



HAL
open science

Functional trait variation of forest understorey plant communities across Europe

Thomas Vanneste, Alicia Valdés, Kris Verheyen, Michael P Perring, Markus Bernhardt-Römermann, Émilie Andrieu, Jörg Brunet, Sara A.O. Cousins, Marc Deconchat, Pallieter de Smedt, et al.

► To cite this version:

Thomas Vanneste, Alicia Valdés, Kris Verheyen, Michael P Perring, Markus Bernhardt-Römermann, et al.. Functional trait variation of forest understorey plant communities across Europe. *Basic and Applied Ecology*, 2019, 34, pp.1-14. 10.1016/j.baae.2018.09.004 . hal-02356900

HAL Id: hal-02356900

<https://hal.science/hal-02356900v1>

Submitted on 28 May 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3 Thomas Vanneste^{a,*}, Alicia Valdés^{b,1}, Kris Verheyen^a, Michael P. Perring^{a,c}, Markus Bernhardt-Römermann^d,
4 Emilie Andrieu^e, Jörg Brunet^f, Sara A. O. Cousins^g, Marc Deconchat^e, Pallieter De Smedt^a, Martin Diekmann^h,
5 Steffen Ehrmannⁱ, Thilo Heinken^j, Martin Hermy^k, Annette Kolb^h, Jonathan Lenoir^b, Jaan Liira^l, Tobias Naaf^m,
6 Taavi Paal^l, Monika Wulf^m, Guillaume Decocq^b and Pieter De Frenne^a

7 ^aForest & Nature Lab, Department of Environment, Faculty of Bioscience Engineering, Ghent University,
8 Geraardsbergsesteenweg 267, BE-9090 Gontrode-Melle, Belgium

9 ^bUR « Ecologie et Dynamique des Systèmes Anthropisés » (EDYSAN, UMR 7058 CNRS-UPJV), Jules Verne
10 University of Picardie, 1 Rue des Louvels, F-80037 Amiens, France

11 ^cEcosystem Restoration and Intervention Ecology (ERIE) Research Group, School of Biological Sciences, The
12 University of Western Australia, 35, Stirling Highway, Crawley WA 6009 Australia

13 ^dInstitute of Ecology and Evolution, Friedrich-Schiller-University Jena, Dornburger Str. 159, D-07743 Jena,
14 Germany

15 ^eUMR 1201 DYNAFOR, INRA, Chemin de Borde Rouge, CS 52627 F-31326 Castanet-Tolosan, France

16 ^fSouthern Sweden Research Centre, Swedish University of Agricultural Sciences, Box 49, SE-230 53 Alnarp,
17 Sweden

18 ^gBiogeography and Geomatics, Department of Physical Geography, Stockholm University, SE-106091
19 Stockholm, Sweden

20 ^hVegetation Ecology and Conservation Biology, Institute of Ecology, FB2, University of Bremen, Leobener Str.,
21 D-28359 Bremen, Germany

22 ⁱGeobotany, Faculty of Biology, University of Freiburg, Schänzlestr. 1, D-79104 Freiburg, Germany

23 ^jInstitute of Biochemistry and Biology, University of Potsdam, Maulbeerallee 3, D-14469 Potsdam, Germany

24 ^kDivision Forest, Nature and Landscape Research, University of Leuven (KU Leuven), Celestijnenlaan 200E,
25 BE-3000 Leuven, Belgium

26 ^lInstitute of Ecology and Earth Sciences, University of Tartu, Lai 40, EE-51005 Tartu, Estonia

27 ^mCentre for Agricultural Landscape Research (ZALF), Eberswalder Strasse 84, D-15374 Müncheberg, Germany

28 * Corresponding author. Tel.: +32 (0)9 264 90 30.

29 E-mail address: Thomas.Vanneste@UGent.be.

30 ¹Present address: Department of Ecology, Environment and Plant Sciences, Stockholm University, Svante
31 Arrhenius väg 20 A, SE-106 91 Stockholm, Sweden

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 ± 15 (mean \pm S.D.)
141 forest patches per window in the eight highly-fragmented landscapes and 52 ± 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 ± 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 D³ (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 18th century, 19th century, 20th
199 century and the 21st 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% (χ^2 test; $P < 0.001$), 9.60%
242 (χ^2 test; $P = 0.002$) and 18.4% (χ^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% (χ^2 test; $P < 0.001$), 37.4% (χ^2 test; $P < 0.001$) and 41.1% (χ^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

401 **Acknowledgements**

402 The data for this study were collected within the framework of the ERA-Net BiodivERsA project smallFOREST,
403 with the national funders ANR (France), MINECO (Spain), FORMAS (Sweden), ETAG (Estonia), DFG
404 (Germany) and BELSPO (Belgium) as part of the 2011 BiodivERsA call for research proposals. TV was funded
405 by a BOF grant [no. 01N02817] from Ghent University. PDF was supported by the European Research Council
406 through the FORMICA project [ERC Starting Grant no. 757833], and KV as well as MP through the

407 PASTFORWARD project [ERC Consolidator Grant no. 614839]. We thank Emilie Gallet-Moron for her help
408 in the data management and Safaa Wasof for assistance with statistical analyses.

