Title:

Increasing liana frequency in the understorey of temperate European forests is driven by ivy

Authors:

Michael P. Perring[1,2,†], Pieter De Frenne[1], Lionel R. Hertzog[1,3], Haben Blondeel[1], Leen Depauw[1], Sybryn L. Maes[1], Safaa Wasof[1], Hans Verbeeck[4], Kris Verheyen[1], and forestREplot[5]

Addresses:

1: Forest & Nature Lab, Department of Environment, Campus Gontrode, Ghent University, Geraardsbergsesteenweg 267, 9090 Melle-Gontrode, BELGIUM

2: Ecosystem Restoration and Intervention Ecology Research Group, School of Biological Sciences, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, AUSTRALIA

3: Terrestrial Ecology Unit (TEREC), Department of Biology, Campus Ledeganck, Ghent University, Ledeganckstraat 35, 9000 Gent, BELGIUM

4: Computational and Applied Vegetation Ecology Lab (CAVElab), Department of Environment, Campus Coupure, Ghent University, Coupure Links 653, 9000 Gent, BELGIUM

5: forestREplot authors and addresses listed on end page

~~* forestREplot Authors:~~

~~Lander Baeten[a], Markus Bernhardt-Römermann[b], Jörg Brunet[c], Guillaume Decocq[d], Martin Diekmann[e], Thomas Dirnböck[f], Tomasz Durak[g], Radim Hédl[h,i], Thilo Heinken[j], Patrick Hommel[k], Martin Kopecký[l,m], František Máliš[n,o], Fraser J.G. Mitchell[p], Tobias Naaf[q], Miles Newman[p], Petr Petřík[l], Kamila Reczyńska[r], Wolfgang Schmidt[s], Tibor Standovár[t], Krzysztof Świerkosz[u], Hans Van Calster[v], Ondřej Vild[h], Monika Wulf[q]~~

~~forestREplot Addresses:~~

~~a: Forest & Nature Lab, Department of Environment, Campus Gontrode, Ghent University, Geraardsbergsesteenweg 267, 9090 Melle-Gontrode, BELGIUM~~

~~b: Institute of Ecology and Evolution, Friedrich Schiller University Jena, Dornburger Str 159, DE-07743 Jena, GERMANY~~

~~c: Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Box 49, 230 53 Alnarp, SWEDEN~~

~~d: Unité de recherche "Ecologie et Dynamique des Systèmes Anthropisés" (EDYSAN, UMR CNRS 7058), Université de Picardie Jules Verne, Amiens, Cedex 1, FRANCE~~

~~e: Vegetation Ecology and Conservation Biology, Institute of Ecology, University of Bremen, Bremen, GERMANY~~

~~f: Environment Agency Austria, Spittelauer Lände 5, 1090 Vienna, AUSTRIA~~

~~g: Department of Plant Physiology and Ecology, University of Rzeszów, ul. Rejtana 16c, 35-959 Rzeszów, POLAND~~

~~h: Department of Vegetation Ecology, Institute of Botany, Czech Academy of Sciences, Lidická 25/27, CZ-60200, Brno, CZECH REPUBLIC~~

~~i: Department of Botany, Faculty of Science, Palacký University in Olomouc, Olomouc, CZECH REPUBLIC~~

~~j: General Botany, Institute of Biochemistry and Biology, University of Potsdam, Maulbeerallee 3, 14469 Potsdam, GERMANY~~

~~k: Wageningen Environmental Research (Alterra), AA Wageningen, THE NETHERLANDS~~

~~l: Institute of Botany, Czech Academy of Sciences, Zámek 1, CZ-252 43, Průhonice, CZECH REPUBLIC~~

~~m: Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, CZ-165 00 Prague 6 – Suchdol, CZECH REPUBLIC~~

~~n: Faculty of Forestry, Technical University in Zvolen, Zvolen, SLOVAKIA~~

~~o: National Forest Centre, Zvolen, SLOVAKIA~~

~~p: Botany Department, School of Natural Sciences, Trinity College Dublin, Dublin 2, IRELAND~~

~~q: Leibniz Centre for Agricultural Landscape Research (ZALF), Müncheberg, GERMANY~~

~~r: Department of Botany, Faculty of Biological Sciences, University of Wrocław, Kanonia 6/8, PL-50-328 Wrocław, POLAND~~

~~s: Department of Silviculture and Forest Ecology of the Temperate Zones, Georg-August-University Göttingen, Büsgenweg 1, D-37077 Göttingen, GERMANY~~

~~t: Department of Plant Systematics, Ecology and Theoretical Biology, L. Eötvös University, Budapest, HUNGARY~~

~~u: Museum of Natural History, University of Wrocław, Sienkiewicza 21, PL-50-335 Wroclaw, POLAND~~

~~v: Research Institute For Nature and Forest, Havenlaan 88 bus 73, 1000 Brussels, BELGIUM~~

[†]: Corresponding Author:

michael.perring@ugent.be; michael.perring@uwa.edu.au

Authorship Statement:

MPP developed the idea with comments from KV and PDF, before separately named authors, other than LRH, commented on a first draft. HB prepared Figure 2. LRH provided statistical assistance, in particular suggesting the logistic regression approach, aiding in its interpretation, and preparing Figure 3, as well as commenting on later drafts. All authors listed under the forestREplot author name contributed data to this initiative, and commented on later drafts. All authors agreed to submission of the manuscript.

