.7-154.9) | 5.1 (4.9-5.3) | S | +0.045 | -0.050 | 18.68 | 10 = |
| SK | Slovak Karst, SK | 32-40 | 10 AF | 500 | 10.9 (3.5-49) | 4.8 (4.5-5.0) | ClayNC | +0.024 | -0.037 | 11.57 | 10↓ |
| SKA | Skåne, SW | 31 | 8 AF, 2 RF | 500 | 30.4 (9.6-95) | 5.3 (4.7-5.8) | ClayNC(6), S(4) | +0.026 | +0.080 | 12.88 | 4 =, 6 🗸 |
| SP | Speulderbos, NL | 57-59 | 5 AF, 5 RF | 100 | 52.7 (24.9-92) | 5.2 (5.0-6.0) | S | +0.019 | -0.009 | 31.11 | 4 =, 6 ↓ |
| ТВ | Tournibus, BE | 48 | 5 AF, 5 RF | 100 | 11.8 (6.3-24) | 5.3 (4.6-5.9) | ClayNC | +0.027 | -0.092 | 18.6 | 10 ↓ |
| W | Wales, UK | 45 | 5 AF, 5 RF | 200 | 44.2 (18.3-91.1) | 5.8 (5.2-6.4) | ClayNC | +0.018 | +0.088 | 8.93 | 10↓ |
| WR | Warburg Reserve, UK | 41 | 5 AF, 5 RF | 100 | 19.5 (14.2-23.7) | 5.4 (4.9-5.8) | ClayC(9), ClayNC(1) | +0.025 | +0.026 | 15 | 5 =, 5 🗸 |
| WW | Wytham Woods, UK | 41 | 5 AF, 5 RF | 100 | 13.2 (6.7-19.9) | 6.0 (5.3-6.3) | ClayNC(7), S(3) | +0.022 | +0.032 | 12.39 | 5↓,5↑ |
| ZV | Zvolen, SK | 51-52 | 10 AF | 500 | 35.5 (6.5-111.7) | 4.7 (4.2-5.2) | ClayNC | +0.024 | -0.027 | 12.64 | 1 =, 9 🗸 |
| | | | | | | | | Mean ± se across regions: | | | |
| | | | | | | | | +0.026 ± | -0.009 ± | 15.70 ± | |
| | | | | | | | | 0.002 | 0.012 | 1.22 | |
| | | | | | | | | (p<0.001) | (p = 0.47) | (p<0.001) | |

3.3.2. Data collection

In 2015 and 2016, we revisited 192 plots across 19 regions in temperate Europe that were established and surveyed at least 17 years ago (**Fig. 1.1A**, **Table 3.1**). The year of the original survey varied between 1928 and 1998 (**Table 3.1**). Depending on the region, plot relocation was based on one or more of the following properties: permanent markings in the field, GPS coordinates, physical maps, plot descriptions, drawings, photographs, and the original composition of the canopy layer (**Appendix A3.1**). Plots were either rectangular or circular, and varied in size between 50 and 2500 m² (**Table 3.1**). To assure comparability between our survey and the original survey, we followed the original definitions of the vegetation layers, which differed among regions (**Appendix A3.2**). A vegetation survey comprised a division of all vascular plants into three layers: herb layer, shrub layer and tree layer. The herb layer typically comprised all herbaceous species and the woody species (e.g. tree and shrub seedlings) below a threshold ranging from 0.25 to 1.3 m (threshold differed between regions; see **Appendix A3.2**). For each layer, we visually estimated the cover (%) of each species, as well as the total cover of the layer. When cover values of the old survey were reported in different cover-abundance scales (e.g. Braun-Blanquet, 1964), we converted these to percentages (**Appendix A3.2**).

In addition to vegetation surveys, we collected samples of the mineral topsoil in each plot (a composited sample from five locations within the plot). We analysed the 0–10 cm samples for pH_{KCl} , proportion of exchangeable base cations, total and Olsen phosphorus (P) concentration (mg kg⁻¹), organic and inorganic carbon (C) and total nitrogen (N) concentration (%), and soil organic matter (%), and the 10–20 cm samples for soil texture (% Clay, % Silt, % Sand). We also collected a 0-10 cm soil sample with a Kopecky ring at the centre of each plot to determine the whole-soil bulk density (see Maes et al. (2019) for further details on soil analyses and properties).

3.3.3. Response variables

We derived six plant community descriptors for both the plots in the old (o) and new (n) surveys. To assess the biodiversity of the herb layer, we used **species richness** (*SR*), **Shannon diversity** (*DIV*), and **species evenness** (*EVEN*). Species richness is the number of species present within the plot. Shannon diversity is a combined measure of species richness and evenness, which weights species by their abundance (Shannon, 1948). Species evenness is the distribution of abundance among species. It ranges from zero to one, with one representing a perfectly equal distribution of all occurring species. We followed Smith and Wilson (1996) to calculate evenness based on the variance in species' abundances (see **Appendix A3.3** for details).

To assess the functional composition of the herb layer, we used community weighted mean (CWM) values for the two traits 'plant height' (*height*) and 'specific leaf area' (*SLA*), and the total cover of

the herb layer species (*COVER*). We gathered trait data from different databases including LEDA (Kleyer et al., 2008) (Appendix A3.4). The total herb cover is the sum of the visually estimated cover of each species in the herb layer. Each response variable was based on the 'strict' herb layer, containing only the herbaceous species, and excluding seedlings and shrub species for three reasons: (i) tree and shrub species do not remain structurally part of the herb layer throughout their life cycle, (ii) many recorded trait values are representative for adult trees, shrubs and climbers and not the juvenile state found in the understorey, and (iii) seedlings were not always included in the original surveys (see Appendix A3.5 for species lists). Nomenclature was standardized manually based on The Plant List (2013).

We used the change in community descriptors between surveys as response variables, calculated as response ratios (RR):

$$RR_X = \frac{\ln(\frac{X_n}{X_0})}{\Delta t}$$
 Equation 3.1

where X is one of the community descriptors, 'n' and 'o' refer to the new and old survey, and Δt is the number of years between surveys. These response ratios are further denoted as RR_{SR}, RR_{DIV}, RR_{EVEN}, RR_{HEIGHT}, RR_{SLA} and RR_{COVER}. The use of ln(X_n/X_o) instead of X_n/X_o has the advantage that increases and decreases in X are treated symmetrically: ln(X_n/X_o) is zero in case of equality (X_n=X_o), and if X_n is k times greater than X_o, the ln-ratio is equidistant from zero as in the situation where X_o is k times greater than X_n.

To improve our understanding of what could be driving the changes in these six main response variables, we evaluated the changes (again calculated as log response ratios) in two additional variables related to the herb layer composition: the proportion (%) of the herb layer cover occupied by (i) forest specialists (RR_{FS}) and (ii) graminoids (RR_{GRAM}) (**Appendix A3.6**). Forest specialists are the species most strongly associated to closed forests, following (Heinken et al., 2019), who provides a comprehensive list of vascular plant species occurring in forests for 24 geographical regions across Western, Central and Northern Europe, assigning each species to one of four different groups with different degrees of association with forests (i.e. as an indication for the habitat preference). The forest specialists ('1.1 species') are the species most strongly associated to closed forests. We used the regional species classification relevant for each study region, as some species are classified as 'forest specialist' in some regions, but not in others. The reason to consider graminoids as well, is that in some regions of our dataset, earlier studies have found that herb cover decreases over time were largely caused by decreases of graminoid species, related to changes in management.

3.3.4. Explanatory variables

3.3.4.1. Site conditions

We included **land-use history (LUH)** as a categorical variable, distinguishing plots in ancient forest (forested since at least 1810) and recent forest (former arable land/grassland forested after 1810) (**Table 3.1**). We did not apply a further distinction between recent forests on former arable land and recent forests on former grassland to avoid a too unbalanced study design (with 135 ancient forest plots and only 31 former arable land plots and 26 former grassland plots). As different effects on the understorey dynamics might be expected between both recent forest categories, due to the lower nutrient-enrichment and soil disturbance on former grasslands compared to former arable land, we compared the effect of the former land use within the recent forests on the six main response variables (see 3.3.3. Response variables) with a Welch Two Sample t-test. We found no significant differences (alpha = 0.05) in the response variables between former grassland plots and former arable land plots. Similarly, this t-test revealed no significant differences in Olsen P contentration at the time of the new survey between both types of recent forest plots.

Soil type was also a categorical variable with three groups, obtained with cluster analysis based on soil texture (% Clay, % Silt, % Sand) and carbonate or inorganic carbon concentration (%) (see Maes et al. (2019) for details of this analysis). 'ClayCarbonate' soils represent silty-clay-carbonate soils with high inorganic carbon concentration and high pH_{KCl} , but low C/N-ratio and litter mass (i.e. faster mineralization). The 'ClayNoCarbonate' soils represent silty-clay soils without the presence of carbonates (low inorganic carbon concentration) and intermediate pH_{KCl} , C/N-ratio and litter mass. The 'Sand' soils represent poor sandy soils with a low inorganic carbon concentration and high pH_{KCl}, **C**/N-ratio and high C/N-ratio and litter mass reflecting higher acidity and lower nutrient concentration (**Table 3.1**).

Since **Olsen P** was not correlated with the soil type groups, and because it is an important nutrient for plant growth that is expected to be affected by past land use (De Keersmaeker et al., 2004), we included the Olsen P concentration (mg kg⁻¹) measured at the new survey as a separate predictor (Maes et al., 2019). We expected soil moisture to affect community traits (Schaffers & Sýkora, 2000) and therefore included a community weighted mean **Ellenberg Indicator Value score for soil moisture (EIV_F)** from the plot's herbaceous community at the old survey (**Table 3.1**). EIVs for moisture range from 1 (species occurs on dry soils) to 9 (species occurs on wet soils) (Diekmann, 2003).

Lastly, we included **plot size** (m²) (**Table 3.1**) as an explanatory variable. We expect plot size to affect community property changes as larger plots have more chance of including infrequent species, which may also be more likely to appear or disappear between surveys.

3.3.4.2. Plot-scale drivers of change

At the plot-level, we expect changes in the cover and composition of the canopy (including both shrub and tree layer) to be the main driver of changes in the herb layer community. Canopy changes between surveys can be the result of changes in the type and intensity of forest management, successional trajectories of the forest canopy and natural disturbances. We included the response ratios (see **Equation 3.1**) of the **canopy cover (RR**_{cc}), the **canopy's shade-casting ability (RR**_{scA}) and the **litter quality** (**RR**_{LQ}) as explanatory variables in our analysis. To calculate the overall canopy cover, we combined cover estimates of all species in the tree and shrub layer using the formula developed by Fischer (2015), which accounts for overlap between species and between layers. We calculated the shade-casting ability (SCA) and litter quality (LQ) as a cover weighted average of, respectively, ordinal SCA and LQ scores (listed in **Appendix A3.7**, respectively adapted from Ellenberg (1996) and Hermy (1985) and complemented with expert knowledge of prof. Kris Verheyen), ranging between 1 (very low SCA and very low decomposition rate, respectively) and 5 (very high SCA and very high decomposition rate, respectively)(see also Van Calster et al., 2008; Verheyen et al., 2012).

Across all regions, both SCA and litter quality increased significantly, while canopy cover did not change (**Appendix A3.8**). We expected these canopy variables (SCA, litter quality and cover) to be related to management changes, and checked this through assigning a 'management change category' to each plot (**Table 3.1**, **Appendix A3.9**), based on management history data obtained via local experts. Only the changes in canopy cover clearly differed among the management intensity categories, with the strongest canopy cover increases where management intensity decreased (**Appendix A3.9**). Inspection of the changes in frequency and cover of the ten most frequent tree and shrub species in the new survey revealed that the increasing importance of shade-casting species is mainly due to the increases of *Acer pseudoplatanus, Carpinus betulus* and *Fagus sylvatica*. The increased litter quality is mainly related to increases of *Acer campestre* (**Appendix A3.8**). These four tree species are all shade tolerant late successional species, which indicates that SCA and litter quality increases are probably related to processes of natural succession with time.

3.3.4.3. Regional-scale drivers of change

At the regional scale, we were interested in the effect of two global climatic drivers and a eutrophication driver on the herb layer composition. We calculated the rate of change of **mean annual temperature** (Δ **MAT**) and **De Martonne aridity index** (Δ **Aridity**) as the difference between the new and the old survey, divided by the number of years between surveys. To derive the mean annual temperature and aridity index at both survey times, we averaged annual values for the 10 years preceding the survey (as per Bernhardt-Römermann et al., 2015; Perring, Bernhardt-Römermann, et al., 2018). We extracted

temperature and precipitation data from the Climate Research Unit (CRU TS v. 4.02; 0.5° resolution) (Harris et al., 2014). The De Martonne aridity index is one of the best known and widely used aridity indices in applied climatology (Croitoru et al., 2013; Hrnjak et al., 2014), and is calculated as follows (De Martonne, 1925):

Aridity_{DM} =
$$\frac{Prec}{MAT + 10}$$
 Equation 3.2

with 'MAT' the mean annual temperature (°C) and 'Prec' the annual amount of precipitation (mm). A lower value of Aridity_{DM} represents drier conditions. The mean annual temperature increased in all regions in between surveys, with an average increase of 0.026°C (± 0.002) per year across all regions (**Table 3.1**). The De Martonne aridity index increased in some and decreased in other regions, with no significant overall trend across regions (**Table 3.1**).

We compiled data on nitrogen (N) deposition for the year 2000 from the EMEP database (http://www.emep.int), which allows deposition data for the whole of Europe to be derived with a resolution of 50 km x 50 km. We applied correction factors from Duprè et al. (2010) to obtain N deposition values for each year in between surveys, and then calculated the average annual rate of **nitrogen deposition (Ndep)** as the cumulative amount of N deposition in between surveys divided by the number of years between surveys. We used the mean value across plots per region for each global-change driver for our analyses. The average N deposition rate between surveys was 15.70 kg N ha⁻¹ (\pm 1.22) per year (**Table 3.1**).

3.3.5. Statistical analyses

We performed all statistical analyses and visualizations in R version 3.6.0 (R Core Team, 2019) with the packages 'vegan', 'nlme', 'MuMIn', 'ggplot2', and 'sjPlot' (Barton, 2019; Lüdecke, 2019; Oksanen et al., 2019; Pinheiro et al., 2019; Wickham et al., 2019).

To check our expectation that initial species pools (at the time of the first survey) between ancient and recent forests were similar, we conducted a permutational multivariate analysis of variance (PERMANOVA) using Bray-Curtis dissimilarities with 999 permutations (based on abundance data; Bray & Curtis (1957)). We visualized the compositional differences in the herb layer with nonmetric multidimensional scaling (NMDS).

To check our expectation that Olsen P concentrations differed between ancient and recent forest plots, we performed linear mixed-effect modelling, including land-use history as a fixed effect and region as a random effect.

We used linear mixed-effect modelling to test which explanatory variables are significantly affecting the chosen response variables. We standardized (scaled and centred) all continuous explanatory variables

prior to analysis to enable comparison of their effect sizes. We applied a logarithmic transformation on 'Olsen P' and 'Plot size' to improve normality. To detect possible multicollinearity among the explanatory variables, we calculated variance inflation factors (VIF) according to Zuur et al. (2009). VIF values were very low (<2), indicating low collinearity.

For each response variable, we fitted a linear mixed-effect model with the following explanatory variables as fixed effects (see '3.3.4. Explanatory variables' for abbreviations):

Response variable ~ LUH + Soil type + $\ln(\text{Olsen P})$ + EIV_F + $\ln(\text{Plot size})$ + RR_{CC} + RR_{SCA} + RR_{LQ} + ΔMAT + $\Delta Aridity$ + Ndep + LUH: RR_{CC} + LUH: RR_{SCA} + LUH: RR_{LQ} + LUH: ΔMAT + LUH: $\Delta Aridity$ + LUH:Ndep + (1 | Region) (3)

where '(1 | Region)' represents the inclusion of a random effect term 'region' with varied intercepts only to account for the hierarchical structure of the data. We also incorporated 'region' as a weights term, i.e. we controlled for heterogeneity in residual spread. With ANOVA, we confirmed that both the random effect term and the weights term significantly (alpha = 0.05) improved the model for each response variable. All models were fit with restricted maximum likelihood (REML). We found no clear patterns in the residuals for each model, based on graphical evaluation (Zuur et al., 2009). We report estimates and 95% confidence intervals for each explanatory variable in each model. We calculated the marginal and conditional R^2 for each fitted model, representing the variance explained by fixed factors and the variance explained by both fixed and random factors, respectively (*MuMIn* package; Nakagawa et al., 2013).

3.4. RESULTS

3.4.1. Land-use legacies

Species pools at the original survey time were similar for ancient and recent forests in most regions. We only found significantly different species pools in two regions (Skåne and Wales) (**Appendix A3.10**).

Overall, Olsen P concentrations were significantly higher in recent forests than ancient forests (p = 0.046) (**Appendix A3.11**), but there were unexpected trends for some regions (Tournibus, Wales and Wytham Woods), with higher Olsen P levels in ancient than recent forests (although not significant). These regions with unexpected patterns in P soil concentrations are characterised by a low P nutrient supply in agriculture (Bomans et al., 2005), so that we can assume a low agricultural intensity in these regions.

The canopy's shade-casting ability was significantly higher in ancient forests than in recent forests, both at the time of the original (p = 0.004) and the new survey (p = 0.004) (Appendix A3.14).

3.4.2. Biodiversity and functional changes

For species richness and Shannon diversity, we observed significant increases or decreases over time in a few regions, but no overall trend across the regions (**Fig. 3.1A** and **3.1B**). Species evenness on the other hand, increased significantly across all regions, with decrease observed only in one region (**Fig. 3.1C**). The total cover of the herb layer decreased significantly between surveys in 14 out of 19 regions and across all regions (**Fig. 3.1D**). We found no significant temporal trends across regions for the community weighted mean trait values of plant height and specific leaf area (SLA) (**Fig. 3.1E** and **3.1F**), although it seems that for plant height, the lack of an overall trend is mainly caused by one region (Warburg Reserve) (**Fig. 3.1A**). Excluding the plots in Warburg Reserve from the dataset resulted in an overall significant increase in plant height across regions. The response ratio of species richness was positively correlated with both the response ratio of Shannon diversity ($r_s = 0.71$; p < 0.001) and total herb cover ($r_s = 0.67$; p < 0.001) (see **Appendix A3.12** for overview of correlations between response variables).

3.4.3. Potential (interactive) drivers of biodiversity and functional changes

We found no significant interactive effects for the three biodiversity measures (**Fig. 3.2**). Olsen phosphorus (P) was the only significant predictor for both the changes in species richness (RR_{SR}) and Shannon diversity (RR_{DIV}), with a positive effect on both response variables (**Fig. 3.2**). For the changes in species evenness (RR_{EVEN}), we found that land-use history and the shade-casting ability (RR_{SCA}) of the canopy were significant predictors. The response ratio of species evenness was higher in ancient forests than in recent forests, and in plots with higher response ratio of the canopy's shade-casting ability (**Fig. 3.2**).

For the change in the total herb cover (RR_{COVER}), we found significant interactive effects between landuse history and four drivers of change, i.e. the rate of N deposition (Ndep) (p < 0.001), the rate of change in mean annual temperature (Δ MAT) (p = 0.006), the response ratio of canopy cover (RR_{CC}) (p = 0.006), and the response ratio of shade-casting ability (RR_{SCA}) (p = 0.015) (**Fig. 3.2**). In *ancient* forests, the response ratio of the total herb cover (RR_{COVER}) was negatively affected by Ndep, RR_{CC} and RR_{SCA} (**Fig. 3.3A, 3.3C** and **3.3D**), but it was not affected by Δ MAT (**Fig. 3.3B**). In *recent* forests, Ndep, RR_{CC} and RR_{SCA} had no or a slightly positive effect on RR_{COVER} (**Fig. 3.3A, 3.3C** and **3.3D**), while Δ MAT had a negative effect on RR_{COVER} (**Fig. 3.3B**).

For the change in community weighted mean plant height (RR_{HEIGHT}), we found significant interactive effects between land-use history and the response ratio of canopy cover (RR_{CC}) (p < 0.001) (**Fig. 3.2**). In

ancient forests, RR_{CC} had a negative effect on RR_{HEIGHT}, while no clear effects were found in *recent* forests (**Fig. 3.3E**).

For the change in community weighted mean SLA (RR_{SLA}), we found significant interactive effects between land-use history and the response ratio of canopy cover (RR_{CC}) (p = 0.020), the response ratio of shade-casting ability (RR_{SCA}) (p = 0.001) and Δ Aridity (p = 0.045) (**Fig. 3.2**). In *ancient* forests, RR_{CC} and RR_{SCA} had a positive effect on RR_{SLA}. In *recent* forests, RR_{CC} had no effect on RR_{SLA}, and RR_{SCA} had a negative effect on RR_{SLA} (**Fig. 3.3F** and **Fig. 3.3G**). Differences in RR_{SLA} responses to Δ Aridity between ancient and recent forests were very minor (**Fig. 3.3H**), and therefore, this only just significant interactive effect will not further be discussed.

The amount of variation explained by the model (reflected by marginal R^2 (R^2m) values; **Fig. 3.2**) was low for the response ratios of species richness (0.16), Shannon diversity (0.11), species evenness (0.13) and total herb cover (0.17), but quite high for the response ratios of the functional traits 'height' (0.41) and 'specific leaf area' (0.30). The conditional R^2 (R^2c) was generally much higher than R^2m (see **Fig. 3.2**), indicating that much of the variation in the response variables can be explained by the random effect term 'region'.

3.4.4. Forest specialists and graminoids

Across all regions, both the proportion of forest specialists (FS) and graminoids (GRAM) did not significantly change between surveys. RR_{FS} increased with increasing canopy cover, but *only* in ancient forests, while no relation was found in recent forests. RR_{GRAM} decreased with higher Olsen P and decreased with higher Ellenberg indicator values for soil moisture (**Appendix A3.6**).



Figure 3.1. Temporal shifts in observed: species richness (SR) (A), Shannon diversity (DIV) (B), species evenness (EVEN) (C), total herb layer cover (COVER) (D), community-weighted mean (CWM) plant height (HEIGHT) (E) and community-weighted mean (CWM) specific leaf area (SLA) (F) across all regions (red triangle) and for the 19 regions separately (black dots). Mean (\pm 95 % confidence interval) log response ratios (RR = In (X_{new}/X_{old})/ Δ t) are shown based on the observed plot values in the old (X_{old}) and new (X_{new}) survey. '*' indicates a significant change, with confidence intervals excluding zero. The region labels refer to **Table 3.1**.



Figure 3.2. Estimates and 95% confidence intervals for each explanatory variable in the six models that were fitted for the six different response variables listed in the legend. Non-significant effects (with confidence intervals including zero) are transparent. Marginal R^2 (R^2m) and conditional R^2 (R^2c) of each model are provided in the legend. RR = log response ratio ($\ln (X_{new}/X_{old})/\Delta t$); LUH = land-use history; RF = recent forest; Ndep = nitrogen deposition; MAT = mean annual temperature; CC = canopy cover; SCA = shade-casting ability of the canopy; LQ = litter quality; EIV-F = Ellenberg indicator value for soil moisture. See **Appendix A3.13** for table with full model results.



Figure 3.3. Interactive effects on total herb cover change (RR_{COVER}) (A-D) between land-use history and rate of nitrogen deposition (A), rate of change in mean annual temperature (B), canopy cover change (RR_{CanopyCover}) (C) and shade-casting ability change (RR_{SCA}) (D). Interactive effects on community-weighted mean (CWM) plant height change (RR_{HEIGHT}) between land-use history and canopy cover change (E). Interactive effects on CWM specific leaf area (SLA) change (RR_{SLA}) (F-H) between land-use history and canopy cover change (F), shade-casting ability change (G), and De Martonne aridity index change (H). Fitted values (dots) and average model estimates of the effects (full lines) with 95% confidence intervals (shading), in which the values of the other continuous variables were set at their observed mean and the factor 'soil type' was set at its reference level ('ClayCarb'), are shown.

3.5. DISCUSSION

Our results confirmed the first part of our hypothesis, i.e. biodiversity and functional herb layer responses to environmental changes depend on land-use history. The second part of our hypothesis, i.e. herb layers in recent forests respond more strongly to environmental changes likely because of higher phosphorus availability, was only confirmed for warming, which mainly affected the herb cover in recent forests. In contrast, ancient forest herb layers were more sensitive to decreased light availability and increased nitrogen deposition than recent forests. Overall, canopy cover and composition seemed to be the main factors controlling herb layer changes over time. Not only differences in P levels, but also differences in the canopy's shade-casting ability between ancient and recent forests played a key role in explaining the dependencies of the herb layer responses on land-use history.

3.5.1. Land-use history and light availability interactions drive biodiversity and functional responses of the herb layer

Across our study regions, the total cover of the herb layer decreased over time, likely indicating lower understorey biomass production, which can affect several functions of the understorey, such as nutrient cycling through decreased retention of nutrients (Landuyt et al., 2019). Petzold et al. (2018) attributed their findings of decreased herb cover to a reduced management intensity. In ancient forests, our findings conform with Petzold et al. (2018), as increasing canopy cover due to reduced management intensity, as well as increasing shade-casting ability resulted in a decrease in total herb cover, which can be explained by a lower light availability and possibly also an increased belowground competition for nutrients and water (Ammer & Wagner, 2002). Surprisingly, in recent forests, stronger increases in cover and shade-casting ability of the canopy seemed to have no effect on cover changes of the herb layer, or even slightly reduced the intensity of cover decline.

In the ancient forests, we could relate the stronger decreases in herb cover with increasing canopy cover to an increase in the share of forest specialists (Heinken et al., 2019) in the community (**Appendix A3.6**). Hence, herb cover losses in ancient forests were mainly caused by the disappearance of species that typically occur in forest openings and cannot withstand very dark closed forest conditions. This observation is in accordance with findings of Penone et al. (2019), who found a negative effect of increased canopy cover on vascular plant abundance in the understorey, but a positive effect on specialisation. In the recent forests however, there were no clear shifts in the share of 'closed forest species' with increasing canopy cover or shade-casting ability. Hence, those species that disappeared in the ancient forest plots that became darker seemed to survive in recent forest plots despite the increased shade levels, suggesting that nutrient availability can alter plant species responsiveness to light availability. Ellenberg (1939) already showed that many herb layer species need a higher nutrient supply to compete successfully with other species under darker conditions. Also Heinken (1995) observed an interaction between nutrient and light availability on the herb layer cover, with nutrient-rich sites having similar herb cover, regardless of light availability, while nutrient-poor sites had much lower cover values under darker conditions. In a recent study, Gilliam (2019) also demonstrated the interaction between nutrient and light availability in the herb layer of temperate forests, where he found that increased nutrient availability caused a shift in factors controlling herb layer dynamics from variation in soil resources to variation in canopy structure.

The idea that the shade-tolerance spectrum of plants is wider on nutrient-rich sites than on nutrient-poor sites was also suggested by Coomes et al. (2009), and is consistent with the hypothesis that species cannot be simultaneously tolerant to multiple environmental stress factors (Niinemets & Valladares, 2006b). Hence, species in recent forest plots, with higher nutrient availability, are potentially more tolerant to darker conditions. A possible mechanistic explanation for this phenomenon is that on richer soils, plants need to allocate fewer resources to roots and below-ground processes when nutrients are plentiful and can therefore allocate more nutrients to their leaves (Tilman, 1988; Whitehead et al., 2002), resulting in a higher photosynthetic capacity (Field & Mooney, 1986) and allowing plants to grow under lower light levels. In addition, belowground competition for nutrients, which is expected to increase with canopy cover (e.g. Ammer & Wagner, 2002), could also explain the higher tolerance of the herb layer to increased canopy cover in the recent forests, where nutrient availability is higher compared to ancient forests.

Coomes et al. (2009) also relate nutrient-rich soils to increased plant species richness, because such soils can support both fast-growing light-demanding species and slow-growing species that tolerate deep shade, resulting in a greater range of shade-tolerance niches among species on nutrient-rich soils. This might explain the positive effect of Olsen P concentration on both species richness and Shannon diversity that we found. For these biodiversity measures, land-use history was however not important, which suggests that the interactive effects of land-use history and light-availability on the herb cover might additionally be related to other differences (other than nutrient availability) between ancient and recent forests. One such difference is the overall lower shade-casting ability in recent forest plots. Hence, it could be that in recent forests, although shade-casting ability increased in general, shade levels have not yet reached threshold levels at which herb cover starts to decline, because of the lower starting levels of shade-casting ability.

The higher overall shade-casting ability values in ancient forests compared to recent forests could also explain the observed interactions between climate warming and land-use history on the herb cover: cover declines in response to warming were only found in recent forests. The forest canopy can buffer plant responses to macroclimate warming (De Frenne, Rodriguez-Sanchez, et al., 2013), with stronger microclimatic cooling effects beneath canopies with higher shade-casting ability (Zellweger et al., 2019). The lower water holding capacity typically found in recent forest soils, in contrast to the well-developed

ancient forest soils with thicker O- and A-horizons, could reinforce the susceptibility of the recent forests' herb layer to climate warming (Greiffenhagen et al., 2006; Von Oheimb et al., 2014), as warming decreases water availability through enhanced evapotranspiration (Rind et al., 1990). Moreover, following the optimal resource partitioning theory, in which plants allocate less carbon to roots with increasing nutrient availability, we can expect plants in recent forests to develop less roots and therefore be more sensitive to the drier conditions associated with climate warming (Mausolf et al., 2018; Thornley, 1972).

Reduced light availability because of increased shade-casting ability was also correlated with the overall increase in species evenness. Lower light levels at the forest floor reduces the dominance of fast-growing, competitive, light-demanding species (Honnay et al., 2002). Therefore, evenness can be expected to increase with increasing shade, as the limited availability of light will reduce competitive exclusion by a few dominant light-demanding species, and will favour more shade tolerant species. This shade-induced loss of dominant competitive species with typically high cover values also explains the negative correlation between total herb cover and evenness. Litter quality was never an important predictor in the models, supporting our idea that canopy changes are mainly affecting the herb layer composition through altering light availability (controlled by canopy cover and shade-casting ability) rather than soil conditions (controlled by litter quality).

Across our 19 study regions, neither the community weighted mean (CWM) values for plant height nor specific leaf area (SLA) exhibited a clear directional change between surveys (although plant height would show a general increase when excluding one region, i.e. Warburg reserve (WR)). The investigated functional traits did not show relationships with climate change and increased N deposition. Instead, the functional composition of the herb layer again seemed to be mainly driven by interactions between landuse history and changes in canopy cover (reflecting management changes) and shade-casting ability. In ancient forests, we could relate increased shade to herb layer communities with lower mean plant height and higher mean specific leaf area (SLA), characteristics associated with the shade tolerant forest specialists that gained importance in ancient forests. As these forest specialists did not increase in recent forests, the absence of clear height and SLA responses to increased shade in these forests is not surprising. Another compositional feature of the herb layer that we assessed was the share of graminoids in the community, as we expected this to be related to SLA changes given the typically lower SLA of graminoids compared to forbs (Scharfy et al., 2011; Vile et al., 2005). The importance of graminoids did however not change significantly across our study regions, and a correlation between graminoid cover proportion and SLA was not confirmed. In contrast to previous studies across spatial gradients at a single point in time (e.g. De Frenne, Graae, et al., 2013), we did not find an increasing importance of taller plants with lower SLA with increasing temperatures, likely because the increased shade levels can attenuate herb layer responses to warming (De Frenne et al., 2015).

When resurveying quasi-permanent plots, observer and relocation errors are non-negligible, (Verheyen et al., 2018). However, changes in community properties can still be detected when a sufficiently large number of plots are combined, as in our study. Moreover, Kopecký and Macek (2015) demonstrated that resurveys are robust to uncertainty in original plot location and, when done properly, provide reliable evidence of decadal changes in plant communities. To minimize the observer error, we performed all resurveys with a team of minimum two researchers (Verheyen et al., 2018). Relocation errors might be present in regions where plots were not permanently marked, although for many regions, the available maps and coordinates were supplemented with photographs, schemes and elaborate field descriptions (**Appendix A3.1**), which should minimize these relocation errors. In addition, whenever possible, we received help from the original surveyor with plot relocation.

3.5.2. Herb covers of ancient and recent forests differ in their sensitivity to warming and N deposition

Increased N deposition was related to decreased herb cover, but only in ancient forests, while stronger warming was related to decreased herb cover only in recent forests (**Fig. 3.3A** and **3.3B**). This suggests that herb layers in ancient forests are more sensitive to N deposition, while herb layers in recent forests are more sensitive to warming. As explained above, the stronger response of recent forest herb covers to warming is likely related to the lower microclimate buffering by canopies with lower shade-casting ability, compared to ancient forests. The loss of herb cover with increased N deposition is typically related to the acidifying effect of nitrogen, which is detrimental for the survival of many (herb) species (Tian & Niu, 2015). This can however not explain the distinct herb cover responses to N deposition between ancient and recent forests, as pH values were very similar for both land-use categories, and hence we would not expect ancient forests. Further (experimental) research is required to understand and confirm the underlying mechanism(s) to these, and our other, observations.

3.5.3. Relating biodiversity and functional changes

Our results suggest that there is nearly no overlap in potential drivers of biodiversity and functional responses of the herb layer. Only the response in total herb cover and species evenness (independent from species richness) share one potential driver, i.e. shade-casting ability. Indeed, we also found negative correlations between these two response variables (total herb cover and species evenness). Over time, the total herb layer cover has declined in the temperate European forests that were studied, and the communities have become more even in the abundance of their species. This suggests that the decline in cover is mainly related to a reduced cover of one or more dominant species, and the overall decreased shade-casting ability seems to be the main potential driver of this observation.

3.6. SYNTHESIS

Herb layer community changes in response to environmental alterations differed between ancient and recent forests. These observations confirm our idea that land-use history should not be overlooked in global change studies. Light availability, related to canopy cover and composition, was the most important environmental driver for functional changes and changes in species evenness in the herb layer. Increased shade had the strongest effect on herb layers in ancient forests, where shade-tolerant forest specialists gained importance, while light-demanding competitive species disappeared, resulting in lower cover, higher species evenness, increased specific leaf area and decreased plant height. In recent forests, effects of increased shade on the herb layer were smaller, which we attribute to: (i) higher shade tolerance of light-demanding species when nutrient levels are higher as a legacy of former agricultural use, and (ii) lower initial shade levels in recent forest, which therefore might not yet have reached critical light levels at which communities start responding. On the other hand, the herb layer cover in recent forests was more responsive to increased temperatures, compared to ancient forests, which we could again relate to canopy properties: communities in ancient forests are likely more buffered to macroclimate warming due to the overall higher shade-casting ability of the canopy.

In general, there seems to be a disconnect between biodiversity and functional responses of the herb layer to environmental changes, and therefore, assessing both types of responses is key to get a more complete understanding of the possible impact of global change on the forest herb layer.







Evaluating structural and compositional canopy characteristics to predict the lightdemanding signature of the forest understorey in mixed, semi-natural temperate forests

After:

Depauw, L., Perring, M.P., Landuyt, D., Maes, S.L., Blondeel, H., De Lombaerde, E., Brūmelis, G., Brunet, J., Closset-Kopp, D., Decocq, G., Den Ouden, J., Härdtle, W., Hédl, R., Heinken, T., Heinrichs, S., Jaroszewicz, B., Kopecký, M., Liepiņa, I., Macek, M., Máliš, F., Schmidt, W., Smart, S.M., Ujházy, K., Wulf, M., Verheyen, K., 2020. Evaluating structural and compositional canopy characteristics to predict the light-demanding signature of the forest understorey in mixed, semi-natural temperate forests.

4.1. ABSTRACT

Light availability at the forest floor affects many forest ecosystem processes, and is often quantified indirectly through easy-to-measure stand characteristics. We investigated how three such characteristics, basal area, canopy cover and canopy closure, are related to each other in structurally complex mixed closed-canopy forests, and how well they can predict the light-demanding signature of the forest understorey (estimated as the mean Ellenberg indicator value for light ('EIV_{LIGHT}') and the proportion of 'forest specialists' within the plots ('%FS')). Furthermore, we asked whether accounting for the shade-casting ability of individual canopy species could improve predictions of EIV_{LIGHT} and %FS.

In 192 study plots from nineteen temperate forest regions across Europe, we measured stand basal area (all stems > 7.5 cm diameter), canopy closure (with a densiometer) and visually estimated the % cover of all plant species in herb (<1m), shrub (1-7m) and tree layer (>7m). We used linear-mixed effect models to assess the relationships between basal area, canopy cover and canopy closure. We performed model comparison, based on R² and AIC, to assess which stand characteristics can predict EIV_{LIGHT} and %FS best, and to assess the importance of the canopy's shade-casting ability.

Canopy closure and cover were weakly related to each other, but showed no relation with basal area. For both EIV_{LIGHT} and %FS, canopy cover was the best predictor. Including the share of high shade-casting species in both the basal area- and cover model improved the model fit for EIV_{LIGHT}, but not for %FS.

The typically expected relationships between basal area, canopy cover and canopy closure were weaker or even absent in structurally complex mixed closed-canopy forests. In these forests, easy-to-measure structural canopy characteristics were weak predictors of the understorey light signature, but accounting for compositional characteristics could improve predictions.

4.2. INTRODUCTION

Light availability at the forest floor is a crucial environmental factor for many forest ecosystem processes. Light is a key resource for the growth and survival of forest understorey plant species (Plue et al., 2013), and affects conditions and processes including the forest microclimate (Gray et al., 2002; Ritter et al., 2005), plant community assembly and diversity (Bartemucci et al., 2006; De Frenne et al., 2015; Jelaska et al., 2006), tree regeneration (Beaudet & Messier, 1998; Kobe et al., 1995; Lin et al., 2014), and litter decomposition (Hobbie et al., 2006). Several studies, focusing on forest understorey trajectories under global change in temperate forests, concluded that light availability has a major impact on the understorey composition (e.g. De Frenne et al., 2015). In a full-factorial experiment on herbaceous communities, Blondeel et al. (2020) found that light, rather than global-change drivers (nitrogen deposition and warming) or past land use, determined development trajectories of forest understorey communities over a period of three years. In our resurvey study in temperate oak forests in South Sweden (Chapter 2), we concluded that light dynamics due to management practices play a key role in shaping the understorey composition development.

This clear importance of light availability for the forest understorey composition suggests that forest management, affecting stand structural attributes, may play a crucial role in controlling understorey development in times of global change. Therefore, in our study, we aim to relate stand structural attributes to the 'light-demanding signature' of the understorey. Stand structural attributes are widely used in forest ecology as proxies for light availability (see Angelini et al. (2015) for a review), especially because direct measurements of light availability at the forest floor are typically costly and time-consuming (Brown et al., 2000). In addition, in vegetation resurvey studies, which provide a unique opportunity to estimate vegetation and environmental changes over the past decades (Kapfer et al., 2017), values of light availability at the forest floor in the past (e.g. at the time of the original survey) are typically not available, and light levels need to be estimated from stand or tree characteristics that were recorded. The lightdemanding signature of the understorey can, for instance, be quantified through calculating the community's mean Ellenberg indicator value for light availability. Ellenberg indicator values indicate species preferences in their fundamental niche, which may characterize the environment in the absence of directly measured variables (Diekmann, 2003). Alternatively, other indicators such as the relative abundance of species restricted to forests vs. species also occurring in the open landscape could provide insight in the light-demanding signature of the understorey (e.g. Heinken et al., 2019).

We focus on three easy-to-measure stand characteristics that can provide indirect estimates of light availability at the forest floor (Parker, 2014). The first one is stand basal area, which can be obtained through various methods, such as field measurements of tree diameter at breast height (e.g. Balandier et al., 2006; Sonohat et al., 2004), measurements with an angle prism (Parker, 2014), and LiDAR techniques (light detection and ranging) (Thomas, Oliver, Lim, & Woods, 2008). Secondly, canopy *cover*, defined as the proportion of ground surface covered by the vertical projection of tree crowns, can be obtained from visual estimation with or without instruments (e.g. a sighting tube), or from aerial photographs (Jennings et al., 1999). Thirdly, canopy *closure* is defined as the proportion of the sky hemisphere obscured by vegetation when viewed from a single point (Jennings et al., 2006; Sercu et al., 2017, Gray et al., 2002). A commonly used alternative is the use of a spherical densiometer (Lemmon, 1957), a handheld device where the number of open squares on a convex mirror surface is recorded (e.g. Lieffers et al., 1999; Plue et al., 2013). Several studies demonstrated that densiometer measurements are a reliable alternative for estimating light availability below the canopy, compared to hemispherical photography (Bellow & Nair, 2003; Parker, 2014).

For the three stand characteristics described above, strong relations with light transmittance have been found in even-aged, homogeneous stands with relatively regular spatial distribution of trees (e.g. Balandier et al., 2006; Parker, 2014; Sonohat et al., 2004). However, relationships might be more complex in seminatural, uneven-aged, mixed, heterogeneous stands with multiple structural layers. The amount of light transmitted by a tree can vary considerably among different species, partly because of their lightinterception strategies (Angelini et al., 2015; Leuschner & Ellenberg, 2017; Montgomery & Chazdon, 2001). For example, Perot et al. (2017) applied species-specific light extinction coefficients to account for the canopy composition when modelling light at the forest floor in oak-pine mixed stands. Hence, stands with similar basal area or canopy cover can have different light levels at the forest floor, depending on the shade-casting ability of the constituent tree species. Additionally, in structurally rich stands, interactions between different layers of the canopy (e.g. tree layer and shrub layer) will ultimately determine the light availability at the forest floor (Sercu et al., 2017).

For this study, we used measurements from 192 plots across 19 regions in temperate European forests, characterized as mixed, semi-natural, closed-canopy forests with a well-developed vertical structure (i.e. the presence of both trees and shrubs with varying heights). Within regions, plots generally had similar tree species in their canopy, but with varying density-levels due to varying management intensities. Among regions, plots differed in their main constituent canopy species. We aimed to:

- (i) assess the relationships between stand basal area, canopy *cover* and canopy *closure*;
- (ii) compare how well stand basal area, canopy cover and canopy closure can predict the lightdemanding signature of the understorey;
- (iii) assess the importance of including the shade-casting ability of individual canopy species to improve predictions of the light-demanding signature of the understorey.

4.3. METHODS

4.3.1. Study site

We selected 192 forest plots, spread across 19 temperate forest regions in Europe (Fig. 1.1A, Table 4.1). The plot selection was part of a vegetation resurvey project on understorey community responses to global change and land-use history across European forests (ERC-project PASTFORWARD, http://www.pastforward.ugent.be/). All plots comprised semi-natural, mixed, closed-canopy forests with a variable tree and shrub layer composition. Plots were predominantly composed of broadleaved species, but a higher occurrence of coniferous species in the easternmost regions with a hemiboreal climate was unavoidable. The five most frequent canopy species across all plots were *Quercus robur/petraea*

(110/192 plots), *Fagus sylvatica* (78/192 plots), *Corylus avellana* (71/192 plots), *Fraxinus excelsior* (69/192 plots) and *Carpinus betulus* (64/192 plots) (see **Appendix A1.2** for an overview of the shrub and tree layer composition of all plots). Within the constraints of plot selection (information on land-use history and a prior understorey vegetation survey were required within the larger project), we tried to minimize differences in parent material and topography among plots. Plots differed in their land-use- and management history: 57 plots were located in recent (post-agricultural forests) and 135 plots in ancient forest (continuously forested since at least 1810). The timing of afforestation of the recent forest sites ranged from 1810 to 1970, but with the majority (47/57) afforested before 1930. 79 out of the 192 plots had a history of coppice(-with-standards) management (see **Table 4.1**).

After we located the centre of the plot, we established a $10x10-m^2$ plot, and a $20x20-m^2$ plot with the same central point. In the $10x10-m^2$ plot, we carried out a vegetation survey, with two surveyors visually estimating and then agreeing on the percentage cover of each vascular plant species in three different layers: herb layer (< 1 m), shrub layer (1-7 m) and tree layer (> 7 m). All measurements were done in May/June 2015/2016.

Table 4.2. Main canopy characteristics and understorey light signature of the 19 forest regions. Overview of the 19 forest regions, their number of plots, their land-use history (AF = ancient forest), their management history (CWS = coppice-with-standards) and their mean values and ranges (in parentheses) of canopy closure, canopy cover, basal area, proportion of the cover occupied by high shade-casting species, mean Ellenberg indicator value (ElV_{LIGHT}) and percentage of forest specialists in the total herb species pool.

| ID | Region, Country | Total nr. of plots (-) | Nr. of AF plots (-) | Nr. of plots with C(WS) history (-) | Mean (range) canopy closure (%) | Mean (range) canopy cover (%) | Mean (range) cover proportion of high shade-casting species (%) | Mean (range) basal area (m² ha-1) | Mean (range) EIVиднт (-) | Mean (range) % forest specialists (%) |
|-----|------------------------|---------------------------------|------------------------------|---|---------------------------------------|-------------------------------------|---|---|--------------------------------|---|
| BI | Bialowieza. PL | 15 | 15 | 0 | 85.0 (70.0 - 95.6) | 77.0 (48.1 - 91.9) | 80.2 (36.2 - 100) | 39.5 (23.2 - 64.4) | 4.1 (3.6 - 4.5) | 78 (67 - 90) |
| BS | Braunschweig, Ge | 10 | 5 | 7 | 80.4 (73.0 - 93.1) | 78.8 (65.8 - 90.4) | 1.7 (0.0 - 12.0) | 26.5 (17.5 - 41.3) | 5.2 (4.7 - 6.2) | 35 (0 - 50) |
| BV | Binnen-Vlaanderen, Be | 9 | 4 | 4 | 80.6 (72.8 - 90.4) | 75.0 (16.4 - 94.2) | 19.4 (0.0 - 52.8) | 33.7 (17.4 - 64.9) | 5.0 (4.2 - 5.6) | 36 (14 - 67) |
| CO | Compiègne, Fr | 10 | 10 | 0 | 83.4 (65.3 - 94.8) | 77.1 (22.5 - 97.2) | 79.9 (39.8 - 100) | 23.4 (10.0 - 46.9) | 5.2 (4.4 - 5.8) | 44 (14 - 60) |
| DE | Devin Wood, CZ | 10 | 3 | 3 | 84.0 (67.8 - 96.9) | 67.9 (44.9 - 88.0) | 37.5 (0.0 - 78.0) | 32.1 (14.2 - 53.5) | 4.5 (3.7 - 5.6) | 55 (31 - 68) |
| GO | Göttingen, Ge | 10 | 10 | 10 | 89.4 (83.6 - 94.8) | 87.1 (69.9 - 96.6) | 84.1 (50.4 - 98.5) | 33.5 (18.5 - 47.9) | 3.2 (2.6 - 3.8) | 88 (72 - 100) |
| КО | Koda Wood, CZ | 10 | 10 | 7 | 92.7 (79.6 - 95.8) | 75.2 (41.7 - 90.8) | 47.0 (4.8 - 76.2) | 34.6 (24.9 - 47.2) | 4.7 (4.2 - 5.2) | 60 (50 - 72) |
| LF | Lyons-la-forêt, Fr | 10 | 10 | 0 | 82.7 (62.1 - 93.1) | 79.9 (55.0 - 98.7) | 96.2 (78.4 - 100) | 21.1 (12.3 - 29.0) | 4.3 (3.6 - 5.1) | 71 (39 - 89) |
| MO | Moricsala, LV | 8 | 5 | 0 | 74.2 (48.0 - 95.4) | 67.0 (41.4 - 94.1) | 39.1 (0.0 - 91.0) | 34.8 (21.8 - 46.4) | 4.2 (3.8 - 4.8) | 72 (60 - 82) |
| PR | Prignitz, Ge | 10 | 5 | 0 | 80.1 (63.2 - 94.8) | 72.6 (49.9 - 95.0) | 31.5 (0.0 - 100) | 46.2 (19.3 - 78.3) | 4.6 (3.6 - 5.8) | 51 (21 - 75) |
| SH | Schleswig-Holstein, Ge | 10 | 5 | 0 | 88.1 (80.0 - 95.0) | 82.0 (15.0 - 97.0) | 92.4 (75.5 - 100) | 40.6 (24.8 - 71.7) | 3.9 (3.0 - 4.8) | 73 (33 - 100) |
| SK | Slovak Karst, SK | 10 | 10 | 10 | 90.9 (84.4 - 96.5) | 84.0 (68.9 - 98.6) | 55.0 (44.9 - 67.9) | 33.7 (25.5 - 49.1) | 4.4 (3.7 - 4.8) | 51 (35 - 75) |
| SKA | Skåne, Sw | 10 | 8 | 0 | 80.1 (61.7 - 98.5) | 71.5 (50.0 - 92.7) | 32.3 (0.0 - 100) | 34.0 (10.2 - 59.1) | 4.5 (3.5 - 5.3) | 61 (37 - 92) |
| SP | Speulderbos, Nl | 10 | 5 | 5 | 90.2 (81.9 - 95.8) | 78.9 (38.6 - 98.0) | 72.7 (21.7 - 100) | 25.0 (16.5 - 40.3) | 5.3 (4.5 - 6.0) | 2 (0 - 12) |
| ТВ | Tournibus, Be | 10 | 5 | 10 | 86.3 (71.9 - 95.2) | 89.8 (80.0 - 95.9) | 23.3 (2.5 - 51.2) | 29.2 (19.5 - 38.3) | 4.5 (4.1 - 5.0) | 58 (41 - 80) |
| W | Wales, UK | 10 | 5 | 5 | 67.8 (51.3 - 91.9) | 56.4 (22.8 - 77.7) | 53.0 (7.4 - 96.8) | 28.9 (13.5 - 38.3) | 4.5 (3.2 - 5.6) | 52 (26 - 83) |
| WR | Warburg Reserve, UK | 10 | 5 | 5 | 66.4 (27.4 - 89.4) | 89.8 (76.4 - 96.5) | 45.4 (0.0 - 95.0) | 31.3 (19.9 - 43.0) | 3.9 (2.5 - 4.5) | 69 (50 - 100) |
| WW | Wytham Woods, UK | 10 | 5 | 5 | 57.8 (34.7 - 75.6) | 68.3 (38.3 - 97.0) | 10.3 (0.0 - 55.7) | 20.7 (10.7 - 38.9) | 4.8 (4.3 - 5.6) | 51 (30 - 64) |
| ZV | Zvolen, SK | 10 | 10 | 8 | 86.4 (72.3 - 96.9) | 76.4 (47.4 - 91.2) | 24.9 (0.0 - 66.7) | 37.9 (29.4 - 44.7) | 4.7 (3.0 - 5.8) | 47 (14 - 100) |

4.3.2. Light-demanding signature of the understorey

We derived two different variables that reflect the light-demanding signature of the understorey. First, we calculated the mean Ellenberg indicator value for light (EIVLIGHT) (Ellenberg et al., 1992). Ellenberg indicator values indicate species environmental preferences in their fundamental niche (Diekmann, 2003). EIVLIGHT ranges from 1 (species can grow in very deep shade and rarely occurs in more open conditions) to 9 (species only occurs in open conditions). Second, we calculated the proportion of species typically related to closed forests (further on referred to as the proportion of 'forest specialists' (FS)). We classified each species in our dataset as either a forest specialist (FS) or not, according to the recently published dataset of Heinken et al. (2019). This dataset presents a comprehensive list of vascular plant species occurring in forests for 24 geographical regions across Western, Central and Northern Europe, assigning each species to one of four different groups with different degrees of association with forests (i.e. as an indication for the habitat preference). The forest specialists ('1.1 species') are the species most strongly associated to closed forests. We used the regional species classification relevant for each study region, as some species are classified as 'forest specialist' in some regions, but not in others. Both variables were based on the 'strict' herb layer, containing only the herbaceous species, and excluding tree seedlings and shrub species, because the latter often do not survive more than one growing season as they germinate independent of suitable site conditions (Yan et al., 2015). Moreover, light requirements of tree species can differ between the seedling and adult stage (Valladares et al., 2016) (see Appendix A3.5 for species lists).

