Functional trait variation of forest understorey plant communities across Europe

Thomas Vanneste\textsuperscript{a,*}, Alicia Valdés\textsuperscript{b,1}, Kris Verheyen\textsuperscript{a}, Michael P. Perring\textsuperscript{a,c}, Markus Bernhardt-Römermann\textsuperscript{d}, Emilie Andrieu\textsuperscript{e}, Jörg Brunet\textsuperscript{f}, Sara A.O. Cousins\textsuperscript{g}, Marc Deconchat\textsuperscript{e}, Pallieter De Smedt\textsuperscript{a}, Martin Diekmann\textsuperscript{h}, Steffen Ehrmann\textsuperscript{i}, Thilo Heiniken\textsuperscript{l}, Martin Hermy\textsuperscript{k}, Annette Kolb\textsuperscript{h}, Jonathan Lenoir\textsuperscript{b}, Jaan Liira\textsuperscript{l}, Tobias Naaf\textsuperscript{m}, Taavi Paal\textsuperscript{l}, Monika Wulff\textsuperscript{m}, Guillaume Decocq\textsuperscript{b}, Pieter De Frenne\textsuperscript{a}

\textsuperscript{a}Forest & Nature Lab, Department of Environment, Faculty of Bioscience Engineering, Ghent University, Geraardsbergsesteenweg 267, BE-9090 Gent/De Pinte, Belgium
\textsuperscript{b}UR «Ecologie et Dynamique des Systèmes Anthropisés» (EDYSAN, UMR 7058 CNRS-UPJV), Jules Verne University of Picardie, 1 Rue des Louwels, F-80037 Amiens, France
\textsuperscript{c}Ecosystem Restoration and Intervention Ecology (ERIE) Research Group, School of Biological Sciences, The University of Western Australia, 35, Stirling Highway, Crawley, WA 6009, Australia
\textsuperscript{d}Institute of Ecology and Evolution, Friedrich-Schiller-University Jena, Dornburger Str. 159, D-07743 Jena, Germany
\textsuperscript{e}UMR 1201 DYNAFOR, INRA, Chemin de Borde Rouge, CS 52627, F-31326 Castanet-Tolosan, France
\textsuperscript{f}Southern Sweden Research Centre, Swedish University of Agricultural Sciences, Box 49, SE-230 53 Alnarp, Sweden
\textsuperscript{g}Biogeography and Geomatics, Department of Physical Geography, Stockholm University, SE-10609 Stockholm, Sweden
\textsuperscript{h}Vegetation Ecology and Conservation Biology, Institute of Ecology, FB2, University of Bremen, Leobener Str., D-28359 Bremen, Germany
\textsuperscript{i}Geobotany, Faculty of Biology, University of Freiburg, Schänzestr. 1, D-79104 Freiburg, Germany
\textsuperscript{j}Institute of Biochemistry and Biology, University of Potsdam, Maulbeerstrasse 3, D-14469 Potsdam, Germany
\textsuperscript{k}Division Forest, Nature and Landscape Research, University of Leuven (KU Leuven), Celestijnlaan 200E, BE-3000 Leuven, Belgium
\textsuperscript{l}Institute of Ecology and Earth Sciences, University of Tartu, Lai 40, EE-51005 Tartu, Estonia
\textsuperscript{m}Centre for Agricultural Landscape Research (ZALF), Eberswalder Strasse 84, D-15374 Müncheberg, Germany

Received 24 May 2018; accepted 20 September 2018
Available online 26 September 2018

Abstract

Global environmental changes are expected to alter the functional characteristics of understorey herb-layer communities, potentially affecting forest ecosystem functioning. However, little is known about what drives the variability of functional traits in forest understories. Here, we assessed the role of different environmental drivers in shaping the functional trait distribution of understorey herbs in fragmented forests across three spatial scales. We focused on 708 small, deciduous forest patches...
located in 16 agricultural landscape windows, spanning a 2500-km macroclimatic gradient across the temperate forest biome in Europe. We estimated the relative effect of patch-scale, landscape-scale and macroclimatic variables on the community mean and variation of plant height, specific leaf area and seed mass. Macroclimatic variables (monthly temperature and precipitation extremes) explained the largest proportion of variation in community trait means (on average 77% of the explained variation). In contrast, patch-scale factors dominated in explaining community trait variation (on average 68% of the explained variation). Notably, patch age, size and internal heterogeneity had a positive effect on the community-level variability. Landscape-scale variables explained only a minor part of the variation in both trait distribution properties. The variation explained by shared combinations of the variable groups was generally negligible. These findings highlight the importance of considering multiple spatial scales in predictions of environmental-change effects on the functionality of forest understories. We propose that forest management sustainability could benefit from conserving larger, historically continuous and internally heterogeneous forest patches to maximise ecosystem service diversity in rural landscapes.

