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Context matters: the landscape matrix determines the population genetic structure of temperate forest herbs across Europe

Tobias Naaf, Jannis Till Feigs, Siyu Huang, Jörg Brunet, Sara Cousins, Guillaume Decocq, Pieter de Frenne, Martin Diekmann, Sanne Govaert, Per-Ola Hedwall, et al.

► To cite this version:

Tobias Naaf, Jannis Till Feigs, Siyu Huang, Jörg Brunet, Sara Cousins, et al.. Context matters: the landscape matrix determines the population genetic structure of temperate forest herbs across Europe. *Landscape Ecology*, 2022, 37 (5), pp.1365-1384. 10.1007/s10980-021-01376-7. hal-03667398

HAL Id: hal-03667398

<https://hal.science/hal-03667398v1>

Submitted on 4 Oct 2022

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1 **Context matters: the landscape matrix determines the population genetic structure of temperate**
2 **forest herbs across Europe**

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24 **Abstract**

25 Context. Plant populations in agricultural landscapes are mostly fragmented and their functional
26 connectivity often depends on seed and pollen dispersal by animals. However, little is known about
27 how the interactions of seed and pollen dispersers with the agricultural matrix translate into gene
28 flow among plant populations.

29 Objectives. We aimed to identify effects of the landscape structure on the genetic diversity within,
30 and the genetic differentiation among, spatially isolated populations of three temperate forest
31 herbs. We asked, whether different arable crops have different effects, and whether the orientation
32 of linear landscape elements relative to the gene dispersal direction matters.

33 Methods. We analysed the species' population genetic structures in seven agricultural landscapes
34 across temperate Europe using microsatellite markers. These were modelled as a function of
35 landscape composition and configuration, which we quantified in buffer zones around, and in
36 rectangular landscape strips between, plant populations.

37 Results. Landscape effects were diverse and often contrasting between species, reflecting their
38 association with different pollen- or seed dispersal vectors. Differentiating crop types rather than
39 lumping them together yielded higher proportions of explained variation. Some linear landscape
40 elements had both a channelling and hampering effect on gene flow, depending on their
41 orientation.

42 Conclusions. Landscape structure is a more important determinant of the species' population
43 genetic structure than habitat loss and fragmentation *per se*. Landscape planning with the aim to
44 enhance the functional connectivity among spatially isolated plant populations should consider that
45 even species of the same ecological guild might show distinct responses to the landscape structure.

46

47

48 **Keywords**

49 arable crops; dispersal vectors; functional connectivity; genetic differentiation; genetic diversity;
50 linear landscape elements

51 **Declarations**

52

53 **Funding**

54 This research was mainly funded by the German Research Foundation (research grants NA 1067/2-1,
55 HO 4742/2-1 and KR 5060/1-1). This includes the research work of JTF, KK, SH, SIJH and TN. CM, PDF,
56 and PV were supported by the European Research Council (ERC Starting Grant FORMICA no. 757833,
57 2018). SG received funding from the Research Foundation Flanders (FWO) (project G0H1517N). TV
58 was funded by the Special Research Fund (BOF) from Ghent University (grant number 01N02817).
59 SAOC was supported by the Bolin Centre for Climate Research. JLi was supported by the Estonian
60 Research Competency Council grant PRG1223 and the European Regional Development Fund
61 EcolChange.

62

63 **Conflicts of interest**

64 We have no conflict of interest to declare.

65

66 **Ethics approval**

67 We have no ethical concerns to declare.

68

69 **Consent to participate**

70 All authors contributed to this study and this manuscript of their own accord.

71

72 **Consent for publication**

73 All authors agree with the content of this manuscript and its publication in Landscape Ecology.

74

75 **Availability of data and material**

76 The microsatellite allele tables for all species and populations as well as population locations are
77 available on DRYAD (<https://doi.org/10.5061/dryad.tb2rbp00k>). The population genetic variables at

78 the node level are published in Naaf et al. 2021 (<https://doi.org/10.1007/s10980-021-01292-w>). The
79 population genetic variables at the link level and all landscape metrics (node and link level) are
80 available on DRYAD as well (<https://doi.org/10.5061/dryad.h70rxwdf>).

81

82 **Authors' contributions**

83 TN, SIJH and KK conceived and designed the study. All authors except JLe and JP were involved in site
84 selection, field work and sampling. JTF, SH, TN and KK performed the molecular lab work and did the
85 allele scoring. TN analyzed the data and wrote the first draft of the manuscript with contributions of
86 JLe, JP, JTF, KK, SH, and SIJH. All authors contributed to revisions and gave final approval for
87 publication.

88

89 **Acknowledgements**

90 We thank LUP Luftbild Umwelt Planung (Potsdam, Germany) for their services in creating the digital
91 land-use maps, Emilie Gallet-Moron (EDYSAN) for the provision of land-use data for the French
92 landscape window and Ute Jahn (ZALF) for technical assistance during GIS work. Basic research work
93 for this study relied on data from the smallFOREST geodatabase ([https://www.u-
94 picardie.fr/smallforest/uk/](https://www.u-picardie.fr/smallforest/uk/)).

95

96 **1. Introduction**

97

98 In many regions on earth, the progressive occupation of land by humans for settlements and
99 agriculture has forced wildlife and wildflowers to live in small remaining fragments of once
100 contiguous natural habitats (Kennedy et al. 2019). Surviving in a system of habitat fragments only
101 succeeds if local populations are functionally connected through the regular exchange of individuals
102 or diaspores. Plants with a limited dispersal potential, low seed production, a transient seed bank
103 and a high age of first sexual reproduction appear poorly equipped to establish such regional
104 population dynamics (Eriksson 1996). Typical temperate forest herbs belong to this group of plants
105 (Whigham 2004) as they evolved within landscapes that used to be covered by forest to a much
106 greater extent (Honnay et al. 2005). Numerous population genetic studies revealed that the
107 functional connectivity among temperate forest herb populations may be strongly reduced in
108 landscapes with a high degree of forest fragmentation. For instance, small, spatially isolated
109 populations often exhibit a reduced allelic richness (Vellend 2004; Jacquemyn et al. 2006; Vandepitte
110 et al. 2007; Kolb and Durka 2013; Naaf et al. 2021) and are strongly genetically differentiated from
111 each other (Jacquemyn et al. 2006; Schmidt et al. 2009; Gentili et al. 2018). However, local
112 populations may maintain a high level of genetic diversity (Culley et al. 2007; Toma et al. 2015) and a
113 low level of genetic differentiation among them (Van Rossum et al. 2002; Tomimatsu and Ohara
114 2003; Jacquemyn et al. 2009) if they are functionally connected by steady gene flow.

115 Gene flow in plants depends on abiotic or biotic vectors that transport seeds or pollen
116 between populations. For many plants, these vectors are animals that actively cross the landscape
117 matrix, i.e. the non-habitat part of the landscape (Murphy and Lovett-Doust 2004). We can therefore
118 assume that the structure of the matrix has a significant impact on gene flow in plants and thus their
119 susceptibility to detrimental effects of habitat loss and fragmentation. Nevertheless, population
120 genetic studies in general (Holderegger et al. 2010) and on forest herbs in particular (e.g., Tomimatsu
121 and Ohara 2003; Jacquemyn et al. 2006; Vandepitte et al. 2007; Kolb and Durka 2013; Gentili et al.
122 2018; but see Westerberg and Saura 1994 and Schmidt et al. 2009) largely ignored the matrix.

123 Several mechanisms of how the matrix may influence the seed and pollen transport among
124 plant populations are conceivable. First, different land-use types may exhibit different degrees of
125 resistance for seed-dispersing animals or pollinators. In general, the landscape permeability for large
126 mammals, such as deer, wild boar or carnivores, increases with forest cover (Coulon et al. 2004;
127 Herrera et al. 2016), while pollinators seem to prefer open landscapes and transport pollen further,
128 when forest cover is low (Kreyer et al. 2004; Kamm et al. 2010). Many mammals avoid proximity to
129 settlements and roads (Trombulak and Frissell 2000; Bonnot et al. 2013). Grasslands and arable fields
130 are avoided by deer and wild boar after harvest when they provide no shelter and little forage
131 biomass (Thurfjell et al. 2009; Morellet et al. 2011). However, maize fields with their specific
132 phenology and structure provide shelter even during late summer and autumn (Keuling et al. 2009;
133 Tillmann 2011) and thus enhance landscape permeability for mammals at a time, when seeds of
134 many forest herb-layer plants are ripe (Heinken and Raudnitschka 2002).

135 Second, land-use types serving as forage or nesting habitat may affect animals' abundance
136 and behaviour. The chance for seeds to be dispersed by birds is directly linked to bird abundance
137 (Garcia et al. 2010) and the abundance of woodland birds in agricultural landscapes increases with
138 increasing forest cover (Heikkinen et al. 2004; Radford and Bennett 2007). Mass-flowering crops such
139 as oilseed rape have been shown to enhance the abundance of bumblebee workers (Westphal et al.
140 2003) and solitary bees (Holzschuh et al. 2013) at the landscape scale. However, whether such an
141 attractive resource pulse results in spill-over to semi-natural habitats and enhanced pollination
142 service to wild plants (Kovacs-Hostyanszki et al. 2013; Ekroos et al. 2015) or a dilution of pollinators
143 and reduced pollination service (Holzschuh et al. 2011, 2016; Riedinger et al. 2015; Proesmans,
144 Smagghe, et al. 2019) needs further investigation. More continuous floral resources in semi-natural
145 habitats such as grasslands or hedgerows may sustain a high pollinator richness and abundance in
146 the long term (Kovacs-Hostyanszki et al. 2013; Riedinger et al. 2015; Bartual et al. 2019). The
147 proximity to such semi-natural habitats has been found to enhance the seed-set of insect-pollinated
148 wild plants in agricultural landscapes (Cussans et al. 2010; Jakobsson and Ågren 2014; Chateil and
149 Porcher 2015; Lindgren et al. 2018). Apart from floral resources, pollinators may depend on further

150 food resources. Larva of aphidophagous hoverflies, for instance, whose preferred adult habitat might
151 be deciduous forest, find their prey mostly in arable fields (Meyer et al. 2009). They can profit from
152 high densities of aphids in cereals as well as in oilseed rape (Haenke et al. 2014).

153 Third, linear landscape elements influence the movement behaviour of seed and pollen
154 dispersal vectors. Roe deer and wild boar, for instance, move preferably along edges such as
155 hedgerows, forest edges and ditches (Saïd and Servanty 2005; Thurfjell et al. 2009; Morellet et al.
156 2011). Bumblebees and honey bees fly preferably along hedgerows or other linear landscape
157 elements (Cranmer et al. 2012; Collett and Graham 2015). However, hedgerows may also act as
158 relative barriers to pollinator movement when their orientation crosses the flight direction (Wratten
159 et al. 2003; Klaus et al. 2015). Busy roads may act as barrier to the movement of large mammals
160 (Trombulak and Frissell 2000; Breyne et al. 2014), and may also restrict bumblebee or hoverfly
161 movement (Lövei et al. 1998; Bhattacharya et al. 2003; Fitch and Vaidya 2021).

162 Although it is evident that the agricultural landscape matrix influences the behaviour of
163 pollen- and seed dispersal vectors, it is unclear how this translates into seed and pollen dispersal
164 rates, and thus functional connectivity, among forest herb populations. Here, we therefore
165 quantified the landscape composition and configuration in terms of both area-based land-use types
166 and linear landscape elements in seven agricultural landscapes across north-western Europe to study
167 their effects on the population genetic structure of three common temperate forest herb species:
168 *Anemone nemorosa* L., *Oxalis acetosella* L. and *Polygonatum multiflorum* (L.) All. All three species are
169 typical, slow-colonizing forest specialists, but differ in their reproduction strategy and associated
170 pollen and seed dispersal vectors. Therefore, we expect them to respond differently to the landscape
171 structure (Table 1). In our understanding, the landscape-scale population genetic structure comprises
172 both the genetic diversity within and the genetic differentiation among local populations. We use it
173 here as an indirect measure of functional connectivity among local plant populations (Aavik et al.
174 2014) and tested the following main hypotheses:

175 H1 Landscape effects on the population genetic structure differ among the three forest herbs
176 because of their association with different pollen and/or seed dispersal vectors.

