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# 1 Functional trait variation of forest understorey plant communities 2 across Europe

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32 **Abstract**

33 Global environmental changes are expected to alter the functional characteristics of understorey herb-layer  
34 communities, potentially affecting forest ecosystem functioning. However, little is known about what drives the  
35 variability of functional traits in forest understories. Here, we assessed the role of different environmental drivers  
36 in shaping the functional trait distribution of understorey herbs in fragmented forests across three spatial scales.  
37 We focused on 708 small, deciduous forest patches located in 16 agricultural landscape windows, spanning a  
38 2500-km macroclimatic gradient across the temperate forest biome in Europe. We estimated the relative effect  
39 of patch-scale, landscape-scale and macroclimatic variables on the community mean and variation of plant height,  
40 specific leaf area and seed mass. Macroclimatic variables (monthly temperature and precipitation extremes)  
41 explained the largest proportion of variation in community trait means (on average 77% of the explained  
42 variation). In contrast, patch-scale factors dominated in explaining community trait variation (on average 68% of  
43 the explained variation). Notably, patch age, size and internal heterogeneity had a positive effect on the  
44 community-level variability. Landscape-scale variables explained only a minor part of the variation in both trait  
45 distribution properties. The variation explained by shared combinations of the variable groups was generally  
46 negligible. These findings highlight the importance of considering multiple spatial scales in predictions of  
47 environmental-change effects on the functionality of forest understories. We propose that forest management  
48 sustainability could benefit from conserving larger, historically continuous and internally heterogeneous forest  
49 patches to maximise ecosystem service diversity in rural landscapes.

50

51 **Keywords:** Agricultural landscapes; biogeography; community ecology; forest understorey; functional trait  
52 diversity; fragmentation; global environmental change; landscape connectivity; macroclimatic gradient; multi-  
53 scale analysis

## 54 **Introduction**

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

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

82 global changes affect ecosystem dynamics and functionality of forest remnants, and can be used to elaborate  
83 guidelines for their conservation and management in an era of environmental change.

84 Here we determined the functional trait distribution of forest herbs as the community-level mean (CM) and  
85 coefficient of variation (CV). We specifically focused on the minimally needed trait spectrum, i.e. the leaf-height-  
86 seed (LHS) trait space (Westoby, 1998), which relies on a combination of easily measurable traits known to  
87 reflect key aspects of ecological strategies amongst vascular plant species (Diaz et al., 2004). (i) Plant height at  
88 maturity determines a species' ability to compete for light and adjust to various forms of environmental stress  
89 (climate, nutrients, etc.) (Westoby, 1998). (ii) Specific leaf area (SLA; leaf area to dry weight ratio) reflects the  
90 trade-off between leaf longevity and the maximum photosynthetic rate (with low/high SLA values resulting in  
91 long/short leaf life-spans, but low/high rates of photosynthesis; Wright et al., 2004), and thus controls the growth  
92 rate of plants as well as their capacity to respond to varying levels of disturbance (Bernhardt-Römermann et al.,  
93 2011). (iii) Seed mass plays an important role in the colonization process as this trait is highly correlated with  
94 seed dispersal distances, seed bank persistence, germination potential of seeds and establishment and survival of  
95 seedlings (with heavier-seeded plants typically having a higher seedling survival rate upon emergence; Coomes &  
96 Grubb, 2003; Moles, Wright, Pitman, Murray, & Westoby, 2009).

97 We aimed at explaining the variation in the functional trait distribution patterns of understorey plant  
98 communities in forest patches of agricultural landscapes along a broad macroclimatic gradient across Europe.  
99 To achieve this, we investigated the relative effects of several environmental drivers acting across different spatial  
100 scales (continental scale, regional/landscape scale and local/patch scale). Our study was explicitly designed to  
101 capture the environmental variability across these scales. In each region, we selected two landscape windows with  
102 a contrasting degree of landscape permeability and habitat connectivity. We assured that these windows  
103 contained forest patches of varying size, age and degree of isolation. The macroclimatic gradient along which the  
104 forest patches were located, assured that the large-scale climatic conditions of temperate Europe are represented  
105 adequately in our study. Moreover, studying plant populations along a broad environmental gradient provides  
106 vital information on the structuring and functioning of ecosystems, and serves as an excellent tool to investigate  
107 the response of individuals, communities or ecosystems to global environmental change (De Frenne, Graae, et  
108 al., 2013). We focus on understorey communities as these represent the vast majority of vascular plant diversity  
109 in temperate forests (Gilliam, 2007). They also play a vital role in forest ecosystem functioning (e.g. litter

110 decomposition and nutrient cycling) as well as the provisioning of ecosystem services (e.g. pollination, tree  
111 regeneration, habitat provisioning, etc.; Ampoorter et al., 2016; Nilsson & Wardle, 2005) and disservices  
112 (Ehrmann et al., 2018). Finally, herbaceous-layer communities are indicators for long-term environmental-  
113 change impacts on forest ecosystems (Förster, Becker, Gerlach, Meesenburg, & Leuschner, 2017; Perring et al.,  
114 2018).