To calculate both the mean EIV_{LIGHT} and the proportion of forest specialists of the herb layer community in each plot, we used presence/absence data. According to Diekmann (2003), the results using presence/absence data should not differ much from the results based on abundances, but most researchers prefer using presence/absence data reasoning that a species' abundance is not only dependent on environmental site conditions, but also on its specific growth form. Hence, mean EIV_{LIGHT} of each plot was calculated as the sum of the EIV_{LIGHT} of each occurring species, divided by the total number of species. The proportion of forest specialists in each plot was calculated as the total number of forest specialists occurring in the plot, divided by the total number of species in the plot. However, in **Appendix A4.1**, we repeated our main analysis (see further: 'predicting understorey light signatures from canopy structure and composition') using abundance-weighted values for both EIV_{LIGHT} and %FS, to check whether this resulted in different responses.

4.3.3. Proxies for light availability at the forest floor: basal area, canopy cover and canopy closure

The **basal area** (m² ha⁻¹) of a forest stand represents the area occupied by tree stems per hectare. For all trees and shrubs within the 20x20-m² plot with a diameter at breast height (DBH) \geq 7.5 cm, we took two measurements of DBH in orthogonal directions, and used the average for the calculation of basal area. For tree stems located on the border or corner of the plot, we divided the calculated stem area by 2 or 4 respectively.

We derived the **canopy cover** (%) in each 10x10-m² plot from the visually estimated cover (%) of all species occurring in the shrub and tree layer. To combine the cover values of the different layers and species, we accounted for overlap by applying a formula described by Fischer (2015). This means that the final canopy cover value of a plot will never exceed 100 %, even when the sum of the cover of all species in the tree and shrub layer is higher than 100%. In **Appendix A4.2**, we repeated our statistical analyses (described below) without applying this formula, and found that overall results and trends were similar, but model fits were slightly better when accounting for overlap through applying the formula.

We measured **canopy closure** (%) with a spherical densiometer at breast height (1.3 m). This small instrument employs a mirror with spherical curvature to visualize the reflection of a large overhead area. A grid is used to estimate percentage of this overhead area covered with forest canopy (Forestry Suppliers, 2008; Lemmon, 1957). We repeated the measurement at five points in each plot: one time in the centre of the plot, and on each corner of the $10x10-m^2$ plot. We averaged the five results to get a final value of canopy closure in the forest plot.

4.3.4. Shade-casting ability of canopy species

The shade-casting ability (SCA) of tree and shrub species is a qualitative index based on expert knowledge from Ellenberg (1996). SCA scores (listed in **Appendix A3.7**, adapted from Ellenberg (1996) and complemented with expert knowledge of prof. Kris Verheyen) range between 1 (very low shade-casting ability) and 5 (very high shade-casting ability) (see also Baeten et al., 2009; Van Calster et al., 2008; Verheyen et al., 2012). To check the reliability of this qualitative index, we compared it to the leaf area index (LAI) values that are available for eleven major Central European tree species (Leuschner & Meier, 2018). For these eleven species, we found high correlations between SCA and LAI (see **Appendix A4.3** for details), suggesting that our SCA-scoring is acceptable. For both canopy cover and basal area, we not only calculated total values for each plot, but also the canopy cover and basal area of the high shade-casting species (with a SCA score of 4 or 5) only. From this, we derived the proportion (%) of the total canopy cover and basal area that is attributed to the high shade-casting species.

4.3.5. Statistical analyses

We performed all statistical analyses and visualizations in R version 3.6.0 (R Core Team, 2019) with the packages 'nlme', 'MuMIn', 'ggplot2', 'mgcv', and 'sjPlot' (Barton, 2019; Lüdecke, 2019; Pinheiro et al., 2019; Wickham et al., 2019; Wood, 2017).

4.3.5.1. Relating basal area, canopy cover and canopy closure (research question 1)

To assess the relationships between the three main stand characteristics, i.e. canopy closure, canopy cover and basal area, we used linear mixed-effect models with one of the variables as the response variable, and another one as the explanatory variable. In addition, for the relationship of both basal area and canopy cover with canopy closure, we also checked whether an exponential relationship fitted the data better. This expectation of an exponential relationship is based on the Lambert-Beer law, expressing light transmittance under a canopy as (Sonohat et al., 2004):

$$T = e^{(-k \ LAI)}$$
Equation 4.1

where T is canopy transmittance (dimensionless), LAI is the canopy leaf area index, and k is an extinction coefficient, which depends mainly on cover properties. Our expectation of an exponential relation is based on the assumption that canopy closure is the complement of canopy transmittance, and LAI is linearly related to basal area and canopy cover (Sonohat et al., 2004). Hence, **Equation 4.1** can be rewritten as:

Canopy Closure = $100 - e^{(\alpha + \beta . X)}$

Equation 4.2

where X is either canopy cover (%) or basal area (m²ha⁻¹), and α and β are respectively the intercept and slope obtained with the linear mixed-effect modelling (after linearizing **Equation 4.2** through a log transformation).

Finally, we also fitted a smoother to the data using a generalized additive mixed model (GAMM), to compare the actual shape of the relationships with the fitted exponential and/or linear relationships.

We started with a model with varying slopes and intercepts for the random effect term 'region', and a weight term to control for heterogeneity in residual spread among the regions. For each model, we used ANOVA to find the most parsimonious model, by checking whether the random slopes, random intercepts and weights term significantly (alpha = 0.05) improved the model. We used R² to assess the strength of the relationships.

4.3.5.2. Predicting understorey light signatures from canopy structure and composition (research questions 2 and 3)

For both response variables, i.e. the mean EIV_{LIGHT} and the proportion of forests specialist, we compared five linear mixed effect models. The first three models contained only one explanatory variable: canopy closure, canopy cover or basal area. The fourth model contains both canopy cover and the proportion of the canopy cover occupied by high shade-casting species as explanatory variables. The fifth model contains both basal area and the proportion of the basal area occupied by high shade-casting species as explanatory variables. We standardized (scaled and centred) all explanatory variables in each model to enable comparison of their effect sizes. In each model, we included a random effect term 'region' with varied intercepts only to account for the hierarchical structure of the data. We also incorporated 'region' as a weight term, i.e. we controlled for heterogeneity in residual spread. With ANOVA, we confirmed that both the random effect term and the weights term significantly (alpha = 0.05) improved the model for each response variable. Including 'region' with both varied intercepts and slopes did not considerably change the overall results, so we will only present the results from the simplest model with only varied intercepts.

All models were fit with restricted maximum likelihood (REML). We found no clear patterns in the residuals for each model, based on graphical evaluation (Zuur et al., 2009). We report estimates and 95% confidence intervals for each explanatory variable in each model. We based our model comparison on both the Akaike Information Criterion (AIC) (Akaike, 1973) and the marginal and conditional R² (Nakagawa & Schielzeth, 2013). The marginal and conditional R² represent the variance explained by fixed factors and the variance explained by both fixed and random factors, respectively (Nakagawa & Schielzeth, 2013). AIC is often used to select the 'best' or 'better' models from a candidate model set, and penalizes for the number of explanatory variables (Burnham & Anderson, 2002). R² values on the other hand, have the advantage that they provide information on the absolute model fit and the amount of variance explained (Nakagawa & Schielzeth, 2013).

4.4. RESULTS

4.4.1. Relating basal area, canopy cover and canopy closure

In general, the fitted relationships between canopy closure, canopy cover and basal area were poor (**Fig. 4.1**). For the first model (canopy closure vs. canopy cover), a mixed-effect model with both random slopes and random intercepts was the most parsimonious model, while for the other two models, the random intercept only model was retained. In each model, the weight term to control for heterogeneity in residual spread among the regions was also retained. Our expectation of exponential relationships with

canopy closure was not confirmed. For the relation between canopy closure and canopy cover, we found a better model fit for the linear model ($R^2m = 0.20$) than for the exponential model ($R^2m = 0.15$) (**Fig. 4.1a**). We did not find any relation between canopy closure and basal area, as both the linear and exponential model had an R^2m value of 0.00 (**Fig. 4.1b**). Similarly, we found no clear relation between canopy cover and basal area ($R^2m = 0.02$; **Fig. 4.1c**). Using a generalized additive mixed model to relate each pair of variables to each other did not result in better model fits, as the adjusted R^2 values of these models were very similar to the R^2m values of the linear and/or exponential relationships, and the shape of the smoothers approached the shape of the linear and/or exponential relationships (**Fig. 4.1**).



Figure 4.1. Relating basal area, canopy cover and canopy closure. (*a*) Linear (black line) and exponential (red line) relationship between canopy closure and canopy cover; (*b*) Linear (black line) and exponential (red line) relationship between canopy closure and basal area; (*c*) linear relationship between basal area and canopy cover. In each plot, the blue line and blue R^2 value represent the result of the generalized additive mixed model. 'Region' was included as a random effect, with random slopes (β) and random intercepts (*a*) only in the second and third set of models (*b*+*c*). Coloured dots represent the actual data points per region. The region labels refer to **Table 4.1**.

4.4.2. Predicting understorey light signatures from canopy structure and composition

We found similar but opposite trends when comparing the five models to predict both the mean EIV_{LIGHT} and the proportion of forest specialists ("%FS'), which are respectively expected to increase and decrease with increasing light availability (**Fig. 4.2**). Canopy closure was a significant predictor for both response variables, but with quite poor model fits ($R^2m = 0.03$ for both models). Canopy cover was also a significant predictor for both response variables, with slightly bigger effect sizes than canopy closure, but still poor model fits ($R^2m = 0.09$ for EIV_{LIGHT}; $R^2m = 0.06$ for %FS). For both response variables, basal area was not a significant predictor ($R^2m = 0.00$ for both models). Adding the percentage of the total canopy cover that is occupied by high shade-casting species as an additional predictor to the canopy cover model improved the model fit for both response variables ($R^2m = 0.19$ for EIV_{LIGHT}; $R^2m = 0.09$ for %FS). Adding the percentage of basal area that is occupied by high shade-casting species as an additional predictor to the canopy cover %FS, the percentage of basal area that is occupied by high shade-casting species did not have additional explanatory power, and R^2m did not increase.

In general, for both response variables, the canopy cover models were the best models, with the lowest AIC-values and the highest R²m-values (**Fig. 4.2**). For mean EIV_{LIGHT}, including the percentage of high shade-casting species clearly improved the model predictions, both for canopy cover and basal area, as this clearly increased R²m-values and decreased AIC-values (**Fig. 4.2a**). For %FS, the benefit of accounting for the shade-casting ability of the canopy species was less clear: for basal area, no model improvements were found, while for canopy cover, R²m increased slightly, but AIC increased as well (Δ AIC = 6.55) (**Fig. 4.2b**).

For all models, conditional R^2 (R^2c) was very high (ranging from 0.68 to 0.84 for EIV_{LIGHT}, and ranging from 0.86 to 0.92 for %FS), which indicates that a large part of the variation in the response variables can be explained by the random effect term 'region' (**Fig. 4.2**).

For the models based on abundance-weighted values for both EIV_{LIGHT} and %FS, instead of presence/absence based values (**Appendix A4.1**), we found very poor model fits (R^2m ranging from 0 to 0.02 for EIV_{LIGHT} and $R^2m = 0$ for all models with %FS as response variable). Canopy closure was the only significant predictor for EIV_{LIGHT}, and canopy cover was the only significant predictor for %FS (but with a very small effect size of only -0.004).




4.5. DISCUSSION

In complex semi-natural mixed closed-canopy forests, relationships between structural characteristics of the canopy are more complex compared to what we can find in the literature for homogenous monospecific stands. The signature for light requirements of the herb layer species was only weakly related to the structural stand characteristics analysed, with canopy cover showing better predictions than canopy closure and basal area. Correlations, however, improved when we took both the canopy structure and the shade-casting ability into account. Yet, the understorey light signature remained largely driven by regional characteristics (e.g. land-use history, management type, soil characteristics or landscape fragmentation).

4.5.1. Relating basal area, canopy cover and canopy closure

In contrast to many other studies, we did not find strong relationships between the three main stand characteristics that we studied, i.e. canopy closure, canopy cover and basal area. For example, Parker (2014) found a very strong logarithmic relationship between canopy closure and basal area ($R^2 = 0.81$) in even-aged pine-dominated forests, and Buckley et al. (1999) found very strong ($R^2 > 0.90$) linear relationships between canopy cover and basal area in both oak and pine stands. Fiala et al. (2006) described the relation between canopy cover and densitometer measurements with a simple linear regression model, and found an R²-value of 0.65 in stands dominated by Douglas-fir, western hemlock, and western redcedar. The lack of clear relationships in our study is probably related to the fact that our analyses focused on much more complex and heterogeneous forest stands, with mixed species and welldeveloped vertical structures. It can be assumed that tree architecture and the light-related characteristics of crowns, branches and leaves can be changed when a tree species grows in mixed stands because of the interactions with other tree species (Perot et al., 2017; Pretzsch, 2014). Differences in crown plasticity between species in mixed stands might also influence the relation between structural stand characteristics, as species with high crown plasticity (such as Fagus sylvatica, a common species in our dataset) can occupy canopy gaps much more effective (Schröter et al., 2012). Also, we are likely investigating smaller ranges of these stand characteristics compared to other studies, because all our plots are situated in mixed closedcanopy forests with relatively high canopy packing and therefore decreased spatial light heterogeneity at the forest floor (Sercu et al., 2017). Furthermore, the presence of a shrub layer in many of our study plots could interfere with the typically expected relations between stand attributes. Especially when light transmittance by the tree layer is high, a complementary shrub layer can exploit this high light availability, and become dense (Sercu et al., 2017). However, shrubs with small stems might not be included in the basal area of the plot, as we needed to set a diameter threshold (in this study at 7.5 cm) to keep DBHmeasurements feasible. This might weaken correlations between basal area and canopy cover/closure.

4.5.2. Predicting understorey light signatures from canopy structure and composition

Of the three investigated stand attributes, canopy cover proved to be the best predictor for the lightdemanding signature of the understorey. This suggests that, in resurvey studies, the lack of data of stand characteristics such as basal area or canopy closure for the original survey is not necessarily a problem, as they are weaker predictors of light availability than the more often available canopy cover values. Indeed, tree and shrub cover estimates are often part of the vegetation survey, and therefore typically available from past vegetation resurveys (e.g. Verheyen et al., 2012).

In contrast to our findings, Alexander et al. (2013) found that canopy closure had a better correlation with EIV_{LIGHT} than canopy cover estimates based on airborne laser scanning (ALS). In theory, canopy closure should indeed provide a better description of the light conditions under a canopy than canopy cover as all the directions in which light reaches a point below the canopy are taken into consideration (Alexander et al., 2013; Jennings et al., 1999). However, this might mainly apply to more open systems or landscapes with forest patches, where light can reach the understorey from the edge of the forest (patch), which is not the case in our plots. The better performance of canopy cover compared to basal area, for predicting the understorey light signature, could be related to the DBH threshold of 7.5 cm that we applied. In contrast to basal area, canopy cover also accounts for smaller shrubs with DBH < 7.5 cm, which can make a considerable difference in plots with a high cover of young shrubs.

Including the species composition of the canopy, through distinguishing high- and low shade-casting species, clearly improved the predictions of the understorey light signature. These results demonstrate that in mixed forests, both canopy structure and canopy composition will determine the light conditions at the forest floor. This is in accordance with several other studies that demonstrated that the simple Lambert-Beer model for light attenuation in forests should be modified for mixed forest stands by applying species-specific values for leaf area index (LAI) and the extinction coefficient (e.g. Cannell and Grace, 1993; Lieffers et al., 1999; Perot et al., 2017). In temperate mixed forests in Flanders, De Lombaerde et al. (2019) also found that tree regeneration (strongly controlled by light availability) depended more on the abundance-weighted shade-casting ability of the canopy, than on the abundance (measured as both canopy cover and basal area) *per se.* However, the relative importance of the canopy composition and structure might depend on the management intensity: Drever and Lertzman (2003) found much weaker dependence of understorey light conditions on the canopy species composition in intensively managed forests, where mainly structural features seemed to be affecting the light conditions at the forest floor.

Overall, we observed that the three easy-to-measure stand characteristics were weak predictors of the light-demanding signature of the understorey in our study plots. These weak relations could be related to the small range within these stand characteristics in the studied forests (**Table 4.1**), which are all closed-canopy forests. Alexander et al. (2013) also found that the correlations between canopy cover estimates and EIV_{LIGHT} increased with increasing variability in canopy cover within a site, and that the lower the variability, the more difficult it was to predict understorey light conditions from the estimates of canopy cover. Similarly, Diekmann (2003) stated that if the light gradient is small, weighted mean indicator values

will differ less between plots, and might be more affected by random spatial fluctuation in species composition than by an underlying gradient of light availability. This can also be related to the very high conditional R² values (compared to the very low marginal R² values) that we found in our models, suggesting that a large part of the variation in the understorey light signature can be explained by the region in which a plot is situated. Hence, regional attributes, such as the soil characteristics, the 'available' species pool, the regional climate, the topography, the land-use- and management history, and the landscape fragmentation and associated dispersal limitations seem to be mainly controlling the understorey composition and its light-demanding signature. For instance, the impact of land-use history on the light-demanding signature of the understorey was assessed by Dzwonko (2001), who found weaker correlations between EIV_{LIGHT} and measured light levels in recent forests, because shade-tolerant specialists had not yet colonized these forests. Differences in management might affect the lightdemanding signature of the understorey through differences in the return interval of light at the forest floor. When this interval is short (e.g. in coppice(-with-standard) systems), light-demanding species can maintain in a vegetative state. Soil characteristics can affect the light-demanding signature of the understorey, through for instance the fact that plant species are often more shade-tolerant on nutrientrich sites (Coomes et al., 2009).

The effect of other (regional) factors appears to be stronger for %FS than for EIV_{LIGHT}, based on the lower R²m and higher R²c values that we found for %FS. This is in accordance with our expectations, as EIV_{LIGHT} has a clear focus on light availability, while the 'forest specialist' classification is based on habitat affinity in general, where other factors, next to light, are important. For example, the share of forest specialists is generally lower on acidic soils than on base-rich soils (Schmidt et al., 2011). Furthermore, the share of forest specialists can also depend on the litter quality and quantity (Decocq & Hermy, 2003), which are affected by canopy characteristics.

Another potential cause of the poor model fits is the occurrence of time lags in the understorey. Temperate forest herb layers are slow-changing systems (Dornelas et al., 2013; Perring, Bernhardt-Römermann, et al., 2018), and understorey communities can display a delayed response to overstorey canopy and light dynamics (Plue et al., 2013). Hence, the current understorey composition might be more strongly related to past light availability (and thus past management) than to the contemporary light conditions (see also our findings in Chapter 5). Time lags can be expected to be stronger for environmental shifts from light to shade (slow changes) than for shifts from shade to light (fast changes) (De Lombaerde et al., 2018). Most of our plots are characterized by an overall reduction in management intensity during the last decades (Kopecký et al., 2013; McGrath et al., 2015), and have therefore slowly shifted from lighter to darker conditions, so it is likely that the understorey community changes are still 'limping behind' (Diekmann, 2003).

Related to these time lags, we might expect to see stronger effects of canopy characteristics on abundance-based understorey responses compared to presence/absence-based responses, as a species will typically not disappear immediately when light conditions become unfavourable, but will decrease in abundance (e.g. Decocq et al., 2005). However, this was not confirmed with a comparison between abundance-based and presence/absence-based responses (**Appendix A4.1**). This comparison mainly illustrated that the effects of canopy characteristics on the understorey light signature are mainly driven by the rare species with low abundances. These less abundant species are given equal weight in the presence/absence analysis, where we found stronger effects of canopy characteristics and higher model fits, while they are given a lower weight than the more abundant species in the abundance-based analyses, where we found small effects and lower model fits. Hence, species turnover appeared to be more important than changes in species abundances for explaining canopy effects on the understorey light signature.

4.6. CONCLUSION

Since intensive management has ceased in many European forests (cfr. McGrath et al., 2015), and protection and restoration of (semi-)natural forest systems is more and more encouraged, it is important to understand how increased structural complexity and species diversity in the overstorey will affect the understorey. Alteration of light regimes is a crucial mechanism in these understorey-overstorey interactions (Bartemucci et al., 2006; Kopecký et al., 2013). Here, we related structural and compositional attributes of the overstorey to the light-demanding signature of the understorey. The typically expected relationships between basal area, canopy cover and canopy closure are weaker or even absent in structurally complex mixed closed-canopy forests, compared to what we found in the literature for homogenous monospecific stands. In such complex and well-developed forest systems, easy-to-measure structural canopy characteristics are weak predictors of the understorey light signature, but accounting for the canopy composition on top of canopy structure can improve predictions. Yet, the understorey light signature remained to be mainly driven by regional characteristics (such as land-use history, management, and soil characteristics) and likely exhibits time lags.







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A general framework for quantifying the effects of land-use history on ecosystem dynamics

After:

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5.1. ABSTRACT

Land-use legacies are important for explaining present-day ecological patterns and processes. However, an overarching approach to quantify land-use history effects on ecosystem properties is lacking, mainly due to the scarcity of high-quality, complete and detailed data on past land use. We propose a general framework for quantifying the effects of land-use history on ecosystem properties, which is applicable (i) to different ecological processes in various ecosystem types and across trophic levels; and (ii) when historical data are incomplete or of variable quality. The conceptual foundation of our framework is that past land use affects current (and future) ecosystem properties through altering the past values of resources and conditions that are the driving variables of ecosystem responses. We describe and illustrate how Markov chains can be applied to derive past time series of driving variables, and how these time series can be used to improve our understanding of present-day ecosystem properties. We present our framework in a stepwise manner, elucidating its general nature. We illustrate its application through a case study on the importance of past light levels for the contemporary understorey composition of temperate deciduous forest. We found that the understorey shows legacies of past forest management: high past light availability lead to a low proportion of 'forest specialists' (i.e. species adapted to dark, closed forest conditions) in the understorey. Our framework can be a useful tool for quantifying the effect of past land use on ecological patterns and processes and enhancing our understanding of ecosystem dynamics by including legacy effects which have often been ignored.

5.2. INTRODUCTION

Ecological memory is defined as 'the capacity of past states or experiences to influence present or future responses of the community' (Padisák, 1992), and as 'the degree to which an ecological process is shaped by past modifications of a landscape' (Peterson, 2002). The importance of ecological memory in plant and ecosystem processes has been demonstrated in a recent study by Ogle et al. (2015), who showed that various ecosystem processes, across biological, temporal and/or spatial scales, were better explained when models take into account antecedent conditions on top of contemporary conditions. Similar patterns have been observed in other ecosystems (Barron-Gafford et al., 2014; Cable et al., 2013; Hawkins & Ellis, 2010; Leuning et al., 2005; Oesterheld et al., 2001; Sala et al., 2012). An ecosystem's ecological memory is (among other factors) caused by the past land use of the system, which influences the past conditions of the system (Schaefer, 2009; Sun et al., 2013).

Past land use can affect ecosystems for thousands of years (Dupouey et al., 2002; Foster et al., 2003; Lunt & Spooner, 2005). The system properties resulting from past land use are called land-use legacies (Foster et al., 2003; Kopecký & Vojta, 2009; Perring et al., 2016). Examples of species and communities affected by past land use include plant community composition in forests (De Frenne, Baeten, et al., 2011;

Dupouey et al., 2002; Flinn & Marks, 2007; Peterken & Game, 1984), grasshoppers in woodlands (Hahn & Orrock, 2015), butterflies in grasslands (Moranz et al., 2012), fish and invertebrates in streams (Harding et al., 1998), and birds in Mediterranean forests and shrublands (De Cáceres et al., 2013). In general, there is increasing evidence that past land use can affect future biodiversity over decades to centuries (Bürgi et al., 2017; Essl et al., 2015).

Given the importance of past land use for explaining current and future ecosystem properties, a standardized method to quantify the effects of past land use is needed. Most existing classification schemes or indices for land use consider only contemporary land-use intensity and are developed for one specific ecosystem type, such as forest, grassland or agricultural land (e.g. Blüthgen et al., 2012; Dietrich et al., 2012; Kahl & Bauhus, 2014; Luyssaert et al., 2011; Schall & Ammer, 2013). They do not capture past land use or historical land-use changes and lack general applicability. More general frameworks for quantifying ecological memory (e.g. Ogle et al., 2015) require a lot of data. Such data, including continuous time series, are often lacking for long-term processes (e.g. time scales of decades or even centuries).

We propose a framework that can help resolve the above-mentioned restrictions, by quantifying the effect of land-use history on ecological processes in different ecosystem types, even when data on past land use is incomplete, uncertain and of low quality or resolution. We do not intend to replace existing methods such as the modelling approach from Ogle et al. (2015); our framework can support and complement existing methods through developing the well-needed and often lacking time series of environmental variables. Our basic postulate is that past land use affects current (and future) ecological properties. This occurs through the past land use altering resources and conditions that are the driving variables of ecosystem and community responses (Perring et al., 2016) (**Fig. 5.1**). Testing this postulate would be aided by time series data of the driving variables, but such series are rarely available. Trajectories of past land use, even if uncertain, are more frequently known (e.g. McGrath et al., 2015).

Here, we provide a general framework to derive time series of driving variables from known land-use history. By defining the driving variables case-specifically, the framework can be used for a wide range of ecological processes and properties within different ecosystems. In this chapter, we describe how Markov chains can be applied to derive time series of driving variables given the known land-use history. Additionally, we provide an illustration of how past values of driving variables can be used to explain current ecosystem properties. Our framework is based on Markov-chain modelling (**box 5.1**), a stochastic modelling approach that is often used to model temporal ecosystem changes, such as successional vegetation change, based on temporal autocorrelation in time series (Balzter, 2000; Golroo, Ph, Eng, & Tighe, 2012; Horn, 1975; Logofet & Lesnaya, 2000; Usher, 1981). Markov chains can deal with different types of data as well as uncertainties or missing data, and can incorporate expert knowledge to describe causal relations in the network when long-term data series are lacking (Golroo et al., 2012) (as also

implemented in Bayesian belief network modelling (Aguilera et al., 2011; Pollino et al., 2007)). Hence, Markov chains are highly suitable when land-use history data are incomplete or uncertain, which is often the case.



Figure 5.1. Rationale of the proposed framework: past land use affects current ecosystem conditions through alteration of the resources and conditions that are the driving variables of ecosystem responses. We describe and illustrate how Markov chains can be applied to derive time series of driving variables given the known land-use history, and we provide an illustration of how time series of driving variables can be used to explain current ecosystem conditions.

We describe our framework step-by-step (section 5.3, **Fig. 5.3**). In each step, we provide a general description of the modelling approach, and illustrate the proposed approach with a specific case study about the effects of past forest management practices on the current understorey composition in temperate forests. We outline some of the main strengths and opportunities of the framework, describe how the model performance could be improved, and discuss the applicability of the framework to assess how past land use influences current ecosystem properties (section 5.4).

Box 5.1: Theoretical background of Markov chains

<u>Markov chains</u> are graphical, multivariate, statistical models, representing dynamic systems wherein variables can go from one state to another over time, with a transition probability that depends on preceding conditions (see **Fig. 1 box 5.1**). A Markov chain consists of **nodes**, representing the system's variables, and **arrows**, representing the causal relations among these variables. Each variable is discrete and characterized by a set of **states** it can manifest (numerical values, discrete classes or qualitative levels) and a **probability distribution** that quantifies the probability of being in one of the states. If such a probability distribution depends on the state of another variable, it is referred to as a **conditional probability**, which quantifies the causal relation represented by an arrow. Through **probabilistic inference**, a Markov chain can infer the probability distribution for a given variable conditional on the state of the other variables in the model (Jensen & Nielsen, 2007).

<u>The order of a Markov chain</u> (Fig. 1 box 5.1) is the number of time steps in the past that influence the probability of the current state (Shamshad et al., 2005).



Figure 1 box 5.1. In the first-order Markov chain (a), the state of X only depends on the state of X at the previous time step. In the second- and third-order Markov chains (b, c), the state of X depends on the state of X at the two and three previous time steps, respectively.

<u>Auxiliary variables</u> can be added to Markov chains to model more complex processes with multiple variables. For example, in **Fig. 2 box 5.1**, the state of the variable X at each time step depends on the state of X at the previous time step (first-order Markov chain), and on the state of the auxiliary variable Y at the current time step.



Figure 2 box 5.1: First-order Markov chain with one auxiliary variable. The state of the variable X at each time step depends on the state of X at the previous time step, and on the state of the auxiliary variable Y at the current time step.

<u>The Transition Probability Matrix (TPM)</u> is the core of a Markov chain, in which each element represents the probability that a variable is in a certain state, at a certain time step, given the state of the previous time step(s) (Golroo et al., 2012; Logofet & Lesnaya, 2000; Shamshad et al., 2005).

Let X be a variable, possessing discrete states S ($S = \{1, 2, ..., m\}$). In general, for a given sequence of time points $t_1 < t_2 < \cdots < t_{n-1} < t_n$, the conditional probability for X to be in a certain state at time t_n is (Balzter, 2000; Logofet & Lesnaya, 2000; Shamshad et al., 2005):

$$P(X_{s}(t_{n})|X(t_{1}),X(t_{2}),...,X(t_{n-1}))$$

Equation 1 box 5.1

In Equation 1 box 5.1, $X(t_n)$ depends on the state of X at all previous time steps $t_1, ..., t_{n-1}$, representing a Markov chain of order n - 1. Equation 2 box 5.1 and Equation 3 box 5.1 show the conditional probabilities for a first- and second-order Markov chain:

$$P(X(t_n)|X(t_{n-1}))$$
 Equation

$$P(X(t_n)|X(t_{n-2}),X(t_{n-1}))$$

These conditional probabilities make up the TPM. For m states, the first-order TPM takes the form (Shamshad et al., 2005):

$$TPM = \begin{bmatrix} p_{1,1} & p_{1,2} & \dots & p_{1,m} \\ p_{2,1} & p_{2,2} & \dots & p_{2,m} \\ \vdots & \vdots & p_{i,j} & \vdots \\ p_{m,1} & p_{m,2} & \dots & p_{m,m} \end{bmatrix}$$
 Equation 4 box 5.1

with $p_{i,j}$ the probability of state *i*, if the previous state was *j*.

Similarly, the second-order TPM takes the form (Shamshad et al., 2005):

$$TPM = \begin{bmatrix} p_{1.1,1} & p_{1.1,2} & \dots & p_{1.1,m} \\ p_{1.2,1} & p_{1.2,2} & \dots & p_{1.2,m} \\ \vdots & \vdots & p_{i,j,k} & \vdots \\ p_{1.m,1} & p_{1.m,2} & \dots & p_{1.m,m} \\ p_{2.1,1} & p_{2.1,2} & \dots & p_{2.1,m} \\ p_{2.2,1} & p_{2.2,2} & \dots & p_{2.2,m} \\ \vdots & \vdots & \ddots & \vdots \\ p_{m.m,1} & p_{m.m,2} & \dots & p_{m.m,m} \end{bmatrix}$$

Equation 5 box 5.1

2 box 5.1

Equation 3 box 5.1

with $p_{i,j,k}$ the probability of state *i*, if the states at the two previous time steps were (in chronological order) *k* and *j*.

In Markov chain studies, a TPM is often derived from empirical evidence or machine learning (Balzter, 2000; Logofet & Lesnaya, 2000; Usher, 1981). However, transition probabilities can also be derived from expert knowledge (Aguilera et al., 2011), a particularly suitable approach when long-term data series are lacking (Golroo et al., 2012; Pollino et al., 2007).

The strength of influence can be calculated for each arrow in a Markov chain based on the Transition Probability Matrix (TPM), and represents a measure for the extra information that is obtained by knowing the value of the parent (i.e. the node where the arrow starts from) (Theijssen et al., 2013). In other words, it quantifies how much the value of the parent node affects the value of the child node (i.e. the node where the arrow arrives).

Belief updating is the process of inserting new information (evidence) on the status of one of the variables in a Markov chain. This will change the probability distribution of other variables in the network,

and lower the uncertainty in the model output (Jensen & Nielsen, 2007). The process of inserting **hard evidence** into the network is called **instantiation**, and comprises assigning a 100% probability to one of the states of a variable. **Soft evidence** provides probabilistic information on the status of a variable (Jensen & Nielsen, 2007).

5.3. STEPWISE EXPLANATION AND ILLUSTRATION OF THE MODELLING FRAMEWORK

In our framework, a Markov chain models the dynamics of the driving variables of the studied ecosystem process. A variable representing the land-use history (called *land-use variable*) is added to the chain as an auxiliary variable (cf. **box 5.1**, **Fig. 5.2**). The final model represents the dynamics of a driving variable, under the assumption that its present state is directly influenced by the current land-use state, and indirectly by past land use, through the past states of the driving variable (**Fig. 5.2**).



Figure 5.2. The Markov-chain model used within the framework presented in this chapter, consisting of a first-order Markov chain (a) with an additional direct effect (b) between the state variable at t-2 and the state variable at t (i.e. second-order Markov chain) and an additional auxiliary variable (c) representing the land-use history of the system.

Below, we describe the modelling approach step-by-step. Each step contains a general explanation and a specific application for a case study. In the case study, we aim to assess the effect of past forest management practices on the current understorey composition, in terms of the proportion of forest specialists (i.e. plant species found mainly in closed forest, as defined for the lowlands of the Czech Republic, cf. Heinken et al., 2019). We use 29 forest plots from Koda Wood (Czech Republic), Zvolen (central Slovakia) and Slovak Karst (south-eastern Slovakia). For each plot, a description of the management history since 1950 and two vegetation surveys (the first in the 1950s, 60s or 70s, depending on the region, and the second in 2015) are available (see **Appendix A5.1**). The plots were originally established in mostly oak-dominated forests managed either as coppice, coppice-with-standards or high

forests. In each region, we resurveyed plots from all three management categories to cover the historical management variability. Between the surveys, the intensity of forest management generally decreased and shifted from historically dominant coppicing to presently high forest management or no regular management in forest reserves. The change in management resulted in a general decline of plant species richness and a spatial homogenization of the vegetation (Hédl, Kopecký, & Komárek, 2010; Kopecký et al., 2013). The species that showed the strongest decline were light-demanding species typical for open oak forests such as *Bupleurum falcatum, Carex montana, Silene nutans, Veronica chamaedrys* agg., *Ajuga generensis, Lotus corniculatus, Campanula persicifolia* and *Tanacetum corymbosum*. In contrast, shade-tolerant, mesic and nutrient-demanding species such as *Alliaria petiolata, Asarum europaeum, Hepatica nobilis, Mercurialis perennis,* and *Neottia nidus-avis* became more frequent in the understorey. The annual *Impatiens parviflora* was the only invasive alien species with higher occurrence across the studied plots. The majority of the species in the study plots were perennials (full species list in **Appendix A5.7**). Tree species regeneration became more abundant, particularly of shade-tolerant tree species such as *Fagus sylvatica* and *Carpinus betulus* (Máliš et al., 2016).

5.3.1. Step 1: defining variables

The ecological process of interest is scrutinised to identify its main *driving variables*. For example, soil pH, soil moisture content, nutrient availability, and light availability are important driving variables for plant community composition trajectories (Klanderud et al., 2015), whereas soil temperature and moisture content are among the main driving variables for soil respiration rates (Ogle et al., 2015). Making an informed choice in this first step is vital, as the chosen driving variable(s) should enable the user to evaluate how land use affects the ecological process of interest. We only consider one driving variable in the further description and illustration of the framework, but the entire process can be repeated for the multiple variables that drive the same ecological process.

In our case study, the ecological process of interest is the shaping of the forest understorey community. We selected light transmittance as the driving variable because the understorey composition changes observed in our study regions were strongly related to the light requirement of understorey plants (Hédl et al., 2010; Kopecký et al., 2013) and light availability is one of the main environmental factors controlling the establishment and growth of plant species in forests (Baeten, Bauwens, et al., 2009; Thomaes et al., 2013; Tinya & Ódor, 2016). Several studies have observed time lags in vegetation response to understorey light conditions (Dölle & Schmidt, 2009; Thomas, Halpern, Falk, Liguori, & Austin, 1999), suggesting that past values of light transmittance can be important for current understorey composition. Light transmittance is defined as the ratio of the amount of solar radiation reaching the understorey to the total incident radiation at the top of the canopy (Parker, 2014). It is a common assumption that using light transmittance (%) rather than absolute values of radiation allows for predictions or estimations without

knowledge on specific climate and weather conditions (Balandier et al., 2009). Light transmittance depends on forest architecture, and is, as such, mostly uninfluenced by the absolute amount of light at the top of the canopy. Light transmittance depends on canopy closure and hence on the time of the year. In the further description of our case study, we consider the light transmittance in July.

After identifying the process-specific driving variable, a suitable variable representing the land use of the system is defined. The chosen *land-use variable* can be related to one or more of the various aspects comprising land use, such as land cover (e.g. grassland, arable land, forest, heathland), fertilizer type and fertilization intensity, soil manipulation (e.g. ploughing, tilling), harvesting (e.g. crop type in arable fields, different management regimes for timber production in forests, litter raking in forests), and should have a potential effect on the driving variable. For example, past fertilization type and intensity can be suitable land-use variables when soil pH is chosen as the driving variable (Koerner et al., 1997).

As the land-use variable in our case study, we selected forest management, given its possible impact on the canopy composition and structure and hence on light transmittance (Thomaes et al., 2014) and the forest understorey (e.g. Kopecký et al., 2013; Perring, Bernhardt-Römermann, et al., 2018; Ujházy et al., 2017; Van Calster et al., 2008). We did not consider other factors affecting light transmittance, such as tree species and phenology, but kept in mind that these could influence the interpretation of the results.

5.3.2. Step 2: discretization of variables

First, to be able to use a driving variable in our Markov chain, the variable needs to be discretized (cf. **box 5.1**) by defining a finite set of ecologically relevant, representative states (Carpinone et al., 2015; Shamshad et al., 2005). In our case study, we defined sensible discrete states for light transmittance, looking at the relationship between light transmittance and understorey community composition in temperate deciduous forests in Europe. We used three threshold values between four light transmittance states: strong shade (0-8%), moderate shade (8-20%), moderate light (20-40%) and strong light (>40%). Many understorey species of temperate deciduous forest benefit from light levels below 8%, when the survival of certain competitors is limited (De Keersmaeker et al., 2004). For some forest understorey species, the survival is higher under moderate levels of shade (8-20%) than under strong shade ($\leq 8\%$) (Thomaes, 2014). Understorey cover reaches an asymptotic maximum at around 40% light transmittance (Balandier et al., 2009).

Second, similar to the driving variable, also the land-use variable needs to be discretized. In our case study, we defined four states of forest management (further on referred to as *land-use states*) that cover a gradient in management intensity, and encompass the typical forest management actions in our study regions:

- Zero cut: no tree fellings or removals, forest under a zero management system or forest in a period in between two interventions of a rotation system;
- Thinning: the removal of a proportion of trees to allow more growing space for the final crop trees (den Ouden et al., 2010) or management actions with similar effects on the canopy structure, such as selection felling of single trees;
- Shelter cut: a method of securing natural tree regeneration under the sparse shelter of old trees that are removed by successive cuttings to admit a gradually increasing amount of light to the seedlings (den Ouden et al., 2010) or the cutting phase in a coppice-with-standards system resulting in a similar forest structure;
- Clear-cut: most or all trees in an area are cut, e.g. the harvesting phase of coppice systems or high forest systems with a clear-felling management.

Third, the magnitude of the time step (Δt) in the chain should be clearly defined. The time step can vary from less than seconds to more than years, depending on the chosen driving and land-use variables, the ecological process considered, and the availability of land-use history data (Carpinone et al., 2015). In our case study, the time step (Δt) is mainly constrained by the temporal resolution of the available land-use history data (section 5.3.5) and set at 10 years. The 10-year time step corresponds well to the typical management cycles in temperate forests (den Ouden et al., 2010; Kerr & Haufe, 2011), but might be too long to detect short-term temporal dynamics in understorey composition. Smaller time steps would have been better to predict light dynamics that drive understorey composition. However, due to the absence of high-resolution land-use history data, high-resolution predictions of light dynamics would be highly uncertain and therefore contain no additional information compared to the light availability data derived from the model with $\Delta t = 10$ years. Moreover, for herbaceaous perennial plants in forests, a time step of 10 years might be a reasonable choice given their high average life span (64 years for forest herb layer species (Ehrlén & Lehtilä, 2002)) and long time needed for full establishment.

5.3.3. Step 3: defining the model

One can adjust the proposed Markov-chain model to the system and the driving variable of interest by defining the appropriate order of the Markov chain. The order of a Markov chain is the number of time steps in the past that can directly influence the current state (Shamshad et al., 2005). In a simple first-order Markov chain, the present state of the modelled variable only depends on the previous state of that variable. However, for some ecological processes, it might be necessary to include higher-order terms to the chain, to account for the possible ecological memory in the dynamics of the driving variables controlling the processes. For example, adding a second-order arrow to the chain, implies that the state of the driving variable at time t can depend both on the previous state (t-1) and the state before that (t-2) (**box 5.1**) (Usher, 1979). The order that should be used when applying the framework will be case-

specific, and depends on the expected ecological memory of the driving variable that is modelled, as well as on the level of complexity that can be dealt with in the Transition Probability Matrix (TPM; see section 5.3.4). When validation data are available, results from chains with different orders can be compared to assess how long influences of the past remain important for contemporary states. In addition, mathematical methods are available to identify whether second-order relations are sufficiently important to include when compared to the first-order relations in the model (BayesFusion, 2017). We show later (see section 5.3.4) that in our particular case study, a first order model was sufficient to model the light dynamics over time.

5.3.4. Step 4: Transition Probability Matrix

The Transition Probability Matrix (TPM; **box 5.1**) quantifies the causal relations between the different variables in the Markov chain (Logofet & Lesnaya, 2000; Shamshad et al., 2005). In the context of this study, expert-based approaches are best suited to derive the TPM. Experts are asked to complete a TPM according to their knowledge and expectations, and to report their confidence in each estimate (Kuhnert et al., 2010; Pollino et al., 2007). These confidence levels are then used to weight the estimates of all experts in a final TPM (Pollino et al., 2007). It is important to clearly define the investigated process and boundary conditions to ensure that different expert estimates are based on the same assumptions and thus comparable.

In our case study, the second-order TPM describes the probability for light transmittance (LT) at time t being in one of the four defined states, given the light transmittance state of the system at time t-1 (i.e. ten years ago) and t-2 (i.e. twenty years ago), and the land-use state (i.e. forest management) at time t (LU). Since both variables (light transmittance and forest management) have four possible states, the second-order TPM contains 64 scenarios = 4 (LT_{t-2}) x 4 (LT_{t-1}) x 4 (LU_t). A team of six experts (all author of this chapter) provided a probability distribution and a confidence level for this probability distribution for each of these 64 scenarios, resulting in one second-order TPM (see Appendix A5.2). Clear guidelines, definitions, boundary conditions and assumptions were provided to all experts (Appendix A5.3). Based on the second-order TPM, we calculated the strength of influence between nodes (see box 5.1) in the Markov chain. We found a strength of influence of 0.03 for the second-order relation (influence of LT_{t-2} on LT_t) and 0.35 for the first-order relation (influence of LT_{t-1} on LT_t). Light transmittance at t thus mainly depended on light transmittance at t-1, and less on light transmittance at t-2. The strength of influence of LU_t on LT_t was 0.49. We concluded that a first-order Markov chain is sufficient to model the light dynamics over time given the land-use trajectory. All further results and figures are from the first-order Markov chain. We derived a first-order TPM by marginalization (i.e. grouping scenarios with the same light transmittance state at t-1 (thus: only differing in the light transmittance state at t-2) and calculating the average probability distribution for each group of scenarios) (Table 5.1, Appendix A5.2). The first-

order TPM describes the probability for light transmittance (LT) at time *t* being in one of the four defined states, given the light transmittance state of the system at time *t*-1 (i.e. ten years ago) and the land-use state at time *t* (LU_{*t*}), and thus contains 16 scenarios = 4 (LT_{*t*-1}) x 4 (LU_{*t*}).

Table 5.3. The first-order Transition Probability Matrix (TPM) derived from the second-order TPM by marginalization. The pie charts represent the average expected probability distribution of light transmittance at t for the 16 different scenarios (i.e. 16 combinations of the land-use state at t and the light transmittance state at (t-1). The full first- and second-order TPMs can be found in *Appendix A5.2*.



