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

Running title: Canopy and understorey light-demand-signature

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ABSTRACT

Questions: 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, were related to each other in structurally complex mixed forests. We also asked how well they can predict the light-demand-signature of the forest understorey (estimated as the mean Ellenberg indicator value for light (‘EIV_{LIGHT}’) and the proportion of ‘forest specialists’ (‘%FS’) within the plots). Furthermore, we asked whether accounting for the shade-casting ability of individual canopy species could improve predictions of EIV_{LIGHT} and %FS.

Location: 192 study plots from nineteen temperate forest regions across Europe

Methods: In each plot, 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 comparisons, based on R^2 and AIC, to assess which stand characteristics can predict EIV_{LIGHT} and %FS best, and to assess whether canopy shade-casting ability can significantly improve model fit.

Results: 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 models improved the model fit for EIV_{LIGHT}, but not for %FS.

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

Keywords: basal area, canopy cover, canopy closure, Ellenberg indicator values, herb layer, light availability, light transmittance, shade-casting ability, temperate forest, understorey

1. 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; Jelaska *et al.* 2006; De Frenne *et al.* 2015), tree regeneration (Kobe *et al.* 1995; Beaudet and Messier 1998; 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) and on the presence of invasive species (e.g. Medvecká *et al.*, 2018). In a multifactor 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 a resurvey study in temperate oak forests in South Sweden, Depauw *et al.* (2019b) concluded that light dynamics due to management practices play a key role in the development of the understorey composition.

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 (e.g. Decocq *et al.*, 2004). This role may become even more important in times of global change. Therefore, in our study, we aim to relate stand structural attributes to the ‘light-demand-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). In turn, we expect light availability to influence the light-demand-signature of the understorey. Relating stand structural attributes to the light-demand-signature offers at least two methodological benefits. First, direct measurements of light availability at the forest floor are typically costly and time-consuming (Brown *et al.* 2000). Additionally, 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 (Depauw *et al.*, 2019a).

The light-demand-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 realized 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 into the light-demand-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 *et al.*, 2008). Secondly, *canopy cover*, defined as the proportion of ground surface covered by a vertical projection from the 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.* 1999). Canopy closure in forests is typically measured with hemispherical photography (e.g. Jelaska *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 and 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, to our knowledge, these relations have not been investigated in semi-natural, uneven-aged, mixed, heterogeneous forest stands with multiple structural layers. More complex relations might be expected in such stands, as the amount of light transmitted by a tree can vary considerably among different species, partly because of their light-interception strategies (Montgomery and Chazdon 2001; Angelini *et al.* 2015; Leuschner and Ellenberg 2017). 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 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 light-demand-signature of the understorey;

(iii) assess the importance of including the shade-casting ability of individual canopy species to improve predictions of the light-demand-signature of the understorey.

2. METHODS

2.1. Study sites

We selected 192 forest plots, spread across 19 temperate forest regions in Europe (**Fig. 1**, **Table 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/). Within this overarching project, plot selection was based on several criteria: (1) existence of historical understorey surveys (not relevant for this study) (2) an intermediate to high soil nutrient availability (C/N < 20), (3) an intermediate water holding capacity (Ellenberg Indicator Value for moisture ranging between 3.5 and 6.5, excluding extremely dry and water-logged sites) and (4) a well-documented land use history. All plots comprised semi-natural, mixed forests with a variable tree and shrub layer composition. Plots were predominantly composed of broadleaved species, but a higher share of coniferous species in the easternmost regions with hemiboreal forests was unavoidable. The four most frequent canopy species across all plots were *Quercus robur/petraea* (110/192 plots), *Fagus sylvatica* (78/192 plots), *Fraxinus excelsior* (69/192 plots) and *Carpinus betulus* (64/192 plots). All plots belonged to the vegetation classes Quercetea robori-petraeae and Carpino-Fagetea sylvaticae (Mucina *et al.* 2016). Within the constraints of plot selection, we tried to minimize differences in parent material and topography among plots. Plots differed in their land-use and forest management history: 57 plots were located in recent (post-agricultural) forests and 135 plots in ancient forests (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 1**).

After we located the centre of the plot, we established a 10x10-m² plot, and a 20x20-m² plot with the same central point. In the 10x10-m² 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, except for the basal area measurements in the Swedish region (Skåne), which we did in November 2014 (but no disturbances occurred in these plots in the meantime).

2.2. Light-demand-signature of the understorey

We derived two different variables that reflect the light-demand-signature of the understorey in each plot. First, we calculated the **mean Ellenberg indicator value for light (EIV_{LIGHT})** (Ellenberg *et al.*, 1992)**.** Ellenberg indicator values indicate species environmental preferences in their realized niche (Diekmann, 2003). EIV_{LIGHT} 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 forest habitat preference in general, irrespective of forest type). 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 (i.e. $\mathrm{EIV}_{\mathrm{LIGHT}}$ and %FS) were based on the ‘strict’ herb layer, containing only the herbaceous species and dwarf shrubs. We excluded tree seedlings and shrub species, because they often do not survive more than one growing season as they germinate independent of suitable site conditions (Yan *et al.* 2015). Moreover, the presence of tree and shrub species in the herb layer might also depend on the occurrence of mast years, and is therefore representative of conditions that encouraged seeding of adults the year before rather than current light conditions (see **Appendix S1** for species lists). Nomenclature was standardized manually based on The Plant List (2013).