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

120

## 121 **Material and methods**

### 122 *Study area*

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

133 We sampled all deciduous forest patches in each landscape window, including both large and small as well as  
134 ancient (i.e. forests that have not been cleared for agriculture over a period of at least 150–400 years) and recent  
135 forests (i.e. forests that have been established on former agricultural land; Flinn & Vellend, 2005). We focused  
136 on deciduous forests as these are the most dominant type of forest remnants in rural landscapes across Europe,

137 and are known to have a diverse understorey species composition. Hence, we excluded coniferous plantations  
138 and stands with more than 40% of coniferous trees in the entire patch area. If a deciduous forest patch was  
139 embedded in a larger coniferous plantation, the coniferous part was not sampled and the deciduous stands were  
140 regarded as a single patch. In total, 708 forest patches were sampled, with an average of  $37 \pm 15$  (mean  $\pm$  S.D.)  
141 forest patches per window in the eight highly-fragmented landscapes and  $52 \pm 13$  (mean  $\pm$  S.D.) forest patches  
142 per window in the eight semi-fragmented landscapes.

#### 143 *Floristic surveys*

144 Species-specific occurrences (presence/absence) of terrestrial vascular plants were collected in all forest patches  
145 at the peak of phenology of the vegetation (May–July 2012). More specifically, we recorded all vascular plant  
146 species (see Valdés et al., 2015 for a complete species list) occurring along parallel transects spaced at 10 m apart,  
147 in accordance with the recommendations of Kirby et al. (1986). Taxonomic agglomerates (e.g. *Rubus fruticosus*  
148 agg.) were treated as single species. The number of transects per patch and the transect length were proportional  
149 to the patch size. The transect direction was chosen randomly, but all transects were situated parallel to each  
150 other such that the entire area was surveyed. The average amount of time spent on these surveys was about two  
151 hours per hectare per person. Finally, we omitted trees and non-seed plants (i.e. ferns and horsetails) to avoid a  
152 bias in the calculation of trait statistics (especially for plant height and seed mass, respectively). This resulted in a  
153 final dataset of 606 species (with an average of  $37.5 \pm 19.7$  species per patch). Following the methodology of  
154 Chao, Colwell, Lin, and Gotelli (2009), we estimated that we detected 85.3 % of all species present in the forest  
155 fragments.

#### 156 *Trait data*

157 We compiled data on functional plant life-history traits from databases as well as personal measurements (see  
158 Appendix A: Table 2). The main data source for all traits was the LEDA database (Kleyer et al., 2008), completed  
159 for plant height by data from Ecoflora (Fitter & Peat, 1994) and for seed mass by D<sup>3</sup> (Hintze et al., 2013) and  
160 the SID databases (Royal Botanic Gardens Kew, 2008). For completion of species with still missing values, the  
161 trait databases shown in Appendix 2 were assessed. In few cases, personal measurements following the protocols  
162 of the LEDA database were used. Remaining gaps in the trait data were relatively scarce (i.e. 0.87%, 2.66% and  
163 4.62% of missing occurrences in the sites  $\times$  traits matrix for plant height, SLA and seed mass, respectively) and  
164 were therefore not interpolated as this would have only a minor influence on the calculation of community-level



165 statistics. Plant height was weakly correlated with SLA (Pearson's  $r = -0.118$ ,  $P = 0.007$ ), while plant height and  
166 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  
167 no significant correlation.

168 Due to limitations in data availability, we used mean functional trait values per species without taking into account  
169 intraspecific trait variability. Yet, this is a rational approach considering the broad scale of our study and the  
170 nature of our predefined hypotheses (following the guidelines of Albert, Grassein, Schurr, Vieilledent, & Violle,  
171 2011). Nonetheless, we acknowledge that incorporating within-species trait variability could further improve the  
172 robustness of our analyses (Albert et al., 2010; Violle et al., 2012), and merits additional research (especially  
173 given the effect of intraspecific trait variation on plant community dynamics and ecosystem functioning; Garnier  
174 et al., 2001).