5.3.5. Step 5: land-use trajectory

Knowledge on past land use can be gathered from natural archives, such as tree-ring series or soil properties, and cultural archives, such as old aerial pictures, historical maps, old management plans, and face-to-face interviews with locals, land owners or managers. The land-use trajectory comprises the translation of what is known about the past land use of the system into a sequence of the possible land-use states defined in section 5.3.2 (step 2). Thus, for each time step in the chain, the land-use state that best describes the situation at that time needs to be determined, and will be entered in the Markov chain as evidence. This can, depending on the certainty of the land-use trajectory, either be done as *hard evidence*,

assigning a 100% probability to the assumed land-use state at each time step, or as *soft evidence*, providing probabilities for the different states of the land-use variable that sum up to 100% (**box 5.1**).

For our case study, two co-authors of this chapter, each with detailed knowledge of the case study regions, investigated the management history of the 29 plots and completed a standardized land-use history questionnaire (**Appendix A5.4**). The historical information was used to assign a land-use state to each 10-year time step for each plot, starting in 1950 (**Appendix A5.5**). Some assumptions were necessary, due to variations in the level of detail of the available historical data (**Appendix A5.5**). To illustrate the possibility of including an uncertain land-use trajectory in the model, we defined three alternative trajectories for one of the Czech plots (Plot KO775; **Table 5.2**). The historical information for this plot mentioned sanitary thinnings of standards in the period 1900-2010. We assumed that every 30 years one of these thinnings affected the plot and used a different timing of this thinning frequency in the three alternative land-use trajectories. Presuming that each alternative is equally likely, each time step between 1950 and 2010 has a 66.6% probability of 'zero cut' and 33.3% probability of 'thinning', which can be included in the model as soft evidence.

Table 5.4. Three alternative land-use (LU) trajectories for one of the Czech plots (KO775), with shifted timings for the sanitary thinnings that took place between 1900 and 2010. The last row shows how alternative trajectories can be combined into one uncertain land-use trajectory, which can be entered in the model as soft evidence.



5.3.6. Step 6: running the model

Numerous software packages can be used to implement and run Markov-chain models. Aside from software packages that are often used for Markov-chain modelling (e.g. R (Spedicato, 2017), MARCA (Stewart, 1996), PRISM (Kwiatkowska et al., 2011)), also software packages primarily designed for Bayesian belief network modelling can be highly suitable (e.g. Netica (Norsys, 1998), Hugin (Hugin, 2008) and GeNie (Druzdzel 1999; http://www.bayesfusion.com))(Landuyt et al., 2013). In our case study, models were implemented and run using the free software package GeNie. We built the model structure (a first-order Markov chain with one auxiliary variable), and entered the weighted-average TPM of the six experts (cf. **Appendix A5.2**). Then, we entered the assumed land-use state for each considered time step, first as hard evidence (i.e. providing probabilities for the different states of the land-use variable

that sum up to 100%) for one of the plots, to illustrate how using hard vs. soft evidence influences the results. For each of the 29 study plots, the model then calculated the probability of each light transmittance state to occur at each time step (for seven time steps of 10 years; from 1950-2020), given the specific land-use trajectory of the plot.

Note that the model can be updated with evidence on the state of the driving variable at certain time steps (in case these data are available). In our case study, we have light transmittance data for time step t_6 (2010-2020). We first used these data to evaluate the model outcomes (section 5.3.7) and then updated the model using the light transmittance data as evidence to generate model outcomes for further analysis (see section 5.3.8 for details).

5.3.7. Step 7: evaluation of model outcomes

The final model output is a probability distribution of the different states of the driving variable at each time step. In other words, the probability for each possible state of the driving variable at each time step is predicted based on the land-use history data and the TPM (**Fig. 5.3**). From the probability distribution output, a user can derive several variables to use in further analyses. Time series of, for instance, the mean expected value, the most probable state to occur or the probability for a certain state to occur (e.g. Dlamini, 2010; Smith et al., 2007) can be used to further investigate and analyse ecological process dynamics. In our case study, we calculated the mean expected value of light transmittance at each time step based on the probability distribution at each time step and the mean value of each light transmittance (LT) state:

mean expected $LT = P_{SS}$. $\overline{SS} + P_{MS}$. $\overline{MS} + P_{ML}$. $\overline{ML} + P_{SL}$. $\overline{SL} = P_{SS}$. 4% + P_{MS} . 14% + P_{ML} . 30% + P_{SL} . 70% Equation 5.1

with \overline{SS} , \overline{MS} , \overline{ML} and \overline{SL} the class means of respectively strong shade, moderate shade, moderate light and strong light; and with P the probability for a light transmittance state to occur.



Figure 5.3. Flowchart illustrating the steps of the framework, applied to our case study. Note that only a few rows of the TPM are shown here as an illustration. The full secondorder TPM, with 64 rows, can be found in *Appendix A5.2*. The data and graphs shown for step 5, 6, 7 and 8 are based on a hypothetical plot with a land-use history as described in Step 5 of the figure. With LT light transmittance, LU land use, SS strong shade, MS moderate shade, ML moderate light and SL strong light.

Metrics to evaluate the performance of models that produce a probabilistic output include confusion tables, k-fold cross-validation, receiver operating characteristic curves, and several performance indices such as spherical pay-off, Schwarz' Bayesian information criterion, and true skill statistic (Marcot, 2012). Another commonly used approach is based on comparing the model performance to the expected percentage of correct classifications if the prediction was made in a random manner (i.e. by a model called random classifier or baseline classifier) (e.g. Genc & Dag 2016). In our case study, we used light transmittance data obtained from the 2015 survey that took place in each of the 29 plots (Appendix A5.1) to evaluate the model performance. We measured light transmittance with a spherical densiometer (Forestry Suppliers, 2008; Lemmon, 1957). For the time step t₆ (2010-2020) for which observed light transmittance data are available, we compared model predictions against predictions of an indifferent baseline classifier (uniform distribution). For each plot, the model performance was expressed as the predicted probability of the observed light transmittance state at the survey time, minus the baseline probability of that state. Since the defined light transmittance classes were unbalanced, baseline probabilities, derived from a uniform distribution, were set to 8%, 12%, 20% and 60%, for the states 'strong shade', 'moderate shade', 'moderate light' and 'strong light', respectively. Positive model performance values, where predicted probability values are higher than their baseline, indicate that model predictions are informative.

In our case study, the model performance differed between plots (**Fig. 5.4**), and for the majority of the plots, the informed model was performing better than the random (baseline) model (more positive than negative values in **Fig. 5.4**). Many of the plots for which the model performed badly were thinned within the 20 years prior to the survey. Thinning events close to the survey hence seemed to decrease the model's performance. Two possible explanations for this observation are: (i) the documented thinnings might not have taken place in or close to the plot, and (ii) the experts who completed the TPM might have wrong expectations about the effect of thinnings on light levels. The experts generally assumed thinnings to increase light levels, but a recent study showed that light levels at the forest floor can be similar in forests with a dense vs. a more open canopy, due to a higher shrub density in the more open forests (Sercu et al., 2017).



Figure 5.4. Measure of model performance for the 29 plots of our case study, calculated as the predicted probability of the observed light transmittance state (at the 2015 survey) minus the baseline probability of that state (based on a uniform distribution). The more positive the value, the better the model predictions. The colours of the bars indicate the observed light transmittance state during the 2015 survey.

Including uncertainty in the timing of thinning events in our model resulted in a more gradual change in predicted average light transmittance over time compared to the cyclic behaviour of light transmittance for thinning events with a certain timing (**Fig 5.5**).Yet, the general trend, i.e. an overall decrease in light transmittance over time, was similar for certain and uncertain land-use trajectories.



Figure 5.5. Comparison between the results of a first-order Markov chain, with and without accounting for uncertainty in the land-use (LU) trajectory (see *Table 5.2*), for one plot from our case study (KO 775) and seven 10-year time steps during 1950-2020.

5.3.8. Step 8: application of model outcomes

For the 29 plots of our case study, we have vegetation data from two surveys (the first survey in the 1950s, 60s or 70s, depending on the region, and the second in 2015; see **Appendix A5.1**). The survey data comprise an estimated cover (in %) for each species in three separate layers, i.e. tree layer (all trees taller than half of the height of the canopy trees), shrub layer (all woody plants taller than 1.3 m not included in the tree layer) and understorey (all plants smaller than 1.3 m). We have data on light transmittance for the 2015 survey, measured with a spherical densiometer, and derived estimates of light transmittance for the first survey through the relationship between the light transmittance and tree and shrub cover data of the second survey (see **Appendix A5.6**). We included the light transmittance data of both time steps (the two survey times) as evidence in our model to calculate a time series of mean expected light transmittance for each plot. We expect that including evidence will make the model results more informative, but we cannot quantify this effect, as there is no validation data available. We did not include uncertainty in the land-use trajectory to obtain the estimated light transmittance over time. We used the obtained time series, combined with the vegetation data from the 2015 survey, to assess the importance of past light levels on the current understorey community composition.

The data from the two surveys provide light transmittance values at two time points, as well as an estimation for light transmittance values in between both surveys, given we assume linear dynamics (**Fig. 5.6a**). Our framework, however, allows uncovering the light transmittance in between surveys, demonstrating that two plots with very similar light levels during both surveys may have experienced completely different light regimes in between surveys (**Fig. 5.6b**).

We used a simple linear model to explore the importance of past light levels for understorey community composition. The response variable was the proportion of forest specialists (i.e. plant species found mainly in closed forest, as defined for the lowlands of the Czech Republic, cf. Heinken, 2019) in the understorey community (all plants smaller than 1.3 m height, including tree species) in the 2015 survey. The explanatory variables were the cumulative light transmittance, i.e. the area under the curve of estimated light transmittance over time (**Fig. 5.6c**), for 10 and 60 years prior to the 2015 survey. As covariates, we included the total number of species present in 2015 and the region (i.e. Koda Wood, Zvolen, or Slovak Karst) of a plot.



Figure 5.6. Graphical illustration of the added value of our framework for a resurvey study, using 3 of our 29 study plots. Light transmittance values are only available at the two survey times. (a) Light transmittance between both surveys can be estimated through linear interpolation. (b) Using our framework, light transmittance in between surveys can be estimated, demonstrating that two plots with similar light levels for both surveys may have experienced completely different light regimes between the surveys. For plot 1 and 3, management interventions are indicated on the figure. Plot 2 was thinned at each time step. (c) The projected time series of light transmittance can be used to calculate, for example, the cumulative light transmittance over the 40 years before a survey.

We found that the cumulative light transmittance over a period of 60 years prior to the survey was a better predictor of the proportion of forest specialists in a plot's understorey community (p = 0.07), compared to the cumulative light transmittance of the recent past (i.e. 10 years prior to the survey) (p = 0.16) (**Fig. 5.7**). This suggests that the current understorey composition is better explained by cumulative light levels over the past 60 years than by the more recently prevailing light levels. Study plots with a higher number of species in the understorey had a lower proportion of forest specialists, and the plots in Zvolen had a lower proportion of forest specialists than in the other two regions. The model explains 43 % of the variation in the proportion of forest specialists ($R^2 = 0.43$); an acceptable R^2 -value for ecological processes. Our findings suggest that management legacies are present in forest understoreys and are in accordance with Thomas et al. (1999) and Dölle and Schmidt (2009), who found that the light-vegetation relationship might be better explained by past light regimes than by current light conditions because of the slowness of plant community changes. Note that our findings are limited by (i) the small sample size and (ii) possible correlation structures among plots in each region that are not accounted for in our simple analysis. All analyses were performed in R 3.3.2 (R Core Team, 2017).



Figure 5.7. Effect sizes of cumulative light transmittance (LT) over the past 10 and 60 years prior to the survey for the proportion of forest specialists in the total species pool. Significant effects are indicated with '*' (p<0.10). The effect sizes of the covariates 'total species number' and 'region' are also shown.

5.4. DISCUSSION

We proposed a framework based on the hypothesis that past land use affects current ecosystem properties through its impact on past values of driving variables (**Fig. 5.1**). We used our framework to model the temporal dynamics of one such driving variable (i.e. light transmittance) based on land-use history data, to look for effects of past land use on current understorey composition in temperate forests. To more thoroughly estimate the past resources and conditions of an ecosystem, the modelling could be repeated for other driving variables relevant for the particular study system.

5.4.1. Strengths of the framework

The strength of the framework is its applicability to different types of ecological processes and ecosystems, while previously developed indices or classification schemes for quantifying land-use legacies were only applicable to specific ecosystems, such as forests (e.g. Schall & Ammer 2013; Kahl & Bauhus 2014), grasslands (e.g. Blüthgen et al., 2012), or agricultural fields (e.g. Dietrich et al., 2012). The modelling framework of Ogle et al. (2015) for quantifying ecological memory is also applicable in different ecosystems, but has the disadvantage of requiring long continuous time series. When such long-term data are unavailable or incomplete, which is often the case, our framework offers the opportunity to derive time series of biologically meaningful driving variables from uncertain or incomplete land-use data.

Markov chains offer the advantage that they can handle low-quality land-use data with high uncertainties since both hard evidence (100% certainty about the land use at a certain time point, e.g. based on photographs) and soft evidence (probabilistic information about the land use at a certain time point, e.g. based on expert information) can be inserted (Jensen & Nielsen, 2007). The general applicability of the proposed framework is further improved by allowing the user to adjust the order of the Markov chain, depending on the expected extent of influences of the past. For our case study, where we model light transmittance over time for a given land-use trajectory, we found very small influences of the second-order term of the Markov chain (based on the Transition Probability Matrix (TPM)), suggesting that light transmittance at the forest floor mainly depended on more recent management events.

5.4.2. Opportunities for improving model performance

The poor model performance that we observed for some of the plots in our case study can have several reasons. We believe the most important reason is the high uncertainty of the data on past land use. As the exact timing of management interventions was often unknown, especially at the plot level, we can't expect to be able to accurately predict light transmittance values at a specific point in time. In addition, the resolution of the Markov chain in the application (i.e. time intervals of 10 years) might be too low to capture small fluctuations in light availability that might have had an impact on the understorey. However, when the aim of the model is to derive general trends in the dynamics of a driving variable, such as cumulative light availability, this bias can be considered less problematic. We illustrated this with one of the plots from our case study (**Fig. 5.5**), where similar general trends were predicted with and without accounting for uncertainty in the land-use trajectory.

Another potential weakness of the framework is the strong dependence of the model output on the quality of the Transition Probability Matrix (TPM), which depends on the knowledge of the consulted experts. However, the TPM might be improved by including literature data and data-learning techniques to estimate the conditional probabilities. The latter, however, requires extensive long-term data, which are often not available. Providing experts with clear guidelines and background information on the investigated process and boundary conditions is key for obtaining high-quality TPMs. In addition, when multiple experts have provided a TPM, running the model with each separate TPM instead of the (weighted) average TPM can provide information on the dependency of the model results on the TPM, and can reveal how some TPMs better fit the data (assuming qualitative validation data is available) than others and should therefore be given more weight in the final TPM.

Finally, information loss through strong simplifications due to the discrete nature of Markov chains can decrease model performance. There is a trade-off between accuracy and complexity, as an increase in the number of states will also increase the number of rows of the TPM. By using ecologically relevant thresholds, information loss through discretization can be minimized.

To deal with the abovementioned issues, a lot can be learned from recent advances in the field of Bayesian belief network modelling, a modelling technique that also works with discrete variables and an identical probabilistic knowledge base that is often derived from a combination of literature data, field data and expert knowledge (see, for example, Murphy (2002)). Within this field, expert knowledge elicitation techniques (e.g. Kuhnert et al., 2010; Pollino et al., 2007), and data assimilation techniques (e.g. Chen & Pollino, 2012; Marcot et al., 2006) to combine different data sources have been developed and optimized.

Marcot (2012) suggests that Bayesian belief networks may best be developed stepwise, starting from a less ambitious model based on expert knowledge, testing and calibrating the model, updating the structure of the model and retesting it until a satisfying performance is reached. In this chapter, we used Markov chains, which are related to Bayesian belief networks and also offer the flexibility to update the model with auxiliary variables, such as the land-use variable in **Fig. 5.2**. They can easily be extended even further, depending on the complexity of the ecological processes that are studied. For example, if next to land use, other variables influence the state of the driving variable, these can be added to the chain as well, and model performance can be tested again. Of course, this will only work if we have temporal data on this additional auxiliary variable and if the relation between this variable and the driving variable can be quantified through experts or data. Besides, the improvement of model performance can only be tested when qualitative validation data is available.

Here, we illustrated one possible approach to validate the model performance. We compared the performance of our 'informed model' (based on expert knowledge for both the model structure and the TPM) to the performance of a 'random classifier model', which makes predictions in a completely random manner. However, alternative approaches could provide further insight in the validity and performance of our model. For example, we could compare our informed model to a model with the same structure (i.e. based on expert knowledge) but using a random TPM instead of an expert-based TPM.

5.4.3. Applicability of the framework

With our framework, we are able to predict time trends of driving variables of ecological processes and properties, for a given land-use history. We believe this is a key step leading to further investigation of how past land use affects current ecosystems. Long time series of measured past resources and conditions are often not available. With the time trends we model, we can reveal some of the likely past behaviour of these resources and conditions (cf. **Fig. 5.6**), allowing us to detect why systems with seemingly similar contemporary resources and conditions can display different properties. In our case study, we derived past light dynamics to assess how current herb layer communities are (partially) shaped by past light availability, and revealed why forest plots with similar current light conditions have different herb layer communities. Several other drivers, such as soil pH, nutrient availability and soil moisture content also

affect herb layer communities (Klanderud et al., 2015). It would therefore be interesting to apply the proposed framework on the other important driving variables, which might be influenced by other landuse variables. It may not always be feasible to determine all driving variables of an ecological process, but gaining insight into the dynamics of a subset of the driving variables will already improve our understanding of the process and its dependence on past land use.

We hope our framework will provide an opportunity for further studies on how past ecosystem properties (i.e. past levels of resources and conditions), controlled by past land use, are affecting contemporary ecological properties and patterns. The modelling approach can easily be translated to different driving variables and different land-use variables and can be extended or adapted depending on the complexity of the study system. We therefore believe the proposed approach is widely applicable in studies where researchers have (some) data on past land use and want to take those into account to achieve a better understanding and better predictions of the contemporary or future ecological state.







General discussion and conclusions

In this PhD, our main objectives were to (i) assess the main environmental change drivers that could explain biodiversity and functional changes in forest understorey communities over time, and (ii) assess how these understorey community responses to environmental change depend on the land-use history of the system. An extensive dataset of vegetation resurveys allowed us to assess actual temporal changes in understorey communities at multiple locations across Europe, and to disentangle the different potential drivers of these changes. Our major findings were (i) that light availability as a local driver of change was more important for explaining understorey community trajectories than the regional global-change drivers (climate and nitrogen deposition) and (ii) that land-use history affected the impact of the environmental change drivers on the understorey community trajectories (see **Fig. 6.1** for an overview of our most important findings).

In this general discussion, we will integrate the findings of the different chapters. Previous land use has steered understorey communities onto trajectories of change, through locally eliminating plants and their diaspores, and through altering the resources and conditions that determine understorey composition. Therefore, we will first discuss the main legacies that we observed from different previous land uses, i.e. the ancient/recent distinction across Europe, and the outland/infield distinction in Skåne (section 6.1). Then, we will elaborate on the importance of light availability, as we found that this was the key driver for understorey community trajectories (section 6.2). Taking these findings together, we will discuss how forest management practices can be used to steer understorey composition under future environmental changes (section 6.3), and we will formulate concrete recommendations for future research avenues (section 6.4).


Figure 6.1. Overview of the main results from Chapter 2 and 3, where we investigated the effects of local- and regional-scale environmental changes on different properties of the herb layer composition. Effects of land-use history (LUH) should be interpreted as the effect of the plot being located on former infield (Chapter 2) or in recent forest (Chapter 3) instead of former outland/ancient forest. Effects of forest management (Chapter 2) should be interpreted as the effect of more intensive management practices. The sign (positive/negative) of the interactive effect of LUH indicates the effect of infield (Chapter 2) or recent forest (Chapter 3) on the slope (estimate) of the effect of the predictor on the response variable. Thus, a positive (negative) interaction means that the slope is higher (lower) in recent forest/former infield than in ancient forest/former outland. SCA = shade-casting ability; SLA = specific leaf area; N = nitrogen; MAT = mean annual temperature.

6.1. LAND-USE LEGACIES IN SOIL AND CANOPY PROPERTIES

Legacies from the former agricultural use were present in the topsoil conditions of our study plots. Across our European dataset, total phosphorus (P) concentrations were higher in recent than in ancient forests, and in Skåne, total P concentrations were higher in former infields compared to former outlands. While we should bear in mind that these differences might partially be related to an initial preference for richer soils for agriculture (Flinn et al., 2005), it is very likely that subsequent fertilization practices have at least reinforced the higher fertility that infield/recent forest soils exhibit. In contrast to the results of Honnay et al. (1999) and Verheyen and Hermy (2001), pH_{KCI} was not related to former agricultural land use, which could be due to a large variety of former agricultural practices across the different countries where we sampled (Graae et al., 2003).

The former agricultural use was also reflected in the canopy structure and composition, but here, we found contradictory results between the Skåne study (Chapter 2) and the study across Europe (Chapter 3). Across Europe, the canopy's shade-casting ability was lower in the recent (post-agricultural) forests than in the ancient forests. We speculate that this might be related to differences in the stage of natural succession between ancient and recent forests. With natural forest succession, the importance of higher shade-casting species increases over time (Connell & Slatyer, 1977), and ancient forests are likely to be in a more 'mature' stage of succession compared to recent forests which only started to develop after the agricultural land use was abandoned. Yet, other factors could also have caused the differences in canopy composition between ancient and recent forests, such as the choice of tree species when reforestation of abandoned agricultural land happened through plantation rather than spontaneously. However, we were not able to test the cause(s) of the different shade-casting abilities in ancient vs. recent forests. In Skåne, on the other hand, we found denser, more shade-casting canopies on former infields than on former outlands, and related this to the higher soil fertility. Similar examples of lower light transmission on richer soils, potentially due to a denser layer of subcanopy trees, have been reported in other parts of the world (e.g. Coomes et al., 2009; Coomes & Grubb, 1996; Tilman, 1988). A possible reason for these opposite findings is that the recent/ancient and infield/outland distinctions are not fully comparable. While the basic idea of the nutrient-enriched vs. nutrient-depleted soils is comparable, forests on former infields/outlands typically developed from semi-open conditions, with already some trees present, to closed stands when livestock grazing (outland) or wooded meadow/coppice management (infield) ceased. As a result, there might be no differences in the successional stage between former infields and outlands, and differences in nutrient availability might be the main driver of differences in canopy composition.

6.2. LOCAL LIGHT DYNAMICS AS KEY DRIVER OF UNDERSTOREY COMPOSITION

In general, we found a higher importance of local-scale drivers, compared to regional-scale drivers, for explaining temporal changes in herb layer composition (Fig. 6.1). In a resurvey study across Europe, Bernhardt-Römermann et al. (2015) also highlighted the importance of local fine-resolution changes in environmental conditions to predict herb layer diversity changes, while coarse-grained environmental conditions (like climate) had no significant effect on diversity changes. Next to the land-use history, the three local-scale drivers that we assessed were canopy cover, shade-casting ability (SCA) of the canopy and litter quality, which are all related to the canopy's structure and composition. Our findings suggest that the **canopy composition** is likely affecting the herb layer mainly through altering the light availability at the forest floor, as litter quality, reflecting the rate of mineralization and nutrient cycling processes (Cornwell et al., 2008), was never an important explanatory variable for herb layer community changes. The low importance of litter quality is unexpected, as several studies have shown that canopy species composition affects the understorey vegetation through their leaf litter quality (Kooijman, 2010; Wulf & Naaf, 2009). Further research focussing on litter depth and quality would be required to derive strong conclusions about the importance of the litter layer for understorey community composition. For canopy cover, we cannot attribute its effect entirely to light availability, as canopy cover can also have an indirect effect on the forest understorey through root competition for water and nutrients (e.g. Ammer and Wagner (2002) found positive correlations between canopy cover and fine-root biomass). As we did not include water and nutrient availability as explanatory variables when analysing herb layer community changes, we cannot disentangle the direct effect of canopy cover through light availability from the indirect effects through resource availability caused by root competition.

Across our study regions, forests have become darker over time because of a shift in canopy composition towards more late-successional shade-casting tree species. In the ancient forest plots, this resulted in a compositional shift towards a higher dominance of 'forest specialists' adapted to dark closed forest conditions, and this was related to (i) a decreased total herb cover, (ii) a decreased mean plant height, (iii) an increased mean specific leaf area (SLA), and (iv) an increased species evenness. Interestingly, the herb layer composition in recent forests was much less sensitive to the decreased light levels. This dependency of the herb layer response on land-use history may be explained by (a combination of) both the legacies in soil conditions – plant species can have a higher shade-tolerance spectrum on nutrient-rich sites (Coomes et al., 2009; Ellenberg, 1939; Niinemets & Valladares, 2006a) – and the legacies in canopy composition – recent forest canopies have a lower SCA, and shade levels might not yet have reached threshold levels at which herb cover starts to decline.

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Similarly, in Skåne, we observed interactions between past agricultural land use and light dynamics (reflected by the management intensity) on the functional composition of the herb layer. Here, our findings mainly illustrated that intensive forest management can suppress legacies from past land use: the lower light-demanding signature of the herb layer on the nutrient-enriched infields compared to the outlands was only observed in plots with a low management intensity. When management intensity was high, the light-demanding signature of the herb layer was similarly high for infield and outland plots. However, while the canopy-related land-use legacies have disappeared with forest management practices, legacies remain present in the soil conditions, and therefore, we expect that compositional differences in the herb layer may re-appear when intensive management ceases and natural forest succession takes over.

Our findings of a lower light-demanding signature in nutrient-enriched former infields compared to outlands in Skåne (Chapter 2) somewhat contradicts our findings from the European study (Chapter 3), where we found that typically more light-demanding species could persist under low light levels when soil nutrient content was high. This might suggest that assessment of changes in community composition should not only be based on indicator values (such as the ones from Ellenberg), as species are plastic in their response to e.g. light availability, depending on other environmental conditions (e.g. soil nutrient content) (Lajoie & Vellend, 2015; Valladares et al., 2006).

Importantly, it should be noted that the light availability gradient in our study was rather small, and did not cover the entire possible range (**Fig. 1.2**). The majority of our plots (179/192) were situated in rather dark closed forests, with a canopy closure of 60% or more. Therefore, extrapolating results and conclusions to forests with a more open canopy should be done with caution.

6.3. FOREST MANAGEMENT AS ADAPTATION TOOL

In general, our findings suggest a high importance of light dynamics for understorey compositional changes. Forest management is a rather straightforward tool to control light levels at the forest floor, and therefore it could be used as a tool for forest adaptation to (future) consequences of global changes (Lindner et al., 2010; Luyssaert et al., 2018; Sousa-Silva et al., 2018). We showed in Chapter 4 that both structural and compositional attributes of the canopy are important to control light availability at the forest floor. Forest managers might actively influence the canopy structure, through thinning, pruning and harvesting. Furthermore, they can change the canopy composition, e.g. by introducing different species, or favouring certain species over others by means of thinning/selective cutting.

6.3.1. Herb cover losses due to climate change and nitrogen deposition

Effects of environmental changes at the regional scale on herb layer composition were generally limited, and only the herb layer productivity (reflected by the total cover of the herb layer) was influenced by climate warming and N deposition. Increased N deposition was related to decreased herb cover, but only in ancient forests, while stronger warming was related to decreased herb cover only in recent forests. This suggests that herb layers in ancient forests are more sensitive to N deposition, while herb layers in recent forests are more sensitive to N deposition.

For climate warming, the different responses in ancient and recent forests are likely related to land-use legacies in the canopy. The more shade-casting ancient forest canopies can cause stronger microclimatic buffering against macroclimate warming (De Frenne, Rodriguez-Sanchez, et al., 2013; Zellweger et al., 2019). Although there are no studies specifically investigating the difference in microclimate buffering capacity between ancient and recent forests, several studies have demonstrated the impact of anthropogenic land use on the microclimate below the canopy. For instance, old-growth forests displayed more buffering of extreme high temperatures than mature plantations (Frey et al., 2016), and the forest cover of former coppices had a weaker impact on the extreme maximum temperatures compared to high forests (Ferrez et al., 2011).

Possibly, when the recent forests further mature and reach similar shade-casting levels as the ancient forests, the negative effects of warming on the herb cover might be mitigated. On the other hand, negative effects of warming on ancient forest herb layers could emerge when temperatures keep increasing during the coming decades (as expected by the IPCC (2014)) and the buffering capacity of the overstorey is no longer sufficient. In any case, this suggests that management actions to limit the negative effects of warming on the herb layer productivity should favour closed canopies with species with a high shade-casting ability. Indeed, persistence of light limitation is often considered as the main mechanism that lowers the understorey's response to global change (see e.g. De Frenne et al., 2015). On the other hand, decreasing the light availability at the forest floor in ancient forests can also have a negative effect on the herb cover, through the disappearance of light-demanding species (as discussed above in section 6.2). However, we should bear in mind that the observed decreases in herb cover can be caused by different community assembly processes, which do not necessarily all have a negative impact on the ecosystem and its functioning. For instance, Bernhardt-Römermann et al. (2015) found that a decrease in herb cover over time was related to an increase in species evenness. We made similar observations in our study across Europe (Chapter 3), and moreover, we could relate the shade-induced cover losses in ancient forests to a shift in species composition, with more dominant light-demanding species disappearing in favour of so-called 'forest specialists', adapted to dark closed forest conditions. As these

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forest specialists have limited survival chances outside the closed forest, because of their limited competitive ability in lighter conditions where other species can occur as well, they may be considered as important biodiversity indicators for forests (Hermy et al., 1999; Peterken, 1974). Hence, if we want to promote the occurrence of these typical forest species in a forest stand, a shaded forest microclimate should be maintained, even if this induces an overall decrease in the total herb cover. In addition, we should keep in mind that many of these typical forest species are related to former coppicing (with standards) practices, and benefit from the regular occurrence of light phases and associated changes in environmental conditions (e.g. soil temperature) (Hermy, 2015). Therefore, small-scale cuttings within the forest interior, leaving the forest microclimate more or less intact, would likely be the best strategy to promote the occurrence of typical forest species.

With regard to nitrogen deposition, it is less clear which land-use legacies are causing the different response in herb layer productivity between ancient and recent forests. If the canopy differences would somehow again be the main cause, this implies that we can not mitigate both the effects of warming and nitrogen deposition through management actions, as a more shade-casting canopy would reduce the negative effect of warming on the herb cover, but increase the negative effect of nitrogen deposition, and vice versa. However, phosphorus legacies in the soil could also be driving the different responses of the herb cover to nitrogen deposition between ancient and recent forests. The loss of herb cover with increased N deposition is typically related to the acidifying effect of nitrogen, causing increased levels of toxic Al³⁺, which is detrimental for the survival of many (herb) species (Tian & Niu, 2015), but several studies have demonstrated that phosphorus might alleviate the toxic effects of Al³⁺ for plants (Iqbal, 2014; Teng et al., 2018). Overall, further research on what is driving the different herb layer responses in ancient vs. recent forests to N deposition would be required to fully understand the mechanism and draw conclusions for management recommendations.

6.3.2. Biodiversity changes and management

Across our European study regions, species richness and Shannon diversity did not show clear directional trends over time, and were not related to the considered environmental change drivers. These findings are in line with several resurvey studies across Europe (e.g. Bernhardt-Römermann et al., 2015; Verheyen et al., 2012), and with a global meta-analysis by Vellend et al. (2013), where no mean temporal change in plant species diversity at the local scale was found. Importantly, these results do not pertain to species losses at the global scale caused by human activities, for which there is a broad scientific consensus (Barnosky et al., 2011; Pereira et al., 2012).

The third biodiversity metric that we investigated, species evenness, increased across Europe. According to Chapin III et al. (2000), environmental changes will influence the relative abundances of species more frequently than the presence or absence of species. They argue that changes in species evenness warrant

increased attention, because evenness usually responds more rapidly to environmental changes than does species richness. Indeed, changes in evenness have important consequences for ecosystems long before a species is threatened by extinction. In our study, the increased evenness is mainly related to an increased SCA of the canopy, and thus a decreased light availability. The reduction of light availability reduces the dominance of fast growing, competitive, light-demanding species with typically high cover (cfr. Bernhardt-Römermann et al., 2015), in favour of more shade-tolerant 'forest specialists' with a more 'even' relative abundance. Note however that this is mainly the case for the ancient forests. In the recent forests, no clear compositional shifts towards a higher proportion of 'forest specialists' was observed, and increases in evenness were less strong. Here, both forest specialists and more light-demanding species can occur together, because of the higher shade-tolerance of the light-demanding species with higher nutrient availability that we hypothesized. In addition, although SCA increased in general, it was lower in recent than in ancient forests. Therefore, it could be that in recent forests, shade levels have not yet reached threshold levels at which only forest specialists can survive, because of the lower starting levels of SCA.

In Skåne, we did observe changes in Shannon diversity over time. The peak in management intensity at the intermediate survey, observed across all plots due to changes in legislations, was reflected in a peak in Shannon diversity, indicating that forest management has a positive effect on herb layer diversity. Other studies have reported similar findings, where forest management has a positive effect on species richness of the understorey vegetation (e.g. Boch et al., 2013; Brunet et al., 1997; Paillet et al., 2010). It is difficult to relate these findings to the European study, where we found no changes in Shannon diversity, but increased evenness with decreased light availability. To understand the different mechanisms behind these observations, further insight into how management intensity is affecting the herb layer diversity in Skåne would be required, as this might be through alterations in e.g. soil pH, organic matter content, bulk density, and nutrient availability, on top of alterations in light availability (Brunet et al., 1997). The peak in understorey diversity at the intermediate survey in Skåne also clearly illustrates that understorey community trajectories over time can be non-linear, and that more complex understorey dynamics can only be revealed with multiple resurveys over time (further discussed in section 6.4).

6.3.3. Assessing the effects of management changes on future herb layer composition

In Chapter 5, we proposed a conceptual framework that allows to relate past land-use changes to contemporary ecosystem properties, through quantifying how past land use has changed the driving variables of the ecosystem properties under study. We illustrated how past light transmittance can be quantified based on information on the historical forest management, and how the present-day understorey composition is more strongly related to these past light levels than to the contemporary light

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availability. We attribute these findings to the occurrence of time lags in understorey community assembly: if there is a shift in environmental conditions, the community composition may respond with a delay, of which the magnitude depends on different mechanisms, such as dispersal and recruitment limitations of new species, or the ability of originally present species to survive in less optimal conditions (Diekmann, 2003; Essl et al., 2015). Earlier studies have also suggested that comprehensive understanding of forest management impacts on understorey plant communities will need to consider time lags in vegetation response (Dölle & Schmidt, 2009; Thomas et al., 1999). These time lags might also partly explain the weak relations between overstorey attributes (basal area, canopy cover and canopy closure) and the light signature of the understorey in Chapter 4.

The occurrence of time lags in the dynamics of understorey communities (reinforced by findings of Perring, Bernhardt-Römermann, et al., 2018) suggests that the management decisions of today may influence the future herb layer composition for many decades. While, in the first place, we developed our framework to improve our understanding of the impact of past land-use changes on contemporary ecosystem properties, it could also provide a useful tool to predict how current forest management decisions might affect future herb layer composition. This would require identification of the key resources and conditions that control understorey composition and that can be altered by forest management practices, such as light availability, soil pH, soil moisture content, and nutrient availability (Brunet et al., 1997; Klanderud et al., 2015). Then, our framework would allow quantifying the dynamics of these resources and conditions for different forest management scenarios, which could further assist in predicting e.g. the response of understorey communities to altered management.

6.4. PERSPECTIVES FOR FUTURE RESEARCH

To investigate how forest understorey communities respond to global change, this study focused on some of the most evident aspects of global change, i.e. climate changes, nitrogen deposition, and landuse changes. Other well-known aspects of global change, such as increased CO₂ and ozone (O₃) concentrations were not investigated here. Yet, there is clear evidence that increased atmospheric CO₂ concentrations can alter plant community composition and diversity through changes in plant physiology and resource availability (Hasegawa et al., 2018; Luo et al., 2011; Morgan et al., 2004; Smith, Knapp, & Collins, 2009), and tropospheric ozone is known to damage plants and reduce plant primary productivity (Ashmore, 2005). Moreover, climate change is causing several pests and diseases, such as the oak processional moth (*Thaumetopoea processionea*) or the Eurasion spruce bark beetle (*lps typographus*), to expand their ranges and increase in numbers (Jönsson et al., 2007, 2011; Rahlenbeck & Utikal, 2015; Ramsfield et al., 2016). These pests and diseases can cause growth loss or even tree death, which can indirectly affect the understorey composition through altering e.g. light availability, microclimate buffering, and nutrient stocks. In addition, an important local scale driver of plant community composition is herbivory (Kempel et al., 2015). Although we made qualitative notes of the level of browsing damage in each study plot, these data were not incorporated in our analyses, due to a lack of time, and because models were already quite complex. However, these data, in combination with local expert knowledge from regional contact persons on e.g. past and present densities of common herbivores such as roe deer would allow further investigation of the impact of herbivory on functional and compositional changes in the understorey. In summary, incorporating these additional (global-change related) regional and local drivers (i.e. CO_2 concentrations, pests and diseases, herbivory) is required to gain a more complete understanding of temperate forest understorey responses to future environmental change. To allow disentangling the impact of all these different drivers on the understorey, analyses across multiple sites would be required. In addition, experimental approaches could be adopted to test the influence of CO_2 (e.g. CO_2 -elevation experiments (Leakey et al., 2009)) or herbivory (e.g. exclusion experiments (Schäfer et al., 2019)).

In this study, we focussed on the effects of climate change through assessing the impact of changes in average climatic conditions, i.e. temperature and precipitation. However, climate change is also causing an increase in the frequency of extreme weather events, such as heat waves, droughts, cyclones and heavy precipitation (IPCC, 2014). Several studies have already indicated that such extreme meteorological events can have a strong impact on forest plants and biodiversity (e.g. Archaux & Wolters, 2006; Bolte, Hilbrig, Grundmann, & Roloff, 2014; Royer et al., 2011). Mausolf et al. (2018) also emphasized the need to consider the 'ecological memory' of forests (e.g. former land use) when assessing or predicting the sensitivity of forest ecosystems to climate extremes, which would be possible using available meteorological data in combination with our extensive European dataset.

Furthermore, while we focussed this study on the understorey for good reasons – i.e. its importance for forest biodiversity and its crucial role in forest functioning – other ecological components such as the tree layer and belowground microbial communities are also key drivers of ecological processes that can be affected by global change. Again, our extensive sampling campaign would allow to explore both global-change effects on these other components and interactions among all ecological components in future studies, as we collected and stored fresh soil samples from each plot (containing the living soil organisms), and recorded tree species and their cover and diameter. In addition, we sampled tree increment cores of the two or three dominant trees in each plot, measured the height of these dominant trees and recorded the distance and diameter of all trees within a distance of 9 m. A study by Maes et al. (2019) within the PASTFORWARD project already assessed the interactive effects of climate change, atmospheric deposition and past forest management on individual tree growth of three study species. Their findings demonstrated that tree growth can be interactively determined by global-change drivers and past forest management. This highlights the importance of considering multiple drivers as well as past land-use changes, not only to assess understorey dynamics – as found in this PhD – but also to predict e.g. tree

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growth. While the study by Maes et al. (2019) focussed on individual tree growth of only three species, this could be extended to other tree species and to the stand-level.

In our study, we were limited to the use of proxies due to lack of actual measurements for some globalchange drivers (e.g. nitrogen deposition from EMEP model data), and other environmental factors (e.g. soil moisture content from Ellenberg indicator values of herb species, light availability from canopy characteristics). It would be useful if future studies address these issues in order to test the validity of our findings. For light availability in particular, which was found to be a key driver for understorey composition, future studies would benefit from direct light measurements using e.g. PAR (photosynthetically active radiation) sensors on top of indirect estimates of light availability (such as canopy cover and canopy closure). Such direct measurements of light transmittance could also help to explain the weak relationships that we found in Chapter 4 between canopy structural and compositional attributes and the light-demanding signature of the understorey. In addition, microclimatic temperature below the canopy may strongly differ from the macroclimatic temperatures obtained from nearby weather stations. We suggested that this microclimatic buffering might explain why negative effects of increased temperatures are only found in recent forests, which have less shade-casting canopies compared to ancient forests. One add-on study in ten PASTFORWARD regions already confirmed that tree species with the highest shade-casting ability indeed exhibit the strongest cooling effects (Zellweger et al., 2019).

Our spatio-temporal approach, based on repeat observations of the same community over time, offers clear benefits compared to space-for-time approaches (e.g. De Frenne, Brunet, et al., 2011; Honnay et al., 1999). While space-for-time studies rely on many assumptions (e.g. Walker et al., 2010) and allow only to hint (and with caution) at potential future responses of forests to temporal variation in environmental drivers, resurvey data extending to several decades allow to obtain more reliable and informative signals to estimate the nature and rate of change over time (Verheyen et al., 2017). However, our study in Skåne, making use of surveys at three points in time, illustrated that herb layer community trajectories are not necessarily linear. Therefore, while many large studies assessing temporal changes in plant communities (e.g. Dornelas et al., 2014; Vellend et al., 2013), including also our European study (Chapter 3), are based on only two observations across time, multiple intermediate surveys could reveal more complex dynamics. Furthermore, conclusions on the direction of community shifts over time could be dependent on the timing of the original survey. For instance, if the intermediate survey (in 1993) in the Skåne study had been the reference survey, we would have concluded that alpha-diversity decreased over time, instead of concluding no net changes in alpha diversity (in reference to the first survey in 1983). Hence, we advocate the establishment of permanent vegetation plots that can be resurveyed at regular time intervals to reveal potential non-linear temporal dynamics in vegetation composition.

To obtain a more mechanistic understanding of some of the findings in this study, which are currently hard to explain, e.g. the negative effect of N deposition in ancient but not in recent forests, our

observational study could be complemented with an experimental approach. This allows a more controlled, mechanistic assessment of forest responses to global changes across soils with a contrasting land-use history through manipulating temperature, N addition and light availability. Within the PASTFORWARD project, such an experiment was set up by Blondeel et al. (2020), but no clear interactive effects between the environmental treatments and agricultural legacy on community development were found. However, the time span of the experiment (three years) might be too short to capture potentially delayed responses of herb layer communities, which typically exhibit slow dynamics (Dornelas et al., 2013; Peterken & Game, 1984). Hence, we propose to further maintain this experiment in order to follow-up the longer-term responses of the understorey communities.

Our study focussed on the interactive effects of land-use history on the one hand and other global-change drivers on the other hand, on the forest herb layer. Other possible interactions between global-change drivers were not assessed. To obtain a more comprehensive understanding of the complex effects of multiple global-change drivers on the forest herb layer dynamics, future research should also consider these other potential interactions (Baeten, De Frenne, Verheyen, Graae, & Hermy, 2010). For instance, altered temperatures (related to climate change) and light levels (related to management changes) could both interact with N deposition, as higher temperatures and light levels can increase mineralization rates and hence N availability for plants (Koch et al., 2007; Van Calster et al., 2007).

Finally, the insights obtained from both the observational and experimental studies within the PASTFORWARD project could be used to develop a phenomenological-mechanistic model that allows predicting trajectories of forest herb community development under different scenarios of global change (Landuyt et al., 2018).

6.5. GENERAL CONCLUSIONS

To conclude, this PhD aimed to improve our understanding of how different global-change drivers affect temporal changes in the herb layer composition in temperate European forests with a contrasting landuse history. This was done through a spatio-temporal study design, which allowed us to determine longterm temporal shifts in community composition across multiple regions spanning gradients in environmental change factors. Our findings clearly demonstrated that responses in herb layer composition to changes in climate, nitrogen deposition and light availability depend on the land-use history of the forests, i.e. based on whether or not the investigated forests had a history of agricultural use. In general, light availability was the most important driver for compositional changes in the herb layer, but time lags should be taken into account, meaning that the present-day herb layer composition might be more related to past (e.g. a few decades ago), rather than current, light levels at the forest floor. Moreover, herb layers in recent forests were less responsive to altered light levels than herb layers in ancient forests. Similarly, the sensitivity of the herb layer to increased temperatures and nitrogen

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deposition depended on the land-use history, as increased temperatures caused decreases in the total cover of the herb layer in recent forests, but not in ancient forests, while increased nitrogen deposition only caused herb cover decreases in ancient forests. These findings clearly demonstrated the importance of land-use legacies from former agricultural use, and importantly, legacies were not only reflected in different soil nutrient contents, but also in differences in canopy composition. In sum, this PhD showed the complexity of forest dynamics in response to different local and regional environmental drivers. We specifically highlight the importance of considering the land-use history of forests in order to make sound predictions for the future development of forests, their biodiversity and functional role, under global change.



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Appendix A1

[Chapter 1]

APPENDIX A1.1. FIELD PROTOCOL

Plots were relocated as detailed as possible by making use of several supports (depending on the availability per study region) including (i) GPS coordinates of the plots, (ii) descriptive maps and notes from previous data collectors, (iii) potential markers that remained from earlier surveys (i.e. for permanent plots) and (iv) previous vegetation surveys. The plot borders were then marked by poles before sampling, using measuring tapes and a prisma to create right angles.

When the plot centre had been located, we first marked the **original plot size** used in the first survey, in order to perform a vegetation survey that can be exactly compared over time. However, since we wanted to also standardize the measurement protocol over all visited plots in the study regions such that surveys can be spatially compared as well, we performed a second vegetation survey using a standard plot size of **10x10 m²**, nested in the original plot which may be larger or smaller (**Fig. A1.1.1**). The centre will remain the centre of both plots. This plot was in turn nested in a larger **20x20 m²** plot used for determining basal area.



Figure A1.1.1. Two examples of the three plot sizes to be used during sampling. The original plot size in dark red (Left: example with original plot > standard $10x10 m^2$ plot – Right: original plot < standard $10x10 m^2$), standard vegetation plot $10x10 m^2$ in dark blue, standard stand structure plot $20x20 m^2$ in dark green. Black dot represents the plot centre and the stars indicate where the four poles will be placed during sampling.

Once plots were established, we performed an extensive and standardized measurement protocol in each plot characterizing:

- General *plot information* (of the larger 20x20 m² plot) consisted of a geographical description (e.g. GPS coordinates, slope), a visual assessment of the potential stand development (e.g. even-aged or uneven-aged stand), as well as of several management aspects (e.g. driving track signs).
- (ii) We characterized the *vegetation*, both in the 'standard' 10x10 m² plot and in the 'original' plot by performing a vegetation survey, comprising a division of all vascular plants into three layers: herb layer, shrub layer and tree layer. For each layer, we visually estimated the cover

(%) of each species, as well as the total cover of the layer. For the survey in the $10x10 \text{ m}^2$ plot, we applied our own standard definitions of the layers to assure spatial comparability across all regions: the herb layer comprised all woody and non-woody vascular plants <1m height, the shrub layer comprised all woody species between 1-7 m and the tree layer comprised all woody species >7m. For the survey in the original plot, we followed the original definitions of the vegetation layers, which differed among regions (see **Appendix A3.2**), to assure comparability between our survey and the original survey.

- (iii) We characterized *stand structure and composition* (in the larger 20x20 m² plot) by performing basal area measurements, i.e. measuring the diameter-at-breast-height (DBH) and recording the species of all trees and shrubs within the plot with DBH > 7.5 cm.
- (iv) We collected information on *individual tree growth* (in the larger 20x20 m² plot) by taking increment cores from a selection of dominant trees, recording the species, and measuring their diameter and height. Since competition can strongly influence tree growth, we also characterized their neighbouring environment by measuring for each cored tree the diameters of all trees (if DBH>7.5 cm) within a radius of 9 m around that tree as well as their distance to the cored tree.
- (v) Finally, we quantified several key resources and (site) conditions in each (smaller 10x10 m²) plot. First, light availability was characterized through performing densiometer measurements at five locations (four corners + centre). Second, we performed a soil profile description to achieve a morphological description of the soil. The soil profile was sampled by means of a soil auger, going to a depth of 50 cm. Diagnostic horizons (O, A, B, E, C, R) were identified, as well as their depth of occurrence (cm) was noted until 50 cm deep. Third, to achieve a physico-chemical description of the soil we sampled the mineral soil, i.e. mixed-soil samples were collected at two intervals (0-10, and 10-20 cm depth) from five locations (four corners + center) in each plot after removing the organic litter, fragmentation and humus layer (OL, OF, OH). The [0-10 cm] soil samples were analyzed for pH, proportion of exchangeable base cations, soil organic matter, total and Olsen phosphorus, as well as inorganic carbon and total nitrogen concentration. The [10-20 cm] soil samples were analyzed for soil texture (%clay, silt, sand). We also collected a soil sample of the [0-10 cm] interval with Kopecky rings at the center of each plot to determine bulk density. Finally, to characterize the organic forest floor, we sampled and quantified the biomass of the organic layer (OL+OF+OH) with a 20x20 cm wooden frame at two locations along a plot diagonal, and made a morphological classification of the humus layer according to Zanella et al. (2011).