409

410 Appendix A. Supplementary data

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

412

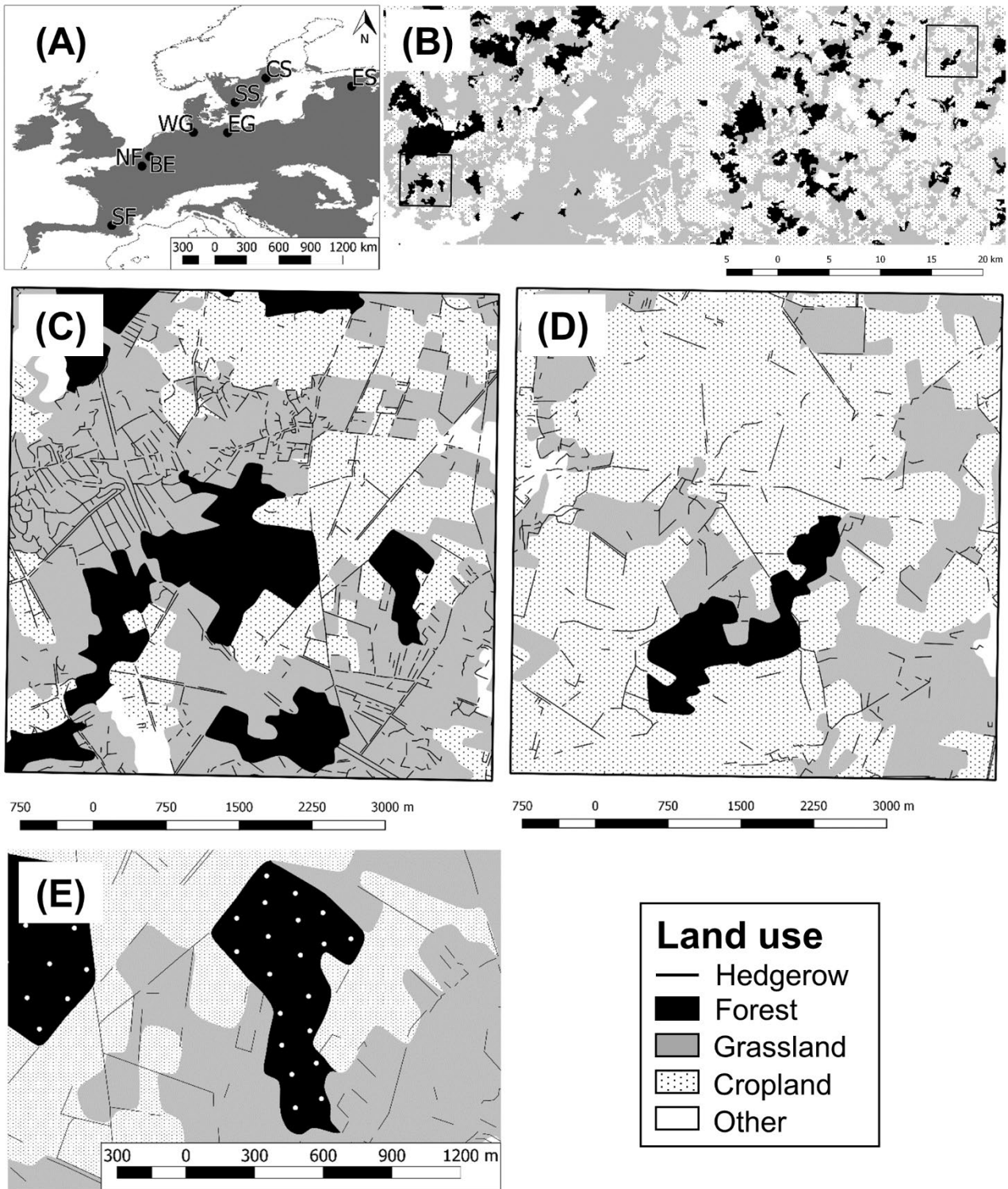
413 References

- 414 Albert, C. H., Grassein, F., Schurr, F. M., Vieilledent, G., & Violle, C. (2011). When and how should
415 intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology,*
416 *Evolution and Systematics*, *13*(3), 217-225. doi:<http://dx.doi.org/10.1016/j.ppees.2011.04.003>
- 417 Albert, C. H., Thuiller, W., Yoccoz, N. G., Douzet, R., Aubert, S., & Lavorel, S. (2010). A multi-trait approach
418 reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits.
419 *Functional Ecology*, *24*(6), 1192-1201. doi:10.1111/j.1365-2435.2010.01727.x
- 420 Ampoorter, E., Selvi, F., Auge, H., Baeten, L., Berger, S., Carrari, E., . . . Verheyen, K. (2016). Driving
421 mechanisms of overstorey-understorey diversity relationships in European forests. *Perspectives in Plant*
422 *Ecology, Evolution and Systematics*, *19*(Supplement C), 21-29.
423 doi:<https://doi.org/10.1016/j.ppees.2016.02.001>
- 424 Barton, K. (2017). MuMIn: Multi-Model Inference. R package version 1.40.0. Retrieved from [https://CRAN.R-](https://CRAN.R-project.org/package=MuMIn)
425 [project.org/package=MuMIn](https://CRAN.R-project.org/package=MuMIn)
- 426 Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4.
427 *Journal of Statistical Software*, *67*(1), 1-48.
- 428 Bernhardt-Römermann, M., Gray, A., Vanbergen, A. J., Bergès, L., Böhner, A., Brooker, R. W., . . . Stadler, J.
429 (2011). Functional traits and local environment predict vegetation responses to disturbance: a pan-
430 European multi-site experiment. *Journal of Ecology*, *99*(3), 777-787. doi:10.1111/j.1365-
431 2745.2011.01794.x
- 432 Brunet, J., Valtinat, K., Mayr, M. L., Felton, A., Lindbladh, M., & Bruun, H. H. (2011). Understorey succession
