Increasing liana frequency in temperate European forest understories is driven by ivy

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The increasing prevalence of woody liana species has been widely observed across the neotropics, but observations from temperate regions are comparatively rare. On the basis of a resurvey database of 1814 (quasi-)permanent plots from across 40 European study sites, with a median between-survey interval of 38 years, and ranging from 1933 (earliest initial survey) to 2015 (most recent resurvey), we found that liana occurrence has also increased in the understories of deciduous temperate forests in Europe. Ivy (*Hedera helix*) is largely responsible for driving this increase across space and time, as its proportional occurrence has grown by an average of 14% per site. Enhanced warming rates, increased shade, and historical management transitions explain only some of the variation in ivy frequency response across the dataset, despite surveys coming from across continental gradients of environmental conditions. Uncovering the mechanisms underlying ivy expansion, and the potential consequences for forest structure and functioning, requires further research. Given the magnitude of increases in understory ivy frequency and its possible impacts, scientists, policy makers, and resource managers must be mindful of the patterns, processes, and implications of potential "lianification" of temperate forests.

Lianas – generally defined as woody perennial vines with the potential to reach tree canopies – have been increasing in frequency, cover, and biomass, particularly in the neotropics, over the past several decades (eg Phillips *et al.* 2002; Schnitzer and Bongers 2011; although note Bongers *et al.* [2020]). However, liana dynamics are understudied in temperate forests, where they are less conspicuous than in the tropics (Schnitzer 2005; Ladwig and Meiners 2015). Although research has shown that liana prevalence has changed in temperate areas, such studies are limited, for instance by having a restricted geographical extent (Londré and Schnitzer 2006) or a narrow focus on a particular species (Heinrichs and Schmidt 2015). Understanding and predicting liana dynamics is important, however, as research in the tropics has demonstrated that lianas can have far-reaching effects on forest biodiversity and structure, as well as on such functions as carbon (C), nutrient, and water cycling (van der Heijden *et al.* 2015; Schnitzer 2018). The potential for consequences of liana expansion on temperate ecosystems has been discussed previously (Ladwig and Meiners 2015), and accumulating evidence suggests that lianas are having major impacts on transpiration (Ichihashi *et al.*

2017) and species composition (Ladwig and Meiners 2009; Madrigal-González *et al.* 2017).

Possible drivers underlying increased liana prevalence in the neotropics 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 and Bongers 2011; Schnitzer and van der Heijden 2019). These factors, along with atmospheric deposition of nutrients and urbanization, also affect temperate forests (Bernhardt-Römermann *et al.* 2015). Certain drivers might be expected to underlie any potential changes in temperate liana frequency, and therefore these drivers might be expected to be associated with observed frequency responses. For instance, warmer winter temperatures may lower the risk of freeze–thaw embolism, which tends to affect lianas more than other woody species (Schnitzer 2005). Frequency responses may be especially marked in the understory, as experimental evidence suggests that temperate climbers would benefit more than self-supporting species from rising CO_2 levels in deep shade (Mohan *et al.* 2006; Zotz *et al.* 2006). This benefit likely arises due to the relatively high investment of liana species in producing leaves, which allows them to take greater advantage of the lower light compensation point for C uptake in shade (Zotz *et al.* 2006). One might therefore expect a general liana response in the understories of temperate forests as well, given lianas' specific ecology, anatomy, morphology, and physiology, and the global rise in CO_2 and temperature.

General liana responses in temperate areas may, however, depend on liana growth strategies and tolerance to environmental conditions. In the understory, lianas can either "actively search" for growth opportunities or "sit-and-wait" for changed

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conditions. In understory shade, and in contrast to lianas in the tropics, some temperate lianas can form dense mats of leaf and stem cover (eg ivy [*Hedera helix*]). Lianas use various climbing mechanisms to ascend to the canopy; temperate lianas exhibit the same suite of climbing mechanisms as tropical lianas, including through adhesion to trees by roots (eg ivy), twining/scrambling (eg honeysuckle [*Lonicera periclymenum*], traveller's joy [*Clematis vitalba*]), and tendril attachments (eg various species of grape [*Vitis* spp]). At the same time, tolerance to environmental conditions and demand for resources vary among liana species. Shadier conditions (eg following a decline in management intensity across European forests; McGrath *et al.* 2015) may be of direct benefit to temperate shade-tolerant lianas but detrimental to more light-demanding liana species, such as grape. Such differences complicate making predictions about whether there will be general responses among temperate liana species or how individual species will respond to changing environmental conditions.