Data Statement:

Data and code used to prepare figures and model results are archived at the Forest & Nature Lab, Ghent University, and are available upon the receipt of a reasonable request to the corresponding author (see also: www.pastforward.ugent.be). Conflicting policies at the time of initial surveys and resurveys, and the wishes of data contributors at the time of data deposition to forestREplot (www.forestreplot.ugent.be), prevent the free unsupervised access to data used in this manuscript.

Conflict of Interest Statement

The lead author is not aware of any conflicts of interest to declare.

Abstract

Increasing woody liana prevalence has been widely observed across the neotropics but observations from temperate regions are rarer. Using a resurvey database of 1814 (quasi-)permanent plots from across 40 European study sites, with a median intersurvey interval of 38 years, and ranging from 1933 (earliest initial survey) to 2015 (latest resurvey), we show that liana occurrences have also increased in the understories of deciduous temperate forests. Ivy drives this increase across space and time, showing an average 14 % proportional occurrence increase per site. Enhanced warming rates, denser shade, and historical management transitions explain some of the variation in ivy frequency response across the whole dataset, despite surveys coming from across continental gradients of environmental conditions. Revealing the mechanisms driving ivy expansion, and any consequences for forest structure and functioning, requires further research. Given the magnitude of ivy frequency increase in the understorey though, and its possible impacts, scientists, policy makers and resource managers need to be mindful of the patterns, processes and implications of any potential 'lianification' of temperate forests.

Keywords:

Broadleaved temperate forest, *Clematis vitalba,* Climate change, Forest management, forestREplot, *Hedera helix*, laurophyllisation, *Lonicera periclymenum*, quasi-permanent plots, resurvey, woody climber

Introduction

Lianas – woody perennial vines with the potential to reach the tree canopy – have been increasing in frequency, cover and biomass particularly across the neotropics in the past decades (e.g. Phillips et al., 2002; Schnitzer & Bongers, 2011). Liana dynamics are understudied in temperate forests, where they are less conspicuous compared to the tropics (Ladwig & Meiners, 2015; Schnitzer, 2005). Some studies have noted changed liana prevalence in temperate areas but they have limited generality e.g. a restricted geographical extent (Londré & Schnitzer, 2006); focused on a particular species (Heinrichs & Schmidt, 2015). Yet understanding and predicting liana dynamics is important. As demonstrated in the tropics, lianas can have far-reaching consequences for forest biodiversity, structure, and functions such as carbon, nutrient and water cycling (Schnitzer, 2018; van der Heijden, Powers, & Schnitzer, 2015). The potential for ecosystem consequences in temperate areas has been discussed (Ladwig & Meiners, 2015), and evidence is accumulating of significant impacts on transpiration (Ichihashi et al., 2017) and species composition (Ladwig & Meiners, 2009; Madrigal-González, Rios, Aragón, & Gianoli, 2017).

Possible drivers explaining generally increased liana prevalence in the tropics include forest fragmentation and disturbance, climate change, increasing intensity of seasonal droughts, shifting rainfall patterns, and rising concentrations of atmospheric carbon dioxide [CO_2] (Schnitzer & Bongers, 2011; Schnitzer & van der Heijden, 2019). These drivers, and others such as atmospheric deposition of nutrients and urbanization, also affect temperate forests (Bernhardt-Römermann et al., 2015). We might expect certain drivers to underlie any potential changes in temperate liana frequency, and thus for these drivers to be correlated with any observed frequency responses. For instance, increasing winter temperatures may lower the risk of freeze-thaw embolism ~~(cell rupture)~~ which tends to affect lianas more than other woody species (Schnitzer, 2005). Any frequency response may be especially marked in the understorey as experimental evidence suggests that temperate climbers would benefit more than self-supporting species from rising [CO_2] in deep shade (Mohan et al., 2006; Zotz, Cueni, & Körner, 2006). This benefit likely arises due to liana species' investment in leaves: a greater relative investment in leaves compared to non-liana species allows them to take more advantage of the lower light compensation point for carbon uptake in shade (Zotz et al., 2006). One might therefore expect a general liana response in the understories of temperate forests too, given lianas' specific ecology, anatomy, morphology and physiology, and the widespread rise in [CO_2] and temperature.

Any general liana response in temperate areas may though depend on liana growth strategies and tolerance to environmental conditions. In the understorey, lianas may actively search for growth opportunities or 'sit-and-wait' for changed conditions. In understorey shade, and generally in contrast to the tropics, some temperate lianas can form dense mats of leaf and stem cover (e.g. ivy; *Hedera helix*). When ascending to the canopy, lianas use various climbing mechanisms. Temperate lianas exhibit the same suite of climbing mechanisms as tropical lianas, including through adhesion to trees by roots (e.g. ivy), twining/scrambling (honeysuckle and traveller's joy; *Lonicera periclymenum* and *Clematis vitalba* respectively) and tendril attachments (grape species; *Vitis* spp.). Simultaneously, tolerance to environmental conditions and demand for resources can vary among liana species. Shadier conditions, for instance following a decline in management intensity across European forests (McGrath et al., 2015) may be of direct benefit to temperate shade-tolerant lianas, while being detrimental to more light-demanding liana species (e.g. *Vitis* spp). These differences make it unclear whether there will be a general liana response in temperate species, or how individual species will respond to changed environmental conditions.