433 in post-agricultural oak forests: Habitat fragmentation affects forest specialists and generalists differently.
434 *Forest Ecology and Management*, *262*(9), 1863-1871. doi:<http://doi.org/10.1016/j.foreco.2011.08.007>
- 435 Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-*
436 *theoretic approach*: Springer-Verlag New York.
- 437 Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in
438 behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and*
439 *Sociobiology*, *65*(1), 23-35. doi:10.1007/s00265-010-1029-6
- 440 Büttner, G. (2014). CORINE Land Cover and Land Cover Change Products. In I. Manakos & M. Braun (Eds.),
441 *Land Use and Land Cover Mapping in Europe: Practices & Trends* (pp. 55-74). Dordrecht: Springer
442 Netherlands.
- 443 Chao, A., Colwell, R. K., Lin, C.-W., & Gotelli, N. J. (2009). Sufficient sampling for asymptotic minimum species
444 richness estimators. *Ecology*, *90*(4), 1125-1133. doi:10.1890/07-2147.1
- 445 Coomes, D. A., & Grubb, P. J. (2003). Colonization, tolerance, competition and seed-size variation within
446 functional groups. *Trends in Ecology & Evolution*, *18*(6), 283-291. doi:[https://doi.org/10.1016/S0169-](https://doi.org/10.1016/S0169-5347(03)00072-7)
447 [5347\(03\)00072-7](https://doi.org/10.1016/S0169-5347(03)00072-7)
- 448 de Bello, F., Lavorel, S., Lavergne, S., Albert, C. H., Boulangeat, I., Mazel, F., & Thuiller, W. (2013).
449 Hierarchical effects of environmental filters on the functional structure of plant communities: a case
450 study in the French Alps. *Ecography*, *36*(3), 393-402. doi:10.1111/j.1600-0587.2012.07438.x
- 451 De Frenne, P., Baeten, L., Graae, B. J., Brunet, J., Wulf, M., Orczewska, A., . . . Verheyen, K. (2011).
452 Interregional variation in the floristic recovery of post-agricultural forests. *Journal of Ecology*, *99*(2), 600-
453 609. doi:10.1111/j.1365-2745.2010.01768.x