Continent-wide resurvey studies in temperate forests offer the opportunity to infer generality of responses to changes in conditions over long time intervals. Results from such surveys, distributed along carefully chosen environmental gradients (eg of climate) and with well-characterized management histories, facilitate assessment of potential drivers of change (Verheyen *et al.* 2017). Using a network of 1814 understory resurvey plots in continuously forested sites (since at least 1800) across Europe, we examined whether and how the frequency of occurrence of temperate lianas has changed over space and time. We then investigated environmental correlates of observed frequency responses. Given the general susceptibility of lianas to cold temperatures, we expected that warmer conditions in a higher CO_2 world have led to a general increase in understory liana frequency over the past several decades (Manzanedo *et al.* 2018). We also examined the effects that historical management transitions and light dynamics may have had on liana response in these widespread temperate forests.

■ Methods

A network of resurvey plots across environmental gradients

We compiled vegetation resurvey data on the forest understory for 1814 (quasi-)permanent plots in 40 single-study sites across Europe (hereafter "sites"; www.forestreplot.ugent.be). Because these data were collated from datasets originally collected for different purposes, there is inherent variation among the plots (WebPanel 2; WebTable 1). The majority of plots (*n* = 1465) were between 100–400 m^2 in size, as is likely typical for forest understory surveys, with size remaining generally consistent between survey time points within a site. All plots were assessed twice by surveyors (all qualified botanists), with a median intercensus interval of 38 years (range 12–75 years, interquartile range of 25–49 years). Initial survey years ranged from 1933 to 1994, and resurveys took place between the years 1987–2015. Plot locations were most likely chosen without regard to the presence or absence of lianas.

The definition of "understory" differed among surveys but was consistent between time points within a site. The understory included lianas, and typically perennial woody and herbaceous species characteristic of a layer below 1.5–2 m in height. Tree and shrub seedlings were ignored in several surveys, even in cases where woody species characteristic of the understory were included. In the event that surveyors had deliberately ignored lianas, we analyzed frequency change data in two ways, first by including sites where no presence of a given liana species was recorded in plots at both survey dates and then by excluding such sites. Overstory tree species were recorded inconsistently across the dataset, but species typically noted included various oaks (*Quercus* spp) and maples (*Acer* spp), and European beech (*Fagus sylvatica*) and European ash (*Fraxinus excelsior*). Stands were primarily either monocultures or mixtures, with conifers present at only a very few sites (WebPanel 2).

We restricted our analyses to understories in "ancient forest" plots, in other words areas that have been under continuous forest cover since at least 1800; note that the designation "ancient" refers to land-use continuity, not to forest stand age or management intensity. Semi-natural forest, of which 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 in Europe (Forest Europe 2015). We also determined the forest management history for each plot from 1800 to the present through questionnaires issued to local experts (see Perring *et al.* [2018] for details). We asked experts to classify plots as managed according to the most prevalent methods in Europe (McGrath *et al.* 2015), which consisted of: *coppicing*, in other words 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*, which involves the use of 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]). We assumed that vegetation change responses were not confounded by immediate post-disturbance successional dynamics because no large-scale management actions (eg clear felling) or stand-scale disturbances (eg widespread storm damage) occurred between surveys for all plots.

Plots within sites also experience considerable variation in local environmental conditions. We estimated environmental variation using cover-weighted Ellenberg indicator values (EIV) of the understory community at the time of the initial survey (Ellenberg *et al.* 2001). The EIV of individual species provides an indication of the demand or tolerance for a given variable based on a species' realized niche, and includes light (EIV_L), pH (as EIV_R), and nutrient (EIV_N) variables. Community metrics of these variables are considered a reasonable approximation of environmental conditions (Diekmann 2003). We calculated changing light dynamics by estimating EIV_L at the time of both the initial and recent surveys. A negative value for the change in EIV_L (ie ΔEIV_L) indicates the community demand for light has decreased, suggesting increased shade over time. We extracted

