

Dominance of individual plant species is more important than diversity in explaining plant biomass in the forest understorey

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Abstract :

Questions

How does plant community diversity influence variation in plant biomass? There are two competing hypotheses: the 'biomass-ratio hypothesis', where biomass is influenced by the abundance and traits of the most dominant species, and the 'diversity hypothesis', where the diversity of organisms influences biomass through mechanisms such as niche complementarity. However, no studies have tested which one of these two hypotheses better explains the variation in plant biomass in the forest understorey.

Location

Temperate deciduous forests in Northern France.

Methods

For the forest understorey, we assessed species diversity and biomass as well as soil and light conditions in 133 forest plots of 100m² each. Using mixed-effect models and after controlling for potential confounding factors, we tested the 'biomass-ratio hypothesis' by relating the relative

abundance of the most dominant species across our study sites and the community-weighted mean values (CWM) of plant traits (leaf area and plant height) to biomass. The 'diversity hypothesis' was tested by relating biomass to various measures of taxonomic, functional and phylogenetic diversity.

Results

Biomass of the forest understorey was mainly related to the relative abundance and the trait values of the most dominant species, supporting the 'biomass-ratio hypothesis'. In contrast with the 'diversity hypothesis', functional diversity indices had a negative impact on biomass. We found no contribution of taxonomic or phylogenetic diversity indices.

Conclusion

The abundance and traits of the most dominant species matter more than taxonomic, functional or phylogenetic diversity of the forest understorey in explaining its biomass. Thus, there is a need for experiments that aim to fully understand keystone species' responses to ongoing changing biotic and abiotic conditions and to predict their effects on ecosystem functioning and processes.



INTRODUCTION

There is growing concern about the consequences of biodiversity loss on ecosystem functioning and services (Loreau et al. 2001; Hooper et al. 2005), with the number of studies steadily growing (Gross et al. 2014; Byrnes et al. 2014; Tilman et al. 2014; Zhu et al. 2016; Duffy et al. 2017). However, most of these studies have dealt with aquatic systems, wetlands

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or grasslands (Díaz & Cabido 2001; Srivastava et al. 2012). Forest ecosystems have only recently come into focus and most available studies focus on the relationship between overstorey diversity and ecosystem functioning (Vilà et al. 2007; Watson et al. 2015; van der Plas et al. 2016; Liang et al. 2016). Yet, forest ecosystems are structurally complex and the influence of other forest tiers, such as the understorey, remains to be investigated (Axmanová et al. 2012; Axmanová et al. 2013; Zhang et al. 2017). For instance, in temperate forests, the forest understorey encompasses a large proportion of vascular plant diversity and plays an important role in ecosystem functioning such as nutrient cycling, organic matter fluxes and as faunal habitat (Whigham 2004; Gilliam 2007). Therefore, it is highly relevant to relate species richness of this key compartment to its above-ground biomass (Axmanová et al. 2012; Axmanová et al. 2013).

Two mutually non-exclusive hypotheses have been proposed to explain variation in ecosystem properties such as biomass (Mokany et al. 2008). First, the ‘biomass-ratio’ or ‘dominance hypothesis’ (Grime 1998) postulates that the effect of individual species on ecosystem properties is related to their relative abundance in the community, and that trait values of the dominant species have a proportionally greater effect. There is some evidence that the ‘biomass-ratio hypothesis’ is relevant to ecosystem processes such as productivity (Garnier et al. 2004; Chanteloup & Bonis 2013), the rate of litter decomposition (Garnier et al. 2004) and the nitrification rate (Laughlin 2011), all of which impact on biomass. Second, the ‘diversity’ or ‘complementarity hypothesis’ proposes that diverse communities have increased influences on ecosystem properties through mechanisms such as complementary resource use and the sampling effect (Tilman et al. 1997). In forest ecosystems, this hypothesis is supported for the overstorey layer and over a wide range of environmental conditions (Hooper et al. 2005; Vilà et al. 2007; Paquette & Messier 2011; Vilà et al. 2013; Zhang & Chen 2015). However, whether the strength and the direction of this relationship

hold for the understorey herb layer has been rarely explored. A notable exception is the study of Zhang et al. (2017), which found that while positive relationships between species richness and above-ground biomass were observed across all vegetation layers, the strength of the effect in the understorey layers was weaker than that for the over-storey layer.

Variation in biomass is largely influenced by available resources and surrounding environmental conditions (Díaz & Cabido 2001; Fridley 2002) and is therefore context-dependent. Consequently, recent work has suggested that factors such as soil pH, light availability, habitat heterogeneity or disturbances may confound with the ‘biomass-ratio’ and the ‘diversity’ hypotheses (Grace et al. 2007; Ma et al. 2010). For instance, in central European oak forests, biomass in the herb layer has been shown to be mainly determined by light availability and to a lesser extent by soil phosphorus concentrations (Axmanová et al. 2013). Thus, environmental factors have a major role in influencing both the potential pool of species and the biomass of keystone species in the habitat (Gough et al. 1994; Schuster & Diekmann 2005). Therefore, one question is how much of the variation in above-ground biomass could be explained by herbaceous plant community diversity after controlling for the different confounding factors involving environmental conditions.