### 175 *Environmental variables*

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

181 The first group of environmental predictors consisted of four macroclimatic variables, using WorldClim  
182 version 1.4 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005): maximum temperature of the warmest month  
183 (MaTWm; BIO5), minimum temperature of the coldest month (MiTCm; BIO6), precipitation of the wettest  
184 month (PWm; BIO13) and precipitation of the driest month (PDm; BIO14). Both MaTWm and MiTCm were  
185 highly correlated with the mean annual temperature (Pearson's  $r = 0.773$  and  $0.943$ , respectively), while PWm  
186 and PD showed a high correlation with the mean annual precipitation (Pearson's  $r = 0.698$  and  $0.956$ ,  
187 respectively). For more details regarding the calculation and selection procedure of these macroclimatic variables,  
188 we refer to Appendix A and Valdés et al. (2015).

189 Next, we calculated 20 variables describing the landscape configuration around each patch, using the Corrine  
190 Land Cover map of 2006 (Büttner, 2014) as well as aerial photographs. We retained only the four most  
191 representative variables, i.e. the proximity index (PROX; McGarigal, Cushman, & Ene, 2002), proportion of  
192 forest (F500) and grassland (G500) in a 100–500 m buffer around each focal patch and proportion of hedgerows

193 (H50) in a 0–50 m buffer around each patch (see Appendix A). These variables provide a measure for the inter-  
194 patch connectivity as well as permeability of the surrounding matrix, and relate to the movements of species  
195 across the landscape.

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

### 211 *Data analyses*

212 We calculated the community-level mean (CM; i.e. mean trait values per patch) and variation (CV; i.e. coefficient  
213 of variation of trait values per patch) for each of the three plant traits. Then, we related these trait statistics to the  
214 12 studied environmental variables using linear mixed-effect models (LMM) with maximum-likelihood model  
215 estimation. In these models, we used the CM and CV of the studied traits as response variable, whereas the 12  
216 environmental variables were included as fixed effect. Furthermore, we included ‘region’ and ‘window type’  
217 (nested within ‘region’) as random intercept terms in the models to account for the hierarchical structure of the  
218 data and potential spatial autocorrelation between plant populations belonging to the same region and landscape  
219 window. The variance inflation factor (VIF) between predictors was greatest for MiTCm (VIF = 7.87) and PDm  
220 (VIF = 9.40) (see Appendix A: Fig. 1, Fig. 2 and Table 3). Therefore, these two variables were not simultaneously

221 included in the models. All response variables were transformed with natural logarithm prior to the analyses to  
222 meet the assumptions of the statistical tests, while the predictor variables were standardized.

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

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

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

239

## 240 **Results**

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

247 biotic heterogeneity and proportion of forests around the patch, but was negatively correlated with the proportion  
248 of grassland and minimum temperature of the coldest month (Table 1).

249 For the variation of plant height, SLA and seed mass, the proportion of variance explained by the environmental  
250 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;  $P <$   
251 0.001, respectively. Notably, the variation of plant height, SLA and seed mass increased significantly with  
252 increasing patch area, patch age and abiotic as well as biotic heterogeneity of the forest patches. In addition, we  
253 detected a negative correlation between the variation of plant height and SLA and proportion of hedgerows  
254 around the patch, while the variation of seed mass responded negatively to increasing minimum temperature of  
255 the coldest month (Fig. 2, Table 1).

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

265

## 266 **Discussion**

267 Our study quantified the functional trait distribution of understorey plant species in fragmented forests along a  
268 macroclimatic gradient, and related the observed patterns to underlying effects of environmental variables at  
269 three different scales (patch-, landscape- and continental scale). We provide evidence for a scale-dependency in  
270 the role of environmental variables shaping the functional trait assemblages of forest fragments. Once large-scale  
271 environmental conditions such as macroclimate have set the community trait means, fine-scale variables

272 determine the variance of plant functional traits around the mean, and may thus explain why communities  
273 support different amounts of trait variation.

#### 274 *Patch-scale variables as main driver of community trait variation in forests*

275 We found strong positive effects of all four patch-scale predictor variables (patch size, patch age, abiotic  
276 heterogeneity and biotic heterogeneity) on the community-level variation of the three studied traits. Indeed,  
277 larger forest patches tend to harbour a higher number of species (*cf.* species-area relationship; Wright, 1983),  
278 and may hence support a broader range of plant strategies. Furthermore, ancient forests are likely to accumulate  
279 more species over time, especially species with life-history traits that limit their dispersal (De Frenne et al., 2011),  
280 and may thus also support a higher variation of functional traits. Older forests also provide a wider variety of  
281 microhabitats related to, for instance, the structural complexity of shrub and tree layer as well as often higher  
282 density of dead wood (Löhmus & Kraut, 2010).