APPENDIX A1.2. SHRUB AND TREE LAYER COMPOSITION

Table A1.2.1. Tree layer composition of each plot in the dataset. Numbers in the table represent the species' cover %. The first one or two letters of the plot ID refer to the region of the plot (see Table 1.1)

| РГОТ | Acer campestre | Acer platanoides | Acer pseudoplatanus | Alnus glutinosa | Alnus incana | Betula pendula | Betula pubescens | Carpinus betulus | Castanea sativa | Crataegus monogyna | Crataegus spec | Fagus sylvatica | Frangula alnus | Fraxinus excelsior | Hedera helix | llex aquifolium | Larix spec | Picea abies | Pinus nigra | Pinus sylvestris | Populus alba | Populus canadensis | Populus canescens | Populus tremula | Prunus avium | Prunus serotina | Pseudotsuga menziesii | Pyrus pyraster | Quercus cerris | Quercus petraea | Quercus pubescens | Quercus robur | Quercus robur/petraea | Quercus rubra | Robinia pseudoacacia | Salix alba | Salix caprea | Sorbus aucuparia | Sorbus torminalis | Tilia cordata | Tilia platyphyllos | Tilia spec | Ulmus glabra | Ulmus minor | Ulmus spec |
|--------|----------------|------------------|---------------------|-----------------|--------------|----------------|------------------|------------------|-----------------|--------------------|----------------|-----------------|----------------|--------------------|--------------|-----------------|------------|-------------|-------------|------------------|--------------|--------------------|-------------------|-----------------|--------------|-----------------|-----------------------|----------------|----------------|-----------------|-------------------|---------------|-----------------------|---------------|----------------------|------------|--------------|------------------|-------------------|---------------|--------------------|------------|--------------|-------------|------------|
| BI2388 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 70 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BI2393 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 |
| BI2592 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BI2606 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 0 |
| BI2960 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 |
| BI6447 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 45 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BI6471 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 45 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 65 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BI6537 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 80 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BI6602 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 60 | 0 | 0 | 0 | 0 | 0 |
| BI6603 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 55 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BI6614 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 45 | 0 | 0 | 10 | 0 | 0 |
| BI6625 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 60 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BI6627 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 60 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BI9366 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 60 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 |
| BI9460 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BS183 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BS192 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 75 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BS195 | 0 | 0 | 0 | 0 | 0 | 33 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BS203 | 0 | 0 | 0 | 0 | 0 | 8.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 58 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BS205 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 55 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BS331 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 55 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BS340 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 60 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BS342 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 70 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BS359 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 58 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BS370 | 0 | 0 | 0 | 0 | 0 | 14 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 55 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BV1011 | 0 | 0 | 0 | 0 | 45 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 45 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BV103 | 0 | 0 | 0 | 2 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BV106 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 6.5 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 4 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BV257 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BV258 | 0 | 0 | 0 | 2.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 58 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2.5 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BV31 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BV42 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BV46 | 0 | 0 | 55 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 33 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 48 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| РІОТ | Acer campestre | Acer platanoides | Acer pseudoplatanus | Alnus glutinosa | Alnus incana | Betula pendula | Betula pubescens | Carpinus betulus | Castanea sativa | Crataegus monogyna | Crataegus spec | Fagus sylvatica | Frangula alnus | Fraxinus excelsior | Hedera helix | llex aquifolium | Larix spec | Picea abies | Pinus nigra | Pinus sylvestris | Populus alba | Populus canadensis | Populus canescens | Populus tremula | Prunus avium | Prunus serotina | Pseudotsuga menziesii | Pyrus pyraster | Quercus cerris | Quercus petraea | Quercus pubescens | Quercus robur | Quercus robur/petraea | Quercus rubra | Robinia pseudoacacia | Salix alba | Salix caprea | Sorbus aucuparia | Sorbus torminalis | Tilia cordata | Tilia platyphyllos | Tilia spec | Ulmus glabra | Ulmus minor | Ulmus spec |
|--------|----------------|------------------|---------------------|-----------------|--------------|----------------|------------------|------------------|-----------------|--------------------|----------------|-----------------|----------------|--------------------|--------------|-----------------|------------|-------------|-------------|------------------|--------------|--------------------|-------------------|-----------------|--------------|-----------------|-----------------------|----------------|----------------|-----------------|-------------------|---------------|-----------------------|---------------|----------------------|------------|--------------|------------------|-------------------|---------------|--------------------|------------|--------------|-------------|------------|
| CO1 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 28 | 0 | 0 | 0 | 65 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CO4.20 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CO4.21 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 0 | 45 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CO4.23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CO4.24 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 80 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CO4.25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 80 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CO4.27 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 45 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 55 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CO5 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 95 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CO6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 55 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CO8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| DE129 | 1.3 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 38 | 0 | 0 | 0 | 0 |
| DE27 | 0 | 45 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 55 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| DE28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 45 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| DE400 | 0 | 10 | 10 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 |
| DE404 | 4 | 0 | 45 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 55 | 0 | 0 | 0 |
| DE408 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| DE411 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 |
| DE412 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 57 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| DE446 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 |
| DE50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GO104 | 0 | 0 | 1.5 | 0 | 0 | 0 | 0 | 11 | 0 | 0 | 0 | 90 | 0 | 3.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GO116 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 70 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GO120 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 85 | 0 | 7.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GO178 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 95 | 0 | 1.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GO182 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 88 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GO216 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7.5 | 0 | 0 | 0 | 0 | 0 | 0 |
| GO237 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| G0548 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 93 | 0 | 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| G0578 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 55 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 0 |
| G083 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 95 | 0 | 1.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| K0775 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 |
| K0777 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 18 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 23 | 35 | 0 | 0 | 0 | 0 | 0 |
| K0778 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 45 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 |
| K0784 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 70 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 |
| K0785 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 65 | 0 | 0 | 0 | 0 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| K0786 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 60 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| K0787 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 65 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| KO789 | õ | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 |
| KO791 | õ | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 70 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 |
| K0792 | õ | 25 | 0 | 0 | 0 | õ | 0 | 0 | 0 | õ | õ | 0 | 0 | õ | õ | 0 | 0 | 0 | 0 | 0 | õ | õ | 0 | 0 | 0 | 0 | õ | 0 | õ | 55 | õ | 0 | 0 | 0 | 0 | õ | õ | õ | 1 | õ | 0 | 0 | 0 | 0 | 0 |
| LF1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

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|----------------|------|---------|------|---------|------|-------|---------|------|------|------|------|----------|------|---------|-----|------|------|------|------|------|-------|------|------|-------|------|------|------|----------|------|------|------|---------|------|------|-------|------|------|------|------|------|------|------|----------|----------|-------|
| | | | snu | | | | | | | yna | | | | | | | | | | | | .s | s | | | | zies | | | | SL | | trae | | acia | | | | | | | | | | |
| | e | les | ataı | a | | m. | ens | sn | ē | 10g | U | | | sior | | ~ | | | | S | | ens | cen | ıla | | a | nen | | | ea | scer | | əd/. | | oac | | | aria | alis | | os | | | | |
| | estr | pior | lqo | JOS | g | dula | esc | etul | ativ | lo L | spe | itica | snu | cel | .× | ium | | | | stri | Da | nad | nes | m | Ę | otin | ga n | ster | rris | etra | ipe | bur | bur | bra | pna | | æ | edn | nin | g | hyll | | ra | ď | 0 |
| | du | atar | eud | luti | Icar | лей | qnc | s be | s es | I SN | sn | ylva | a al | sex | hel | ifol | ec | oies | igra | /lve | s alk | cal | s ca | s tre | avit | sero | tsug | yras | s ce | s pe | s pu | s ro | s ro | s ru | pse | ра | pre | auc | tor | dat | typ | S | glab | nin | bed |
| ⊢ | .cal | d. | sd. | S g | s in | lla p | lla p | inu | ane | aeg | aeg | IS SI | gul | inu | era | nbe | c sp | a at | s ni | s s) | snlr | snlr | snlr | snlr | snu | SUL | iopi | s p | LCU | LCU | LCU | rcu | lici | lici | nia | alb | cal | sn | . Sn | cor | pla | spe | ns € | us r | ns s |
| -O- | cer | vcer | cer | lhu | Nu | letu | etu | arp | ast | rat | Crat | agu | ran | rax | led | ex | arix | ice | inu | inu | 1do | ldo | 1do | ldo | run | run | seu | , Jru | Jue | Jue | Jue | Sue | Jue | Sue | idoli | alix | alix | orb | orb | ilia | ilia | ilia | <u>n</u> | <u>n</u> | ull I |
| LF10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 83 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LF12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 70 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LF14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 17 | 0 | 0 | 0 | 80 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LF15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 68 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LF16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 38 | 0 | 0 | 0 | 63 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LF3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 97 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LF5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 55 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LF7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 98 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LF9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | /0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.5 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| MO12 | 0 | 50 0 | 0 | 0 | 0 | 0 | 3 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 45 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 35 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| M012 M018 | 0 | 28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 0 |
| M019 | 0 | 75 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 45 | 0 | 0 | 0 | 0 | 0 | 50 | õ | 0 | 0 | 0 | 0 | õ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13 | 0 | 0 | 0 | õ | 0 | 0 | 0 |
| MO20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 60 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 8 | 0 | 0 | 0 | 0 | 0 |
| MO22 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| M08 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 15 | 0 | 0 | 0 | 0 | 0 |
| M09 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PR122 | 0 | 0 | 0 | 66 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PR125 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PR156 | 0 | 0 | 30 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PR1/U | 0 | 0 | 0 | 80 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PR190 DR107 | 0 | 0 | 23 | 35 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PR204 | 0 | 0 | 0 | 23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PR26 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 |
| PR63 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 95 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PR68 | 0 | 0 | 0 | 50 | 0 | 1.5 | 0 | 1.5 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SH1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 97 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SH10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 93 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SH2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 88 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SH3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 92 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SH4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 90 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SH5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | /5 02 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3П7 SH8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 95 70 | 0 | 50 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SH9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 96 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SKA124 | 0 | 0 | 0 | õ | 0 | 0 | 0 | 60 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | õ | õ | 20 | 0 | 0 |
| SKA133 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 80 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| SKA2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SKA35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 60 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Appendix to Chapter 1

| LOT | Acer campestre | Acer platanoides | Acer pseudoplatanus | Alnus glutinosa | Alnus incana | setula pendula | setula pubescens | Carpinus betulus | Castanea sativa | Crataegus monogyna | Crataegus spec | agus sylvatica | rangula alnus | raxinus excelsior | ledera helix | lex aquifolium | arix spec | oicea abies | oinus nigra | oinus sylvestris | opulus alba | opulus canadensis | opulus canescens | opulus tremula | runus avium | ^o runus serotina | seudotsuga menziesii | yrus pyraster | Juercus cerris | Juercus petraea | Juercus pubescens | Juercus robur | Quercus robur/petraea | Juercus rubra | kobinia pseudoacacia | ialix alba | ialix caprea | orbus aucuparia | orbus torminalis | ilia cordata | ilia platyphyllos | ïlia spec | Jlmus glabra | Jlmus minor | Jlmus spec |
|--------|----------------|------------------|---------------------|-----------------|--------------|----------------|------------------|------------------|-----------------|--------------------|----------------|----------------|---------------|-------------------|--------------|----------------|-----------|-------------|-------------|------------------|-------------|-------------------|------------------|----------------|-------------|-----------------------------|----------------------|---------------|----------------|-----------------|-------------------|---------------|-----------------------|---------------|----------------------|------------|--------------|-----------------|------------------|--------------|-------------------|-----------|--------------|-------------|------------|
| SKA71 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SKA80 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 70 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 70 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SKA89 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 60 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SKA9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SKA92 | Õ | Ő | 10 | 0 | 0 | 0 | õ | 0 | 0 | 0 | 0 | 5 | 0 | 0 | õ | 0 | Õ | 0 | 0 | 0 | 0 | 0 | 0 | Õ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | õ | 0 | 0 | 0 | Õ | 0 | Õ | 0 | Õ | 0 | 0 | 0 | 0 |
| SKA96 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 60 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SKI 1 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SKR20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 38 | 0 | 0 | 0 | 0 | 0 | 0 |
| SKR26 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 55 | 0 | 0 | 0 | 45 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 0 |
| SKR32 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 70 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 45 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SKR34 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 65 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SKR35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 70 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SKT16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 68 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SKT22 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 65 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SKT23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 43 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SKT26 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP1A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 95 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP1B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 55 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP2A | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 60 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP2B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 60 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP3A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 98 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP3B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 97 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP4A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 33 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP4B | 0 | 0 | 0 | 0 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 45 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP5A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 75 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP5B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| TB106 | 0 | 0 | 18 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| TB109 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| TB115B | 0 | 0 | 33 | 7.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| TB120 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 58 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| TB140 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| TB146 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 78 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| TB151 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 55 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| TB181 | 0 | 0 | 70 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 11 |
| TB80 | 0 | 0 | 33 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| TB97 | 0 | 0 | 10 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 90 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WAS10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WAS11 | 0 | 0 | 53 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WAS12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WAS14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 45 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WAS16 | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | _ | | | | | | | | | | | | |
|-------|---------------|-----------------|--------------------|----------------|-------------|---------------|-----------------|-----------------|----------------|-------------------|--------------|-----------------|--------------|------------------|-------------|---------------|-----------|-----------|-----------|----------------|-------------|-------------------|------------------|----------------|------------|---------------|----------------------|---------------|---------------|----------------|------------------|--------------|----------------------|--------------|---------------------|-----------|-------------|-----------------|------------------|-------------|------------------|----------|-------------|------------|-----------|
| ŌŢ | cer campestre | cer platanoides | cer pseudoplatanus | Inus glutinosa | inus incana | etula pendula | etula pubescens | arpinus betulus | astanea sativa | ataegus monogyna. | ataegus spec | agus sylvatica | angula alnus | axinus excelsior | edera helix | ex aquifolium | arix spec | cea abies | nus nigra | nus sylvestris | opulus alba | opulus canadensis | opulus canescens | opulus tremula | unus avium | unus serotina | seudotsuga menziesii | /rus pyraster | uercus cerris | uercus petraea | uercus pubescens | uercus robur | uercus robur/petraea | uercus rubra | obinia pseudoacacia | alix alba | alix caprea | orbus aucuparia | orbus torminalis | lia cordata | lia platyphyllos | lia spec | lmus glabra | lmus minor | lmus spec |
| | Ă | Ă | Ă | Ā | Ā | ä | ä | <u> </u> | <u> </u> | Ū | Ū | <u><u> </u></u> | <u> </u> | <u> </u> | Ĭ | <u> </u> | <u>_</u> | Pi | Pi | Pi | <u> </u> | <u> </u> | <u> </u> | <u> </u> | 4 | <u> </u> | å | <u></u> | <u> </u> | ď | ď | <u> </u> | ď | <u>a</u> | Ř | Š | Š | Š | Š | i E | H | F | <u> </u> | | |
| WPY1 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WPY2 | 0 | 0 | 65 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WPY3 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WPY4 | 0 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 68 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WPY7 | 0 | 0 | 45 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WR1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 95 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WR10 | 0 | 0 | 48 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WR2 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 85 | 0 | 5.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WR3 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 90 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WR4 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 80 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WR5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 35 | 0 | 75 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WR6 | 3 | 0 | 70 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WR7 | 5 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 68 | 0 | 0 | 0 | 18 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WR8 | 0 | 0 | 36 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 84 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WR9 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 65 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WW1 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WW10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WW2 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WW3 | 80 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WW4 | 10 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WW5 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WW6 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WW7 | 0 | 0 | 68 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 23 | 0 | 80 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WW8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WW9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| ZVD14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 17 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| ZVD16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 70 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| ZVD29 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 63 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 |
| ZVD31 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 83 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| ZVD33 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| ZVG24 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 63 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| ZVG25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| ZVG26 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 80 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| ZVG62 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 73 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| ZVY7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 74 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Appendix to Chapter 1

| РОТТ | Acer campestre | Acer platanoides | Acer pseudoplatanus | Alnus incana | Betula pendula | Betula pubescens | Betula spec | Carpinus betulus | Castanea sativa | Clematis vitalba | Cornus mas | Cornus sanguinea | Cornus spec | Corylus avellana | Crataegus laevigata | статаевих птоповупа Статаевих ѕрес | Euonymus europaeus | Fagus sylvatica | Frangula alnus | Fraxinus excelsior | Hedera helix | Humulus lupulus | llex aquifolium | Ligustrum vulgare | Lonicera periclymenum | Lonicera xylosteum | Picea abies | Populus canescens | Populus tremula | Prunus avium | Prunus pagus Prunus serotina | Prunus spinosa | Quercus cerris | Quercus petraea | Quercus pubescens | Quercus robur | Ribes rubrum | Robinia pseudoacacia | Salix caprea | Sambucus nigra | Sambucus racemosa | Sorbus aria | Sorbus aucuparia | Sorbus torminalis | Staphylea pinnata | Tilia cordata | Tilia platyphyllos | Ulmus glabra Ulmus minor |
|--------|----------------|------------------|---------------------|--------------|----------------|------------------|-------------|------------------|-----------------|------------------|------------|------------------|-------------|------------------|---------------------|---------------------------------------|--------------------|-----------------|----------------|--------------------|--------------|-----------------|-----------------|-------------------|-----------------------|--------------------|-------------|-------------------|-----------------|--------------|---------------------------------|----------------|----------------|-----------------|-------------------|---------------|--------------|----------------------|--------------|----------------|-------------------|-------------|------------------|-------------------|-------------------|---------------|--------------------|-----------------------------|
| BI2388 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 (| 0 0 |
| BI2393 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 (| 0 0 |
| BI2592 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 (| 0 0 |
| BI2606 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 (| 0 0 |
| BI2960 | 0 | 37 | 0 0 | 0 | 0 | 0 | 0 | 37 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 (| 0 0 |
| BI6447 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |
| BI6471 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 (| 0 0 |
| BI6537 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |
| BI6602 | 0 | 0 | 0 0 |) 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 (| 0 0 |
| BI6603 | 0 | 0 | 0 0 |) 0 | 0 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |
| BI6614 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 65 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 2 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 . | 1 0 |
| BI6625 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 39 | 0 (| 0 0 |
| BI6627 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 38 | 0 | 0 | 0 | 0 | 0 | 18 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 (| 0 0 |
| BI9366 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 (| 0 0 |
| BI9460 | 0 | 0 | 0 0 |) 0 | 0 | 0 | 0 | 1.5 | 0 | 0 | 0 | 0 | 0 0 | 0.5 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4.5 | 0 (| 0 0 |
| BS183 | 0 | 0 | 0 0 |) 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 12 | 0 | 0 | 0 | 0 | 0 0 | 0 | 3 | 0 | 0 | 0 | 0 | 12 | 0 | 0 | 0 | 0 (| 0 0 |
| BS192 | 0 | 0 | 0 0 |) 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 6.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 4. | 5 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 (| 0 0 |
| BS195 | 0 | 0 | 0 0 |) 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 45 | 0 | 0 | 10 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 (| 0 0 |
| BS203 | 0 | 0 | 0 0 |) 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 33 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 0. | 5 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 1.5 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 (| 0 0 |
| BS205 | 0 | 0 | 0 0 |) 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 1.5 | 6 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 (| 0 0 |
| BS331 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4.5 | 0 | 0 | 0 | 0 | 0 | 0 50 | 0 | 0 | 7.5 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 (| 0 0 |
| BS340 | 0 | 0 | 0 0 |) 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 0 | 0 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 25 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 35 | 0 | 0 | 0 | 0 (| 0 0 |
| BS342 | 0 | 0 | 0 0 |) 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 (| 0 0 |
| BS359 | 0 | 0 | 0 0 |) 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 0 | 0 | 2 | 6.5 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 4 | 0 | 0 | 1.8 | 0 | 0 | 0 | 0 (| 0 0 |
| BS370 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 2 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.5 | 0 | 0 | 0 | 0 (| 0 0 |
| BV1011 | 0 | 0 | 0 0 |) 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |
| BV103 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 25 | 0 | 0 | 0 | 0 | 0 4 | 0 | 0 | 0 | 3 | 0 | 0 | 5 | 0 | 0 | 0 | 0 (| 0 0 |
| BV106 | 0 | 0 (| 0.5 2 | . 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 5 C | 2 | 1 | 0 | 43 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |
| BV257 | 0 | 0 | 10 0 |) () | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |
| BV258 | 0 | 0 | 0 1. | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0.5 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 1.5 | 1.8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |
| BV31 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 60 |
| BV42 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 40 | 0 2 | 5 0 | 0 | 0 | 0 | 2.5 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 1.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 38 |
| BV46 | 0 | 0 | 55 3 | 0 | 0 | 0 | 0 | 0 | 2.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 1 | .5 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |
| BV510 | 0 | 0 3 | 1.5 3. | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 7.5 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |
| CO1 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 01 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |
| CO4.20 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 13 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0. | 50 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |
| CO4.21 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 50 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 (| 0 0 |
| CO4.25 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 10 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |
| CO4.27 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |
| CO5 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 15 | 0 | 0 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |
| CO6 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 6.5 | 0 | 0 | 0 | 0 | 55 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 06 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 (| 0 0 |
| CO8 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 30 | 0 | 0 | 0 | 0 | 45 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |

Table A.1.2.2. Shrub layer composition of each plot in the dataset. Numbers in the table represent the species' cover %. The first one or two letters of the plot ID refer to the region of the plot (see Table 1.1)

| РГОТ | Acer campestre | Acer platanoides | Acer pseudoplatanus | Alnus glutinosa | Alnus incana | Betula pendula | Betula pubescens | Betula spec | Carpinus betulus | Castanea sativa Clomotic vitolko | ciematis vitalba Cornus mas | Cornus sanguinea | Cornus spec | Corylus avellana | Crataegus laevigata Crataegus monogyna | Crataegus spec | Euonymus europaeus | Fagus sylvatica | Frangula alnus | Fraxinus excelsior | Hedera helix | Humulus lupulus | liex aquirolium Ligustrum vulgare | Lonicera periclymenum | Lonicera xylosteum | Picea abies | Populus canescens | Prunus avium | Prunus padus | Prunus serotina | Prunus spinosa | Quercus cerris | Quercus peu aea Quercus pubescens | Quercus robur | Quercus rubra | Ribes rubrum | Robinia pseudoacacia | Salix caprea | Sambucus racemosa | Sorbus aria | Sorbus aucuparia | Sorbus torminalis Stanhvlea ninnata | Tilia cordata | Tilia platyphyllos | Ulmus glabra | Ulmus minor |
|----------------|----------------|------------------|---------------------|-----------------|--------------|----------------|------------------|-------------|------------------|-------------------------------------|--------------------------------|------------------|-------------|------------------|---|----------------|--------------------|-----------------|----------------|--------------------|--------------|-----------------|--------------------------------------|-----------------------|--------------------|-------------|-------------------|--------------|--------------|-----------------|----------------|----------------|--------------------------------------|---------------|---------------|--------------|----------------------|--------------|-------------------|-------------|------------------|--|---------------|--------------------|--------------|-------------|
| DE129 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 (| 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 0 | 0 | 0 | 0 (| 0 |
| DE27 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (|) () | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 0 | 0 | 0 | 0 (| 0 |
| DE28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 10 | 0 | 0 | 0 | 0 0 | 1.5 | 0 | 0 | 0 | 2 | 0 | 0 0 |) () | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 0 | 0 | 2 | 0 (| 0 |
| DE400 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 3 | 30 | 0 0. | .5 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 (| 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 0 | 0 | 10 | 0 (| 0 |
| DE404 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 45 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 |) 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 0 | 0 | 0 | 1 (| 0 |
| DE408 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 20 | 0 (| 0 | 0 | 0 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 (|) 2 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 15 | 50 | 0.5 | 0 (| 0 |
| DE411 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 05 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0.5 | 50 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 2 | 0 | 10 | 0 (| 0 |
| DE412 | 1.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | 0 15 | 0 | 0 | 0 | 0 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 (| 0.5 | 5 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | | 0 (|) 2.5 | 0 | 0 | 0 | 0 | 00 |) () | 0 | 0 | 0 5 | 0 | 0 | 0 (| 0 |
| GO104 | 0 | 0 | 1.8 | 0 | 0 | 0 | 0 | 0 3 | 3.5 | | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 1.5 | 0 | 0 | 0 | | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | | | 0 0 | 0 | 0 | 0 | 0 | | | 0 | 0 | 0 0 | 0 | 0 | 1.5 (| 0 |
| GO120 GO179 | 0 | 0 | 1.5 | 0 | 0 | 0 | 0 | 0 | 0 | | | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | | , 0 , 0 | 0 | 0 | 0 | | | 0 | 0 | | | | 0 | 0 | 0 | 0 | | | 0 | 0 | 0 0 | 0 | 0 | | 0 |
| GO178 | 0 | 0 | 75 | 0 | 0 | 0 | 0 | 0 | 0 | | 0 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 32 | 0 | 0 | 05 | | , 0) 0 | 0 | 0 | 0 | | | 0 | 0 | | |) ()) () | 0 | 0 | 0 | 0 | | | 0 | 0 | 0 0 | 0 | 0 | 5 (| 0 |
| GO102 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | | 0 | Ő | 0 | 0 | 0 0 | 0 | Ő | 15 | 0 | 40 | 0 | 0 0 | 0 | Ő | Ő | 0 | 0 0 | 0 | 0 | õ | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 0 | 0 | 0 | 0 0 | 0 05 0 | 0 | Ő | 0 0 | 0 |
| G0237 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 60 | 0 | 2 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0.5 | 1.5 (| 0 |
| GO548 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 0 | 0 | 0 | 0 0 | 0 |
| GO578 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 0 | 0 (| 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 0 | 0 | 0.5 | 15 (| 0 |
| GO83 | 0 | 0 | 28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 3.5 | 0 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 0 | 0 | 0 | 1.5 (| 0 |
| KO775 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 |) 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 0 | 0.5 | 0 | 0 (| 0 |
| KO778 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0.5 | 50 | 0 | 7 | 0 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 (|) () | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 3 0 | 1 | 0 | 0 (| 0 |
| KO784 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 1 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (|) () | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 (| 0 |
| KO785 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 1 | | | | 0 | 0 | 1 0 | 0 | 0 | 0 | 0 | 0 | 0 | | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | | | 0 0 | 0 | 0 | 0 | 0 | | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 0 | 0 |
| KU786 | 18 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | | 0 1.5 | 0 3 1E | 0 | 1 | 0 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | | 0 | 0 | 0 | 0 | | | 0 | 0 | | |) U | 0 | 0 | 0 | 0 | | | 0 | 0 | | 1 | 0 | | 6 |
| K0789 | 1 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0. | 0 10 | | 0 0 | 15 | 0 | q | 00 | 0 | 0 | 12 | 0 | 0 | 0 | | , 0) 0 | 0 | 0 | 0 | | | 0 | 0 | | |) ()) () | 0 | 0 | 0 | 0 | | | 0 | 0 | 0.5 0 | 0 | 0 | | 0 |
| K0791 | 2.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | 0 0 | 0 | 25 | 0 | 00 | 0 | 0 | 1 | 0 | 0 | 0 | 0 0 |) 0 | 0 | 15 | 0 | 0 0 | 0 | 0 | 0 | | 0 0 |) 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 1 | 0 | 0 0 | 0 | 0 | 0 0 | 0 |
| KO792 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 2 | 20 | 0 0 | 0 0 | 10 | 0 | 0 | 0 0 | 2 | 0 | 0 | 0 | 0.5 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 (| 0 |
| LF1 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 2 | 3 (| 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 13 | 0 | 0 | 0 | 0 0 |) 0 | 0 | 0 | 0 | 0 0 | 2.5 | 5 0 | 0 | 0 0 | 0 0 | 0 0 | 0.5 | 0 | 0 | 0 0 | .5 (|) 0 | 0 | 0 | 0 0 | 0 | 0 | 0 (| 0 |
| LF10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 |).5 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 0 | 0 | 0 | 0 0 | 0 |
| LF12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 2 | 25 (| 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 0 | 0 | 0 | 0 (| 0 |
| LF14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 0 | 0 | 0 | 0 (| 0 |
| LF15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 5.5 | 0 | 0 | 0 | 0 0 | 5 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 0 | 0 | 0 | 0 (| 0 |
| LF16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 (| 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 (| 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 (| 0 |
| | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 23 | 0 | 0 | 0 | 0 / | 5 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | | | 0 0 | 0 | 0 | 0 | 0 | |) () | 0 | 0 | 0 0 | 0 | 0 | 0 0 | 0 |
| LF9 MO11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 1 E | 0 | 0 | | | 0 | 0 | 0 | 0 0 | 0 | 0 | 23 | 0 | 0 | 0 | | 0 | 0 | 0 | 0 | | | 0 | 0 | | |) U | 0 | 0 | 0 | 0 | | | 0 | 0 | 0 0 | 0 | 0 | | 0 |
| MO12 | 0 | 0 | 0 | 0 | 0 | 0 | 1.5 | 0 | 0 | | 0 0 | 0 | 0 | 10 | 00 | 0 | 0 | 0 | 55 | 0 | 0 | | , 0) 0 | 0 | 0 | 0 | | | 0 | 0 | | | 5 0 1 0 | 0 | 0 | 0 | 0 | | | 0 | 0 | 0 0 | 0 | 0 | | 0 |
| M012 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | 5 0 n n | 0 | 0 | 10 | 00 | 0 | 0 | 0 | 0.5 | 0 | 0 | | , 0) 0 | 0 | 0 | 0 | 0 0 | | 55 | 0 | | |) 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 05 | 0 | 0 0 | 0 |
| M019 | ŏ | Ő | Ő | 0 | 0 | 0 | 0 | 0 | 0 | | 0 0 | 0 | Ő | 0 | 0 0 | Ő | Ő | 0 | 0 | õ | 0 | 0 0 | 0 | Ő | õ | 2 | 0 0 | 0 | 0 | õ | 0 0 | 0 0 | 5 0 | Ő | 0 | õ | 0 | 0 0 | 0 | Ő | 0 | 0 0 | 0.5 | õ | 0 0 | 0 |
| MO20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 3 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 1 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 4 | 0 | 0 (| 0 |
| M022 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 |) 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 |) () | 0 | 6 | 0 0 | 0 | 0 | 0 (| 0 |
| M08 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 43 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 0 | 1 | 0 | 0 0 | 0 |
| PR122 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 03 | 90 | 0 | 0 | 0 0 | 0 | 0 | 0 0 | 0 |
| PR125 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 0 | 0 | 0 | 0 0 | 0 |
| PR156 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0.5 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 0 | 0 | 0 | 0 0 | 0 |
| PR170 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 0 | 0 | 0 | 68 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 (| 0 |
| PR196 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 0 | 0 | 0 | 25 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 | 0 | 0 | 0 | 0 0 | 0 | 4 | 0 | | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 2 | 0 0 | 0 | 0 | 0 (| 0 |
| PK197 | 0 | 9.5 | 0 | 0 | U | 0 | 0 | 0 | U | υΟ | U 0 | 0 | 0 | 40 | υ 0 | 0 | 0 | U | U | U | U | υ (| 0 1 | 0 | 0 | 0 | υΟ | 0 | 2.5 | U | U | υ (| J 0 | 0 | 0 | 0 | 0 | υ | J 0 | 0 | U | υ 0 | 0 | U | 0 (| U |

Appendix to Chapter 1

| PLOT | Acer campestre | Acer platanoides | Acer pseudoplatanus | Alnus glutinosa | Alnus incana | Betula pendula | Betula pubescens | Betula spec | Carpinus betulus | Castanea sauva Clematis vitalha | Cornus mas | Cornus sanguinea | Cornus spec | Corylus avellana | Crataegus laevigata Crataegus monogyna | Crataegus spec | Euonymus europaeus | Fagus sylvatica | Frangula ainus | Fraxinus excelsior Lodora bolix | Humulus lubulus | llex aquifolium | Ligustrum vulgare | Lonicera periclymenum | Lonicera xylosteum | Picea abies | Populus tremula | Prunus avium | Prunus padus | Prunus serotina | Prunus spinosa Onercus cerris | Quercus petraea | Quercus pubescens | Quercus robur | Quercus rubra | Ribes rubrum | Robinia pseudoacacia | salıx caprea Sambucus nigra | Sambucus racemosa | Sorbus aria | Sorbus aucuparia | Sorbus torminalis | Staphylea pinnata | lillia corgata Tilia platvohvillos | Ulmus glabra | Ulmus minor |
|--------|----------------|------------------|---------------------|-----------------|--------------|----------------|------------------|-------------|------------------|------------------------------------|-------------|------------------|-------------|------------------|---|----------------|--------------------|-----------------|----------------|------------------------------------|-----------------|-----------------|-------------------|-----------------------|--------------------|-------------|-----------------|--------------|--------------|-----------------|----------------------------------|-----------------|-------------------|---------------|---------------|--------------|----------------------|--------------------------------|-------------------|-------------|------------------|-------------------|-------------------|---------------------------------------|--------------|-------------|
| PR204 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 0 |) () |) () | 0 | 0 | 3 | 0 0 | 0.5 | 0 | 0 | 0 0 | .5 (|) () | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 3.5 | 0 (| D 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 3.5 | 0 | 0 | 0 | 0 | 0 | 0 C | 0 | 0 |
| PR26 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 |) () | 0 (| 0 | 0 | 12 | 0 0 | 0 | 0 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 C | 0 | 25 |
| PR68 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 |) () | 0 (| 0 | 0 | 15 | 0 0 | 0 | 0 | 3 | 0 | 0 0. | 5 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 23 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 2.5 | 0 | 0 | 0 | 0 | 0 | 0 C | 0 | 0 |
| SH10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |) () | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0.5 | 0 | 0 | 0 | 0 | 0 | 0 C | 0 | 0 |
| SH7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 |) () | 0 (| 0 | 0 | 0 | 0 0 | 0 | 0 | 0.5 | 0 | 0 0 |) () | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 C | 0 | 0 |
| SH8 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 0 |) () | 0 (| 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 |) () | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 C | 0 | 0 |
| SH9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 |) () | 0 (| 0 | 0 | 0 | 0 0 | 0 | 0 | 2 | 0 | 0 0 |) () | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 C | 0 | 0 |
| SKA124 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 (|) () |) () | 0 | 0 | 1 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 1 0 | 0 | 0 |
| SKA35 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |) () | 0 | 0 | 20 | 0 0 | 0 | 0 | 0 | 3 | 0 0 | 0 0 | 0 | 0 | 0 | 1 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 5 | 0 | 0 | 0 0 | 0 | 0 |
| SKA71 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |) 0 | 0 | 0 | 40 | 0 0 | 0 | 0 | 5 | 0 | 3 (| 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 2 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 20 | 0 |
| SKA80 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 (| 0 0 |) 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 2 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 |
| SKA89 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 (| 0 0 |) () | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 |
| SKA9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |) () | 0 | 0 | 85 | 0 0 | 0 | 0 | 0 | 0 | 0 (| 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 |
| SKA92 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 (|) () |) () | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 (| 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 |
| SKA96 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (|) () |) () | 0 | 0 | 10 | 0 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 5 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 |
| SKL1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 (|) () |) 29 | 0 | 0 | 0 | 0 0 | 2 | 0 | 0 | 0 | 0 (| 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 |
| SKR20 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 4 | 40 (|) () | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 (| 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 |
| SKR26 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 |) () | 8 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | |) () | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0.5 | 0 | 0 0 | 0 | 0 |
| SKR3Z | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | 0 | 0 | 0 0 | 0.5 0 | 1 | 0 | 0 | 0 | | 0 0 | 0 | 0 | 0 | 0 | | | 0 | 0 | 0 0 | 5 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 5 0 | 0 | |
| SKR34 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 4 | 46 (05 (| | | 0 | 0 | 0 | 0 0 | 1 | 0 | 0 | 0 | | 0 0 | 0 | 0 | 0 | 0 | | | 0 | 0 | 0 0 | 5 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 5 0 | 0.5 | , 0 |
| SKIID | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 : | 95 (25 (|) () (|) / \ 10 | 0 | 0 | 0 | 0 0 | 1 | 0 | 0 | 0 | | 0 0 | 0 | 0 | 0 | 0 | | | 0 | 0 | 0 0 | | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 5 0 | 0 | 0 |
| SK122 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 35 (24 (|) () (| 0 10 | 0 | 0 | 0 | 0 0 | 1 | 0 | 0 | 0 | |) ()) () | 0 | 0 | 0 | 0 | | | 0 | 0 | 0 0 | 5 U 5 O | | 0 | 0 | 0 | 0 | 0 | | 0 | 0 | 0 | 0 | 0 | 5 0 5 0 | 0 | 0 |
| SKT25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 1 | 24 (| ט נ ח נ | | 0 | 0 | 0 0 | | 0 | 0 | 0 | 0 | | , 0 , 0 | 0 | 0 | 0 | 0 | | | 0 | 0 | | 5 0 5 0 | | 0 | 0 | 0 | 0 | 0 | | 0 | 0 | 0 | 0 | 0 | 5 0 5 0 | 0 | 0 |
| SP1A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0. 0 | 0 0 | ן ה ה ה |) 0.J | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | n | | , 0 , 0 | 25 | 0 | 0 | 0 | | | 0 | 0 | | 5 0 7 0 | | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 50 10 | 0 | 0 |
| SP2A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | , 0 1 0 | 0 | 0 | 0 | 0 | 00 | 0 | 0 | 10 | n | | , 0 , 0 | 2.5 | 0 | 1 | 0 | 0 0 | | 0 | 0 | 0 0 | 5 0 1 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 5 0 1 0 | 0 | 0 |
| SP2R | 0 | 0 | ñ | 0 | ñ | 0 0 | n n | 0 0 | 0 0 | , 0 1 0 | 0 | 0 | 0 | n n | 0 0 | ñ | 0 | 18 | n | | , 0) 0 | 0 | ñ | Ô | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 5 0 5 0 | 0 | 0 | 0 | 0 | ñ | 0 | 0 0 | ñ | ñ | 2 | 0 0 | 0 0 | n n | 0 | 0 |
| SP3B | 0 | õ | Ő | 0 | 0 | 0 | 0 | õ | 0 0 | 0 | 0 | Ő | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 6 | õ | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 50 | 0 | 0 | 0 | 0 | õ | 0 | 0 0 | 0 | Ő | 0 | 0 | 0 | 0 0 | 0 | 0 |
| SP4A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 |) 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 9 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 |
| SP4B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 |) 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 80 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 |
| SP5A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 |) 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0.5 | 0 | 0 | 0 0 | 0 | 0 |
| SP5B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 |) () | 0 | 0 | 0 | 0 0 | 0 | 0 | 30 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0.5 | 0 | 0 | 0 C | 0 | 0 |
| TB106 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 53 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 C | 0 | 0 |
| TB109 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 |) () | 0 | 0 | 61 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0.5 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 C | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 C | 0 | 0 |
| TB115B | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 65 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 C | 0 | 0 |
| TB120 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 |) () | 0 | 0 | 85 | 0 0 | 0 | 0 | 0 | 0 2 | .5 (| 0 0 | 0 | 0 | 4 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 C | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 C | 0 | 0 |
| TB140 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 |) () | 0 | 0 | 60 | 0 0 | 0 | 0 | 0 | 0 | 7 (| 0 0 | 0 | 0 | 2 | 0 | 0 0 | 0 | 0 | 0 | 0 (| D 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 1.5 | 0 | 0 | 0 C | 0 | 0 |
| TB146 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 |) () | 0 | 0 | 80 | 0 0 | 0.5 | 0 | 0 | 0 | 4 (| 0 (| 0.5 | 0 | 0.5 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 C | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0.5 | 0 | 0 | 0 C | 0 | 0 |
| TB151 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 |) () | 0 | 0 | 86 | 0 0 | 1.5 | 0 | 0 | 0 | 0 0 | 0 (| 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| D 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 C | 0 | 0 |
| TB181 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 (| 0 | 0 | 55 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| D 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 |
| TB80 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 4 | 40 (| 0 0 | 0 (| 0 | 0 | 40 | 0 0 | 0 | 0 | 0 | 2 | 0 0 | 5 0 | 0 | 0 | 2.5 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0.5 | 0 | 0 | 0 0 | 0 | 0 |
| TB97 | 0 | 0 | 5 | 0 | 0 | 2 | 0 | 0 | 0 (| 0 0 | 0 0 | 0 | 0 | 45 | 0 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 1 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 |
| WAS10 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 5 | 0 0 | 0 | 0 | 4 | 0 | 1 4 | 1 0 | 12 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 |
| WAS11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (|) () | 0 | 0 | 0 | 1 | 0 0 | 0 | 0 | 27 | 0 | 0 (|) () | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 |
| WAS12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (|) () | 0 | 0 | 0 | 3.5 | 0 0 | 0 | 0 | 0.5 | 0 | 2 (| 0_0 | 5 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 2.5 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 |
| WAS14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (|) () | 0 | 0 | 0 | 10 | 0 0 | 0 | 0 | 15 | 0 | 00. | 5 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 |
| WAS16 | 0 | 0 | 1.5 | 0 | 0 | 25 | υ | U | 0 (|) (|) () | 0 | 0 | 7 | υ 0 | 0 | 0 | 0.5 | υ | υ |) O | 0 | 0 | 0 | 0 | υ Ο | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | υ Ο | 0 | 0 | 3 | 0 | 0 | U 0 | 0 | 0 |

| PLOT | Acer campestre | Acer platanoides | Acer pseudoplatanus | Alnus glutinosa | Alnus incana | Betula pendula | Betula pubescens | Betula spec | Carpinus betulus | Castanea sativa | Clematis vitalba | Cornus mas | Cornus sanguinea | Cornus spec | Crataegus laevigata | Crataegus monogyna | Crataegus spec | Euonymus europaeus | Fagus sylvatica | Frangula alnus | Fraxinus excelsior | Hedera helix | Humulus lupulus Ilex activitations | Ligustrum vulgare | Lonicera periclymenum | Lonicera xylosteum | Picea abies | Populus canescens | Populus tremula | Prunus avium | Prunus pagus Drunus cerotina | Prunus spinosa | Quercus cerris | Quercus petraea | Quercus pubescens | Quercus robur | Quercus rubra Ribes rubrum | Robinia pseudoacacia | Salix caprea | Sambucus nigra | Sambucus racemosa | Sorbus aria | Sorbus aucuparia | Sorbus torminalis | Staphylea pinnata | Tilia cordata | Tilia platyphyllos | Ulmus glabra Ulmus minor | |
|----------|----------------|------------------|---------------------|-----------------|--------------|----------------|------------------|-------------|------------------|-----------------|------------------|------------|------------------|-------------|---------------------|--------------------|----------------|--------------------|-----------------|----------------|--------------------|--------------|---------------------------------------|-------------------|-----------------------|--------------------|-------------|-------------------|-----------------|--------------|---------------------------------|----------------|----------------|-----------------|-------------------|---------------|-------------------------------|----------------------|--------------|----------------|-------------------|-------------|------------------|-------------------|-------------------|---------------|--------------------|-----------------------------|---|
| WPY1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 1 | 5 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 |) () | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 | - |
| WPY2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | .5 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| WPY3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 |).5 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| D C |) 3 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| WPY4 | 0 | 0 | 1.5 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0.5 | 0 | 0 | 0 | 0 10 | 0 (| 0 | 0 | 0 | 0 | 0 | 0 1 | 5 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 (| 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| WPY7 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| WR10 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| WR2 | 6.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 8. | 5 0 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| WR3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 0 0 | 0 | 0 | 0 | 0 | 25 | 0 2 | 25 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| WR4 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| WR5 | 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 65 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 00 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 00 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| WR6 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 30 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 | |
| WR7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | |
| WR8 | 0 | 0 | 1/ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 1 | 0 | 0 | 0 | 0 | 0 | 0 1 | 15 | 0 | | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| WK9 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | / | 0 2: | | 0 | 0 | 0 | 0 | 0 | 0 | | | | 0 | 0 | 0 | 0 | 0 | | | | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 40 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | | | | 0 | 0 | 0 | 0 | 0 | | | | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| VV VV 10 | 0 | 0 | 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | | 0 | 0 | 0 | 0 | 0 | | | | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| VV VV Z | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 60 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 0 | | | | 0 | 0 | 0 | 0 | 0 | | | | 0 | 0 | 0 | 0 | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| WW4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 70 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | 0 | 0 | 0 | 0 | 0 | 0 | | | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| WW5 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 50 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | | 0 | 0 | 0 | Ő | 0 | 0 | 0 0 | | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 45 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| WW6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| WW7 | 0 | 0 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 10 | 0 | 20 | 0 | 0 | 0 | - 0 6 | | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| ZVD16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0 | 3 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| ZVD29 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 63 | 0 | 0 | 0 | 0 | 0 0 |).5 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 | 0.5 | 8.5 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| ZVD31 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | o c | 0 | 0 | 2.5 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| ZVD33 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 06 | 60 | 0 | 0 | 0 | 0 | 0 7 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| o c | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| ZVG24 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0.5 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | o c | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | o c | 0 | 4.5 | 2.5 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| ZVG25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 12 | 0 | 0 | 0 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| D C | 0 (| 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 0 | |
| ZVG62 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 2 | 20 | 0 | 0 | 0 | 0 | 0 0. | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 (| 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |
| ZVY7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 65 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 (| 0 0 | 0 (| 0 | 0 | 0 | 0 | 0 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 0 | |

Appendix to Chapter 1

Appendix A2

[Chapter 2]

APPENDIX A2.1. LAND-USE AND MANAGEMENT CLASSIFICATION FOR

ALL 62 PLOTS

| Plot | 1983 management | 1993 management | 2014 management | Final management category | Infield/outl |
|-----------|----------------------|----------------------|----------------------|---------------------------|--------------|
| | (see Fig. A2.2.1 for | (see Fig. A2.2.1 for | (see Fig. A2.2.1 for | с с <i>,</i> | and |
| | definitions) | definitions) | definitions) | | |
| 76 | M2 | M0 | Managed | High | in |
| 65 | MO | MO | Managed | low | out |
| 113 | MO | MO | Managed | Low | in |
| 62 | MO | MO | Managed | Low | out |
| 30 | M2 | MO | Unmanaged | Low | in |
| 9 | MO | MO | Unmanaged | Low | in |
| 15 | MO | MO | Unmanaged | Low | in |
| 35 | MO | MO | Unmanaged | Low | out |
| 53 | MO | MO | Unmanaged | Low | in |
| 71 | MO | MO | Unmanaged | Low | out |
| 96 | MO | MO | Unmanaged | Low | in |
| 105 | MO | MO | Unmanaged | Low | in |
| 123 | MO | MO | Unmanaged | Low | in |
| 68 | MO | MO | Unmanaged | Low | in |
| 70 | MO | MO | Unmanaged | Low | in |
| 70 | MO | MO | Unmanaged | Low | out |
| 92 81 | MO | MO | Unmanaged | Low | in |
| 95 | MO | MO | Unmanaged | Low | in |
| 112 | MO | MO | Unmanaged | Low | in |
| 12/ | MO | MO | Unmanaged | Low | in |
| 125 | MO | MO | Unmanaged | Low | in |
| 67 | M2 | M1 | Managed | High | out |
| 120 | MO | | Managed | High | out |
| £0 | MO | | Unmanaged | low | in |
| 03 | MO | | Unmanaged | Low | in |
| 97 122 | IVIU MO | | Unmanaged | Low | in |
| 122 | IVIU MO | | Unmanaged | Low | in |
| 50 104 | IVIU MO | | Unmanaged | Low | 1/1 in |
| 104 | | | Unmanaged | LOW | 10 |
| 2 | IVIZ | IVIZ | Managed | High | out |
| 17 | IVIZ | IVIZ | Managed | High | out |
| 1/ | IVI2 | IVI2 | Managed | High | in in |
| 82 | IVIZ | IVIZ | Managed | High | in |
| 92 | IVIU M2 | M2 | ivianaged | High | out |
| 111 | M2 | M2 | Unmanaged | LOW | out |
| 11 | MO | M2 | Unmanaged | Low | in |
| 80 | MU | M2 | Unmanaged | LOW | in |
| 124 | MU | M2 | Unmanaged | Low | in |
| 120 | MO | M2 | Unmanaged | Low | in |
| 89 | M2 | M3 | Managed | High | out |
| 103 | M2 | M3 | Managed | High | out |
| 18 | M2 | M3 | Managed | High | in |
| 42 | M2 | M3 | Managed | High | out |
| 59 | M2 | M3 | Managed | High | in |
| /8 | M2 | M3 | Managed | High | out |
| 129 | M2 | M3 | Managed | High | out |
| 85 | MO | M3 | Managed | High | in |
| 86 | MO | M3 | Managed | High | in |
| 44 | M2 | M3 | Unmanaged | High | out |
| 128 | M2 | M3 | Unmanaged | High | in |
| 137 | M2 | M3 | Unmanaged | High | out |
| 45 | M2 | M3 | Unmanaged | High | out |
| 49 | M2 | M3 | Unmanaged | Low | out |
| 21 | M0 | M3 | Unmanaged | High | in |
| 90 | MO | M3 | Unmanaged | High | in |
| 79 | M0 | M3 | Unmanaged | High | in |
| 106 | MO | M3 | Unmanaged | High | in |

| Plot | 1983 management | 1993 management | 2014 management | Final management category | Infield/outl |
|------|----------------------|----------------------|----------------------|---------------------------|--------------|
| | (see Fig. A2.2.1 for | (see Fig. A2.2.1 for | (see Fig. A2.2.1 for | | and |
| | definitions) | definitions) | definitions) | | |
| 132 | M0 | M4 | Managed | High | out |
| 73 | MO | M4 | Managed | High | in |
| 47 | M0 | M4 | Unmanaged | High | in |
| 55 | M0 | M4 | Unmanaged | High | in |
| 140 | M0 | M5 | Unmanaged | High | out |
| 139 | M0 | M5 | Unmanaged | High | out |

APPENDIX A2.2. DETERMINING THE LEVEL OF RECENT MANAGEMENT INTENSITY FOR EACH PLOT

To characterize the recent management intensity level in each plot, we distinguished between plots that were more intensively disturbed over the period 1983-2014, and plots that were less intensively disturbed. We combined the different management classification approaches applied during the three surveys to reach a final management category, as shown schematically in **Fig. A2.2.1**.