Figure 1. Examples of focal liana species found in the understory of temperate deciduous forests across Europe: (a) ivy (*Hedera helix*), shown here in the understory of a deciduous forest in Viroinval, Belgium; (b) honeysuckle (*Lonicera periclymenum*), shown here in a hedgerow in Campine, Belgium; and (c) traveller's joy (*Clematis vitalba*), shown here in the understory of a deciduous forest in Viroinval.

data for site-level climatic conditions and atmospheric nitrogen deposition from online databases. Additional details regarding environmental variation across plots and sites, and the methods used to assess these, are presented in WebPanel 3 and WebTables 2–4. We are aware that EIV provides only an indirect depiction of environmental conditions, and that direct characterization of prevailing environmental conditions is necessary for advancing understanding of forest ecology.

For each plot, we extracted the percentage cover (total of foliage and stem) in the understory of three native liana species typically found in temperate European forests: ivy, traveller's joy, and honeysuckle (Figure 1). Although all three species are lianas, their ecological tolerances and growth forms differ considerably. No records of other temperate lianas (eg *Lonicera caprifolium*, *Vitis* spp, *Parthenocissus* spp) were found in the dataset used in our analysis.

Quantifying trends in liana frequency

For a given liana species at the time of each survey at each site, we tallied the number of understory plots in which it occurred, then summed these values across species to produce 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. Our primary objective was to address the questions of whether the frequency change of individual liana species in understory communities and the total frequency change across European forest sites differed from zero.

A paired *t* test was used to examine whether the proportion of understory plots occupied per site at the time of the resurvey differed from the proportion of occupied understory plots per site at the time of the initial survey. We calculated "proportion of occupied plots" as the number of plots in which a given liana species was observed in a site divided by the total number of surveyed plots in that site (ie 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 prevented a robust trend investigation,

although qualitative conclusions on frequency change remain unaltered when examining subsets of the data (WebPanel 4).

Investigating potential drivers of frequency change

To investigate potential drivers of liana frequency change across the dataset, we specifically asked how the probability of presence in a plot of a given liana species i at the time of the resurvey ($t2$, ie 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 framework (*lme4* package in R):

$$
\begin{aligned}
i_{t2} \sim {}& i_{t1} + \text{years between surveys} \\
& + log \text{ (plot size)} + \text{altitude} + \text{EIV}_{NR} \\
& + \text{EIV}_{L} + MAT + MAP + \Delta\text{EIV}_{L} + \Delta T \\
& + \Delta N + \Delta P + \text{management transition} \\
& + (1|\text{site}) \qquad\qquad\qquad\qquad \text{Equation (1)}.
\end{aligned}
$$

Given our expectations (ie the importance of environmental changes, management transitions and light dynamics), we focused on changes between surveys in shade (as estimated by ΔEIV_{L}), mean annual temperature (ΔT), and mean annual precipitation (ΔP); the mean N deposition rate (ΔN) between surveys; and management transitions since 1800. We accounted for methodological covariates (eg plot size), plot conditions at the time of the initial survey (eg MAT, EIV_{L}), and the nesting of plots within sites (details provided in WebTable 2).