© 2018 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

**Keywords:** Agricultural landscapes; Biogeography; Community ecology; Forest understorey; Functional trait diversity; Fragmentation; Global environmental change; Landscape connectivity; Macroclimatic gradient; Multi-scale analysis

---

### Introduction

The major drivers of global change, that is, climate and land-use changes, are causing long-term shifts in the biodiversity and functioning of forest ecosystems (Sala et al., 2000; Hansen et al., 2001). Indeed, previous studies have reported a warming-induced reshuffling in the composition of forest plant communities (Walther, 2010). Furthermore, habitat fragmentation may aggravate the impact of climate change on forest ecosystems by impeding the movements of species across the landscape (Honnay et al., 2002; Skov & Svenning, 2004). Forest herbs are particularly susceptible to these interactive global-change effects due to their dispersal limitation (De Frenne et al., 2011; Verheyen, Honnay, Motzkin, Hermy, & Foster, 2003). Many forest plants are likely not able to rapidly track favourable environmental conditions, and their persistence may depend on the conservation of existing forest habitats within their actual distribution range (Honnay et al., 2002). From this perspective, small forest remnants may serve as refugia for forest herbs or even form stepping-stones for their migration across the landscape. Likewise, exactly these patches account for some key ecosystem services (e.g. sources of wood and fibre production, pollination, carbon sequestration, etc.; see review by Decocq et al., 2016).

The response of forest ecosystems to environmental changes as well as their capacity to deliver ecosystem services is strongly defined by changes in plant functional trait diversity (i.e. the distribution of functional life-history traits among coexisting species) (Diaz, Cabido, & Casanoves, 1998; Violle, Reich, Pacala, Enquist, & Kattge, 2014). Indeed, various abiotic and biotic drivers (ecological filters) acting across different scales shape the functional trait composition within and across communities (Keddy, 1992; Zobel, 1997; Violle et al., 2007). Large-scale environmental factors (e.g. macroclimate) determine which ecological strategies are more viable at a given site, and may thus shape the community-level mean of plant traits. Local environmental variation (e.g. microclimate, edaphic heterogeneity and biotic interactions), on the other hand, provides opportunities for niche partitioning, and may explain why communities support a wider distribution of ecological strategies (de Bello et al., 2013; Stark, Lehman, Crawford, Enquist, & Blonder, 2017). Finally, landscape-scale factors (e.g. landscape connectivity) affect the movements of species among habitat patches, and may thus also modify the distribution of traits in community assemblages (e.g. by selecting species based on their dispersal traits; Favre-Bac, Mony, Burel, Seimandid-Corda, & Ernoult, 2017). However, the relative importance of these environmental drivers in structuring the functional trait distribution of forest plant communities across multiple spatial scales (from local to continental) still needs to be quantified. This knowledge is key to develop a deeper understanding of how global changes affect ecosystem dynamics and functionality of forest remnants, and can be used to elaborate guidelines for their conservation and management in an era of environmental change.

Here we determined the functional trait distribution of forest herbs as the community-level mean (CM) and coefficient of variation (CV). We specifically focused on the minimally needed trait spectrum, i.e. the leaf-height-seed (LHS) trait space (Westoby, 1998), which relies on a combination of easily measurable traits known to reflect key aspects of ecological strategies amongst vascular plant species (Diaz et al., 2004). (i) Plant height at maturity determines a species’ ability to compete for light and adjust to various forms of environmental stress (climate, nutrients, etc.) (Westoby, 1998). (ii) Specific leaf area (SLA; leaf area to dry weight ratio) reflects the trade-off between leaf longevity and the maximum photosynthetic rate (with low/high SLA values resulting in long/short leaf life-spans, but low/high rates of photosynthesis; Wright et al., 2004), and thus controls the growth rate of plants as well as their capacity to respond to varying levels of disturbance (Bernhardt-Römermann et al., 2011). (iii) Seed mass plays an important role in the colonization process
as this trait is highly correlated with seed dispersal distances, seed bank persistence, germination potential of seeds and establishment and survival of seedlings (with heavier-seeded plants typically having a higher seedling survival rate upon emergence; Coomes & Grubb, 2003; Moles, Wright, Pitman, Murray, & Westoby, 2009).

We aimed at explaining the variation in the functional trait distribution patterns of understorey plant communities in forest patches of agricultural landscapes along a broad macroclimatic gradient across Europe. To achieve this, we investigated the relative effects of several environmental drivers acting across different spatial scales (continental scale, regional/landscape scale and local/patch scale). Our study was explicitly designed to capture the environmental variability across these scales. In each region, we selected two landscape windows with a contrasting degree of landscape permeability and habitat connectivity. We assured that these windows contained forest patches of varying size, age and degree of isolation. The macroclimatic gradient along which the forest patches were located, assured that the large-scale climatic conditions of temperate Europe are represented adequately in our study. Moreover, studying plant populations along a broad environmental gradient provides vital information on the structuring and functioning of ecosystems, and serves as an excellent tool to investigate the response of individuals, communities or ecosystems to global environmental change (De Frenne, Graae et al., 2013). We focus on understorey communities as these represent the vast majority of vascular plant diversity in temperate forests (Gilliam, 2007). They also play a vital role in forest ecosystem functioning (e.g. litter decomposition and nutrient cycling) as well as the provisioning of ecosystem services (e.g. pollination, tree regeneration, habitat provisioning, etc.; Nilsson & Wardle, 2005; Ampoorter et al., 2016) and disservices (Ehrmann et al., 2018). Finally, herbaceous-layer communities are indicators for long-term environmental-change impacts on forest ecosystems (Förster, Becker, Gerlach, Meesenburg, & Leuschner, 2017; Perring et al., 2018).

More specifically, we addressed the following hypotheses: (i) macroclimatic factors, as overall ecological filters, mainly affect the community trait means of understorey herbs in forest fragments, (ii) landscape configuration around the forest patches determines the dispersal success of species, and may therefore also influence the functional trait distribution of plant communities in fragmented forests, and (iii) patch-scale factors such as patch age, size and internal heterogeneity contribute mostly to community trait variation within fragmented systems.