During the 1983 survey, no field notes on management were taken. Hence, the 1983 classification was performed a posteriori, by the 1993 surveyor (Jörg Brunet), based on the following reasoning: As the canopy was relatively closed in almost all plots, I assume that plots that had been thinned within 10 years before sampling, only experienced a light thinning, corresponding ca. to class M2. That's why I classified plots as either M0 (= no management 1973-83) or M2 (possibly light thinning 1973-1978). I base some of the class 2 estimates on the fact that the planted oak stands have to be thinned regularly every 5-10 years according to good silvicultural practice. For many of the semi-natural stands, I assume no management during 1973-1983. This seems reasonable also because management activity in Swedish hardwood forest was generally low prior to 1984, when the Swedish Broadleaves Act was ratified.

In 1993, plots were classified based on observed canopy thinning and soil disturbance using a six-degree scale (Brunet et al., 1996).

In 2014, plots were again classified using a two-degree scale. Plots that seemed to be thinned less than 10 years before the survey were classified as *managed*, while plots where the last thinning took place more than 10 years ago were classified as *unmanaged*. Plots located in nature reserves were also classified as *unmanaged* in 2014. In our final decision on the management category of each plot (see **Fig. A2.2.1**), we gave the most weight to the 1993 classification, given its higher level of detail, and the least weight to the 1983 classification, given its high uncertainty. In November 2014, surveyors visited 35 of the 62 plots and made more detailed notes on management that confirmed the classifications reached here.

It should be noted that, although we used one overall management classification for the entire 1983-2014 period, there was an overall increase in management activity after the ratification of the *Swedish Broadleaves Act* in 1984, which prescribed that oak/hornbeam stands larger than 0.5 ha must not be converted to spruce, but regenerated with oak or other temperate hardwoods. After 1993, however, management activity decreased again due to changes in the Swedish forest policy that now gave more importance to the environmental goal of forests whereby biodiversity was to be secured and ecosystems conserved (Simonsson et al., 2015). While these overall temporal shifts in management intensity are not included in our management classification, it is important to keep them in mind during the interpretation and discussion of the results.



Figure A2.2.1. Management classification for each survey time, and decision scheme for the final overall management category that was applied in this study.



Figure A2.2.2. Differences in the number of stumps counted in 2014, between plots classified as 'High' and 'Low' managed, for a subset of 35 plots out of 62.

APPENDIX A2.3. DETAILS ON SOIL SAMPLING AND ANALYSES DURING OUR OWN SAMPLING CAMPAIGN IN 2014

We collected two mineral soil samples (0 - 5 cm) for chemical analyses in each plot (samples were taken from five locations in the plot, as shown in **Fig. A2.3.1**, and mixed) after removing the organic litter (OL), fragmentation (OF), and humus (OH) layers. One sample was stored in the freezer until analysis in the laboratory was possible, the other sample was dried at 40°C for 24 hours before analysis. We sieved all samples with a 2 mm sieve before analysis.

For analyzing pH_{KCl} , 10 g of the fresh soil was extracted using 50 mL 0.2 M KCl, shaken for two hours and measured after sedimentation with a pH meter Orion 920A with pH electrode model Ross sure-flow 8172 BNWP, Thermo Scientific Orion, USA. For all other chemical analyses of the soil, we used the dried soil samples. All P-concentrations were measured colorimetrically according to the malachite green procedure (Lajtha et al., 1999). Total P was extracted after complete destruction of the soil samples with HClO4 (65%), HNO3 (70%) and H2SO4 (98%) in teflon bombs for 4 h at 150°C. Bioavailable or Olsen P, which is available for plants within one growing season (Gilbert et al., 2009), was extracted in NaHCO3 (POlsen; according to ISO 195 11263:1994(E)). Total C (%) and N (%) concentration was quantified by combusting samples at 1150°C which releases all C and N and then measuring the combustion gases for thermal conductivity in a CNS elemental analyser (vario Macro Cube, Elementar, Germany).



Figure A2.3.1. The five locations within the 20x20 m² plot where we took a soil sample to obtain a representative mixed-soil sample.

APPENDIX A2.4. SOIL DATA FOR 1983 AND 2014

Table A2.4.1. t-tests to compare soil variables (0 - 5 cm depth) between former infield and former outfield plots. For both plot groups, the mean value and standard error (se) are given, as well as the degrees of freedom (df), the t-statistic and the p-value.

| | Infield (n=39) (mean ± se) | Outland (n=23) (mean ± se) | df | t-statistic | p-value |
|-----------------|-------------------------------|-------------------------------|----|-------------|---------|
| 1983 | (| (| | | |
| Clay (%) | 3.16 ± 0.56 | 1.58 ± 0.25 | 60 | 2.08 | 0.041 |
| pH (KCl) | 3.73 ± 0.06 | 3.56 ± 0.08 | 60 | 1.73 | 0.089 |
| 2014 | | | | | |
| Total C (%) | 5.89 ± 0.36 | 5.02 ± 0.27 | 60 | 1.70 | 0.095 |
| Total N (%) | 0.43 ± 0.03 | 0.37±0.02 | 60 | 1.64 | 0.106 |
| Total P (mg/kg) | 541.16 ± 20.8 | 439.13 ± 39.2 | 60 | 2.53 | 0.014 |

Table A2.4.2. t-tests to compare soil variables (0 - 5 cm depth) between plots with high and low management intensity. For both plot groups, the mean value and standard error (se) are given, as well as the degrees of freedom (df), the t-statistic and the p-value.

| | High intensity management (n=31) (mean ± se) | Low intensity management (n=31) (mean ± se) | df | t-statistic | p-value |
|-----------------|--|---|----|-------------|---------|
| 1983 | | | | | |
| Clay (%) | 2.22 ± 0.36 | 2.93 ± 0.66 | 60 | -0.94 | 0.351 |
| pH (KCl) | 3.54 ± 0.06 | 3.79 ± 0.07 | 60 | -2.70 | 0.009 |
| 2014 | | | | | |
| Total C (%) | 5.70 ± 0.35 | 5.43 ± 0.37 | 60 | 0.53 | 0.600 |
| Total N (%) | 0.41 ± 0.02 | 0.40 ± 0.03 | 60 | 0.21 | 0.832 |
| Total P (mg/kg) | 454.59 ± 28.9 | 552.03 ± 26.3 | 60 | -2.49 | 0.015 |

APPENDIX A2.5. SHADE-CASTING ABILITY SCORES

Table A2.5.1. Shade-casting ability (SCA) scores (1: very low shade-casting ability; 5: very high shade-casting ability) for tree and shrub species in the canopy layer, adapted from Ellenberg (1996) and complemented with expert knowledge of prof. Kris Verheyen.

| Species | SCA | Species | SCA | |
|----------------------|-----|--------------------|-----|--|
| Acer campestre | 3 | Tilia cordata | 4 | |
| Acer platanoides | 4 | Tilia platyphyllos | 4 | |
| Acer pseudoplatanus | 4 | Ulmus glabra | 4 | |
| Alnus glutinosa | 3 | Ulmus laevis | 3 | |
| Alnus incana | 3 | Ulmus minor | 3 | |
| Betula pendula | 1 | Ulmus procera | 3 | |
| Betula pubescens | 1 | Ulmus spp. | 3 | |
| Betula spp. | 1 | | | |
| Carpinus betulus | 5 | | | |
| Castanea sativa | 3 | | | |
| Cornus mas | 2 | | | |
| Cornus sanguinea | 2 | | | |
| Corylus avellana | 3 | | | |
| Fagus sylvatica | 5 | | | |
| Fraxinus excelsior | 3 | | | |
| Larix decidua | 1 | | | |
| Larix spp. | 1 | | | |
| Picea abies | 4 | | | |
| Pinus sylvestris | 1 | | | |
| Populus alba | 2 | | | |
| Populus canescens | 2 | | | |
| Populus spp. | 2 | | | |
| Populus tremula | 2 | | | |
| Populus x canadensis | 2 | | | |
| Prunus avium | 3 | | | |
| Prunus padus | 3 | | | |
| Quercus petraea | 3 | | | |
| Quercus robur | 2 | | | |
| Quercus rubra | 3 | | | |
| Quercus spp. | 2.5 | | | |
| Quercus x rosacea | 2.5 | | | |
| Robinia pseudoacacia | 3 | | | |
| Salix alba | 2 | | | |
| Salix caprea | 2 | | | |
| Sambucus nigra | 3 | | | |
| Sorbus aria | 2 | | | |
| Sorbus aucuparia | 2 | | | |
| Sorbus domestica | 2 | | | |
| Sorbus torminalis | 2 | | | |

APPENDIX A2.6. SHADE-CASTING ABILITY OF THE TREE LAYER



Figure A2.6.1. Comparison between shade-casting abilities of the tree layer for the four different plot categories, based on their management intensity (high/low) and past land use (infield/outland), and given for each of the three survey years (1983, 1993 and 2014).

APPENDIX A2.7. VEGETATION DATA MANIPULATION

Impact of grouping herb and shrub layer into understorey layer

In 2014, surveyors distinguished three vegetation layers: the tree layer containing all woody species above 5 m, the shrub layer, containing the woody species with a height between 0.5 and 5 m, and the herb layer containing all non-woody vascular plants and the woody species below 0.5 m. However, in 1983 and 1993, surveyors only distinguished between the understorey, comprising all vascular plants below 5 m height, and the canopy, comprising all vascular plants above 5 m height. Therefore, we only considered these two layers, and transformed the 2014 dataset to this standard. We used pairwise t-tests to check whether the relevant response variables (i.e. Shannon diversity, Bray-Curtis dissimilarity, Ellenberg N and L values) in 2014 were significantly different when based on either the entire understorey (i.e. everything < 5 m), or the strict herb layer (< 0.5 m). We only found significant differences for Ellenberg L values (**Table A2.7.1**), but these differences were very small (-0.07 units of Ellenberg L when looking at the strict herb layer instead of the entire understorey), and therefore we assumed that the grouping of the herb and shrub layer in the 2014 dataset will have a negligible impact on the results of our analyses.

| 2014 | | Based on strict herb layer (< 0.5m) (mean ± se) | Based on understorey (< 5m) (mean ± se) | df | t | p-value |
|--------------------------|------------------------------|---|---|----|-------|----------|
| Understorey diversity | Shannon diversity | 1.97 ± 0.08 | 1.99 ± 0.07 | 61 | -0.37 | 0.715 |
| | Bray-Curtis dissimilarity | 0.84 ± 0.01 | 0.86 ± 0.01 | 61 | -0.17 | 0.864 |
| Soil conditions | Ellenberg N | 4.93 ± 0.10 | 4.92 ± 0.11 | 61 | 0.90 | 0.371 |
| Light conditions | Ellenberg_L | 4.95 ± 0.07 | 5.02 ± 0.07 | 61 | -5.33 | 0.000*** |

Table A2.7.1. Results of pairwise t-test to compare the 2014 response variables, based on either the strict herb layer or the understorey

Results with Corylus avellana in the understorey

An exceptional case in the 2014 dataset was the species *Corylus avellana*, which was always treated as a shrub species if it was higher than 0.5 m. Hence, even when the individual was higher than 5 m, it was not added to the tree layer, which resulted in the entire cover of *C. avellana* being regarded as understorey in the 2014 dataset. As the species often creates a shading canopy in the study plots, we expect it to be more closely related to trees, in terms of its effect on the understorey composition and dynamics. Therefore, we decided to arbitrarily move all *C. avellana* in the entire dataset (1983, 1993 and 2014) to the tree layer, rather than the understorey. To check whether this decision had a big impact on the results, we repeated our analyses with a dataset where *C. avellana* was in the understorey. We concluded that the effect on the results was minor (**Fig. A2.7.1, A2.7.2** and **A2.7.3**; **Tables A2.7.2** and **A2.7.3**).

Table A2.7.2. Plot characteristics in 1983, at the beginning of the sampling period. Mean values and standard errors are shown for the plots on former infields and outland. The last three columns contain the degrees of freedom (df), the t-statistic and the p-value of the Welch Two Sample t-test that was performed to check whether the differences between infield and outland plots were significant. All results are based on the dataset where Corylus avellana is part of the understorey.

| | | Infield (n=39) | Outland (n=23) | df | t-statistic | p- |
|--------------------------|------------------------------|----------------|-----------------|-------|-------------|--------|
| | | (mean ± se) | (mean ± se) | ui | t-statistic | value |
| Understorey diversity | Shannon diversity | 2.10 ± 0.08 | 1.97 ± 0.09 | 49.44 | 1.09 | 0.280 |
| | Bray-Curtis dissimilarity | 0.81 ± 0.01 | 0.82 ± 0.01 | 47.47 | -1.06 | 0.294 |
| Soil conditions | Ellenberg N | 4.97 ± 0.16 | 4.40 ± 0.18 | 53.00 | 2.36 | 0.022* |
| Light conditions | Ellenberg L | 5.03 ± 0.09 | 5.22 ± 0.11 | 48.70 | -1.40 | 0.168 |



Figure A2.7.1. Temporal changes in mean values of the four response variables representing understorey diversity and composition. The level of recent disturbance by forest management is indicated by the line color (red = high; blue = low), while the past land use category is indicated by the line type (continuous = infield; dotted = outland). Below each figure, the significant predictors that were retained in the final model are shown, with their level of significance ('***' for p < 0.001; '**' for p < 0.01; '*' for p < 0.0.5). Interactions between predictors are indicated with ':'. All results are based on the dataset where Corylus avellana is part of the understorey.


Figure A2.7.2. NMDS of understorey composition for each survey year. In the upper row, red dots represent former infield plots and the species in red are the indicator species of infield plots; blue dots represent former outland plots and the species in blue are the indicator species of outland plots. In the lower row, red dots represent plots with high levels of management intensity and their respective indicator species are shown in red; blue dots represent plots with low levels of management intensity and their respective indicator species are shown in blue. The arrows indicate the variables characterizing the soil and overstorey of the plots, i.e. soil pH, soil clay and total P content, tree cover, and shade-casting ability. All results are based on the dataset where Corylus avellana is part of the understorey.

Appendix to Chapter 2

Table A2.7.3. Linear mixed effect modelling results for the four response variables representing understorey diversity and composition. PLU = Past Land Use; RM = Recent Management. For each response variable, the estimates, standard errors (se) and p-values are given for the predictors that were retained in the optimal model. For each optimal model, the marginal and conditional R^2 (R^2m and R^2c respectively) are also given. All results are based on the dataset where Corylus avellana is part of the understorey.

| UNDERSTOREY DIVERS | ITY | | | | | |
|--------------------|-----------|-----------|-----------|-----------|------------|------------|
| | Shannon | diversity | | Bray-Curt | is dissimi | larity |
| | estimate | SE | p-value | estimate | SE | p-value |
| PLU | - | - | - | - | - | - |
| RM | - | - | - | - | - | - |
| Year(1993) | 0.251 | 0.070 | 0.0005*** | 0.002 | 0.005 | 0.7462 |
| Year(2014) | -0.156 | 0.070 | 0.0279* | 0.041 | 0.005 | 0.0000**** |
| PLU:RM | - | - | - | - | - | - |
| Year(1993): PLU | - | - | - | - | - | - |
| Year(2014): PLU | - | - | - | - | - | - |
| Year(1993): RM | - | - | - | - | - | - |
| Year(2014): RM | - | - | - | - | - | - |
| | | | | | | |
| | R²m | R²c | | R²m | R²c | |
| | 0.10 | 0.48 | | 0.183 | 0.645 | |
| PLANT COMMUNITY D | ESCRIPTOR | S | | | | |
| | Ellenberg | Ν | | Ellenberg | L | |
| | estimate | SE | p-value | estimate | SE | p-value |
| PLU | -0.457 | 0.222 | 0.0437* | -0.139 | 0.163 | 0.3950 |
| RM | - | - | - | -0.369 | 0.149 | 0.0160* |
| Year(1993) | 0.068 | 0.062 | 0.2722 | 0.131 | 0.043 | 0.0029** |
| Year(2014) | 0.167 | 0.062 | 0.0077** | -0.046 | 0.043 | 0.2850 |
| PLU:RM | - | - | - | 0.606 | 0.253 | 0.0201* |
| Year(1993): PLU | - | - | - | - | - | - |
| Year(2014): PLU | - | - | - | - | - | - |

R²c

0.79

R²m

0.13

Year(1993): RM Year(2014): RM

-

R²m

0.06

_

R²с

0.86



Figure A2.7.3. (a) Mean and standard error of the NMDS-coordinates for each survey year and for each plot category (resulting in 12 possible combinations of year, past land use and recent management level). The level of recent disturbance by forest management is indicated by the line colour (red = high; blue = low), while the past land use category is indicated by the line type (continuous = infield; dotted = outland). The black arrows visualize the trajectories of the understorey compositions over time. (b) Correlation of relevant plot characteristics (orange arrows: soil clay and total P content, soil pH, cover and shade-casting ability (SCA) of the tree layer) and community descriptors (green arrows: mean Ellenberg N and L values) with the plot positions on the NMDS ordination figure. The length of the arrows indicates the degree of correlation. All results are based on the dataset where Corylus avellana is part of the understorey.

APPENDIX A2.8. AIC MODEL COMPARISON RESULTS

Table A2.8.1. Results of the model comparison based on Akaike's Information Criterion (AIC). The left column indicates which explanatory variables and interactions are included in the model, next to Plot ID as a random intercept (always included). In the column 'delta', the difference between the model's AIC value and the lowest AIC value of all models is shown. The model with the lowest AIC (delta = 0) can be considered the most optimal model. Abbreviations: SHAN = Shannon diversity; BRAY = Bray-Curtis dissimilarity; PLU = Past land use; RM = Recent management

| | SHAN | | BRAY | | Ellenberg L | | Ellenberg N | |
|--------------------------------------|-------|-------|--------|-------|-------------|-------|-------------|-------|
| | AIC | delta | AIC | delta | AIC | delta | AIC | delta |
| ~1 | 269.1 | 21.2 | -629.6 | 67.6 | 185.0 | 16.7 | 336.8 | 3.9 |
| ~PLU | 270.1 | 22.2 | -628.0 | 69.2 | 185.3 | 17.0 | 334.9 | 2.0 |
| ~RM | 271.1 | 23.3 | -628.0 | 69.3 | 184.4 | 16.1 | 335.1 | 2.2 |
| ~PLU+RM | 272.1 | 24.3 | -626.7 | 70.6 | 185.7 | 17.4 | 334.9 | 2.0 |
| ~Year | 247.8 | 0.0 | -697.3 | 0.0 | 171.0 | 2.7 | 334.8 | 1.9 |
| ~Year+PLU | 248.9 | 1.0 | -695.6 | 1.7 | 171.3 | 3.0 | 332.9 | 0.0 |
| ~Year+RM | 249.9 | 2.1 | -695.5 | 1.7 | 170.5 | 2.2 | 333.1 | 0.2 |
| ~Year+PLU+RM | 251.0 | 3.2 | -694.3 | 3.0 | 171.8 | 3.5 | 333.0 | 0.0 |
| ~PLU+RM+PLU:RM | 274.1 | 26.2 | -625.7 | 71.6 | 182.2 | 13.9 | 336.0 | 3.1 |
| ~Year+PLU+RM+PLU:RM | 253.0 | 5.2 | -693.2 | 4.1 | 168.3 | 0.0 | 334.1 | 1.2 |
| ~PLU+Year+PLU:Year | 251.2 | 3.4 | -693.2 | 4.1 | 173.6 | 5.3 | 333.9 | 0.9 |
| ~PLU+RM+Year+PLU:Year | 253.4 | 5.6 | -691.7 | 5.5 | 174.2 | 5.9 | 334.0 | 1.0 |
| ~PLU+RM+Year+PLU:Year+PLU:RM | 255.5 | 7.6 | -690.6 | 6.7 | 170.7 | 2.4 | 335.2 | 2.3 |
| ~RM+Year+RM:Year | 253.0 | 5.2 | -694.3 | 3.0 | 173.8 | 5.5 | 335.0 | 2.1 |
| ~PLU+RM+Year+RM:Year | 254.2 | 6.3 | -693.0 | 4.3 | 175.1 | 6.8 | 334.9 | 2.0 |
| ~PLU+RM+Year+RM:Year+PLU:RM | 256.2 | 8.4 | -691.8 | 5.4 | 171.7 | 3.4 | 336.1 | 3.2 |
| ~PLU+RM+Year+RM:Year+PLU:Year | 256.1 | 8.3 | -689.3 | 8.0 | 178.3 | 10.0 | 336.3 | 3.4 |
| ~PLU+RM+Year+RM:Year+PLU:Year+PLU:RM | 258.2 | 10.4 | -688.1 | 9.1 | 174.9 | 6.6 | 337.5 | 4.6 |

APPENDIX A2.9. BACKWARDS MODEL SELECTION FOR EACH YEAR

SEPARATELY

Table A2.9.1. Linear mixed effect modelling results for each survey year and for the four response variables representing understorey diversity and composition. PLU = Past Land Use; RM = Recent Management. For each response variable, the estimates, standard errors (se) and p-values are given for the predictors that were retained in the optimal model. For each optimal model, the marginal and conditional R^2 (R^2m and R^2c respectively) are also given.

| Shannon di | versity | | | | | | | | |
|--------------------|-----------|-------|---------|----------|-------|---------|----------|-------|---------|
| | 1983 | | | 1993 | | | 2014 | | |
| | estimate | SE | p-value | estimate | SE | p-value | estimate | SE | p-value |
| PLU | - | - | - | - | - | - | - | - | - |
| RM | - | - | - | - | - | - | - | - | - |
| PLU:RM | - | - | - | - | - | - | - | - | - |
| | | | | | | | | | |
| | R²m | R²c | | R²m | R²c | | R²m | R²c | |
| | 0 | 0.88 | | 0 | 0.88 | | 0 | 0.88 | |
| Bray-Curtis | dissimila | rity | | | | | | | |
| | 1983 | | | 1993 | | | 2014 | | |
| | estimate | SE | p-value | estimate | SE | p-value | estimate | SE | p-value |
| PLU | - | - | - | - | - | - | - | - | - |
| RM | - | - | - | - | - | - | - | - | - |
| PLU:RM | - | - | - | - | - | - | - | - | - |
| | | | | | | | | | |
| | R²m | R²c | | R²m | R²c | | R²m | R²c | |
| | 0 | 0.88 | | 0 | 0.88 | | 0 | 0.88 | |
| Ellenberg N | I | | | | | | | | |
| | 1983 | | | 1993 | | | 2014 | | |
| | estimate | SE | p-value | estimate | SE | p-value | estimate | SE | p-value |
| PLU | -0.567 | 0.252 | 0.0281 | - | - | - | - | - | - |
| RM | - | - | - | - | - | - | 0.390 | 0.197 | 0.0528 |
| PLU:RM | - | - | - | - | - | - | - | - | - |
| | | | | | | | | | |
| | R²m | R²c | | R²m | R²c | | R²m | R²c | |
| | 0.08 | 0.89 | | 0 | 0.88 | | 0.06 | 0.88 | |
| Ellenberg L | | | | | | | | | |
| | 1983 | | | 1993 | | | 2014 | | |
| | estimate | SE | p-value | estimate | SE | p-value | estimate | SE | p-value |
| PLU | -0.108 | 0.185 | 0.5612 | -0.131 | 0.161 | 0.4157 | - | - | - |
| RM | -0.376 | 0.169 | 0.0301 | -0.414 | 0.147 | 0.0067 | - | - | - |
| PLU:RM | 0.600 | 0.288 | 0.0413 | 0.669 | 0.250 | 0.0097 | - | - | - |
| | | | | | | | | | |
| | R²m | R²c | | R²m | R²c | | R²m | R²c | |
| | 0.11 | 0.89 | | 0.17 | 0.90 | | 0 | 0.88 | |

APPENDIX A2.10. DETAILS OF LINEAR MIXED EFFECT MODELLING

RESULTS FOR THE FOUR RESPONSE VARIABLES

Table A2.10.1. Linear mixed effect modelling results for the four response variables representing understorey diversity and composition. PLU = Past Land Use; RM = Recent Management. For each response variable, the estimates, standard errors (se) and p-values are given for the predictors that were retained in the optimal model. For each optimal model, the marginal and conditional R^2 (R^2m and R^2c respectively) are also given.

| Understorey diversity | | | | | | |
|-----------------------|--|---|--|---|---|--|
| Shanno | Shannon diversity | | | Bray-Curtis dissimilarity | | |
| estimate | SE | p-value | estimate | SE | p-value | |
| - | - | - | - | - | - | |
| - | - | - | - | - | - | |
| 0.269 | 0.068 | 0.0001 | 0.000 | 0.005 | 0.9196 | |
| -0.069 | 0.068 | 0.3115 | 0.042 | 0.005 | <0.0001 | |
| - | - | - | - | - | - | |
| - | - | - | - | - | - | |
| - | - | - | - | - | - | |
| - | - | - | - | - | - | |
| - | - | - | - | - | - | |
| R²m | R²c | | R²m | R²c | | |
| 0.08 | 0.48 | | 0.17 | 0.67 | | |
| | rsity Shanno estimate - - 0.269 -0.069 - - - - - - R ² m 0.08 | Shannon diversi estimate SE - - - - 0.269 0.068 -0.069 0.068 - - - - | Shannon diversity estimate SE p-value - - - - - - - - - 0.269 0.068 0.0001 -0.069 0.068 0.3115 - - - - - </td <td>Shannon diversity Bray-Cu estimate SE p-value estimate - - - - - - - - - - - - - - - - 0.269 0.068 0.0001 0.000 -0.069 0.068 0.3115 0.042 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -</td> <td>Shannon diversity Bray-Curtis dissi estimate SE p-value estimate SE - - - - - - - - - - - - - - - 0.269 0.068 0.0001 0.000 0.005 -0.069 0.068 0.3115 0.042 0.005 - - - - - - - - - - -0.069 0.068 0.3115 0.042 0.005 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -<</td> | Shannon diversity Bray-Cu estimate SE p-value estimate - - - - - - - - - - - - - - - - 0.269 0.068 0.0001 0.000 -0.069 0.068 0.3115 0.042 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - | Shannon diversity Bray-Curtis dissi estimate SE p-value estimate SE - - - - - - - - - - - - - - - 0.269 0.068 0.0001 0.000 0.005 -0.069 0.068 0.3115 0.042 0.005 - - - - - - - - - - -0.069 0.068 0.3115 0.042 0.005 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -< | |

Plant community descriptors

| | Fllenber | σN | | Fllenber | σl | |
|-----------------|----------|----------|---------|----------|------------|---------|
| | | в | nualua | | 6 - | n value |
| | estimate | SE | p-vuiue | estimate | SE | p-value |
| PLU | -0.461 | 0.230 | 0.0498 | -0.133 | 0.167 | 0.4279 |
| RM | - | - | - | -0.375 | 0.153 | 0.0174 |
| Year(1993) | 0.067 | 0.064 | 0.2971 | 0.140 | 0.045 | 0.0023 |
| Year(2014) | 0.160 | 0.064 | 0.0139 | -0.051 | 0.045 | 0.2582 |
| PLU:RM | - | - | - | 0.613 | 0.260 | 0.0219 |
| Year(1993): PLU | - | - | - | - | - | - |
| Year(2014): PLU | - | - | - | - | - | - |
| Year(1993): RM | - | - | - | - | - | - |
| Year(2014): RM | - | - | - | - | - | - |
| | | | | | | |
| | R²m | R²c | | R²m | R²c | |
| | 0.06 | 0.86 | | 0.13 | 0.79 | |

APPENDIX A2.11. INDICATOR SPECIES ANALYSIS

Table A2.11.1. Indicator species per plot category and per year. For each set of indicator species, the mean Ellenberg indicator values for nutrients (N) and light (L) are shown, as well as their proportion of the understorey cover within the plot category. For the mean Ellenberg indicator values, t-tests were conducted to check for significant differences between contrasting plot categories (i.e. infield vs. outland in the upper row, and high vs. low management intensity in the lower row). Significant differences (alpha < 0.05) are indicated with '*'.

| 1983 | | 19 | 93 | 2014 | | |
|---|---|--|--|---|---|--|
| Infield | Outland | Infield | Outland | Infield | Outland | |
| Acer platanoides | Agrostis capillaris | Aegopodium podagraria | Acer pseudoplatanus | Convallaria majalis | Acer pseudoplatanus | |
| Aegopodium podagraria | Carex pilulifera | Convallaria majalis | Carex pilulifera | Mercurialis perennis | Athyrium filix-femina | |
| Anthriscus sylvestris | Dryopteris carthusiana | Hepatica nobilis | Dryopteris carthusiana | Poa nemoralis | Avenella flexuosa | |
| Convallaria majalis | Juncus effusus | Poa nemoralis | Festuca ovina | Stellaria media | Betula pendula | |
| Poa nemoralis | Juniperus communis | Rubus saxatilis | Fraxinus excelsior | Tilia cordata | Hypericum perforatum | |
| Rubus saxatilis | Lysimachia europaea | Tilia cordata | Juncus effusus | | Luzula pilosa | |
| Silene dioica | Rubus idaeus | | Ribes uva-crispa | | Picea abies | |
| | Veronica officinalis | | Salix caprea | | | |
| Mean Ellenberg N = 6.14* | Mean Ellenberg N = 3.71* | Mean Ellenberg N = 4.83 | Mean Ellenberg N = 4.43 | Mean Ellenberg N = 5.60 | Mean Ellenberg N = 4.00 | |
| Mean Ellenberg L = 5.67 | Mean Ellenberg L = 6.38 | Mean Ellenberg L = 5.33 | Mean Ellenberg L = 5.50 | Mean Ellenberg L = 4.80 | Mean Ellenberg L = 4.86 | |
| % of total cover = 13.4 % | % of total cover = 6.68 % | % of total cover = 9.45 % | % of total cover = 2.21 % | % of total cover = 14.5 % | % of total cover = 13.3 % | |
| | | | | | | |
| High | Low | High | Low | High | Low | |
| High Betula pendula | Low Aegopodium podagraria | High Acer pseudoplatanus | Low Anthriscus sylvestris | High Acer pseudoplatanus | Low Melica nutans | |
| High Betula pendula Dryopteris carthusiana | Low Aegopodium podagraria Acer platanoides | High Acer pseudoplatanus Betula pendula | Low Anthriscus sylvestris Hepatica nobilis | High Acer pseudoplatanus Betula pubescens | Low Melica nutans Mercurialis perennis | |
| High Betula pendula Dryopteris carthusiana Fagus sylvatica | Low Aegopodium podagraria Acer platanoides Hepatica nobilis | High Acer pseudoplatanus Betula pendula Juncus effusus | Low Anthriscus sylvestris Hepatica nobilis Melica nutans | High Acer pseudoplatanus Betula pubescens Carex pilulifera | Low Melica nutans Mercurialis perennis Tilia cordata | |
| High Betula pendula Dryopteris carthusiana Fagus sylvatica | Low Aegopodium podagraria Acer platanoides Hepatica nobilis Melica nutans | High Acer pseudoplatanus Betula pendula Juncus effusus Stellaria holostea | Low Anthriscus sylvestris Hepatica nobilis Melica nutans Mercurialis perennis | High Acer pseudoplatanus Betula pubescens Carex pilulifera | Low Melica nutans Mercurialis perennis Tilia cordata | |
| High Betula pendula Dryopteris carthusiana Fagus sylvatica | Low Aegopodium podagraria Acer platanoides Hepatica nobilis Melica nutans Mercurialis perennis | High Acer pseudoplatanus Betula pendula Juncus effusus Stellaria holostea Taraxacum vulgare | Low Anthriscus sylvestris Hepatica nobilis Melica nutans Mercurialis perennis Prunus padus | High Acer pseudoplatanus Betula pubescens Carex pilulifera | Low Melica nutans Mercurialis perennis Tilia cordata | |
| High Betula pendula Dryopteris carthusiana Fagus sylvatica | Low Aegopodium podagraria Acer platanoides Hepatica nobilis Melica nutans Mercurialis perennis Polygonatum multiflorum | High Acer pseudoplatanus Betula pendula Juncus effusus Stellaria holostea Taraxacum vulgare | Low Anthriscus sylvestris Hepatica nobilis Melica nutans Mercurialis perennis Prunus padus Rubus saxatilis | High Acer pseudoplatanus Betula pubescens Carex pilulifera | Low Melica nutans Mercurialis perennis Tilia cordata | |
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| High Betula pendula Dryopteris carthusiana Fagus sylvatica | Low Aegopodium podagraria Acer platanoides Hepatica nobilis Melica nutans Mercurialis perennis Polygonatum multiflorum Rubus saxatilis Scrophularia nodosa Ulmus glabra | High Acer pseudoplatanus Betula pendula Juncus effusus Stellaria holostea Taraxacum vulgare | Low Anthriscus sylvestris Hepatica nobilis Melica nutans Mercurialis perennis Prunus padus Rubus saxatilis Ulmus glabra | High Acer pseudoplatanus Betula pubescens Carex pilulifera | Low Melica nutans Mercurialis perennis Tilia cordata | |
| High Betula pendula Dryopteris carthusiana Fagus sylvatica Mean Ellenberg N = 3 | Low Aegopodium podagraria Acer platanoides Hepatica nobilis Melica nutans Mercurialis perennis Polygonatum multiflorum Rubus saxatilis Scrophularia nodosa Ulmus glabra Mean Ellenberg N = 5.78 | High Acer pseudoplatanus Betula pendula Juncus effusus Stellaria holostea Taraxacum vulgare Mean Ellenberg N = 4.50 | Low Anthriscus sylvestris Hepatica nobilis Melica nutans Mercurialis perennis Prunus padus Rubus saxatilis Ulmus glabra Mean Ellenberg N = 5.57 | High Acer pseudoplatanus Betula pubescens Carex pilulifera Mean Ellenberg N = 3.00 | Low Melica nutans Mercurialis perennis Tilia cordata Mean Ellenberg N = 5.00 | |
| High Betula pendula Dryopteris carthusiana Fagus sylvatica Mean Ellenberg N = 3 Mean Ellenberg L = 5 | Low Aegopodium podagraria Acer platanoides Hepatica nobilis Melica nutans Mercurialis perennis Polygonatum multiflorum Rubus saxatilis Scrophularia nodosa Ulmus glabra Mean Ellenberg N = 5.78 Mean Ellenberg L = 4 | High Acer pseudoplatanus Betula pendula Juncus effusus Stellaria holostea Taraxacum vulgare Mean Ellenberg N = 4.50 Mean Ellenberg L = 6.00 | Low Anthriscus sylvestris Hepatica nobilis Melica nutans Mercurialis perennis Prunus padus Rubus saxatilis Ulmus glabra Mean Ellenberg N = 5.57 Mean Ellenberg L = 4.71 | High Acer pseudoplatanus Betula pubescens Carex pilulifera Mean Ellenberg N = 3.00 Mean Ellenberg L = 5.33 | Low Melica nutans Mercurialis perennis Tilia cordata Mean Ellenberg N = 5.00 Mean Ellenberg L = 3.67 | |

Appendix A3

[Chapter 3]

APPENDIX A3.1. PLOT RELOCATION

| Bialowieza, PL X X X Photographs Bi Bialowieza, PL X X X Photographs Bi Bianschweig, GE X X X X BW Binnen- X X X X CO Compisene, FR X X X Info on topography DE Devin, CZ X X X Info on topography GO Göttingen, GE X X X Info on topography GO Göttingen, GE X X X Info on topography GO Moda, CZ X X X Info on topography IF Lyons-la-forêt, FR X X X X MO Moricsala, LV X X X X SH Schleswig X X X X SK Slowak Karst, SK X X X X X SW Wales, UK X X X X X SW Wales, UK X X X X X SW Wales, UK X X X X X | ID | Region, Country | Permanent | Coordinates | Maps | Schemes | Canopy | Textual | Other |
|--|-------|--------------------|-----------|-------------|------|---------|-------------|-------------|------------------|
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| IB Tournibus, BE X X W Wales, UK X X WR Warburg Reserve, UK X X WW Wytham Woods, UK X X ZV Zvolen, SK X X X X Info on topography | 5P | Speulderbos, NL | | | X | X | X | | |
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| WR Warburg Reserve, UK X WW Wytham Woods, UK X ZV Zvolen, SK X X X Info on topography | W | Wales, UK | | | X | | | | |
| WW Wytham Woods, UK X ZV Zvolen, SK X X X Info on topography | WR | warburg Reserve, | Х | | | | | | |
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| | 7\/ | | v | | v | | v | v | Info on |
| | 2.0 | LVUICH, SK | ^ | | ^ | | ~ | ^ | topography |

APPENDIX A3.2. VEGETATION DATA: STANDARDIZING LAYER DEFINITIONS AND COVER SCALES

WW & WR – Wytham Woods & Warburg reserve

| Layers | yers Definition Ab | | Abundance estimates per species | | |
|--------|--------------------|---|------------------------------------|---|---|
| Old | New | Old | New | Old | New |
| Tree | Tree | >2.5 m | >2.5 m | Cover % estimate along the diagonal of the plot | Cover % estimate along the diagonal of the plot |
| Shrub | Shrub | 0.5-2.5 m | 0.5-2.5 m | NO: only total cover (%) along the diagonal of the plot | NO: only total cover (%) along the diagonal of the plot |
| Herb | Herb | 0-0.5 m; no woody species included (no seedlings) | 0-0.5 m; including seedlings | measured as frequency in 13 circlets (0.1 m ² circular quadrats) across the diagonals → see conversion table | Cover (%) estimate in the whole plot |

Conversion table:

| Frequency recorded in original survey | Assumed cover (%) |
|---------------------------------------|-------------------|
| 0 and not present in the 10x10 plot | 0 |
| 0 (but present in the 10x10 plot) | 0.5 |
| 1 | 3.8 |
| 2 | 11.5 |
| 3 | 19.2 |
| 4 | 26.9 |
| 5 | 34.6 |
| 6 | 42.3 |
| 7 | 50 |
| 8 | 57.7 |
| 9 | 65.4 |
| 10 | 73.1 |
| 11 | 80.8 |
| 12 | 88.5 |
| 13 | 96.2 |

LF - Lyons-la-forêt

| Layers | | Definition | | Abundance estimates p | per species |
|--------|-------|--|--|---|--|
| Old | New | Old | New | Old | New |
| Tree | Tree | canopy trees and dominated trees (>7m) | canopy trees and dominated trees (>7m) | Braun-Blanquet scale → see conversion table | Cover (%) estimate in the whole plot |
| Shrub | Shrub | 1-7 m | 1-7 m | Braun-Blanquet scale → see conversion table | Cover (%) estimate in the whole plot |
| Herb | Herb | herbaceous layer including undershrub and young saplings (<1m) | herbaceous layer including undershrub and young saplings (<1m) | Braun-Blanquet scale → see conversion table | Cover (%) estimate in the whole plot |

Conversion table:

| Braun-Blanquet | Assumed cover (%) |
|----------------|-------------------|
| r | 0.5* |
| + | 0.5 |
| 1 | 3 |
| 2 | 15 |
| 3 | 37.5 |
| 4 | 62.5 |
| 5 | 87.5 |

TB - Tournibus

| Layers | | Definition | | Abundance estimates per species | | |
|--------|-------|--|--|--|----------------------|--|
| Old | New | Old | New | Old | New | |
| Tree | Tree | >7m (except Corylus avellana) | >7m (except Corylus avellana) | Cover (%) in plot (except for plot TB115B: only presence/absence data) | Cover (%) in plot | |
| Shrub | Shrub | 1-7 m (and all Corylus avellana >1m) | 1-7 m (and all Corylus avellana >1m) | Cover (%) in plot (except for plot TB115B: only presence/absence data) | Cover (%) in plot | |
| Herb | Herb | <1 m | <1 m | Cover (%) in plot | Cover (%) in plot | |

BV - Binnen-Vlaanderen

| Layers | | Definition | | Abundance estima species | ites per |
|--------|-------|--|--|--|----------------------|
| Old | New | Old | New | Old | New |
| Tree | Tree | All woody species in the top canopy | All woody species in the top canopy | Londo scale → see conversion table | Cover (%) in plot |
| Shrub | Shrub | all woody species > 1m height and not in the canopy (i.e. subcanopy) + seedlings > 0.25m | all woody species > 1m height and not in the canopy (i.e. subcanopy) + seedlings > 0.25m | Londo scale → see conversion table | Cover (%) in plot |
| Herb | Herb | All herbaceous species and seedlings < 0.25m | All herbaceous species and seedlings < 0.25m | Londo scale → see conversion table | Cover (%) in plot |

Conversion table:

| Londo scale | Assumed cover (%) | Londo scale | Assumed cover (%) |
|-------------|-------------------|-------------|-------------------|
| present | 0.5 | 2/3 | 25 |
| r1 | 1 | 3 | 30 |
| r2 | 2 | 3/4 | 35 |
| r4 | 4 | 4 | 40 |
| p1 | 1 | 4/5 | 45 |
| p2 | 2 | 5- | 50 |
| р4 | 4 | 5 | 50 |
| a1 | 1 | 5+ | 50 |
| a2 | 2 | 5/6 | 55 |
| a4 | 4 | 6 | 60 |
| m1 | 1 | 6/7 | 65 |
| m2 | 2 | 7 | 70 |
| m4 | 4 | 7/8 | 75 |
| 1- | 9 | 8 | 80 |
| 1+ | 14 | 8/9 | 85 |
| 1/2 | 15 | 9 | 90 |
| 2 | 20 | | |

PR - Prignitz

| Layers | | Definition | | Abundance estimates per species | | |
|---------------------|---------------------|---|---|--|---|--|
| Old | New | Old | New | Old | New | |
| Tree: T1 + T2 | Tree: T1 + T2 | Plot specific: looking at structure to define height ranges of tree and shrub layer, and using T1 and T2 in case there are two | Plot specific: looking at structure to define height ranges of tree and shrub layer, and using T1 and T2 in case there | cover (%) Spring AND summer survey → final value for each species is the highest of the two | cover (%) | |
| | | distinct tree layers | layers | cover (%) value was calculated from T1 and T2 estimates, according to Fischer (2015) | For final analysis, one cover (%) value was calculated from T1 and T2 estimates, according to Fischer (2015) | |
| Shrub | Shrub | Plot specific: looking at structure to define height ranges of tree and shrub layer | Plot specific: looking at structure to define height ranges of tree and shrub layer | cover (%) Spring AND summer survey → final value for each species is the highest of the two | cover (%) | |
| Herb | Herb | All species < tallest herbaceous species | All species < tallest herbaceous species | scale of Barkman, Doing, and Segal (1964)→ see conversion table Spring AND summer survey → final value for each species is the highest of the two | cover (%) | |

Conversion table:

| Scale of Barkman et al. (1964) | | | | |
|--------------------------------|-----------------|--------------------------------|-------------------------|--|
| Code | Cover (%) range | Number of individuals | Assumed cover (%) value | |
| .+r | | 1 or 2 individuals in the plot | 0.5 | |
| .+p | <1% | 3-20 individuals in the plot | 0.5 | |
| .+a | 1-2% | 3-20 individuals in the plot | 1.5 | |
| .+b | 2-5% | 3-20 individuals in the plot | 3.5 | |
| 1p | <1% | 20-100 individuals in the plot | 0.5 | |
| 1a | 1-2% | 20-100 individuals in the plot | 1.5 | |
| 1b | 2-5% | 20-100 individuals in the plot | 3.5 | |
| 2m | <5% | >100 individuals in the plot | 3.5 | |
| 2a | 5-12,5% | >100 individuals in the plot | 8.75 | |
| 2b | 12,5-25% | >100 individuals in the plot | 18.75 | |
| 3a | 25-37,5% | number of indiv doesn't matter | 31.25 | |
| 3b | 37,5-50% | number of indiv doesn't matter | 43.75 | |
| 4a | 50-62,5% | number of indiv doesn't matter | 56.25 | |
| 4b | 62,5-75% | number of indiv doesn't matter | 68.75 | |
| 5a | 75-87,5% | number of indiv doesn't matter | 81.25 | |
| 5b | 87,5-100% | number of indiv doesn't matter | 93.75 | |

BS – Braunschweig

| Layers | | Definition | | Abundance estimates p | er species |
|--------|-------|-------------------------|-------------------------|---|------------|
| Old | New | Old | New | Old | New |
| Tree | Tree | Structurally defined | Structurally defined | Braun-Blanquet scale → see conversion table | cover (%) |
| Shrub | Shrub | Structurally defined | Structurally defined | Braun-Blanquet scale → see conversion table | cover (%) |
| Herb | Herb | Structurally defined | Structurally defined | Braun-Blanquet scale → see conversion table | cover (%) |

Conversion table:

| Braun-Blanquet | Assumed cover (%) |
|----------------|-------------------|
| r | 0.5* |
| + | 0.5 |
| 1 | 3 |
| 2 | 15 |
| 3 | 37.5 |
| 4 | 62.5 |
| 5 | 87.5 |

GO - Göttingen

| Layers | | Definitio | n | Abundance estimates per specie | S |
|--------|-------|-----------|------------|---|---|
| Old | New | Old | New | Old | New |
| Tree | Tree | >5m | >5m | Braun-Blanquet scale → see conversion table | cover (%) in Summer |
| Shrub | Shrub | 0.5-5m | 0.5- 5m | Spring AND summer survey → final value for each species is the highest of the two Braun-Blanquet scale → see conversion table | cover (%) in Summer |
| Herb | Herb | <0.5m | <0.5m | Spring AND summer survey → final value for each species is the highest of the two Braun-Blanquet scale → see conversion table | cover (%) in Spring cover (%) in Summer |
| | | | | Spring AND summer survey → final value for each species is the highest of the two | Spring AND summer survey → final value for each species is the highest of the two |