- 454 De Frenne, P., Graae, B. J., Rodríguez-Sánchez, F., Kolb, A., Chabrierie, O., Decocq, G., . . . Verheyen, K.
 455 (2013). Latitudinal gradients as natural laboratories to infer species' responses to temperature. *Journal*
 456 *of Ecology*, *101*(3), 784-795. doi:10.1111/1365-2745.12074
- 457 De Frenne, P., Rodríguez-Sánchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M., . . . Verheyen,
 458 K. (2013). Microclimate moderates plant responses to macroclimate warming. *Proceedings of the*
 459 *National Academy of Sciences*, *110*(46), 18561-18565.
- 460 Decocq, G., Andrieu, E., Brunet, J., Chabrierie, O., De Frenne, P., De Smedt, P., . . . Wulf, M. (2016).
 461 Ecosystem Services from Small Forest Patches in Agricultural Landscapes. *Current Forestry Reports*,
 462 *2*(1), 30-44. doi:10.1007/s40725-016-0028-x
- 463 Diaz, S., Cabido, M., & Casanoves, F. (1998). Plant functional traits and environmental filters at a regional scale.
 464 *Journal of Vegetation Science*, *9*(1), 113-122. doi:10.2307/3237229
- 465 Diaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., . . . Zak, M. R. (2004).
 466 The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*,
 467 *15*(3), 295-304. doi:10.1111/j.1654-1103.2004.tb02266.x
- 468 Dupré, C., & Ehrlén, J. (2002). Habitat configuration, species traits and plant distributions. *Journal of Ecology*,
 469 *90*(5), 796-805. doi:10.1046/j.1365-2745.2002.00717.x
- 470 Dwyer, L. M., & Merriam, G. (1981). Influence of Topographic Heterogeneity on Deciduous Litter
 471 Decomposition. *Oikos*, *37*(2), 228-237. doi:10.2307/3544470
- 472 Ehrmann, S., Ruyts, S. C., Scherer-Lorenzen, M., Bauhus, J., Brunet, J., Cousins, S. A. O., . . . Liira, J. (2018).
 473 Habitat properties are key drivers of *Borrelia burgdorferi* (s.l.) prevalence in *Ixodes ricinus* populations
 474 of deciduous forest fragments. *Parasites & Vectors*, *11*(1), 23. doi:10.1186/s13071-017-2590-x
- 475 Favre-Bac, L., Mony, C., Burel, F., Seimandi-Corda, G., & Ernoult, A. (2017). Connectivity drives the functional
 476 diversity of plant dispersal traits in agricultural landscapes: the example of ditch metacommunities.
 477 *Landscape Ecology*, *32*(10), 2029-2040. doi:10.1007/s10980-017-0564-1
- 478 Fitter, A. H., & Peat, H. J. (1994). The Ecological Flora Database. *Journal of Ecology*, *82*, 415-425.
- 479 Flinn, K. M., & Vellend, M. (2005). Recovery of forest plant communities in post-agricultural landscapes.
 480 *Frontiers in Ecology and the Environment*, *3*(5), 243-250. doi:10.1890/1540-
 481 9295(2005)003[0243:ROFPCI]2.0.CO;2
- 482 Förster, A., Becker, T., Gerlach, A., Meesenburg, H., & Leuschner, C. (2017). Long-term change in understorey
 483 plant communities of conventionally managed temperate deciduous forests: effects of nitrogen
 484 deposition and forest management. *Journal of Vegetation Science*, *28*(4), 747-761.
 485 doi:10.1111/jvs.12537
- 486 Garnier, E., Laurent, G., Bellmann, A., Debain, S., Berthelie, P., Ducout, B., . . . Navas, M. L. (2001).
 487 Consistency of species ranking based on functional leaf traits. *New Phytologist*, *152*(1), 69-83.
 488 doi:10.1046/j.0028-646x.2001.00239.x
- 489 Gilliam, F. S. (2007). The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems.
 490 *Bioscience*, *57*(10), 845-858. doi:10.1641/B571007
- 491 Graae, B. J., Vandvik, V., Armbruster, W. S., Eiserhardt, W. L., Svenning, J.-C., Hylander, K., . . . Lenoir, J.
 492 (2017). Stay or go - how topographic complexity influences alpine plant population and community
 493 responses to climate change. *Perspectives in Plant Ecology, Evolution and Systematics*.
 494 doi:<https://doi.org/10.1016/j.ppees.2017.09.008>
- 495 Hansen, A. J., Neilson, R. P., Dale, V. H., Flather, C. H., Iverson, L. R., Currie, D. J., . . . Bartlein, P. J. (2001).
 496 Global Change in Forests: Responses of Species, Communities, and Biomes: Interactions between
 497 climate change and land use are projected to cause large shifts in biodiversity. *Bioscience*, *51*(9), 765-
 498 779. doi:10.1641/0006-3568(2001)051[0765:GCIFRO]2.0.CO;2
- 499 Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated
 500 climate surfaces for global land areas. *International Journal of Climatology*, *25*(15), 1965-1978.
 501 doi:10.1002/joc.1276
- 502 Hintze, C., Heydel, F., Hoppe, C., Cunze, S., König, A., & Tackenberg, O. (2013). D-3: The Dispersal and
 503 Diaspore Database - Baseline data and statistics on seed dispersal. *Perspectives in Plant Ecology*
 504 *Evolution and Systematics*, *15*(3), 180-192. doi:DOI 10.1016/j.ppees.2013.02.001
- 505 Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B., & Hermy, M. (2002). Possible effects of
 506 habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters*, *5*(4), 525-
 507 530. doi:10.1046/j.1461-0248.2002.00346.x
- 508 Jamoneau, A., Sonnier, G., Chabrierie, O., Closset-Kopp, D., Saguez, R., Gallet-Moron, E., & Decocq, G. (2011).
 509 Drivers of plant species assemblages in forest patches among contrasted dynamic agricultural landscapes.
 510 *Journal of Ecology*, *99*(5), 1152-1161. doi:10.1111/j.1365-2745.2011.01840.x

