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1 **Response of understory plant communities and traits to past land**
2 **use and coniferous plantation**

3
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20
21

22 **Abstract**

23 **Questions:** How did past land use and conifer plantation affect understory plant communities? What
24 plant traits explain understory vegetation response to agricultural past land use and coniferous
25 plantation?

26 **Location:** Forest of Orléans (50 000 ha), Loiret, northern central France.

27 **Methods:** Canopy cover, herb layer composition, litter and soil properties were measured in 80 100 m²
28 plots sampled in plantations of *Pinus sylvestris* or *P. nigra* vs. natural regenerations of *Quercus petraea*
29 and *Q. robur* along a gradient of forest continuity (using historical maps and aerial photos from 1840,
30 1949 and 2006). We related 15 plant traits to past land use and tree species using RLQ and fourth-corner
31 analyses.

32 **Results:** The magnitude of past land use effect largely exceeded that of coniferous plantation. Post-
33 agricultural forests, even 150 years after afforestation, differed from ancient forests in soil properties
34 (thinner humus layer, higher phosphorus content, higher pH and lower C/N ratio) and plant traits.
35 Ancient forests hosted more forest core species, stress-tolerant, competitive species and bryophytes, but
36 fewer ruderals, annuals/biennials, shrubs and trees and nutrient-demanding species, and had lower
37 specific leaf area and higher leaf dry matter content. Conifer plantations had a thicker humus layer,
38 lower pH and higher C/N ratio than deciduous forests, and hosted more light-demanding species but less
39 forest core species. Importantly, differences in soil and plant traits between conifer plantations and
40 naturally regenerated deciduous stands were discernible in both recent and ancient forests, indicating
41 that tree species lastingly influence ecosystem functioning.

42 **Conclusions:** Past land use and coniferous plantation resulted in different understory plant communities
43 and traits under pine plantations and naturally regenerated oak stands. These differences were driven by
44 soil acidification, litter decomposition rate, light conditions, canopy development, soil disturbance, stand
45 management, and dispersal and recruitment limitations. Coniferous plantations slowed down the
46 recovery of post-agricultural forests to ancient deciduous forest conditions. Applying natural
47 regeneration and favouring native deciduous tree species thus helps recreate or maintain ancient forest
48 plant communities.

49
50 **Keywords:** ancient forest, coniferous plantation, functional trait, land use history, tree species
51 substitution, restoration.

52
53 **Nomenclature:** French BDTFX flora nomenclature and European BDNBE bryophyte nomenclature
54 (<http://www.tela-botanica.org>).

55 **Introduction**

56 Two major changes have occurred in European forest landscapes over the last 250 years. First, forest
57 cover has globally increased in many European countries since the Industrial Revolution (Mather et al.
58 1999) due to rural exodus and agricultural land set-aside (Cramer et al. 2008). In France and several
59 other European countries, many former agricultural lowlands have been planted with *Pinus* and *Picea*
60 species (see <http://inventaire-forestier.ign.fr/spip/spip.php?rubrique80> and Leuschner et al. (2013)).
61 Second, large areas of deciduous forests have been converted to coniferous forests in western and
62 central Europe since the beginning of the 20th century, to develop more profitable industrial forestry
63 (Wulf & Heinken 2008). There is still intense debate on whether plantation forests help to maintain
64 biodiversity or instead degrade it (Bremer & Farley 2010). Some authors consider that plantations can
65 accelerate the regeneration of native understory species and thus help conserve biodiversity (Boothroyd-
66 Roberts et al. 2013), while others have shown no effect or a decrease in the number or the diversity of
67 forest species (Aubin et al. 2008; Tullus et al. 2013). The value of plantations for biodiversity actually
68 depends on several factors that are not always easy to disentangle: (i) tree species identity (ii) the nature
69 of the earlier land cover (iii) proximity to native vegetation source, (iv) plantation silviculture and (v)
70 soil conditions.

71 The role of tree species on understory plant communities is largely documented (Barbier et al. 2008).
72 The overstory directly affects the understory through its impact on light availability (Wulf & Naaf 2009)
73 and by competition for water and nutrients (Barbier et al. 2009), especially on acidic sites (Hårdtle et al.
74 2003). Canopy composition also indirectly affects understory through litter quality and decomposability
75 (Hagen-Thorn et al. 2004), which influences topsoil nutrient availability and acidity (Augusto et al.
76 2015), the soil fauna (Reich et al. 2005) and the recruitment and growing conditions of seeds (Baeten et
77 al. 2009a). Understory plant composition differs between coniferous and deciduous stands and can
78 depend on the deciduous tree species being compared (Barbier et al. 2008).

79 Past land use lastingly influences forest soil properties and understory vegetation, which gave rise to the
80 concept of ancient forest (AF) and ancient forest species (AFS) (Hermy & Verheyen 2007). Forest soils
81 on former arable fields are mostly differentiated from ancient forest by higher soil pH and phosphorus
82 content, and lower nitrogen and carbon content (Sciama et al. 2009; De Schrijver et al. 2012). The
83 association between forest continuity and ancient forest species is mainly related to their low dispersal
84 capacity and low recruitment success in post-agricultural forests (Hermy & Verheyen 2007); recruitment
85 of ancient forest species in post-agricultural forests is partly determined by interspecific competition,
86 soil characteristics and light availability (Baeten et al. 2009b).