Continent-wide resurvey studies in temperate forests offer the opportunity to infer generality of response to changed environmental conditions over long time intervals. Results from such surveys, distributed along carefully chosen environmental gradients (e.g. of climate) and with well-characterised management histories, allow assessment of potential change drivers (Verheyen et al., 2017). Here, using a network of 1814 understorey resurvey plots in continuously forested sites (since at least 1800) across Europe, we ask how temperate liana frequency of occurrence has changed over space and time. We then investigate environmental correlates of observed frequency responses. Given the general susceptibility of lianas to cold temperatures ~~and the potential benefit of increased [CO_2] for understorey liana growth~~, we expected warmer conditions in a higher [CO_2] world to have led to a general increase in understorey liana frequency (see also Manzanedo et al., 2018). We also considered that historical management transitions and light dynamics may affect liana response in these widespread temperate forests.

Methods

A network of resurvey plots across environmental gradients

We compiled vegetation resurvey data on the forest understorey for 1814 (quasi-) permanent plots spread across 40 European single-study sites (hereafter "sites") (www.forestreplot.ugent.be). These data were collated from available datasets originally collected for different purposes, so there is inherent variation as described in WebPanel 1. Methodologically, the majority of plots (*n* = 1465) are between 100 and 400 m^2, as is likely typical for forest understorey surveys, with a generally consistent size between survey time points within a site. Surveyors, all qualified botanists, assessed plots twice, with a median intercensus interval of 38 years (range 12 to 75 years, interquartile range of 25 to 49 years). Initial survey years ranged from 1933 to 1994, and resurveys took place between 1987 and 2015. As far as we are aware, plots were initially located without regard to the presence or absence of lianas.

The definition of the understorey differed among sites but was consistent between time points within a site. The understorey included lianas, and typically perennial woody and herbaceous species characteristic of a layer below 1.5 to 2m in height. Some surveys ignored tree and shrub seedlings, even while including woody species characteristic of the understorey. In case this meant that surveyors had ignored lianas, we analysed frequency change data in two ways: we included or we excluded sites when all plots within a site had no recorded presence of a given liana species at both survey dates. Surveyors did not consistently record overstorey tree species across the dataset, but typical species noted were oaks (*Quercus* spp.), beech (*Fagus sylvatica*), maples (*Acer* spp.) and ash (*Fraxinus excelsior*). Stands could be monocultures or mixtures, and very few sites had mixtures with conifers (WebPanel 1).

We restricted our analyses to understories in ancient forest plots i.e. continuously forested since at least 1800. Note that designation as 'ancient' refers to the continuity of land use; it does not refer to forest stand age nor the intensity of management. ~~We are not aware of figures outlining the extent of continuously forested sites in Europe, as opposed to forest cover extent following e.g. agricultural abandonment. However, s~~Semi-natural forest (ancient forest is a subset) occupies 87 % of European forests, with broadleaved forests covering 90.4 million ha of the 215 million ha of total forest area (Forest Europe, 2015). We also characterised forest management history for each plot, from 1800 to present, through questionnaires issued to local experts (details in Perring et al., 2018). We asked experts to classify plots as managed according to prevalent methods in Europe (McGrath et al., 2015): *coppicing* (harvesting of multi-stemmed trees and shrubs with relatively short rotation time and regrowth from rootstock, and with occasional single stemmed 'standard' trees, collectively termed here 'coppice-with-standards'); *high forest* (longer rotation times with recruitment from seed and harvesting of (generally) single stemmed trees for timber), or *unmanaged*. We derived management transitions based on these categories (see Perring et al., 2018). No large-scale management actions (e.g. clear felling), or stand-scale disturbances (e.g. widespread storm damage), took place between surveys, so we assume that vegetation change responses were not confounded with immediate post-disturbance successional dynamics.

Plots within sites also have variation in local environmental characteristics. We estimated environmental variation using cover-weighted Ellenberg Indicator Values (EIV) of the understorey community at the time of the initial survey (Ellenberg, Weber, Düll, Wirth, & Werner, 2001). Individual species' EIV suggest the demand or tolerance for a given variable based on a species' realised niche, and include light (EIV_L), pH (as EIV_R) and nutrients (EIV_N). Community metrics of these values are considered a reasonable approximation of environmental conditions (Diekmann, 2003). We estimated changing light dynamics by taking account of the EIV_L at the time of the recent and initial survey~~ (Table S6)~~. A negative value for the absolute change in EIV_L i.e. ΔEIV_L indicates the community demand for light has decreased, suggesting increased shade over time. We extracted site-level climate and atmospheric nitrogen deposition data from online databases. Further details on the environmental variation across plots and sites, and the methods used to assess these, can be found in Supplementary Information (WebPanel 2, and WebTables 2, 3 and 4). We are aware that EIV characterise the environment indirectly; direct environmental characterisation is important for moving understanding forward in forest ecological research.