Studies that aim to test the ‘diversity hypothesis’ to explain the variation in above-ground biomass usually focus on taxonomic diversity (e.g. species richness), although other components of biodiversity may be stronger predictors of ecosystem properties (Tilman 1999). For example, functional diversity has increasingly been used (Cadotte et al. 2009; Flynn et al. 2011), using various metrics accounting for functional richness, functional evenness and functional divergence (Mason et al. 2005; Villéger et al. 2008; Laliberté & Legendre 2010). However, this approach presents some shortcomings, such as, for example, the *a priori* choice of traits (Petchey & Gaston 2006; Cadotte et al. 2009; Thompson et al. 2015). In contrast, phylogenetic diversity (i.e. a measure of the evolutionary relatedness of

species in communities; Srivastava et al. 2012) can capture the functional difference between species due to unmeasured traits (Flynn et al. 2011; Srivastava et al. 2012; Thompson et al. 2015). Phylogenetic diversity indices rely on the assumption that phylogenetically related species are likely to share similar functional traits (Losos 2008; Wiens et al. 2010; but see Cavender-Bares et al. 2009; Narwani et al. 2015). Moreover, phylogenetic diversity has been shown to be a good predictor of ecosystem productivity (Cadotte et al. 2009; Flynn et al. 2011; Thompson et al. 2015). To our knowledge, no study has investigated the efficacy of multiple components of biodiversity to explain the variation in above-ground plant biomass in the forest understorey.

In this study, we aim to test which one of the ‘biomass-ratio’ or the ‘diversity’ hypotheses best explains plant biomass in the forest understorey, after controlling for the potential confounding effects of light availability and soil factors (e.g. soil pH, phosphorus, moisture and C:N ratio).

MATERIALS AND METHODS

Study design

We selected nine 5 km by 5 km landscape windows representative of temperate lowlands deciduous forests and land uses in Northern France (Hauts-de-France, N49°25'–50°11'; E1°52'–3°55'; alt. 60–220 m; Fig. 1). In each window, only forest sites capable of containing a 100m² quadrat distant from at least 10m from the closest edge were retained. We then randomly selected 15 sites per window, giving 135. The climate in the studied area is oceanic with mean annual temperature and total annual rainfall of 10°C and 700 mm, respectively.

Field sampling

Within each of the 135 sites, we randomly set a 100m² plot, and measured the following:

(1) *The cover of all vascular plant species* present was scored, separately for the tree (>12 m), shrub (1-12 m) and understorey (<1 m) layers, using a numeric scale: 0.1, 0.5, 3, 7.5, 17.5,

37.5, 62.5, and 87.5 %. Between 2007 and 2008, all 100m² plots were visited twice, in spring (April–May, collecting only vernal species) and in summer (June–September, collecting remaining species) to cover the entire growing season here in Northern France. Aggregate taxa (e.g. *Taraxacum officinale* agg. or *Rubus fruticosus* agg.) were treated as single species.

(2) *The biomass* of the forest understorey was harvested in three 1m² quadrats that were placed at 0, 2.25 and 7.10 m along a random diagonal of the 100m² plot (Fig. 1c). All herbs and lianas creeping on the ground as well as saplings <1m high were harvested, and oven-dried (at 60-65°C for 72 hours), and weighed. We summed the two harvest values (i.e. spring and summer) to report the average above-ground biomass of the forest understorey in each plot.

Plant functional traits

For the 162 plant species that we recorded, we compiled values for (i) *lateral spread* (LS, ordinal scale), (ii) *plant height* (H; m), and (iii) *specific leaf area* (SLA; mm².mg⁻¹) from existing databases (Lambinon et al. 2004; Grime et al. 2007; Kleyer et al. 2008; Landolt et al. 2010). Annual lateral spread is scaled from 1 for therophytes (limited lateral spread) to 5 for perennials (radial spread per year >1 m).

Environmental co-variables factors

To account for the effect of potentially confounding factors, we measured and collected five sets of abiotic variables.

(1) *Soil chemical properties* were measured for organic matter content, total nitrogen (*N*), available phosphorus (Olsen *P*) and *pH_{water}* following AFNOR French norms (X31-109, X31-111, X31-113 and X31-104, respectively). For this, three soil samples from the 0-10 cm horizon, after litter removal, were collected along the diagonal of the 100m² plot.

(2) *Light availability to the forest understorey* was measured using two indices: the percentage cover of the canopy, and the shade casting ability of the canopy species (Verheyen et al. 2012). The percentage cover of each layer (trees: >12 m, shrubs: 1-12 m) was visually estimated in the field. The combined cover of woody layers (trees and shrubs) or total canopy cover hereafter served as a proxy for light reaching the herb layer and was computed following Fischer (2015). Second, the shade casting ability index (SCA) is an expert-based, species-specific index that varies between 1 and 5 (low to high shade casting ability of the canopy tree species; Verheyen et al. 2012). Community weighted mean (CWM) values of the SCA index were calculated for each individual 100m² plot based on the index of each individual tree weighted by its cover within the plot.