To calculate both the mean $\mathrm{EIV}_{\mathrm{LIGHT}}$ 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 $\mathrm{EIV}_{\mathrm{LIGHT}}$ of each plot was calculated as the sum of the $\mathrm{EIV}_{\mathrm{LIGHT}}$ of each occurring species, divided by the total number of species. For combined taxa (occurring 7 times in the list of 286 species in total; e.g. *Cardamine hirsuta/flexuosa*), we used mean $\mathrm{EIV}_{\mathrm{LIGHT}}$ of both species. For taxa identified at the genus level only (occurring 26 times in the list of 286 species in total; e.g. *Festuca* spec.), we used the mean $\mathrm{EIV}_{\mathrm{LIGHT}}$ of all species of the genus that were present in our full dataset. We do not expect this to distort our analysis, because combined taxa and taxa identified at the genus level were rare, and because values obtained by averaging across all species within a genus generally yields midrange values that do not have the ability to shift a community's light-demand-signature. 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. In **Appendix S2**, we repeated our main analysis (see further: 'Predicting understorey light-demand-signatures from canopy structure and composition') using abundance-weighted values for both EIV_{LIGHT} and %FS, to check the sensitivity of our main findings to this methodological choice.

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

The **basal area** (m^2 ha^{-1}) of a forest stand typically represents the area occupied by tree stems per hectare. For all trees and shrubs within the 20x20-m^2 plot with a diameter at breast height (DBH) ≥ 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-m^2 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 S3**, 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. Another alternative would have been to assess total cover independent of species identity (e.g. as done with hemispherical photographs (Rich 1990)). This approach, however, does not account for overlapping crowns which have the potential to reduce light availability significantly and would not allow testing whether correcting for overlap (as explained above) is important or not.

We measured **canopy closure** (%) with a spherical densiometer held 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 (Lemmon 1957; Forestry Suppliers 2008). 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-m² plot. We averaged the five results to get a final value of canopy closure in the forest plot.

2.4. Shade-casting ability of canopy species

We expected that in these mixed forests, canopy characteristics other than structure may affect light availability. In particular, we expected the shade-casting ability of species to influence light availability. The shade-casting ability (SCA) of tree and shrub species is a qualitative index based on expert knowledge from Ellenberg (1996). SCA scores (**Appendix S4**) 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 S5** for details), suggesting that our SCA-scoring is acceptable. For both canopy cover and basal area, we not only calculated total SCA 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.

2.5. 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’ (Wood 2017; Barton 2019; Lüdecke 2019; Pinheiro *et al.* 2019; Wickham *et al.* 2019).

2.5.1. *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. We started with a model with varying slopes and intercepts for the random effect term ‘region’, and a weights 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 R^2 to assess the strength of the relationships.

2.5.2. *Predicting understorey light-demand-signatures from canopy structure and composition (research questions 2 and 3)*

For both understorey response variables, i.e. the mean EIV_{LIGHT} and the proportion of forest 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 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. Including ‘region’ with both varied intercepts and slopes did not considerably change the overall results, so we present the results from the simplest model, i.e. with 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 R^2 (Nakagawa & Schielzeth 2013). The marginal R^2 (R^2m) and conditional R^2 (R^2c) represent the variance explained by fixed factors and the variance explained by both fixed and random factors, respectively (Nakagawa and 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 and Anderson 2002). R^2 values on the other hand, have the advantage that they provide information on the absolute model fit and the amount of variance explained (Nakagawa and Schielzeth 2013).

3. RESULTS

3.1. Relating basal area, canopy cover and canopy closure

In general, the fitted relationships between canopy closure, canopy cover and basal area were poor (**Fig. 2**). 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 weights term to control for heterogeneity in residual spread among the regions was also retained. While canopy closure and canopy cover were weakly related (**Fig. 2a**), we did not find any relation between canopy closure and basal area, and between canopy cover and basal area, indicated by R^2m values of 0 and 0.02, respectively (**Fig. 2b-c**).

3.2. Predicting understorey light-demand-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. 3**). 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 basal area model only improved the model fit for mean EIV_{LIGHT} ($R^2m = 0.12$). For %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 R^2m values (**Fig. 3**). 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 R^2m values and decreased AIC-values (**Fig. 3a**). 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, R^2m increased slightly, but AIC increased as well ($\Delta AIC = 6.55$) (**Fig. 3b**).

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. 3**).

For the models based on abundance-weighted values for both EIV_{LIGHT} and %FS (**Appendix S2**), instead of presence/absence based values, 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. DISCUSSION

In complex, semi-natural, mixed forests, relationships between structural characteristics of the canopy are more complex compared to literature findings for homogeneous 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-demand-signature remained largely driven by regional characteristics (e.g. land-use history, management type, soil characteristics, climate or landscape fragmentation).