Conversion table:

| Braun-Blanquet | Assumed cover (%) |
|----------------|-------------------|
| r | 0.5* |
| + | 0.5 |
| 1 | 3 |
| 2 | 15 |
| 3 | 37.5 |
| 4 | 62.5 |
| 5 | 87.5 |

| Layers | | Definition | | Abundance estimate | es per |
|------------------------|-------|--|---|---|-----------|
| | | | | species | |
| Old | New | Old | New | Old | New |
| Tree: T1, T2, T3 | Tree | T1: trees above main canopy level T2: main canopy level T3: from ½ of the height of the main tree layer (t2), but below main canopy layer | T1+T2+T3 from the old definition combined (i.e. everything > ½ main canopy level) | Zlatník's scale → see conversion table For final analysis, one cover (%) value was calculated from T1, T2 and T3 estimates, according to Fischer (2015) | cover (%) |
| Shrub: S1, S2 | Shrub | S1: from 1.3 m up to $\frac{1}{2}$ of the height of the main tree layer (T2) S2: all woody species up to 1.3 m (including low shrubs and tree saplings) \rightarrow for final analysis, S2 was considered part of the herb layer | S1 from the old definition (from 1.3 m up to ½ main canopy level) | Zlatník's scale → see conversion table | cover (%) |
| Herb: HL+JL | Herb | HL: herbaceous species JL: tree seedlings up to ca. 30 cm | S2 + HL + JL from the old definition combined (i.e. all herbs + everything <1.3m) | Zlatník's scale → see conversion table | cover (%) |

KO - Koda Wood

Conversion table:

| Zlatník's scale | | | | |
|-----------------|---|-------------------|--|--|
| Code | Description | Assumed cover (%) | | |
| - | rare (up to 3 individual per plot) | 0.5 | | |
| + | sparse (more than 3 individuals, but below 1 % cover) | 0.5 | | |
| 1 | coverage up 5 % of the plot | 3 | | |
| -2 | coverage 5–15 % of the plot | 10 | | |
| +2 | coverage 15–25 % of the plot | 20 | | |
| -3 | coverage 25–37 % of the plot | 31 | | |
| +3 | coverage 37–50 % of the plot | 43.5 | | |
| -4 | coverage 50–62 % of the plot | 56 | | |
| +4 | coverage 62–75 % of the plot | 68.5 | | |
| -5 | coverage 75–87 % of the plot | 81 | | |

DE - Devin Wood

+5

| Layers | | Definition | | Abundance estima species | tes per |
|--------|-------|--|--|---|-----------|
| Old | New | Old | New | Öld | New |
| Т | Tree | all woody species higher than 1/2 of the height of the main tree layer | all woody species higher than 1/2 of the height of the main tree layer | Braun-Blanquet → see conversion table | cover (%) |
| S | Shrub | all woody species between 1.3m and 1/2 of the height of the main tree layer | all woody species between 1.3m and 1/2 of the height of the main tree layer | Braun-Blanquet → see conversion table | cover (%) |
| H+J | Herb | H: all herbaceous species (including climbers) J: woody species below 1.3 m height | all herbaceous species (including climbers)+ woody species below 1.3 m height | Braun-Blanquet → see conversion table | cover (%) |

Conversion table:

| Braun-Blanquet | Assumed cover (%) |
|----------------|-------------------|
| r | 0.5* |
| + | 0.5 |
| 1 | 3 |
| 2 | 15 |
| 3 | 37.5 |
| 4 | 62.5 |
| 5 | 87.5 |

| Layers | | Definition | | Abundance estimate | es per |
|------------------------|-------|--|---|--|-----------|
| | | | | species | |
| Old | New | Old | New | Old | New |
| Tree: T1, T2, T3 | Tree | T1: trees above main canopy level T2: main canopy level T3: from ½ of the height of the main tree layer (t2), but below main canopy layer | T1+T2+T3 from the old definition combined (i.e. everything > ½ main canopy level) | Zlatník's scale → see conversion table For final analysis, one cover (%) value was calculated from T1, T2 and T3 estimates, according to Fischer (2015) | cover (%) |
| Shrub: S1, S2 | Shrub | S1: from 1.3 m up to ½ of the height of the main tree layer (T2) S2: all woody species up to 1.3 m (including low shrubs and tree saplings) → for final analysis, S2 was considered part of the herb layer | S1 from the old definition (from 1.3 m up to ½ main canopy level) | Zlatník's scale → see conversion table | cover (%) |
| Herb: HL+JL | Herb | HL: herbaceous species JL: tree seedlings up to ca. 30 cm | S2 + HL + JL from the old definition combined (i.e. all herbs + everything <1.3m) | Zlatník's scale → see conversion table | cover (%) |

ZV & SK – Zvolen & Slovak Karst

Conversion table:

| Zlatník's scale | | | | |
|-----------------|---|-------------------|--|--|
| Code | Description | Assumed cover (%) | | |
| _ | rare (up to 3 individual per plot) | 0.5 | | |
| + | sparse (more than 3 individuals, but below 1 % cover) | 0.5 | | |
| 1 | coverage up 5 % of the plot | 3 | | |
| -2 | coverage 5–15 % of the plot | 10 | | |
| +2 | coverage 15–25 % of the plot | 20 | | |
| -3 | coverage 25–37 % of the plot | 31 | | |
| +3 | coverage 37–50 % of the plot | 43.5 | | |
| -4 | coverage 50–62 % of the plot | 56 | | |
| +4 | coverage 62–75 % of the plot | 68.5 | | |
| -5 | coverage 75–87 % of the plot | 81 | | |
| +5 | coverage 87–100 % of the plot | 93.5 | | |

| Layers | | Definition | | Abundance estimates p | er species |
|--------------|--|--|---|---|---|
| Old | New | Old | New | Old | New |
| Trees | Tree + Shrub | All woody species > 1.3 m | All woody species > 1.3 m height and with diameter at breast height (DBH) > 5 cm | DBH-class for each individual was noted (see DBH-table below) For final dataset: - Calculated basal area m ² /ha, based on mid points of DBH classes - Omitted individuals with DBH <5 cm for comparability | DBH-class for each individual with DBH > 5 cm was noted For final dataset: - Calculated basal area m ² /ha, based on mid points of DBH classes |
| Regeneration | Herb (because of upper limit of 1.3 m) | 0.25-1.3m | 0.25-1.3m | Only presence/absence data | Only presence/absence data |
| Ground flora | Herb | <0.25 m (including woody species) | <0.25 m (including woody species) | Cover (%) | Cover (%) |

W - Wales

DBH-table:

| Mid-point (cm) | DBH-class | DBH-range (cm) | Mid-point (cm) | DBH-class | DBH-range (cm) |
|----------------|-----------|----------------|----------------|-----------|----------------|
| 2.5 | 1 | 0-5 | 82.5 | 17 | 80-85 |
| 7.5 | 2 | 5-10 | 87.5 | 18 | 85-90 |
| 12.5 | 3 | 10-15 | 92.5 | 19 | 90-95 |
| 17.5 | 4 | 15-20 | 97.5 | 20 | 95-100 |
| 22.5 | 5 | 20-25 | 102.5 | 21 | 100-105 |
| 27.5 | 6 | 25-30 | 107.5 | 22 | 105-110 |
| 32.5 | 7 | 30-35 | 112.5 | 23 | 110-115 |
| 37.5 | 8 | 35-40 | 117.5 | 24 | 115-120 |
| 42.5 | 9 | 40-45 | 122.5 | 25 | 120-125 |
| 47.5 | 10 | 45-50 | 127.5 | 26 | 125-130 |
| 52.5 | 11 | 50-55 | 132.5 | 27 | 130-135 |
| 57.5 | 12 | 55-60 | 137.5 | 28 | 135-140 |
| 62.5 | 13 | 60-65 | 142.5 | 29 | 140-145 |
| 67.5 | 14 | 65-70 | 147.5 | 30 | 145-150 |
| 72.5 | 15 | 70-75 | 152.5 | 31 | 150-155 |
| 77.5 | 16 | 75-80 | 157.5 | 32 | 155-160 |

CO - Compiègne

| Layers | | Definition | | Abundance estimates per s | species |
|--------|-------|------------|-----------|--|--|
| Old | New | Old | New | Old | New |
| Tree | Tree | > 8 m | > 8 m | Braun-Blanquet scale → see conversion table | Braun-Blanquet scale $ ightarrow$ see conversion table |
| Shrub | Shrub | 1.5 – 8 m | 1.5 – 8 m | Braun-Blanquet scale $ ightarrow$ see conversion table | Braun-Blanquet scale $ ightarrow$ see conversion table |
| Herb | Herb | < 1.5 m | < 1.5 m | Braun-Blanquet scale $ ightarrow$ see conversion table | Braun-Blanquet scale $ ightarrow$ see conversion table |

Conversion table:

| Braun-Blanquet | Assumed cover (%) |
|----------------|-------------------|
| r | 0.5* |
| + | 0.5 |
| 1 | 3 |
| 2 | 15 |
| 3 | 37.5 |
| 4 | 62.5 |
| 5 | 87.5 |
| i | 0.1 |

SP - Speulderbos

| Layers | | Definition | | Abundance estimates per s | pecies |
|--------|-------|------------|-----------|--|-----------|
| Old | New | Old | New | Old | New |
| Tree | Tree | 0 – 0.5 m | 0 – 0.5 m | Braun-Blanquet → see conversion table | cover (%) |
| Shrub | Shrub | 0.5 – 5 m | 0.5 – 5 m | Braun-Blanquet → see conversion table | cover (%) |
| Herb | Herb | > 5 m | > 5 m | Braun-Blanquet → see conversion table | cover (%) |

Conversion table:

| Braun-Blanquet | Assumed cover (%) |
|----------------|-------------------|
| r | 0.5* |
| + | 0.5 |
| 1 | 3 |
| 2 | 15 |
| 3 | 37.5 |
| 4 | 62.5 |
| 5 | 87.5 |

SH - Schleswig-Holstein

| Layers | | Definition | | Abundance estimates pe | r species |
|--------------------|------------------|-------------------------------------|-----------------------------|--|---|
| Old | New | Old | New | Old | New |
| Layer 1 Layer 2 | Tree: T1 + T2 | Layer 1: upper canopy | T1: upper canopy | Braun-Blanquet → see conversion table | cover (%) |
| | | Layer 2: lower canopy | T2: lower canopy | For final analysis, one cover (%) value was calculated from T1 and T2 estimates, according to Fischer (2015) | For final analysis, one cover (%) value was calculated from T1 and T2 estimates, according to Fischer (2015) |
| Layer 4 | Shrub | 1 – 4 m | 1–4 m | Braun-Blanquet → see conversion table | cover (%) |
| Layer 6 | Herb | <1 m; including woody species | <1 m; including woody | Braun-Blanquet → see conversion table | cover (%) |
| | | | species | Note: in some plots, only presence of the | |
| | | | | spring geophytes | |
| | | | | (Anemone nemorosa | |
| | | | | and <i>Ficaria verna</i>) was | |
| | | | | recorded, without cover estimates \rightarrow for final | |
| | | | | analysis, these species | |
| | | | | were omitted from both | |
| | | | | the old and new survey | |

Conversion table:

| Code | Cover (%) range | Number of individuals | Assumed cover (%) |
|------|-----------------|-----------------------|-------------------|
| r | ≤1% | 1 individual | 0.5* |
| + | ≤1% | 2-5 individuals | 0.5 |
| 1 | ≤5% | 6-50 individuals | 3 |
| 2m | ≤5% | >50 individuals | 3 |
| 2a | 5% - 15% | - | 10 |
| 2b | 16% - 25% | - | 20 |
| 3 | 26% - 50% | - | 37.5 |
| 4 | 51% - 75% | - | 62.5 |
| 5 | 76% - 100% | - | 87.5 |

MO - Moricsala

| Layers | | Definition | | Abundance estimates per species | |
|--------|-------|--|-----------------------------------|---|--|
| Old | New | Old | New | Old | New |
| Tree | Tree | Woody species with DBH>10cm | Woody species with DBH>10cm | Basal area (m²/ha) | Basal area (m²/ha) |
| Shrub | Shrub | Woody species with DBH<10cm | Woody species with DBH<10cm | Number/ha In final dataset: converted to basal area (m²/ha), assuming an average diameter of 5 cm for all shrubs | Number/ha In final dataset: converted to basal area (m²/ha), assuming an average diameter of 5 cm for all shrubs |
| Herb | Herb | Herbaceous species (no seedlings) | Herbaceous species | Frequency of occurrence in 10 subplots (1x1m) → See conversion table | Frequency of occurrence in 10 subplots (1x1m) → See conversion table |
| | | | | | 0.1 indicates presence in total plot, but not in one of the subplots, however, this was NOT done in the old survey, so this data was omitted in final dataset |

Conversion table:

| Frequency | Assumed cover (%) |
|-----------|-------------------|
| 0 | 0 |
| 1 | 5 |
| 2 | 15 |
| 3 | 25 |
| 4 | 35 |
| 5 | 45 |
| 6 | 55 |
| 7 | 65 |
| 8 | 75 |
| 9 | 85 |
| 10 | 95 |

BI - Bialowieza

| Layers | | Definition | | Abundance estimates per species | | |
|--------|-------|------------------------|-----------------------|---------------------------------|----------------|--|
| Old | New | Old | New | Old | New | |
| Trees: | Tree: | a1 – dominant tree | a1 – dominant tree | Braun-Blanquet | cover (%) | |
| a1 | a1 | crowns (tops in the | crowns (tops in the | ightarrow see conversion | | |
| a2 | a2 | sun) | sun) | table | For final | |
| | | a2 – subdominant | a2 – subdominant | | analysis, one | |
| | | and shadow tolerant | and shadow tolerant | For final analysis, | cover (%) | |
| | | trees with tops of | trees with tops of | one cover (%) | value was | |
| | | crowns in the lower | crowns in the lower | value was | calculated | |
| | | part of the layer a1 | part of the layer a1 | calculated from | from a1 and | |
| | | (except Corylus | (except Corylus | a1 and a2 | a2 estimates, | |
| | | avellana, which is | avellana, which is | estimates, | according to | |
| | | always b/c layer) | always b/c layer) | according to | Fischer (2015) | |
| | | | | Fischer (2015) | | |
| b | Shrub | bush and tree | bush and tree | Braun-Blanquet | cover (%) | |
| 2 | onnub | undergrowth laver | undergrowth laver | \rightarrow see conversion | | |
| | | higher than knee | higher than knee | table | | |
| | | height (ca. 50 cm) but | height (ca. 50 cm) | | | |
| | | not reaching the | but not reaching the | | | |
| | | layer a | layer a | | | |
| | | - | - | | | |
| С | Herb | herb layer (all non- | herb layer (all non- | Braun-Blanquet | cover (%) | |
| | | woody plants and | woody plants and | ightarrow see conversion | | |
| | | woody plants if lower | woody plants if lower | table | | |
| | | than knee height – | than knee height – | | | |
| | | approximately 50 cm) | approximately 50 | | | |
| | | | cm) | | | |

Conversion table:

| Braun-Blanquet | Assumed cover (%) |
|----------------|-------------------|
| r | 0.5* |
| + | 0.5 |
| 1 | 3 |
| 2 | 15 |
| 3 | 37.5 |
| 4 | 62.5 |
| 5 | 87.5 |
| (+) | 0.1 |

SKA - Skåne

| Layers | | Definition | | Abundance esti | mates per species |
|-------------|-------|---|---|----------------|-------------------|
| Old | New | Old | New | Old | New |
| Tree | Tree | Vegetation > 5 m | Vegetation > 5 m | cover (%) | cover (%) |
| / | Shrub | / | / | / | / |
| Understorey | Herb | Vegetation < 5 m | Vegetation < 5 m | cover (%) | cover (%) |
| | | For final analysis, all woody species in the understorey layer with a cover (%) of > 1 % were assigned to the shrub layer | For final analysis, all woody species in the understorey layer with a cover (%) of > 1 % were assigned to the shrub layer | | |

APPENDIX A3.3. CALCULATION OF SPECIES EVENNESS

Similarly to Bernhardt-Römermann et al. (2015), we selected E_{var} to estimate evenness. E_{var} is based on the variance in abundance over the species, an intuitive way to measure evenness (Smith & Wilson, 1996). E_{var} is calculated with the following formula:

$$E_{var} = 1 - \frac{2}{\pi} \arctan\left(\sum_{s=1}^{S} \left(\ln(x_s) - \sum_{t=1}^{S} \ln(x_t)/S\right)^2/S\right)$$

Where x_s and x_t are the cover values of species s and t respectively (where t represents all remaining species in a plot given s is the focal species), and S is the total number of species in the vegetation plot. Evar is not impacted by richness or symmetry because it is based solely on variance in species' abundances (Smith & Wilson, 1996).

APPENDIX A3.4. TRAIT DATA SOURCES

We sourced trait values for specific leaf area (SLA) and plant height as shown in Table A3.4.1.

Table A3.4.1. Trait database sources for species within our dataset. E: (Fitter & Peat, 1994), http://www.ecoflora.org.uk [March 2017]; L: (Kleyer et al., 2008); O: Own measurements; R: (Jäger & Werner, 2005).

| Trait | Units | Data source |
|--------------------------|--------|-------------|
| Plant height | m | L, E, O, R |
| Specific leaf area (SLA) | mm²/mg | L, O |

Trait values of plant height (m) and SLA (mm² mg⁻¹) were available for all species that occurred in more than 5% of the plots with a mean cover value of more than 1%. In all but one plot a minimum of 80% of the total herbaceous vegetation cover was represented by species having trait attribute values, which is considered a cut-off at which trait environment relationships are robust (Pakeman, 2014). For plot ZV-D33 in Zvolen, the cover share of species for which no SLA value is available exceeded the threshold of 20%. The plot only contained three herbaceous species, each with a cover value of only 0.5%. One of these three species was *Neottia nidus-avis*, a rare nonphotosynthetic orchid for which no SLA values exist, resulting in a cover share of 33.3% of missing trait values. This issue was not further addressed, as we expect its impact to be small on the results for the entire dataset of 192 plots.

APPENDIX A3.5. HERB LAYER SPECIES LISTS: INCLUDED AND EXCLUDED SPECIES

Included herbaceous species:

Achillea millefolium Achillea setacea Aconitum lycoctonum Aconitum vulparia Actaea spicata Adoxa moschatellina Aegopodium podagraria Agrimonia eupatoria Agrostis canina Agrostis capillaris Agrostis gigantea Agrostis spec Agrostis stolonifera Agrostis vinealis Ajuga genevensis Ajuga reptans Ajuga spec Alliaria petiolata Allium flavum Allium scorodoprasum Allium senescens Allium ursinum Anemone nemorosa Anemone ranunculoides Anemone spec Anemone sylvestris Angelica sylvestris Anthericum ramosum Anthericum spec Anthoxanthum odoratum Anthriscus nitida Anthriscus sylvestris Aquilegia vulgaris Arabidopsis arenosa Arabis hirsuta Arctium lappa Arctium nemorosum Arctium tomentosum Arrhenatherum elatius Artemisia absinthium Arum maculatum Asarum europaeum Asperula tinctoria Asplenium spec Aster amellus Astragalus glycyphyllos

Ballota nigra Blackstonia perfoliata Blechnum spicant Brachypodium pinnatum Brachypodium sylvaticum Bromus benekenii Bromus ramosus Bromus spec Bromus sterilis Brvonia dioica Buglossoides purpurocaerulea Bupleurum falcatum Calamagrostis arundinacea Calamagrostis canescens Calamagrostis epigejos Calamagrostis spec Calamagrostis villosa Caltha palustris Campanula bononiensis Campanula glomerata Campanula latifolia Campanula patula Campanula persicifolia Campanula rapunculoides Campanula rotundifolia Campanula trachelium Cardamine amara Cardamine bulbifera Cardamine flexuosa Cardamine hirsuta Cardamine hirsuta/flexuosa Cardamine impatiens Cardamine pratensis Cardamine spec Carduus spec Carex acutiformis Carex arenaria Carex canescens Carex caryophyllea Carex digitata Carex flacca Carex michelii Carex montana Carex muricata Carex nigra Carex pallescens

Carex remota Carex spec Carex sylvatica Centaurea jacea Centaurium umbellatum Cephalanthera damasonium Cephalanthera rubra Cerastium fontanum Ceratocapnos claviculata Chaerophyllum aromaticum Chaerophyllum temulum Chamaenerium angustifolium Chrysosplenium alternifolium Chrysosplenium oppositifolium Circaea alpina Circaea lutetiana Circaea x intermedia Cirsium arvense Cirsium oleraceum Cirsium palustre Cirsium vulgare Clematis recta Clinopodium vulgare Conopodium major Convallaria majalis Convolvulus spec Corydalis cava Corydalis solida Crepis paludosa Cruciata glabra Cynoglossum germanicum Cytisus scoparius Dactylis glomerata Dactylorhiza fuchsii Dactylorhiza maculata Danthonia decumbens Daphne mezereum Daucus carota Deschampsia cespitosa Deschampsia flexuosa Dictamnus albus Digitalis grandiflora Digitalis purpurea Dryopteris affinis Dryopteris carthusiana Dryopteris dilatata

Dryopteris spec Echium vulgare Elymus caninus Elymus hispidus Elymus repens Epilobium angustifolium Epilobium hirsutum Epilobium montanum Epilobium spec Epilobium tetragonum Epipactis helleborine Epipactis purpurata Epipactis spec Equisetum arvense Equisetum pratense Equisetum sylvaticum Equisetum telmateia Euphorbia amygdaloides Euphorbia cyparissias Euphorbia epithymoides Euphorbia esula Falcaria vulgaris Fallopia convolvulus Fallopia convolvulus/dumetorum Fallopia dumetorum Fallopia spec Festuca altissima Festuca filiformis Festuca gigantea Festuca heterophylla Festuca ovina Festuca pseudovina Festuca rubra Festuca rupicola Festuca rupicola/ovina Festuca spec Festuca valesiaca Ficaria verna Filipendula ulmaria Fragaria moschata Fragaria vesca Fragaria vesca/moschata Gagea lutea Gagea spathacea Galeopsis angustifolia Galeopsis bifida/tetrahit

Appendix to Chapter 3

Astragalus spec Athyrium filix-femina Atropa belladonna Galium aparine Galium boreale Galium glaucum Galium intermedium

Galium mollugo Galium odoratum Galium palustre Galium pumilum Galium saxatile Galium spec Galium sylvaticum Galium verum Genista germanica Genista pilosa Genista tinctoria Gentiana cruciata Geranium molle Geranium robertianum Geranium sanguineum Geranium svlvaticum Geum rivale Geum urbanum Glechoma hederacea Glechoma hirsuta Gymnocarpium dryopteris Hacquetia epipactis Helictotrichon pubescens Hepatica nobilis Heracleum sphondylium Hieracium bifidum Hieracium lachenalii Hieracium laevigatum Hieracium murorum Hieracium pilosella Hieracium sabaudum Hieracium sabaudum/racemosum Hieracium spec Hierochloe australis Holcus lanatus Holcus mollis Holcus spec Hordelymus europaeus Hyacinthoides non-scripta Hypericum elodes Hypericum hirsutum Hypericum maculatum Hypericum montanum Hypericum perforatum Hypericum pulchrum

Carex pendula Carex pilosa Carex pilulifera Hypericum tetrapterum Impatiens glandulifera Impatiens noli-tangere Impatiens parviflora Impatiens parviflora/nolitangere Inula conyza Inula conyzae Inula ensifolia Inula salicina Iris pseudacorus Iris variegata Isopyrum thalictroides Jacobaea vulgaris Juncus conglomeratus Juncus effusus Juncus inflexus Juncus spec Juncus tenuis Knautia arvensis Lactuca muralis Lamium galeobdolon Lamium maculatum Lamium spec Lapsana communis Laserpitium latifolium Lathraea squamaria Lathyrus linifolius Lathyrus niger Lathyrus pratensis Lathyrus vernus Lembotropis nigricans Leopoldia comosa Leucanthemum vulgare Leucojum vernum Lilium martagon

Lotus corniculatus Luzula campestris Luzula forsteri Luzula luzuloides Luzula multiflora Luzula pilosa Luzula sylvatica Lycopodium annotinum Lycopodium clavatum Lysimachia nemorum Lysimachia nummularia Lysimachia vulgaris Maianthemum bifolium Dryopteris filix-mas Dryopteris polypodioides

Medicago lupulina Melampyrum nemorosum Melampyrum pratense Melampyrum spec

Melica ciliata Melica nutans Melica picta Melica uniflora Melittis melissophyllum Mentha aquatica Mentha arvensis Mentha spec Mercurialis perennis Milium effusum Moehringia trinervia Molinia caerulea Monotropa hypopitys Myosotis arvensis Myosotis palustris/scorpioides Myosotis spec Myosotis sylvatica Nardus stricta Nasturtium microphyllum Neottia nidus-avis Neottia ovata **Omphalodes** scorpioides Orchis purpurea Origanum vulgare Ornithogalum umbellatum Orthilia secunda Oxalis acetosella Parietaria officinalis Paris quadrifolia Persicaria hydropiper Petasites hybridus

> Peucedanum cervaria Phalaris arundinacea Phleum phleoides Phyteuma spicatum Pilosella spec Pimpinella major Pimpinella saxifraga Platanthera bifolia Poa angustifolia Poa annua Poa nemoralis Poa pratensis Poa remota Poa spec

Galeopsis spec Galeopsis tetrahit Galium album Poa stiriaca Poa trivialis Polygala chamaebuxus Polygala spec

Polygonatum multiflorum Polygonatum odoratum Polygonatum verticillatum Polvpodium vulaare Potentilla alba Potentilla erecta Potentilla reptans Potentilla spec Potentilla sterilis Prenanthes purpurea Primula elatior Primula spec Primula veris Primula vulgaris Prunella vulgaris Pteridium aquilinum Pulmonaria mollis Pulmonaria obscura Pulmonaria officinalis Pulmonaria spec Pyrola rotundifolia Ranunculus acris Ranunculus auricomus Ranunculus bulbosus Ranunculus cassubicus Ranunculus flammula Ranunculus lanuginosus Ranunculus polyanthemos Ranunculus repens Ribes rubrum Ribes spec

> Ribes uva-crispa Rosa canina Rosa corymbifera Rosa pendulina Rosa spec Rubus caesius Rubus fruticosus Rubus idaeus Rubus saxatilis Rubus saxatilis Rubus spec Rumex acetosa Rumex acetosella Rumex obtusifolia

Rumex sanguineus Salvia pratensis Sanicula europaea Scrophularia auriculata Scrophularia nodosa Securigera varia Sedum maximum Sedum telephium Senecio aquaticus Senecio ovatus Serratula tinctoria Silene dioica Silene latifolia Silene nutans Silene vulgaris Sisymbrium strictissimum Solanum dulcamara Solidago virgaurea Stachys officinalis Stachys sylvatica

Stellaria aquatica Stellaria holostea Stellaria media Stellaria nemorum Succisa pratensis Symphytum officinale Symphytum tuberosum Tamus communis Tanacetum corymbosum Taraxacum officinale Taraxacum spec Teucrium chamaedrys Teucrium scorodonia Thalictrum aquilegiifolium Torilis arvensis Torilis japonica Trientalis europaea Trifolium alpestre Trifolium medium Trifolium montanum Trifolium repens Umbilicus rupestris Urtica dioica Vaccinium myrtillus Vaccinium uliginosum Vaccinium vitis-idaea Valeriana officinalis Verbascum austriacum Verbascum nigrum

Veronica chamaedrys Veronica hederifolia Veronica montana Veronica officinalis Vicia angustifolia Vicia cassubica Vicia cracca Vicia dumetorum Vicia sepium Vicia sepium/dumetorum Vicia spec Vicia tetrasperma Vinca minor Vincetoxicum hirundinaria Viola collina Viola hirta Viola hirta/collina Viola mirabilis Viola odorata Viola reichenbachiana Viola reichenbachiana/riviniana Viola riviniana Viola spec Waldsteinia geoides

Excluded tree, shrub and climber species (seedlings) present in the herb layer:

Abies alba Acer campestre Acer platanoides Acer pseudoplatanus Acer spec Acer tataricum Alnus glutinosa Alnus incana Berberis vulgaris Betula pendula Betula pubescens Betula spec Carpinus betulus Castanea sativa Clematis vitalba Cornus mas Cornus sanguinea Cornus spec Corylus avellana Cotoneaster integerrimus Cotoneaster spec Crataegus laevigata Crataegus monogyna Crataegus spec Euonymus europaeus Euonymus verrucosus Fagus sylvatica Frangula alnus Fraxinus angustifolia Fraxinus excelsior Hedera helix Humulus lupulus Ilex aquifolium

Juglans regia Juniperus communis Larix decidua Larix spec Ligustrum vulgare Lonicera caprifolium Lonicera periclymenum Lonicera spec Lonicera xylosteum Malus sylvestris Other shrubs Picea abies Picea spec Pinus nigra Pinus spec Pinus sylvestris Populus alba Populus canescens Populus spec Populus tremula Prunus avium Prunus mahaleb Prunus padus Prunus serotina Prunus spec Prunus spinosa Pseudotsuga menziesii Pyrus communis Pyrus pyraster Quercus cerris Quercus petraea Quercus pubescens Quercus robur

Quercus robur/petraea Quercus rubra Quercus spec Quercus X intermedia Rhamnus cathartica Rhamnus frangula Robinia pseudoacacia Salix caprea Salix spec Salix triandra Sambucus nigra Sambucus nigra laciniata Sambucus racemosa Sambucus spec Sorbus aria Sorbus aucuparia Sorbus torminalis Staphylea pinnata Taxus baccata Thuja plicata Tilia cordata Tilia platyphyllos Tilia spec Ulmus glabra Ulmus minor Ulmus spec unknown seedling spec Viburnum lantana Viburnum opulus Viburnum spec Tilia cordata/platyphyllos Ruscus aculeatus

APPENDIX A3.6. ADDITIONAL ANALYSIS FOR COMMUNITY COMPOSITION

We performed an additional analysis to get an insight in the potential shifts in species composition that can be linked to the observed interactive effects of land-use history and global-change drivers on the functional signature of the herb layer. For each plot in the dataset, we calculated the response ratio (RR) of the share (%) of the total herb cover that is occupied by (i) **forest specialists (RR_{FS})** (following Heinken et al. (2019)), and (ii) **graminoids (RR_{GRAM})**. Then, we fitted the following linear mixed-effect model with these response ratios as the response variable (similar to the analyses in the main manuscript):

Response variable ~ LUH + Soil type + ln(Olsen P) + EIV_F + ln(Plot size) + RR_{CC} + RR_{SCA} + RR_{LQ} + Δ MAT + Δ Aridity + Ndep + LUH:RR_{CC} + LUH:RR_{SCA} + LUH:RR_{LQ} + LUH: Δ MAT + LUH: Δ Aridity + LUH:Ndep + (1 | Region)

with LUH = land-use history, EIV_F = Ellenberg indicator value for soil moisture content, CC = canopy cover, SCA = shade-casting ability, LQ = litter quality, Δ MAT = rate of change in mean annual temperature, Δ Aridity = rate of change in mean De Martonne aridity index, Ndep = rate of nitrogen deposition. '(1 | Region)' represents the inclusion of a random effect term 'region' with varied intercepts only to account for the hierarchical structure of the data. We also incorporated 'region' as a weights term, i.e. we controlled for heterogeneity in residual spread. With ANOVA, we confirmed that both the random effect term and the weights term significantly (alpha = 0.05) improved the model for each response variable. All models were fit with restricted maximum likelihood (REML). We found no clear patterns in the residuals for each model, based on graphical evaluation (Zuur et al., 2009).

We found a significant (p=0.003) interactive effect between land-use history and the change in canopy cover (RR_{CC}) on the change in cover share of forest specialists (RR_{FS}) (**Table A3.6.1**). In *ancient* forests, RR_{FS} increased with increasing RR_{CC} , while in *recent* forest, RR_{CC} had no or even a slightly negative effect on RR_{FS} (**Fig. A3.6.3A**). We also found an interactive effect between land-use history and the change in the De Martonne drought index (**Table A3.6.1**), but based on **Fig. A3.6.3B**, the effects in both directions are very minor.



Figure A3.6.1. Temporal shifts in the cover share (%) of forest specialists (A) and graminoids (B) across all regions (red triangle) and for the 19 regions separately (black dots). Mean (\pm 95 % confidence interval) log response ratios (In (X_{new}/X_{old})/ Δ t) are shown based on the plot values in the old and new survey. '*' indicates a significant change, with confidence intervals excluding zero. The region labels refer to **Table 3.1** in the main text.



Figure A3.6.2. Estimates and 95% confidence intervals for each explanatory variable in the two additional models that were fitted for the two response variables listed in the legend. Non-significant effects (with confidence intervals including zero) are transparent. Marginal $R^2 (R^2m)$ and conditional $R^2 (R^2c)$ of each model are provided in the legend. RR = log response ratio ($ln (X_{new}/X_{old})/\Delta t$); LUH = land-use history; RF = recent forest; Ndep = nitrogen deposition; MAT = mean annual temperature; CC = canopy cover; SCA = shade-casting ability of the canopy; LQ = litter quality; EIV-F = Ellenberg indicator value for soil moisture. See **Table A3.6.1** for full model results.

Table A3.6.1. Estimates (Est), confidence intervals (CI) and p-values from the additional linear mixed-effect models with RR cover share of forest specialists (left) and graminoids (right) as response variable. LUH = land-use history; RF = recent forest; CWM = community weighted mean; EIV-F = Ellenberg indicator value for moisture; SCA = Shade-casting ability; MAT = mean annual temperature; Ndep = nitrogen deposition.

| | RR cover share forest specialists | | | RR cover share graminoids | | |
|------------------------|-----------------------------------|------------------|-------|---------------------------|------------------|-------|
| Predictors | Est | CI | р | Est | CI | p |
| (Intercept) | -0.0004 | -0.0089 - 0.0082 | 0.933 | -0.0186 | -0.03630.0009 | 0.039 |
| Plot size | 0.0000 | -0.0032 - 0.0032 | 0.993 | -0.0073 | -0.0161 - 0.0014 | 0.101 |
| Soil type (ClayNoCarb) | 0.0021 | -0.0040 - 0.0083 | 0.496 | 0.0071 | -0.0060 - 0.0202 | 0.287 |
| Soil type (Sand) | -0.0005 | -0.0096 - 0.0085 | 0.908 | 0.0107 | -0.0075 - 0.0290 | 0.246 |
| LUH (RF) | 0.0056 | -0.0011 - 0.0122 | 0.103 | 0.0048 | -0.0062 - 0.0157 | 0.390 |
| Olsen P | -0.0014 | -0.0033 - 0.0004 | 0.135 | -0.0045 | -0.00830.0007 | 0.022 |
| EIV-F | 0.0004 | -0.0019 - 0.0028 | 0.732 | 0.0061 | 0.0011 - 0.0110 | 0.016 |
| RR CC | 0.0036 | 0.0012 - 0.0060 | 0.004 | -0.0043 | -0.0096 - 0.0011 | 0.116 |
| RR SCA | 0.0019 | -0.0010 - 0.0048 | 0.199 | -0.0029 | -0.0077 - 0.0018 | 0.225 |
| RR LQ | 0.0020 | -0.0004 - 0.0044 | 0.099 | -0.0020 | -0.0076 - 0.0035 | 0.470 |
| ΔΜΑΤ | 0.0001 | -0.0074 - 0.0077 | 0.972 | 0.0051 | -0.0090 - 0.0192 | 0.452 |
| ΔAridity | -0.0031 | -0.0105 - 0.0043 | 0.384 | 0.0055 | -0.0096 - 0.0205 | 0.453 |
| Ndep | -0.0033 | -0.0106 - 0.0040 | 0.351 | -0.0126 | -0.0264 - 0.0011 | 0.068 |
| LUH:Ndep | -0.0008 | -0.0083 - 0.0067 | 0.833 | 0.0039 | -0.0072 - 0.0151 | 0.486 |
| LUH:∆MAT | 0.0043 | -0.0044 - 0.0130 | 0.327 | -0.0063 | -0.0181 - 0.0055 | 0.296 |
| LUH:∆Aridity | 0.0078 | 0.0021 - 0.0135 | 0.008 | -0.0052 | -0.0165 - 0.0062 | 0.370 |
| LUH:RR CC | -0.0057 | -0.00940.0019 | 0.003 | 0.0053 | -0.0030 - 0.0136 | 0.211 |
| LUH:RR SCA | -0.0018 | -0.0071 - 0.0035 | 0.504 | 0.0028 | -0.0065 - 0.0120 | 0.554 |
| LUH:RR LQ | 0.0015 | -0.0057 - 0.0087 | 0.681 | 0.0087 | -0.0025 - 0.0198 | 0.128 |
| Observations | 185 | | | 185 | | |
| R²m | 0.31 | | | 0.15 | | |
| R²c | 0.85 | | | 0.42 | | |


Figure A3.6.3. (A) Interactive effects between land-use history and the response ratio (RR) of canopy cover on the response ratio of the cover (%) share of forest specialists (FS) in the herb layer. (B) Interactive effects between land-use history and the change in the De Martonne aridity index (with lower values indicating drier conditions) on the response ratio of the cover (%) share of forest specialists (FS) in the herb layer. Fitted values (dots) and average model estimates of the effects (full lines), in which the values of the other continuous variables were set at their observed mean, are shown. AF = ancient forest; RF = recent forest.

APPENDIX A3.7. SHADE-CASTING ABILITY (SCA) AND LITTER QUALITY (LQ) SCORES

Table A3.7.1. Shade-casting ability (SCA) scores (1: very low shade-casting ability; 5: very high shade-casting ability) adapted from Ellenberg (1996) and complemented with expert knowledge of prof. Kris Verheyen. Litter quality (LQ) scores (1: very slow decomposition rate; 5: very fast decomposition rate) adapted from Hermy (1985) and complemented with expert knowledge of prof. Kris Verheyen.

| Species | SCA | LQ | Species | SCA | LQ |
|----------------------------|-----|-----|----------------------|-----|-----|
| Acer campestre | 3 | 4 | Quercus pubescens | 3 | 1.5 |
| Acer platanoides | 4 | 3 | Quercus robur | 2 | 1 |
| Acer pseudoplatanus | 4 | 3 | Quercus rubra | 4 | 1 |
| Alnus glutinosa | 3 | 4 | Robinia pseudoacacia | 1 | 4 |
| Alnus incana | 3 | 3 | Rosa canina | 2 | 5 |
| Betula pendula | 1 | 2 | Rosa spec | 2 | 5 |
| Betula pendula x pubescens | 1 | 2 | Salix aurita | 2 | 5 |
| Betula pubescens | 1 | 2 | Salix caprea | 2 | 5 |
| Betula spec | 1 | 2 | Salix spec | 2 | 5 |
| Carpinus betulus | 5 | 3 | Salix triandra | 1 | 5 |
| Castanea sativa | 3 | 1 | Salix x mollissima | 2 | 5 |
| Cornus mas | 3 | 5 | Sambucus nigra | 3 | 5 |
| Cornus sanguinea | 3 | 5 | Sambucus racemosa | 3 | 5 |
| Corylus avellana | 3 | 3 | Sorbus aria | 3 | 3 |
| Crataegus laevigata | 3 | 3 | Sorbus aucuparia | 2 | 3 |
| Crataegus monogyna | 3 | 3 | Sorbus torminalis | 3 | 3 |
| Euonymus europaeus | 3 | 4 | Tilia cordata | 4 | 4 |
| Fagus sylvatica | 5 | 1 | Tilia platyphyllos | 4 | 4 |
| Frangula alnus | 2 | 5 | Ulmus glabra | 4 | 5 |
| Fraxinus excelsior | 3 | 5 | Ulmus minor | 4 | 5 |
| llex aquifolium | 5 | 2 | Ulmus spec | 3 | 5 |
| Larix decidua | 1 | 1 | Viburnum opulus | 3 | 4 |
| Picea abies | 4 | 1 | | | |
| Pinus nigra | 1 | 1 | | | |
| Pinus sylvestris | 1 | 2.5 | | | |
| Populus spec | 2 | 3.5 | | | |
| Populus tremula | 2 | 3 | | | |
| Prunus avium | 3 | 4 | | | |
| Prunus padus | 3 | 4 | | | |
| Prunus serotine | 3 | 3 | | | |
| Prunus spinose | 3 | 5 | | | |
| Quercus cerris | 3 | 1.5 | | | |

3

1.5

Quercus petraea

APPENDIX A3.8. CHANGES IN CANOPY COVER, SCA AND LQ

For two regions in the UK (WW and WR; **Table 3.1**), no cover values per species were available for the canopy, and therefore, shade-casting ability (SCA) and litter quality (LQ) could not be calculated. To avoid the exclusion of both regions from our dataset, we assigned an SCA and LQ value to these plots, equal to the mean SCA and LQ value of all plots in the remaining 17 regions. For two other regions (MO and W), the shrub and tree layer were recorded as basal area (m² ha⁻¹) instead of cover percentage (see **Appendix A3.2** for details). As we are only considering the relative changes in canopy cover, SCA and LQ between surveys, using response ratios, we do not expect this to have an impact on the results.



Figure 3.8.1. Temporal shifts in canopy cover (A), shade-casting ability (B) and litter quality (C) across all regions (red triangle) and for the 19 regions separately (black dots). Mean (\pm 95 % confidence interval) log response ratios (ln (X_{new}/X_{old})/ Δ t) are shown based on the plot values in the old and new survey. '*' indicates a significant change, with confidence intervals excluding zero. The region labels refer to **Table 3.1** in the main text.

Table 3.8.1. Overview of the ten most frequent tree and shrub species across the different regions in the new surveys, their average cover in the plots where they occurred and the trends in frequency and cover compared to the original survey. Shade-casting ability (SCA) and litter quality (LQ) scores (see appendix G) of the species are also shown. The species are ranked according to their increase in frequency in between both surveys. Note: two regions, i.e. Wales (W) and Moricsala (MO), are not included in this analysis, as we do not have data on the shrub species for these regions. Both the mean frequency % and cover % per species are calculated by first deriving the average value per region, and then taking the overall mean of these values.

| | Frequency | Change in | Cover (%) | Change in cover | | |
|------------------------|-------------------------|--------------------------------|------------------|------------------------------------|---------------|--------------|
| Species | (%) in new survey | compared to original survey | in new survey | (%) compared to original survey | SCA- score | LQ- score |
| Fraxinus excelsior | 50.0 | -5.9 | 19.5 | -4.6 | 3 | 5 |
| Sorbus aucuparia | 29.4 | -5.6 | 3.3 | 0.9 | 2 | 3 |
| Corylus avellana | 51.3 | -2.8 | 23.1 | 3.4 | 3 | 3 |
| Tilia cordata | 40.0 | 0.0 | 13.1 | 1.3 | 4 | 4 |
| Quercus robur | 42.5 | 1.8 | 27.5 | -10.0 | 2 | 1 |
| Quercus petraea | 58.6 | 3.0 | 33.9 | 3.6 | 3 | 1.5 |
| Carpinus betulus | 56.7 | 3.0 | 29.0 | 6.5 | 5 | 3 |
| Acer pseudoplatanus | 35.0 | 7.3 | 21.3 | 10.1 | 4 | 3 |
| Fagus sylvatica | 57.7 | 10.0 | 39.9 | 4.4 | 5 | 1 |
| Acer campestre | 51.4 | 24.3 | 15.6 | 2.5 | 3 | 4 |

APPENDIX A3.9. MANAGEMENT INFORMATION

Table A3.9.1. Overview of land-use and management information per plot. The first two characters of the plot ID represent the region of the plot. LUH = land-use history; AF = ancient forest; RF = recent forest. 'Previous land cover' indicates how the land was used before afforestation (in case of recent forests). Year afforestation' indicates the year in which afforestation took place (in case of recent forests). 'Management transition(s)' indicates the main management regimes that have been applied since 1850, or since the year of afforestation, with HF = high forest, ZM = zero management, CWS = coppice with standards, WP = wood pasture. 'Year transition 1 and 2' represent the year in which potential shifts from one management regime to another have taken place. Δ Management indicates whether management intensity has increased, decreased or stayed the same over time.