(3) *The surrounding landscape* was described as percentage cover of grasslands, forests (deciduous and coniferous) and croplands within a 500m radius around the focal plot.

(4) *The distance to the closest edge of the forest* from the centre of the 100m² plot was calculated.

(5) *Ellenberg indicator values (EIV)* were used to estimate local environmental conditions for light (*L*), soil nutrients (*N*), soil pH (*R*) and soil moisture (*F*) (Ellenberg et al. 1999). Ellenberg et al. (1999) ranked most of the central European vascular plant species according to the position of their realised optimum along the above-mentioned ecological gradients. For each of these environmental variables, unweighted *EIVs* of all species co-occurring in each plot were averaged.

Explanatory variables

To explain biomass of the forest understorey (the response variable), we used four groups of variables capturing the ‘biomass-ratio’ and ‘diversity’ hypotheses (see below) together with the potential confounding factors due to local environmental conditions (see the ‘Statistical analyses’ section for the selection of the covariates) as explanatory variables.

(1) *Dominance*: To investigate the relative importance of "abundant" species on total biomass, we used two approaches. First, a CWM of trait values was calculated for each quantitative trait (i.e. SLA and height) (Díaz et al. 2007; Lavorel et al. 2008). CWM is a direct extension of the 'biomass-ratio hypothesis' (Grime 1998) and represents functional dominance (sometimes called functional identity) (Mokany et al. 2008). Second, for the two most dominant species across our whole study area, namely *Ivy* (*Hedera helix* L.) and *Blackberry* (*Rubus fruticosus* L.), we calculated their covers relative to the total cover of all species in each plot. *Ivy* and *Blackberry* were selected as the collected biomass was always high when *Ivy* and/or *Blackberry* was present in the plot and because of their high cover values in the dataset (Fig. 2).

(2) *Taxonomic diversity (TD)*: Four indices were computed: species richness (i.e. number of species per plot; *SR*); Shannon's diversity (H'); Simpson's diversity (D); and Pielou's equitability ($J' = H'/\ln(SR)$).

(3) *Functional diversity (FD)*: We used three traits: lateral spread (*LS*), plant height (*H*); and specific leaf area (*SLA*) (Appendix S1). We first computed a principal coordinate analysis (PCoA) on the matrix of species-by-species Gower distances, corrected using Cailliez's method (Cailliez 1983) to avoid negative eigenvalues. The resulting axes were used to build the multidimensional trait space within which three complementary FD indices were computed: functional richness (*FRic*), functional evenness (*FEve*), and functional divergence (*FDiv*) (Villéger et al. 2008; Mouchet et al. 2010; Laliberté & Legendre 2010). *FRic* measures the n -dimensional functional hypervolume enclosing all species co-occurring in the community. A low *FRic* value means that part of the studied trait space is unused (Mason et al. 2005). By contrast, *FEve* measures evenness in abundance distributions in the n -dimensional trait space (a convex hull). Values close to 0 mean that some species are tightly packed in only some parts of the n -dimensional trait space. *FDiv* quantifies how species

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diverge, in terms of Euclidean distances (weighted by their abundance), from the centre of gravity of the n -dimensional trait space. $FDiv$ also ranges from 0 to 1: values close to 1 mean a high degree of functional niche differentiation among species (Mouchet et al. 2010), whilst values approach 0 when highly abundant species are very close to the centre of gravity relative to rare species (Villéger et al. 2008). Further, we computed *Rao's Q* quadratic entropy (Botta-Dukát 2005; Laliberté & Legendre 2010), which estimates how species are dispersed in the n -dimensional trait space (Laliberté & Legendre 2010). $FEve$ and *Rao's Q* are unaffected by species richness and outliers, and have no loss of information associated with reduced space ordination and subsequent calculations (Villéger et al. 2008; Laliberté & Legendre 2010). Note that when computing $FRic$ and $FDiv$, the number of species co-occurring within the focal community must always exceed the number of PCoA axes retained to build the n -dimensional trait space. For that reason, only 133 (out of 135) plots could be used for computation of $FRic$, any bias being insignificant. Calculations of all functional diversity indices used the package 'FD' (Laliberté et al. 2014) implemented in R version 3.4.1.

(4) *Phylogenetic diversity (PD)*: We first extracted a phylogenetic tree for the 162 vascular plant species occurring in our study from a dated, ultrametric super tree containing 4685 Central European vascular plant species (Durka & Michalski 2012). The final tree included 155 tips and 150 internal nodes (Appendix S1). We computed four complementary metrics. First, we computed the *Faith's PD* index, which is the minimum tree length containing all the taxa to the root of the tree (Faith 1992). Then, we computed phylogenetic species' variability (PSV ; Helmus et al. 2007), which measures the variance among species of a community in the value of a hypothetical neutral trait evolving under a Brownian motion model; a higher phylogenetic relatedness produces lower values of PSV than expected by chance. Third, we computed phylogenetic species richness (PSR ; Helmus et al. 2007) which

is *PSV* multiplied by the number of species in the focal community and indicates species richness of a community after discounting species relatedness; it decreases towards zero as relatedness among species increases. Finally, we computed the phylogenetic species evenness (*PSE*; Helmus et al. 2007) which is a modification of *PSV* that incorporates relative species covers; the maximum value of 1 is reached only if species' abundances are equal and the species' phylogeny is a star, i.e. the community has no phylogenetic structure. All *PD* indices were calculated using the package 'pez' (Pearse et al. 2014) in R version 3.4.1.