From the fitted model, we derived the presence probability for each liana species i in the resurvey given the initial survey absence of that species ($i_{t1} = 0$). This allowed examination of the effect of various environmental change drivers on increases in liana frequencies. We first predicted the probability of resurvey presence in the absence of any change for a given focal driver, and 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. Predictions for each forest management transition were derived using average values for other predictor variables. Analysis of
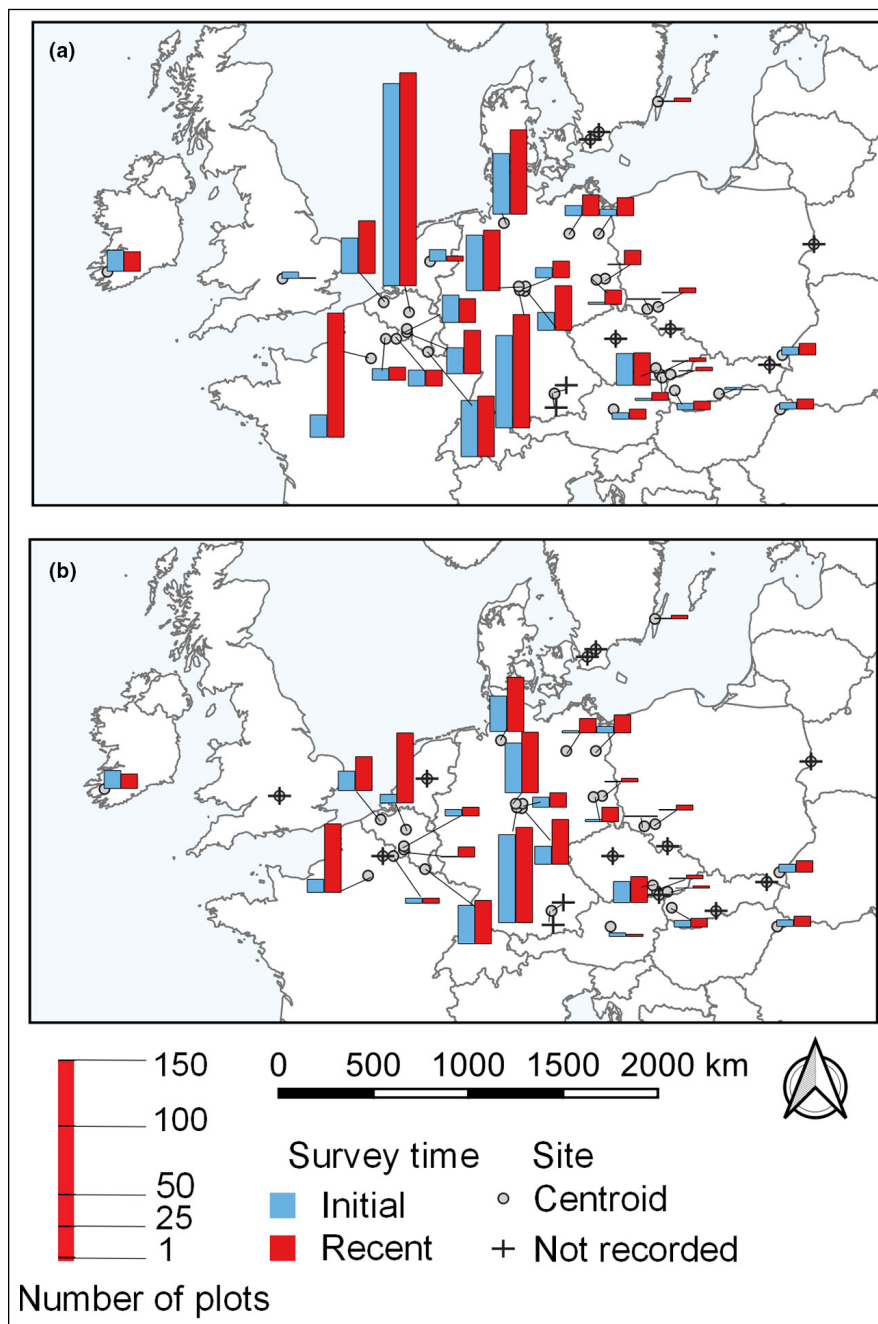
Figure 2. (a) Liana frequency has increased in temperate deciduous forests across Europe over the past several decades. Of the three liana species used to determine overall trends, (b) ivy is primarily responsible for driving overall liana response, whereas traveller's joy and honeysuckle are less frequent and do not exhibit consistent directional change (see WebFigure 1 and WebTable 5 for raw results, and WebTables 6–8 for statistical results).

potential drivers of frequency change assessed only those liana species present in more than ten sites at the time of the initial survey and the resurvey in order to encompass enough of an environmental gradient that relationships could be tested adequately. To gain further understanding about the potential drivers of change, we calculated the degree of variation that could be uniquely attributed to focal terms by subtracting a reduced model R^2 (without the focal term) from the full model R^2 (including the focal term), while also considering changes in AIC between these

models. All statistical analyses were conducted in R (v3.6.0; R Core Team 2019).