| | Previous | | Year | Management | Year | Year | AManagement | |
|--------|----------|-------------|---------------|-----------------|--------------|--------------|---------------|--|
| FLOT | LOH | land cover | afforestation | transition(s) | transition 1 | transition 2 | Δivianagement | |
| BI2388 | AF | NA | NA | HF to ZM | 1921 | NA | Decrease | |
| BI2393 | AF | NA | NA | HF to ZM | 1921 | NA | Decrease | |
| BI2592 | AF | NA | NA | HF to ZM | 1921 | NA | Decrease | |
| BI2606 | AF | NA | NA | HF to ZM | 1921 | NA | Decrease | |
| BI2960 | AF | NA | NA | HF to ZM | 1921 | NA | Decrease | |
| BI6447 | AF | NA | NA | HF to ZM | 1979 | NA | Decrease | |
| BI6471 | AF | NA | NA | HF to ZM | 1979 | NA | Decrease | |
| BI6537 | AF | NA | NA | HF to ZM | 1985 | NA | Decrease | |
| BI9366 | AF | NA | NA | HF to ZM | 1974 | NA | Decrease | |
| BI9460 | AF | NA | NA | HF to ZM | 1974 | NA | Decrease | |
| BS192 | AF | NA | NA | Coppice to HF | 1995 | NA | Decrease | |
| BS195 | AF | NA | NA | Coppice to HF | 1995 | NA | Decrease | |
| BS203 | AF | NA | NA | Coppice to HF | 2014 | NA | Decrease | |
| BV257 | AF | NA | NA | Coppice to HF | 1950 | NA | Decrease | |
| BS205 | RF | Arable land | 1860 | CWS to HF | 1950 | NA | Decrease | |
| BS331 | RF | Arable land | 1843 | HF throughout | NA | NA | Decrease | |
| BV42 | AF | NA | NA | Coppice to HF | 1950 | NA | Decrease | |
| BS359 | RF | Arable land | 1840 | Coppice to HF | 1950 | NA | Decrease | |
| CO1 | AF | NA | NA | HF to ZM | 1970 | NA | Decrease | |
| CO4.27 | AF | NA | NA | HF to ZM | 1970 | NA | Decrease | |
| CO5 | AF | NA | NA | HF to ZM | 1970 | NA | Decrease | |
| CO6 | AF | NA | NA | HF to ZM | 1970 | NA | Decrease | |
| CO8 | AF | NA | NA | HF to ZM | 1970 | NA | Decrease | |
| DE129 | AF | NA | NA | CWS to HF to ZM | 1935 | 1946 | Decrease | |
| DE400 | AF | NA | NA | CWS to HF to ZM | 1935 | 1946 | Decrease | |
| BS183 | RF | Arable land | 1860 | HF throughout | NA | NA | Unchanged | |
| DE446 | AF | NA | NA | CWS to HF to ZM | 1935 | 1946 | Decrease | |
| GO120 | AF | NA | NA | CWS to HF to ZM | 1860 | 1992 | Decrease | |
| GO548 | AF | NA | NA | CWS to HF to ZM | 1860 | 1997 | Decrease | |
| GO83 | AF | NA | NA | CWS to HF to ZM | 1860 | 1970 | Decrease | |
| KO775 | AF | NA | NA | CWS to HF | 1899 | NA | Decrease | |
| K0777 | AF | NA | NA | CWS to HF | 1940 | NA | Decrease | |
| KO778 | AF | NA | NA | CWS to HF | 1923 | NA | Decrease | |

| PLOT | LUH | Previous land cover | Year afforestation | Management transition(s) | Year transition 1 | Year transition 2 | ΔManagement |
|--------|-----|------------------------|-----------------------|-----------------------------|----------------------|----------------------|-------------|
| KO784 | AF | NA | NA | CWS to HF | 1931 | NA | Decrease |
| KO785 | AF | NA | NA | CWS to HF | 1924 | NA | Decrease |
| KO791 | AF | NA | NA | CWS to HF | 1883 | NA | Decrease |
| KO792 | AF | NA | NA | CWS to HF | 1884 | NA | Decrease |
| MO20 | AF | NA | NA | HF to ZM | 1912 | NA | Decrease |
| BS370 | RF | Heathland | 1810 | HF throughout | NA | NA | Unchanged |
| BV31 | RF | Grassland | 1912 | Coppice to HF | 1950 | NA | Decrease |
| PR125 | AF | NA | NA | WP to HF to ZM | 1990 | NA | Decrease |
| PR156 | AF | NA | NA | WP to HF | 1860 | NA | Decrease |
| PR170 | AF | NA | NA | WP to HF | 1860 | NA | Decrease |
| BV258 | RF | Grassland | 1900 | Coppice to HF | 1950 | NA | Decrease |
| BV1011 | RF | Grassland | 1912 | HF throughout | NA | NA | Unchanged |
| PR26 | AF | NA | NA | WP to HF to ZM | 1995 | NA | Decrease |
| BV46 | RF | Grassland | 1912 | HF throughout | NA | NA | Unchanged |
| PR68 | AF | NA | NA | WP to HF | NA | NA | Decrease |
| BV106 | RF | Grassland | 1900 | HF throughout | NA | NA | Unchanged |
| SKA124 | AF | NA | NA | WP to HF to ZM | 1990 | NA | Decrease |
| SKA133 | AF | NA | NA | WP to HF to ZM | 1990 | NA | Decrease |
| SKA71 | AF | NA | NA | HF to ZM | 1980 | NA | Decrease |
| SKA80 | AF | NA | NA | WP to HF to ZM | 1990 | NA | Decrease |
| SKA9 | AF | NA | NA | WP to ZM | 1978 | NA | Decrease |
| SKA96 | AF | NA | NA | WP to HF to ZM | 1980 | NA | Decrease |
| SKL1 | AF | NA | NA | Coppice to WP to ZM | 1900 | 1985 | Decrease |
| SKR20 | AF | NA | NA | Coppice to HF to ZM | 1950 | 1980 | Decrease |
| SKR26 | AF | NA | NA | Coppice to HF to ZM | 1950 | 1980 | Decrease |
| SKR32 | AF | NA | NA | Coppice to HF to ZM | 1950 | 1990 | Decrease |
| SKR34 | AF | NA | NA | Coppice to HF | 1950 | NA | Decrease |
| SKR35 | AF | NA | NA | Coppice to HF to ZM | 1950 | 1980 | Decrease |
| SKT16 | AF | NA | NA | Coppice to HF to ZM | 1960 | 1995 | Decrease |
| SKT22 | AF | NA | NA | CWS to HF to ZM | 1950 | 1980 | Decrease |
| SKT23 | AF | NA | NA | CWS to HF to ZM | 1950 | 1990 | Decrease |
| SKT26 | AF | NA | NA | Coppice to HF | 1950 | NA | Decrease |
| SP2B | AF | NA | NA | Coppice to HF | 1936 | NA | Decrease |
| SP3B | AF | NA | NA | CWS to HF | 1900 | NA | Decrease |
| SP4B | AF | NA | NA | Coppice to HF | 1939 | NA | Decrease |
| SP5B | AF | NA | NA | HF to ZM | 1980 | NA | Decrease |
| TB106 | AF | NA | NA | CWS to HF | 1961 | NA | Decrease |
| TB115B | AF | NA | NA | CWS to HF | 1961 | NA | Decrease |
| DE408 | RF | Arable land | 1935 | HF to ZM | 1946 | NA | Decrease |
| TB181 | AF | NA | NA | CWS to HF | 1961 | NA | Decrease |
| TB80 | AF | NA | NA | CWS to HF | 1961 | NA | Decrease |
| TB97 | AF | NA | NA | CWS to HF | 1961 | NA | Decrease |
| DE411 | RF | Arable land | 1935 | HF to ZM | 1946 | NA | Decrease |
| DE412 | RF | Arable land | 1935 | HF to ZM | 1946 | NA | Decrease |
| DE404 | RF | Grassland | 1870 | HF to ZM | 1946 | NA | Decrease |
| DE50 | RF | Grassland | 1870 | HF to ZM | 1946 | NA | Decrease |

| | | Previous | Year | Management | Year | Year | |
|----------|-----|-------------|---------------|---------------------|--------------|--------------|-------------|
| PLOT | LUH | land cover | afforestation | transition(s) | transition 1 | transition 2 | ΔManagement |
| DE27 | RF | Grassland | 1860 | HF to ZM | 1946 | NA | Decrease |
| WPY1 | AF | NA | NA | CWS to ZM | 1947 | NA | Decrease |
| WPY2 | AF | NA | NA | CWS to ZM | 1947 | NA | Decrease |
| WPY3 | AF | NA | NA | CWS to ZM | 1947 | NA | Decrease |
| WPY4 | AF | NA | NA | CWS to ZM | 1947 | NA | Decrease |
| WPY7 | AF | NA | NA | CWS to ZM | 1947 | NA | Decrease |
| WR1 | AF | NA | NA | Coppice to ZM | 1955 | NA | Decrease |
| DE28 | RF | Grassland | 1860 | HF to ZM | 1946 | NA | Decrease |
| WR2 | AF | NA | NA | Coppice to ZM | 1955 | NA | Decrease |
| WR3 | AF | NA | NA | Coppice to ZM | 1955 | NA | Decrease |
| WR4 | AF | NA | NA | Coppice to ZM | 1955 | NA | Decrease |
| WR5 | AF | NA | NA | Coppice to ZM | 1955 | NA | Decrease |
| M011 | RF | Grassland | 1912 | ZM throughout | NA | NA | Unchanged |
| M012 | RF | Grassland | 1912 | ZM throughout | NA | NA | Unchanged |
| M022 | RF | Grassland | 1912 | ZM throughout | NA | NA | Unchanged |
| WW1 | AF | NA | 1945 | CWS to ZM | 1955 | NA | Decrease |
| PR122 | RF | Arable land | 1970 | WP throughout | NA | NA | Unchanged |
| WW2 | AF | NA | NA | CWS to ZM | 1955 | NA | Decrease |
| WW3 | AF | NA | NA | CWS to ZM | 1955 | NA | Decrease |
| WW4 | AF | NA | NA | CWS to ZM | 1955 | NA | Decrease |
| WW5 | AF | NA | NA | CWS to ZM | 1955 | NA | Decrease |
| PR63 | RF | Grassland | 1900 | HF throughout | NA | NA | Unchanged |
| PR196 | RF | Grassland | 1881 | HF throughout | NA | NA | Unchanged |
| PR197 | RF | Grassland | 1881 | HF throughout | NA | NA | Unchanged |
| ZVD14 | AF | NA | NA | Coppice to HF to ZM | 1958 | 1985 | Decrease |
| ZVD16 | AF | NA | NA | Coppice to HF to ZM | 1965 | 1975 | Decrease |
| ZVD29 | AF | NA | NA | HF throughout | NA | NA | Decrease |
| ZVD31 | AF | NA | NA | Coppice to HF to ZM | 1958 | 1985 | Decrease |
| ZVD33 | AF | NA | NA | Coppice to HF to ZM | 1958 | 1985 | Decrease |
| ZVG24 | AF | NA | NA | Coppice to HF to ZM | 1958 | 1985 | Decrease |
| ZVG25 | AF | NA | NA | Coppice to HF to ZM | 1958 | 1985 | Decrease |
| ZVG62 | AF | NA | NA | Coppice to HF to ZM | 1958 | 1985 | Decrease |
| ZVY7 | AF | NA | NA | HF throughout | NA | NA | Decrease |
| PR204 | RF | Grassland | 1879 | HF throughout | NA | NA | Unchanged |
| SH3 | RF | Arable land | 1955 | HF throughout | NA | NA | Unchanged |
| SH1 | RF | Grassland | 1905 | HF throughout | NA | NA | Unchanged |
| SH2 | RF | Grassland | 1905 | HF throughout | NA | NA | Unchanged |
| SH4 | RF | Arable land | 1890 | HF throughout | NA | NA | Unchanged |
| LF1 | AF | NA | NA | HF throughout | NA | NA | Increase |
| LF10 | AF | NA | NA | HF throughout | NA | NA | Increase |
| LF12 | AF | NA | NA | HF throughout | NA | NA | Increase |
| LF14 | AF | NA | NA | HE throughout | NA | NA | Increase |
| LF15 | AF | NA | NA | HE throughout | NA | NA | Increase |
| LF16 | AF | NA | NA | HE throughout | NA | NA | Increase |
| 1 F3 | ΔF | NΔ | NA | HEthroughout | NΔ | NΔ | Increase |
| 15 | | NΔ | NA | HE throughout | NΔ | NΔ | Increase |
| LĽĴ | AL | 11/1 | IN/A | ine thioughout | IN/A | NA . | iiici ease |

| | | Due 1 | N | NA | No | N | |
|--------|-----------|------------------------|-----------------------|-------------------------------|----------------------|----------------------|-------------|
| PLOT | LUH | Previous land cover | Year afforestation | IVIanagement transition(s) | Year transition 1 | Year transition 2 | ΔManagement |
| LF7 | AF | NA | NA | HF throughout | NA | NA | Increase |
| LF9 | AF | NA | NA | HF throughout | NA | NA | Increase |
| BI6602 | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| BI6603 | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| BI6614 | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| BI6625 | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| BI6627 | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| SH9 | RF | Arable land | 1890 | HF throughout | NA | NA | Unchanged |
| SKA35 | RF | Heathland | 1900 | HF throughout | NA | NA | Unchanged |
| BS340 | AF | NA | NA | CWS throughout | NA | NA | Unchanged |
| BS342 | AF | NA | NA | Coppice throughout | NA | NA | Unchanged |
| BV103 | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| BV510 | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| CO4.20 | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| CO4.21 | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| CO4.23 | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| CO4.24 | AF | NA | NA | HE throughout | NA | NA | Unchanged |
| CO4.25 | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| SKA2 | RF | Heathland | 1880 | HE throughout | NA | NA | Unchanged |
| SP4A | RF | Arable land | 1840 | CWS to HF | 1935 | NA | Decrease |
| SP2A | RF | Arable land | 1820 | Coppice to HF | 1943 | NA | Decrease |
| SP1A | RF | Arable land | 1924 | HE throughout | ΝΔ | NA | Unchanged |
| SP3A | RF | Arable land | 1890 | HEthroughout | NΔ | NA | Unchanged |
| SP5A | RE | Arable land | 1884 | HEthroughout | NA | | Unchanged |
| GO104 | ΔΕ | | 1004 NA | | 1860 | | Unchanged |
| 60116 | | NA | | CWS to HE | 1880 | | Unchanged |
| GO110 | | NA | | CWS to HE | 1880 | | Unchanged |
| GO173 | | | | | 1000 | | Unchanged |
| 60182 | | | | | 1900 | | Unchanged |
| 60210 | | | | | 1990 | | Unchanged |
| G0237 | | | | | 1960 | | Unchanged |
| KO796 | | | | | 1900 | | Unchanged |
| KU780 | | | | | | | Unchanged |
| KU787 | | | | | | | Unchanged |
| KU789 | | NA Arabia land | NA 1004 | HF throughout | NA 1001 | NA | Unchanged |
| 1B151 | KF | Arable land | 1904 | CWS to HF | 1961 | NA | Decrease |
| 18146 | KF A F | Arable land | 1903 | | 1901 | NA | Decrease |
| | AF | NA | NA | ∠ivi throughout | NA | NA | Unchanged |
| M019 | AF | NA | NA | ZIVI throughout | NA | NA | Unchanged |
| M08 | AF | NA | NA | ZIVI throughout | NA | NA | Unchanged |
| M09 | AF | NA | NA | | NA | NA | Unchanged |
| тв140 | RF | Arable land | 1902 | CWS to HF | 1961 | NA | Decrease |
| TB120 | RF | Arable land | 1901 | CWS to HF | 1961 | NA | Decrease |
| SH10 | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| TB109 | RF | Arable land | 1900 | CWS to HF | 1961 | NA | Decrease |
| WAS10 | RF | Grassland | 1870 | HF to ZM | 1950 | NA | Decrease |
| SH5 | AF | NA | NA | HF throughout | NA | NA | Unchanged |

| DIOT | 1110 | Previous | Year | Management | Year | Year | AManagament |
|-------|------|-------------|---------------|---------------|--------------|--------------|---------------|
| PLUT | LOH | land cover | afforestation | transition(s) | transition 1 | transition 2 | Δινιαπαgement |
| SH6 | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| SH7 | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| SH8 | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| WAS11 | RF | Grassland | 1870 | HF to ZM | 1950 | NA | Decrease |
| WAS12 | RF | Grassland | 1870 | HF to ZM | 1950 | NA | Decrease |
| WAS14 | RF | Grassland | 1870 | HF to ZM | 1950 | NA | Decrease |
| SKA89 | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| SKA92 | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| WAS16 | RF | Grassland | 1870 | HF to ZM | 1950 | NA | Decrease |
| SP1B | AF | NA | NA | HF throughout | NA | NA | Unchanged |
| WR10 | RF | Arable land | 1893 | HF throughout | NA | NA | Unchanged |
| WR6 | RF | Arable land | 1893 | HF throughout | NA | NA | Unchanged |
| WR7 | RF | Arable land | 1893 | HF throughout | NA | NA | Unchanged |
| WR8 | RF | Arable land | 1893 | HF throughout | NA | NA | Unchanged |
| WR9 | RF | Arable land | 1893 | HF throughout | NA | NA | Unchanged |
| WW10 | RF | Arable land | 1945 | HF throughout | NA | NA | Increase |
| WW6 | RF | Arable land | 1945 | HF throughout | NA | NA | Increase |
| WW7 | RF | Arable land | 1945 | HF throughout | NA | NA | Increase |
| WW8 | RF | Arable land | 1945 | HF throughout | NA | NA | Increase |
| WW9 | RF | Arable land | 1945 | HF throughout | NA | NA | Increase |
| ZVG26 | AF | NA | NA | Coppice to HF | 1958 | NA | Unchanged |



Figure A3.9.1. Changes in shade-casting ability (RR_{SCA}; A), canopy cover (RR_{CC}; B) and litter quality (RR_{LQ}; C) for the three categories of management intensity change (increase, decrease or unchanged; see *Table A3.9.1*).

APPENDIX A3.10. COMPARISON OF INITIAL SPECIES POOLS BETWEEN ANCIENT AND RECENT FORESTS

We checked whether the initial species pools (at the time of the first survey) were similar between ancient and recent forests, within each region where both land-use histories occurred. We conducted a permutational multivariate analysis of variance (PERMANOVA; vegan package;Oksanen et al. (2019)) using Bray-Curtis dissimilarities with 999 permutations (based on abundance data; Bray and Curtis (1957)). To visualize the compositional differences in the herb layer, we used nonmetric multidimensional scaling (NMDS) (**Fig. A3.10.1**).

Overall, we found that species pools at the original survey time were similar for ancient and recent forests in most regions. We only found significantly different species pools in two regions (Skåne and Wales) (**Fig. A3.10.1**, **Table A3.10.1**).



Figure A3.10.1. Nonmetric multidimensional scaling (NMDS) of herb layer composition at the original survey time for the regions with both ancient and recent forest plots. Regions for which the PERMANOVA analysis showed a significantly different composition between ancient and recent plots (*Table A3.10.1*) are marked with a '*' in the legend.

| Region | Df | SumsofSqs | MeanSqs | F.Model | R ² | р |
|--------|----|-----------|---------|---------|----------------|-------|
| | 1 | 0.1114 | 0.1114 | 0.8317 | 0.1217 | 0.531 |
| MO | 6 | 0.8036 | 0.1339 | | 0.8783 | |
| | 7 | 0.915 | | | 1 | |
| | 1 | 0.3582 | 0.3582 | 1.3129 | 0.141 | 0.348 |
| SH | 8 | 2.1826 | 0.2728 | | 0.859 | |
| | 9 | 2.5407 | | | 1 | |
| | 1 | 0.771 | 0.771 | 2.5543 | 0.242 | 0.03 |
| SKA | 8 | 2.4146 | 0.3018 | | 0.758 | |
| | 9 | 3.1856 | | | 1 | |
| | 1 | 0.3709 | 0.3709 | 1.1744 | 0.128 | 0.328 |
| ТВ | 8 | 2.5267 | 0.3158 | | 0.872 | |
| | 9 | 2.8976 | | | 1 | |
| | 1 | 0.7184 | 0.7184 | 3.3261 | 0.2937 | 0.014 |
| W | 8 | 1.728 | 0.216 | | 0.7063 | |
| | 9 | 2.4464 | | | 1 | |
| | 1 | 0.4327 | 0.4327 | 2.3761 | 0.229 | 0.052 |
| WR | 8 | 1.4568 | 0.1821 | | 0.771 | |
| | 9 | 1.8895 | | | 1 | |
| | 1 | 0.2095 | 0.2095 | 0.8812 | 0.0992 | 0.502 |
| WW | 8 | 1.9019 | 0.2377 | | 0.9008 | |
| | 9 | 2.1114 | | | 1 | |
| | 1 | 0.3881 | 0.3881 | 1.1424 | 0.125 | 0.339 |
| DE | 8 | 2.7177 | 0.3397 | | 0.875 | |
| | 9 | 3.1058 | | | 1 | |
| | 1 | 0.5805 | 0.5805 | 2.7428 | 0.2553 | 0.066 |
| PR | 8 | 1.693 | 0.2116 | | 0.7447 | |
| | 9 | 2.2735 | | | 1 | |
| | 1 | 0.2206 | 0.2206 | 1.1684 | 0.1274 | 0.286 |
| BS | 8 | 1.5105 | 0.1888 | | 0.8726 | |
| | 9 | 1.7311 | | | 1 | |
| | 1 | 0.4235 | 0.4235 | 1.3169 | 0.1583 | 0.314 |
| SP | 7 | 2.2512 | 0.3216 | | 0.8417 | |
| | 8 | 2.6747 | | | 1 | |
| | 1 | 0.1339 | 0.1339 | 0.396 | 0.0535 | 0.954 |
| BV | 7 | 2.3675 | 0.3382 | | 0.9465 | |
| | 8 | 2.5014 | | | 1 | |

Table A3.10.1. Results of PERMANOVA analyses for the regions with both ancient and recent forest plots.

APPENDIX A3.11. OLSEN P CONCENTRATIONS IN RECENT VS. ANCIENT FORESTS

We compared Olsen P concentrations between plots in recent and ancient forests (in the regions where both types occurred). With linear mixed-effect modelling, including region as a random effect, we found that land-use history (LUH) had a significant effect on the Olsen P concentrations, with higher values in recent forests (**Table A3.11.1**). We observed unexpected trends for some regions (Tournibus, Wales and Wytham Woods), with higher Olsen P levels in ancient than recent forests (although not significant) (**Fig. A3.11.1**). These regions with unexpected patterns were all characterised by a negative P balance. The P balance is a proxy for the agricultural intensity of a region, and reflects the actual application and withdrawal (harvest) of Phosphorus on the field (Bomans et al., 2005).

| | | Olsen P | |
|------------------------------------|------------|---------------|--------|
| Predictors | Estimates | CI | p |
| (Intercept) | 24.69 | 16.27 – 33.10 | <0.001 |
| RF | 8.02 | 0.23 - 15.82 | 0.046 |
| Random Effects | | | |
| σ^2 | 445.91 | | |
| $\tau_{00 \text{ Region}}$ | 130.40 | | |
| ICC | 0.23 | | |
| N Region | 12 | | |
| Observations | 117 | | |
| Marginal R^2 / Conditional R^2 | 0.027 / 0. | .247 | |

Table A3.11.5. Linear mixed-effect modelling results of Olsen P ~ LUH + (1 | Region). RF = recent forest.



Figure A3.11.2. Olsen P concentrations in ancient and recent forest plots, for regions in which both types occurred. Regions in which the difference in Olsen P between ancient and recent forest was significant, are indicated with '*' (only PR and SP). Regions are ranked according to their P balance (i.e. the actual application and withdrawal (harvest) of P on the field), a proxy of agricultural intensity. P balance values: MO, SH, SKA, TB, W, WR, and WW < 0 kg P/ha; DE and PR: 0-5 kg P/ha; BS: 5-10 kg P/ha; SP: 10-15 kg P/ha; BV: >20 kg P/ha.



APPENDIX A3.12. CORRELATIONS BETWEEN RESPONSE VARIABLES

Figure A3.12.1. Overview of the correlations between response variables. The lower left panel shows the Pearson's correlation coefficient. The upper right panel shows the data points and a smoother (red line).

APPENDIX A3.13. MODEL RESULTS

Table A3.13.1. Estimates (Est), confidence intervals (CI) and p-values from the linear mixed-effect models with the response ratio (RR) of the three biodiversity measures as response variable. See main text for a description of the response variables and predictors. LUH = land-use history; RF = recent forest; CWM = community weighted mean; EIV-F = Ellenberg indicator value for moisture; CC = canopy cover; SCA = Shade-casting ability; LQ = litter quality; MAT = mean annual temperature; Ndep = nitrogen deposition.

| | | RR species richness | | F | R Shannon diversity | | | RR species evenness | | | |
|------------------------|---------|---------------------|-------|---------|---------------------|-------|---------|---------------------|-------|--|--|
| Predictors | Est | CI | р | Est | CI | р | Est | CI | р | | |
| (Intercept) | -0.0015 | -0.0074 - 0.0045 | 0.625 | 0.0009 | -0.0044 - 0.0062 | 0.746 | 0.0087 | 0.0029 - 0.0145 | 0.003 | | |
| Plot size | 0.0027 | -0.0001 - 0.0056 | 0.062 | -0.0001 | -0.0026 - 0.0025 | 0.953 | -0.0010 | -0.0037 - 0.0018 | 0.476 | | |
| Soil type (ClayNoCarb) | 0.0009 | -0.0028 - 0.0046 | 0.634 | -0.0007 | -0.0050 - 0.0037 | 0.756 | -0.0006 | -0.0049 - 0.0037 | 0.792 | | |
| Soil type (Sand) | -0.0005 | -0.0066 - 0.0055 | 0.858 | -0.0012 | -0.0068 - 0.0044 | 0.673 | -0.0021 | -0.0081 - 0.0039 | 0.494 | | |
| LUH (RF) | -0.0024 | -0.0067 - 0.0020 | 0.289 | -0.0008 | -0.0050 - 0.0035 | 0.725 | -0.0042 | -0.00800.0003 | 0.033 | | |
| Olsen P | 0.0014 | 0.0001 - 0.0027 | 0.038 | 0.0013 | 0.0002 - 0.0025 | 0.024 | 0.0000 | -0.0011 - 0.0012 | 0.979 | | |
| EIV-F | 0.0008 | -0.0009 - 0.0025 | 0.347 | 0.0011 | -0.0003 - 0.0025 | 0.128 | 0.0004 | -0.0011 - 0.0019 | 0.597 | | |
| RR CC | -0.0005 | -0.0024 - 0.0013 | 0.583 | -0.0001 | -0.0015 - 0.0014 | 0.928 | -0.0001 | -0.0018 - 0.0016 | 0.897 | | |
| RR SCA | 0.0007 | -0.0007 - 0.0020 | 0.356 | 0.0001 | -0.0013 - 0.0016 | 0.844 | 0.0021 | 0.0005 - 0.0037 | 0.011 | | |
| RR LQ | 0.0007 | -0.0011 - 0.0025 | 0.461 | -0.0003 | -0.0019 - 0.0012 | 0.677 | 0.0005 | -0.0012 - 0.0021 | 0.573 | | |
| ΔΜΑΤ | -0.0001 | -0.0059 - 0.0057 | 0.970 | -0.0004 | -0.0050 - 0.0043 | 0.873 | -0.0019 | -0.0067 - 0.0030 | 0.419 | | |
| ΔAridity | -0.0004 | -0.0063 - 0.0055 | 0.884 | -0.0008 | -0.0044 - 0.0028 | 0.632 | -0.0012 | -0.0061 - 0.0036 | 0.596 | | |
| Ndep | 0.0000 | -0.0049 - 0.0049 | 0.993 | -0.0017 | -0.0062 - 0.0028 | 0.423 | 0.0008 | -0.0036 - 0.0052 | 0.714 | | |
| LUH:Ndep | -0.0002 | -0.0044 - 0.0040 | 0.915 | -0.0015 | -0.0078 - 0.0047 | 0.627 | -0.0016 | -0.0055 - 0.0022 | 0.397 | | |
| LUH:∆MAT | -0.0029 | -0.0084 - 0.0026 | 0.301 | 0.0003 | -0.0076 - 0.0081 | 0.941 | 0.0000 | -0.0047 - 0.0047 | 0.988 | | |
| LUH:∆Aridity | -0.0043 | -0.0091 - 0.0006 | 0.082 | -0.0027 | -0.0061 - 0.0007 | 0.125 | -0.0025 | -0.0064 - 0.0014 | 0.208 | | |
| LUH:RR CC | -0.0007 | -0.0031 - 0.0018 | 0.583 | 0.0008 | -0.0014 - 0.0029 | 0.472 | -0.0003 | -0.0029 - 0.0023 | 0.809 | | |
| LUH:RR SCA | -0.0001 | -0.0025 - 0.0023 | 0.915 | -0.0013 | -0.0040 - 0.0014 | 0.328 | -0.0024 | -0.0055 - 0.0007 | 0.128 | | |
| LUH:RR LQ | -0.0006 | -0.0055 - 0.0043 | 0.809 | 0.0009 | -0.0033 - 0.0051 | 0.665 | 0.0020 | -0.0017 - 0.0057 | 0.292 | | |
| Observations | 185 | | | 185 | | | 185 | | | | |

Appendix to Chapter 3

Table A3.13.2. Estimates (Est), confidence intervals (CI) and p-values from the linear mixed-effect models with the response ratio (RR) of the total cover of the herb layer and the community weighted mean trait values for 'plant height' and 'specific leaf area (SLA)'. See main text for a description of the response variables and predictors. LUH = land-use history; RF = recent forest; CWM = community weighted mean; EIV-F = Ellenberg indicator value for moisture; CC = canopy cover; SCA = Shade-casting ability; LQ = litter quality; MAT = mean annual temperature; Ndep = nitrogen deposition.

| | | RR total herb cover | | | RR plant height | | | RR SLA | | | |
|------------------------|---------|---------------------|--------|---------|------------------|--------|---------|------------------|--------|--|--|
| Predictors | Est | CI | р | Est | CI | p | Est | CI | р | | |
| (Intercept) | -0.0235 | -0.03420.0128 | <0.001 | -0.0024 | -0.0081 - 0.0033 | 0.412 | -0.0007 | -0.0029 - 0.0015 | 0.546 | | |
| Plot size | 0.0003 | -0.0046 - 0.0051 | 0.918 | -0.0024 | -0.0050 - 0.0002 | 0.075 | 0.0006 | -0.0004 - 0.0017 | 0.221 | | |
| Soil type (ClayNoCarb) | 0.0022 | -0.0055 - 0.0098 | 0.576 | 0.0046 | 0.0010 - 0.0081 | 0.012 | 0.0005 | -0.0014 - 0.0025 | 0.601 | | |
| Soil type (Sand) | 0.0015 | -0.0087 - 0.0116 | 0.776 | 0.0119 | 0.0060 - 0.0178 | <0.001 | 0.0004 | -0.0022 - 0.0030 | 0.769 | | |
| LUH (RF) | 0.0075 | 0.0004 - 0.0145 | 0.039 | -0.0034 | -0.0076 - 0.0008 | 0.111 | 0.0001 | -0.0015 - 0.0016 | 0.947 | | |
| Olsen P | 0.0004 | -0.0016 - 0.0023 | 0.694 | -0.0007 | -0.0016 - 0.0002 | 0.113 | -0.0005 | -0.0011 - 0.0002 | 0.172 | | |
| EIV-F | 0.0001 | -0.0017 - 0.0019 | 0.940 | -0.0027 | -0.00420.0013 | <0.001 | -0.0004 | -0.0011 - 0.0003 | 0.293 | | |
| RR CC | -0.0027 | -0.00460.0007 | 0.007 | -0.0047 | -0.00620.0032 | <0.001 | 0.0017 | 0.0008 - 0.0025 | <0.001 | | |
| RR SCA | -0.0050 | -0.00830.0018 | 0.002 | -0.0010 | -0.0021 - 0.0001 | 0.074 | 0.0009 | -0.0000 - 0.0019 | 0.051 | | |
| RR LQ | 0.0002 | -0.0025 - 0.0030 | 0.871 | 0.0007 | -0.0009 - 0.0022 | 0.400 | 0.0002 | -0.0006 - 0.0011 | 0.581 | | |
| ΔΜΑΤ | -0.0011 | -0.0103 - 0.0080 | 0.794 | 0.0006 | -0.0047 - 0.0058 | 0.826 | -0.0010 | -0.0028 - 0.0007 | 0.215 | | |
| ΔAridity | -0.0036 | -0.0135 - 0.0064 | 0.456 | 0.0001 | -0.0055 - 0.0056 | 0.982 | -0.0003 | -0.0017 - 0.0011 | 0.630 | | |
| Ndep | -0.0074 | -0.0151 - 0.0003 | 0.059 | 0.0028 | -0.0020 - 0.0075 | 0.234 | -0.0002 | -0.0017 - 0.0014 | 0.809 | | |
| LUH:Ndep | 0.0087 | 0.0042 - 0.0133 | <0.001 | -0.0027 | -0.0066 - 0.0012 | 0.179 | -0.0006 | -0.0026 - 0.0013 | 0.519 | | |
| LUH:ΔMAT | -0.0095 | -0.01620.0027 | 0.006 | 0.0025 | -0.0018 - 0.0069 | 0.256 | 0.0009 | -0.0017 - 0.0035 | 0.507 | | |
| LUH:∆Aridity | 0.0061 | -0.0019 - 0.0140 | 0.134 | -0.0012 | -0.0055 - 0.0032 | 0.602 | -0.0013 | -0.00250.0000 | 0.045 | | |
| LUH:RR CC | 0.0055 | 0.0016 - 0.0094 | 0.006 | 0.0047 | 0.0020 - 0.0074 | 0.001 | -0.0015 | -0.00280.0002 | 0.020 | | |
| LUH:RR SCA | 0.0064 | 0.0013 - 0.0116 | 0.015 | -0.0001 | -0.0037 - 0.0035 | 0.942 | -0.0022 | -0.00350.0009 | 0.001 | | |
| LUH:RR LQ | 0.0026 | -0.0051 - 0.0103 | 0.503 | -0.0049 | -0.0100 - 0.0003 | 0.063 | -0.0012 | -0.0031 - 0.0007 | 0.224 | | |
| Observations | 185 | | | 185 | | | 185 | | | | |

APPENDIX A3.14. COMPARISON OF CANOPY COVER AND SCA

BETWEEN SURVEYS AND BETWEEN LAND-USE HISTORIES

We compared canopy cover and SCA between plots in recent and ancient forests. With linear mixedeffect modelling, including region as a random effect, we found that land-use history (LUH) had a significant effect on SCA, with higher values in ancient forests for both survey times. Canopy cover on the other hand, was not related to land-use history (**Table A3.14.1**, **Fig. A3.14.1**).

Table A3.14.6. Linear mixed-effect modelling results of SCA ~ LUH + (1 | Region) and Canopy cover ~ LUH + (1 | Region). RF = recent forest.

| | SC | A (original su | rvey) | S | CA (new surv | ey) | Cover (original survey) | | | Cover (new survey) | | |
|----------------------------|--------|----------------|--------|--------|--------------|--------|-------------------------|--------------|--------|--------------------|--------------|--------|
| Predictors | Est | CI | р | Est | CI | р | Est | CI | р | Est | CI | p |
| (Intercept) | 3.50 | 3.12 – 3.88 | <0.001 | 3.72 | 3.37 – 4.06 | <0.001 | 0.80 | 0.76 – 0.84 | <0.001 | 0.80 | 0.75 – 0.84 | <0.001 |
| LUH [RF] | -0.33 | -0.550.10 | 0.004 | -0.26 | -0.430.08 | 0.004 | 0.01 | -0.03 - 0.05 | 0.766 | -0.02 | -0.07 – 0.03 | 0.376 |
| Random Effec | ts | | | | | | | | | | | |
| σ2 | 0.36 | | | 0.22 | | | 0.01 | | | 0.02 | | |
| ICC | 0.65 | | | 0.71 | | | 0.30 | | | 0.20 | | |
| Ν | 19 Reg | gion | | 19 Reg | gion | | 17 Re | gion | | 17 Reg | ion | |
| Observations | 191 | | | 192 | | | 173 | | | 174 | | |
| Marginal R ² / | | | | | | | | | | | | |
| Conditional R ² | 0.021 | / 0.656 | | 0.018 | / 0.720 | | 0.000 | / 0.303 | | 0.005 / | 0.199 | |



Figure A3.14.1. Boxplots of canopy cover (A) and shade-casting ability (B) for both surveys (O = Old and N = New) and for ancient and recent forest plots.

Appendix A4

[Chapter 4]

APPENDIX A4.1. PREDICTING UNDERSTOREY LIGHT SIGNATURES FROM CANOPY CHARACTERISTICS USING ABUNDANCE-WEIGHTED RESPONSE VARIABLES

We repeated our main analysis (i.e. 'predicting understorey light signatures from canopy structure and composition') using abundance-weighted values for both EIV_{LIGHT} and %FS, instead of presence/absence based values, to check whether this resulted in different responses (**Fig. A4.1.1**). All models showed very poor model fits (R²m ranging from 0 to 0.02 for EIV_{LIGHT} and R²m = 0 for all models with %FS as response variable). Canopy closure was the only significant predictor for EIV_{LIGHT}, and canopy cover was the only significant predictor for %FS (but with a very small effect size of only - 0.004). Overall, comparing these results to the results for the presence/absence based responses, illustrates that the effects of canopy characteristics on the understorey light signature are mainly driven by the rare species with low abundances. These less abundant species are given equal weight in the presence/absence analysis, where we found stronger effects of canopy characteristics and higher model fits, while they are given a lower weight than the more abundant species in the abundance-based analyses, where we found small effects and lower model fits.





APPENDIX A4.2. RESULTS OF STATISTICAL ANALYSES WHEN USING CANOPY COVER VALUES THAT WERE NOT CORRECTED FOR OVERLAPPING LAYERS

The methods to obtain the results shown in **Fig. A4.2.1** and **Fig. A4.2.2** are identical to the methods described in the main text of Chapter 4, except that canopy cover values were obtained by simply taking the sum of the cover of all shrub and tree species, instead of applying the formula described by Fischer (2015) to account for overlap. Therefore, canopy cover values can be higher than 100 % here.

For both analyses, the overall results and trends were very similar to the results and trends obtained when including the correction for overlap (**Fig. 4.1** and **Fig. 4.2**), but model fits were slightly better when accounting for overlap through applying the formula.



Figure A4.2.1. Relating basal area, canopy cover and canopy closure, with canopy cover calculated as the sum of all tree and shrub species (i.e. not accounting for overlap between species/layers). (a) Linear (black line) and exponential (red line) relationship between canopy closure and canopy cover; (b) Linear (black line) and exponential (red line) relationship between canopy closure and basal area; (c) linear relationship between basal area and canopy cover. In all three models, 'region' was included as a random effect, with random slopes (β) and random intercepts (a) only in the second and third set of models (b+c). Coloured dots represent the actual data points per region. The region labels refer to **Table 1.1**.





APPENDIX A4.3. CORRELATION BETWEEN SCA-SCORES AND LAI FOR ELEVEN MAJOR CENTRAL EUROPEAN TREE SPECIES

For eleven major Central European tree species, we compared our shade-casting ability (SCA) scores to the leaf area index (LAI) obtained from Leuschner and Meier (2018) (**Fig. A4.3.1**). There was a positive and strong correlation between the two variables, Pearson's r = 0.85, p < 0.001.



Figure A4.3.1. Correlation between leaf area index (LAI) and shade-casting ability scores (SCA) for eleven major Central European tree species (Leuschner & Meier, 2018).

Appendix A5

[Chapter 5]

APPENDIX A5.1. THE 29 STUDY PLOTS

| Site | ID | Latitude | Longitude | Size | First survey | Second survey |
|--------------|-------|-----------|-----------|--------|--------------|---------------|
| Koda Wood | KO775 | 49.936408 | 14.096280 | 400 m² | 1957 | 2015 |
| (Czech | K0777 | 49.939641 | 14.093676 | 400 m² | 1957 | 2015 |
| Republic) | KO778 | 49.940555 | 14.098687 | 400 m² | 1957 | 2015 |
| | KO784 | 49.934512 | 14.100819 | 400 m² | 1957 | 2015 |
| | KO785 | 49.932949 | 14.107652 | 400 m² | 1957 | 2015 |
| | KO786 | 49.930361 | 14.104681 | 400 m² | 1957 | 2015 |
| | KO787 | 49.927881 | 14.103873 | 400 m² | 1957 | 2015 |
| | KO789 | 49.927086 | 14.106577 | 400 m² | 1957 | 2015 |
| | KO791 | 49.933729 | 14.117787 | 400 m² | 1957 | 2015 |
| | KO792 | 49.934928 | 14.120776 | 400 m² | 1957 | 2015 |
| Slovak Karst | SKT26 | 48.612010 | 20.542656 | 500 m² | 1975 | 2015 |
| (Slovakia) | SKR32 | 48.603473 | 20.579832 | 500 m² | 1975 | 2015 |
| | SKR35 | 48.606473 | 20.584043 | 500 m² | 1975 | 2015 |
| | SKT23 | 48.610453 | 20.535703 | 500 m² | 1975 | 2015 |
| | SKR20 | 48.611833 | 20.588566 | 500 m² | 1975 | 2015 |
| | SKT16 | 48.617928 | 20.537832 | 500 m² | 1975 | 2015 |
| | SKR26 | 48.611279 | 20.579970 | 500 m² | 1975 | 2015 |
| | SKR34 | 48.606714 | 20.579944 | 500 m² | 1975 | 2015 |
| | SKT22 | 48.607992 | 20.538759 | 500 m² | 1975 | 2015 |
| Zvolen | ZVD29 | 48.642060 | 19.285881 | 500 m² | 1963 | 2015 |
| (Slovakia) | ZVG26 | 48.626299 | 19.345731 | 500 m² | 1964 | 2015 |
| | ZVG24 | 48.617755 | 19.342796 | 500 m² | 1964 | 2015 |
| | ZVD14 | 48.627717 | 19.311616 | 500 m² | 1963 | 2015 |
| | ZVD33 | 48.629151 | 19.312970 | 500 m² | 1963 | 2015 |
| | ZVY7 | 48.639690 | 19.288793 | 500 m² | 1963 | 2015 |
| | ZVG25 | 48.623646 | 19.342791 | 500 m² | 1964 | 2015 |
| | ZVG62 | 48.626821 | 19.332363 | 500 m² | 1964 | 2015 |
| | ZVD31 | 48.624698 | 19.311915 | 500 m² | 1963 | 2015 |
| | ZVD16 | 48.636102 | 19.309211 | 500 m² | 1963 | 2015 |

Table A5.1.1. The location, size and survey years of the 29 study plots

APPENDIX A5.2. WEIGHTED-AVERAGE FINAL TPMS

The final TPM was calculated as the weighted average of the probability estimates provided by the six experts, using their provided confidence levels as a weighting factor:

$$\bar{x}^* = \frac{\sum_{i=1}^N w_i x_i}{\sum_{i=1}^N w_i}$$

with N the number of experts, w_i the confidence levels and x_i the probability estimates.

The weighted standard deviation was calculated as:

$$\sqrt{\frac{\sum_{i=1}^{N} w_i (x_i - \bar{x}^*)^2}{\frac{M-1}{M} \sum_{i=1}^{N} w_i}}$$

with \bar{x}^* the weighted average and M the number of non-zero weights.

Table A5.2.1. Second-order TPM with the weighted average (± standard deviation) probabilities of the six experts

| | Licht | Licht | Probability | distribution f | or light transr | nittance at t |
|---------------------------|---------------------------|---------------------------|-----------------|-------------------|-------------------|---------------|
| Management action at t | transmittance at (t-1) | transmittance at (t-2) | Strong shade | Moderate shade | Moderate light | Strong light |
| | | | (0-8%) | (8-20%) | (20-40%) | (40-100%) |
| Zero cut | Strong shade | Strong shade | 0.90±0.00 | 0.10±0.00 | 0.00±0.00 | 0.00±0.00 |
| Zero cut | Strong shade | Moderate shade | 0.88±0.04 | 0.12±0.04 | 0.00±0.00 | 0.00±0.00 |
| Zero cut | Strong shade | Moderate light | 0.85±0.10 | 0.13±0.09 | 0.01±0.04 | 0.00±0.00 |
| Zero cut | Strong shade | Strong light | 0.86±0.08 | 0.12±0.05 | 0.02±0.04 | 0.00±0.00 |
| Zero cut | Moderate shade | Strong shade | 0.42±0.15 | 0.5±0.15 | 0.08±0.04 | 0.00±0.00 |
| Zero cut | Moderate shade | Moderate shade | 0.37±0.11 | 0.53±0.11 | 0.10±0.00 | 0.00±0.00 |
| Zero cut | Moderate shade | Moderate light | 0.43±0.13 | 0.47±0.13 | 0.10±0.00 | 0.00±0.00 |
| Zero cut | Moderate shade | Strong light | 0.36±0.16 | 0.51±0.17 | 0.12±0.04 | 0.02±0.04 |
| Zero cut | Moderate light | Strong shade | 0.15±0.09 | 0.5±0.18 | 0.28±0.19 | 0.07±0.08 |
| Zero cut | Moderate light | Moderate shade | 0.19±0.24 | 0.41±0.15 | 0.34±0.17 | 0.07±0.05 |
| Zero cut | Moderate light | Moderate light | 0.11±0.03 | 0.45±0.19 | 0.37±0.15 | 0.08±0.05 |
| Zero cut | Moderate light | Strong light | 0.08±0.05 | 0.42±0.12 | 0.43±0.05 | 0.07±0.05 |
| Zero cut | Strong light | Strong shade | 0.02±0.04 | 0.20±0.06 | 0.50±0.15 | 0.28±0.20 |
| Zero cut | Strong light | Moderate shade | 0.00±0.00 | 0.12±0.10 | 0.55±0.19 | 0.32±0.15 |
| Zero cut | Strong light | Moderate light | 0.00±0.00 | 0.15±0.05 | 0.54±0.16 | 0.32±0.14 |
| Zero cut | Strong light | Strong light | 0.01±0.03 | 0.08±0.10 | 0.52±0.19 | 0.39±0.17 |
| Thinning | Strong shade | Strong shade | 0.20±0.10 | 0.50±0.12 | 0.26±0.14 | 0.04±0.05 |
| Thinning | Strong shade | Moderate shade | 0.18±0.11 | 0.50±0.12 | 0.28±0.14 | 0.04±0.05 |
| Thinning | Strong shade | Moderate light | 0.22±0.11 | 0.50±0.12 | 0.24±0.16 | 0.04±0.05 |
| Thinning | Strong shade | Strong light | 0.20±0.12 | 0.47±0.13 | 0.28±0.16 | 0.05±0.06 |
| Thinning | Moderate shade | Strong shade | 0.05±0.05 | 0.39±0.25 | 0.46±0.18 | 0.11±0.11 |
| Thinning | Moderate shade | Moderate shade | 0.05±0.05 | 0.41±0.25 | 0.44±0.19 | 0.10±0.11 |
| Thinning | Moderate shade | Moderate light | 0.05±0.05 | 0.34±0.21 | 0.49±0.14 | 0.12±0.10 |
| Thinning | Moderate shade | Strong light | 0.05±0.05 | 0.34±0.21 | 0.49±0.14 | 0.12±0.10 |

Probability distribution for light transmittance at t Light Light Moderate Management Strong Moderate transmittance transmittance Strong light light action at t shade shade at (t-1) at (t-2) (0-8%) (8-20%) (20-40%) (40-100%) Thinning Moderate light Strong shade 0.03±0.05 0.09±0.12 0.5±0.19 0.39±0.21 Thinning Moderate light Moderate shade 0.03±0.05 0.12±0.17 0.48±0.18 0.37±0.22 Thinning Moderate light Moderate light 0.01±0.04 0.12±0.17 0.50±0.18 0.37±0.22 Thinning Moderate light Strong light 0.01±0.04 0.06±0.08 0.50±0.19 0.43±0.17 Strong light Thinning Strong shade 0.00±0.00 0.01±0.04 0.06±0.09 0.93±0.12 Thinning Strong light Moderate shade 0.00±0.00 0.02±0.07 0.09±0.18 0.88±0.24 Thinning Moderate light Strong light 0.00±0.00 0.01±0.04 0.08±0.15 0.91±0.18 Thinning Strong light Strong light 0.00±0.00 0.00±0.00 0.10 ± 0.16 0.90±0.16 Strong shade Shelter cut Strong shade 0.05±0.07 0.25±0.13 0.54±0.11 0.16±0.12 Shelter cut Strong shade Moderate shade 0.03±0.07 0.26±0.13 0.54±0.11 0.17±0.13 Shelter cut Strong shade Moderate light 0.03±0.07 0.26±0.13 0.55±0.11 0.16±0.12 Shelter cut Strong shade Strong light 0.04±0.07 0.28±0.14 0.53±0.12 0.15±0.12 Shelter cut Moderate shade Strong shade 0.00±0.00 0.13±0.14 0.64±0.13 0.23±0.14 Shelter cut Moderate shade Moderate shade 0.00±0.00 0.13±0.14 0.64±0.13 0.23±0.14 Shelter cut Moderate light Moderate shade 0.00±0.00 0.13±0.16 0.63±0.15 0.25±0.14 Shelter cut Moderate shade Strong light 0.01±0.03 0.10±0.14 0.63±0.16 0.26±0.13 Shelter cut Moderate light Strong shade 0.00±0.00 0.03±0.05 0.40±0.22 0.57±0.26 Shelter cut Moderate light Moderate shade 0.00±0.00 0.03±0.05 0.40±0.22 0.57±0.26 Shelter cut Moderate light Moderate light 0.00±0.00 0.03±0.05 0.43±0.26 0.54±0.30 Moderate light Shelter cut Strong light 0.00±0.00 0.03±0.05 0.35±0.17 0.62±0.20 Shelter cut Strong light Strong shade 0.00±0.00 0.00±0.00 0.12±0.21 0.88±0.21 Shelter cut Strong light Moderate shade 0.00±0.00 0.01±0.04 0.08±0.16 0.91±0.19 Shelter cut Strong light Moderate light 0.00±0.00 0.00±0.00 0.07±0.13 0.93±0.13 0.00±0.00 Shelter cut Strong light Strong light 0.00±0.00 0.06±0.11 0.94±0.11 Strong shade Clear-cut Strong shade 0.00±0.00 0.00±0.00 0.02±0.04 0.98±0.04 0.00±0.00 Clear-cut Strong shade Moderate shade 0.00±0.00 0.02±0.04 0.98±0.04 Clear-cut Moderate light 0.00±0.00 Strong shade 0.00±0.00 0.02±0.04 0.98±0.04 0.00±0.00 Clear-cut Strong shade Strong light 0.00±0.00 0.02±0.04 0.98±0.04 Strong shade 0.00±0.00 Clear-cut Moderate shade 0.02±0.06 0.06±0.16 0.92±0.22 0.00±0.00 Clear-cut Moderate shade Moderate shade 0.02±0.06 0.06±0.16 0.92±0.22 Clear-cut Moderate shade Moderate light 0.00±0.00 0.02±0.06 0.06±0.16 0.92±0.22 0.00±0.00 Clear-cut Moderate shade Strong light 0.02±0.06 0.06±0.16 0.92±0.22 0.00±0.00 0.00±0.00 Clear-cut Moderate light Strong shade 0.05±0.13 0.95±0.13 0.00±0.00 0.00±0.00 Moderate light Clear-cut Moderate shade 0.05±0.13 0.95±0.13 Moderate light 0.00±0.00 0.00±0.00 Clear-cut Moderate light 0.05±0.13 0.95±0.13 0.00±0.00 0.00±0.00 Clear-cut Moderate light Strong light 0.05±0.13 0.95±0.13 0.00±0.00 0.00±0.00 Clear-cut Strong light Strong shade 0.01±0.04 0.99±0.04 0.00±0.00 0.00±0.00 Moderate shade Clear-cut Strong light 0.01±0.04 0.99±0.04 0.00±0.00 0.00±0.00 Moderate light Clear-cut Strong light 0.01±0.04 0.99±0.04 Clear-cut Strong light Strong light 0.00±0.00 0.00±0.00 0.02±0.04 0.98±0.04

Table A5.2.2. First-order TPM, derived from the second-order TPM by marginalization, i.e. grouping scenarios with the same combination of light transmittance at t-1 and management at t (thus: only differing in the light transmittance at t-2) and calculating the average probability distribution for each group of scenarios.

| | Light | Probability | y distribution f | or light transmit | ttance at t |
|---------------------------|---------------------------|------------------------|------------------------------|-------------------------------|---------------------------|
| Management action at t | transmittance at (t-1) | Strong shade (0-8%) | Moderate shade (8-20%) | Moderate light (20-40%) | Strong light (40-100%) |
| Zero cut | Strong shade | 0.87 | 0.12 | 0.01 | 0.00 |
| Zero cut | Moderate shade | 0.40 | 0.50 | 0.10 | 0.00 |
| Zero cut | Moderate light | 0.13 | 0.44 | 0.36 | 0.07 |
| Zero cut | Strong light | 0.01 | 0.14 | 0.53 | 0.33 |
| Thinnings | Strong shade | 0.20 | 0.49 | 0.27 | 0.04 |
| Thinnings | Moderate shade | 0.05 | 0.37 | 0.47 | 0.11 |
| Thinnings | Moderate light | 0.02 | 0.10 | 0.50 | 0.39 |
| Thinnings | Strong light | 0.00 | 0.01 | 0.08 | 0.90 |
| Shelter cut | Strong shade | 0.04 | 0.26 | 0.54 | 0.16 |
| Shelter cut | Moderate shade | 0.00 | 0.12 | 0.64 | 0.24 |
| Shelter cut | Moderate light | 0.00 | 0.03 | 0.39 | 0.57 |
| Shelter cut | Strong light | 0.00 | 0.00 | 0.08 | 0.91 |
| Clear cut | Strong shade | 0.00 | 0.00 | 0.02 | 0.98 |
| Clear cut | Moderate shade | 0.00 | 0.02 | 0.06 | 0.92 |
| Clear cut | Moderate light | 0.00 | 0.00 | 0.05 | 0.95 |
| Clear cut | Strong light | 0.00 | 0.00 | 0.01 | 0.99 |

APPENDIX A5.3. GUIDELINES AND BACKGROUND INFORMATION FOR EXPERTS WHO COMPLETED THE TPM

Land-use history and ecological memory

It is known that land-use history can affect ecosystems for decades to centuries. Many researchers have for example demonstrated that community composition can reflect past land-use for years, and that plant community composition, structure and function in post-agricultural forests can remain distinct from ancient forests, even centuries after abandonment (De Frenne, Baeten, et al., 2011; Dupouey et al., 2002; Flinn & Marks, 2007; Peterken & Game, 1984). Why land-use history has such an impact on community composition (among other ecosystem characteristics) becomes clear when considering the concept of ecological memory in plant and ecosystem processes. *Ecological memory has been defined as 'the capacity of past states or experiences to influence present or future responses of the community*' (Padisák, 1992), and as 'the degree to which an ecological process is shaped by its past modifications of a landscape' (Peterson, 2002). Ogle et al. (2015)compared models including antecedent conditions to simple models without antecedent conditions. For different types of ecosystem models, they found better model fits when incorporating antecedent conditions. Other studies have also proven that more variation in the observed data can be explained when including antecedent variables into the model (Barron-Gafford et al., 2014; Cable et al., 2013; Hawkins & Ellis, 2010; Leuning et al., 2005; Oesterheld et al., 2001; Sala et al., 2012).