Statistical analyses

We first assessed Pearson's correlations among the 13 variables used to describe local environmental conditions in order to avoid multi-collinearity issues in our models (Appendix S2). Mean Ellenberg values for R (*meanR*) were highly correlated with soil *pH*. Percentage cover of forest (*Prop-forest*) and percentage cover of croplands (*Prop-croplands*) within a 500m radius around the focal plot were highly negatively correlated. In addition, *Prop-forest* was also correlated with *meanR* and the distance to the closest forest edge (*Edge-distance*) variables (Appendix S2). Except for *Prop-forest* and *meanR*, the above-mentioned variables were all used as covariates. Fitting a more parsimonious model (i.e. a model with a minimal set of predictor variables) throughout a stepwise regression technique did not give different results/conclusions than fitting the full model. For that reason, we decided to report only the results from the full models in order to take into account all the potential determinants of biomass in the forest understorey. We first analysed the respective effects of the 11 selected environmental covariates on biomass (hereafter, the baseline model).

We fitted 16 'mono-faceted' candidate models (i.e. one per dominance/diversity index) and used Akaike's Information Criterion (AIC) value to compare model performances, preferring the models with the lowest AIC (Burnham & Anderson 2003). Furthermore, based on the best mono-faceted models and multi-collinearity issues (see Appendix S3 for

Pearson's correlation values among the 16 dominance/diversity variables explored in this study), we then fitted one 'multi-faceted' model, including all dominance/diversity indices at once, to test potential confounding effects between the studied dominance/diversity indices.

The response variable (biomass) was Box-Cox transformed (Box & Cox 1964) to improve normality and all the continuous explanatory variables were standardized, i.e., the value for each variable was subtracted from its mean and divided by its standard deviation (Schiele 2010). To account for the sampling structure of our study design, we used linear mixed-effect models (LMMs) with the *windows* variable (a factor variable with 9 levels) as a random intercept term in all our LMMs. Statistical analyses were performed using the packages 'lme4', 'forecast', 'moments', 'multcomp' and 'MuMIn' in the software R version 3.4.1.

RESULTS

Mean values for each soil variable were used as a proxy for resource availability. Soil *pH* ranges from 3 to 7.8 (mean \pm SD: 4.9 ± 1.4) and available *P* ranges between 2.15 to 74.6 (mean \pm SD: 12.4 ± 8.7) mg Olsen-P.kg⁻¹ across the 135 studied plots. Biomass in the understorey ranged from 7.3 to 464.4 g m⁻² (mean \pm SD: 130 ± 102.5) across the study area.

The results of the baseline model (i.e. the model that tests the relative contribution of the 11 environmental covariates on biomass) showed that both *Prop-croplands* (i.e. percentage of croplands within a 500m radius) and soil *pH* had positive relationships (*p*-value < 0.05; Table 1, Fig. 3a, b) with biomass.

Results from the 16 mono-faceted models (Table 2) showed that the effect of the relative abundance of *Ivy* on biomass was positive and its effect size the highest (*p*-value << 0.05; Table 2d). The community-weighted mean trait values for SLA (CWM_{SLA}) were found to negatively relate to biomass (*p*-value = 0.01; Table 2d). Among *FD* indices (Table 2b), only *Rao's Q* index had a negative relationship with biomass. Neither taxonomic nor

phylogenetic indices showed any significant effect (Table 2a, c). Among the environmental covariates, *Prop-croplands* had a positive relationship with biomass in all mono-faceted models, except for the model including *Ivy*. Soil *pH* also had a positive relationship with biomass in all mono-faceted models except the ones including *Ivy* and *FDiv*. Interestingly, in the mono-faceted model that includes *Ivy* with all the environmental covariates, only *meanF* (mean Ellenberg value for moisture) had a positive relationship with biomass (p -value = 0.047) (Fig. 3c).

The multi-faceted model includes *Pielou J*, *Rao's Q*, *PSE*, *Ivy* and *CWM_{SLA}* indices (Table 3). Only *Ivy* (i.e. its relative abundance) had a positive relationship with biomass (p -value = 0.001; Fig. 3d), while none of the investigated diversity indices did (Table 3a-c). Among the environmental covariates, only *meanF* had a positive relationship with biomass (Table 3e; Fig. 3c).