87 Understory-overstory relationships have generally been investigated without considering past land use
88 (Barbier et al. 2008; Kooijman 2010). Although several studies on land use legacies have investigated
89 the influence of tree species or regeneration mode (Aubin et al. 2008; Tullus et al. 2013; Thomaes et al.
90 2014), these have several limitations: (i) they did not include ancient forests as a control in their

91 sampling design, (ii) they explored a very short gradient of age since afforestation (<40 years) and (iii)
92 they rarely compared deciduous and coniferous species. To our knowledge, only one study investigated
93 the two gradients (Wulf & Heinken 2008) and found that deciduous stands did not guarantee higher
94 richness of forest specialists, and underlined the role of former land use on the colonisation of forest
95 species. There is still a need to explore the combined effects of past land use and tree species in more
96 detail (Thomaes et al. 2012), in particular how conifer introduction can influence the recovery rate of
97 understory plant communities to ancient forest conditions, using ancient coniferous forests as a control.
98 Our aim was to investigate to what extent conifer plantations modified the composition and the traits of
99 understory plant communities in recent and ancient forests compared with similar sites with deciduous
100 tree species, addressing the three following questions:

101 (1) How did past land use and tree species affect understory plant communities and their traits and
102 which of the two drivers was more influential?

103 (2) How did understory plant succession differ between conifers and deciduous forests in post-
104 agricultural stands?

105 (3) What plant traits (ecological performance, resource requirement, persistence, regeneration, or
106 dispersion traits) explain understory plant response to past land use and conifer plantation?

107 We assumed that understory communities were close in deciduous and coniferous post-agricultural
108 forests then diverged with increasing time since afforestation, due to several ecological filters: soil
109 acidification and litter accumulation, more pronounced in coniferous stands (Augusto et al. 2015),
110 subcanopy layer development, greater and faster in naturally regenerated deciduous stands, canopy
111 cover conditions, more open in pine forests (Augusto et al. 2003) and soil disturbance, more frequent in
112 plantations (Boch et al. 2013). We expected traits related to ecological performance, resource
113 requirement, persistence, regeneration and dispersion were linked to forest continuity (Verheyen et al.
114 2003), and traits related to ecological performance, resource requirement and regeneration were
115 associated with tree species (Barbier et al. 2008), but which of the two gradients was more influential on
116 plant communities and traits was difficult to predict. Following Wulf and Heiken (2008), we also
117 hypothesised that migration of forest core species [*sensu* Pellissier et al. (2013)] into recent coniferous
118 forests would be delayed compared with deciduous forests, due to both dispersal and recruitment
119 limitations.

120 **Methods**

121 **Study area, land use and forest management history**

122 The study was conducted in the Forest of Orléans (48°00'28" N, 2°09'39" E), which contains a central
123 block of ancient forest covering about 35,000 ha (Fig. 1). Elevation ranges from 107 to 174 m, climate is
124 oceanic, and mean annual precipitation is about 700 mm. The study area was dominated by oak (*Q.*

125 *petraea* and *Q. robur*), pine (*Pinus nigra* subsp. *laricio* var. *corsicana* and *P. sylvestris*) and mixed oak-
126 pine forests.

127 Forest cover reconstruction was based on two sources: historical maps of 1840 (Etat-Major map) and
128 aerial photographs taken in 1949. Forest patches in 1840 were vectorised following a precise protocol
129 (Favre et al. 2013) and then georeferenced with ArcGIS version 10.0 using about one reference point per
130 km². Land use in 1949 was checked on aerial photos. Current forest cover maps dating from 2006 were
131 provided by the French National Forest Inventory (www.inventaire-forestier.ign.fr).

132 Three forest age classes were defined in current forests: ancient forests (AF) (patches present in 1840,
133 1949 and 2006), intermediate-age forests (IF) (patches absent in 1840, present in 1949 and 2006), and
134 recent forests (RF) (patches absent in 1840 and 1949, present in 2006). In the following, the term "post-
135 agricultural forests" includes intermediate-age forests and recent forests.

136
137 These maps and other documents on State forest management history showed that the study area had
138 undergone two major changes in land use and forest management since the beginning of the 19th
139 century. First, a 23% net increase in forest area occurred between 1840 (59,300 ha) and 2006
140 (73,200 ha), the resultant of a gain (21,700 ha) and a loss (-7,800 ha), ancient forest thus covering
141 51,500 ha (Fig. 1). Second, conifers were extensively planted on former agricultural lands but also on
142 former deciduous forests. Conifers currently represent 40% of forest cover, compared with 6% of the
143 total in 1870, and were absent in 1840. For historical reasons, we cannot separate the effects of
144 regeneration mode from the effect of overstory composition, because Corsican and Scotch pines were
145 planted, whereas most of the time sessile and pedunculate oaks were naturally regenerated.

146 **Sampling design**

147 We selected 80 sampling points crossing two types of dominant tree species composition (TSC):
148 coniferous, mainly *P. sylvestris* and *Pinus nigra* subsp. *laricio* var. *corsicana*, noted CON vs. deciduous,
149 mainly *Quercus petraea* - *Q. robur*, noted DEC; and the three classes of forest temporal continuity
150 (FTC): ancient, intermediate-age and recent forests (Table 1). To reduce stand variability, we selected
151 forest stands that were between 40 and 100 years old and only considered "pure stands" with more than
152 70% of the total basal area of either coniferous or deciduous species.