177 H2 Different arable crops (oilseed rape, maize, other cereals) have different effects on the forest
178 herbs' population genetic structure due to their differential effect on the associated pollen
179 and/or seed dispersal vectors.

180 H3 Linear landscape elements may have a channelling or impeding effect on gene flow
181 depending on their orientation in relation to gene dispersal pathways.

182

183

184 **2. Material and Methods**

185

186 *2.1. Study species*

187 The three studied forest herbs were selected for being typical, common slow-colonizing forest
188 specialists (Verheyen et al. 2003; Schmidt et al. 2014). They all exhibit strong clonal growth, but also
189 regular seedling recruitment (Holderegger et al. 1998; Berg 2002; Kosiński 2012). They flower in
190 spring and are pollinated by insects (Klotz et al. 2002). However, they differ in their reproduction
191 strategy. *Oxalis acetosella* has been found to produce most of its seeds from cleistogamous flowers
192 (Berg and Redbo-Torstensson 1998), thus it is less dependent on insect pollinators for sexual
193 reproduction. According to our own research, however, *O. acetosella* is mainly outcrossing (Naaf et
194 al. 2021). *Anemone nemorosa* and *Polygonatum multiflorum* are mainly and strictly outcrossing,
195 respectively (Müller et al. 2000; Kosiński 2012). *Oxalis acetosella* and *A. nemorosa* are pollinated by a
196 wide range of pollinators, including hoverflies, wild bees and honey bees (Shirreffs 1985; Redbo-
197 Torstensson and Berg 1995; Stehlik and Holderegger 2000; Naaf et al. 2021). In contrast,
198 *P. multiflorum* is mostly pollinated by long-tongued bumblebees (Kosiński 2012; Naaf et al. 2021). All
199 three species have a low seed-dispersal potential and are classified as autochorous (Müller-Schneider
200 1986). In addition, seeds of *A. nemorosa* are dispersed by some short-distance vectors such as ants
201 and slugs (Türke et al. 2012). Seeds of *O. acetosella* were found in the fur of wild boar by several
202 independent studies, though at low quantities (Mrotzek et al. 1999; Heinken and Raudnitschka
203 2002). The fleshy berries of *P. multiflorum* may suggest endozoochorous dispersal (Müller-Schneider

204 1986). In fact, however, they are toxic and probably rarely dispersed by birds and mid-sized
205 carnivores such as martens (Ehrlén and Eriksson 1993; Schaumann and Heinken 2002), while short-
206 distance dispersal by small rodents might occur more often (Ehrlén and Eriksson 1993).

207

208

209 2.2. Population genetic structure

210 We compiled population genetic data from seven 5 × 5 km² landscape windows spread across north-
211 western Europe from North France, over Belgium, West Germany, East Germany and South Sweden
212 up to Central Sweden and Estonia (Figure 1a, b). All landscape windows represent typical agricultural
213 landscapes, in which forest fragments are embedded in an agricultural matrix interfused by small
214 settlement areas and roads (see land-use maps in Supp. Inf. S1). We studied up to six forest herb
215 populations from each species in each landscape windows. *Oxalis acetosella* had too few occurrences
216 in Belgium to be included in the analysis of this landscape window. *Polygonatum multiflorum* did not
217 occur in the landscape window of Central Sweden. The final number of surveyed populations was
218 therefore 42, 34 and 36 for *A. nemorosa*, *O. acetosella* and *P. multiflorum*, respectively. Population
219 sizes varied by several orders of magnitude both within and among species ranging from 15 flowering
220 shoots in the smallest *P. multiflorum* population up to >12*10⁶ flowering shoots in the largest
221 *A. nemorosa* population (Table S2). Geographic distances among populations within landscape
222 windows ranged between 214 and 5518 m and were similarly distributed for each species (Table S2).
223 The population genetic data for these populations comprised four measures of within-population
224 genetic diversity, i.e. allelic richness (A_r), expected heterozygosity (H_e), observed heterozygosity (H_o)
225 and the inbreeding coefficient $F = 1 - H_o/H_e$, as well as two measures of among-population genetic
226 differentiation for each pair of populations within landscapes, i.e. G''_{ST} and D_{PS} (Table S2). While G''_{ST}
227 is the recommended genetic differentiation measure with microsatellite markers (Meirmans and
228 Hedrick 2011), D_{PS} equals 1 minus the proportion of shared alleles and therefore facilitates an
229 intuitive interpretation. The genetic data were based on species-specific sets of nuclear microsatellite
230 markers, which comprised six, nine and six markers with a total number of 102, 61 and 149 alleles for

231 *A. nemorosa*, *O. acetosella* and *P. multiflorum*, respectively (Supp. Inf. S3). While *O. acetosella* and
232 *P. multiflorum* are diploid, *A. nemorosa* was treated as tetraploid (Stehlik and Holderegger 2000). For
233 details on genetic analyses and the calculation of population genetic variables see Naaf et al. (2021),
234 in which we studied the effects of habitat loss and fragmentation *per se*.

235

236

237 2.3. Landscape metrics

238 As a basis for our landscape analysis, we created digital land-use maps for all landscape windows
239 based on recent orthophotos and additional, region-specific data (Supp. Inf. S1). Moreover, for all
240 arable fields, we determined the dominance of three different crop types, i.e. oilseed rape, maize
241 and other cereals, over the preceding decade (2008 – 2017) based on data generated within the
242 European Integrated Administration and Control System (IACS) (European Commission 2020; Supp.
243 Inf. S4). To quantify the composition and configuration of area-based and linear landscape elements,
244 we calculated a set of landscape metrics (Table 1) in (a) buffer zones around each herb population
245 (node-level analysis, Figure 1c, e.g. Schmidt et al. 2009) and (b) rectangular landscape strips
246 connecting the centres of each pair of herb populations within landscape windows (link-level
247 analysis, Figure 1d, e.g. Braunisch et al. 2010). Several buffer distances were chosen to reflect range
248 sizes and forage distances of potential seed and pollen dispersal vectors (Table 1): 125 m, 250 m, 500
249 m, 1000 m and 2000 m. Similarly, we chose several width-to-length ratios for the landscape strips
250 connecting the herb populations to account for the fact that different pollen and seed dispersal
251 vectors have different sight distances for their orientation and thus will move more or less linearly
252 through the landscape: 1:7, 1:5, 1:3, 1:2 and 2:3. For each buffer zone and landscape strip, we
253 calculated the percent cover of different area-based land-use types, the relative length of different
254 linear landscape elements (= total length divided by buffer or strip area, respectively) and two index
255 measures, i.e. the Shannon diversity of land-use types and the density of all land-use patch edges
256 (Table 1). Since the effect that a linear landscape element exerts on gene dispersal might depend on
257 its orientation relative to the movement direction of vectors (orthogonal vs. parallel), we calculated

258 also the orthogonal and parallel length component of each linear landscape element (Figure 1c, d). In
259 buffer zones, the parallel direction corresponds to the direction from the midpoint of the linear
260 element to the population centre. In landscape strips, the parallel direction corresponds to the
261 connection line between population centres. The orthogonal-to-parallel length ratio was then used
262 as conditioning variable in statistical models (see below). Moreover, the effect of settlement areas on
263 gene dispersal vectors might depend on the relative proportion of sealed or built-up area vs.
264 unsealed green areas, such as gardens. The latter might serve as forage habitat for pollinators,
265 particularly, when many fruit trees or ornamental shrubs can be found there (Cussans et al. 2010;
266 Goulson et al. 2010; Nakamura and Kudo 2019). Therefore, we used also the proportion of green
267 settlement area as conditioning variable in statistical models.

268

269

270 *2.4. Data analysis*

271 To study the effects of landscape metrics on genetic diversity (node level) and pairwise genetic
272 differentiation (link level), we used linear mixed-effects models (LMMs) separately for each species
273 with landscape window as random intercept. We fitted these models with the function `lme` of the R
274 package `nlme` (Pinheiro et al. 2019). At the link level, we took the correlation among population pairs
275 including a common population into account by defining a correlation structure within the `lme`
276 function using the function `corMLPE` (Pope 2020; maximum likelihood population-effects models
277 sensu Clarke et al. 2002). Prior to modelling, all variables were Box-Cox-transformed to increase the
278 symmetry of their distribution and then centred and scaled to yield standardized regression
279 coefficients. We were interested here in marginal effects of the landscape metrics that they exert on
280 genetic variables in addition to those exerted by some basic population genetic determinants, which
281 had been studied earlier (Naaf et al. 2021). At the node level, these basic determinants were
282 population size, i.e. the total number of flowering shoots in a population, and the degree of spatial
283 isolation measured by Hanski's (1994) incidence function model (see Naaf et al. 2021 for details). At
284 the link level, the basic determinant was edge-to-edge geographical distance. Therefore, all models

285 included population size and isolation or geographic distance, respectively, as fixed effects that could
286 not be removed during model selection. At the link level, we also allowed for interactions between
287 basic determinant and landscape metrics, which was not possible at the node level due to the limited
288 sample size (node level 30-42 vs. link level 78-104; Supp. Inf. S6).

289 To identify the most important predictors among the large number of landscape metrics and
290 to avoid collinearity, our statistical modelling followed three steps. First, we identified for each
291 landscape metric (Table 1) its most influential buffer distance (node level) or width-to-length ratio
292 (link level) as the one yielding the lowest AIC_c in LMMs containing only one landscape metric at a
293 time. To account for curvilinear or unimodal relationships these models contained also a quadratic
294 term if this lowered AIC_c . Models for linear landscape elements and settlement area included also
295 the interaction with a corresponding conditioning variable (Table 1). Models at the link level included
296 also an interaction term with geographic distance if this lowered AIC_c . In the following steps, we
297 considered only those most influential landscape metrics that showed a significant effect in the
298 single-metric models at a level of $\alpha = 0.15$ based on a likelihood ratio test against the reduced model
299 without the landscape metric in question.

300 Second, we checked for collinearity among the remaining landscape metrics. Any correlations
301 with $|r| \geq 0.7$ were not tolerated. In case of intrinsic collinearity, we used principal components
302 analysis to calculate a principal component of the collinear variables. In case of collinearity among
303 variables that are not obviously ecologically related, we chose the one yielding the highest
304 importance value in the final average model (see below) and excluded the other one (keeping the
305 collinearity in mind for our interpretation). In the special case of percent cover of arable land, we
306 allowed either the percent cover of different crop types (RAPE, MAIZE, CEREAL; Table 1) or the
307 percent cover of arable land in general (ARABLE) to be included to see which version explained a
308 higher proportion of variation in the final average model (see below).

309 Third, all remaining metrics entered the global model, which was then used for model
310 selection followed by multi-model inference with the R package MuMIn (Barton 2019). In this step,
311 we fitted models using ML estimation for all subsets of predictors allowing for a maximum of four

312 and nine landscape metric terms in models at the node and link level, respectively, given the limited
313 sample size. All models with a $\Delta AIC_C < 2$ were refit with REML estimation and then subjected to full
314 model averaging (Grueber et al. 2011). For each term in the average model, we calculated an
315 importance value as the sum of the Akaike weights over all component models, in which the term
316 appeared. This importance value ranges between 0 and 1 with a value of 1 indicating that the
317 corresponding term occurs in all component models. Any term with an importance value ≥ 0.5 will be
318 reported and interpreted. To quantify the amount of variation in genetic variables explained by the
319 landscape metrics, we calculated the difference between the marginal R^2 for the average model and
320 the marginal R^2 for the basic model including only the basic population genetic determinants. For the
321 visualization of any important effects (i.e., those with an importance value ≥ 0.5), we used the single
322 best model that included all important terms.

323

324

325 **3. Results**

326

327 *3.1. Landscape effects at the node level*

328 Out of the 16 landscape metrics considered, 15 were involved in at least one important landscape
329 effect (i.e., with an importance value ≥ 0.5) on a genetic diversity variable (Table 2). The proportion
330 of variation explained uniquely by the landscape effects was mostly larger than the proportion
331 explained by the basic population genetic determinants, population size and spatial isolation
332 (Table 2).