- 511 Keddy, P. A. (1992). Assembly and Response Rules - 2 Goals for Predictive Community Ecology. *Journal of*
512 *Vegetation Science*, 3(2), 157-164. doi:Doi 10.2307/3235676
- 513 Kirby, K. J., Bines, T., Burn, A., Mackintosh, J., Pitkin, P., & Smith, I. (1986). Seasonal and observer differences
514 in vascular plant records from British woodlands. *journal of ecology*, 74(1), 123-131.
515 doi:10.2307/2260353
- 516 Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., . . . Peco, B. (2008).
517 The LEDA Traitbase: A database of life-history traits of Northwest European flora. *Journal of Ecology*,
518 96, 1266-1274.
- 519 Kolk, J., & Naaf, T. (2015). Herb layer extinction debt in highly fragmented temperate forests - Completely paid
520 after 160 years? *Biological Conservation*, 182, 164-172.
521 doi:<https://doi.org/10.1016/j.biocon.2014.12.004>
- 522 Kraft, N. J. B., Godoy, O., & Levine, J. M. (2015). Plant functional traits and the multidimensional nature of
523 species coexistence. *Proceedings of the National Academy of Sciences*, 112(3), 797-802.
- 524 Kuznetsova, A., Brockhoff, P., & Christensen, R. (2017). lmerTest Package: Tests in Linear Mixed Effects
525 Models. *Journal of Statistical Software*, 82(13), 1-26. doi: 10.18637/jss.v082.i13
- 526 Lamanna, C., Blonder, B., Violle, C., Kraft, N. J. B., Sandel, B., Šimová, I., . . . Enquist, B. J. (2014). Functional
527 trait space and the latitudinal diversity gradient. *Proceedings of the National Academy of Sciences of the*
528 *United States of America*, 111(38), 13745-13750. doi:10.1073/pnas.1317722111
- 529 Legendre, P., & Legendre, L. (2006). *Numerical ecology*. Amsterdam: Elsevier.
- 530 Lenoir, J., Hattab, T., & Pierre, G. (2017). Climatic microrefugia under anthropogenic climate change:
531 implications for species redistribution. *Ecography*, 40(2), 253-266. doi:10.1111/ecog.02788
- 532 Lidestav, G., & Berg Lejon, S. (2013). Harvesting and silvicultural activities in Swedish family forestry - behavior
533 changes from a gender perspective. *Scandinavian Journal of Forest Research*, 28(2), 136-142.
534 doi:10.1080/02827581.2012.701324
- 535 Liira, J., Jürjendal, I., & Paal, J. (2014). Do forest plants conform to the theory of island biogeography: the case
536 study of bog islands. *Biodiversity and Conservation*, 23(4), 1019-1039. doi:10.1007/s10531-014-0650-5
- 537 Liira, J., & Paal, T. (2013). Do forest-dwelling plant species disperse along landscape corridors? *Plant Ecology*,
538 214(3), 455-470. doi:10.1007/s11258-013-0182-1
- 539 Lõhmus, A., & Kraut, A. (2010). Stand structure of hemiboreal old-growth forests: Characteristic features,
540 variation among site types, and a comparison with FSC-certified mature stands in Estonia. *Forest Ecology*
541 *and Management*, 260(1), 155-165. doi:<https://doi.org/10.1016/j.foreco.2010.04.018>
- 542 Lõhmus, K., Paal, T., & Liira, J. (2014). Long-term colonization ecology of forest-dwelling species in a
543 fragmented rural landscape - dispersal versus establishment. *Ecology and Evolution*, 4(15), 3113-3126.
544 doi:10.1002/ece3.1163
- 545 McGarigal, K., Cushman, S. A., & Ene, E. (2002). FRAGSTATS v4: Spatial Pattern Analysis Program for
546 Categorical and Continuous Maps.
- 547 Moles, A. T., Ackerly, D. D., Webb, C. O., Tweddle, J. C., Dickie, J. B., Pitman, A. J., & Westoby, M. (2005).
548 Factors that shape seed mass evolution. *Proceedings of the National Academy of Sciences of the United*
549 *States of America*, 102(30), 10540-10544.
- 550 Moles, A. T., Warton, D. I., Warman, L., Swenson, N. G., Laffan, S. W., Zanne, A. E., . . . Leishman, M. R.
551 (2009). Global patterns in plant height. *Journal of Ecology*, 97(5), 923-932. doi:10.1111/j.1365-
552 2745.2009.01526.x
- 553 Moles, A. T., Wright, I. J., Pitman, A. J., Murray, B. R., & Westoby, M. (2009). Is there a latitudinal gradient in
554 seed production? *Ecography*, 32(1), 78-82. doi:10.1111/j.1600-0587.2008.05613.x
- 555 Mori, A. S., Furukawa, T., & Sasaki, T. (2013). Response diversity determines the resilience of ecosystems to
556 environmental change. *Biological Reviews*, 88(2), 349-364. doi:10.1111/brv.12004
- 557 Naaf, T., & Kolk, J. (2015). Colonization credit of post-agricultural forest patches in NE Germany remains 130-
558 230 years after reforestation. *Biological Conservation*, 182, 155-163.
559 doi:<https://doi.org/10.1016/j.biocon.2014.12.002>
- 560 Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R² from generalized linear
561 mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133-142. doi:10.1111/j.2041-
562 210x.2012.00261.x
- 563 Nilsson, M. C., & Wardle, D. A. (2005). Understorey vegetation as a forest ecosystem driver: evidence from the
564 northern Swedish boreal forest. *Frontiers in Ecology and the Environment*, 3(8), 421-428. doi:Doi
565 10.2307/3868658
- 566 Opedal, Ø. H., Armbruster, W. S., & Graae, B. J. (2015). Linking small-scale topography with microclimate,
567 plant species diversity and intra-specific trait variation in an alpine landscape. *Plant Ecology & Diversity*,
568 8(3), 305-315. doi:10.1080/17550874.2014.987330