153 **Floristic survey, humus form and soil data collection**

154 At each of the 80 sampling points, the presence of understory vascular species (pteridophytes and
155 phanerogams) and terricolous bryophytes below 2 m in height were recorded in one 10 × 10 m plot
156 between June 9 and July 22, 2011. The vegetation belongs to the phytosociological sub-alliance of
157 *Quercenion robori-petraeae* Rivas Mart. 1975. We also measured canopy cover of different strata and
158 humus form, and analysed soil samples to measure pH H₂O, organic carbon content (C_{org}), total nitrogen
159 content (N content), potentially available phosphorus content and other soil parameters at two depths (0-

160 5 cm and 15-20 cm). Appendix S1 gives a detailed presentation of forest stand and soil data protocol.
161 Soil types were cambisols, dystric cambisols, planosols, entic podzols and podzols (WRB 2015).
162 Topsoil texture was mostly sand or loamy sand with a predominantly clay horizon (silty clay, sandy clay
163 or clay) appearing between 30 and 70 cm. Moderate waterlogging was observed between 24 and 68 cm.
164 pH H₂O ranged from 3.9 to 5.7 and humus form varied from mesomull to dysmoder according to the
165 classification of Ponge et al. (2002).

166 **Plant traits**

167 We investigated plant traits that were previously related to forest understory succession after land
168 abandonment (Hermy & Verheyen 2007) and that could vary according to tree species (Barbier et al.
169 2008). We selected 15 species traits and ecological features, and classified them according to their
170 ecological function (Table 2): ecological performance, resource requirement, persistence, regeneration
171 and dispersal ability (Verheyen et al. 2003; Violle et al. 2007). Trait values were extracted from several
172 databases (Catminat, Ecoplant, Ellenberg, LEDA, Bioflor and D³). Although plant features related to
173 ecological performance are not functional traits, we use the term "plant traits" to simplify. Details on
174 plant traits are provided in Appendix S2. Detailed hypotheses on the expected relationships between
175 each trait and the two gradients we investigated are presented in Appendix S3.

176 **Data analyses**

177 *Soil and stand variations among sites*

178 Preliminary analyses checked for soil and stand variations among sites (Appendix S1). To reduce the
179 number of predictors in our analyses, we selected a short list of five environmental variables that are
180 recognised to vary with forest continuity and tree species and reflected nutrient richness, light
181 availability and past disturbance regime (Thomaes et al. 2012): humus index (litter effect on understory
182 plants), pH H₂O (nutrient balance between exchangeable H/Al and exchangeable cations), phosphorus
183 content (legacy of former agricultural use) and light conditions: lower and upper canopy cover (CC 2–
184 8 m and CC > 8 m).

185 *Plant communities*

186 To test how plant community composition varied with forest continuity and tree species, we first applied
187 canonical correspondence analysis to the L-table after Hellinger transformation with forest continuity
188 and tree species as explanatory variables. We conducted permutation tests to analyse the effects of the
189 two factors and their interaction using 9999 permutations. We then performed a pCCA using forest
190 continuity and tree species as constraints and humus index, pH H₂O, log(P₂O₅+1), CC 2–8 m and CC >
191 8 m as conditions to test whether forest continuity and tree species effects persisted after controlling for
192 resource gradient differences. We did not apply RLQ, a method to directly analyse trait-environment
193 relationships (Kleyer et al. 2012), because this approach is not adapted to test the effect of a set of

194 variables after controlling for the effect of covariates (Jamil et al. 2013). Between-class RLQ is
195 available (Dray et al. 2014), but impossible to apply when one aims at removing the effect of several
196 variables, whereas partial canonical correspondence analysis (pCCA) is suited for this purpose (Borcard
197 et al. 1992).

198 ***Plant traits***

199 To analyse how species traits were influenced by forest continuity and tree species and which of the two
200 gradients had a greater influence, we adopted the analysis framework proposed by Dray *et al.* (2014):
201 we used RLQ to obtain a graphical display and related values of projections and fourth-corner analysis
202 (Legendre et al. 1997) for testing statistical relationships between traits and environmental variables.
203 RLQ was used to provide a simultaneous ordination and analyse the joint structure of three tables: R
204 (environmental gradients: forest continuity, tree species, humus index, pH H₂O, log(P₂O₅+1), CC 2–8 m
205 and CC > 8 m), L (plant presence data) and Q (species traits).

206 A multivariate test using permutation method was applied to evaluate the global significance of the trait-
207 environment relationships [see (Dray et al. 2014) and Appendix S4]. Using permutation method, we also
208 tested the links between RLQ axes and traits or environmental variables to interpret the main pattern of
209 variation and correlation (Dray et al. 2014). As the L-table contained presence-absence data only,
210 categorical trait variation reflected change in proportion of each trait category. Fourth-corner was lastly
211 applied to test the significance of bivariate associations between each trait, or each trait category, and
212 each environmental variable. The link was measured by a Pearson correlation coefficient for two
213 quantitative variables (trait and environmental variable), by a Pearson Chi² and G statistic for two
214 qualitative variables and by a Pseudo-F and Pearson r for one quantitative variable and one qualitative
215 variable. We used 9999 permutations in all randomization procedures, and the false discovery rate
216 method (FDR) to adjust *P* values for multiple testing. See Appendix S4 for more details on RLQ and
217 fourth-corner analysis.

218 Finally, to test whether migration of forest core species [*sensu* Pellissier et al. (2013)] into recent
219 coniferous forests would be delayed compared with deciduous forests, we ran a two-way ANOVA to
220 test the effects of forest continuity, tree species composition and their interaction on the number of
221 forest core species at plot scale.

222

223 All statistical analyses were performed using *R* software (version 3.2.5, R Foundation for Statistical
224 Computing, Vienna, AT); we used the package *ade4* for RLQ and fourth-corner analysis (Dray et al.
225 2014) and the package *vegan* for CCA and pCCA.