333 Some of the landscape metrics had contrasting effects for different species. With increasing
334 cover of arable land, allelic richness of *A. nemorosa* increased, but decreased for *P. multiflorum*
335 (Figures 2a and k). Expected heterozygosity of *A. nemorosa* increased with increasing maize cover in
336 the landscape, whereas for *O. acetosella*, expected heterozygosity was highest at a lower-than-
337 average maize cover (Figures 2d and h). Expected and observed heterozygosity of *A. nemorosa* also
338 appeared to benefit from a high settlement cover in the landscape, while expected and observed

339 heterozygosity of *P. multiflorum* decreased with increasing settlement cover (Figures 2c, e, m, and
340 n).

341 The differentiation of crop types resulted mostly in higher marginal R^2 -values than
342 considering arable land in general, even though often only a single crop type yielded importance
343 (Table 2a, b) or several crop types were highly correlated and were thus united in a principal
344 component (Table 2c). All crop types had unique effects. The inbreeding coefficient of *A. nemorosa*
345 populations was highest with an oilseed rape cover slightly above the mean (Figure 2f). As stated
346 above, maize cover affected the expected heterozygosity of *A. nemorosa* and *O. acetosella*
347 differently. Allelic richness and expected heterozygosity of *P. multiflorum* populations decreased
348 with increasing cover of cereals and oilseed rape, which was, however, at the same time negatively
349 correlated with grassland cover (Table 2, Figure 2k).

350 Linear landscape elements affected genetic diversity mostly independent of their prevalent
351 orientation relative to the gene dispersal direction, with one exception (Figure 3g): water courses
352 orthogonal to the gene flow direction reduced observed heterozygosity in *P. multiflorum*
353 populations, while water courses pointing towards the populations enhanced observed
354 heterozygosity.

355 The spatial scale, at which the species' genetic diversity responded to the landscape
356 structure, was variable both across genetic diversity variables and landscape metrics (Table 2).
357 Often, landscape effects were similarly high at several buffer distances (results not shown). For
358 *P. multiflorum*, the majority (75%) of important landscape effects were most pronounced at a buffer
359 distance ≥ 1000 m. No clear pattern occurred for the other two species.

360

361

362 3.2. Landscape effects at the link level

363 Twelve landscape metrics were involved in at least one important landscape effect on a genetic
364 differentiation measure (Table 3). The proportion of variation explained uniquely by the landscape
365 effects generally exceeded 90% of the total variation explained by fixed effects. This means that

366 geographic distance alone had little explanatory power. It determined, however, the magnitude and
367 direction of several landscape effects (Figure 3).

368 Two landscape metrics had contrasting effects for the different species, forest cover and
369 arable land. Genetic differentiation among *A. nemorosa* populations measured by D_{PS} was highest
370 with an intermediate forest cover (Figure 2g), while for *O. acetosella*, D_{PS} was highest with a high
371 forest cover (Figure 3d). When distance between populations was short, a high forest cover reduced
372 G''_{ST} among both *O. acetosella* and *P. multiflorum* populations. However, when distance between
373 population was far, a high forest cover enhanced G''_{ST} among *O. acetosella* populations, but reduced
374 it among *P. multiflorum* populations (Figures 3c and h). A high cover of arable land generally
375 increased D_{PS} between *O. acetosella* populations (Figure 2j), whereas for *A. nemorosa*, it either
376 increased or decreased D_{PS} depending on whether the distance between populations was short or
377 far, respectively (Figure 3b).

378 Of the different crop types, only oilseed rape had a unique effect (Figure 3e). For short
379 distances between *O. acetosella* populations, G''_{ST} was highest, when oilseed rape cover was high.
380 With far distances between *O. acetosella* populations, G''_{ST} was highest, when oilseed rape cover
381 was intermediate, but lowest when oilseed rape cover was either very high or low.

382 Two of the eight effects of linear landscape elements depended on the orientation of the
383 landscape elements relative to the landscape strip (Table 3). For *O. acetosella*, woody linear elements
384 running parallel to the landscape strip had little effect, but those running orthogonal to the
385 landscape strip enhanced D_{PS} among populations (Figure 3f). For *P. multiflorum*, roads running
386 parallel to the landscape strip reduced G''_{ST} among populations, whereas those running orthogonal
387 to the landscape strip enhanced G''_{ST} (Figure 3i).

388 The width-to-length ratio of the landscape strips, at which genetic differentiation among
389 populations was influenced most, was variable (Table 3). There was no clear difference among
390 species. Most landscape effects (81%) were most pronounced at an intermediate width-to-length
391 ratio (1:5 to 1:2).

392

393

394 **4. Discussion**

395

396 Our results show that gene flow among spatially isolated forest herb populations in agricultural
397 landscapes is influenced by a multitude of different land-use types and landscape elements that act
398 at different spatial scales. The composition and configuration of the landscape prove here to be more
399 important determinants of the forest herbs' landscape-scale population genetic structure than the
400 size of local populations and their geographic distance to each other.

401

402 *4.1. Forest herbs respond differently to the landscape structure (H1)*

403 Each species not only responded to a different set of landscape metrics, but also showed contrasting
404 responses when affected by the same landscape metric (Tables 2 and 3). These contrasting responses
405 were most pronounced for the cover of forest, arable land and settlements. Forest cover in
406 landscape strips among populations affected the genetic differentiation among populations of all
407 three species. For *O. acetosella*, a high forest cover in the landscape increased genetic differentiation
408 among populations, particularly when distances among populations were far (Figures 3c and d),
409 indicating that forest hampers far-distance gene dispersal. While forests do not represent
410 insurmountable barriers for bees, they appear to enhance landscape resistance for forage flights
411 (Kreyer et al. 2004; Goulson et al. 2010; Kamm et al. 2010; Zurbuchen et al. 2010). In contrast,
412 *P. multiflorum* showed the lowest genetic differentiation among populations, when forest cover was
413 high (Figure 3h). This stands in contrast to the observation that forest increases landscape resistance
414 to bumblebee flights (Kreyer et al. 2004; Goulson et al. 2010). In fact, one of the most important
415 pollinators of *P. multiflorum*, *Bombus pascuorum* (Naaf et al. 2021), was found to use floral resources
416 in forests and open habitats at similar rates and at similar distances from their nests (Kreyer et al.
417 2004). Thus, for this bumblebee species, forests do not represent barriers but even allow *B.*
418 *pascuorum* to practice its typical trap line behaviour and to visit several *P. multiflorum* populations
419 on a single forage flight (Kreyer et al. 2004). Moreover, there is ample evidence that seed dispersal

420 by both woodland birds (Heikkinen et al. 2004; Garcia et al. 2010) and carnivores (Herrera et al.
421 2016) is enhanced with a high forest cover. Finally, genetic differentiation among *A. nemorosa*
422 populations was highest with an intermediate forest cover in the landscape (Table 3, Figure 2g). This
423 relationship might reflect a trade-off between effects that limit and promote gene flow. As
424 mentioned above, a high forest cover might restrict bee movement through the landscape. However,
425 it allows also a high richness and abundance of forest-dwelling hoverflies (Meyer et al. 2009;
426 Proesmans, Bonte, et al. 2019; Schirmel et al. 2018) and a short distance to other *A. nemorosa*
427 populations.

428 Besides forest, the cover of arable land affected the species' population genetic structure
429 differently. While a high cover of arable land appeared to facilitate gene flow among *A. nemorosa*
430 populations (Figure 2a and 3b), it apparently restricted gene flow among populations of *O. acetosella*
431 (Figure 2j) and *P. multiflorum* (Figure 2k). One gene-dispersal vector for *A. nemorosa* that benefits
432 from arable land are aphidophagous hoverflies. Many hoverflies, which prefer forests and hedgerows
433 as their adult habitat, prefer cropland as their larval habitat, where they feed on aphid colonies
434 (Meyer et al. 2009). In fact, several studies found positive relationships between the abundance and
435 species richness of aphidophagous hoverflies and the proportion of arable land in the landscape
436 (Jauker et al. 2009; Meyer et al. 2009; Haenke et al. 2014). Thus, high abundances of aphidophagous
437 hoverfly species, such as *Melanostoma scalare*, *Platycheirus albimanus* or *Syrphus ribesii*, which are
438 important pollinators of *A. nemorosa* (personal observations), might be responsible for the positive
439 effect of arable land on allelic richness and its negative effect on genetic differentiation among
440 *A. nemorosa* populations. This is apparently not true for *O. acetosella*, for which genetic
441 differentiation among populations increased with increasing cover of arable land in the landscape.
442 Since the most dominant crop types, i.e. cereals and maize (Supp. Inf. S4), do not provide any floral
443 resources during spring, they occur at the cost of more valuable habitats for pollinators, such as
444 grasslands (Jakobsson and Ågren 2014; Bartual et al. 2019). The trade-off between arable land and
445 grassland was even clearer for *P. multiflorum*, for which allelic richness and expected heterogeneity
446 decreased with increasing cover of arable land at the cost of grassland (Table 2, Figure 2k). Many

447 bumblebee species benefit from a high grassland cover in the landscape because grasslands may
448 provide both nesting sites and floral resources (Goulson et al. 2010; Vray et al. 2019). Also, the
449 occupancy of forest patches by woodland birds appears to be positively affected by the amount of
450 grassland in contrast to the amount of arable fields in the surrounding landscape (Radford and
451 Bennett 2007; Montague-Drake et al. 2009).

452 Moreover, settlements and roads affected the forest herbs differently. Close to villages, the
453 road network is particularly dense. Therefore, the effects of settlement area and road density were
454 often confounded (Table 2). For *P. multiflorum*, the lower genetic diversity in populations less than
455 1 km away from settlements (Figures 2l-n) implies that here, the inflow of new alleles via pollen or
456 seeds occurs at lower rates than at far distance from settlements. Two mechanisms, corresponding
457 to different gene dispersal vectors, might explain this pattern. First, woodland birds might avoid
458 landscapes with more settlements and roads (Dunford and Freemark 2005; Rüdissler et al. 2015) and
459 therefore transport *P. multiflorum* seeds less often into nearby forest patches. However, woodland
460 birds were found to respond most strongly to landscape composition at a smaller spatial scale of 100
461 to 500 m (Rüdissler et al. 2015). Second, settlements in our agricultural landscapes consist mostly of
462 rural villages with many gardens. Gardens are important forage habitats for bumblebees in rural
463 landscapes (Goulson et al. 2010; Nakamura and Kudo 2019). The flowering period of fruit trees such
464 as *Malus* spp., *Pyrus* spp. or *Prunus* spp. as well as ornamental shrubs such as *Syringa vulgaris*
465 overlaps with that of *P. multiflorum*. These ample floral resources might attract bumblebees and
466 reduce bumblebee abundance and their pollination service in nearby forest patches (Nakamura and
467 Kudo 2019; Proesmans, Smagghe, et al. 2019). Interestingly, at a smaller spatial scale (250 m), the
468 inbreeding coefficient for *P. multiflorum* was negatively related to settlement area (Figure 2o),
469 indicating that *P. multiflorum* populations very close to villages might benefit from bumblebee
470 spill-over (Cussans et al. 2010). In contrast to *P. multiflorum*, *A. nemorosa* appeared to benefit from
471 settlement areas in the landscape (250-500 m), at least in terms of expected and observed
472 heterozygosity (Figures 2c and e). Close to villages, different foraging, resting or nesting habitats for
473 pollinators, such as gardens and hedgerows, have a relatively high density. They might sustain a high

474 abundance of pollinators (Cussans et al. 2010; Garratt et al. 2017; Schirmel et al. 2018; Bartual et al.
475 2019), which then spill over to nearby forest patches to feed on pollen of *A. nemorosa* in early spring.

476 In general, there was no clear difference in the spatial scale, at which the three species
477 responded to the landscape structure. The prevalent buffer distances ≥ 1000 m for *P. multiflorum*
478 reflect its association with far-flying bumblebees. Important pollinator species such as *Bombus*
479 *pascuorum* and *B. pratorum* (Naaf et al. 2021) may forage over distances > 1800 m (Redhead et al.
480 2016) and > 670 m (Knight et al. 2005), respectively.