- 569 Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology,*
570 *Evolution, and Systematics*, 37(1), 637-669. doi:10.1146/annurev.ecolsys.37.091305.110100
- 571 Perring, M. P., Bernhardt-Römermann, M., Baeten, L., Midolo, G., Blondeel, H., Depauw, L., . . . Verheyen,
572 K. (2018). Global environmental change effects on plant community composition trajectories depend
573 upon management legacies. *Global Change Biology*, 24(4), 1722-1740 doi:10.1111/gcb.14030
- 574 Price, J., Tamme, R., Gazol, A., de Bello, F., Takkis, K., Uria-Diez, J., . . . Pärtel, M. (2017). Within-community
575 environmental variability drives trait variability in species-rich grasslands. *Journal of Vegetation Science*,
576 28(2), 303-312. doi:10.1111/jvs.12487
- 577 Renton, M., Shackelford, N., & Standish, R. J. (2012). Habitat restoration will help some functional plant types
578 persist under climate change in fragmented landscapes. *Global Change Biology*, 18(6), 2057-2070.
579 doi:10.1111/j.1365-2486.2012.02677.x
- 580 Roy, V., & de Blois, S. (2008). Evaluating hedgerow corridors for the conservation of native forest herb diversity.
581 *Biological Conservation*, 141(1), 298-307. doi:<http://doi.org/10.1016/j.biocon.2007.10.003>
- 582 Royal Botanic Gardens Kew. (2008). *Seed Information Database (SID)*.
- 583 Sala, O. E., Stuart Chapin, F., Iii, Armesto, J. J., Berlow, E., Bloomfield, J., . . . Wall, D. H. (2000). Global
584 Biodiversity Scenarios for the Year 2100. *Science*, 287(5459), 1770.
- 585 Sercu, B. K., Baeten, L., van Coillie, F., Martel, A., Lens, L., Verheyen, K., & Bonte, D. (2017). How tree
586 species identity and diversity affect light transmittance to the understory in mature temperate forests.
587 *Ecology and Evolution*, 4(24), 10861-10870. doi:10.1002/ece3.3528
- 588 Skov, F., & Svenning, J.-C. (2004). Potential impact of climatic change on the distribution of forest herbs in
589 Europe. *Ecography*, 27(3), 366-380. doi:10.1111/j.0906-7590.2004.03823.x
- 590 Stark, J., Lehman, R., Crawford, L., Enquist, B. J., & Blonder, B. (2017). Does environmental heterogeneity
591 drive functional trait variation? A test in montane and alpine meadows. *Oikos*, 126(11), 1650-1659.
592 doi:10.1111/oik.04311
- 593 Tamme, R., Hiiesalu, I., Laanisto, L., Szava-Kovats, R., xe, & rtel, M. (2010). Environmental heterogeneity,
594 species diversity and co-existence at different spatial scales. *Journal of Vegetation Science*, 21(4), 796-
595 801.
- 596 Valdés, A., Lenoir, J., Gallet-Moron, E., Andrieu, E., Brunet, J., Chabrierie, O., . . . Decocq, G. (2015). The
597 contribution of patch-scale conditions is greater than that of macroclimate in explaining local plant
598 diversity in fragmented forests across Europe. *Global Ecology and Biogeography*, 24(9), 1094-1105.
599 doi:10.1111/geb.12345
- 600 Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., & Foster, D. R. (2003). Response of forest plant species
601 to land-use change: a life-history trait-based approach. *Journal of Ecology*, 91(4), 563-577.
602 doi:10.1046/j.1365-2745.2003.00789.x
- 603 Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., . . . Messier, J. (2012). The return
604 of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution*, 27(4),
605 244-252. doi:<https://doi.org/10.1016/j.tree.2011.11.014>
- 606 Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept
607 of trait be functional! *Oikos*, 116(5), 882-892. doi:10.1111/j.0030-1299.2007.15559.x
- 608 Violle, C., Reich, P. B., Pacala, S. W., Enquist, B. J., & Kattge, J. (2014). The emergence and promise of
609 functional biogeography. *Proceedings of the National Academy of Sciences*, 111(38), 13690-13696.
- 610 Walther, G.-R. (2010). Community and ecosystem responses to recent climate change. *Philosophical*
611 *Transactions of the Royal Society B: Biological Sciences*, 365(1549), 2019.
- 612 Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199(2), 213-227.
613 doi:10.1023/A:1004327224729
- 614 Wright, D. H. (1983). Species-Energy Theory: An Extension of Species-Area Theory. *Oikos*, 41(3), 496-506.
615 doi:10.2307/3544109
- 616 Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., . . . Villar, R. (2004). The
617 worldwide leaf economics spectrum. *Nature*, 428, 821. doi:10.1038/nature02403
- 618 Wulf, M., & Kolk, J. (2014). Plant species richness of very small forests related to patch configuration, quality,
619 heterogeneity and history. *Journal of Vegetation Science*, 25(5), 1267-1277. doi:10.1111/jvs.12172
- 620 Zobel, M. (1997). The relative of species pools in determining plant species richness: an alternative explanation
621 of species coexistence? *Trends in Ecology & Evolution*, 12(7), 266-269.
622 doi:[https://doi.org/10.1016/S0169-5347\(97\)01096-3](https://doi.org/10.1016/S0169-5347(97)01096-3)