226 **Results**

227 **Plant communities**

228 The CCA applied to the floristic matrix composed of 80 sampling points and 197 species showed that
229 12.6% of the total variance was explained by forest continuity, tree species and their interaction. The
230 projected inertias on the first three factorial axes were 43, 25 and 16%, respectively. Permutation tests
231 showed that the first two factorial axes and main effects were highly significant ($P < 0.001$) and the
232 interaction was very significant ($P = 0.004$). Ancient, intermediate-age and recent forests were ordered
233 along the first axis and the second, orthogonal axis discriminated between oak and pine stands (Fig. 2).
234 Community dissimilarity between oak and pine was present along the forest continuity gradient but was
235 much higher in recent compared to ancient forest. Plant turn-over from ancient to recent forest was
236 slightly higher for pine. A partial CCA using forest continuity and tree species as constraints and humus
237 index, pH H₂O, log(P₂O₅+1), CC 2–8 m and CC > 8 m as conditions indicated that 8.5% of the total
238 variance was explained by forest continuity and tree species, while the other environmental variables
239 explained 14.0% of the total variance. Permutation tests showed that the main effects and interaction
240 were still significant (forest continuity: $P = 0.001$; tree species: $P = 0.002$ and interaction: $P = 0.02$).
241 Individual plant species response to past land use and conifer plantation are presented in Appendices S5
242 and S6.

243 **Plant traits**

244 RLQ analysis showed that plant traits were significantly related to forest continuity, tree species and
245 environmental variables (permutation tests for *model 2* and *model 4*: $P < 0.0001$, see Appendix S4 for
246 description of *models 2* and *4*). The first two axes of the RLQ accounted for 95% of the total inertia
247 (87% and 8% respectively). The variance of the environmental scores (R-table) was almost entirely
248 preserved on the first two axes (98%). The variance of the trait scores (Q-table) was also well preserved
249 (40% on the first axis and 58% on the first two axes).

250 The first ordination axis of the RLQ was associated with forest continuity and contrasted ancient forests
251 (negative values) and recent forests (positive values), intermediate-age forests being roughly in the
252 middle (Fig. 3a and Table 3). The second axis was related to tree species, and differentiated deciduous
253 stands (positive values) from coniferous ones (negative values, Table 3). Humus index and canopy cover
254 above 8 m were negatively associated with the first axis (higher values in ancient forest and lower
255 values in recent forest), while pH H₂O and P content displayed the opposite trend (lower values in
256 ancient forest and higher values in recent forest; Fig. 3a and Table 3). Canopy cover 2–8 m was
257 positively associated with the second ordination axis, indicating higher subcanopy cover in deciduous
258 stands (Fig. 3a and Table 3).

259 Since the first two RLQ axes were respectively closely related to forest continuity and tree species, the
260 correlations between these gradients and plant traits were easy to infer. All the traits were correlated
261 with at least one RLQ axis (Fig. 3b and Table 4). However, the traits or trait categories that correlated
262 with the first axis (forest continuity) differed from the traits that correlated with the second axis (tree
263 species): only seed length and zoochory were significantly correlated with the first two axes (Table 4).

264 Forest core species, leaf dry matter content and bryophytes were highly, negatively correlated with the
265 first axis ($P < 0.001$), indicating increasing values from recent to ancient forest (Table 4). C-coordinate,
266 S-coordinate and seed length were also negatively correlated but to a lower extent ($P < 0.01$ or 0.05).
267 Conversely, R-coordinate, indicator value for soil pH and soil nitrogen (N), specific leaf area and
268 annuals/biennials were highly positively correlated with the first axis, indicating decreasing values from
269 recent to ancient forest. Perennial herbs, species reproducing by seed and vegetatively (sv.vvs),
270 barochory and zoochory were also positively correlated with the first axis ($P < 0.01$ or $P < 0.05$). Bivariate
271 associations between categories of forest continuity and species traits indicated that peripheral species
272 and shrubs/trees were associated with recent forests, while larger seeds and earlier end-of-flowering
273 characterised intermediate forests (Table 5).
274 Seed weight and length, myrmecochory and zoochory were positively associated with the second axis
275 ($P < 0.01$) with higher values in deciduous forests (Table 4). Conversely, indicator value for light, start
276 and end of flowering, anemochory and seed bank longevity index were negatively associated with the
277 second axis ($P < 0.01$), meaning that these traits had higher values in coniferous stands. In addition,
278 proportion of forest core species was higher in deciduous forests (Table 5), proportion of annuals and
279 biennials was particularly high in recent pine plantations (Fig. 3b), and several species were located in
280 this bottom right corner of the first RLQ factorial map (Appendix S7). We noted that the associations
281 between the second axis of RLQ and traits (Table 4) and bivariate associations between tree species and
282 traits (Table 5) were not consistent: only forest core species and indicator value for L were significantly
283 related to tree species in Table 5, meaning that the associations between the second RLQ axis and traits
284 should be interpreted with caution.
285 The *ad-hoc* two-way ANOVA applied to forest core species richness revealed that the effects of forest
286 continuity and tree species were significant ($P < 0.001$ and $P < 0.01$ respectively) but not the interaction:
287 species richness increased from recent to ancient forest and was higher under oak (Fig. 4).

288 Discussion

289 Our results showed that forest continuity and tree species acted as ecological filters on the taxonomic
290 and functional composition of forest understory plant communities. Plant trait composition varied along
291 the forest continuity and tree species gradients according to ecological performance, resource
292 requirement, persistence, regeneration and dispersal ability. As past land use was correlated to the first
293 RLQ axis (87% of total inertia) while tree species was correlated to the second one (8%), our results
294 indicated that the magnitude of past land use effect on plant functional composition was globally
295 stronger than the effect of tree species, in line with Kelemen *et al.* (2014).