4.1. 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 densiometer measurements with a simple linear regression model, and found an R^2 value of 0.65 in stands dominated by Douglas-fir, western hemlock, and western red cedar. 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 well-developed 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 (Pretzsch 2014; Perot *et al.* 2017). 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 effectively (Schröter *et al.* 2012). Also, we are likely investigating smaller ranges of these stand characteristics compared to other studies, because most of our plots are situated in mixed closed-canopy 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 DBH-measurements feasible, but they will have been included in canopy cover/closure measurements. This might weaken correlations between basal area and canopy cover/closure.

4.2. Predicting understorey light-demand-signatures from canopy structure and composition

Of the three investigated stand attributes, canopy cover proved to be the best predictor for the light-demand-signature of the understorey. This suggests that, in resurvey studies, the lack of data for stand characteristics such as basal area or canopy closure in 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). On the other hand, canopy cover is a more subjective measure, compared to basal area or canopy closure, stressing the need to standardize these measurements especially when different surveyors are involved (Morrison 2016). In this study, this estimation error was reduced by performing two independent estimates of canopy cover, after which the two surveyors agreed upon the final reported value. As this approach led to the best predictor (out of the three we tested) for the understorey's light-demand-signature, we propose the use of this method for future studies.

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 (Jennings *et al.* 1999; Alexander *et al.* 2013). 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-demand-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 or tree regeneration. Moreover, basal area does not take into account species attributes such as crown shape, leaf inclination and crown- and foliage health.

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-demand-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 1**), which are mostly 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 R^2 values (compared to the very low marginal R^2 values) that we found in our models, suggesting that a large part of the variation in the understorey light-demand-signature can be explained by the region in which a plot is situated. Regional differences in canopy attributes (e.g. species composition) can partly explain this, but also many other regional attributes, such as the soil characteristics, the 'available' species pool, the regional climate, the topography, the land-use and forest management history, and the landscape fragmentation and associated dispersal limitations are likely controlling the understorey composition and its light-demand-signature. For instance, the impact of land-use history on the light-demand-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 light-demand-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 be maintained. Soil characteristics can also affect the light-demand-signature of the understorey, as plant species are often more shade-tolerant on nutrient-rich 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 R^2m and higher R^2c 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 and 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 *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 (Depauw *et al.*, 2019a). Ash *et al.* (1976) studied understorey composition in coppiced woodlands and found that many perennials can persist throughout the entire coppice cycle. 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 S2**). This comparison mainly illustrated that the effects of canopy characteristics on the understorey light signature were mainly driven by the rare species with low abundances. These less abundant species were given equal weight in the presence/absence analysis, where we found stronger effects of canopy characteristics and higher model fits, while they were 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.

5. CONCLUSION

The typically expected relationships between basal area, canopy cover and canopy closure were weaker or even absent in structurally complex mixed forests, compared to literature findings for homogeneous monospecific stands. In complex and well-developed forest systems, easy-to-measure structural canopy characteristics are weak predictors of the understorey's light-demand-signature, but accounting for the canopy composition on top of canopy structure can improve predictions. Although the predictive abilities of all considered canopy density variables were rather weak, canopy cover turned out to be the best predictor for the understorey's light-demand-signature. Therefore, this variable remains a valid proxy for light availability in forest vegetation studies, even in complex, mixed stands. Yet, the understorey light-demand-signature appeared to mainly be driven by regional characteristics (presumably land-use history, forest management, and soil characteristics) and likely exhibited time lags.

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Author contributions

LD and KV conceived of the research idea; all authors helped with data collection; LD performed statistical analyses; LD, with contributions from MPP, DL and KV, wrote the paper; all authors discussed the results and commented on the manuscript.

Data accessibility

We intend to archive all data used in this paper on our public website: www.pastforward.ugent.be.

REFERENCES

Akaike, H. (1973). Information Theory and an Extension of the Maximum Likelihood Principle. In Petrov, B.N. & Csaki, F. (eds.), Proceedings of the 2nd International Symposium on Information Theory, pp. 267–281. Budapest: Akademiai Kiado.

Alexander, C., Moeslund, J.E., Bøcher, P.K., Arge, L., & Svenning, J.-C. (2013). Airborne laser scanner (LiDAR) proxies for understory light conditions. Remote Sensing of Environment 134: 152–161.

Angelini, A., Corona, P., Chianucci, F., & Portoghesi, L. (2015). Structural attributes of stand overstory and light under the canopy. Annals of Silvicultural Research 39: 23–31.

Ash, J.E., & Barkham, J.P. (1976). Changes and variability in field layer of a coppiced woodland in Norfolk, England. Journal of Ecology 64: 697–712.

Baeten, L., Bauwens, B., De Schrijver, A., De Keersmaeker, L., Van Calster, H., Vandekerkhove, K. *et al.* (2009). Herb layer changes (1954–2000) related to the conversion of coppice-with-standards forest and soil acidification. Applied Vegetation Science 12: 187–197.

Balandier, P., Sonohat, G., Sinoquet, H., Varlet-Grancher, C., & Dumas, Y. (2006). Characterisation, prediction and relationships between different wavebands of solar radiation transmitted in the understorey of even-aged oak (Quercus petraea, Q. robur) stands. Trees 20: 363–370.

Bartemucci, P., Messier, C., & Canham, C.D. (2006). Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec. Canadian Journal of Forest Research 36: 2065–2079.

Barton, K. (2019). MuMIn: Multi-Model Inference.