481

482 4.2. Distinguishing crop types matters (H2)

483 In nine out of 11 landscape effects, in which arable crops were involved (Tables 2 and 3), a
484 differentiation of crop types resulted in higher proportions of explained variation than merging the
485 different crop types into arable land in general. In particular oilseed rape and maize had distinct
486 effects, which is remarkable considering that both crop types represent relatively young elements in
487 European landscapes that were more or less absent seven decades ago (Knoema 2020). There was
488 thus limited time for them to leave their imprint in the forest herbs' population genetic structure. We
489 had expected to find any effects of oilseed rape or maize most likely for *O. acetosella* given its
490 shorter generation time compared to *A. nemorosa* and *P. multiflorum* (Naaf et al. 2021). Indeed,
491 oilseed rape affected the genetic differentiation among populations of *O. acetosella* (Figure 3e),
492 while maize influenced genetic diversity within its populations (Figures 2h and i). The high genetic
493 differentiation among *O. acetosella* populations separated by a matrix of high oilseed rape cover
494 might reflect a dilution effect (Holzschuh et al. 2011 2016). The flowering periods of oilseed rape and
495 *O. acetosella* greatly overlap and oilseed rape is highly attractive for various pollinators (Haenke et al.
496 2014; Riedinger et al. 2015). The attraction of pollinators by oilseed rape might lead to diluted
497 pollinators in adjacent forests (Holzschuh et al. 2011; Van Reeth et al. 2019), where *O. acetosella*
498 plants might receive little compatible pollen from other forest patches. However, when oilseed rape
499 cover in the landscape strip was very high and distances between populations were > 2300 m, we
500 observed a reduced genetic differentiation among *O. acetosella* populations (Figure 3e). In this case,

501 the landscape strip crossed large parts of the landscape window. A permanently high oilseed rape
502 cover across the landscape window might result in positive population growth rates of pollinators
503 and thus higher abundances in the long term. For instance, the abundance of solitary bees was found
504 to be enhanced by a high oilseed rape cover in the preceding year (Riedinger et al. 2015).

505 The negative effect of maize cover on expected heterozygosity of *O. acetosella* populations
506 (Figure 2h) indicates that a high cover of maize reduces the inflow of new alleles. Also the inbreeding
507 coefficient of *O. acetosella* populations increased with maize cover, potentially reflecting pollen
508 limitation (Figure 2i). However, this increase levelled off and changed into a decrease when maize
509 cover was very high. Since pollen limitation is unlikely to decrease, when maize cover is very high,
510 enhanced seed dispersal might prevent inbreeding under these circumstances. Maize fields are a
511 very attractive forage and shelter habitat for wild boar during summer and autumn (Keuling et al.
512 2009; Tillmann 2011), when the cleistogamous seeds of *O. acetosella* are ripe (Berg and Redbo-
513 Torstensson 1998). Some of these animals appear to move regularly between the maize fields and
514 forests (Keuling et al. 2009) and might thus disperse seeds of *O. acetosella*.

515 Despite its longer generation time, also *A. nemorosa* showed some responses to oilseed rape
516 and maize. Populations with a high oilseed rape cover in the surrounding landscape showed an
517 increased inbreeding signal (Figure 2f). Although *A. nemorosa* starts flowering earlier than oilseed
518 rape, there might be an overlapping flowering period of one or two weeks. Thus, as with
519 *O. acetosella*, the increased inbreeding signal might result from pollinator dilution (Holzschuh et al.
520 2011; Van Reeth et al. 2019). The positive effect of maize cover on expected heterozygosity of
521 *A. nemorosa* populations (Figure 2d) was unexpected (Table 1) and difficult to explain. Given the
522 young history of maize in our landscapes in relation to the long generation time of *A. nemorosa*, this
523 result should be considered with caution.

524

525

526 4.3. The orientation of linear landscape elements matters (H3)

527 Our results show that linear landscape elements, including woody line elements, water courses,
528 herbaceous fringes and roads, influence the movement of gene dispersal vectors across the
529 landscape. The orientation of the linear landscape elements was important in three out of 16 effects
530 (Tables 2 and 3). Here, the linear landscape elements appeared to have a promoting or hampering
531 effect on gene flow as hypothesized, depending on whether they were predominantly oriented
532 parallel or orthogonal to the gene dispersal pathways (Figures 3f, g, and i). These results confirm the
533 observation that linear landscape elements may not just channel animal movements, but may also
534 act as relative barrier (Wratten et al. 2003; Levey et al. 2005; Saïd and Servanty 2005; Krewenka et al.
535 2011; Klaus et al. 2015; Fitch and Vaidya 2021).

536 At large spatial scales (2000 m radius around populations), orthogonal and parallel
537 orientations of linear landscape elements can be expected to be balanced. For this situation, we
538 found a strong positive effect of road density on the inbreeding coefficient of *P. multiflorum*
539 populations, indicating that roads restrict outbreeding (Table 2, Figure 2p). Whether this effect is
540 mediated through pollen or seed dispersers or both remains unclear. Bumblebees as well as many
541 rodents seem to be reluctant to cross roads (Trombulak and Frissell 2000; Bhattacharya 2003).

542 Also at the 2000 m scale, there was a strong unimodal response of allelic richness in
543 *A. nemorosa* populations to the density of woody linear elements (Table 2, Figure 2b). These
544 appeared to promote allelic richness up to an above-average density in the landscape. This effect
545 might result from a higher abundance of pollinators in landscapes with a high hedgerow density and
546 spill-over from hedgerows to adjacent forests. Hedgerows represent important resting and foraging
547 habitats for both hoverflies (Haenke et al. 2014; Garratt et al. 2017; Schirmel et al. 2018) and bees
548 (Garratt et al. 2017; Bartual et al. 2019). The subsequent decrease in allelic richness at an even higher
549 density of woody linear elements was mainly due to the French populations (Figure 2b). On the one
550 hand, this decrease could result from an increasing resistance that woody linear elements constitute
551 for pollinator movements (Wratten et al. 2003; Krewenka et al. 2011; Klaus et al. 2015). This
552 interpretation would be analogous to that of the unimodal effect of forest cover on genetic
553 differentiation among *A. nemorosa* populations (see above, Figure 2g). On the other hand, the high

554 hedgerow density in the French landscape window is rather recent and established only in the 19th
555 century (Jamoneau et al. 2012). Thus, the time passed since then might not suffice for the hedgerows
556 to leave their imprint in the genetic diversity of *A. nemorosa* populations.

557

558

559 **5. Conclusions**

560

561 Our study shows that, more than habitat loss and fragmentation *per se*, the composition and
562 configuration of the agricultural landscape matrix exerts significant control over the population
563 genetic structure, and thus the functional connectivity, in fragmented temperate forest herb
564 populations. Although we could only discuss rather than reveal the underlying mechanisms of the
565 observed landscape effects, it became obvious that a multitude of mechanisms are at work in our
566 landscapes. In this respect, our study has generated many hypotheses, which deserve to be tested in
567 depth. The observed landscape effects turned out to be rather species-specific. Nevertheless, they
568 are general in the sense that they were consistent across multiple agricultural landscapes across
569 Europe.

570 Landscape planning with the aim to enhance the functional connectivity among spatially
571 isolated plant populations in agricultural landscapes should consider that (a) species of the same
572 ecological guild (e.g., forest herbs) might respond quite differently to the landscape structure, if they
573 are associated with different pollen or seed dispersal vectors; (b) it may be worth to differentiate
574 crop types rather than merging them into arable crops in general given their distinct effects on
575 functional connectivity; and (c) linear landscape elements that are mostly perceived as relative
576 barriers for animals, such as roads, may also have a channelling effect on their movement and thus
577 promote gene flow, whereas linear landscape elements that are mostly perceived as connecting
578 corridors, such as hedgerows, may also act as barrier for gene dispersal vectors.

579

580

581

582 **References**

583 Aavik T, Holderegger R, Bolliger J (2014) The structural and functional connectivity of the grassland

584 plant *Lychnis flos-cuculi*. *Heredity* 112(5):471-478. <https://doi.org/10.1038/hdy.2013.120>

585 Barton K (2019) MuMIn: Multi-Model Inference. R package version 1.43.15.

586 Bartual AM, Sutter L, Bocci G et al (2019) The potential of different semi-natural habitats to sustain

587 pollinators and natural enemies in European agricultural landscapes. *Agric Ecosyst Environ*

588 279:43-52. <https://doi.org/10.1016/j.agee.2019.04.009>

589 Berg H (2002) Population dynamics in *Oxalis acetosella*: the significance of sexual reproduction in a

590 clonal, cleistogamous forest herb. *Ecography* 25(2):233-243. <https://doi.org/10.1034/j.1600->

591 0587.2002.250211.x

592 Berg H, Redbo-Torstensson P (1998) Cleistogamy as a bet-hedging strategy in *Oxalis acetosella*, a

593 perennial herb. *J Ecol* 86(3):491-500. <https://doi.org/10.1046/j.1365-2745.1998.00272.x>

594 Bhattacharya M, Primack RB, Gerwein J (2003) Are roads and railroads barriers to bumblebee

595 movement in a temperate suburban conservation area? *Biol Conserv* 109(1):37-45.

596 [https://doi.org/10.1016/s0006-3207\(02\)00130-1](https://doi.org/10.1016/s0006-3207(02)00130-1)

597 Bonnot N, Morellet N, Verheyden H et al (2013) Habitat use under predation risk: hunting, roads and

598 human dwellings influence the spatial behaviour of roe deer. *Eur J Wildl Res* 59(2):185-193.

599 <https://doi.org/10.1007/s10344-012-0665-8>

600 Braunisch V, Segelbacher G, Hirzel AH (2010) Modelling functional landscape connectivity from

601 genetic population structure: a new spatially explicit approach. *Mol Ecol* 19(17):3664-3678.

602 <https://doi.org/10.1111/j.1365-294X.2010.04703.x>

603 Breyne P, Mergeay J, Casaer J (2014) Roe deer population structure in a highly fragmented

604 landscape. *Eur J Wildl Res* 60(6):909-917. <https://doi.org/10.1007/s10344-014-0859-3>

605 Chateil C, Porcher E (2015) Landscape features are a better correlate of wild plant pollination than

606 agricultural practices in an intensive cropping system. *Agric Ecosyst Environ* 201:51-57.

607 <https://doi.org/10.1016/j.agee.2014.12.008>

608 Clarke RT, Rothery P, Raybould AF (2002) Confidence limits for regression relationships between
609 distance matrices: Estimating gene flow with distance. *J Agric Biol Env Stat* 7(3):361-372.
610 <https://doi.org/10.1198/108571102320>

611 Collett TS, Graham P (2015) Insect navigation: do honeybees learn to follow highways? *Current*
612 *Biology* 25(6):R240-R242. <https://doi.org/10.1016/j.cub.2014.11.003>

613 Coulon A, Cosson JF, Angibault JM et al (2004) Landscape connectivity influences gene flow in a roe
614 deer population inhabiting a fragmented landscape: an individual-based approach. *Mol Ecol*
615 13(9):2841-2850. <https://doi.org/10.1111/j.1365-294X.2004.02253.x>

616 Cranmer L, McCollin D, Ollerton J (2012) Landscape structure influences pollinator movements and
617 directly affects plant reproductive success. *Oikos* 121(4):562-568.
618 <https://doi.org/10.1111/j.1600-0706.2011.19704.x>

619 Culley TM, Sbita SJ, Wick A (2007) Population genetic effects of urban habitat fragmentation in the
620 perennial herb *Viola pubescens* (Violaceae) using ISSR markers. *Ann Bot* 100(1):91-100.
621 <https://doi.org/10.1093/aob/mcm077>

622 Cussans J, Goulson D, Sanderson R, Goffe L, Darvill B, Osborne JL (2010) Two bee-pollinated plant
623 species show higher seed production when grown in gardens compared to arable farmland. *Plos*
624 *One* 5(7):10. <https://doi.org/10.1371/journal.pone.0011753>

625 Dunford W, Freemark K (2005) Matrix matters: Effects of surrounding land uses on forest birds near
626 Ottawa, Canada. *Landsc Ecol* 20(5):497-511. <https://doi.org/10.1007/s10980-004-5650-5>

627 Ehrlén J, Eriksson O (1993) Toxicity in fleshy fruits: A non-adaptive trait? *Oikos* 66(1):107-113.
628 <https://doi.org/10.2307/3545202>

629 Ekroos J, Jakobsson A, Wideen J, Herbertsson L, Rundlof M, Smith HG (2015) Effects of landscape
630 composition and configuration on pollination in a native herb: a field experiment. *Oecologia*
631 179(2):509-518. <https://doi.org/10.1007/s00442-015-3370-y>

632 Eriksson O (1996) Regional dynamics of plants: A review of evidence for remnant, source-sink and
633 metapopulations. *Oikos* 77(2):248-258.