296 Role of past land use

297 Previous cultivation has long-lasting effects on the upper forest soil horizon, e.g. nitrogen and carbon
298 depletion, phosphorus enrichment, and soil pH rise (Hermy & Verheyen 2007; Berthrong *et al.* 2009;

299 Brudvig et al. 2013). Overall, land use legacies on topsoil chemical properties are related to three
300 processes: (i) soil acidification and base cation loss caused by nutrients being redistributed from soils to
301 biomass in aggrading forest ecosystems (Jobbagy & Jackson 2003), (ii) lower rates of nitrification and
302 higher nitrate leaching in the soil, which may result from increased soil acidity (Hermy & Verheyen
303 2007), and (iii) past amendment and fertiliser application (lime and manure) in former agricultural soils
304 that have enriched soil P and base cation levels (Compton & Boone 2000). As expected, we found a
305 pronounced agricultural legacy on understory plant communities and progressive recovery to ancient
306 forest communities, as evidenced by the first axis of the CCA (Fig. 2). As resource gradients (nutrient
307 and light) did not explain all the variability in plant community composition (see pCCA), this strongly
308 suggests that factors other than local habitat quality constrained the establishment of forest understory
309 plants in post-agricultural forests, *e.g.* time since disturbance, distance to propagule source and species
310 dispersal capacity. After deforestation and subsequent cultivation, species typical of ancient forests are
311 soon lost from the soil seed bank (Hermy & Verheyen 2007). After the abandonment of agriculture, the
312 land is colonised by open habitat herbaceous plants, but ruderal species rapidly disappear and are
313 replaced by competitive species (pioneer trees and shrubs) (Hermy & Verheyen 2007). In our study,
314 plant C-S-R signature was characterised by a strong decrease in R-component and an increase in C and
315 S-components from recent to ancient forest. The variation in R-component can be linked to ploughing
316 and other forms of soil disturbance and the increase in C-axis to land abandonment and increased
317 competitive exclusion (Hunt et al. 2004). Long after the reconstitution of a dominant tree layer, the plant
318 communities still differ from ancient forests: many plants typical of ancient forests are lacking due to
319 their limited dispersal capacity (Hermy & Verheyen 2007). In accordance with previous studies
320 (Verheyen et al. 2003; Bergès et al. 2016), we showed that proportion of zoochory was slightly higher
321 and seed length lower in recent forests (Table 4).

322 Plant communities in recent forests were characterised by a larger proportion of nutrient-demanding,
323 ruderal and short-lived species, but also tree and shrub species. Some of the shrubs in our recent forests
324 could be considered as relicts from previous stages in vegetation succession (Verheyen & Hermy 2001).
325 The lower specific leaf area and higher leaf dry matter content detected in ancient forests confirms that
326 species in environments with resource stress displayed these functional features compared with
327 resource-rich environments (higher soil pH and N and P availability), such as recent forests (Cornelissen
328 et al. 2003). Analogous responses of specific leaf area and leaf dry matter content to land use change
329 were noted in grasslands, where abandonment of land tended to favour species with reduced acquisition
330 capacities and increased nutrient conservation efficiency (Garnier et al. 2007).

331 **Role of tree species composition**

332 Many conifer species, but not all (Barbier et al. 2008), tend to acidify soils more than deciduous trees
333 through several processes (Verstraeten et al. 2013; Augusto et al. 2015). Although we detected
334 significant differences in pH, C/N and phosphorus content between deciduous and coniferous stands

335 (Table S1 and Fig. S1), the fourth-corner analysis did not detect any significant associations between
336 plant resource requirements (indicator values for pH and N) and tree species composition (Tables 4 and
337 5). This may be because RLQ is simply an ordination of the fourth-corner statistics and so does not
338 build a truly multi-trait multi-environment model in the sense of regression analysis, *i.e.* is unable to
339 reveal additive effects (Jamil et al. 2013). In our case, variations in soil properties were much stronger
340 along the forest continuity gradient than between deciduous and coniferous forests: indeed, tree species
341 effect was significant only after correcting for forest continuity effect (data not shown). Plant functional
342 composition differed between oak and pine mainly for shade tolerance (Table 5), in line with a less
343 dense canopy cover between 2 and 8 m under pine (Fig. S1) and the highest indicator value for light
344 detected for the understory vegetation under *P. sylvestris* among six tree species (Augusto et al. 2003).
345 The higher proportion of anemochory and lighter and shorter seeds in pine plantations (Table 4) could
346 also be explained by their more open subcanopy, which could facilitate seed dispersal by wind. A higher
347 proportion of vernal plants, which must bloom before canopy leaf expansion, could explain the earlier
348 period of flowering observed in oak (Table 4).

349 **Role of regeneration mode and forest management**

350 Regardless of tree species, site preparation before plantation implies more intense forest floor and
351 topsoil disturbances (*e.g.* ploughing and soil scarification) compared with naturally regenerated
352 deciduous stands (Balandier et al. 2006). This could explain why recent pine plantations exhibited
353 higher proportions of ruderal and wind-dispersed species (Boch et al. 2013). Weed control by
354 mechanical or herbicide release treatments can also deeply modify plant communities and promote the
355 establishment of species adapted to disturbance (Balandier et al. 2006). Pine plantations in post-
356 agricultural forests had a low proportion of ant-dispersed species, which can be explained by their
357 reduced colonisation capacity after removal from a site (Aubin et al. 2008), and hosted plants with a
358 higher seed bank longevity (Table 4), which is a strategy to survive in case of frequent site disturbances.
359 Conserving a substantial part of the pre-existing plant communities in plantation forests thus has a
360 positive impact on plant diversity and vegetation recovery (Hartley 2002).
361 Likewise, the silviculture applied to the stand plays a role because it modifies light transmittance to the
362 ground and causes regular soil disturbance due to logging machines (Verstraeten et al. 2013). Moreover,
363 shrub and subcanopy strata can be controlled during thinnings at the thicket, sapling and pole stages of
364 the stand and could mitigate soil acidification in pine plantations (Van Nevel et al. 2014). Silviculture in
365 conifer plantations prevents natural development of a dense tree subcanopy, as shown by the much
366 lower canopy cover between 2 and 8 m under pine (Fig. 3a and Fig. S1). On the other hand, intense litter
367 and topsoil disturbances could also occur in oak to favour natural deciduous regeneration in actively
368 managed stands. Consequently, our results cannot be interpreted as pure tree effects, but rather a
369 combination of tree species effect and their associated management (Thomaes et al. 2012).