Beaudet, M., & Messier, C. (1998). Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. Canadian Journal of Forest Research 28: 1007–1015.

Bellow, J.G., & Nair, P.K.R. (2003). Comparing common methods for assessing understory light availability in shaded-perennial agroforestry systems. Agricultural and Forest Meteorology 114: 197–211.

Blondeel, H., Perring, M.P., Depauw, L., De Lombaerde, E., Landuyt, D., De Frenne, P., & Verheyen, K. (2020). Light and warming drive forest understorey community development in different environments. Global Change Biology. doi: 10.1111/gcb.14955

Brown, N., Jennings, S., Wheeler, P., & Nabe-Nielsen, J. (2000). An improved method for the rapid assessment of forest understorey light environments. Journal of Applied Ecology 37: 1044–1053.

Buckley, D.S., Isebrands, J.G., & Sharik, T.L. (1999). Practical field methods of estimating canopy cover, PAR, and LAI in Michigan oak and pine stands. Northern Journal of Applied Forestry 16: 25–32.

Burnham, K.P., & Anderson, D.R. (2002). Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, Berlin.

Van Calster, H., Baeten, L., Verheyen, K., De Keersmaeker, L., Dekeyser, S., Rogister, J.E., & Hermy, M. (2008). Diverging effects of overstorey conversion scenarios on the understorey vegetation in a former coppice-with-standards forest. Forest Ecology and Management 256: 519–528.

Cannell, M.G.R., & Grace, J. (1993). Competition for light: detection, measurement, and quantification. Canadian Journal of Forest Research 23: 1969–1979.

Coomes, D.A., Kunstler, G., Canham, C.D., & Wright, E. (2009). A greater range of shade-tolerance niches in nutrient-rich forests: An explanation for positive richness-productivity relationships? Journal of Ecology 97: 705–717.

De Lombaerde, E., Verheyen, K., Van Calster, H., & Baeten, L. (2019). Tree regeneration responds more to shade casting by the overstorey and competition in the understorey than to abundance per se. Forest Ecology and Management 450:.

De Lombaerde, E., Verheyen, K., Perring, M.P., Bernhardt-Römermann, M., Van Calster, H., Brunet, J. *et al.* (2018). Responses of competitive understorey species to spatial environmental gradients inaccurately explain temporal changes. Basic and Applied Ecology 30: 52–64.

Decocq, G., Aubert, M., Dupont, F., Alard, D., Saguez, R., Wattez-Franger, A. *et al.* (2004). Plant diversity in a managed temperate deciduous forest: Understorey response to two silvicultural systems. Journal of Applied Ecology 41: 1065–1079.

Decocq, G., Aubert, M., Dupont, F., Bardat, J., Saguez, A.W.-F.R., de Foucault, B. *et al.* (2005). Silviculture-driven vegetation change in a European temperate deciduous forest. Annals of Forest Science 62: 313–323.

Decocq, G., & Hermy, M. (2003). Are there herbaceous dryads in temperate deciduous forests? Acta Botanica Gallica 150: 373–382.

Depauw, L., Landuyt, D., Perring, M.P., Blondeel, H., Maes, S.L., Kopecký, M. *et al.* (2019). A general framework for quantifying the effects of land-use history on ecosystem dynamics. Ecological Indicators 107:1-11.

Depauw, L., Perring, M.P., Brunet, J., Maes, S.L., Blondeel, H., De Lombaerde, E. *et al.* (2019). Interactive effects of past land use and recent forest management on the understorey community in temperate oak forests in South Sweden. Journal of Vegetation Science 30: 917–928.

Diekmann, M. (2003). Species indicator values as an important tool in applied plant ecology – a review. Basic and Applied Ecology 4: 493–506.

Dornelas, M., Magurran, A.E., Buckland, S.T., Chao, A., Chazdon, R.L., Colwell, R.K. *et al.* (2013). Quantifying temporal change in biodiversity: challenges and opportunities. Proceedings of the Royal Society B: Biological Sciences 280: 1–10.

Drever, C.R., & Lertzman, K.P. (2003). Effects of a wide gradient of retained tree structure on understory light in coastal Douglas-fir forests. Canadian Journal of Forest Research 33: 137–146.

Dzwonko, Z. (2001). Assessment of light and soil conditions in ancient and recent woodlands by Ellenberg indicator values. Journal of Applied Ecology 38: 942–951.

Ellenberg, H. (1996). Vegetation Mitteleuropas mit den Alpen in o¨kologischer, dynamischer und historischer Sicht. Ulmer, Stuttgart, DE.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., & Paulissen, D. (1992). Zeigerwerte von Pflanzen in Mitteleuropa. Göttingen.

Fiala, A.C.S., Garman, S.L., & Gray, A.N. (2006). Comparison of five canopy cover estimation techniques in the western Oregon Cascades. Forest Ecology and Management 232: 188–197.

Fischer, H.S. (2015). On the combination of species cover values from different vegetation layers. Applied Vegetation Science 18: 169–170.

Forestry Suppliers. (2008). Using Forest Densiometers.

De Frenne, P., Rodríguez-Sánchez, F., De Schrijver, A., Coomes, D.A., Hermy, M., Vangansbeke, P., & Verheyen, K. (2015). Light accelerates plant responses to warming. Nature Plants 1: 1–3.