**Materials and methods**

**Study area**

Data on plant species occurrences were gathered from deciduous forest patches in eight regions, spanning a macroclimatic gradient of c. 2500 km across the nemoral and boreo-nemoral zones of Europe (see also Valdés et al., 2015; Fig. 1). In each region, two 5 km × 5 km agricultural landscape windows were selected with contrasting degree of connectivity between forest patches. The first window (henceforth referred to as ‘highly-fragmented system’), was chosen to consistently represent a poorly connected landscape with primarily isolated forest patches, separated by an intensively managed agricultural matrix of open arable fields. The other window (hereafter referred to as ‘semi-fragmented system’) contains forest patches which are, to some extent, connected by woody corridors (e.g. hedgerows and tree lines), and embedded in a less disturbed matrix. This landscape was thus considered more permeable to species movements between habitat patches. For each window, landscape metrics and climatic characteristics are given in Supplementary Appendix A: Table 1.

We sampled all deciduous forest patches in each landscape window, including both large and small as well as ancient (i.e. forests that have not been cleared for agriculture over a period of at least 150 years) and recent forests (i.e. forests that were established on former agricultural land; Flinn & Vellend, 2005). We focused on deciduous forests as these are the most dominant type of forest remnants in rural landscapes across Europe, and are known to have a diverse understorey species composition. Hence, we excluded coniferous plantations and stands with more than 40% of coniferous trees in the entire patch area. If a deciduous forest patch was embedded in a larger coniferous plantation, the coniferous part was not sampled and the deciduous stands were regarded as a single patch. In total, 708 forest patches were sampled, with an average of 37 ± 15 (mean ± S.D.) forest patches per window in the eight highly-fragmented landscapes and 52 ± 13 (mean ± S.D.) forest patches per window in the eight semi-fragmented landscapes.

**Floristic surveys**

Species-specific occurrences (presence/absence) of terrestrial vascular plants were collected in all forest patches at the peak of phenology of the vegetation (May–July 2012). More specifically, we recorded all vascular plant species (see Valdés et al., 2015 for a complete species list) occurring along parallel transects spaced at 10 m apart, in accordance with the recommendations of Kirby et al. (1986). Taxonomic agglomerates (e.g. Rubus fruticosus agg.) were treated as single species. The number of transects per patch and the transect length were proportional to the patch size. The transect direction was chosen randomly, but all transects were situated parallel to each other such that the entire area was surveyed. The average amount of time spent on these surveys was about two hours per hectare. Finally, we omitted trees and non-seed plants (i.e. ferns and horsetails) to avoid a bias in the calculation of trait statistics (especially for plant height and seed mass, respectively). This resulted in a final dataset of 606 species (with an average of 37.5 ± 19.7 species per
Fig. 1. (A) Continental scale: map showing the locations of the eight study regions, spanning a latitudinal gradient of c. 2500 km. The grey area represents the temperate forest biome of Europe (adapted from Olson et al. 2001). Country codes: SF = Southern France, NF = Northern France, BE = Belgium, WG = Western Germany, EG = Eastern Germany, SS = Southern Sweden, CS = Central Sweden, ES = Estonia. (B) Landscape scale: each region comprised two 5 km × 5 km landscape windows, embedded in a fragmented agricultural matrix consisting of mainly croplands, grasslands/pastures and isolated forest patches (example from western Germany). (C) Landscape scale: ‘semi-fragmented system’ with higher amount of woody corridors and a more permeable landscape matrix. (D) Landscape scale: ‘highly-fragmented system’ with lower amount of woody corridors and a landscape matrix predominantly consisting of intensively managed croplands. (E) Patch scale: fragmented forest patch with the location of the sampling plots (white points) used for the vegetation surveys. This figure was partly adapted from Valdés et al. (2015).
patch). Following the methodology of Chao, Colwell, Lin, and Gotelli (2009), we estimated that we detected 85.3% of all species present in the forest fragments.

Trait data

We compiled data on functional plant life-history traits from databases as well as personal measurements (see Supplementary Appendix A: Table 2). The main data source for all traits was the LEDA database (Kleyer et al., 2008), completed for plant height by data from Ecoflora (Fitter & Peat, 1994) and for seed mass by D³ (Hintze et al., 2013) and the SID databases (Royal Botanic Gardens Kew, 2008). For completion of species with still missing values, the trait databases shown in Supplementary Appendix A: Table 2 were assessed. In few cases, personal measurements following the protocols of the LEDA database were used. Remaining gaps in the trait data were relatively scarce (i.e. 0.87%, 2.66% and 4.62% of missing occurrences in the sites × traits matrix for plant height, SLA and seed mass, respectively) and were therefore not interpolated as this would have only a minor influence on the calculation of community-level statistics. Plant height was weakly correlated with SLA (Pearson’s \( r = -0.118 \), \( P = 0.007 \), while plant height and seed mass (Pearson’s \( r = 0.073 \), \( P = 0.098 \)) as well as SLA and seed mass (Pearson’s \( r = 0.018 \), \( P = 0.677 \)) showed no significant correlation.