In this project, we will follow this line of thought and apply it to the concept of driving variables of forest understorey communities. We expect that *when studying the composition of the herb layer community, more variation can be explained if – in addition to current values of a driving variable –antecedent values of this variable are taken into account as well. In other words: time trends of a driving variable will lead to better predictions of the forest understory community composition, compared to simply using current values of the driving variable as a predictor for community composition.* Examples of typical driving variables of the forest herb layer are light availability, soil pH and nutrient availability.

Framework for estimating time series of driving variables, based on Markov chains

To evaluate the role of the past in ecosystem development, data sets with extensive temporal information (i.e. time series of studied driving variables) are necessary (Ogle et al., 2015). In reality, however, such time series are often lacking. In contrast, data on land-use history is often available, or can still be traced

relatively easy. Therefore, we developed a framework to estimate time series of driving variables, based on knowledge of the land-use over the considered time interval.

The framework is based on the concept of **Markov chains**. A Markov chain represents a system of elements going from one state to another over time, where the probability of going to a certain next state depends on preceding conditions. The behaviour of a Markov chain can be described by a so-called **'Transition Probability Matrix' (TPM)**, in which each element represents the probability that an asset in a given state at a given time will shift to another state or remain in the same state during a time step (Golroo et al., 2012; Shamshad et al., 2005). The advantage of Markov chains is that they can handle incompleteness or lack of long-term data by incorporating expert knowledge to set up the TPM (Golroo et al., 2012).

For our framework, we will apply a second-order Markov chain as shown in **Figure**. We assume that the value of the driving variable (DV) at a certain time step t will be directly affected by three other variables:

- The land-use (LU) at time step t
- The value of the driving variable at t-1 (the previous time step)
- The value of the driving variable at t-2 (the time step before the previous time step)



Figure A5.3.1. Schematic representation of the second order Markov chain where our framework is based on. DV = driving variable; LU = land-use. The value of the driving variable (DV) at time t will depend on (1) the land-use (LU) at time t (blue arrows); (2) the value of the DV at time (t-1) (green arrows); (3) the value of the DV at time (t-2) (red arrows)

Important features of a Markov chain

• Time step Δt

An important feature of a Markov chain is the length of Δt . The choice of the length of each time step will depend on the time-scale of the processes that are modelled. It is important to define Δt before creating the TPM, since it will strongly influence the predictions/estimations that are made for the TPM. Appendix to Chapter 5

• Discrete classes for each element

For each element in the network, discrete classes have to be defined. Examples can be found below.

• Transition Probability Matrix

This is the most important feature of the network that has to be created. As stated above, it describes the behaviour of the Markov chain. For the network shown in A3.1, the TPM would be a matrix that describes the probability distribution for DV at time t, given the values for LU at time t, DV at time (t-1) and DV at time (t-2). The TPM contains a row for each possible scenario, i.e. each possible combination of the values for LU(t), DV(t-1) and DV(t-2). The number of rows in the TPM will depend on the number of classes that are defined for each element.

An illustration of the framework for light availability

In our study, we would like to illustrate the framework for the driving variable 'light availability', which is very important for the forest understory community.

The states that were defined for each element in the network are shown in Table A5.3.1.

We chose to quantify light availability using 'light transmittance' of the forest stand, which is the ratio of the light that reaches the understory to the total incident light at the top of the canopy. Again, classes were confined based on relevant thresholds for forest herb layer species. Therefore, the nonlinear relation between light availability and the forest herb cover was taken into account. Light availability in a forest context is mainly dependent on management interventions, so we defined four possible management actions that will have a clear impact on light availability at the forest floor. *Table A5.3.1.* Light classes and management classes that will be applied in the illustration of the framework: estimating light availability time series for a given forest management history. Note that light availability is quantified as light transmittance (LT)

| Light classes | | Managemei | nt classes |
|----------------|-----------|-------------|--|
| Strong shade | 0–8% LT | Zero cut | No fellings or removals are carried out. |
| Moderate shade | 8-20% LT | Thinning | The removal of a proportion of trees from a forest to allow more growing space for the final crop trees. Note: for this illustration, we will classify very similar management actions, like selection felling, as 'thinning' as well. |
| Moderate light | 20-40% LT | Shelter cut | A method of securing natural tree reproduction under the shelter of old trees which are removed by successive cuttings to admit to the seedlings a gradually increasing amount of light. Note: given the similar forest structure resulting from it, also 'coppice with standards' will be classified here. |
| Strong light | >40% LT | Clear-cut | Most or all trees in an area are uniformly cut down. Note: we will also consider the harvesting of the wood in a coppice system as a clear-cut action. |

• Time step Δt

The length of the time step Δt is chosen at **10 years**. We expect this to be a time interval long enough so that relevant changes will be noticeable, and short enough so that no important events will be missed.

• Boundary conditions

In order to create a sensible TPM, based on input of different experts, it is important to define some boundary conditions for the system that is under study. We will investigate the behaviour of light availability over time in **temperate forests**. When assessing light availability, we will assume we are estimating light transmittance of a **European temperate deciduous forest in the month July**.

• Transition probability matrix

The Markov chain is shown in **Fig. A5.3.2**. We now need to create a TPM in order to run the model and make actual predictions of how the variable will behave over time, given a certain management history.

Appendix to Chapter 5



Figure A5.3.2. Markov chain for light transmittance and management actions (MA)

The TPM for light will consist of 64 rows: 4 management-classes x 4 light-classes at $(t-1) \ge 4$ light-classes at (t-2) = 64 scenarios.

For each scenario, a probability distribution has to be determined for light at t. This means that for each of the four light-classes possible at t, the probability has to be estimated that light at t will actually be within this class, given a certain management practice at t and a certain light state at t-1 and t-2.

An example of some TPM-rows and their interpretation are given in Table A5.3.2.

Table A5.3.2. Example of two possible lines for a TPM for the light-model. For the first line, the expert expects that if there was moderate and strong shade at the forest floor, resp. 20 years and 10 years before t, and if there has just been a clear-cut at t, then there is a 90 % chance that there will be strong light at the forest floor, and 10 % chance that there will be moderate light at the forest floor at t. For the second line, the expert expects that if the light availability at the forest floor was characterized as 'strong shade' during the 20 years before t, and if there just have been thinnings at t, then there is a 10 % chance that there will still be strong shade at t, while chances for moderate shade, moderate light and strong light at t are resp. 70%, 20% and 0%. Note that the sum of probabilities should always be 100%. LT = Light transmittance.

| Management (t) | LT (t-2) | LT (t-1) | | LT (| t) | |
|----------------|-------------------|-----------------|------------------------|---------------------------|----------------------------|---------------------------|
| | | | Strong shade (0-8%) | Moderate shade (8-20%) | Moderate light (20-40%) | Strong light (40-100%) |
| Clear-cut | Moderate shade | Strong shade | 0% | 0% | 10% | 90% |
| Thinnings | Strong shade | Strong shade | 10% | 70% | 20% | 0% |

• Extra necessary input: confidence levels

An extra column is provided in each TPM to indicate how confident you are about your answer for each specific row/scenario. We request all experts to always indicate their confidence for each scenario. When calculating the final TPM, based on the input of multiple experts, we will take this confidence level into

account, by assigning more weight to values that are entered with more confidence. The possible confidence levels are: 1 (very unconfident), 2 (rather unconfident), 3 (quite confident), 4 (very confident).

APPENDIX A5.4. ILLUSTRATION OF HISTORICAL QUESTIONNAIRE COMPLETED BY LOCAL EXPERTS (CO-

AUTHORS OF CHAPTER 5: MARTIN KOPECKÝ AND FRANTIŠEK MÁLIŠ) OF THE THREE FOREST REGIONS

| lanagement periods | | 1 1050 1000 1 1000 1 BIED, defensions 1 | | | |
|--|--|---|--|---|--|
| anagement periods 185 | 0-1900 1900-1990 1990-2015 | 1950-1980 1980- INFO: definitions | | | |
| reconstruct the ma pe/intensity. Three I periods, please cor | nagement history of this plo key examples are given belo itact us). | t, we ask you to DIVIDE THE HISTOR w to inform you better how to make th | Y OF THE PLOT, STARTING IN 1850, IN A FEW P hese divisions in a correct way. Note, the maximu | PERIODS, depo Im number of | ending on the changes in management periods is 10 (if you want to enter more thar |
| EXAMPLE 1 – C Assume you know while, the CWS 4 different perio choose the year | onversion scenario(s) ow the forest was first managed management was abandoned, a ds: 1850-1880 (coppice); 1880- r when some management prac | l as coppice, but then there was a transition and the forest became a high forest under 1955 (coppice-with-standards); 1955-presen tice was decided to be abandoned, but cho | n towards coppice-with-standards (CWS): the first CWS group selection management, with the first group cutting nt (group selection high forest). So this example shows t lose the year in which the new system came into force. | cut – leaving so g occurring in 19 the importance | me standards to grow – was made in 1880. After 155. Here, you can make a division of the history ir of choosing the correct time interval limits: do not |
| EXAMPLE 2 – Sp Assume a partic present. The fir high forest). So | pontaneous forest succession af jular agricultural land use was ab st cuttings within the single-tree this example shows the importa | ter abandonment of past land use andoned in 1840 and after that, spontanec selection system took place in 1920. Here, Ince of distinguishing between a spontaneou | ous forest succession occurred until a high forest manag you can make a division of the history in 2 periods: 185 us succession period and the enforcement of an actual r | ement system v 0-1920 (zero m management sy | with single-tree selection was put into force until anagement); 1920-present (single-tree selection /stem once the forest has become mature enough |
| EXAMPLE 3 – Re Assume a partic | eforestation after abandonment sular agricultural land was abando nent system was put into force. | of past land use oned in 1840 and the land was planted with After this, no other serious management o | tree species in 1840 and put under a clearcut managen changes occurred until present. Here, you can make a d | nent system. T livision of the his | he last clearcut took place in 1900 when a high itory in 2 periods: 1850-1900 (clearcut system); |
| 1900-present (h | igh forest). | | | | |
| 1900-present (h NOTE that tend | igh forest). ing & thinning operations are co | nsidered part of a management system, so | o they do not constitute a management change, hence | do not imply a i | new time period. |
| NOTE that tend | igh forest). ing & thinning operations are co | nsidered part of a management system, so | o they do not constitute a management change, hence | do not imply a i | new time period. |
| NOTE that tend ce you have entere | igh forest). ing & thinning operations are cou d a period, please ENTER TH | nsidered part of a management system, so HE MAIN MANAGEMENT TYPE for this | o they do not constitute a management change, hence period in the boxes on the right. You can either c | do not imply a i choose from a | new time period. list or type your own short description. |
| NOTE that tend ce you have entere | igh forest). ing & thinning operations are co d a period, please ENTER Th ater a CORRESPONIDING TA | nsidered part of a management system, so HE MAIN MANAGEMENT TYPE for this | o they do not constitute a management change, hence period in the boxes on the right. You can either o | do not imply a i choose from a | new time period. list or type your own short description. |
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| Interventions/disturbances tree laver | |
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| not, species,) were present and/or which | |
| Frequency of thinning: mowing management (removal of clippings | |
| Type of thinning: | |
| Intensity of thinning: Description of smaller management related | |
| disturbances in the herb layer (Examples: | |
| related disturbances (Examples: Hazelnut gathering, litter raking, hay cutting, litter raking, leaf | |
| burning, potash making, wild fruit fodder, etc.) | |
| collecting, lime kin, etc.) | |
| Description of non-management | |
| related disturbances (Examples: ash Description of pests or diseases affecting the borb layer | |
| disease, bark stripping, other pests | |
| or diseases, storm camage, etc.) | |
| | |
| - Specific questions for management type 'Coppice' | |
| What was/is the average rotation time used? | _ |
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| | _ |
| Which species were/are used? | |
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| Were there some types of soil processing applied? (tilling before planting, addition of nutrients, etc.)? | |
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| storical information on plot(s) " | | | X |
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| Management periods 1850-1900 1900-1990 1990-2015 IN | FO: definitions | | |
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| Year of tending: | | Description of which grazers (domestic or | |
| Frequency of thinning: | | not, species,) were present and/or which mowing management (removal of clippings | |
| Type of thinning: | | or not,) was applied | |
| Intensity of thinning: | | Description of smaller management related disturbances in the herb layer (Examples: | |
| Description of smaller management related disturbances (Examples: burning, potash making, wild fruit collecting, lime kiln, etc.) | | Hazeluut gathering, litter raking, hay cutting, honey, acorn gathering, cone gathering, leaf fodder, etc.) | |
| Description of non-management related disturbances (Examples: ash dieback, bark beetle, dutch elm disease, bark stripping, other pests or diseases, storm damage, etc.) | | Description of pests or diseases affecting the herb layer | |
| Which tree species were used What was/is the average rotation time used? | | | |
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| Historical information on plot(s) " | |
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| Interventions/disturbances tree layer | Interventions/disturbances herb layer |
| Year of tending: | Description of which grazers (domestic or |
| Frequency of thinning: | not, species,) were present and/or which mowing management (removal of clippings |
| Type of thinning: | or not,) was applied |
| Intensity of thinning: | Description of smaller management related |
| Description of smaller management | disturbances in the herb layer (Examples: Hazelnut gathering, litter raking, hay cutting, |
| related disturbances (Examples: burning, potash making, wild fruit | honey, acorn gathering, cone gathering, leaf fodder, etc.) |
| collecting, lime kiln, etc.) | |
| Description of non-management | |
| dieback, bark beetle, dutch elm | herb layer |
| or diseases, storm damage, etc.) | |
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| Please try to describe what is known about the management: | |
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APPENDIX A5.5. MANAGEMENT HISTORY DATA FOR EACH PLOT

Table A5.5.1. Final land-use trajectory of each plot, with the colours indicating the assumed land-use state at each time step. t0 = 1950-1960; t1 = 1960-1970; t2 = 1970-1980; t3 = 1980-1990; t4 = 1990-2000; t5 = 2000-2010; t6 = 2010-2020. Note that the land-use state 'shelter cut' never appeared in the land-use trajectories from 1950-2020 in our case study plots.

| PLOT | t ₀ | t1 | t ₂ | t ₃ | t4 | t5 | t ₆ | PLOT | t ₀ | t ₁ | t ₂ | t ₃ | t4 | t ₅ | t ₆ | PLOT | t ₀ | t1 | t2 | t₃ | t4 | t ₅ | t ₆ |
|----------|----------------|----|----------------|----------------|----|----|----------------|-------|----------------|----------------|----------------|----------------|----|----------------|----------------|-------|----------------|----|----|----|----|----------------|----------------|
| KO775 | | | | | | | | SKR20 | | | | | | | | ZVD14 | | | | | | | |
| КО777 | | | | | | | | SKR26 | | | | | | | | ZVD16 | | | | | | | |
| KO778 | | | | | | | | SKR32 | | | | | | | | ZVD29 | | | | | | | |
| KO784 | | | | | | | | SKR34 | | | | | | | | ZVD31 | | | | | | | |
| KO785 | | | | | | | | SKR35 | | | | | | | | ZVD33 | | | | | | | |
| KO786 | | | | | | | | SKT16 | | | | | | | | ZVG24 | | | | | | | |
| KO787 | | | | | | | | SKT22 | | | | | | | | ZVG25 | | | | | | | |
| KO789 | | | | | | | | SKT23 | | | | | | | | ZVG26 | | | | | | | |
| KO791 | | | | | | | | SKT26 | | | | | | | | ZVG62 | | | | | | | |
| KO792 | | | | | | | | | | | | | | | | ZVY7 | | | | | | | |
| Zero cut | | | | | | | | | | | | | | | | | | | | | | | |

Clear cut

To reach these land-use trajectories, some assumptions were necessary, due to variations in the level of detail of the available historical data. Below, we provide a summary of the management history data for each plot, obtained from the historical questionnaire (**Appendix A5.4**). Final decisions and assumptions are <u>underlined</u>.

KO 775

1848-1899: Coppice with standards, rotation time 30 years. Extra info states that age of coppiced wood was 45 years in 1944. We assumed last harvest in 1899 (thus 1890-1900), and thus shelter cut in 1890-1900 and 30 years earlier, i.e. 1860-1870.

1899-2015: High forest, no knowledge on forestry practice. No regular thinning, mostly sanitary thinning of standards and singling-out of coppice stools. There has not yet been a clear-cut since switch to high forest management. Rotation time ca 100 years. <u>We estimated that on average every 30 years one of these actions</u> <u>might have affected the plot. So thinning in 1920-1930, 1950-1960 and 1980-1990.</u>

KO 777

1848-1940: Coppice with standards, rotation time 30 years. Extra info other document states that age of coppiced wood was 4 years in 1944. <u>We assumed last harvest in 1940 (thus 1930-1940)</u>, and thus shelter cut in 1930-1940 and 30 years earlier, i.e. 1900-1910 and 1870-1880.

1940-2015: High forest, no knowledge on forestry practice. No regular thinning, mostly sanitary thinning of standards and singling-out of coppice stools. There has not yet been a clear-cut since switch to high forest management. <u>We estimated that on average every 30 years one of these actions might have affected the plot. So thinning in 1960-1970 and 1990-2000.</u>

KO 784

1848-1931: Coppice with standards, rotation time 30 years. Extra info other document states that age of coppiced wood was 14 years in 1944. <u>We assumed last harvest in 1930 (thus 1920-1930)</u>, and thus shelter cut in 1920-1930 and 30 years earlier, i.e. 1890-1900 and 1860-1870.

1931-2015: High forest, no knowledge on forestry practice. No regular thinning, mostly sanitary thinning of standards and singling-out of coppice stools. There has not yet been a clear-cut since switch to high forest management. <u>We estimated that on average every 30 years one of these actions might have affected the plot. So thinning in 1950-1960 and 1980-1990.</u>

KO 785

1848-1924: Coppice with standards, rotation time 30 years. Extra info other document states that age of coppiced wood was 20 years in 1944. <u>We assumed last harvest in 1924 (thus 1920-1930)</u>, and thus shelter cut in 1920-1930 and 30 years earlier, i.e. 1890-1900 and 1860-1870.

1924-2015: High forest, no knowledge on forestry practice. No regular thinning, mostly sanitary thinning of standards and singling-out of coppice stools. There has not yet been a clear-cut since switch to high forest management. <u>We estimated that on average every 30 years one of these actions might have affected the plot. So thinning in 1950-1960 and 1980-1990.</u>

KO 786

1850-1895: High forest, no knowledge on forestry practice. Nothing mentioned about thinning. Clearcut in 1895. We assumed zero cut for all the periods < 1890-1900, and then clear-cut in 1890-1900.

1895-2015: High forest, clear felling. Last clear-cut in 1895. Heavy thinning. <u>We assumed nothing happened</u> the first 20 years after the clear-cut. After that, we assumed thinning in every period, because 'heavy thinning' is mentioned.

KO 787

1850-2015: High forest clear felling. No regular thinning, but sanitary thinning of single trees. Last clearcut around 1903. Intensity of thinning = heavy. Rotation ca 100 years. <u>We assumed thinning for every period</u> <u>before 1903. Then a clear-cut in 1900-1910. Then 2 periods of no intervention (zero cut). Then again thinning every</u> <u>period.</u>

KO 789

1850-2015: High forest clear felling. No regular thinning, but sanitary thinning of single trees. Last clearcut around 1988. Intensity of thinning = heavy. Rotation ca 80 years. <u>We assumed a clear-cut in 1908 and in</u> <u>1988. Before 1908, we assumed thinning every period (since thinning was heavy). After the clear-cut (1900-1910) we</u> <u>assumed 2 periods of no intervention after this. Then thinning for every period. Then a clear-cut in 1980-1990. Then 2</u> <u>periods of no intervention (zero cut). Then again thinning every period.</u>

KO 791

1848-1883: coppice with standards, rotation 30 years. Based on tree ages (see extra info document), there was a *shelter cut in 1853 and in 1883*.

1883-2015: High forest, no knowledge on forestry practice. No regular thinning, mostly sanitary thinning of standards and singling-out of coppice stools. There has not yet been a clear-cut since switch to high forest management. <u>We estimated that on average every 30 years one of these actions might have affected the plot. So thinning in 1910-1920, 1940-1950, 1970-1980 and 2000-2010.</u>

KO 792

1848-1884: coppice with standards, rotation 30 years. Based on tree ages (see extra info document), there was a *shelter cut in 1850 and in 1884.*

1883-2015: High forest, no knowledge on forestry practice. No regular thinning, mostly sanitary thinning of standards and singling-out of coppice stools. There has not yet been a clear-cut since switch to high forest management. <u>We estimated that on average every 30 years one of these actions might have affected the plot. So thinning in 1910-1920, 1940-1950, 1970-1980 and 2000-2010.</u>

KO 778

1848-1923: coppice with standards, rotation 30 years. Based on tree ages (see extra info document), there was a *shelter cut in 1850 and in 1923. Given the 30 years rotation time, we also assumed a shelter cut in between, i.e.* <u>1880-1890</u>

1923-2015: High forest, no knowledge on forestry practice. No regular thinning, mostly sanitary thinning of standards and singling-out of coppice stools. There has not yet been a clear-cut since switch to high forest management. <u>We estimated that on average every 30 years one of these actions might have affected the plot. So</u> thinning in 1950-1960, 1980-1990. Not in 2010-2020, since we would have noticed this during fieldwork.

ZVD14

1850-1958: coppice, 30 years. We assumed clear-cut in 1850-1860, 1880-1890, 1910-1920, 1940-1950. Zero cut in between.

1958-1965: conversion from coppice to HF, thinning every 10 years, both from below and above. Conversion was done through selective cutting (or thinning), once or twice per decennium. <u>We assumed</u> <u>thinning in 1950-1960.</u>

1966-1985: conversion from coppice to HF, thinning every 20 years, both from below and above. Exact thinning dates (and even harvest volumes) are known: 1966 and 1984. <u>We put in thinning in 1960-1970 and 1980-1990. Zero cut in between.</u>

1985-2015: Zero management. Zero cut for all periods.

ZVD16

1850-1958: coppice, 30 years. We assumed clear-cut in 1850-1860, 1880-1890, 1910-1920, 1940-1950. Zero cut in between.

1958-1965: conversion from coppice to HF, thinning every 10 years, both from below and above. Conversion was done through selective cutting (or thinning), once or twice per decennium. <u>We assumed</u> <u>thinning in 1950-1960 and in 1960-1970.</u>

1966-1975: conversion from coppice to HF, thinning every 5 years, both from below and above. Exact thinning dates (and even harvest volumes) are known: 1968 and 1973. <u>We put in thinning in 1960-1970 and 1970-1980.</u>

1976-2015: Zero management. Zero cut for all periods.

ZVD29 and ZVY7

1850-1966: High forest, no knowledge on forestry practice. Rotation times varied: 100-120 years. <u>We</u> assumed thinning in every period. (see next period)

1966-1980: High forest, shelterwood. Since 1966, exact years of harvesting were known: 1966, 1971, 1973 and 1980. Before 1966, probably similar management and frequencies, but no details given. <u>We assumed</u> <u>thinning in every period. We chose not to put 'shelter cut' because they mention 1/3 of wood volume per decennium is</u> <u>removed. In case of shelter cut, a bigger portion of total wood volume is removed.</u>

1980-2015: High forest, shelter wood. Only salvage logging after disturbances, but probably outside of the plot areas. *Zero cut for every period.*

ZVD31

1850-1958: coppice, 30 years. We assumed clear-cut in 1850-1860, 1880-1890, 1910-1920, 1940-1950. Zero cut in between.

1958-1965: conversion from coppice to HF, thinning every 10 years, both from below and above. Conversion was done through selective cutting (or thinning), once or twice per decennium. <u>We assumed</u> <u>thinning in 1950-1960.</u>

1966-1985: conversion from coppice to HF, thinning every 20 years, both from below and above. Exact thinning dates (and even harvest volumes) are known: 1966 and 1984. <u>We put in thinning in 1960-1970 and 1980-1990. Zero cut in between.</u>

1985-2015: Zero management. Only salvage logging after disturbances, but probably outside of the plot areas. *Zero cut for all periods.*

ZVD33

1850-1958: coppice, 30 years. We assumed clear-cut in 1850-1860, 1880-1890, 1910-1920, 1940-1950. Zero cut in between.

1958-1965: conversion from coppice to HF, thinning every 10 years, both from below and above. Conversion was done through selective cutting (or thinning), once or twice per decennium. <u>We assumed</u> <u>thinning in 1950-1960.</u>

1966-1985: conversion from coppice to HF, thinning both from below and above. Exact thinning dates (and even harvest volumes) are known: 1966, 1967, 1970, 1978 and 1984. <u>We put in thinning in 1960-1970</u>, <u>1970-1980 and 1980-1990</u>.

1985-2015: Zero management. Only salvage logging after disturbances, but probably outside of the plot areas. *Zero cut for all periods.*

ZVG24

1850-1958: coppice, 30 years. We assumed clear-cut in 1850-1860, 1880-1890, 1910-1920, 1940-1950. Zero cut in between.

1958-1965: conversion from coppice to HF, thinning every 10 years, both from below and above. Conversion was done through selective cutting (or thinning), once or twice per decennium. <u>We assumed</u> <u>thinning in 1950-1960.</u> 1966-1985: conversion from coppice to HF, thinning both from below and above. Exact thinning dates (and even harvest volumes) are known: 1968, 1976, 1983 and 1984. <u>We put in thinning in 1960-1970, 1970-1980 and 1980-1990.</u>

1985-2015: Zero management. Only salvage logging after disturbances, but probably outside of the plot areas. *Zero cut for all periods.*

ZVG25

1850-1958: coppice, 30 years. We assumed clear-cut in 1850-1860, 1880-1890, 1910-1920, 1940-1950. Zero cut in between.

1958-1965: conversion from coppice to HF, thinning every 10 years, both from below and above. Conversion was done through selective cutting (or thinning), once or twice per decennium. <u>We assumed</u> <u>thinning in 1950-1960.</u>

1966-1985: conversion from coppice to HF, thinning both from below and above. Exact thinning dates (and even harvest volumes) are known: 1969, 1970, 1973 and 1980. <u>We put in thinning in 1960-1970, 1970-1980 and 1980-1990.</u>

1985-2015: Zero management. In the 90's, some damaged trees were harvested. <u>Thinning in 1990-2000. In</u> 2006, wind created a gap very close (next) to the plot. However, we assume it will not have a big impact in light availability in the plot, so was not considered a thinning.

ZVG26

1850-1958: coppice, 30 years. We assumed clear-cut in 1850-1860, 1880-1890, 1910-1920, 1940-1950. Zero cut in between.

1958-1965: conversion from coppice to HF, thinning every 10 years, both from below and above. Conversion was done through selective cutting (or thinning), once or twice per decennium. <u>We assumed</u> <u>thinning in 1950-1960.</u>

1966-2015: conversion from coppice to HF, thinning both from below and above. Exact thinning dates (and even harvest volumes) are known: 1969, 1973, 1980, 1987, 1991, 1992 and 2008. <u>We put in thinning</u> in 1960-1970, 1970-1980, 1980-1990, 1990-2000 and 2000-2010.

ZVG62

1850-1958: coppice, 30 years. We assumed clear-cut in 1850-1860, 1880-1890, 1910-1920, 1940-1950. Zero cut in between.

1958-1965: conversion from coppice to HF, thinning every 10 years, both from below and above. Conversion was done through selective cutting (or thinning), once or twice per decennium. <u>We assumed</u> <u>thinning in 1950-1960.</u>

1966-1985: conversion from coppice to HF, thinning both from below and above. Exact thinning dates (and even harvest volumes) are known: 1969, 1975 and 1984. <u>We put in thinning in 1960-1970, 1970-1980</u> <u>and 1980-1990.</u>

1985-2015: Zero management. Only salvage logging after disturbances, but probably outside of the plot areas. *Zero cut for all periods.*

SKT16

1850-1900: Coppice, rotation time 40 years, charcoal production stopped after 1950

1900-1959: coppice, rotation time 40 years

We assumed last clear-cut in 1930-1940, thus also clear-cut in 1890-1900 and in 1850-1860. Zero cut in between.

1960-1979: conversion to high forest, thinning frequency = 10 years, thinning both from below and above. We assumed thinning in 1960-1970 and 1970-1980

1980-1994: Conversion to high forest (without grazing), thinning frequency = 5-10 years, thinning both from below and above. Definitely two thinnings in period 1980-1990. <u>*Thinning in 1980-1990.*</u>

1995-2015: zero management. Zero cut from 1990 onwards.

SKT22

1850-1900 Coppice, rotation time 40 years, charcoal production stopped after 1950

1900-1949: coppice, rotation time 40 years

We assumed last clear-cut in 1930-1940 (not later, because thinning started in 1950, and it's not realistic that they would happen so fast after a clear-cut), thus also clear-cut in 1890-1900 and in 1850-1860. Zero cut in between.

1950-1979: conversion to high forest (with grazing), thinning frequency = 10 years, thinning both from below and above. <u>We assumed thinning in every period.</u>

1980-2015: zero management, recently (last few years), two individual mature oaks were thrown by wind in the southern part of the plot. <u>We assumed zero cut</u>, except for the period 2010-2020, where we put thinning, as a reflection of the windthrom.

SKT23

1850-1900: Coppice, rotation time 40 years, charcoal production stopped after 1950

1900-1949: coppice, rotation time 40 years

We assumed last clear-cut in 1930-1940 (not later, because thinning started in 1950, and it's not realistic that they would happen so fast after a clear-cut), thus also clear-cut in 1890-1900 and in 1850-1860. Zero cut in between.

1950-1979: conversion to high forest, thinning frequency = 10 years, thinning both from below and above. <u>We assumed thinning in every period.</u>

1980-1988: conversion to high forest, thinning frequency = 10 years, thinning both from below and above. Definitely one thinning operation mentioned in management plans. <u>*Thinning in 1980-1990.*</u>

1989-2015: zero management. Zero cut from 1990 onwards.

SKT26

1850-1900: Coppice, rotation time 40 years, charcoal production stopped after 1950

1900-1949: coppice, rotation time 40 years

We assumed last clear-cut in 1930-1940 (not later, because thinning started in 1950, and it's not realistic that they would happen so fast after a clear-cut), thus also clear-cut in 1890-1900 and in 1850-1860. Zero cut in between.

1950-1979: conversion to high forest, thinning frequency = 10 years, thinning both from below and above. <u>We assumed thinning in every period</u>

1980-1988: zero management. Zero cut in 1980-1990.

1989-2015: Conversion to high forest, thinning frequency = 10 years, thinning both from below and above. Presently, the stand has low density of old trees after thinning operations and three tree layers are visible. Upper (main canopy) - formed by old oaks, middle - formed by hornbeam (originated in previous period) and the lower tree layer formed by hornbeam and Acer campestre. This lower layer originates in this period. *We assumed thinning in every period from 1990 onwards*.

SKR20 and SKR26

1850-1949: Coppice, rotation time 40 years, charcoal production stopped after 1950. <u>We assumed last clear-</u> cut in 1930-1940 (not later, because thinning started in 1950, and it's not realistic that they would happen so fast after a clear-cut), thus also clear-cut in 1890-1900 and in 1850-1860. Zero cut in between.

1950-1979: conversion to high forest, thinning frequency = 10 years, thinning both from below and above. <u>We assumed thinnings in all periods</u>

1980-1988: zero management. Zero cut in 1980-1990.

1989-2015: zero management. Some disturbances causing small gaps were mentioned, but not clear in which periods they took place. *We assumed zero cut for all the periods.*

SKR32

1850-1900: Coppice, rotation time 40 years, charcoal production stopped after 1950

1900-1949: coppice, rotation time 40 years

We assumed last clear-cut in 1930-1940 (not later, because thinning started in 1950, and it's not realistic that they would happen so fast after a clear-cut), thus also clear-cut in 1890-1900 and in 1850-1860. Zero cut in between.

1950-1979: conversion to high forest, thinning frequency = 10 years, thinning both from below and above. <u>We assumed thinning in all periods</u>

1980-1988: conversion to high forest, thinning frequency = 10 years, thinning both from below and above. Definitely one thinning operation mentioned in management plans. <u>*Thinning in 1980-1990.*</u>

1989-2015: zero management. Zero cut from 1990 onwards.

SKR34

1850-1949: Coppice, rotation time 40 years, charcoal production stopped after 1950 <u>We assumed last clearcut in 1930-1940 (not later, because thinning started in 1950, and it's not realistic that they would happen so fast after a</u> <u>clear-cut</u>), thus also clear-cut in 1890-1900 and in 1850-1860. Zero cut in between.

1950-2015: conversion to high forest, thinning frequency = 10 years, thinning both from below and above. <u>We assumed thinning in all periods</u>

SKR35

1850-1949: Coppice, rotation time 40 years, charcoal production stopped after 1950 <u>We assumed last clearcut in 1930-1940 (not later, because thinning started in 1950, and it's not realistic that they would happen so fast after a</u> clear-cut), thus also clear-cut in 1890-1900 and in 1850-1860. Zero cut in between.

1950-1980: conversion to high forest, thinning frequency = 10 years, thinning both from below and above. Thinnings are clearly mentioned in the first decade: 1950-1960. <u>We assumed thinning in every period.</u>

1980-2015: zero management. Zero cut for every period.

APPENDIX A5.6. DERIVATION OF THE BEST MODEL PREDICTORS FOR LIGHT TRANSMITTANCE IN THE 29 FOREST PLOTS

To estimate the light transmittance in a forest plot during the second survey, we used a spherical densiometer. This small instrument employs a mirror with spherical curvature to visualize the reflection of a large overhead area. The mirror is divided into a grid of 24 squares to enable estimating the percentage of the overhead area covered with forest canopy. The person measuring the light transmittance pictures four imaginary dots in the quarters of each grid square, counts the number of dots in a canopy opening and multiplies this number with 1.04 (Forestry Suppliers, 2008; Lemmon, 1957). Light transmittance was measured at five points in each plot: in the centre and two times on the two diagonals. The five measurements were averaged to get a final value of light transmittance for the plot.

Estimates of light transmittance at the time of the first survey were derived through the relationships between tree and shrub cover data and light transmittance at the second survey.

A linear model was set up, with the densiometer values as response variable and nine different descriptors of canopy composition as predictors: the cover of the shrub layer, tree layer and the combination of shrub and tree layer for shade-tolerant species, shade-intolerant species, and all species together (**Table A5.6.1**). Shade-tolerant species were the species with shade tolerance ≥ 3 according to Niinemets and Valladares (2006); overlap between species or layers was taken into account by using the formula of Fischer (2015) to calculate the total cover of the different layers.

To derive the optimal model, we used the *dredge* function (package MuMIn in R; Barton, 2016), which generates a set of models with combinations (subsets) of the nine predictors. We retained the model with the lowest AIC_c, the second-order Akaike Information Criterion for small sample sizes. The model including the predictors 'total cover of the tree layer' and 'cover of the shade-tolerant species of both tree and shrub layer combined' predicted the measured light transmittance the best ($\mathbf{R}^2 = 0.42$; p < 0.001; **Table A5.6.2**).

 Table A5.6.1.
 The nine predictor variables

| Variable |
|---|
| Overall cover of the shrub and tree layer |
| Cover of shade-tolerant species in the shrub and tree layer |
| Cover of shade-intolerant species in the shrub and tree layer |
| Overall cover of the shrub layer |
| Cover of shade-tolerant species in the shrub layer |
| Cover of shade-intolerant species in the shrub layer |
| Overall cover of the tree layer |
| Cover of shade-tolerant species in the tree layer |
| Cover of shade-intolerant species in the tree layer |

Table A5.6.2. The optimal linear model including only two predictors

| | Estimate | Std. Error | t-value | Pr (> t) |
|---|----------|------------|---------|-----------|
| Intercept | 1.84 | 0.53 | 3.50 | 0.002 |
| Overall cover of the tree layer | 1.72 | 0.71 | 2.40 | 0.023 |
| Cover of shade-tolerant species in the shrub and tree layer | -1.74 | 0.44 | -3.95 | <0.001 |

APPENDIX A5.7. SPECIES LIST

Below, we provide a list of all species that were present in the understorey community in the 29 case study plots, according to a vegetation survey performed in 2015. We defined 'understorey' as all species smaller than 1.3 m height, thus including small tree and shrub species. The forest specialists are highlighted (**bold text**). These species are found mainly in closed forest, as defined for the lowlands of the Czech Republic, cf. Heinken et al. (2019).

Nomenclature: The Plant List (2013). Version 1.1. Published on the Internet; http://www.theplantlist.org/ (accessed January 2019)

Abies alba Acer campestre Acer platanoides Acer pseudoplatanus Acer tataricum Achillea millefolium Actaea spicata Adoxa moschatellina Aegopodium podagraria Agrimonia eupatoria Agrostis spec Ajuga genevensis Ajuga reptans Ajuga spec Alliaria petiolata Allium senescens Anemone nemorosa Anemone sylvestris Anthericum ramosum Anthericum spec Anthoxanthum odoratum Anthriscus nitida Anthriscus sylvestris Aquilegia vulgaris

Arabidopsis arenosa Arabis hirsuta Arctium tomentosum Asarum europaeum Asperula tinctoria Astragalus glycyphyllos Astragalus spec Athyrium filix-femina Atropa belladonna Berberis vulgaris Brachypodium pinnatum Brachypodium sylvaticum Bromus benekenii Bromus spec Cornus spec Corylus avellana Cotoneaster integerrimus Cotoneaster spec Crataegus laevigata Crataegus spec Cruciata glabra Dactylis glomerata Daphne mezereum Deschampsia cespitosa Deschampsia flexuosa Digitalis grandiflora Dryopteris carthusiana Dryopteris filix-mas Elymus caninus Epilobium angustifolium Epilobium montanum Epilobium spec Epipactis helleborine Epipactis spec Euonymus europaeus Euonymus verrucosus Euphorbia amygdaloides Euphorbia cyparissias

Fagus sylvatica Fallopia dumetorum Festuca gigantea Festuca heterophylla Festuca ovina Festuca rubra Festuca rupicola/ovina Festuca spec Fragaria moschata Fragaria vesca Fragaria vesca/moschata

Frangula alnus **Fraxinus angustifolia** Fraxinus excelsior Impatiens parviflora Inula conyza Inula ensifolia Inula salicina Juniperus communis Lactuca muralis Lamium galeobdolon Lamium maculatum Lapsana communis Laserpitium latifolium Lathyrus niger Lathyrus vernus Lembotropis nigricans Leucanthemum vulgare Ligustrum vulgare Lilium martagon Lonicera spec Lonicera xylosteum Lotus corniculatus Luzula luzuloides Luzula pilosa Lysimachia nummularia Maianthemum bifolium Malus sylvestris Melampyrum nemorosum Melampyrum pratense Melampyrum spec Melica nutans Melica picta Melica uniflora Melittis melissophyllum Mentha spec Mercurialis perennis Milium effusum Moehringia trinervia

Molinia caerulea **Monotropa hypopitys** Myosotis spec Pulmonaria obscura Pulmonaria officinalis Pulmonaria spec Pyrus pyraster Quercus cerris Quercus petraea Quercus robur Ranunculus auricomus Rhamnus cathartica Ribes uva-crispa Rosa canina agg. Rosa pendulina Rosa spec Rubus fruticosus Rubus idaeus Rubus spec Sambucus nigra Sanicula europaea Scrophularia nodosa Securigera varia Sedum maximum Sedum telephium Senecio ovatus Serratula tinctoria

Silene nutans Silene vulgaris Solanum dulcamara Solidago virgaurea Sorbus aria Sorbus aucuparia **Sorbus torminalis** Stachys officinalis **Stellaria holostea** Symphytum tuberosum Tanacetum corymbosum

Taraxacum spec Teucrium chamaedrys Thalictrum aquilegiifolium

Calamagrostis arundinacea

Calamagrostis villosa Campanula bononiensis Campanula glomerata Campanula patula Campanula persicifolia Campanula rapunculoides Campanula rotundifolia **Campanula trachelium** Cardamine bulbifera Cardamine impatiens Carex caryophyllea Carex digitata Carex flacca Carex michelii Carex montana

Carex muricata agg. Carex pallescens

Carex pilosa

Carex pilulifera Carex spec **Carex sylvatica Carpinus betulus** Centaurea jacea **Cephalanthera damasonium Cephalanthera rubra** Chaerophyllum aromaticum Chaerophyllum temulum **Circaea lutetiana**

Clematis recta Clinopodium vulgare **Convallaria majalis** Cornus mas Cornus sanguinea Galeopsis spec Galium album Galium aparine Galium boreale Galium glaucum Galium intermedium Galium mollugo Galium odoratum Galium sylvaticum Genista germanica Genista pilosa Genista tinctoria Geranium robertianum Geranium sanquineum Geum urbanum Glechoma hederacea

Glechoma hirsuta Gymnocarpium dryopteris

Hacquetia epipactis Hedera helix Hepatica nobilis Heracleum sphondylium Hieracium bifidum Hieracium lachenalii

Hieracium murorum Hieracium pilosella Hieracium sabaudum/racemosum Hieracium spec **Hierochloe australis**

Hordelymus europaeus

Hypericum hirsutum Hypericum montanum Hypericum perforatum Myosotis sylvatica Neottia nidus-avis Oxalis acetosella Paris quadrifolia Phyteuma spicatum Picea abies Pilosella spec Pimpinella major Platanthera bifolia Poa angustifolia Poa nemoralis Poa remota Poa stiriaca Poa trivialis Polygala chamaebuxus Polygala spec Polygonatum multiflorum Polygonatum odoratum Polygonatum verticillatum Polypodium vulgare Populus tremula Potentilla alba Potentilla erecta Prenanthes purpurea

Primula elatior Primula spec

Primula veris Primula vulgaris Prunus avium

Prunus spec Prunus spinosa Pteridium aquilinum Pulmonaria mollis Tilia cordata Tilia platyphyllos Tilia spec Torilis japonica Trifolium alpestre Trifolium medium Trifolium montanum Trifolium repens Ulmus alabra Ulmus minor Ulmus spec Urtica dioica Vaccinium myrtillus Verbascum austriacum Verbascum nigrum Veronica chamaedrys

Veronica officinalis Viburnum lantana

Viburnum opulus Viburnum spec Vicia cassubica Vicia cracca Vicia sepium Vicia spec

Vicia tetrasperma Vincetoxicum hirundinaria

Viola hirta Viola hirta/collina **Viola mirabilis Viola reichenbachiana/riviniana Viola riviniana** Viola spec **Waldsteinia geoides**



CURRICULUM VITAE

Curriculum vitae

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Peer-review scientific articles included in Web of Science

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Non-peer-reviewed scientific articles

Depauw, L., & Maes, S. (2015). forestREplot: a global database of temperate forest herb layer resurvey plots. *BRITISH ECOLOGICAL SOCIETY BULLETIN*, *46*(3), 31–34.

Depauw, L., Verheyen, K., & Van Renthergem, T. (2013). Het belang van houtige vegetatiestroken voor de reductie van verkeersgeluid. *BOSREVUE*, (46), 2–5.

MSc. Thesis

Het belang van houtige vegetatiestroken voor de reductie van verkeersgeluid. ForNaLab, Ghent University. Supervisors: Prof. Dr. Ir. Kris Verheyen & Prof. Dr. Ir. Timothy Van Renthergem

Participation in congresses, symposia or workshops

Oral presentations

Depauw, L., Maes, S., Perring, M. P., Verheyen, K. PASTFORWARD (2014-2019). Development trajectories of temperate forest plant communities under global change: combining hindsight and forecasting. ForestREplot workshop Ghent. 08.12.2014. Ghent, Belgium.

Depauw, L., Maes, S., Blondeel, H. Oude bossen in een nieuwe omgeving. Secundaire schoolpresentatie VABI Roeselare. 6.02.2018 and 7.02.2019.

Depauw, L., Perring, M. P., Brunet, J., Maes, S. L., Blondeel, H., De Lombaerde, E., De Groote, R., & Verheyen, K. Effects of past land use and recent forest management on the understorey community in temperate oak forests in South Sweden. ForNaLab Symposium. 30.11.2018. Gontrode, Belgium

Depauw, L., Landuyt, D., Perring, M. P., Blondeel, H., Maes, S. L., Kopecký, M., Máliš, F., Vanhellemont, M., & Verheyen, K. A general framework for quantifying the effects of land-use history on ecosystem dynamics. 3rd Restoring Forest Conference: Regeneration and Ecosystem Function for the Future (IUFRO). 12.09.2017. Lund, Sweden.

Poster presentations

Depauw, L., Maes, S., & Verheyen, K. (2014). Pastforward: development trajectories of temperate forest plant communities under global change: combining hindsight and forecasting. *BES and SFÉ Joint annual meeting, Abstracts.* Presented at the BES and SFÉ 2014 Joint annual meeting.

Scientific awards

Toekomstboom (2013). Beste studentenscriptie in het vakgebied van bosecologie en bosbeheer uit Nederland en Vlaanderen. Awarded by Stichting Toekomstboom.

Scientific courses

- 2018 Speed Reading-Snellezen Doctoral Schools, Universiteit Gent.
- 2015 Module 9 of the course in Statistics 2014-2015: Multilevel Analysis for Grouped and Longitudinal Data – Center for Statistics & Institute for Continuing Education in Science

Supervision of MSc thesis students

2014-2015: Robbe De Groote: Impact of global change drivers on temperate forest understorey plant dynamics: a case study from Skåne (southern Sweden). Supervisors: Prof. dr. ir. Kris Verheyen, dr. ir. Lander Baeten

2014-2015: Emiel De Lombaerde: Drivers behind temporal changes in the understorey of deciduous temperate forests: a case study from Öland (southern Sweden). Supervisors: Prof. dr. ir. Kris Verheyen, dr. ir. Lander Baeten.