634 European Commission (2020) Integrated administration and control system (IACS).
635 [https://ec.europa.eu/info/food-farming-fisheries/key-policies/common-agricultural-
636 policy/financing-cap/financial-assurance/managing-payments_en](https://ec.europa.eu/info/food-farming-fisheries/key-policies/common-agricultural-
636 policy/financing-cap/financial-assurance/managing-payments_en). Accessed 10 August 2021

637 Fitch G, Vaidya C (2021) Roads pose a significant barrier to bee movement, mediated by road size,
638 traffic and bee identity. *J Appl Ecol* 58(6):1177-1186.
639 <https://doi.org/https://doi.org/10.1111/1365-2664.13884>

640 Garcia D, Zamora R, Amico GC (2010) Birds as suppliers of seed dispersal in temperate ecosystems:
641 conservation guidelines from real-world landscapes. *Conserv Biol* 24(4):1070-1079.
642 <https://doi.org/10.1111/j.1523-1739.2009.01440.x>

643 Garratt MPD, Senapathi D, Coston DJ, Mortimer SR, Potts SG (2017) The benefits of hedgerows for
644 pollinators and natural enemies depends on hedge quality and landscape context. *Agric Ecosyst
645 Environ* 247:363-370. <https://doi.org/10.1016/j.agee.2017.06.048>

646 Gentili R, Solari A, Diekmann M et al (2018) Genetic differentiation, local adaptation and phenotypic
647 plasticity in fragmented populations of a rare forest herb. *Peerj* 6:26.
648 <https://doi.org/10.7717/peerj.4929>

649 Goulson D, Lepais O, O'Connor S et al (2010) Effects of land use at a landscape scale on bumblebee
650 nest density and survival. *J Appl Ecol* 47(6):1207-1215. [https://doi.org/10.1111/j.1365-
651 2664.2010.01872.x](https://doi.org/10.1111/j.1365-
651 2664.2010.01872.x)

652 Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and
653 evolution: challenges and solutions. *J Evol Biol* 24(4):699-711. [https://doi.org/10.1111/j.1420-
654 9101.2010.02210.x](https://doi.org/10.1111/j.1420-
654 9101.2010.02210.x)

655 Haenke S, Kovacs-Hostyanszki A, Frund J et al (2014) Landscape configuration of crops and
656 hedgerows drives local syrphid fly abundance. *J Appl Ecol* 51(2):505-513.
657 <https://doi.org/10.1111/1365-2664.12221>

658 Hanski I (1994) A practical model of metapopulation dynamics. *J Anim Ecol* 63(1):151-162.
659 <https://doi.org/10.2307/5591>

660 Heikkinen RK, Luoto M, Virkkala R, Rainio K (2004) Effects of habitat cover, landscape structure and

661 spatial variables on the abundance of birds in an agricultural-forest mosaic. *J Appl Ecol*
662 41(5):824-835. <https://doi.org/10.1111/j.0021-8901.2004.00938.x>

663 Heinken T, Raudnitschka D (2002) Do wild ungulates contribute to the dispersal of vascular plants in
664 central European forests by epizoochory? A case study in NE Germany. *Forstwiss Centralbl*
665 121(4):179-194.

666 Herrera JM, Teixeira IdS, Rodriguez-Perez J, Mira A (2016) Landscape structure shapes carnivore-
667 mediated seed dispersal kernels. *Landsc Ecol* 31(4):731-743. [https://doi.org/10.1007/s10980-](https://doi.org/10.1007/s10980-015-0283-4)
668 015-0283-4

669 Holderegger R, Buehler D, Gugerli F, Manel S (2010) Landscape genetics of plants. *Trends Plant Sci*
670 15(12):675-683. <https://doi.org/10.1016/j.tplants.2010.09.002>

671 Holderegger R, Stehlik I, Schneller JJ (1998) Estimation of the relative importance of sexual and
672 vegetative reproduction in the clonal woodland herb *Anemone nemorosa*. *Oecologia* 117(1-
673 2):105-107. <https://doi.org/10.1007/s004420050637>

674 Holzschuh A, Dainese M, Gonzalez-Varo JP et al (2016) Mass-flowering crops dilute pollinator
675 abundance in agricultural landscapes across Europe. *Ecol Lett* 19(10):1228-1236.
676 <https://doi.org/10.1111/ele.12657>

677 Holzschuh A, Dormann CF, Tschardt T, Steffan-Dewenter I (2011) Expansion of mass-flowering
678 crops leads to transient pollinator dilution and reduced wild plant pollination. *Proc R Soc B-Biol*
679 *Sci* 278(1723):3444-3451. <https://doi.org/10.1098/rspb.2011.0268>

680 Holzschuh A, Dormann CF, Tschardt T, Steffan-Dewenter I (2013) Mass-flowering crops enhance
681 wild bee abundance. *Oecologia* 172(2):477-484. <https://doi.org/10.1007/s00442-012-2515-5>

682 Honnay O, Jacquemyn H, Bossuyt B, Hermy M (2005) Forest fragmentation effects on patch
683 occupancy and population viability of herbaceous plant species. *New Phytol* 166(3):723-736.
684 <https://doi.org/10.1111/j.1469-8137.2005.01352.x>

685 Jacquemyn H, Brys R, Adriaens D, Honnay O, Roldan-Ruiz I (2009) Effects of population size and forest
686 management on genetic diversity and structure of the tuberous orchid *Orchis mascula*. *Conserv*
687 *Genet* 10(1):161-168. <https://doi.org/10.1007/s10592-008-9543-z>

688 Jacquemyn H, Brys R, Honnay O, Hermy M, Roldan-Ruiz I (2006) Sexual reproduction, clonal diversity
689 and genetic differentiation in patchily distributed populations of the temperate forest herb *Paris*
690 *quadrifolia* (Trilliaceae). *Oecologia* 147(3):434-444. <https://doi.org/10.1007/s00442-005-0287-x>

691 Jakobsson A, Agren J (2014) Distance to semi-natural grassland influences seed production of insect-
692 pollinated herbs. *Oecologia* 175(1):199-208. <https://doi.org/10.1007/s00442-014-2904-z>

693 Jamoneau A, Chabrierie O, Closset-Kopp D, Decocq G (2012) Fragmentation alters beta-diversity
694 patterns of habitat specialists within forest metacommunities. *Ecography* 35(2):124-133.
695 <https://doi.org/10.1111/j.1600-0587.2011.06900.x>

696 Jauker F, Diekötter T, Schwarzbach F, Wolters V (2009) Pollinator dispersal in an agricultural matrix:
697 opposing responses of wild bees and hoverflies to landscape structure and distance from main
698 habitat. *Landsc Ecol* 24(4):547-555. <https://doi.org/10.1007/s10980-009-9331-2>

699 Kamm U, Gugerli F, Rotach P, Edwards P, Holderegger R (2010) Open areas in a landscape enhance
700 pollen-mediated gene flow of a tree species: evidence from northern Switzerland. *Landsc Ecol*
701 25(6):903-911. <https://doi.org/10.1007/s10980-010-9468-z>

702 Kennedy CM, Oakleaf JR, Theobald DM, Baruch-Mordo S, Kiesecker J (2019) Managing the middle: A
703 shift in conservation priorities based on the global human modification gradient. *Glob Change*
704 *Biol* 25(3):811-826. <https://doi.org/10.1111/gcb.14549>

705 Keuling O, Stier N, Roth M (2009) Commuting, shifting or remaining? Different spatial utilisation
706 patterns of wild boar *Sus scrofa* L. in forest and field crops during summer. *Mamm Biol*
707 74(2):145-152. <https://doi.org/10.1016/j.mambio.2008.05.007>

708 Klaus F, Bass J, Marholt L, Müller B, Klatt B, Kormann U (2015) Hedgerows have a barrier effect and
709 channel pollinator movement in the agricultural landscape. *J Landsc Ecol* 8(1):22.
710 <https://doi.org/https://doi.org/10.1515/jlecol-2015-0001>

711 Klotz S, Kühn I, Durka W (2002) BIOLFLOR - Eine Datenbank mit biologisch-ökologischen Merkmalen
712 zur Flora von Deutschland. Bundesamt für Naturschutz, Bonn

713 Knight ME, Martin AP, Bishop S et al (2005) An interspecific comparison of foraging range and nest
714 density of four bumblebee (*Bombus*) species. *Mol Ecol* 14(6):1811-1820.

715 <https://doi.org/10.1111/j.1365-294X.2005.02540.x>

716 Knoema (2020) Production statistics – crops, crops processed.

717 <https://knoema.com/FAOPRDSC2020/production-statistics-crops-crops-processed>. Accessed 10

718 August 2021

719 Kolb A, Durka W (2013) Reduced genetic variation mainly affects early rather than late life-cycle

720 stages. *Biol Conserv* 159:367-374. <https://doi.org/10.1016/j.biocon.2012.11.019>

721 Kosiński I (2012) Generative reproduction dynamics in populations of the perennial herb

722 *Polygonatum multiflorum* (Asparagaceae). *Ann Bot Fenn* 49(4):217-228.

723 <https://doi.org/10.5735/085.049.0401>

724 Kovacs-Hostyanszki A, Haenke S, Batary P et al (2013) Contrasting effects of mass-flowering crops on

725 bee pollination of hedge plants at different spatial and temporal scales. *Ecol Appl* 23(8):1938-

726 1946. <https://doi.org/10.1890/12-2012.1>

727 Krewenka KM, Holzschuh A, Tschardt T, Dormann CF (2011) Landscape elements as potential

728 barriers and corridors for bees, wasps and parasitoids. *Biol Conserv* 144(6):1816-1825.

729 <https://doi.org/10.1016/j.biocon.2011.03.014>

730 Kreyer D, Oed A, Walther-Hellwig K, Frankl R (2004) Are forests potential landscape barriers for

731 foraging bumblebees? Landscape scale experiments with *Bombus terrestris* agg. and *Bombus*

732 *pascuorum* (Hymenoptera, Apidae). *Biol Conserv* 116(1):111-118.

733 [https://doi.org/10.1016/s0006-3207\(03\)00182-4](https://doi.org/10.1016/s0006-3207(03)00182-4)

734 Levey DJ, Bolker BM, Tewksbury JJ, Sargent S, Haddad NM (2005) Effects of landscape corridors on

735 seed dispersal by birds. *Science* 309(5731):146-148. <https://doi.org/10.1126/science.1111479>

736 Lindgren J, Lindborg R, Cousins SAO (2018) Local conditions in small habitats and surrounding

737 landscape are important for pollination services, biological pest control and seed predation.

738 *Agric Ecosyst Environ* 251:107-113. <https://doi.org/10.1016/j.agee.2017.09.025>

739 Lövei GL, Macleod A, Hickman JM (1998) Dispersal and effects of barriers on the movement of the

740 New Zealand hover fly *Melanostoma fasciatum* (Dipt., Syrphidae) on cultivated land. *J Appl*

741 *Entomol* 122(2-3):115-120.

742 Meirmans PG, Hedrick PW (2011) Assessing population structure: F-ST and related measures. Mol
743 Ecol Resour 11(1):5-18. <https://doi.org/10.1111/j.1755-0998.2010.02927.x>

744 Meyer B, Jauker F, Steffan-Dewenter I (2009) Contrasting resource-dependent responses of hoverfly
745 richness and density to landscape structure. Basic Appl Ecol 10(2):178-186.
746 <https://doi.org/10.1016/j.baae.2008.01.001>

747 Montague-Drake RM, Lindenmayer DB, Cunningham RB (2009) Factors affecting site occupancy by
748 woodland bird species of conservation concern. Biol Conserv 142(12):2896-2903.
749 <https://doi.org/10.1016/j.biocon.2009.07.009>

750 Morellet N, Van Moorter B, Cargnelutti B et al (2011) Landscape composition influences roe deer
751 habitat selection at both home range and landscape scales. Landsc Ecol 26(7):999-1010.
752 <https://doi.org/10.1007/s10980-011-9624-0>

753 Mrotzek R, Halder M, Schmidt W (1999) The effect of wild boars for the dispersal of plant diaspores.
754 Verh Ges Ökol 29:437-443.