DISCUSSION

Our objective was to test which of the 'biomass-ratio' or the 'diversity' hypotheses is more important in explaining biomass in the forest understorey of temperate deciduous forests. Our results showed that the 'biomass-ratio hypothesis' explains more variation in biomass in the forest understorey than the 'diversity hypothesis'. Contrary to what was expected under the 'diversity hypothesis', when significant, we found a negative relationship between functional diversity and above-ground biomass in the forest understorey, suggesting higher biomass in functionally-poor understorey plant communities, which further advocates in favour of the 'biomass-ratio hypothesis'. Furthermore, we did not find evidence for taxonomic nor phylogenetic diversity in explaining above-ground biomass in the forest understorey, suggesting that species richness *per se* may not be a good predictor of biomass.

The relative abundance of the most dominant species (*Hedera helix*), as well as community weighted mean trait values (CWM) for specific leaf area (SLA), were highly related to biomass supports the ‘biomass-ratio hypothesis’. While a close relationship between the CWM trait values for SLA and above-ground biomass production is expected under the ‘biomass-ratio hypothesis’, there is no consensus in the literature about the slope of this relationship. In our study, we found a negative relationship between biomass and CWM for SLA, which contradicts the results of other studies (e.g. Chanteloup & Bonis 2013). Our result could be explained by the fact that plants with thicker leaves (hence low SLA) may have higher photosynthetic rates and, consequently, higher biomass production (Thumma et al. 2001; Marron et al. 2005). Interestingly, while our most abundant species (*Hedera helix*) was the best predictor of biomass in our study, our second most abundant species (*Rubus fruticosus*) did not show any significant effect. This result highlights the importance of *Hedera helix* as a keystone species in the forest system and may suggest that different species could have unique contributions to ecosystem functioning and processes (Naeem 1998). That may further raise the importance of considering the consequence of the loss/gain of a keystone species on ecosystem functioning under the context of climate change. For instance, *Hedera helix* increases in abundance in temperate Europe as a result of mild winters (Heinrichs & Schmidt 2014), with important consequences for biomass and carbon sequestration in the forest understorey.

None of taxonomic, functional or phylogenetic diversity explains the biomass in the forest understorey of temperate deciduous forests. In contrast to many previous studies (e.g. Loreau et al. 2001; Hooper et al. 2005), our study showed that taxonomic diversity was not related to biomass of the forest understorey, perhaps because we are missing communities with very low species richness (Hooper et al. 2005; Chanteloup & Bonis 2013). For instance,

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it has been shown that a significant effect of species richness on biomass production disappeared when species richness increased beyond a minimum (generally around four or five) (Hooper et al. 2005; Chanteloup & Bonis 2013). In our communities, the minimum species richness was four species, lacking very low values for species richness.

Among the functional diversity indices, only *Rao's Q* index had a significant, but negative, relationship with biomass. Although surprising at first glance, this may be explained by the dominance of highly competitive and productive species within communities with a low level of *FD* (Mokany et al. 2008; Chanteloup & Bonis 2013). This is consistent with Mokany et al. (2008), who demonstrated that root biomass in temperate native grasslands was negatively related to *FD*, and that high root biomass was likely achieved by a less diverse community with most species present possessing large roots. This pleads for the 'biomass-ratio hypothesis': the relative abundance of the most dominant species is more important than *FD per se*. However, while *Rao's Q* index was significant in the mono-faceted model, its effect disappeared in the multi-faceted model, suggesting a confounding effect with the other dominance/diversity variables.

We did not find any effect of phylogenetic diversity on biomass production either, irrespective of the model type (mono- or multi-faceted). Although it has been acknowledged that *PD* indices should complement *FD* indices to capture unmeasured components of *FD* (Flynn et al. 2011), recent attention has been given to the pitfalls of integrating phylogenetics into studies of community assembly (Gerhold et al. 2015; Kraft et al. 2015) and ecosystem functioning (Narwani et al. 2015; Venail et al. 2015). For example, *PD* has no influence on ecosystem functioning whenever the functional variation among species is not explained by their phylogenetic relatedness (Venail et al. 2015). Despite our expectation of low *PD*

variability among our plots (due to a relatively small studied area with the same regional species pool), we tested PD. PD failed to predict above-ground biomass and thus, we were proved correct.

Abiotic factors typically explain a significant amount of the variation in ecosystem properties such as biomass (Loreau et al. 2001; Axmanová et al. 2012) and an increasing number of studies have demonstrated that changes in environmental conditions could alter the shape of the relationship between biodiversity and ecosystem functioning (Steudel et al. 2012; Isbell et al. 2013). In this context, soil phosphorus availability and moisture have been shown to be important factors influencing the forest understorey biomass in temperate forests (Axmanová et al. 2011). However, we did not find any effect of phosphorus availability on biomass in our study. Interestingly, while *pH* and *Prop-croplands* (percentage of croplands within a 500m radius) had significant effects in the baseline model (i.e. the model that tests the relative contribution of the environmental covariates on biomass), they were no longer significant in the mono-faceted model that includes *Ivy* (as an abundance score). In addition, in that model only soil moisture (as mean Ellenberg values) showed a significant positive relationship with biomass. This could mean that the abundance of *Ivy* is significantly related to these environmental variables. In order to test this hypothesis, we ran an additional linear mixed-effects model where the relationship of environmental variables to the relative abundance of *Ivy* was tested (Appendix S4), and it was only significantly related to soil *pH*. Taken together, this suggests that *Hedera helix* appears a good bio-indicator of soil *pH* here and that it may act as a biotic mediator of changes in these abiotic conditions.