Gray, A.N., Spies, T.A., & Easter, M.J. (2002). Microclimatic and soil moisture responses to gap formation in coastal Douglas-fir forests. Canadian Journal of Forest Research 32: 332–343.

Heinken, T., Diekmann, M., Liira, J., Orczewska, A., Brunet, J., Chytrý, M. *et al.* (2019). European forest vascular plant species list (Version 1). figshare. . doi: 10.6084/m9.figshare.8095217.v1

Hobbie, S.E., Reich, P.B., Oleksyn, J., Ogdahl, M., Zytkowiak, R., Hale, C., & Karolewski, P. (2006). Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87: 2288–97.

Jelaska, S.D., Antonić, O., Božić, M., Križan, J., & Kušan, V. (2006). Responses of forest herbs to available understory light measured with hemispherical photographs in silver fir-beech forest in Croatia. Ecological Modelling 194: 209–218.

Jennings, S.B., Brown, N.D., & Sheil, D. (1999). Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. Forestry: An International Journal of Forest Research 72: 59–74.

Kapfer, J., Hédl, R., Jurasinski, G., Kopecký, M., Schei, F.H., & Grytnes, J.-A. (2017). Resurveying historical vegetation data – opportunities and challenges. Applied Vegetation Science 20: 164–171.

Kobe, R.K., Pacala, S.W., Silander Jr., J.A., & Canham, C.D. (1995). Juvenile tree survivorship as a component of shade tolerance. Ecological Applications 5: 517–532.

Kopecký, M., Hédl, R., & Szabó, P. (2013). Non-random extinctions dominate plant community changes in abandoned coppices. Journal of Applied Ecology 50: 79–87.

Lemmon, P.E. (1957). A New Instrument for Measuring Forest Overstory Density. Journal of Forestry 55: 667–668.

Leuschner, C., & Ellenberg, H. (2017). Ecology of Central European forests: vegetation ecology of Central Europe, vol I. Springer, Switzerland.

Leuschner, C., & Meier, I.C. (2018). The ecology of Central European tree species: Trait spectra, functional trade-offs, and ecological classification of adult trees. Perspectives in Plant Ecology, Evolution and Systematics 33: 89–103.

Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, F., & Comeau, P.G. (1999). Predicting and managing light in the understory of boreal forests. Canadian Journal of Forest Research 29: 796–811.

Lin, F., Comita, L.S., Wang, X., Bai, X., Yuan, Z., Xing, D., & Hao, Z. (2014). The contribution of understory light availability and biotic neighborhood to seedling survival in secondary versus old-growth temperate forest. Plant Ecology 215: 795–807.

Lüdecke, D. (2019). sjPlot: Data Visualization for Statistics in Social Science.

McGrath, M.J., Luyssaert, S., Meyfroidt, P., Kaplan, J.O., Bürgi, M., Chen, Y. *et al.* (2015). Reconstructing European forest management from 1600 to 2010. Biogeosciences 12: 4291–4316.

Medvecká, J., Jarolímek, I., Hegedušová, K., Škodová, I., Bazalová Slabejová, D., Botková, K., & Šibíková, M. (2018). Forest habitat invasions – Who with whom, where and why. Forest Ecology and Management 409: 468–478.

Montgomery, R.A., & Chazdon, R.L. (2001). Forest structure, canopy architecture, and light transmittance in tropical wet forests. Ecology 82: 2707–2718.

Morrison, L.W. (2016). Observer error in vegetation surveys: a review. Journal of Plant Ecology 9: 367–379.

Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J., Raus, T., Čarni *et al.* (2016). Vegetation of Europe: hierarchical floristic classification systemof vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19: 3–264.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4: 133–142.

Parker, W.C. (2014). The relationship of stand structure with canopy transmittance: Simple models and practical methods for managing understory light conditions in eastern white pine (Pinus strobus L.)-dominated forests. The Forestry Chronicle 90: 489–497.

Perot, T., Mårell, A., Korboulewsky, N., Seigner, V., & Balandier, P. (2017). Modeling and predicting solar radiation transmittance in mixed forests at a within-stand scale from tree species basal area. Forest Ecology and Management 390: 127–136.

Perring, M.P., Bernhardt-Römermann, M., Baeten, L., Midolo, G., Blondeel, H., Depauw, L. *et al.* (2018). Global environmental change effects on plant community composition trajectories depend upon management legacies. Global Change Biology 24: 1722–1740.

Pinheiro, J., Bates, D., & R Core Team. (2019). nlme: Linear and Nonlinear Mixed Effects Models.

Plue, J., Van Gils, B., De Schrijver, A., Peppler-Lisbach, C., Verheyen, K., & Hermy, M. (2013). Forest herb layer response to long-term light deficit along a forest developmental series. Acta Oecologica 53: 63–72.

Pretzsch, H. (2014). Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. Forest Ecology and Management 327: 251–264.

R Core Team. (2019). R: A language and environment for statistical computing.

Rich, P.M. (1990). Characterizing plant canopies with hemispherical photographs. Remote Sensing Reviews 5: 13–29.