755 Müller N, Schneller JJ, Holderegger R (2000) Variation in breeding system among populations of the
756 common woodland herb *Anemone nemorosa* (Ranunculaceae). Plant Syst Evol 221(1-2):69-76.
757 <https://doi.org/10.1007/bf01086381>

758 Müller-Schneider P (1986) Verbreitungsbiologie der Blütenpflanzen Graubündens. Veröff geobot Inst
759 ETH Stift Rübel Zürich 85:1-263.

760 Murphy HT, Lovett-Doust J (2004) Context and connectivity in plant metapopulations and landscape
761 mosaics: does the matrix matter? Oikos 105(1):3-14. <https://doi.org/10.1111/j.0030-1299.2004.12754.x>

762

763 Naaf T, Feigs JT, Huang S et al (2021) Sensitivity to habitat fragmentation across European landscapes
764 in three temperate forest herbs. Landsc Ecol. <https://doi.org/10.1007/s10980-021-01292-w>

765 Nakamura S, Kudo G (2019) The influence of garden flowers on pollinator visits to forest flowers:
766 comparison of bumblebee habitat use between urban and natural areas. Urban Ecosystems
767 22(6):1097-1112. <https://doi.org/10.1007/s11252-019-00891-5>

768 Pinheiro J, Bates D, DebRoy S, Sarkar D, Team RC (2019) nlme: Linear and nonlinear mixed effects

769 models. R package version 3.1-143.

770 Pope N (2020) corMLPE: A correlation structure for symmetric relational data. R package version
771 0.0.2.

772 Proesmans W, Bonte D, Smaghe G, Meeus I, Verheyen K (2019) Importance of forest fragments as
773 pollinator habitat varies with season and guild. *Basic Appl Ecol* 34:95-107.
774 <https://doi.org/10.1016/j.baae.2018.08.004>

775 Proesmans W, Smaghe G, Meeus I, Bonte D, Verheyen K (2019) The effect of mass-flowering
776 orchards and semi-natural habitat on bumblebee colony performance. *Landsc Ecol* 34(5):1033-
777 1044. <https://doi.org/10.1007/s10980-019-00836-5>

778 Radford JQ, Bennett AF (2007) The relative importance of landscape properties for woodland birds in
779 agricultural environments. *J Appl Ecol* 44(4):737-747. [https://doi.org/10.1111/j.1365-
780 2664.2007.01327.x](https://doi.org/10.1111/j.1365-2664.2007.01327.x)

781 Redbo-Torstensson P, Berg H (1995) Seasonal cleistogamy - a conditional strategy to provide
782 reproductive assurance. *Acta Bot Neerl* 44(3):247-256.

783 Redhead JW, Dreier S, Bourke AFG et al (2016) Effects of habitat composition and landscape
784 structure on worker foraging distances of five bumble bee species. *Ecol Appl* 26(3):726-739.
785 <https://doi.org/10.1890/15-0546>

786 Riedinger V, Mitesser O, Hovestadt T, Steffan-Dewenter I, Holzschuh A (2015) Annual dynamics of
787 wild bee densities: attractiveness and productivity effects of oilseed rape. *Ecology* 96(5):1351-
788 1360. <https://doi.org/10.1890/14-1124.1>

789 Ruedisser J, Walde J, Tasser E, Fruehauf J, Teufelbauer N, Tappeiner U (2015) Biodiversity in cultural
790 landscapes: influence of land use intensity on bird assemblages. *Landsc Ecol* 30(10):1851-1863.
791 <https://doi.org/10.1007/s10980-015-0215-3>

792 Saïd S, Servanty S (2005) The influence of landscape structure on female roe deer home-range size.
793 *Landsc Ecol* 20(8):1003-1012. <https://doi.org/10.1007/s10980-005-7518-8>

794 Schaumann F, Heinken T (2002) Endozoochorous seed dispersal by martens (*Martes foina*, *M.*
795 *martes*) in two woodland habitats. *Flora* 197(5):370-378.

796 00053

797 Schirmel J, Albrecht M, Bauer PM, Sutter L, Pfister SC, Entling MH (2018) Landscape complexity
798 promotes hoverflies across different types of semi-natural habitats in farmland. *J Appl Ecol*
799 55(4):1747-1758. <https://doi.org/10.1111/1365-2664.13095>

800 Schmidt M, Mölder A, Schönfelder E, Engel F, Schmiedel I, Culmsee H (2014) Determining ancient
801 woodland indicator plants for practical use: A new approach developed in northwest Germany.
802 *For Ecol Manag* 330(0):228-239. <https://doi.org/http://dx.doi.org/10.1016/j.foreco.2014.06.043>

803 Schmidt T, Arens P, Smulders MJM et al (2009) Effects of landscape structure on genetic diversity of
804 *Geum urbanum* L. populations in agricultural landscapes. *Flora* 204(7):549-559.
805 <https://doi.org/10.1016/j.flora.2008.07.005>

806 Shirreffs DA (1985) Biological flora of the British isles - *Anemone nemorosa* L. *J Ecol* 73(3):1005-1020.
807 <https://doi.org/10.2307/2260164>

808 Stehlik I, Holderegger R (2000) Spatial genetic structure and clonal diversity of *Anemone nemorosa* in
809 late successional deciduous woodlands of Central Europe. *J Ecol* 88(3):424-435.
810 <https://doi.org/10.1046/j.1365-2745.2000.00458.x>

811 Thurfjell H, Ball JP, Ahlen PA, Kornacher P, Dettki H, Sjöberg K (2009) Habitat use and spatial patterns
812 of wild boar *Sus scrofa* (L.): agricultural fields and edges. *Eur J Wildl Res* 55(5):517-523.
813 <https://doi.org/10.1007/s10344-009-0268-1>

814 Tillmann JE (2011) Bewertung von Maisäckern als Lebensraum für die Tierwelt der Agrarlandschaft
815 mit Hilfe von Fotofallen. *Umw Raum* 2:43-58.

816 Toma Y, Imanishi J, Yokogawa M et al (2015) Factors affecting the genetic diversity of a perennial
817 herb *Viola grypceras* A. Gray var. *grypceras* in urban fragmented forests. *Landsc Ecol*
818 30(8):1435-1447. <https://doi.org/10.1007/s10980-015-0197-1>

819 Tomimatsu H, Ohara M (2003) Genetic diversity and local population structure of fragmented
820 populations of *Trillium camschatcense* (Trilliaceae). *Biol Conserv* 109(2):249-258.
821 [https://doi.org/10.1016/s0006-3207\(02\)00153-2](https://doi.org/10.1016/s0006-3207(02)00153-2)

822 Trombulak SC, Frissell CA (2000) Review of ecological effects of roads on terrestrial and aquatic

823 communities. *Conserv Biol* 14(1):18-30. <https://doi.org/10.1046/j.1523-1739.2000.99084.x>

824 Türke M, Andreas K, Gossner MM et al (2012) Are gastropods, rather than ants, important dispersers
825 of seeds of myrmecochorous forest herbs? *Am Nat* 179(1):124-131.
826 <https://doi.org/10.1086/663195>

827 Van Reeth C, Michel N, Bockstaller C, Caro G (2019) Influences of oilseed rape area and aggregation
828 on pollinator abundance and reproductive success of a co-flowering wild plant. *Agric Ecosyst*
829 *Environ* 280:35-42. <https://doi.org/10.1016/j.agee.2019.04.025>

830 Van Rossum F, Echchgadda G, Szabadi I, Triest L (2002) Commonness and long-term survival in
831 fragmented habitats: *Primula elatior* as a study case. *Conserv Biol* 16(5):1286-1295.
832 <https://doi.org/10.1046/j.1523-1739.2002.01162.x>

833 Vandepitte K, Jacquemyn H, Roldan-Ruiz I, Honnay O (2007) Landscape genetics of the self-
834 compatible forest herb *Geum urbanum*: effects of habitat age, fragmentation and local
835 environment. *Mol Ecol* 16(19):4171-4179. <https://doi.org/10.1111/j.1365-294X.2007.03473.x>

836 Vellend M (2004) Parallel effects of land-use history on species diversity and genetic diversity of
837 forest herbs. *Ecology* 85(11):3043-3055. <https://doi.org/10.1890/04-0435>

838 Verheyen K, Honnay O, Motzkin G, Hermy M, Foster DR (2003) Response of forest plant species to
839 land-use change: a life-history trait-based approach. *J Ecol* 91(4):563-577.
840 <https://doi.org/10.1046/j.1365-2745.2003.00789.x>

841 Vray S, Rollin O, Rasmont P, Dufrêne M, Michez D, Dendoncker N (2019) A century of local changes in
842 bumblebee communities and landscape composition in Belgium. *J Insect Conserv* 23(3):489-501.
843 <https://doi.org/10.1007/s10841-019-00139-9>

844 Westerbergh A, Saura A (1994) Gene flow and pollinator behavior in *Silene dioica* populations. *Oikos*
845 71(2):215-224. <https://doi.org/10.2307/3546269>

846 Westphal C, Steffan-Dewenter I, Tschardt T (2003) Mass flowering crops enhance pollinator
847 densities at a landscape scale. *Ecol Lett* 6(11):961-965. <https://doi.org/10.1046/j.1461-0248.2003.00523.x>

848

849 Whigham DE (2004) Ecology of woodland herbs in temperate deciduous forests. *Annu Rev Ecol Evol*

850 Syst 35:583-621. <https://doi.org/10.1146/annurev.ecolsys.35.021103.105708>

851 Wratten SD, Bowie MH, Hickman JM, Evans AM, Sedcole JR, Tylianakis JM (2003) Field boundaries as
852 barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land. *Oecologia*
853 134(4):605-611. <https://doi.org/10.1007/s00442-002-1128-9>

854 Zurbuchen A, Bachofen C, Müller A, Hein S, Dorn S (2010) Are landscape structures insurmountable
855 barriers for foraging bees? A mark-recapture study with two solitary pollen specialist species.
856 *Apidologie* 41(4):497-508. <https://doi.org/10.1051/apido/2009084>

857

859 **Table 1** Landscape metrics used to study the effects of the landscape composition and configuration on the population genetic structure of the temperate forest herbs
 860 *Anemone nemorosa*, *Oxalis acetosella*, and *Polygonatum multiflorum*. For each landscape metric, the columns provide the definition and the expected effects on gene flow based
 861 on available literature (references indicated by superscripts are provided in Table S5.1). The minimum, median and maximum value of each landscape metric across all populations
 862 for a 1000 m buffer zone is given in parentheses. The potential mechanisms via pollen- or seed-dispersal vectors behind expected effects are detailed in Table S5.2