283 Forest patches with higher levels of abiotic heterogeneity (here quantified as topography) generally provide a  
284 wider array of edaphic conditions, microclimates and potential resources, which could in turn support the co-  
285 occurrence of species with differing trait values in the understorey (Opedal, Armbruster, & Graae, 2015; Stark  
286 et al., 2017). For instance, topographic complexity typically enhances microclimatic variability (Graae et al., 2017;  
287 Lenoir et al., 2017) and contributes to local heterogeneity in soil texture, soil moisture availability and litter  
288 decomposition (Dwyer & Merriam, 1981). Likewise, we assume that a higher heterogeneity in the canopy  
289 structure, and thus degree of canopy closure, also promotes functional diversity of understorey herbs by locally  
290 modifying environmental conditions such as light transmittance (Sercu et al., 2017) and below-canopy  
291 temperatures (De Frenne, Rodríguez-Sánchez, et al., 2013; Lenoir et al., 2017).

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

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

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

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

318 In addition to macroclimate, some patch- and landscape-scale variables also showed a significant, but weaker  
319 effect on the community trait means. For instance, the negative correlation between patch age and understorey  
320 plant height could be related to the fact that older forests commonly host more small forest specialist species  
321 (Verheyen et al., 2003; and see Appendix A: Fig. 4). Recent forests, on the other hand, typically lack these slow-  
322 colonizing specialists (Brunet et al., 2011; Naaf & Kolk, 2015), and are often dominated by tall, competitive herbs  
323 (e.g. *Urtica dioica*) due to the higher resource availability (e.g. soil phosphorous) or more open tree canopies  
324 (Flinn & Vellend, 2005). Likewise, we found that the mean plant height was negatively affected by the abiotic  
325 (topographic) and biotic (canopy) heterogeneity of the forests. The mean seed mass, however, increased with  
326 biotic patch heterogeneity. According to Wulf and Kolk (2014), the number of geophytes and small forest  
327 specialists with heavy seeds increases with forest patch heterogeneity, while the number of generalists was not

328 affected in their study. Forest specialists thus tend to respond positively to the higher number of small-scale  
329 suitable habitats, whereas generalists require less specific growing conditions and are mainly affected by moisture  
330 and nutrient availability (see also Dupré & Ehrlén, 2002). Consequently, we expect that an increase in small-scale  
331 heterogeneity may cause a proportionally higher rise in the number of forest specialist relative to generalists, thus  
332 implying a decrease in community mean plant height as well as an increase in community mean seed mass.

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

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

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

349 As expected, the variation partitioning demonstrated that macroclimatic drivers contributed most to the variation  
350 in community-mean traits, while patch-scale factors mainly determined functional trait variation, particularly for  
351 plant height and SLA (see also Stark et al., 2017). Specifically, it has been shown that environmental drivers  
352 might act as 'hierarchical filter' shaping community assemblages across different spatial scales (de Bello et al.,  
353 2013; Kraft, Godoy, & Levine, 2015; Zobel, 1997). For instance, de Bello et al. (2013) argued that species are  
354 selected hierarchically from the regional species pool, according to certain trait attributes optimizing their growth  
355 and reproduction in a given area. In this filtering process, large-scale environmental factors such as macroclimate

356 primarily shape the functional trait composition (i.e. community-average traits), whereas local-scale  
357 environmental variables (e.g. microclimate heterogeneity) ultimately determine relative trait abundances, and  
358 may thus explain differences in community functional diversity.

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

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

372 Alternatively, fragmentation through land-use changes not only implies a loss of connectivity, but also leads to a  
373 progressive conversion of forests into smaller and younger patches (Flinn & Vellend, 2005). This is reflected  
374 more clearly in the stand structure and patch characteristics of these forests, and may have a much stronger,  
375 negative impact on the functional diversity of understorey plant communities. In particular, many forest  
376 specialists display life-history traits that make them susceptible to habitat loss and degradation (Brunet et al.,  
377 2011), and will be among the first to disappear from the regional pool of species. Yet, even if the present-day  
378 landscape configuration is maintained, time lags in the local extinction of forest specialists following habitat  
379 fragmentation may still be expected (Kolk & Naaf, 2015). Thus, incorporating information on historical land-use



380 changes and past landscape connectivity, when studying the effects of global change on functional diversity in  
381 temperate forest understories, could be the subject of future evaluation of forest functional research.