370 **Understorey succession differed between pine plantations and naturally regenerated oak stands**

371 Soil chemical parameters in recent forests under oak and pine were very close and confirmed that pre-
372 afforestation site conditions were comparable (Fig. S1). Litter accumulation was higher and litter
373 degradation lower under pine, and these differences increased with time after pine plantation (Fig. S1).
374 In contradiction with our initial hypothesis and with the patterns observed on soil, CCA indicated higher
375 composition similarity between deciduous and coniferous ancient forests than between corresponding
376 recent forests (Fig. 2), *i.e.* a convergence between pine and oak plant succession with increasing forest
377 continuity. To explain the higher dissimilarity in recent forests, we noted that recent pine plantations
378 displayed a higher proportion of short-lived species (Fig. 3b). Floristic difference between pine
379 plantations and deciduous stands in recent forests (Fig. 2) may be related to a higher maintenance of
380 ruderal and nutrient-demanding species due to more intense initial site disturbances combined with
381 lower canopy cover under pine (Thomaes et al. 2014). Then, the effect of the disturbance tends to
382 dissipate progressively after the stand-initiating disturbance (Fourrier et al. 2015), and other ecological
383 filters take over: soil acidification and phosphorus diminution reduced the pool of ruderal and nutrient-
384 demanding species and subcanopy development reduced light-loving competitors and promoted the
385 establishment of shade-tolerant forest herbs (De Keersmaecker et al. 2011). Increasing soil acidification
386 and litter accumulation in intermediate and ancient pine plantations limited the colonisation of acid-
387 intolerant forest species, while promoting acid-tolerant forest species (Thomaes et al. 2013), which
388 partly explains why plant dissimilarity between pines and oaks persisted in intermediate and ancient
389 forests (Fig. 2).

390 In accordance with our initial hypothesis, oak forests hosted a slightly higher proportion of forest core
391 species (Table 5) and a significantly higher number of forest core species (Fig. 4), which suggests that
392 migration or recruitment of forest specialists were delayed in pine plantations on farmlands. This
393 contrasts with the comparably efficient migration of herbaceous forest specialists into recent coniferous
394 and deciduous stands observed by Wulf and Heinken (2008). Our result is consistent with previous
395 experiments that underlined that acidifying tree species could severely limit germination and survival of
396 ancient forest species (Thomaes et al. 2014).

397 Overall, understorey succession in post-agricultural stands varied between pine plantations and naturally-
398 regenerated oak stands, and differences persisted in ancient forests. In line with Fourrier *et al.* (2015),
399 we attributed these differences to the intensity of the initial disturbance, and then to tree species and
400 contrasting stand management.

401 **Conclusion**

402 Plant communities and traits in pine plantations under recent and ancient forests differed from similar
403 sites with pedunculate and sessile oaks. Past land use and tree species substitution had combined effects
404 on topsoil chemical properties, plant community and plant traits, and the impacts of past land use were
405 globally stronger than those of conifer plantation. This hierarchy has to be validated in other ecological

406 contexts and tree species. Understory plant succession differed between pine plantations and naturally-
407 regenerated oak stands, under the influence of several ecological drivers: soil disturbance and understory
408 vegetation removal at the beginning, and then tree species and stand management during stand
409 development, where soil acidification, litter accumulation, canopy cover and dispersal and recruitment
410 limitations play a major role. Our study underlines the slow process of recovery of recent forests
411 towards ancient forest plant communities. In our study area, conifer plantation resulted in a long-lasting
412 distinct taxonomic and functional trait composition. In ancient deciduous forests, we therefore advise
413 applying natural regeneration and favouring native deciduous tree species to maintain or restore ancient
414 forest plant communities.

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424 **References**

- 425 Aubin, I., Messier, C. & Bouchard, A. 2008. Can plantations develop understory biological and physical
426 attributes of naturally regenerated forests? *Biological Conservation* 141: 2461-2476.
- 427 Augusto, L., De Schrijver, A., Vesterdal, L., Smolander, A., Prescott, C. & Ranger, J. 2015. Influences
428 of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate
429 and boreal forests. *Biological Reviews* 90: 444-466.
- 430 Augusto, L., Dupouey, J.L. & Ranger, J. 2003. Effects of tree species on understory vegetation and
431 environmental conditions in temperate forests. *Annals of Forest Science* 60: 823-831.
- 432 Baeten, L., Bauwens, B., De Schrijver, A., De Keersmaeker, L., Van Calster, H., Vandekerckhove, K.,
433 Roelandt, B., Beeckman, H. & Verheyen, K. 2009a. Herb layer changes (1954-2000) related to the
434 conversion of coppice-with-standards forest and soil acidification. *Applied Vegetation Science* 12:
435 187-197.
- 436 Baeten, L., Hermy, M. & Verheyen, K. 2009b. Environmental limitation contributes to the differential
437 colonization capacity of two forest herbs. *Journal of Vegetation Science* 20: 209-223.
- 438 Balandier, P., Collet, C., Miller, J.H., Reynolds, P.E. & Zedaker, S.M. 2006. Designing forest vegetation
439 management strategies based on the mechanisms and dynamics of crop tree competition by
440 neighbouring vegetation. *Forestry* 79: 3-27.