Landscape metric	Definition (min, median, max)	Expected effect on gene flow among populations ^a			
		Species: Vector:	<i>Anemone nemorosa</i> <i>Oxalis acetosella</i> hoverflies, bees	<i>Oxalis acetosella</i> wild boar, deer	<i>Polygonatum multiflorum</i> bumblebees
Area-based metrics					
	Percent cover of ...				
FOREST	deciduous forest (2.5; 8; 23.6)	- 40, 46, 81, 84, 0 51, 86, + 30, 50, 54, 59, 60, 70	+ 55, 56	- 22, 40, 46, 81, 84, 0 51	+ 5, 9, 20, 29, 31, 34, 38, 63, 67, 78
GRASS	grassland in general (2.9; 18.7; 78.9)	0+ 3, 11, 39, 45, 66, 72, 73	0+ 2, 71	0+ 22, 37, 80	0+ 5, 23, 52, 63
SEM-NAT-GRASS	semi-natural grassland (0; 1.3; 7.3)	+ 3, 11, 39, 45, 66, 72, 73	0+ 2, 71	- 64, + 11, 17, 22, 61, 80	+ 5, 23, 52, 63
SEM-NAT-VEG	other semi-natural vegetation (0; 0.7; 8.9)	+ 3, 11, 39, 66, 72	0	- 64, + 11, 17, 61	+ 23
ARABLE	arable land in general (10.6; 58.8; 81.9)	- 27, -+ 25, 50, 74	+ 2, 58, 71	- 27	- 5, 29, 63, 67, 68
RAPE	arable land cultivated with oilseed rape (0; 4; 17.3)	- 35, 36, 53, 79, -+ 44, + 7, 25, 65	0	- 17, 35, 36, 0 22, -+ 44, 83, + 26, 33, 43, 82	- 5, 29, 63, 67, 68
MAIZE	arable land cultivated with maize (0; 8.1; 43.4)	- 27	+ 2, 8, 32, 41, 71, 76	- 27	- 5, 29, 63, 67, 68
CEREAL	arable land cultivated with other cereals (2; 21.4; 52.4)	-+ 25, 50, 74	+ 2, 58, 71	0	- 5, 29, 63, 67, 68
ORCHARD	traditional grassland orchards (0; 0.1; 3)	- 35, + 3, 11, 39, 66, 72	0	- 61	0
SETTLE	settlement area (0; 4.3; 19)	0	- 8, 13	- 57, -+ 15, 22	- 5, 13, 67
	+ conditioning variable: PROPGREEN = Prop. of green urban areas				
Linear landscape elements					
	Relative length [m ha ⁻¹] of ...				
LWOOD	hedgerows and tree lines (0.4; 27.3; 135.3)	- 85, -+ 12, 42, 45, + 1, 16, 21, 25, 59, 70	-+ 69, 75	-+ 12, 14, 21, 42	0+ 18, 24, 47, + 4, 5, 20, 34, 38
	+ conditioning variable: O:P_LWOOD = Orthogonal-to-parallel ratio				
LWATER	water courses (incl. draining ditches) (0.9; 11.8; 37.3)	-+ 12, + 1	-+ 69, 75	-+ 12	0
	+ conditioning variable: O:P_LWATER = Orthogonal-to-parallel ratio				
LFRINGE	broad herbaceous fringes (0; 3.3; 21.3)	-+ 12,	-+ 69, 75	-+ 12, 43,	0+ 5, 52, 63
	+ conditioning variable: O:P_LFRINGE = Orthogonal-to-parallel ratio	+ 3, 11, 39, 45, 66, 72, 73		+ 11, 17, 22, 37, 61	
LROAD	roads (0.7; 15.6; 36.2)	- 48, -+ 12	-+ 10, 13, 69, 75, 77	-+ 6, 12	- 5, 13, 19
	+ conditioning variable: O:P_LROAD = Orthogonal-to-parallel ratio				
Index metrics					
SHANNON	Diversity of land-use types (0.9; 1.7; 2.1)	+ 11, 72	0	+ 11, 72	+ 29, 67
EDGEDEN	Land-use parcel edge density [m ha ⁻¹] (55; 131; 294)	-+ 49, + 28, 72	- 62, 69	+ 72	- 69, + 67, 72

863 ^a Effect codes: - negative, + positive, -+ negative or positive depending on conditions, 0 no effect, 0+ no or positive effect depending on conditions

864 **Table 2** Summary of landscape effects on allelic richness (A_r), expected (H_e) and observed heterozygosity (H_o) and
865 the inbreeding coefficient (F) as resulting from linear mixed-effects models at the node level, separately for (a)
866 *Anemone nemorosa*, (b) *Oxalis acetosella*, and (c) *Polygonatum multiflorum*. All important effects (importance
867 value ≥ 0.5 , see main text), are symbolized as follows: / positive effect, \ negative effect, X interactive effect (see
868 Figure 3), \cap and U unimodal effect with maximum and minimum, respectively, at an intermediate level of the
869 landscape metric, / \cap , \ \cap and /U asymmetric unimodal effects with positive or negative trend, respectively. In
870 addition, R^2 values for each model are provided: marginal R^2 (variation explained by fixed effects, i.e. jointly by
871 basic population genetic determinants and landscape metrics), landscape R^2 (variation explained uniquely by
872 landscape metrics) and the percentage of the marginal R^2 that can be uniquely attributed to landscape effects
873 (%Landscape). See Table 1 for explanations on variable names. Numbers added to the variable names correspond
874 to the most influential buffer distance in meters. See Table S6.1 for complete model results. Visualizations of the
875 effects are presented in Figures 2, 3, and S6.1 to S6.3

Landscape metrics	A_r	H_e	H_o	F
(a) <i>Anemone nemorosa</i>				
FOREST_2000			\	
ARABLE_2000	/			
RAPE_500				/ \cap
MAIZE_1000		/		
pcSETTLE_250 ^a			/U	
pcSETTLE_500 ^b		/		
LROAD_250				\ \cap
LWOOD_2000	/ \cap			
LFRINGE_500	\			
Marginal R^2	0.74	0.38	0.60	0.48
Landscape R^2	0.56	0.29	0.58	0.41
% Landscape	76.4	74.9	97.7	84.7
(b) <i>Oxalis acetosella</i>				
SEMSTATGRASS_1000			U	
SEMSTATVEG_500		/ \cap	/	
MAIZE_250		\ \cap		
MAIZE_1000				/ \cap
pcLWOODGRASS_1000 ^c				/
LFRINGE_2000				\
LROAD_500	\cap			
EDGEEDEN_125			\	
Marginal R^2	0.42	0.57	0.42	0.47
Landscape R^2	0.08	0.30	0.19	0.47
% Landscape	19.5	53.0	45.2	99.5
(c) <i>Polygonatum multiflorum</i>				
FOREST_2000				/
SEMSTATGRASS_250		\cap		
pcARABvsGRASS_2000 ^d	\	\		
SETTLE_250				\
SETTLE_1000	\	\		
pcSETTLE_1000 ^e			\	
LWATER_1000			X	
LWATER_2000	/			
SHANNON_250	/			
LROAD_2000				/
Marginal R^2	0.76	0.38	0.19	0.58

Landscape R^2	0.42	0.24	0.01	0.42
% Landscape	55.9	63.6	4.1	72.3

876 ^a Principal component from SETTLE_250 ($r = 0.94$) and LROAD_250 ($r = 0.94$)

877 ^b Principal component from SETTLE_500 ($r = 0.93$), LROAD_500 ($r = 0.89$) and EDGEDEN_500 ($r = 0.90$)

878 ^c Principal component from GRASS_1000 ($r = 0.94$) and LWOOD_1000 ($r = 0.94$)

879 ^d Principal component from CEREAL_2000 ($r = 0.97$), RAPE_2000 ($r = 0.90$), and GRASS_2000 ($r = -0.95$)

880 ^e Principal component from SETTLE_1000 ($r = 0.95$) and LROAD_1000 ($r = 0.95$)

881

882 **Table 3** Summary of landscape effects on measures of pairwise genetic differentiation (G''_{ST} and D_{PS}) as resulting
883 from MLPE models at the link level, separately for (a) *Anemone nemorosa*, (b) *Oxalis acetosella*, and (c)
884 *Polygonatum multiflorum*. All important effects, i.e. those with an importance value ≥ 0.5 (see main text), are
885 symbolized as follows: / positive effect, \ negative effect, X interactive effect (see Figure 3), \cap and U unimodal
886 effect with maximum and minimum, respectively, at an intermediate level of the landscape metric, / \cap , \ \cap and
887 /U asymmetric unimodal effects with positive or negative trend, respectively. In addition, R^2 values for each
888 model are provided: marginal R^2 (variation explained by fixed effects, i.e. jointly by basic population genetic
889 determinants and landscape metrics), landscape R^2 (variation explained uniquely by landscape metrics) and the
890 percentage of the marginal R^2 that can be uniquely attributed to landscape effects (%Landscape). See Table 1 for
891 explanations on variable names. The ratio added to each variable name corresponds to the most influential
892 width-to-length ratio of the landscape strips. See Table S6.2 for complete model results. Visualizations of the
893 effects are presented in Figures 2, 3, and S6.1 to S6.3

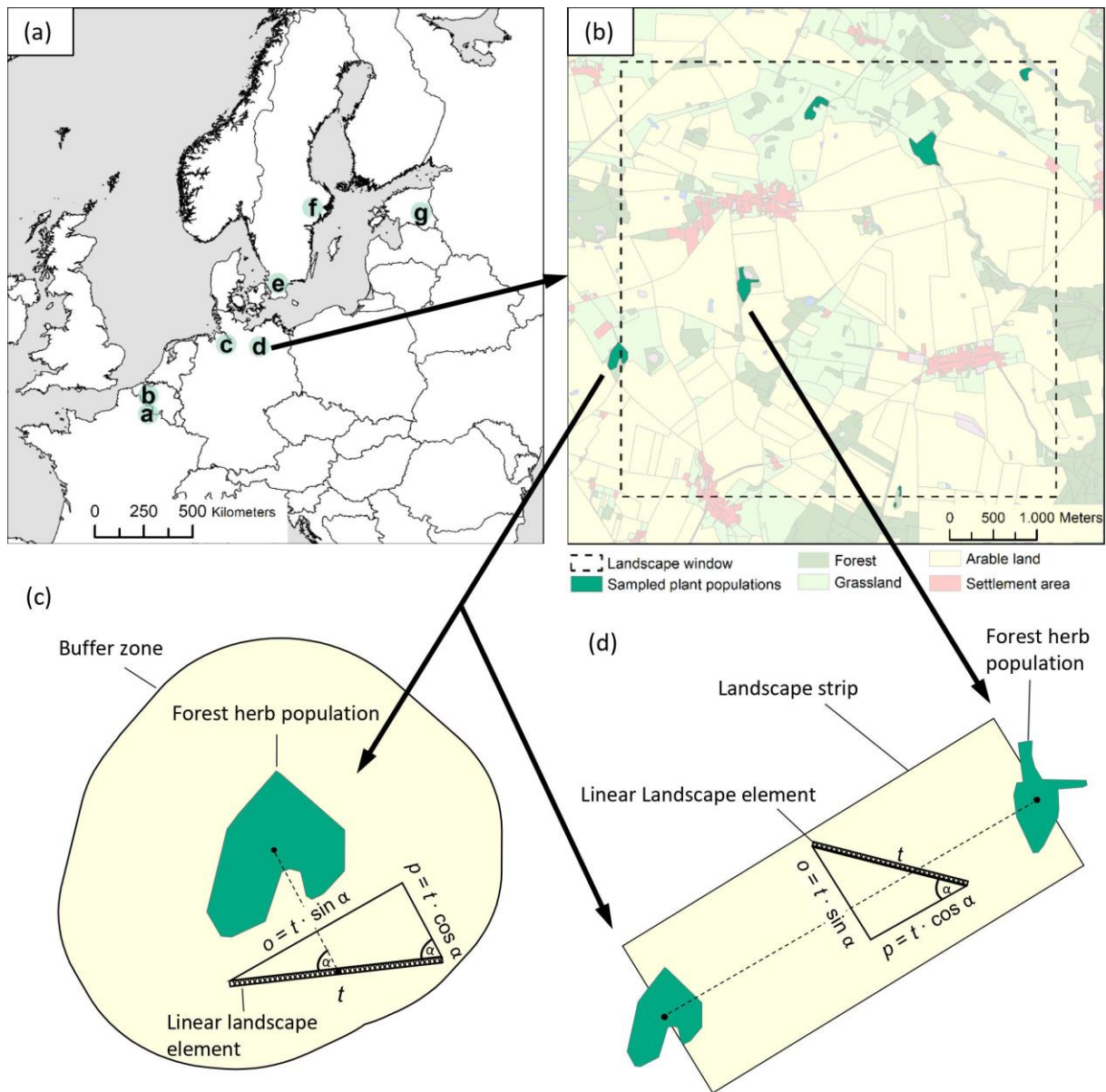
894

Landscape metrics	G''_{ST}	D_{PS}
(a) <i>Anemone nemorosa</i>		
FOREST_1:3	/	\cap
pcARABvsGRASS_1:3 ^a	X	
pcARABvsGRASS_1:2 ^b		X
LFRINGE_1:3	/	/
Marginal R^2	0.16	0.25
Landscape R^2	0.16	0.25
% Landscape	99.2	100.0
(b) <i>Oxalis acetosella</i>		
FOREST_1:3	X	X
ARABLE_1:3		/
RAPE_1:2	X	
LWOOD_1:7		X
LWATER_1:3	\	
LROAD_1:5	\	
SHANNON_2:3		\
Marginal R^2	0.11	0.10
Landscape R^2	0.11	0.09
% Landscape	99.9	99.4
(c) <i>Polygonatum multiflorum</i>		
FOREST_1:2	X	
SEMSTATGRASS_1:3	/U	/
ORCHARD_2:3		/
LWOOD_1:5		\
LROAD_1:7	X	
LROAD_1:2		\
Marginal R^2	0.18	0.33
Landscape R^2	0.17	0.30
% Landscape	95.7	91.4