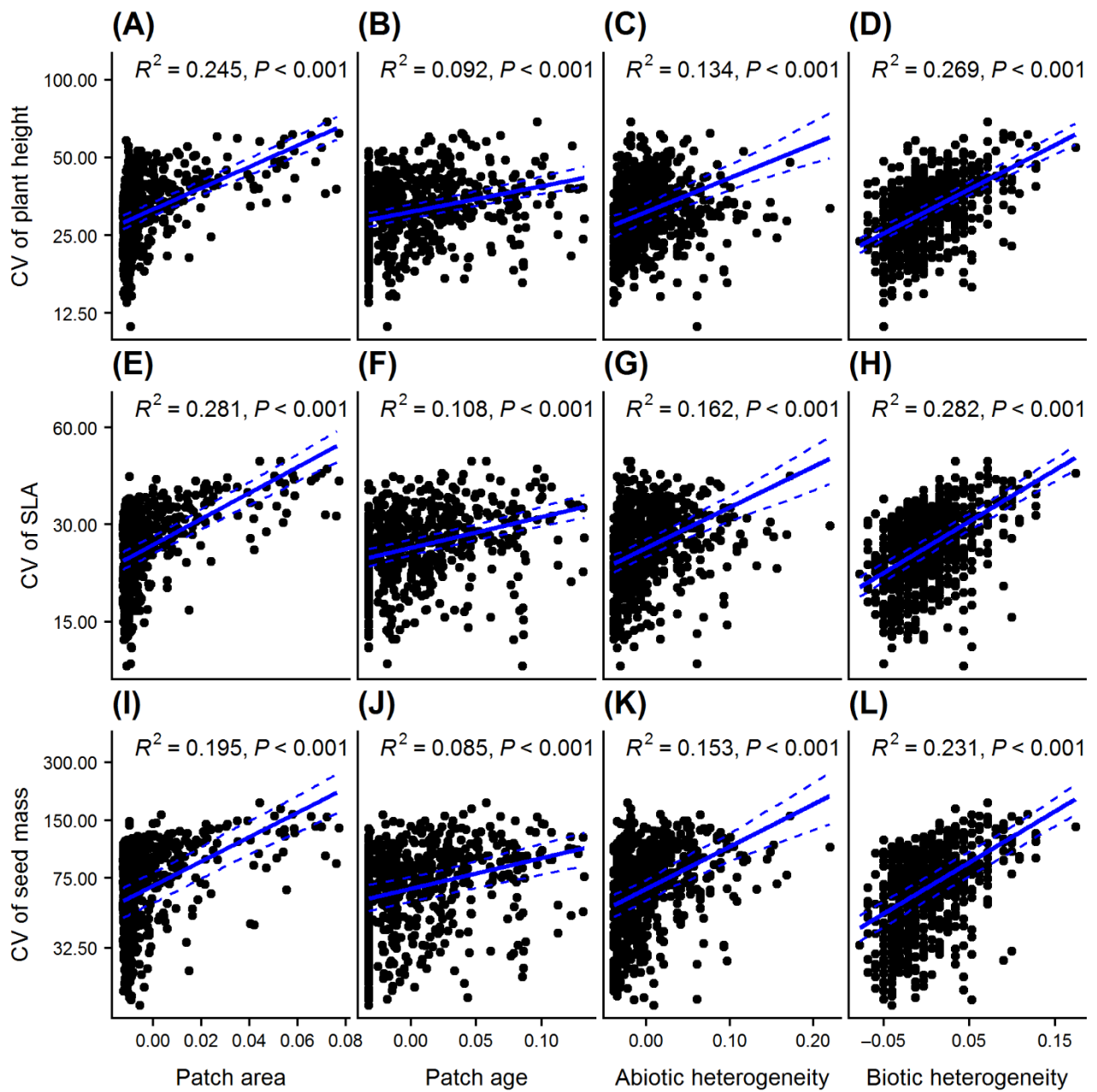


625

626

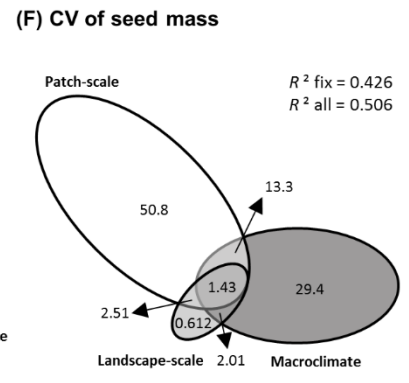
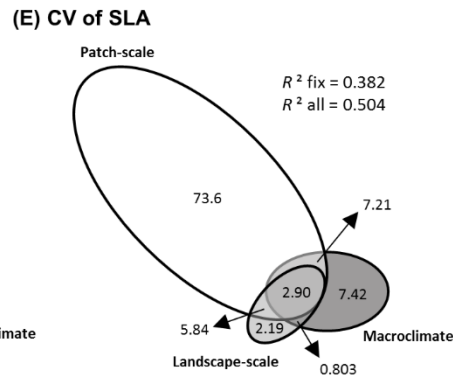
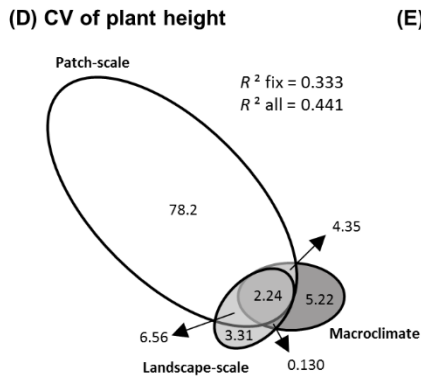
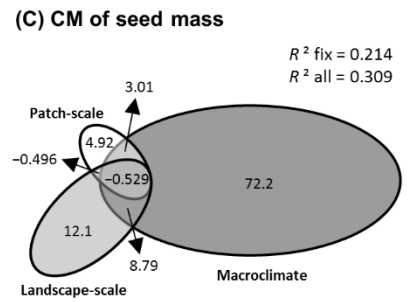
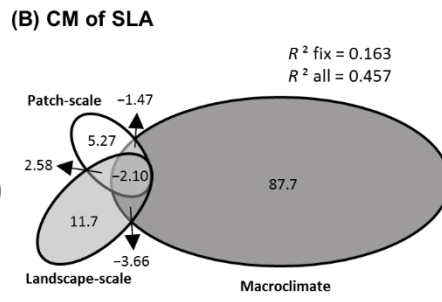
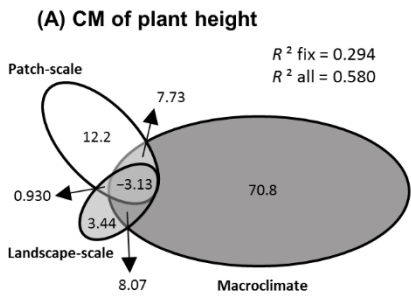
627 **Fig. 1** (A) Continental scale: map showing the locations of the eight study regions, spanning a latitudinal gradient
628 of *c.* 2500 km. The grey area represents the temperate forest biome of Europe (adapted from Olsen et al. 2001).
629 Country codes: SF = Southern France, NF = Northern France, 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).

638



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 χ^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
Community mean (CM)	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 ± 0.007	-0.006 ± 0.002 *	-0.046 ± 0.024 .
Patch age (AGE)	-0.030 ± 0.007 ***	0.002 ± 0.003	0.034 ± 0.025
Abiotic heterogeneity (ABIO_H)	-0.027 ± 0.011 *		
Biotic heterogeneity (BIO_H)	-0.017 ± 0.007 *	0.002 ± 0.003	0.070 ± 0.026 **
Proximity index (PROX)		0.004 ± 0.002 .	
Proportion of forest (F500)	-0.016 ± 0.010 .	-0.004 ± 0.004	0.069 ± 0.035 *
Proportion of grassland (G500)	0.018 ± 0.010 .	-0.010 ± 0.004 *	-0.092 ± 0.037 *
Proportion of hedgerows (H50)		0.003 ± 0.003	0.046 ± 0.027 .