Results

Ivy drives the increase in frequency of lianas in forest understories across Europe

Total liana frequency of occurrence in understory plots was 38.7% higher in resurveys than in initial surveys (from 581–806 plots) across Europe, an increase driven primarily by changes in ivy occurrence (Figure 2; WebTables 5 and 6). Notably, ivy has increased in absolute terms by 70% (from 288 instances recorded in the initial surveys to 496 instances recorded in the resurveys out of the 1814 total plots). Controlling for survey effort, that constitutes a 9% average increase in the proportion of occupied understory plots per site (an average that rises to nearly 14% when sites with zero occupancy of ivy at both surveys are excluded; WebTables 7 and 8). This increase in ivy presence occurred across European forest sites (Figure 2b); of the 27 sites where ivy was observed in the initial survey, its frequency had increased in 23 sites at the time of the resurvey, and remained unchanged or in slight decline in four other sites.

Of the other liana species, travellers' joy increased in understory plot frequency by 113% but was relatively infrequent in the dataset (identified in nine sites, increasing from 23 to 49 occurrences in total; WebTable 5; WebFigure 1). Honeysuckle prevalence was similar to that of ivy in the understory at the time of initial surveys, but little change in its frequency was detected at the time of the resurveys (–3.3% in overall occurrence, declining from 270 to 261 plots). This limited "whole of dataset change" masks among-site differences: most sites experienced stasis or slight declines/increases, whereas a substantial reduction in honeysuckle frequency (from 146 to 108 plots) was observed in Tournibus, Belgium, a site in which ivy frequency increased considerably from the initial survey to the resurvey (WebTable 5; WebFigure 1). Geographically, sites in which lianas were largely absent from the understory, or in which liana frequency was low, were located primarily in the north and east of Europe.

Evidence for focal drivers affecting liana frequency responses

Changes in temperature and light regime, along with historical management transitions, explain limited variation in ivy

frequency responses when presence in initial surveys across the entire dataset is taken into account (Table 1). Unmeasured differences among sites and ivy's presence in the initial survey drive most of the explained variation. However, the likelihood of finding ivy in a plot in a resurvey despite it being absent from the initial survey is clearly enhanced by higher rates of warming and reduced by high forest management alone, whereas the effect of increasing shade is weaker (Figure 3). The probability of honeysuckle occurring in a resurvey declines when high forests transitioned to unmanaged forests, with limited evidence for site-scale drivers affecting the likelihood of honeysuckle being present in the resurvey when it was absent at the time of the initial survey (WebTables 9 and 10).

◾ Discussion

Liana frequency increase in European temperate forest understories driven by ivy

To the best of our knowledge, this study is the first to show that lianas are becoming more abundant across a broad geographical extent in the understories of deciduous temperate forests. In contrast to the neotropics, where liana increase occurs across multiple species, strata, and growth patterns, a single understory species – ivy – is primarily responsible for the trends we observed in Europe. Not only is the magnitude of ivy response notable, additional analyses suggested that its response is singular among broad-leaved evergreen species and woody species that have the capacity to climb; indeed, it is arguably unique among *all* species recorded within this understory (WebPanel 5). 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 occurring immediately prior to or between survey times. We observed an increased ivy presence in these relatively undisturbed, interior forest plots despite the general expectation for liana increases to be strongly associated with disturbance and at forest edges (eg Matthews *et al.* 2016). The limited richness of liana species in the dataset precludes statements regarding changes in liana diversity, however.

Potential drivers of frequency change meet ecological expectations

With observational data, it is not possible to identify the causal driver(s) and mechanism(s) underlying the observed responses. Understanding the mechanisms responsible for these patterns may help guide forest management decisions in response to any increased prevalence of lianas. However, the wide environmental gradients and variation in management conditions do permit the drawing of tentative inferences about the relationships between increasing ivy frequency and changes in temperatures, light regimes, and management over time.

Table 1. Focal variable estimates for ivy (*Hedera helix*) presence in resurveys using logistic regression (Equation 1)

Focal variable	Ivy presence in resurvey		
	Standardized parameter estimate (± 95% CI)	ΔAIC[†]	% unique variation explained by focal fixed effect[‡]
Ivy presence at initial survey	**2.6 (2.2 to 3.0)**	−161	20.6
Warming (ΔT)	**0.9 (0.2 to 1.7)**	−2.7	4.4
Change in light availability (ΔEIV$_L$)	**−0.28 (−0.5 to −0.1)**	−5.3	2.8
Management transition*	−0.07 (−0.8 to 0.7) CWS to HF to 0 **−1.1 (−2.0 to −0.2) HF throughout** −0.1 (−0.9 to 0.7) HF to 0	−0.74	0.5
Nitrogen deposition (ΔN)	−0.5 (−1.1 to 0.1)	−0.76	0.9
Precipitation change (ΔP)	0.1 (−0.4 to 0.7)	1.7	0.4