In general, none of the dominance/diversity metrics investigated in this study were sufficient to explain the observed variation in biomass of the understorey plant communities in Northern France. This suggests that we are either missing important environmental variables that are highly variable across the study area or that other components of

biodiversity that we did not investigate yet may matter. Intraspecific genetic diversity is a potential candidate that we did not investigate here. For instance, it has already been demonstrated that it can shape net primary productivity and ecosystem functioning (Crutsinger et al. 2006; Breza et al. 2012). We argue that there is no single measure that can capture all components of biodiversity, but that all together are important to complete the puzzle. Further investigations accounting for all these components of biodiversity (both interspecific and intraspecific) and focusing on temperate deciduous forest ecosystems where the understorey plant communities play an important role in ecosystem functioning should be carried out to disentangle the drivers of plant biomass.

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AUTHOR CONTRIBUTIONS

SW, JL and GD conceived and designed the experiments as well as the analytical framework. SW, JL, AJ, RS, LB, AV and GD collected the data. TH prepared the phylogeny as well as provided help to compute the functional and phylogenetic diversity metrics. EGM provided maps and GIS support. SW analysed the data with the support of JL and wrote the manuscript with JL, KV and GD. All authors provided feedbacks on the initial version of the manuscript.

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TABLES

Table 1. Summary table of the linear mixed-effect model (LMM) testing the relationship between biomass and environmental drivers. Environmental factors are soil *pH*; available soil phosphorus (*P*); soil carbon-nitrogen ratio; canopy cover; shade casting ability (*SCA*); mean Ellenberg values for light (*meanL*), nitrogen (*meanN*) and soil humidity (*meanF*); percentage cover of grasslands (*Prop-grasslands*) and croplands (*Prop-croplands*) within a 500m radius around the focal plot, and the distance to the closest edge of the forest (*Edge-distance*). The R^2 values represent the total variance explained by both fixed and random factors (i.e. the entire model). Parameters with significant relations are depicted in bold.

| Parameter | Estimate | <i>p</i> -value |
|-----------------------|-------------|----------------------------|
| (Intercept) | 7.6 | <10⁻⁴ |
| Soil pH | 0.45 | 0.04 |
| Available P | -0.023 | 0.9 |
| Carbon:Nitrogen | 0.2 | 0.4 |
| Canopy cover | -0.14 | 0.4 |
| SCA | 0.17 | 0.32 |
| MeanL | 0.20 | 0.31 |
| MeanN | 0.33 | 0.16 |
| MeanF | 0.10 | 0.15 |
| Prop-grasslands | 0.28 | 0.37 |
| Prop-croplands | 0.76 | 0.008 |
| Edge-distance | 0.26 | 0.23 |
| AIC | 562.5 | |
| R^2 | 0.28 | |

Table 2. Summary table of mono-faceted models for all the linear mixed-effect models (LMMs) testing the relationship between biomass and dominance, taxonomic, functional, and phylogenetic diversities. Note that all LMMs also include environmental confounding variables (see Table 1 for the list of environmental variables) as fixed effects. The R^2 values represent the total variance explained by the entire model. The rows of dominance/diversity indices having a significant relationship to biomass (i.e., p-value <0.05) are in bold. Parameters for confounding environmental factors are not shown.

| Indices | Parameter | Estimate | p-value | R^2 | AIC |
|--------------|-------------------------|---------------|----------------------------|-------------|---------------|
| Taxonomic | Species richness | 0.049 | 0.8 | 0.28 | 564.43 |
| | Shannon H | -0.204 | 0.26 | 0.28 | 563.26 |
| | Simpson D | -0.19 | 0.28 | 0.28 | 563.34 |
| | Pielou J | -0.258 | 0.12 | 0.29 | 562.12 |
| Functional | Functional richness | -0.194 | 0.28 | 0.28 | 563.37 |
| | Functional divergence | -0.249 | 0.14 | 0.28 | 562.42 |
| | Functional evenness | -0.248 | 0.13 | 0.29 | 562.23 |
| | RaoQ | -0.356 | 0.028 | 0.29 | 559.83 |
| Phylogenetic | Phylo. spp. variability | 0.054 | 0.83 | 0.28 | 564.45 |
| | Phylo. spp. richness | -0.021 | 0.91 | 0.28 | 564.49 |
| | Phylo. spp. evenness | -0.226 | 0.2 | 0.29 | 562.9 |
| | Faith PD | -0.04 | 0.83 | 0.28 | 564.46 |
| Dominance | CWM.SLA | -0.426 | 0.014 | 0.3 | 558.66 |
| | CWM.height | -0.261 | 0.11 | 0.28 | 562.12 |
| | Ivy | 0.884 | <10⁻⁴ | 0.37 | 545.53 |
| | Blackberry | -0.044 | 0.8 | 0.28 | 564.45 |