For each plot, we extracted the percentage cover (total of foliage and stem) in the understorey of three native liana species (woody vines potentially capable of reaching the tree canopy), typical for these European forests: ivy, traveller's joy and honeysuckle (Figure 1). Although all these species are lianas, their ecological tolerances and growth forms vary. There were no records of other temperate lianas (e.g. *Lonicera caprifolium*, *Vitis* spp., *Parthenocissus* spp.) in this dataset.

Quantifying trends in liana frequency

For a given liana species at each survey in each site, we tallied the number of understorey plots it occurred in. We summed these values across species, to give a total frequency of lianas per site per survey. We then calculated the difference in frequency of occurrence between surveys for each species, and for the total frequency of lianas combined, for each site. Using a t-test, we aimed to answer: Is the frequency change of individual liana species in understorey communities, and the total frequency change, across European forest sites different from zero?

We used a paired t-test to investigate whether the proportion of understorey plots occupied per site at the time of the resurvey was different to the proportion of occupied understorey plots per site at the time of the initial survey. We calculated "proportion of occupied plots" as the number of plots occupied by a given liana species in a site divided by the total number of surveyed plots in a site i.e. controlling for survey effort. In a supplementary analysis, we considered whether there was a temporal trend in liana frequency change. As noted therein, the distribution of our data prevent a robust trend investigation, although qualitative conclusions on frequency change remain unaltered (see WebPanel 3: *A temporal trend in liana frequency change?* and WebTables 11,12,13,14,15,16,17,18).

Investigating potential drivers of frequency change

To investigate potential drivers of frequency change we specifically asked how the probability of presence in a plot of a given liana species i at the time of the resurvey ($t2$, i.e. i_{t2}) depended on change drivers, given the liana species i's occupancy status at the initial survey. To derive these probabilities, we first fitted a logistic regression with a binomial error structure and a logit link in a generalized linear mixed model (GLMM) framework (`lme4` package in R) (Equation [1]):

$$i_{t2} \sim i_{t1} + Years\ between\ surveys + \log\ (Plot\ size) + Altitude + EIV_{NR} + EIV_{L} + MAT + MAP + \Delta EIV_{L} + \Delta T + \Delta N + \Delta P + Management\ transition + (1\ |Site)$$

Equation [1]

Given our expectations (i.e. the importance of environmental changes, management transitions and light dynamics), we focussed on change between surveys in shade (as estimated by ΔEIV_L), mean annual temperature (ΔT), and mean annual precipitation (ΔP), the mean N deposition rate (ΔN), and the management transition since 1800. We accounted for methodological covariates (e.g. plot size), plot conditions at the time of the initial survey (e.g. MAT, $\mathrm{EIV_L}$), and the nesting of plots within sites (as further explained in WebTable 2).

From the fitted model, we derived the presence probability for liana species *i* at the resurvey given the initial survey absence of that species ($i_{t1} = 0$). This allowed investigation of the effect of various environmental change drivers on the increase in liana frequencies. We first predicted the probability of resurvey presence in the absence of any change for a given focal driver, and we then derived another prediction of resurvey presence with the average (across sites) observed change in the focal driver. We set all other variables to their observed means in both models. We derived predictions for each forest management transition using average values for other predictor variables. The investigation of potential drivers of frequency change only assessed those liana species present in more than 10 sites at the time of the initial and resurvey to cover enough environmental space to test relationships. To gain further understanding on potential drivers of change, we also calculated the amount of variation that we can uniquely attribute to focal terms by subtracting a reduced model R^2 (without the focal term) from the full model R^2 (including the focal term), also considering the change in AIC between these models. We carried out all statistical analyses in R 3.6.0 (R Core Team, 2019).

Results

Ivy drives the increase in frequency of lianas in the understorey across Europe

Across the European dataset analysed, total liana frequency of occurrence in understorey plots has increased by 38.7 % between surveys (from 581 to 806 plots), driven by an increase in ivy (Figure 2, WebTable 5 and WebTable 6). Notably, ivy has increased in absolute terms by 70 %, from 288 presences at the time of initial surveys, to 496 presences at resurveys, out of 1814 plots in total. Controlling for survey effort, that is an average increase in the proportion of occupied understorey plots per site of 9 % (nearly 14 % if we remove sites with zero occupancy of ivy at both surveys (WebTable 7 and WebTable 8)). We observe this increase in ivy across European forest sites (Figure 2b): twenty-three of twenty-seven sites with ivy presence at the time of the initial survey showed an increase in frequency of occurrence by the time of the resurvey while two sites remained unchanged. Only two sites exhibited any decline, and this was slight.