Due to limitations in data availability, we used mean functional trait values per species without taking into account intraspecific trait variability. Yet, this is a rational approach considering the broad scale of our study and the nature of our predefined hypotheses (following the guidelines of Albert, Grassein, Schurr, Vieilledent, & Violle, 2011). Nonetheless, we acknowledge that incorporating within-species trait variability could further improve the robustness of our analyses (Albert et al., 2010; Violle et al., 2012), and merits additional research (especially given the effect of intraspecific trait variation on plant community dynamics and ecosystem functioning; Garnier et al., 2001).

Environmental variables

For each studied forest patch, three types of environmental variables (i.e. patch-scale, landscape-scale and macroclimatic variables) were calculated using a Geographic Information System (GIS) software (ArcGIS 9.3, ESRI). For each type, only the four most meaningful and representative variables were retained [based on a principal component analysis (PCA); 12 environmental variables per patch in total] to avoid overweighting of one type over the others in the statistical analysis and facilitate between-group comparisons (Valdés et al., 2015).

The first group of environmental predictors consisted of four macroclimatic variables, using WorldClim version 1.4 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005): maximum temperature of the warmest month (MaTWm; BIO5), minimum temperature of the coldest month (MiTCm; BIO6), precipitation of the wettest month (PWm; BIO6) and precipitation of the driest month (PDm; BIO14). Both MaTWm and MiTCm were highly correlated with the mean annual temperature (Pearson’s \( r = 0.773 \) and 0.943, respectively), while PWm and PD showed a high correlation with the mean annual precipitation (Pearson’s \( r = 0.698 \) and 0.956, respectively). For more details regarding the calculation and selection procedure of these macroclimatic variables, we refer to Supplementary Appendix A and Valdés et al. (2015).

Next, we calculated 20 variables describing the landscape configuration around each patch, using the Corine Land Cover map of 2006 (Büttner, 2014) as well as aerial photographs. We retained only the four most representative variables, i.e. the proximity index (PROX; McGarigal, Cushman, & Ene, 2002), proportion of forest (F500) and grassland (G500) in a 100–500 m buffer around each focal patch and proportion of hedgerows (HS50) in a 0–50 m buffer around each patch (see Supplementary Appendix A). These variables provide a measure of inter-patch connectivity as well as permeability of the surrounding matrix, and relate to the movements of species across the landscape.

Finally, four patch-level variables were computed. Patch area (AREA) was determined after digitizing all forest fragments using recent aerial photographs (all taken after the year 2000). To estimate patch age (AGE), we reconstructed historical changes in forest cover based on land-use maps from the 18th century, 19th century, 20th century and the 21st century. Specifically, we calculated an area-weighted age index \( A_i = \sum p_iage_i \), where \( p_i \) is the proportion of the total surface area of a focal patch that existed continuously between the time of each historical map and the year 2012, and \( age_i \), the estimated age of the historical maps relative to 2012 (the year of the vegetation surveys). Both features are considered important drivers of understory species diversity in forests (De Frenne et al., 2011; Valdés et al., 2015), and may therefore have a profound influence on the functional diversity of fragmented systems. Likewise, small-scale differences in topography and canopy cover strongly modify local environmental conditions (e.g. light availability, microclimate and soil conditions) (Graae et al., 2017; Lenoir, Hattab, & Pierre, 2017), and may promote randomness, or even divergence, of trait values in the understory herb layer. To account for these effects, we used the topographic variability (coefficient of variation of elevation) as proxy for abiotic heterogeneity (ABIOH), and total woody species diversity within each patch as proxy for biotic heterogeneity (BIOH). Further details on the calculation of these variables are provided in Supplementary Appendix A.

Data analyses

We calculated the community-level mean (CM; i.e. mean trait values per patch) and variation (CV; i.e. coefficient of variation of trait values per patch) for each of the three
plant traits. Then, we related these trait statistics to the 12 studied environmental variables using linear mixed-effect models (LMM) with maximum-likelihood model estimation. In these models, we used the CM and CV of the studied traits as response variable, whereas the 12 environmental variables were included as fixed effect. Furthermore, we included ‘region’ and ‘window type’ (nested within ‘region’) as random intercept terms in the models to account for the hierarchical structure of the data and potential spatial autocorrelation between plant populations belonging to the same region and landscape window. The variance inflation factor (VIF) between predictors was greatest for MiTCm (VIF = 7.87) and PDM (VIF = 9.40) (see Supplementary Appendix A: Figs. 1 and 2 and Table 3). Therefore, these two variables were not simultaneously included in the models. All response variables were transformed with natural logarithm prior to the analyses to meet the assumptions of the statistical tests, while the predictor variables were standardized.

To come up with the most parsimonious models, we adopted a model selection procedure according to Burnham and Anderson (2002). In particular, for each of the response variables (CM and CV of the three plant traits), we constructed candidate models with all possible combinations of the 12 explanatory variables, but always excluded one out of the two collinear variables (MiTCm and PDM) unless the other variable dropped out. Next, we ranked these models based on the small sample unbiased Akaike Information Criteria (AICc) (Burnham & Anderson, 2002). Finally, to account for model selection uncertainty, we performed conditional model averaging of parameter estimates across all candidate models with a ΔAICc < 2 (Burnham, Anderson, & Huyvaert, 2011).