Table 3. Summary table of the multi-faceted model for the linear mixed-effect model (LMM) testing the relationship between biomass and several indices representing the four studied components of plant community structure including dominance (cf. the ‘biomass-ratio hypothesis’), taxonomic diversity, functional diversity and phylogenetic diversity. Note that this LMM also includes confounding environmental variables as fixed effects with the *windows* variable (i.e., a factor variable with 9 levels) as a random intercept term. The R^2 represent the total variance explained by both fixed and random factors (i.e. the entire model). Significant p-values (<0.05) are in bold.

| Indices | Parameter | Estimate | p-value |
|-------------------|----------------------|-----------------|----------------|
| | Intercept | 7.582 | |
| Taxonomic | Pielou J | 0.133 | 0.474 |
| Functional | RaoQ | -0.236 | 0.165 |
| Phylogenetic | Phylo. spp. evenness | -0.185 | 0.265 |
| Dominance | CWM _{SLA} | -0.165 | 0.349 |
| | Ivy | 0.776 | 0.001 |
| Abiotic factors | Soil pH | 0.125 | 0.558 |
| | Available P | -0.008 | 0.96 |
| | Carbon:Nitrogen | 0.142 | 0.401 |
| | Canopy cover | -0.183 | 0.247 |
| | SCA | 0.098 | 0.539 |
| | MeanL | 0.079 | 0.677 |
| | MeanN | 0.3 | 0.161 |
| | MeanF | 0.368 | 0.038 |
| | Prop-grasslands | 0.008 | 0.967 |
| | Prop-croplands | 0.473 | 0.076 |
| | Edge-dist | 0.382 | 0.068 |
| Model performance | AIC | 549.7 | |
| | R^2 | 0.38 | |