- 441 Barbier, S., Balandier, P. & Gosselin, F. 2009. Influence of several tree traits on rainfall partitioning in
442 temperate and boreal forests: a review. *Annals of Forest Science* 66.
- 443 Barbier, S., Gosselin, F. & Balandier, P. 2008. Influence of tree species on understory vegetation
444 diversity and mechanisms involved - A critical review for temperate and boreal forests. *Forest*
445 *Ecology and Management* 254: 1-15.
- 446 Bergès, L., Avon, C., Arnaudet, L., Archaux, F., Chauchard, S. & Dupouey, J.L. 2016. Past landscape
447 explains forest periphery-to-core gradient of understory plant communities in a reforestation
448 context. *Diversity and Distributions* 22: 3-16.
- 449 Berthrong, S.T., Jobbagy, E.G. & Jackson, R.B. 2009. A global meta-analysis of soil exchangeable
450 cations, pH, carbon, and nitrogen with afforestation. *Ecological Applications* 19: 2228-2241.
- 451 Boch, S., Prati, D., Muller, J., Socher, S., Baumbach, H., Buscot, F., Gockel, S., Hemp, A.,
452 Hessenmoller, D., Kalko, E.K.V., Linsenmair, K.E., Pfeiffer, S., Pommer, U., Schoning, I., Schulze,
453 E.D., Seilwinder, C., Weisser, W.W., Wells, K. & Fischer, M. 2013. High plant species richness
454 indicates management-related disturbances rather than the conservation status of forests. *Basic and*
455 *Applied Ecology* 14: 496-505.
- 456 Boothroyd-Roberts, K., Gagnon, D. & Truax, B. 2013. Can hybrid poplar plantations accelerate the
457 restoration of forest understory attributes on abandoned fields? *Forest Ecology and Management*
458 287: 77-89.
- 459 Borcard, D., Legendre, P. & Drapeau, P. 1992. Partialling out the spatial component of ecological
460 variation. *Ecology* 73: 1045-1055.
- 461 Bremer, L.L. & Farley, K.A. 2010. Does plantation forestry restore biodiversity or create green deserts?
462 A synthesis of the effects of land-use transitions on plant species richness. *Biodiversity and*
463 *Conservation* 19: 3893-3915.
- 464 Brudvig, L.A., Grman, E., Habeck, C.W., Orrock, J.L. & Ledvina, J.A. 2013. Strong legacy of
465 agricultural land use on soils and understory plant communities in longleaf pine woodlands. *Forest*
466 *Ecology and Management* 310: 944-955.
- 467 Compton, J.E. & Boone, R.D. 2000. Long-term impacts of agriculture on soil carbon and nitrogen in
468 New England forests. *Ecology* 81: 2314-2330.
- 469 Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter
470 Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G. & Poorter, H. 2003. A handbook
471 of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian*
472 *Journal of Botany* 51: 335-380.
- 473 Cramer, V.A., Hobbs, R.J. & Standish, R.J. 2008. What's new about old fields? Land abandonment and
474 ecosystem assembly. *Trends in Ecology & Evolution* 23: 104-112.
- 475 De Keersmaecker, L., Vandekerckhove, K., Verstraeten, A., Baeten, L., Verschelde, P., Thomaes, A.,
476 Hermy, M. & Verheyen, K. 2011. Clear-felling effects on colonization rates of shade-tolerant forest
477 herbs into a post-agricultural forest adjacent to ancient forest. *Applied Vegetation Science* 14: 75-83.

- 478 De Schrijver, A., Vesterdal, L., Hansen, K., De Frenne, P., Augusto, L., Achat, D.L., Staelens, J.,
479 Baeten, L., De Keersmaecker, L., De Neve, S. & Verheyen, K. 2012. Four decades of post-
480 agricultural forest development have caused major redistributions of soil phosphorus fractions.
481 *Oecologia* 169: 221-234.
- 482 Dray, S., Choler, P., Doledec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S. & ter Braak, C.J.F. 2014.
483 Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental
484 variation. *Ecology* 95: 14-21.
- 485 Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Pauliflen, D. 1992. Zeigerwerte von
486 Pflanzen in Mitteleuropa. *Scripta geobotanica* 18: 1-258.
- 487 Favre, C., Grel, A., Granier, E., Cosserat-Mangeot, R., Bachacou, J. & Dupouey, J.L. 2013.
488 Digitalisation des cartes anciennes. Manuel pour la vectorisation de l'usage des sols et le
489 géoréférencement des minutes 1:40000 de la carte d'Etat-Major (v. 12.7.3). In, pp. 54. INRA.
- 490 Fourier, A., Bouchard, M. & Pothier, D. 2015. Effects of canopy composition and disturbance type on
491 understorey plant assembly in boreal forests. *Journal of Vegetation Science* 26: 1225-1237.
- 492 Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas,
493 H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Leps, J.,
494 Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V.P., Quested, H., Quetier, F., Robson,
495 M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J.P., Thebault, A., Vile, D. &
496 Zarovali, M.P. 2007. Assessing the effects of land-use change on plant traits, communities and
497 ecosystem functioning in grasslands: A standardized methodology and lessons from an application
498 to 11 European sites. *Annals of Botany* 99: 967-985.
- 499 Gégout, J.C., Coudun, C., Bailly, G. & Jabiol, B. 2005. EcoPlant: A forest site database linking floristic
500 data with soil and climate variables. *Journal of Vegetation Science* 16: 257-260.
- 501 Hagen-Thorn, A., Callesen, I., Armolaitis, K. & Nihlgard, B. 2004. The impact of six European tree
502 species on the chemistry of mineral topsoil in forest plantations on former agricultural land. *Forest*
503 *Ecology and Management* 195: 373-384.
- 504 Härdtle, W., von Oheimb, G. & Westphal, C. 2003. The effects of light and soil conditions on the
505 species richness of the ground vegetation of deciduous forests in northern Germany (Schleswig-
506 Holstein). *Forest Ecology and Management* 182: 327-338.
- 507 Hartley, M.J. 2002. Rationale and methods for conserving biodiversity in plantation forests. *Forest*
508 *Ecology and Management* 155: 81-95.
- 509 Hermy, M. & Verheyen, K. 2007. Legacies of the past in the present-day forest biodiversity: a review of
510 past land-use effects on forest plant species composition and diversity. *Ecological Research* 22:
511 361-371.
- 512 Hintze, C., Heydel, F., Hoppe, C., Cunze, S., König, A. & Tackenberg, O. 2013. D-3: The Dispersal and
513 Diaspore Database - Baseline data and statistics on seed dispersal. *Perspectives in Plant Ecology*
514 *Evolution and Systematics* 15: 180-192.