Finally, we performed a variation partitioning among the three groups of explanatory variables (patch-scale, landscape-scale and macroclimatic) according to Legendre and Legendre (2006). We constructed LMMs containing each time one, two or three groups of explanatory variables, and determined the proportion of variation explained by the fixed factors (marginal \( R^2 \), \( R^2_m \)) according to Nakagawa and Schielzeth (2013). Subsequently, we calculated the amount of variation explained by the unique and shared contribution of patch-scale, landscape-scale and macroclimatic variables, and expressed this relative to the total amount of variation explained by the fixed factors in the global model (containing all three groups of explanatory variables).

All statistical analyses were performed in R using the packages ‘lme4’ (Bates, Mächler, Bolker, & Walker, 2015), ‘lmerTest’ (Kuznetsova, Brockhoff, & Christensen, 2017) and ‘MuMin’ (Barton, 2017).

Results

In the most parsimonious models, the 12 environmental variables explained 31.0% (\( \chi^2 \) test; \( P < 0.001 \)), 9.60% (\( \chi^2 \) test; \( P = 0.002 \)) and 18.4% (\( \chi^2 \) test; \( P < 0.001 \)) of the total variance in mean plant height, SLA and seed mass, respectively. More precisely, mean plant height responded negatively to patch age, abiotic and biotic patch heterogeneity and precipitation of the wettest month, whereas the minimum temperature of the coldest month and the precipitation of the driest month had a strong positive effect. The mean SLA was related negatively to patch area and proportion of grassland around the patch. The mean seed mass increased with increasing biotic heterogeneity and proportion of forests around the patch, but was negatively correlated with the proportion of grassland and minimum temperature of the coldest month (Table 1).

For the variation of plant height, SLA and seed mass, the proportion of variance explained by the environmental predictors in the best model was 31.6% (\( \chi^2 \) test; \( P < 0.001 \)), 37.4% (\( \chi^2 \) test; \( P < 0.001 \)) and 41.1% (\( \chi^2 \) test; \( P < 0.001 \)), respectively. Notably, the variation of plant height, SLA and seed mass increased significantly with increasing patch area, patch age and abiotic as well as biotic heterogeneity of the forest patches. In addition, we detected a negative correlation between the variation of plant height and SLA and proportion of hedgerows around the patch, while the variation of seed mass responded negatively to increasing minimum temperature of the coldest month (Fig. 2, Table 1).

The variation partitioning revealed that, among all fixed effects, the unique effect of macroclimatic variables accounted for the largest proportion of explained variation in the mean plant traits (70.8%, 87.7% and 73.2% of the explained variation for plant height, SLA and seed mass, respectively), whereas the percentage of variation explained by patch- and landscape variables was negligible. For the variation of the plant traits, however, patch-scale variables accounted for the largest prediction value (78.2%, 73.6% and 50.8% of the explained variation for plant height, SLA and seed mass, respectively), followed by macroclimatic conditions and finally by landscape-scale variables. The percentages of variation shared by the different groups of environmental variables were generally low (on average 2.88% of the explained variation across the three plant traits; Fig. 3). The results of the variation partitioning are thus highly consistent with the LMMs, demonstrating the robustness of our findings.

Discussion

Our study quantified the functional trait distribution of understory plant species in fragmented forests along a macroclimatic gradient, and related the observed patterns to underlying effects of environmental variables at three different scales (patch-, landscape- and continental scale). We provide evidence for a scale-dependency in the role of environmental variables shaping the functional trait assemblages of forest fragments. Once large-scale environmental condi-
Table 1. Results of the mixed model selection and averaging across the best candidate models relating the community-level mean (CM) and coefficient of variation (CV) of the studied plant traits (plant height, SLA and seed mass) to the 12 environmental variables. Values of Akaike Information Criterion (AIC), marginal $R^2$ ($R^2_m$) and conditional $R^2$ ($R^2_c$) are shown for the best model. The values inside the table represent parameter estimates $\pm$ standard error, resulting from model averaging across all models with a $\Delta$AIC < 2. The significance of each predictor variable was obtained from a $\chi^2$ test, and is indicated as: ***P < 0.001; **P < 0.01; *P < 0.05; P < 0.1, with n = 708 forest patches. Blank spaces indicate that the variable was not included in the average model.

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>Plant height</th>
<th>SLA</th>
<th>Seed mass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Community mean (CM)</td>
<td>AIC = −588</td>
<td>$R^2_m = 0.310$</td>
<td>$R^2_c = 0.184$</td>
</tr>
<tr>
<td>Patch area (AREA)</td>
<td>−0.006 ± 0.007</td>
<td>−0.006 ± 0.002*</td>
<td>−0.046 ± 0.024</td>
</tr>
<tr>
<td>Patch age (AGE)</td>
<td>−0.030 ± 0.007***</td>
<td>0.002 ± 0.003</td>
<td>0.034 ± 0.025</td>
</tr>
<tr>
<td>Abiotic heterogeneity (ABIO_H)</td>
<td>−0.027 ± 0.011*</td>
<td>0.002 ± 0.003</td>
<td>0.070 ± 0.026**</td>
</tr>
<tr>
<td>Proximity index (PROX)</td>
<td>0.004 ± 0.002.</td>
<td>0.004 ± 0.002.</td>
<td>0.046 ± 0.027</td>
</tr>
<tr>
<td>Proportion of forest (F500)</td>
<td>−0.016 ± 0.010.</td>
<td>−0.004 ± 0.004</td>
<td>0.069 ± 0.035*</td>
</tr>
<tr>
<td>Proportion of grassland (G500)</td>
<td>0.018 ± 0.010.</td>
<td>−0.010 ± 0.004*</td>
<td>−0.092 ± 0.037*</td>
</tr>
<tr>
<td>Proportion of hedgerows (H50)</td>
<td>0.003 ± 0.003</td>
<td>0.004 ± 0.003</td>
<td>0.046 ± 0.027</td>
</tr>
<tr>
<td>Minimum temperature warmest month (MaTm)</td>
<td>−0.302 ± 0.041</td>
<td>−0.088 ± 0.016</td>
<td>−0.061 ± 0.077</td>
</tr>
<tr>
<td>Precipitation wettest month (PWm)</td>
<td>−0.066 ± 0.034*</td>
<td>0.003 ± 0.013</td>
<td>−0.031 ± 0.060</td>
</tr>
<tr>
<td>Precipitation driest month (PDm)</td>
<td>0.105 ± 0.047*</td>
<td>0.029 ± 0.015.</td>
<td>0.029 ± 0.015.</td>
</tr>
</tbody>
</table>