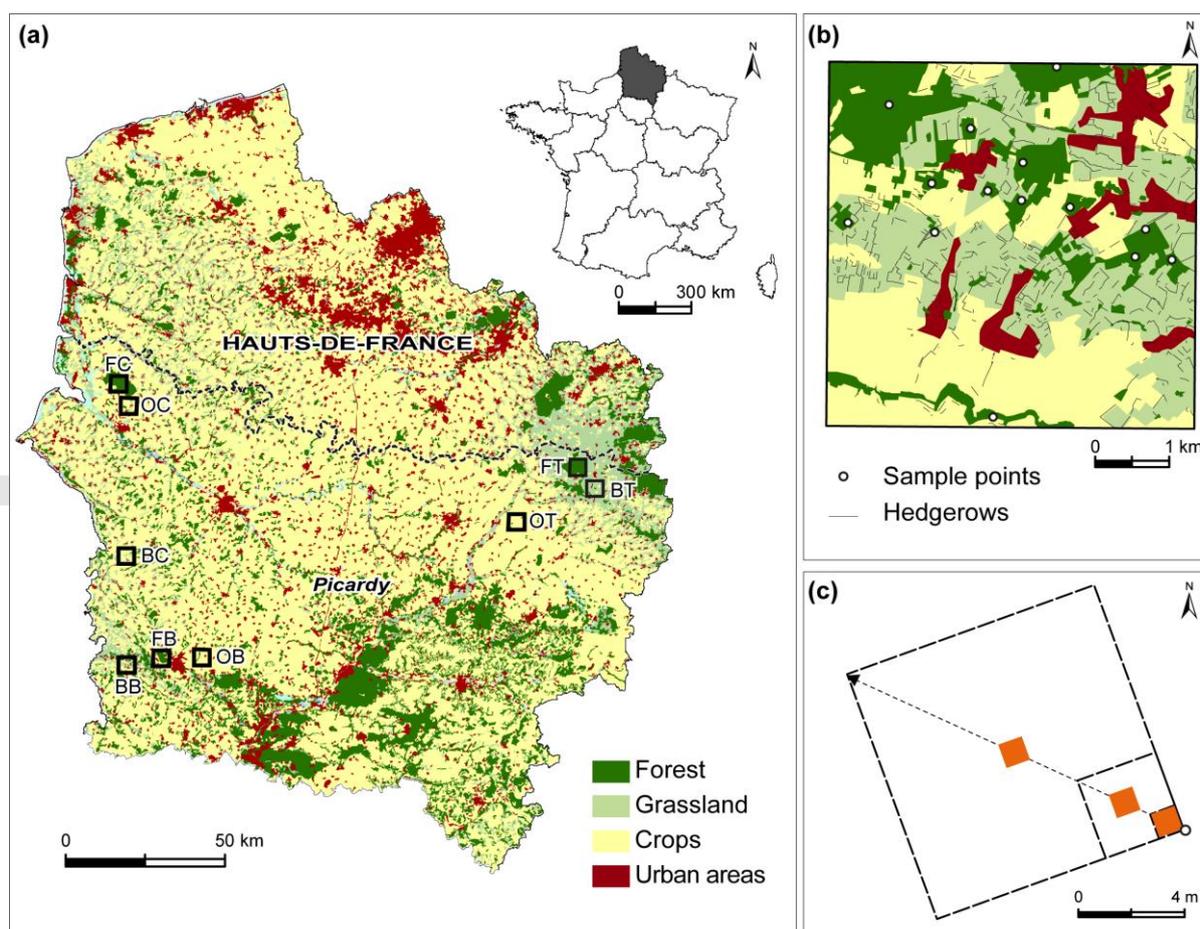
SUPPORTING INFORMATION

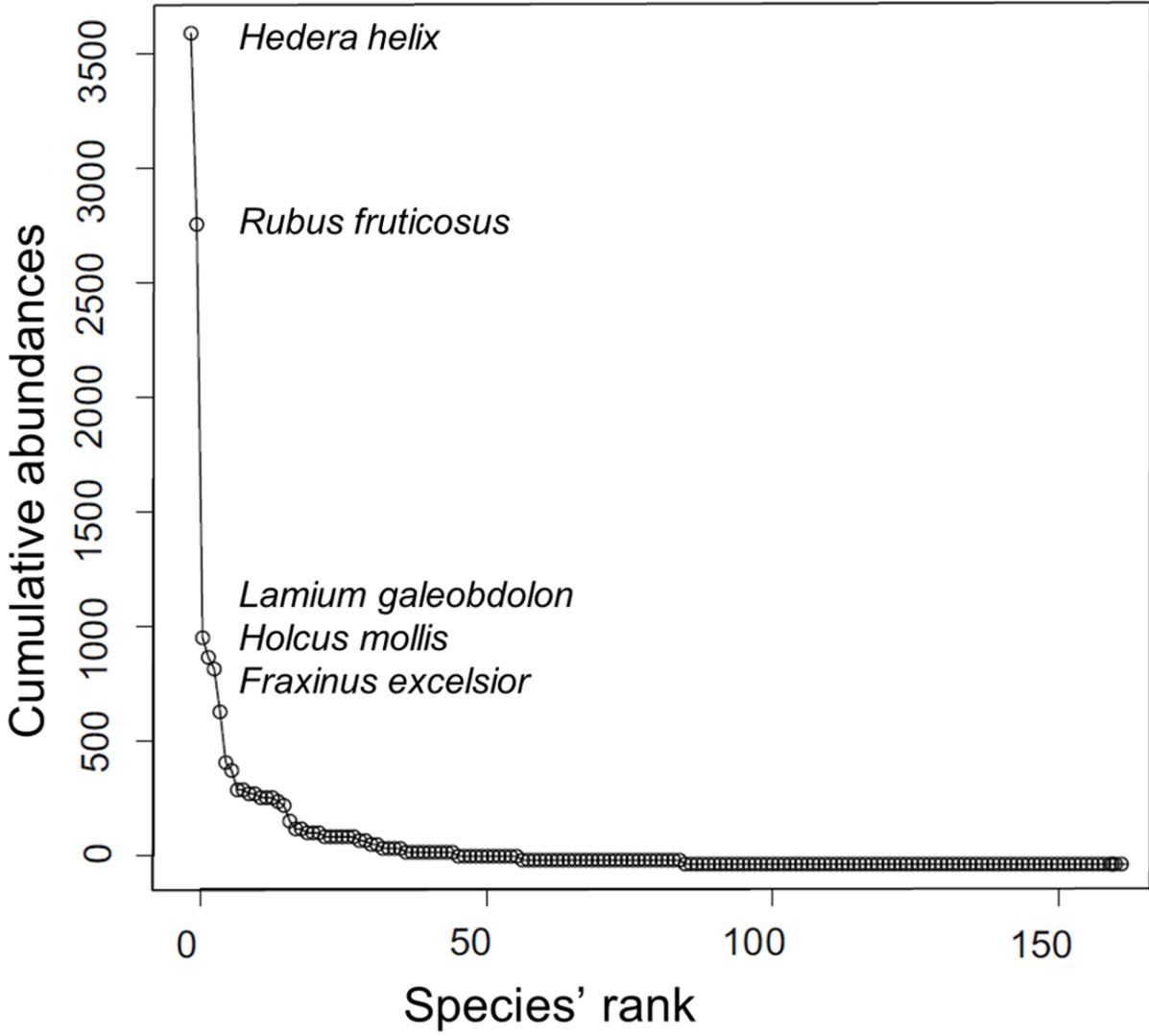
Appendix S1: Variation in species' life-history traits over the phylogenetic tree of the 162 studied forest plant species occurring within our study area.

Appendix S2: Pearson's correlations among the 13 variables used to describe local environmental conditions.

Appendix S3: Pearson's correlations among all dominance/ diversity variables explored in this study (16 indices).

Appendix S4: Summary table of the linear mixed-effect model (LMM) testing the relationship between Ivy (*Hedera helix. L*) and environmental drivers.





Biomass (g, BoxCox transformed)