Ritter, E., Dalsgaard, L., & Einhorn, K.S. (2005). Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. Forest Ecology and Management 206: 15–33.

Schmidt, M., Culmsee, H., Boch, S., Heinken, T., Müller, J., & Schmiedel, I. (2011). Anwendungsmöglichkeiten von Waldartenlisten für Gefäßpflanzen, Moose und Flechten. In Schmidt, M., Kriebitzsch, W.-U., & Ewald, J. (eds.), Waldartenlisten der Farn- und Blütenpflanzen, Moose und Flechten Deutschlands. BfN-Skritpen 299: 25-45.,

Schröter, M., Härdtle, W., & von Oheimb, G. (2012). Crown plasticity and neighborhood interactions of European beech (Fagus sylvatica L.) in an old-growth forest. European Journal of Forest Research 131: 787–798.

Sercu, B.K., Baeten, L., van Coillie, F., Martel, A., Lens, L., Verheyen, K., & Bonte, D. (2017). How tree species identity and diversity affect light transmittance to the understory in mature temperate forests. Ecology and Evolution 7: 10861–10870.

Sonohat, G., Balandier, P., & Ruchaud, F. (2004). Predicting solar radiation transmittance in the understory of even-aged coniferous stands in temperate forests. Annals of Forest Science 61: 629–641.

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

Thomas, V., Oliver, R.D., Lim, K., & Woods, M. (2008). LiDAR and Weibull modeling of diameter and basal area. Forestry Chronicle 84: 866–875.

Verheyen, K., Baeten, L., De Frenne, P., Bernhardt-Römermann, M., Brunet, J., Cornelis, J. *et al.* (2012). Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. Journal of Ecology 100: 352–365.

Wickham, H., Chang, W., Henry, L., Pedersen, T.L., Takahashi, K., Wilke, C., & Woo, K. (2019). ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics.

Wood, S.N. (2017). Generalized Additive Models: An Introduction with R. Chapman and Hall/CRC.

Yan, Y., Zhang, C., Wang, Y., Zhao, X., & von Gadow, K. (2015). Drivers of seedling survival in a temperate forest and their relative importance at three stages of succession. Ecology and Evolution 5: 4287–4299.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., & Smith, G.M. (2009). Mixed effect models and extensions in ecology with R. Springer, New York.

Table 1. Main canopy characteristics and understorey light-demand-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 (EIV_{LIGHT}) and percentage of forest specialists in the total herb species pool.*

ID	Region, Country	Total no. of plots (-)	No. of AF plots (-)	No. of plots with CWS (-)	Mean (range) canopy closure (%)	Mean (range) canopy cover (%)	Mean (range) basal area (m^2 ha^{-1})	Mean (range) cover proportion of high shade-casting species (%)	Mean (range) EIV_{LIGHT} (-)	Mean (range) % forest specialists (%)
BI	Bialowieza, PL	15	15	0	85.0 (70.0 - 95.6)	77.0 (48.1 - 91.9)	39.5 (23.2 - 64.4)	80.2 (36.2 - 100)	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)	26.5 (17.5 - 41.3)	1.7 (0.0 - 12.0)	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)	33.7 (17.4 - 64.9)	19.4 (0.0 - 52.8)	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)	23.4 (10.0 - 46.9)	79.9 (39.8 - 100)	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)	32.1 (14.2 - 53.5)	37.5 (0.0 - 78.0)	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)	33.5 (18.5 - 47.9)	84.1 (50.4 - 98.5)	3.2 (2.6 - 3.8)	88 (72 - 100)
KO	Koda Wood, CZ	10	10	7	92.7 (79.6 - 95.8)	75.2 (41.7 - 90.8)	34.6 (24.9 - 47.2)	47.0 (4.8 - 76.2)	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)	21.1 (12.3 - 29.0)	96.2 (78.4 - 100)	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)	34.8 (21.8 - 46.4)	39.1 (0.0 - 91.0)	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)	46.2 (19.3 - 78.3)	31.5 (0.0 - 100)	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)	40.6 (24.8 - 71.7)	92.4 (75.5 - 100)	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)	33.7 (25.5 - 49.1)	55.0 (44.9 - 67.9)	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)	34.0 (10.2 - 59.1)	32.3 (0.0 - 100)	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)	25.0 (16.5 - 40.3)	72.7 (21.7 - 100)	5.3 (4.5 - 6.0)	2 (0 - 12)
TB	Tournibus, Be	10	5	10	86.3 (71.9 - 95.2)	89.8 (80.0 - 95.9)	29.2 (19.5 - 38.3)	23.3 (2.5 - 51.2)	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)	28.9 (13.5 - 38.3)	53.0 (7.4 - 96.8)	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)	31.3 (19.9 - 43.0)	45.4 (0.0 - 95.0)	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)	20.7 (10.7 - 38.9)	10.3 (0.0 - 55.7)	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)	37.9 (29.4 - 44.7)	24.9 (0.0 - 66.7)	4.7 (3.0 - 5.8)	47 (14 - 100)