382

## 383 **Conclusion**

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

400

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409

410 Appendix A. Supplementary data

411 Supplementary data associated with this article can be found, in the online version, at XXXXX.

412

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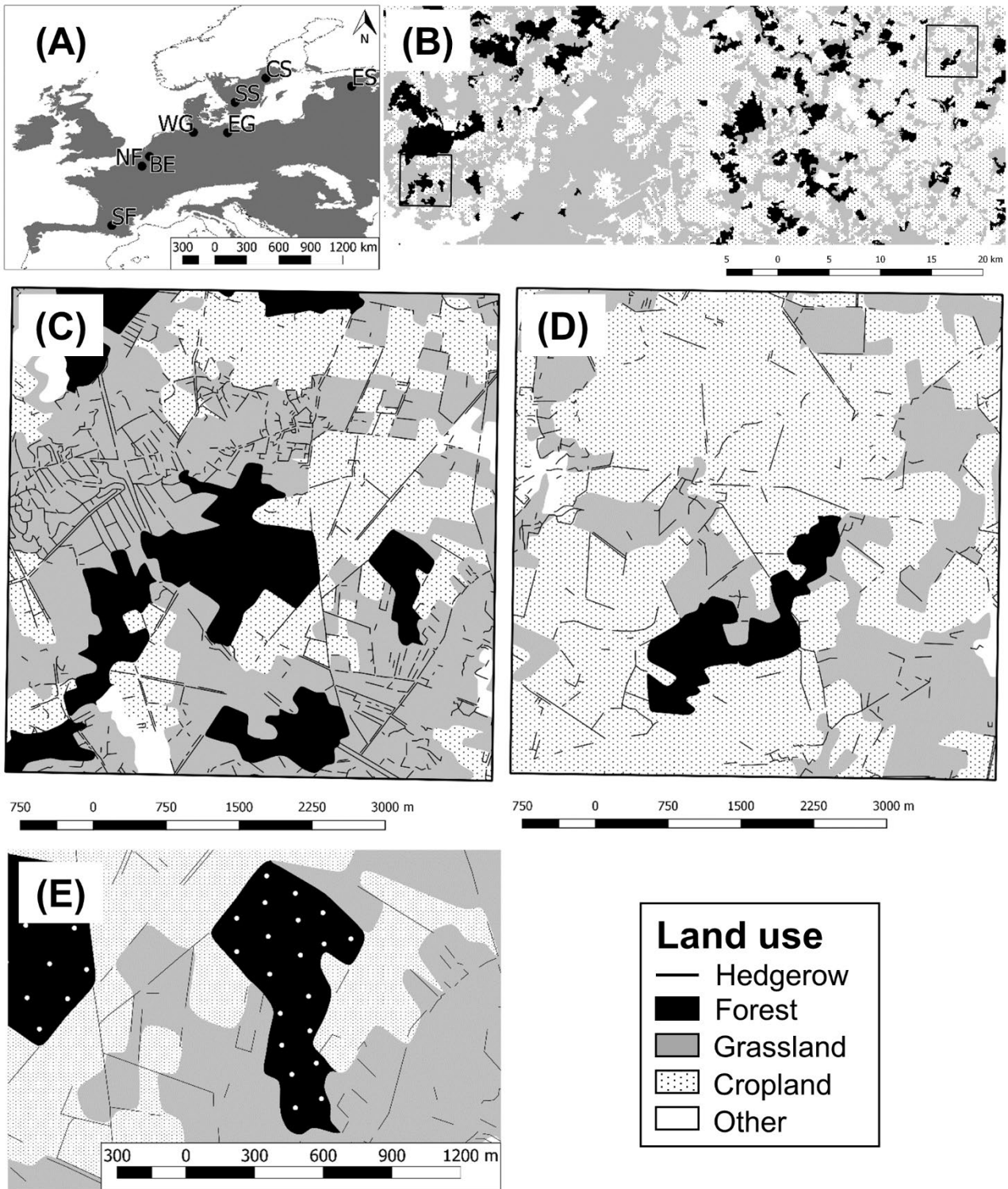
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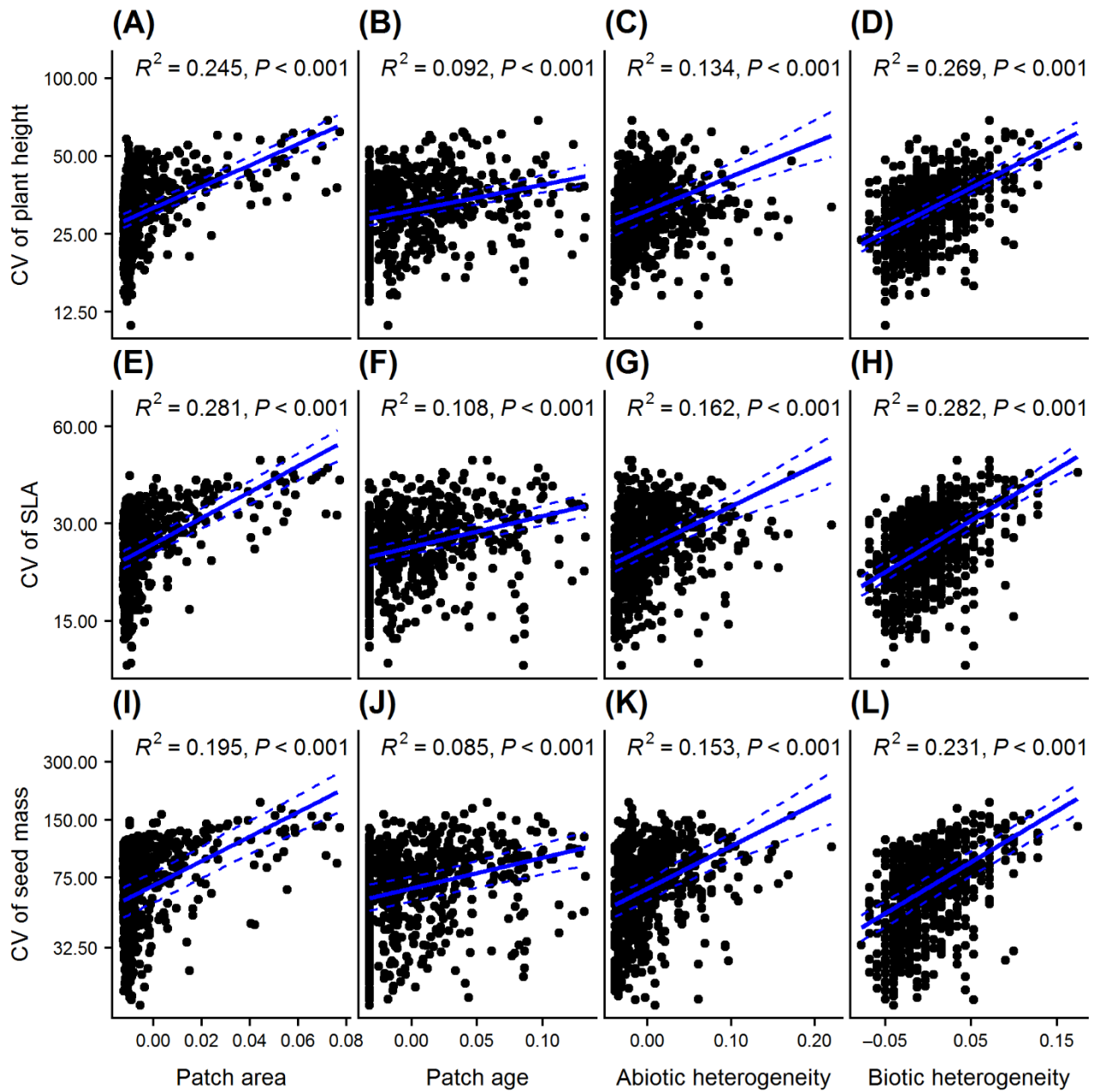