Of the other liana species, travellers' joy (*Clematis vitalba*) increased in understorey plot frequency by 113 % but was relatively infrequent in the dataset (found in 9 sites, going from 23 to 49 occurrences in total (WebTable 5, WebFigure 1)). Honeysuckle (*Lonicera periclymenum*) had a similar prevalence to ivy in the understorey at the time of the initial survey, but barely changed in frequency (- 3.3% in overall occurrence from 270 to 261 plots). This limited 'whole of dataset change' masks among-site differences: stasis or slight declines/increases characterise most sites, while we find a large drop in honeysuckle frequency (from 146 to 108 plots) in Tournibus, Belgium, a site with a large increase in ivy frequency (WebTable 5, WebFigure 1). We generally observed that sites without any liana presence in the understorey, or with low liana frequencies, are in the north and east of Europe.

Evidence for focal drivers affecting liana frequency responses

Changing temperature, light regimes, and historical management transitions explain limited unique variation in ivy frequency responses when we take presence at the initial survey across the whole dataset into account (Table 1). Unmeasured differences among sites, and ivy's presence at the initial survey, drive most of the variation explained~~; focal drivers account for limited unique additional variation (Table 1)~~. Despite this, the likelihood of finding ivy in a plot at a resurvey, given it was absent at the initial survey, is clearly increased by greater rates of warming and decreased by high forest management, while the impact of denser shade is less strong (Figure 3). The probability of finding honeysuckle at a resurvey declines when high forests became unmanaged, with limited evidence for site-scale drivers affecting the likelihood of finding honeysuckle when it is absent at the initial survey (WebTable 9 and WebTable 10).

Discussion

Ivy drives an increase in liana frequency in the understories of ancient deciduous temperate forests distributed across northern Europe

For the first time, to our knowledge, we have demonstrated that lianas are increasing in frequency of occurrence across a broad geographical extent in the understories of temperate forests. Contrary to the neotropics, where liana increase occurs across multiple species, strata, and growth habits, the pattern reported here is driven by a single understorey species, the evergreen, root-climbing plant ivy. Not only is the magnitude of response for ivy striking, additional analyses show it is a singular response among broad-leaved evergreen species and woody species that have the capacity to climb. Indeed, it is arguably unique among *any* species recorded within this understorey dataset (see WebPanel 4: "*A unique response of ivy frequency…?*" and associated WebTables 19 and 20). Interestingly, the properties of the surveyed forest sites argue against an increasing response due to post-disturbance successional processes. This is because they have been continuously forested since 1800, predominantly with deciduous trees, and with no large-scale disturbances immediately prior to, or between surveys. We observed an increased ivy presence in these relatively undisturbed forest interior plots despite the general expectation for lianas to increase with disturbance and at forest edges (e.g. Matthews, Schmit, & Campbell, 2016). The limited richness of liana species in the dataset precludes statements regarding liana diversity change.

Significant potential drivers of frequency change meet ecological expectations

With observational data, we cannot causally demonstrate the driver(s) and mechanism(s) underlying the observed responses. Understanding any mechanism may of course aid forest management decisions in response to the increased prevalence. The wide environmental gradients and variation in management conditions do allow us to draw tentative inference from the relationships among greater ivy frequency and warmer temperatures, light regimes and historical management transitions.

The effect of these potential drivers fits with our understanding of ivy's ecology. Warming is expected to favour it, perhaps due to susceptibility to freezing, and/or perhaps because of the genus' tropical evolutionary origins (Metcalfe, 2005) i.e. ivy might 'like' warmer conditions in any season. Ivy is also expected to take advantage of shadier conditions in the understorey, particularly with enhanced [CO_2] (Zotz et al., 2006). In contrast, increasing shade (a general response across the forests analysed here) is likely to compromise honeysuckle, as it tends to increase with increasing light availability. This variable ecology between liana species may also explain the tendency for contrasting cover responses of these two species in forests that have undergone transitions to being unmanaged (see WebPanel 5 and WebFigures 3, 4, 5 and 6).

Causes and consequences of ivy frequency change

The causes and consequences of ivy increase in the understorey remain unknown. Although our analysis explained some variation in frequency at the resurvey with potential focal drivers, the extent of this explanation is limited in comparison to among-site differences and the explanatory power of initial survey ivy presence. However, the consistent Europe-wide ivy pattern also suggests that drivers at that scale may underlie responses (Senf et al., 2018). Increasing frequency could relate to diaspore pressure, which in turn will relate to the proximity of reproductive adults. For ivy in particular, a transition to the adult (flowering) form only occurs once it has gained height or exposure to light, and has therefore transitioned from the understorey. Unfortunately, our data lacked sufficient coverage of overstorey liana presence, and knowledge on surrounding landscape parameters (e.g. the potential for garden escapes), to assess potential diaspore pressure, dispersal and recruitment processes. This highlights the requirement to extend liana research across temperate forest strata.