895 ^a Principal component from CEREAL_1:3 ($r = 0.95$), RAPE_1:3 ($r = 0.90$) and GRASS_1:3 ($r = -0.92$)

896 ^b Principal component from CEREAL_1:2 ($r = 0.96$), RAPE_1:2 ($r = 0.90$) and GRASS_1:2 ($r = -0.92$)

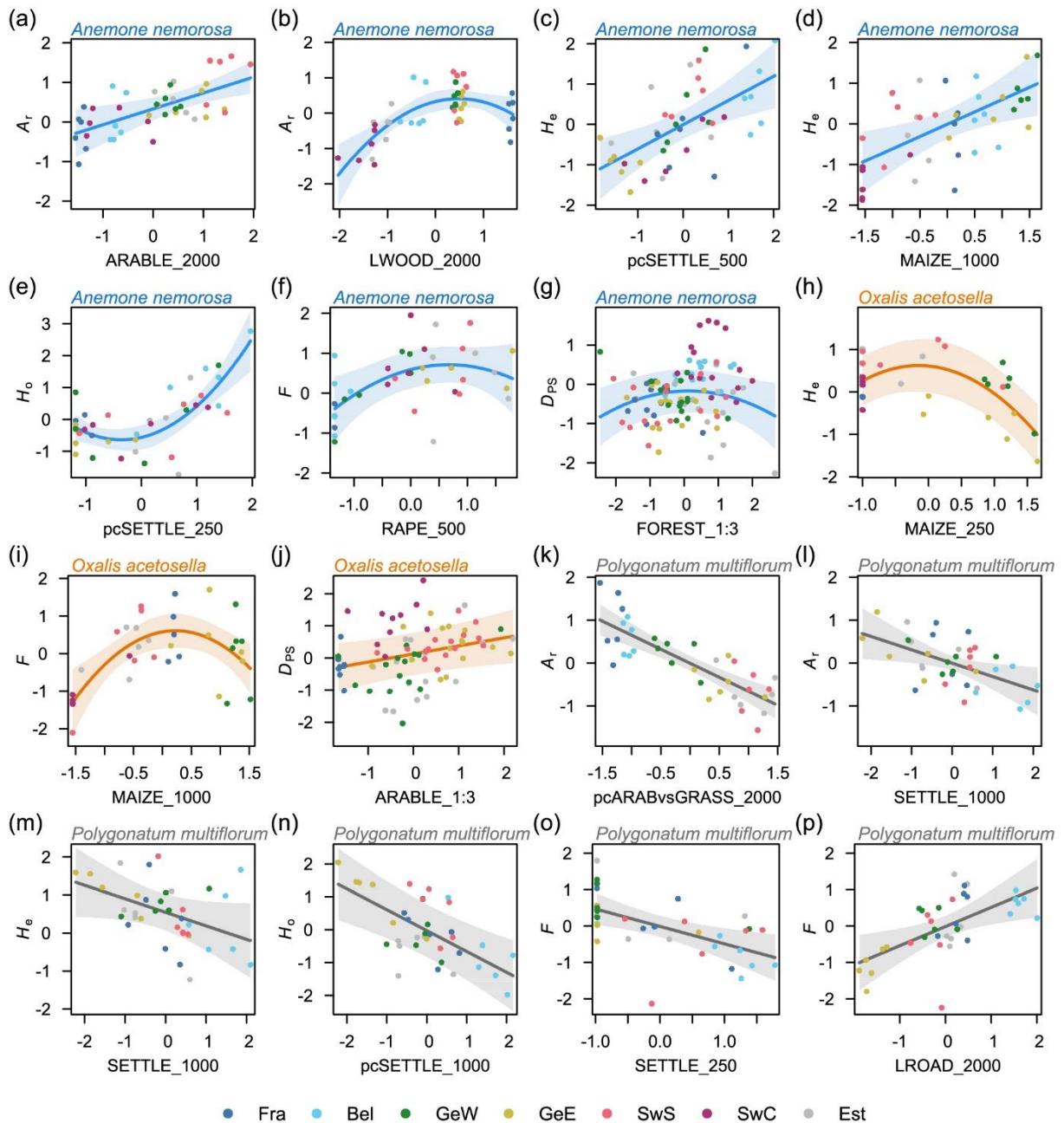
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901 **Fig. 1** Overview on the study design. The seven $5 \times 5 \text{ km}^2$ landscape windows (a) are spread across
 902 temperate Europe from North France (A) over Belgium (B), West Germany (C), East Germany (D), and
 903 South Sweden (E) up to Central Sweden (F) and Estonia (G). In each agricultural landscape, we
 904 surveyed up to six populations of each species, here exemplified for *Polygonatum multiflorum* in East
 905 Germany (b). See Supp. Inf. 1 for detailed land-use maps of each landscape window, including
 906 locations of all sampled populations. The landscape surrounding the populations was analysed at the
 907 node level, i.e., in buffer zones of distances between 125 and 2000 m (c), and at the link level, i.e. in

908 landscape strips between populations with width-to-length ratios between 1:7 and 2:3 (d). For linear
909 landscape elements within buffer zones and landscape strips, we calculated not only the total length
910 (t), but also the parallel (p) and orthogonal (o) length component in relation to the gene dispersal
911 direction
912
913



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915 **Fig. 2** Visualization of landscape effects (cf. Tables 2 and 3) on population genetic variables of

916 *Anemone nemorosa* (*A. nem.*), *Oxalis acetosella* (*O. ace.*) and *Polygonatum multiflorum* (*P. mul.*).

917 Shown are those effects, which are directly related to our hypotheses and therefore discussed in the

918 main text. Panels display the partial slopes and residuals as well as the 95% confidence band. All

919 variables are scaled in standard deviation units. Colours of partial residuals represent the different

920 landscape windows: France (Fra), Belgium (Be), West Germany (GeW), East Germany (GeE), South

921 Sweden (SwS), Central Sweden (SwC), and Estonia (Est). Population genetic variables are allelic

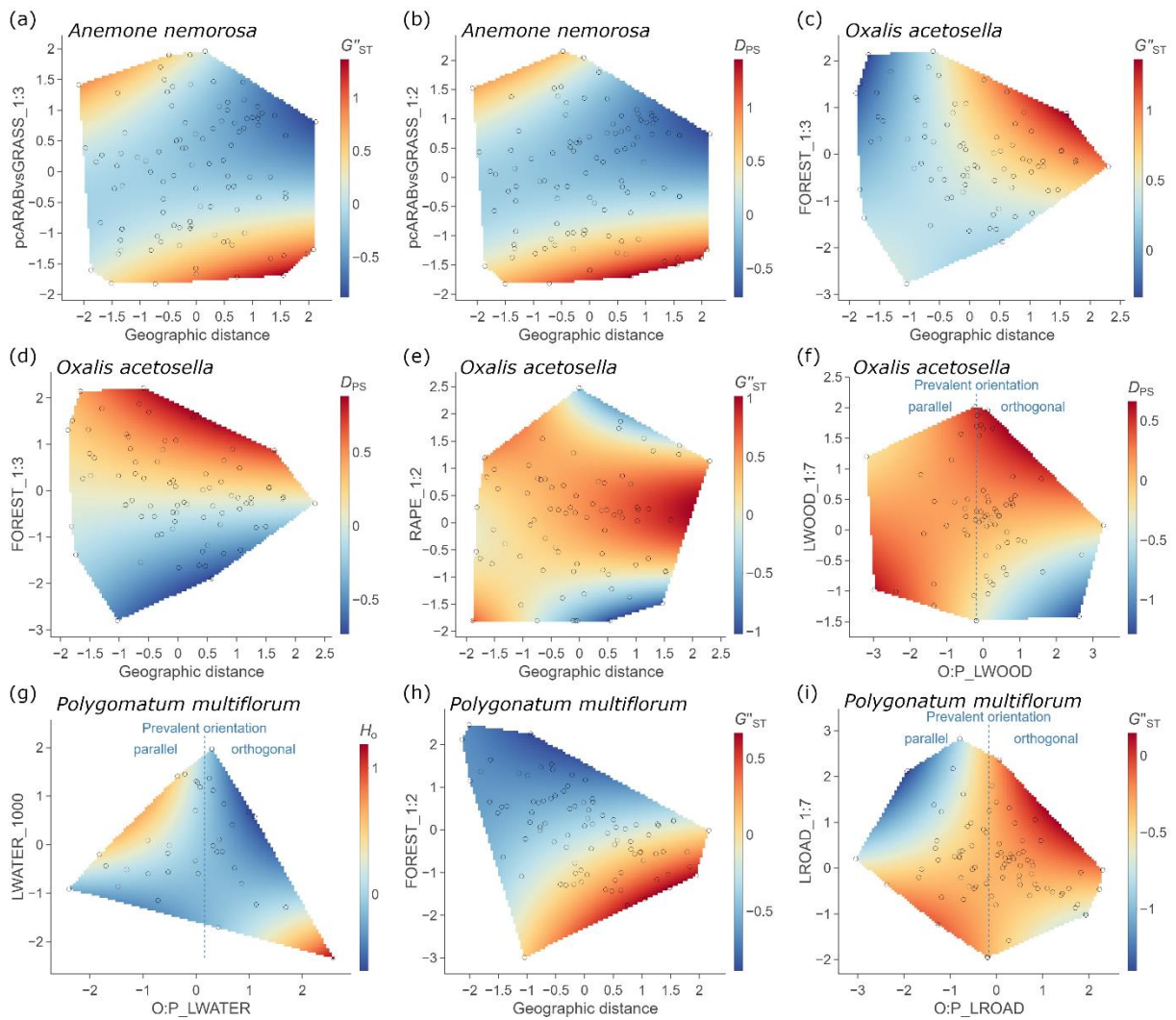
922 richness (A_r), expected (H_e) and observed heterozygosity (H_o), inbreeding index (F), and genetic

923 differentiation (D_{ps}). The landscape metrics ARABLE, FOREST, MAIZE, RAPE, and SETTLE refer to the
924 percent cover of arable land, deciduous forest, maize, oilseed rape and settlement area, respectively.
925 LWOOD and LROAD refer to the relative length of hedgerows/tree lines and roads, respectively.
926 pcSETTLE is a principal component reflecting settlement area, road density and edge density (cf.
927 Table 2). pcARABvsGRASS is a principal component reflecting the trade-off between arable land
928 (cereals and oilseed rape) on the one hand and grassland on the other hand (cf. Table 2). Numbers or
929 ratios added to the variable names correspond to the most influential buffer distance in meters or
930 the most influential width-to-length ratio of the landscape strips, respectively

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Fig. 3 Visualizations of interactive effects (cf. Tables 2 and 3) of landscape metrics (x- and y-axis) on

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population genetic variables of *Anemone nemorosa* (*A. nem.*), *Oxalis acetosella* (*O. ace.*) and

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Polygonatum multiflorum (*P. mul.*) as heatmap. Only the area covered by the values of both

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explanatory variables (overlaid as points) is plotted. All variables are scaled in standard deviation

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units. Population genetic variables are measures of genetic differentiation (D_{PS} and G''_{ST}) and

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observed heterozygosity (H_0). The landscape metrics FOREST and RAPE refer to the percent cover of

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deciduous forest and oilseed rape, respectively. LROAD, LWATER and LWOOD refer to the relative

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length of roads, water courses and hedgerows/treelines, respectively. The prefix O:P refers to

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orthogonal-to-parallel length ratio. pcARABvsGRASS is a principal component reflecting the trade-off

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between arable land (cereals and oilseed rape) on the one hand and grassland on the other hand (cf.

945 Table 3). Numbers or ratios added to the variable names correspond to the most influential buffer
946 distance in meters or the most influential width-to-length ratio of the landscape strips, respectively
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948