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627 **Fig. 1** (A) Continental scale: map showing the locations of the eight study regions, spanning a latitudinal gradient  
628 of *c.* 2500 km. The grey area represents the temperate forest biome of Europe (adapted from Olsen et al. 2001).  
629 Country codes: SF = Southern France, NF = Northern France, BE = Belgium, WG = Western Germany, EG =  
630 Eastern Germany, SS = Southern Sweden, CS = Central Sweden, ES = Estonia). (B) Landscape scale: each region  
631 comprised two 5 km × 5 km landscape windows, embedded in a fragmented agricultural matrix consisting of  
632 mainly croplands, grasslands/pastures and isolated forest patches (example from western Germany). (C)  
633 Landscape scale: ‘semi-fragmented system’ with higher amount of woody corridors and a more permeable  
634 landscape matrix. (D) Landscape scale: ‘highly-fragmented system’ with lower amount of woody corridors and a  
635 landscape matrix predominantly consisting of intensively managed croplands. (E) Patch scale: fragmented forest  
636 patch with the location of the sampling plots (white points) used for the vegetation surveys. This figure was partly  
637 adapted from Valdés et al. (2015).

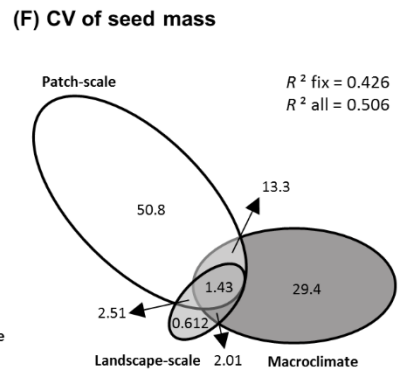
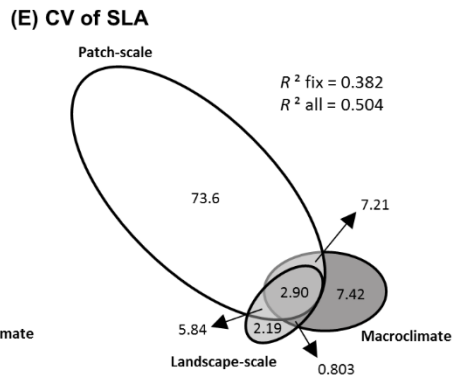
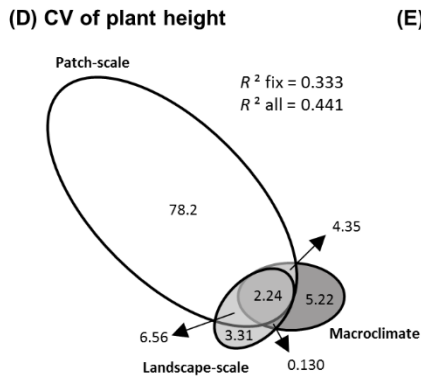
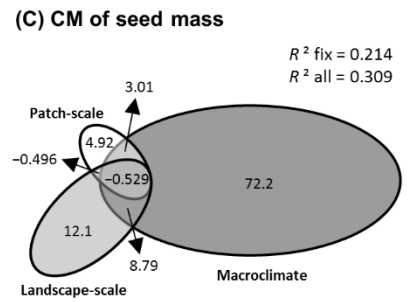
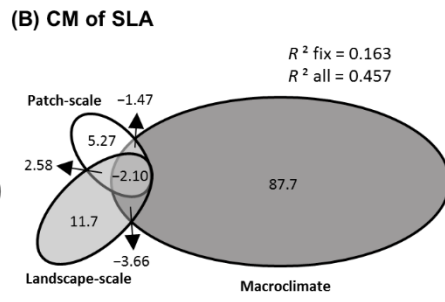
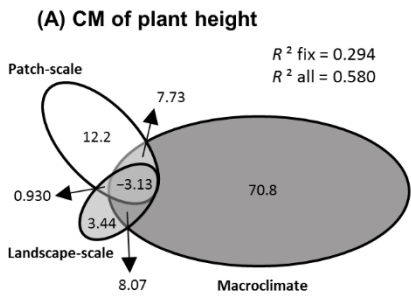
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640 **Fig. 2** Relationship between the community-level coefficient of variation (CV) of plant height (A-D), SLA (E-H)  
641 and seed mass (I-L), on the one hand, and patch area (A, E, I), patch age (B, F, J), abiotic patch heterogeneity  
642 (C, G, K) and biotic patch heterogeneity (D, H, L), on the other hand. The *blue line* denotes a linear mixed-  
643 effect model (LMM;  $P < 0.05$ ) with the predictor variables as fixed effect and ‘region’ as well as ‘window type’  
644 (nested within ‘region’) as random intercept terms. The *dashed line* represents a 95% confidence interval. All  
645 response variables (CV of plant height, CV of SLA and CV of seed mass) were transformed with natural  
646 logarithm, whereas predictor variables (patch area, patch age, abiotic heterogeneity and biotic heterogeneity) were  
647 standardized by subtracting the mean and dividing by the standard deviation (S.D.).

648



650 **Fig. 3** Results of the variation partitioning for the community-level mean (CM) plant height (A), SLA (B) and  
651 seed mass (C) as well as the community-level coefficient of variation (CV) for plant height (D), SLA (E) and seed  
652 mass (F) across the three groups of environmental variables (patch-, landscape- and macroclimatic scale). The  
653 amount of variation explained by pure and shared contributions of each variable group was calculated as a  
654 percentage of the total variation explained by the fixed factors in the global model (including the three groups of  
655 explanatory variables), and represented by ellipses with the ellipse area proportional to the percentage of variation  
656 explained. Values of marginal  $R^2$  ( $R_m^2$ ) and conditional  $R^2$  ( $R_c^2$ ) of the global models are shown for each response  
657 variable. Variation partitioning was based on a linear mixed-effect model (LMM) with the predictor variables as  
658 fixed effect and 'region' as well as 'window type' (nested within 'region') as random intercept terms. Note that  
659 these results strongly reflect the patterns shown in Fig. 2 and Table 1, based on the LMMs separately.