Full model

AIC: 1209; R^2 fixed effects: 34.8%; R^2 fixed and random effects: 46.9%

Notes: CI: confidence interval. Values in bold have CIs that do not overlap with zero. 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 are provided in WebTable 9, along with those for honeysuckle (*Lonicera periclymenum*). [†]Change in AIC is negative if the reduced model (ie a model fitted to Equation 1 without the focal variable) has a greater AIC than the full model (given by Equation 1). [‡]Percent unique variation explained was calculated as (full model R^2 − reduced model R^2), where the reduced model was fitted without the focal variable. *Management transitions: CWS to HF to 0: "coppice-with-standards to high forest to unmanaged"; HF throughout: "high forest throughout"; HF to 0: "high forest to unmanaged".

The effect of these potential drivers fits with our understanding of ivy's ecology. Warming is expected to benefit ivy, possibly due to its susceptibility to freezing and/or because of the genus' tropical evolutionary origins (Metcalfe 2005); that is, ivy might "like" warmer conditions in any season. Ivy is also expected to benefit from shadier conditions in the understory, particularly as CO_2 concentrations continue to increase (Zotz *et al.* 2006). In contrast, greater shade (a general response across the forests analyzed here) is likely to be detrimental to honeysuckle, as this species tends to "prefer" higher levels of available light (WebPanel 6). This variable ecology between liana species may also explain the tendency for contrasting cover responses of these two species in forests that have transitioned to being unmanaged (WebPanel 6).

Causes and consequences of changes in ivy frequency

The reasons for and impacts of greater ivy occurrence in the understory of European temperate forests remain unknown. Although our analysis explained some variation in frequency at the time of the resurveys due to potential focal drivers, the extent of this explanation is limited in comparison to
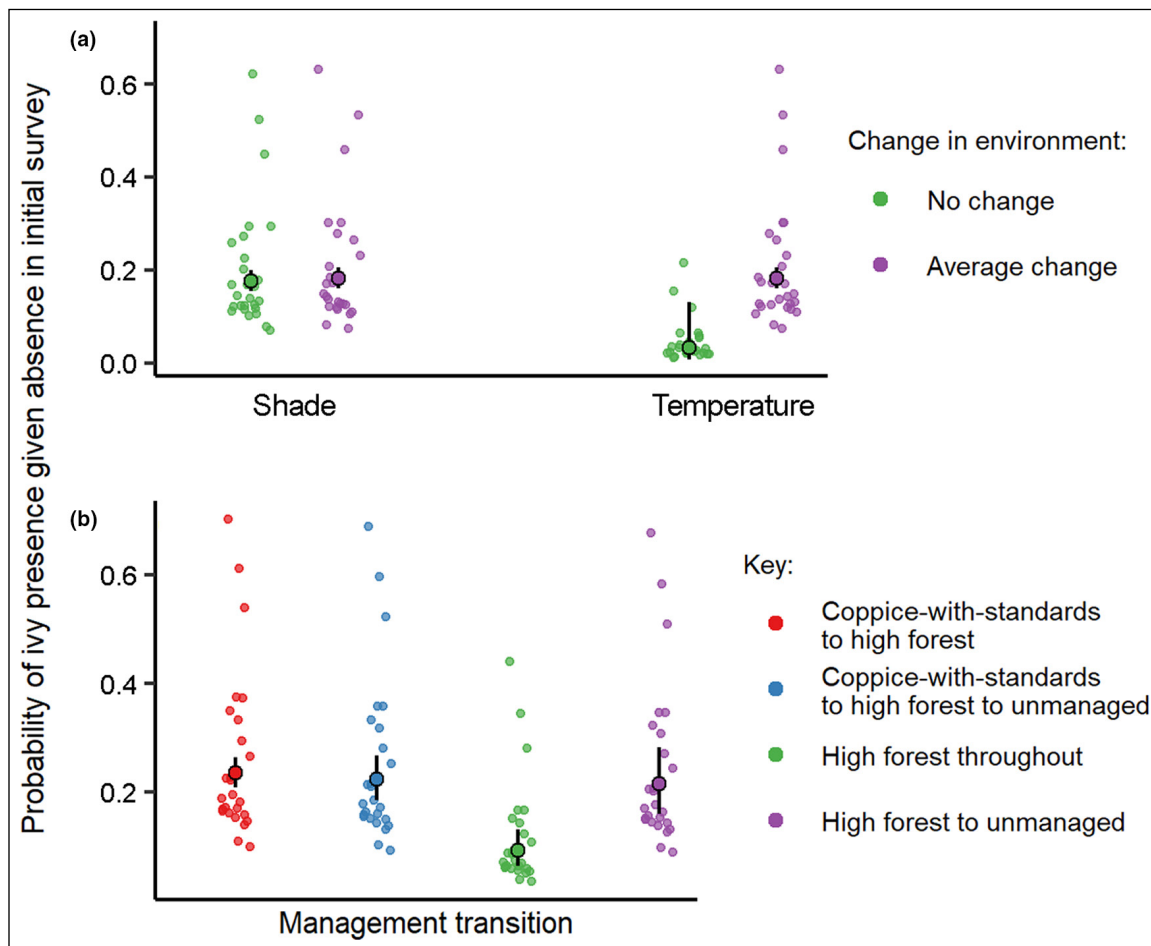
Figure 3. Predicted change in the probability of presence (± 95% confidence interval) for ivy in resurveys in cases where it was absent in the initial survey, with (a) enhanced shade and warming temperatures, and (b) management transitions. In panel (a), green symbols with black outline show the mean probability of presence in the absence of any change for the focal variable between surveys across the whole of Europe; purple symbols with black outline show the mean probability of presence given the average across-dataset change in the focal variable. In panel (b), predictions are made for different forest management transitions. A continually managed "high forest" system has a much lower probability of ivy occurring in the resurvey when absent from the initial survey, and when compared to other widespread management transitions in European forestry (details of which provided in the main text). In both figures, dots represent the site-specific probabilities and show the wide degree of variation in predicted probability of ivy presence at the site level.