This increased research effort needs to consider whether increasing understorey ivy prevalence has consequences for forest biodiversity, structure, and function. The evergreen nature of ivy may allow it to increase the growing season length of the understorey (and overstorey), and thus fix more carbon at times when conditions are favourable, especially prior to overstorey leaf flushing in trees. Indeed, ivy alone has been demonstrated to drive biomass accumulation in the understorey (Wasof et al., 2018) while it may alter tree regeneration and consequently influence overstorey, as well as understorey, composition (including through allelopathy Ladwig, Meiners, Pisula, & Lang, 2012). In general, species in the understorey require increased consideration in global change research given their (sometimes significant) contribution to whole forest functioning (Landuyt et al., 2019). Temperate lianas, especially ivy's adult form, can enhance biodiversity in forests through the provision of useful habitat and resources for other organisms (Metcalfe, 2005). Finally, there is an increased tree mortality risk were ivy to reach the canopy since it can make host trees more susceptible to windfall (e.g. Schnitzler & Heuzé, 2006).

Concluding remarks

Lianas, particularly ivy, have long had a culturally and economically important role in European society, been an important component of domestic and wild ungulate browse, and provided indications of past climate variability (see WebPanel 6: *The cultural, scientific and economic significance of temperate liana species*). Our results encourage experimental (e.g. liana removal studies) and observational research on the functional and structural consequences of increased liana prevalence in temperate as well as tropical areas, across other forest types and strata, and across levels of biodiversity. If such a research programme demonstrates that temperate lianas can have important structural and functional implications, then predictive forest dynamic models will need to account for lianas in temperate as well as tropical forests (di Porcia e Brugnera et al., 2019; Verbeeck & Kearsley, 2016), and resource managers may need to adapt to potential temperate "lianification".

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Supplementary References in WebPanel 7.

Tables

Table 1: Focal variable estimates for ivy presence at the resurvey using logistic regression (Equation [1]); values in bold have confidence intervals that do not overlap with 0. We also report the change in AIC with the removal of a given focal variable, and amount of variation explained by a given focal variable. Parameter values for all terms in Equation [1] provided in WebTable 9, along with those for honeysuckle.

Focal variable	**Ivy Presence at Resurvey**		
	Standardized Parameter Estimate (±95% Confidence Interval)	**ΔAIC**[a]	**% Unique variation explained by focal fixed effect**[b]
Ivy presence at initial survey	**2.6 (2.2 - 3.0)**	−161	20.6
Warming (ΔT)	**0.9 (0.2 - 1.7)**	−2.7	4.4
Change in light availability (ΔEIV_L)	**−0.28 (−0.5 - −0.1)**	−5.3	2.8
Management transition[c]	−0.07 (−0.8 - 0.7) CWS to HF to 0 **−1.1 (−2.0 - −0.2)** **HF throughout** −0.1 (−0.9 - 0.7) HF to 0	−0.74	0.5
Nitrogen deposition (ΔN)	−0.5 (−1.1 - 0.1)	−0.76	0.9
Precipitation change (ΔP)	0.1 (−0.4 - 0.7)	1.7	0.4
Full Model			
AIC: 1209	R^2 fixed effects: 34.8%	R^2 fixed and random effects: 46.9%	

[a]: Change in AIC is negative if the reduced model i.e. a model fitted to Equation [1] without the focal variable, has a greater AIC than the full model (given by Equation [2]).

[b]: % Unique variation explained calculated as: (full model R^2 – reduced model R^2) where the reduced model is fitted without the focal variable.

[c]: Management transitions: CWS to HF to 0 is "coppice-with-standards to high forest to unmanaged", HF throughout is "high forest throughout", and HF to 0 is "high forest to unmanaged".

Figures

See images for Perring_Fig1a, Perring_Fig1b, and Perring_Fig1c submitted separately.