660

661 **Tables**

662 **Table 1** Results of the mixed model selection and averaging across the best candidate models relating the  
663 community-level mean (CM) and coefficient of variation (CV) of the studied plant traits (plant height, SLA and  
664 seed mass) to the 12 environmental variables. Values of Akaike Information Criterion (AIC), marginal  $R^2$  ( $R_m^2$ )  
665 and conditional  $R^2$  ( $R_c^2$ ) are shown for the best model. The values inside the table represent parameter estimates  
666  $\pm$  standard error, resulting from model averaging across all models with a  $\Delta\text{AIC} < 2$ . The significance of each  
667 predictor variable was obtained from a  $\chi^2$  test, and is indicated as: \*\*\*  $P < 0.001$ ; \*\*  $P < 0.01$ ; \*  $P < 0.05$ ; .  $P <$   
668 0.1, with  $n = 708$  forest patches. Blank spaces indicate that the variable was not included in the average model.

Explanatory variables	Plant height	SLA	Seed mass
<b>Community mean (CM)</b>	AIC = -588	AIC = -1870	AIC = 1238
	$R_m^2 = 0.310$	$R_m^2 = 0.096$	$R_m^2 = 0.184$
	$R_c^2 = 0.544$	$R_c^2 = 0.475$	$R_c^2 = 0.314$
Patch area (AREA)	$-0.006 \pm 0.007$	$-0.006 \pm 0.002$ *	$-0.046 \pm 0.024$ .
Patch age (AGE)	$-0.030 \pm 0.007$ ***	$0.002 \pm 0.003$	$0.034 \pm 0.025$
Abiotic heterogeneity (ABIO_H)	$-0.027 \pm 0.011$ *		
Biotic heterogeneity (BIO_H)	$-0.017 \pm 0.007$ *	$0.002 \pm 0.003$	$0.070 \pm 0.026$ **
Proximity index (PROX)		$0.004 \pm 0.002$ .	
Proportion of forest (F500)	$-0.016 \pm 0.010$ .	$-0.004 \pm 0.004$	$0.069 \pm 0.035$ *
Proportion of grassland (G500)	$0.018 \pm 0.010$ .	$-0.010 \pm 0.004$ *	$-0.092 \pm 0.037$ *
Proportion of hedgerows (H50)		$0.003 \pm 0.003$	$0.046 \pm 0.027$ .
Maximum temperature warmest month (MaTWm)	$-0.002 \pm 0.041$	$-0.008 \pm 0.016$	$-0.061 \pm 0.077$
Minimum temperature coldest month (MiTCm)	$0.085 \pm 0.034$ *	$0.026 \pm 0.017$	$-0.203 \pm 0.073$ **
Precipitation wettest month (PWm)	$-0.066 \pm 0.034$ *	$0.003 \pm 0.013$	$-0.031 \pm 0.060$
Precipitation driest month (PDm)	$0.105 \pm 0.047$ *	$0.029 \pm 0.015$ .	
<b>Community coefficient of variation (CV)</b>	AIC = -110	AIC = -324	AIC = 534
	$R_m^2 = 0.316$	$R_m^2 = 0.374$	$R_m^2 = 0.411$
	$R_c^2 = 0.439$	$R_c^2 = 0.511$	$R_c^2 = 0.501$
Patch area (AREA)	$0.036 \pm 0.009$ ***	$0.033 \pm 0.008$ ***	$0.050 \pm 0.015$ ***
Patch age (AGE)	$0.034 \pm 0.010$ ***	$0.035 \pm 0.008$ ***	$0.060 \pm 0.015$ ***
Abiotic heterogeneity (ABIO_H)	$0.047 \pm 0.027$ ***	$0.052 \pm 0.012$ ***	$0.093 \pm 0.022$ ***
Biotic heterogeneity (BIO_H)	$0.112 \pm 0.010$ ***	$0.102 \pm 0.009$ ***	$0.172 \pm 0.016$ ***
Proximity index (PROX)	$0.013 \pm 0.008$	$0.008 \pm 0.007$	$0.008 \pm 0.013$
Proportion of forest (F500)	$0.015 \pm 0.013$	$0.010 \pm 0.011$	$0.016 \pm 0.021$
Proportion of grassland (G500)	$0.026 \pm 0.014$ .	$0.015 \pm 0.012$	$-0.006 \pm 0.022$
Proportion of hedgerows (H50)	$-0.027 \pm 0.010$ **	$-0.024 \pm 0.009$ **	$-0.022 \pm 0.016$

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Maximum temperature warmest month (MaT <sub>Wm</sub> )	$-0.010 \pm 0.027$		$-0.124 \pm 0.041^{**}$
Minimum temperature coldest month (MiT <sub>Cm</sub> )	$0.020 \pm 0.027$	$-0.008 \pm 0.025$	
Precipitation wettest month (P <sub>Wm</sub> )	$-0.033 \pm 0.023$	$-0.035 \pm 0.023$	$-0.032 \pm 0.036$
Precipitation driest month (P <sub>Dm</sub> )	$0.016 \pm 0.031$	$-0.029 \pm 0.029$	$-0.048 \pm 0.046$

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