Community coefficient of variation (CV)

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>Plant height</th>
<th>SLA</th>
<th>Seed mass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Community mean (CM)</td>
<td>AIC = −110</td>
<td>$R^2_m = 0.316$</td>
<td>$R^2_c = 0.411$</td>
</tr>
<tr>
<td>Patch area (AREA)</td>
<td>0.036 ± 0.009***</td>
<td>0.033 ± 0.008***</td>
<td>0.050 ± 0.015***</td>
</tr>
<tr>
<td>Patch age (AGE)</td>
<td>0.034 ± 0.010***</td>
<td>0.035 ± 0.008***</td>
<td>0.060 ± 0.015***</td>
</tr>
<tr>
<td>Abiotic heterogeneity (ABIO_H)</td>
<td>0.047 ± 0.027***</td>
<td>0.052 ± 0.012***</td>
<td>0.093 ± 0.022***</td>
</tr>
<tr>
<td>Biotic heterogeneity (BIO_H)</td>
<td>0.112 ± 0.010***</td>
<td>0.102 ± 0.009***</td>
<td>0.172 ± 0.016***</td>
</tr>
<tr>
<td>Proximity index (PROX)</td>
<td>0.013 ± 0.008</td>
<td>0.008 ± 0.007</td>
<td>0.008 ± 0.013</td>
</tr>
<tr>
<td>Proportion of forest (F500)</td>
<td>0.015 ± 0.013</td>
<td>0.010 ± 0.011</td>
<td>0.016 ± 0.021</td>
</tr>
<tr>
<td>Proportion of grassland (G500)</td>
<td>0.026 ± 0.014.</td>
<td>0.015 ± 0.012</td>
<td>−0.006 ± 0.022</td>
</tr>
<tr>
<td>Proportion of hedgerows (H50)</td>
<td>−0.027 ± 0.010***</td>
<td>−0.024 ± 0.009***</td>
<td>−0.022 ± 0.016</td>
</tr>
<tr>
<td>Minimum temperature warmest month (MaTm)</td>
<td>−0.010 ± 0.027</td>
<td>−0.024 ± 0.009**</td>
<td>−0.124 ± 0.041**</td>
</tr>
<tr>
<td>Maximum temperature coldest month (MiTCm)</td>
<td>0.020 ± 0.027</td>
<td>−0.008 ± 0.025</td>
<td>−0.006 ± 0.022</td>
</tr>
<tr>
<td>Precipitation wettest month (PWm)</td>
<td>−0.033 ± 0.023</td>
<td>−0.035 ± 0.023</td>
<td>−0.032 ± 0.036</td>
</tr>
<tr>
<td>Precipitation driest month (PDm)</td>
<td>0.016 ± 0.031</td>
<td>−0.029 ± 0.029</td>
<td>−0.048 ± 0.046</td>
</tr>
</tbody>
</table>

The effect of abiotic heterogeneity, biotic heterogeneity, proximity index, patch area, age, and other factors such as patch size, patch age, abiotic heterogeneity and biotic heterogeneity on the community-level variation of the three studied traits. Indeed, larger forest patches tend to harbour a higher number of species (cf. species-area relationship; Wright, 1983), and may hence support a broader range of plant strategies. Furthermore, ancient forests are likely to accumulate more species over time, especially species with life-history traits that limit their dispersal (De Frenne et al., 2011), and may thus also support a higher variation of functional traits. Older forests also provide a wider variety of microhabitats related to, for instance, the structural complexity of shrub and tree layer as well as often higher density of dead wood (Lõhmus & Kraut, 2010).