FIGURES

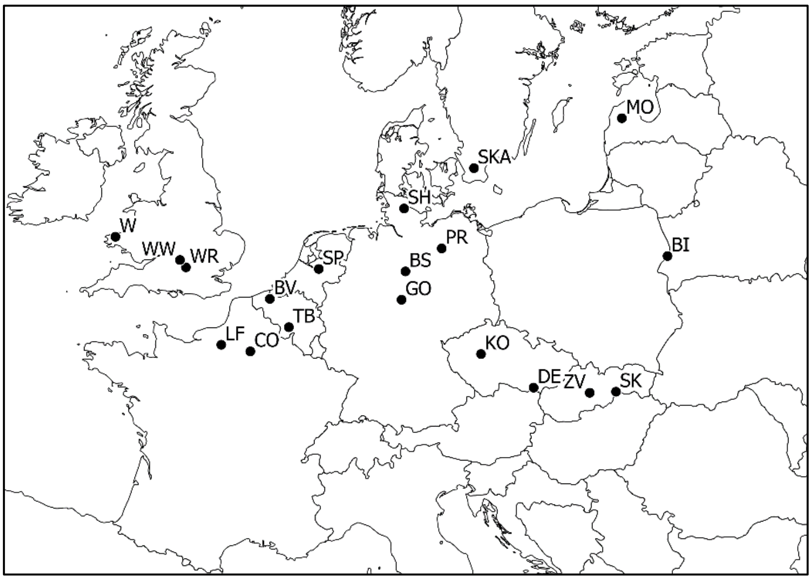

Figure 1. Geographical distribution of the 19 forest regions (the labels refer to Table 1)

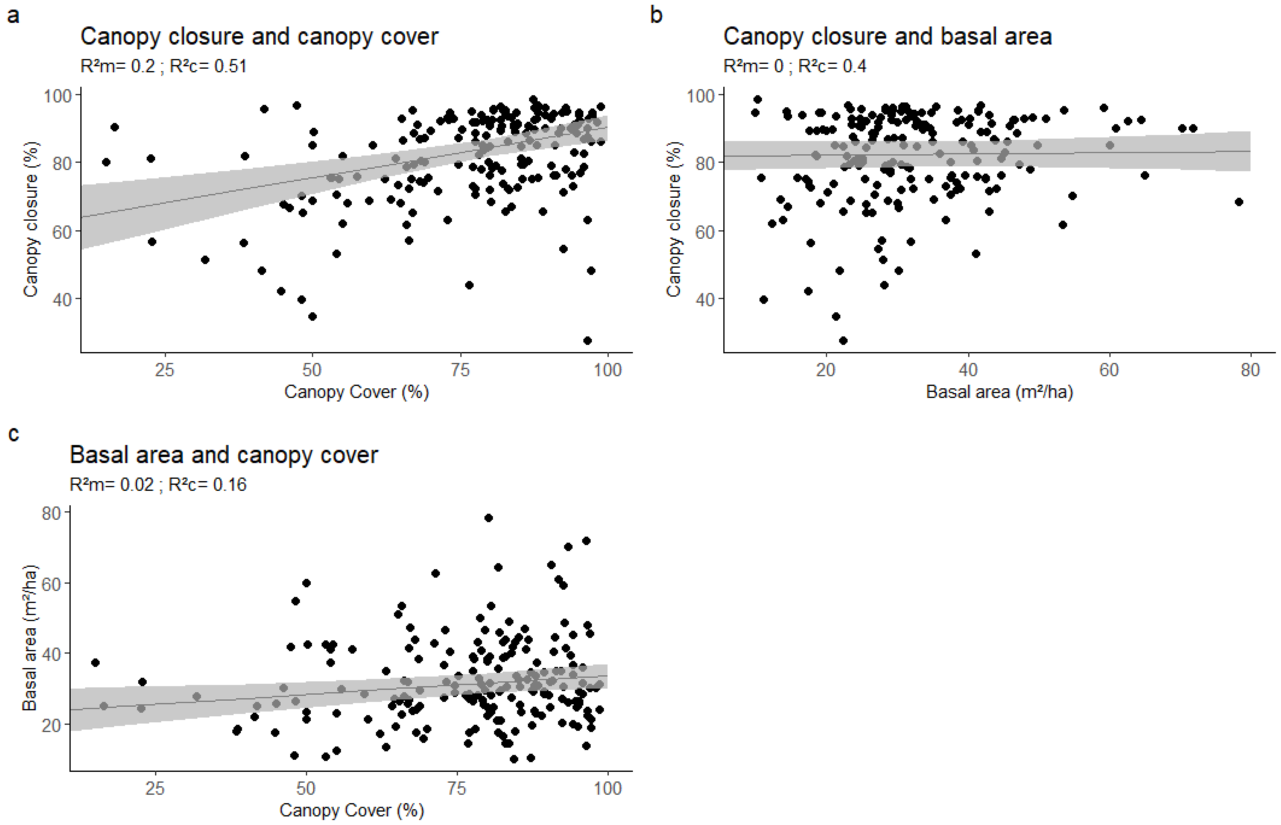

Figure 2. Relationship between basal area, canopy cover and canopy closure, visualised through linear mixed effect models. *'Region' was included as a random slope and intercept in (a), and as a random intercept only in (b) and (c).* R^2m *and* R^2c *represent the variance explained by fixed factors and the variance explained by both fixed and random factors, respectively.*