Figure 1

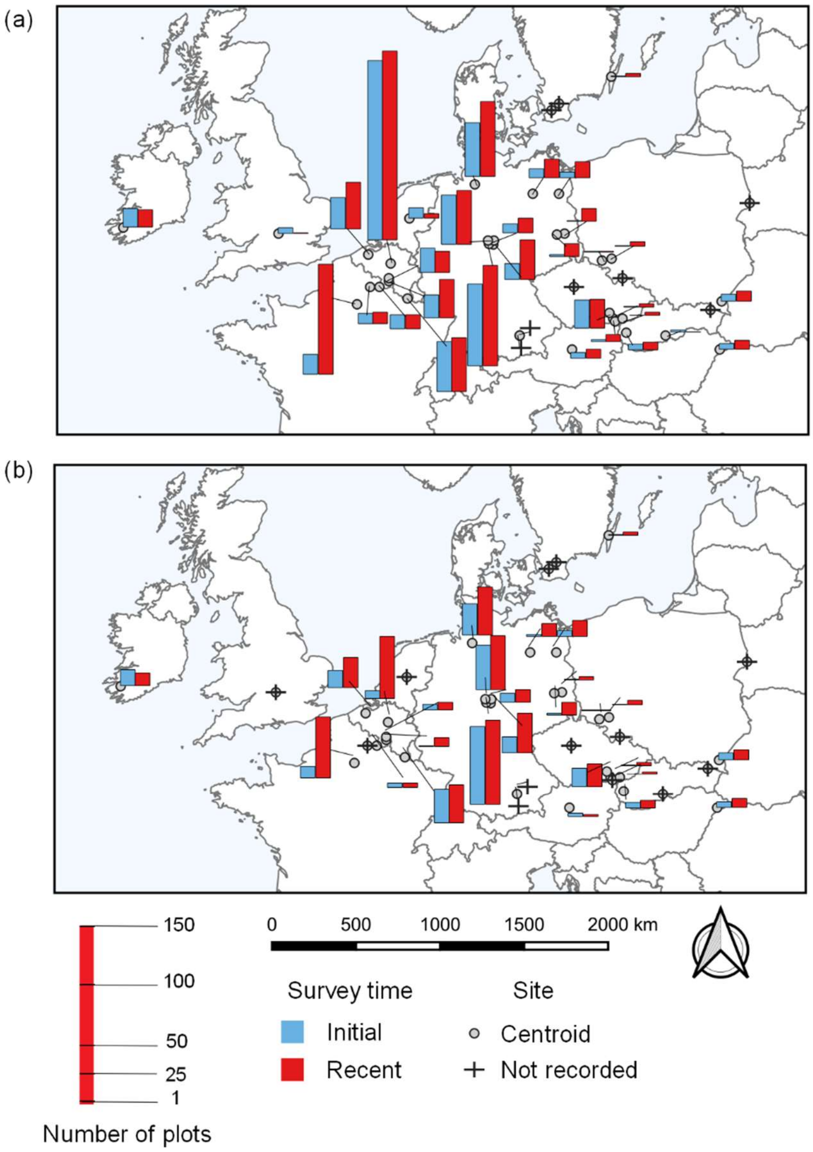

Figure 2

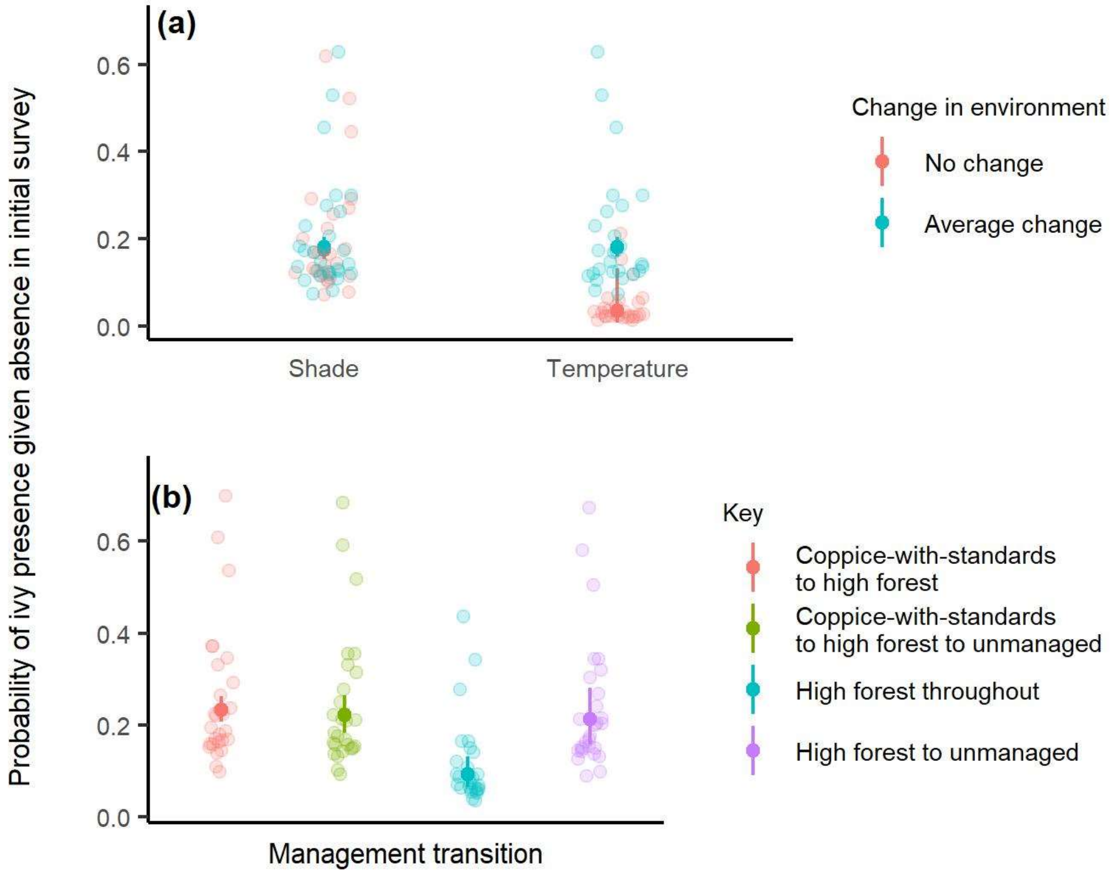
(a)
Probability of ivy presence given absence in initial survey
0.6
0.4
0.2
0.0
Shade
Temperature
Change in environment
No change
Average change
(b)
0.6
0.4
0.2
0.0
Management transition
Key
Coppice-with-standards to high forest
Coppice-with-standards to high forest to unmanaged
High forest throughout
High forest to unmanaged

Figure 3

Figure Captions

Figure 1: Example images of focal liana species found in the understorey of temperate deciduous forests across Europe showing (a) ivy, (b) honeysuckle, and (c) traveller's joy. Figures 1a & 1c taken in the understorey of a deciduous forest in the Viroinval, Belgium, courtesy of Seppe Lenders, and Fig 1b showing flowering honeysuckle in a hedgerow in the Campine, Belgium, courtesy of Sanne Van Den Berge.