that of among-site differences and the explanatory power of ivy being present at the time of the initial survey. However, the consistent Europe-wide pattern of changes in ivy frequency also suggests that drivers at the continental 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, transition to the adult (flowering) form only occurs once the plant has reached a certain height or exposure to light, and has therefore moved out of the understory. Unfortunately, our data lacked sufficient coverage of overstory liana presence and information about surrounding landscape parameters (eg potential for garden escapes) to assess potential diaspore pressure, dispersal, and recruitment processes, underscoring the need to extend research on lianas across temperate forest strata.

Studies focusing on the potential consequences that increasing understory ivy may have on forest biodiversity, structure,

and function are needed. The evergreen nature of ivy may allow it to increase the growing season length of the understory (and overstory), and thus fix more C at times when conditions are favorable, especially prior to overstory leaf flushing in trees. Indeed, research has demonstrated that ivy may not only drive biomass accumulation in the understory (Wasof *et al.* 2018) but also alter tree regeneration, thereby influencing overstory composition (including through allelopathic effects; Ladwig *et al.* 2012). In general, species in the understory require increased consideration in global change research given their (sometimes substantial) contribution to forest functioning (Landuyt *et al.* 2019). Temperate lianas, and especially ivy in the adult form, can promote biodiversity in forests through the provision of useful habitat and resources for other organisms (Metcalfe 2005). Finally, tree mortality may be higher in the presence of climbing ivy, as it can increase host tree susceptibility to windfall (eg Schnitzler and Heuzé 2006).

Conclusions

Lianas, particularly ivy, have long played key cultural and economic roles in European society, and are also an important component of domestic and wild ungulate browse; moreover, lianas provide indications of past climate variability (WebPanel 7). Our results encourage further experimental (eg liana removal studies) and observation-based research on the functional and structural consequences of increased liana prevalence in temperate as well as tropical areas, and across other forest types, strata, and levels of biodiversity. If such a research program 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 (Verbeeck and Kearsley 2016; di Porcia e Brugnera *et al.* 2019), and resource managers may need to adapt to the "lianification" of future temperate forests.

Acknowledgements

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■ Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2266/suppinfo