Forest patches with higher levels of abiotic heterogeneity (here quantified as topography) generally provide a wider array of edaphic conditions, microclimates and potential resources, which could in turn support the co-occurrence of species with differing trait values in the understorey (Oppedal, Armbruster, & Graae, 2015; Stark et al., 2017). For instance, topographic complexity typically enhances microclimatic variability (Graae et al., 2017; Lenoir et al., 2017) and contributes to local heterogeneity in soil texture, soil moisture availability and litter decomposition (Dwyer & Merriam, 2011).
Fig. 2. Relationship between the community-level coefficient of variation (CV) of plant height (A–D), SLA (E–H) and seed mass (I–L), on the one hand, and patch area (A, E, I), patch age (B, F, J), abiotic patch heterogeneity (C, G, K) and biotic patch heterogeneity (D, H, L), on the other hand. The blue line denotes a linear mixed-effect model (LMM; $P < 0.05$) with the predictor variables as fixed effect and ‘region’ as well as ‘window type’ (nested within ‘region’) as random intercept terms. The dashed line represents a 95% confidence interval. All response variables (CV of plant height, CV of SLA and CV of seed mass) were transformed with natural logarithm, whereas predictor variables (patch area, patch age, abiotic heterogeneity and biotic heterogeneity) were standardized by subtracting the mean and dividing by the standard deviation (S.D.). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Likewise, we assume that a higher heterogeneity in the canopy structure, and thus degree of canopy closure, also promotes functional diversity of understorey herbs by locally modifying environmental conditions such as light transmittance (Sercu et al., 2017) and below-canopy temperatures (De Frenne, Rodríguez-Sánchez et al., 2013; Lenoir et al., 2017).

In addition to these patch-scale effects, we detected a strong negative impact of the number of hedgerows around a forest patch on the variation of plant height and SLA. Long-term continuity of woody corridors is commonly seen as a crucial factor supporting species-rich plant communities in small forest patches (Roy & de Blois, 2008; Liira & Paal, 2013). The hedgerows in our landscape windows, however, are likely too young to act as efficient migration corridors for forest herbs (Valdés et al., 2015), and might therefore not contribute to a divergence in functional trait attributes. Alternatively, well-connected landscapes (with many corridors) might reflect the historical land use, e.g. as remnants of cleared forests or forests used as wooded pastures, both of
which may have homogenised the distribution of leaf traits in understorey herb-layer communities.

Finally, apart from the negative effect of temperature on seed mass variation, macroclimatic factors contributed poorly to explaining functional trait variation in the forest fragments. This is corroborated by the weak relationship between latitude and the variation of plant traits, particularly for plant height and SLA (see Supplementary Appendix A: Fig. 3). Moreover, if macroclimate would have been the main driver of functional diversity, we would have expected a significant reduction in the number of viable plant strategies—and thus functional diversity—towards higher latitudes (Lamanna et al., 2014). Yet, our results indicate that patch characteristics may decrease the effect of large-scale environmental conditions, and ultimately explain why understorey herb communities in forest remnants exhibit different amounts of variation in their life-history traits.

Macroclimatic variables as primary filter to define community trait means in forests

Overall, macroclimatic variables had the greatest effect on the mean plant traits, suggesting large-scale filtering of species according to specific limiting conditions (Keddy, 1992). For instance, a higher precipitation in the driest month positively affected the mean plant height, supporting the findings of Moles, Warton et al. (2009) that water availability constitutes one of the key limiting factors for plant height at a species level. Likewise, the positive effect of temperature on the mean plant height and seed mass in our study is corroborated by large-scale observational studies of plant functional trait variation (Moles et al., 2005; De Frenne, Graae et al., 2013). Yet, we acknowledge that macroclimatic variables did not have a significant effect on the mean SLA. Most likely, this can be attributed to the fact that we focused on forest herbs, and SLA is therefore a direct reflection of species adaptations to shade (Löhmus, Paal, & Liira, 2014) rather than macroclimate.

In addition to macroclimate, some patch- and landscape-scale variables also showed a significant, but weaker effect on the community trait means. For instance, the negative correlation between patch age and understorey plant height could be related to the fact that older forests commonly host more small forest specialist species (Verheyen et al., 2003; and see Supplementary Appendix A: Fig. 4). Recent forests, on the other hand, typically lack these slow-colonizing specialists (Brunet et al., 2011; Naaf & Kolk, 2015), and are often dominated by tall, competitive herbs (e.g. Urtica dioica) due to the higher resource availability (e.g. soil phosphorous) or...
more open tree canopies (Flinn & Vellend, 2005). Likewise, we found that the mean plant height was negatively affected by the abiotic (topographic) and biotic (canopy) heterogeneity of the forests. The mean seed mass, however, increased with biotic patch heterogeneity. According to Wulf and Kolk (2014), the number of geophytes and small forest specialists with heavy seeds increases with forest patch heterogeneity, while the number of generalists was not affected in their study. Forest specialists thus tend to respond positively to the higher number of small-scale suitable habitats, whereas generalists require less specific growing conditions and are mainly affected by moisture and nutrient availability (see also Dupré & Ehrén, 2002). Consequently, we expect that an increase in small-scale heterogeneity may cause a proportionally higher rise in the number of forest specialists relative to generalists, thus implying a decrease in community mean plant height as well as an increase in community mean seed mass.

SLA responded negatively to patch size, which could be the result of larger patches being more easily managed towards efficient timber production (Lidestav & Berg Lejon, 2013) or having more interior edges (e.g. forests roads) dominated by light-demanding, low-SLA species. Forest patches surrounded by a larger proportion of grasslands had a lower average SLA and seed mass. Most likely, these forests receive a higher input of open-landscape species (with low SLA and low seed mass) and wind-dispersing plants (with low seed mass) from the surrounding pastures and meadows into the forest edges (Jamoneau et al., 2011; Löhms et al., 2014).