Maximum temperature warmest month (MaTWm)	-0.002 ± 0.041	-0.008 ± 0.016	-0.061 ± 0.077
Minimum temperature coldest month (MiTCm)	0.085 ± 0.034 *	0.026 ± 0.017	-0.203 ± 0.073 **
Precipitation wettest month (PWm)	-0.066 ± 0.034 *	0.003 ± 0.013	-0.031 ± 0.060
Precipitation driest month (PDm)	0.105 ± 0.047 *	0.029 ± 0.015 .	
Community coefficient of variation (CV)	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 ± 0.009 ***	0.033 ± 0.008 ***	0.050 ± 0.015 ***
Patch age (AGE)	0.034 ± 0.010 ***	0.035 ± 0.008 ***	0.060 ± 0.015 ***
Abiotic heterogeneity (ABIO_H)	0.047 ± 0.027 ***	0.052 ± 0.012 ***	0.093 ± 0.022 ***
Biotic heterogeneity (BIO_H)	0.112 ± 0.010 ***	0.102 ± 0.009 ***	0.172 ± 0.016 ***
Proximity index (PROX)	0.013 ± 0.008	0.008 ± 0.007	0.008 ± 0.013
Proportion of forest (F500)	0.015 ± 0.013	0.010 ± 0.011	0.016 ± 0.021
Proportion of grassland (G500)	0.026 ± 0.014 .	0.015 ± 0.012	-0.006 ± 0.022
Proportion of hedgerows (H50)	-0.027 ± 0.010 **	-0.024 ± 0.009 **	-0.022 ± 0.016

Maximum temperature warmest month (MaT _{Wm})	-0.010 ± 0.027		$-0.124 \pm 0.041^{**}$
Minimum temperature coldest month (MiT _{Cm})	0.020 ± 0.027	-0.008 ± 0.025	
Precipitation wettest month (PW _m)	-0.033 ± 0.023	-0.035 ± 0.023	-0.032 ± 0.036
Precipitation driest month (PD _m)	0.016 ± 0.031	-0.029 ± 0.029	-0.048 ± 0.046

669
670