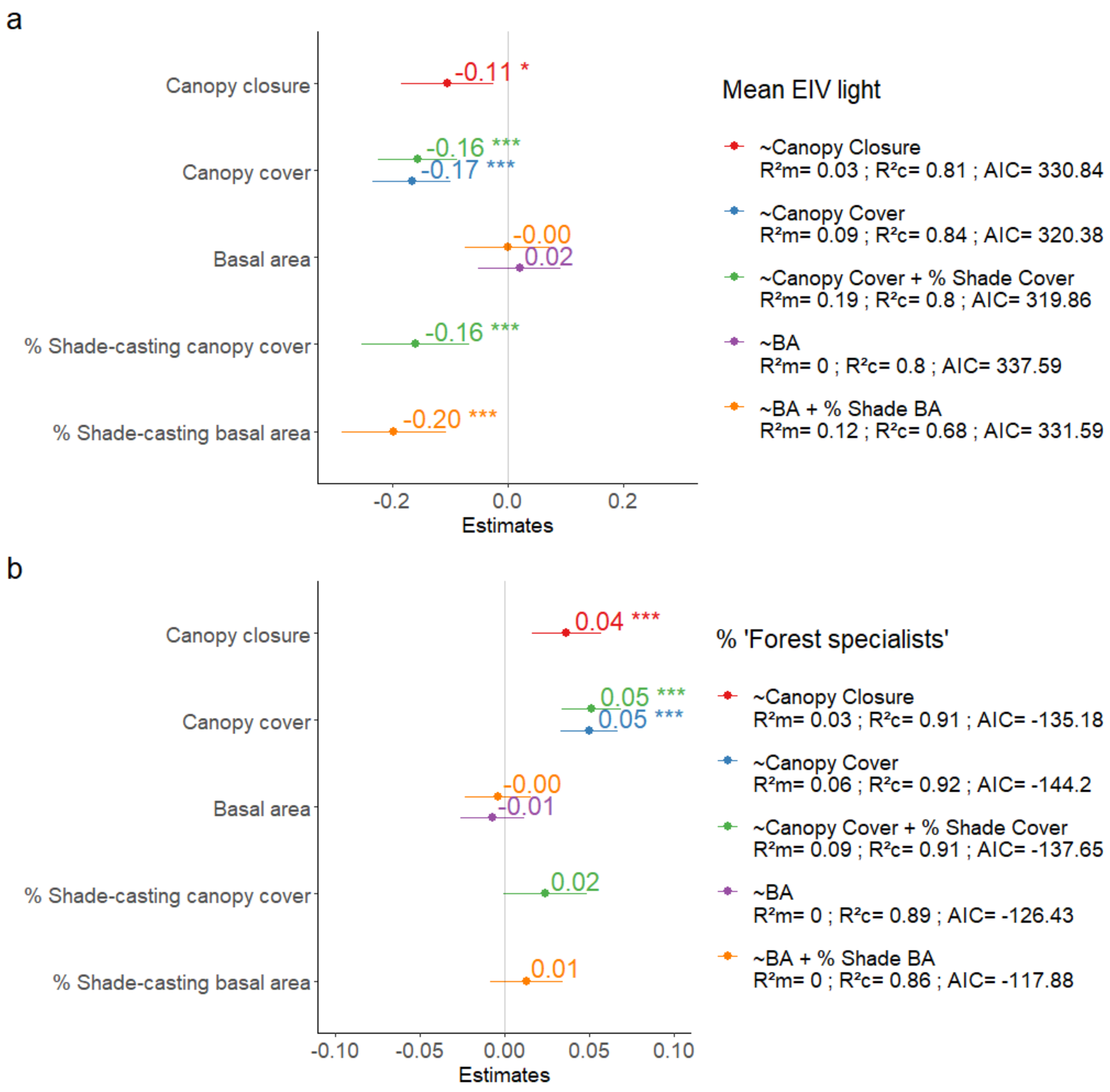

Figure 3. Predicting understorey light-demand-signatures from canopy structure and composition. *Results of comparing five models for two different response variables, i.e. the mean EIV$_{LIGHT}$ (a) and the percentage of forest specialists in the community (b). The five models that we compared, with their respective marginal and conditional R^2 (R^{2}m and R^{2}c, respectively) and AIC-values, are shown in the legend. The figure shows the model estimates and 95% confidence intervals for each explanatory variable. BA stands for basal area. '% Shade Cover' and '% Shade BA' represent the percentage of respectively the canopy cover and the basal area that is occupied by high shade-casting canopy species. Bivariate plots (i.e. light-demand-signature as a function of given explanatory variable(s)) are shown in* ***Appendix S6****.*

SUPPLEMENTARY INFORMATION

Appendix S1. Herb layer species lists: included and excluded species

Appendix S2. Predicting understorey light-demand-signatures from canopy characteristics using abundance-weighted response variables

Appendix S3. Results of statistical analyses when using canopy cover values that were not corrected for overlapping layers

Appendix S4. Shade-casting ability (SCA) scores

Appendix S5. Correlation between SCA-scores and Leaf Area Index (LAI) for eleven major Central European tree species

Appendix S6. Bivariate plots for all fitted models for predicting understorey light-demand-signatures