Finally, it should be noted that, in some cases, the explanatory power ($R^2$) of the studied environmental variables was low (especially for the mean SLA and seed mass). We argue that other fine-scale environmental factors, which were not directly measured in this study, could partly drive functional diversity in the studied forest patches. Previous studies have reported that soil characteristics (Price et al., 2017), microclimate (Stark et al., 2017) and local light conditions (Lii, Jürjendal, & Paal, 2014) may play a key role in shaping the functional composition of plant communities. Besides, several non-environmental factors, such as biotic interactions, may influence functional diversity at a community-level (Tamme et al., 2010). Given this, we could expect that part of the variation in the studied plant traits arises from interactions between coexisting species within a forest patch (Moles, Warton et al., 2009).

**Scale-dependency in drivers of the community trait means and variation of forests**

As expected, the variation partitioning demonstrated that macroclimatic drivers contributed most to the variation in community-mean traits, while patch-scale factors mainly determined functional trait variation, particularly for plant height and SLA (see also Stark et al., 2017). Specifically, it has been shown that environmental drivers might act as ‘hierarchical filters’ shaping community assemblages across different spatial scales (Zobel, 1997; de Bello et al., 2013; Kraft, Godoy, & Levine, 2015). For instance, de Bello et al. (2013) argued that species are selected hierarchically from the regional species pool, according to certain trait attributes optimizing their growth and reproduction in a given area. In this filtering process, large-scale environmental factors such as macroclimate primarily shape the functional trait composition (i.e. community-average traits), whereas local-scale environmental variables (e.g. microclimate heterogeneity) ultimately determine relative trait abundances, and may thus explain differences in community functional diversity.

**Environmental-change effects on the functional trait distribution of forest understories**

Under climate change, species are predicted to shift their ranges towards higher latitudes (and higher elevations in mountainous regions) in the coming decades (Parmesan, 2006). As a result, numerous forest ecosystems will likely experience a shift in their plant functional assemblages, which may in turn affect their functioning. However, for many species, these projected range shifts may be, at least partly, inhibited due to the fragmentation of present-day landscapes (Renton, Shackelford, & Standish, 2012). Habitat fragmentation per se may also alter the functional trait distribution of forests by filtering plant species with strategies adapted to low habitat availability and high levels of patch isolation (Favre-Bac et al., 2017). In particular, plant species with dispersal traits helping them to overcome adverse effects of habitat isolation are selected from the regional species pool, leading to an overall convergence of trait values. In our study, however, landscape-scale variables related to habitat connectivity and landscape permeability had only a minor influence on both community trait means and variation. We argue that trait variation in our study area is not subject to direct landscape filtering, but shows a more stochastic pattern, which is driven by factors acting both at a continental and at a patch level.

Alternatively, fragmentation through land-use changes not only implies a loss of connectivity, but also leads to a progressive conversion of forests into smaller and younger patches (Flinn & Vellend, 2005). This is reflected more clearly in the stand structure and patch characteristics of these forests, and may have a much stronger, negative impact on the functional diversity of understory plant communities. In particular, many forest specialists display life-history traits that make them susceptible to habitat loss and degradation (Brunet et al., 2011), and will be among the first to disappear from the regional pool of species. Yet, even if the present-day landscape configuration is maintained, time lags in the local extinction of forest specialists following habitat fragmentation may still be expected (Kolk & Naaf, 2015). Thus,
incorporating information on historical land-use changes and past landscape connectivity, when studying the effects of global change on functional diversity in temperate forest understories, could be the subject of future evaluation of forest functional research.

Conclusion

While community-mean traits have been repeatedly linked to mean environmental conditions over large spatial scales, we demonstrated that local environmental factors (e.g. patch size, patch age, abiotic and biotic heterogeneity of the patch, etc.) provide a better predictor of functional trait diversity in fragmented forests. Given the role of small forest patches as biodiversity reservoirs and their potential to improve multifunctionality of degraded landscapes (Decocq et al., 2016), we suggest that better-informed guidelines for their management and conservation in an agricultural framework are urgently needed. With this in mind, our results are relevant to improve projections of future environmental-change impacts on the biodiversity and functioning of forest remnants, and have implications for the future management of fragmented systems. Forest managers, policymakers and landscape planners could benefit from prioritizing the conservation of larger, older and more heterogeneous forests, as these have a higher functional diversity and therefore potentially a higher resilience to global environmental changes (Mori, Furukawa, & Sasaki, 2013) as well as a higher potential to safeguard ecosystem service delivery in human-transformed landscapes (Decocq et al., 2016). Conversely, our findings suggest that land management strategies aiming to improve the ecosystem service supply of heavily fragmented systems should prioritize on specific patch-scale characteristics of forests (e.g. size, history, tree composition, etc.), before scaling up to a landscape level (e.g. increasing functional connectivity or improving the overall landscape permeability).

Acknowledgements

The data for this study were collected within the framework of the ERA-Net BiodivERsA project smallFOREST, with the national funders ANR (France), MINECO (Spain), FORMAS (Sweden), ETAG (Estonia), DFG (Germany) and BELSPO (Belgium) as part of the 2011 BiodivERsA call for research proposals. TV was funded by a BOF grant [no. 01N02817] from Ghent University. PDF was supported by the European Research Council through the FORMICA project [ERC Starting Grant no. 757833], and KV as well as MP through the PAST FORWARD project [ERC Consolidator Grant no. 614839]. We thank Emilie Gallet-Moron for her help in the data management and Safaai Wasof for assistance with statistical analyses.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.baee.2018.09.004.

References


Royal Botanic Gardens Kew. (2008). *Seed Information Database (SID).*