Figure 2: **(a) Absolute liana frequency has generally increased over time in temperate deciduous forests across Europe.** Of the three liana species included in these total amounts, ivy **(b)** drives the response while traveller's joy and honeysuckle are less frequent and do not exhibit consistent directional change (see WebFigure S1, and WebTables 6 to 8 for statistical results).

Figure 3: **Predicted change in the probability of presence (± 95% CI) for ivy at the resurvey, given absence at the initial survey, with (a) enhanced shade and warming temperatures; and (b) management transitions.** In panel (a), solid pink symbols give the mean probability of presence in the absence of any change for the focal variable between surveys across the whole of Europe, and light blue symbols the mean probability of presence given the average across-dataset change in the focal variable (lines give the 95% CI). In panel (b), predictions are made for different forest management transitions. A continually managed high forest system has a much lower probability of finding ivy in a resurvey when absent intially, and compared to other widespread management transitions in European forestry (as explained in the main text~~ and the SI~~). In both figures, transparent symbols represent the site-specific probabilities and show the wide variation in the predicted probability of ivy presence at the site level.

forestREplot Authors:

Lander Baeten[a], Markus Bernhardt-Römermann[b], Jörg Brunet[c], Guillaume Decocq[d], Martin Diekmann[e], Thomas Dirnböck[f], Tomasz Durak[g], Radim Hédl[h,i], Thilo Heinken[j], Patrick Hommel[k], Martin Kopecký[l,m], František Máliš[n,o], Fraser J.G. Mitchell[p], Tobias Naaf[q], Miles Newman[p], Petr Petřík[l], Kamila Reczyńska[r], Wolfgang Schmidt[s], Tibor Standovár[t], Krzysztof Świerkosz[u], Hans Van Calster[v], Ondřej Vild[h], Monika Wulf[q]

forestREplot Addresses:

a: Forest & Nature Lab, Department of Environment, Campus Gontrode, Ghent University, Geraardsbergsesteenweg 267, 9090 Melle-Gontrode, BELGIUM
b: Institute of Ecology and Evolution, Friedrich Schiller University Jena, Dornburger Str 159, DE-07743 Jena, GERMANY
c: Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Box 49, 230 53 Alnarp, SWEDEN

d: Unité de recherche “Ecologie et Dynamique des Systèmes Anthropisés” (EDYSAN, UMR CNRS 7058), Université de Picardie Jules Verne, Amiens, Cedex 1, FRANCE
e: Vegetation Ecology and Conservation Biology, Institute of Ecology, University of Bremen, Bremen, GERMANY
f: Environment Agency Austria, Spittelauer Lände 5, 1090 Vienna, AUSTRIA
g: Department of Plant Physiology and Ecology, University of Rzeszów, ul. Rejtana 16c, 35-959 Rzeszów, POLAND
h: Department of Vegetation Ecology, Institute of Botany, Czech Academy of Sciences, Lidická 25/27, CZ-60200, Brno, CZECH REPUBLIC
i: Department of Botany, Faculty of Science, Palacký University in Olomouc, Olomouc, CZECH REPUBLIC
j: General Botany, Institute of Biochemistry and Biology, University of Potsdam, Maulbeerallee 3, 14469 Potsdam, GERMANY
k: Wageningen Environmental Research (Alterra), AA Wageningen, THE NETHERLANDS
l: Institute of Botany, Czech Academy of Sciences, Zámek 1, CZ-252 43, Průhonice, CZECH REPUBLIC
m: Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, CZ-165 00 Prague 6 – Suchdol, CZECH REPUBLIC
n: Faculty of Forestry, Technical University in Zvolen, Zvolen, SLOVAKIA
o: National Forest Centre, Zvolen, SLOVAKIA
p: Botany Department, School of Natural Sciences, Trinity College Dublin, Dublin 2, IRELAND
q: Leibniz Centre for Agricultural Landscape Research (ZALF), Müncheberg, GERMANY
r: Department of Botany, Faculty of Biological Sciences, University of Wrocław, Kanonia 6/8, PL-50-328 Wrocław, POLAND
s: Department of Silviculture and Forest Ecology of the Temperate Zones, Georg-August-University Göttingen, Büsgenweg 1, D-37077 Göttingen, GERMANY
t: Department of Plant Systematics, Ecology and Theoretical Biology, L. Eötvös University, Budapest, HUNGARY
u: Museum of Natural History, University of Wrocław, Sienkiewicza 21, PL-50-335 Wroclaw, POLAND
v: Research Institute For Nature and Forest, Havenlaan 88 bus 73, 1000 Brussels, BELGIUM