- 515 Hunt, R., Hodgson, J.G., Thompson, K., Bungener, P., Dunnett, N.P. & Askew, A.P. 2004. A new
516 practical tool for deriving a functional signature for herbaceous vegetation. *Applied Vegetation*
517 *Science* 7: 163-170.
- 518 Jamil, T., Ozinga, W.A., Kleyer, M. & Ter Braak, C.J.F. 2013. Selecting traits that explain species-
519 environment relationships: A generalized linear mixed model approach. *Journal of Vegetation*
520 *Science* 24: 988-1000.
- 521 Jobbagy, E.G. & Jackson, R.B. 2003. Patterns and mechanisms of soil acidification in the conversion of
522 grasslands to forests. *Biogeochemistry* 64: 205-229.
- 523 Kelemen, K., Kriván, A. & Standovár, T. 2014. Effects of land-use history and current management on
524 ancient woodland herbs in Western Hungary. *Journal of Vegetation Science* 25: 172-183.
- 525 Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschod, P.,
526 van Groenendael, J.M., Klimes, L., Klimesova, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D.,
527 Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Gotzenberger, L., Hodgson, J.G., Jackel,
528 A.K., Kuhn, I., Kunzmann, D., Ozinga, W.A., Romermann, C., Stadler, M., Schlegelmilch, J.,
529 Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E. &
530 Peco, B. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European
531 flora. *Journal of Ecology* 96: 1266-1274.
- 532 Kleyer, M., Dray, S., de Bello, F., Leps, J., Pakeman, R.J., Strauss, B., Thuiller, W. & Lavorel, S. 2012.
533 Assessing species and community functional responses to environmental gradients: which
534 multivariate methods? *Journal of Vegetation Science* 23: 805-821.
- 535 Kooijman, A. 2010. Litter quality effects of beech and hornbeam on undergrowth species diversity in
536 Luxembourg forests on limestone and decalcified marl. *Journal of Vegetation Science* 21: 248-261.
- 537 Kühn, I., Durka, W. & Klotz, S. 2004. BiolFlor - a new plant-trait database as a tool for plant invasion
538 ecology. *Diversity and Distributions* 10: 363-365.
- 539 Legendre, P., Galzin, R. & HarmelinVivien, M.L. 1997. Relating behavior to habitat: Solutions to the
540 fourth-corner problem. *Ecology* 78: 547-562.
- 541 Leuschner, C., Wulf, M., Bäuchler, P. & Hertel, D. 2013. Soil C and nutrient stores under Scots pine
542 afforestations compared to ancient beech forests in the German Pleistocene: The role of tree species
543 and forest history. *Forest Ecology and Management* 310: 405-415.
- 544 Mather, A.S., Fairbairn, J. & Needle, C.L. 1999. The course and drivers of the forest transition: The case
545 of France. *Journal of Rural Studies* 15: 65-90.
- 546 Pellissier, V., Bergès, L., Nedeltcheva, T., Schmitt, M.C., Avon, C., Cluzeau, C. & Dupouey, J.L. 2013.
547 Understorey plant species show long-range spatial patterns in forest patches according to distance-
548 to-edge. *Journal of Vegetation Science* 24: 9-24.
- 549 Ponge, J.F., Chevalier, R. & Loussot, P. 2002. Humus index: An integrated tool for the assessment of
550 forest floor and topsoil properties. *Soil Science Society of America Journal* 66: 1996-2001.

- 551 Reich, P.B., Oleksyn, J., Modrzyński, J., Mrozinski, P., Hobbie, S.E., Eissenstat, D.M., Chorover, J.,
552 Chadwick, O.A., Hale, C.M. & Tjoelker, M.G. 2005. Linking litter calcium, earthworms and soil
553 properties: a common garden test with 14 tree species. *Ecology Letters* 8: 811-818.
- 554 Sciama, D., Augusto, L., Dupouey, J.L., Gonzalez, M. & Dominguez, C.M. 2009. Floristic and
555 ecological differences between recent and ancient forests growing on non-acidic soils. *Forest
556 Ecology and Management* 258: 600-608.
- 557 Thomaes, A., De Keersmaecker, L., De Schrijver, A., Baeten, L., Vandekerckhove, K., Verstraeten, G. &
558 Verheyen, K. 2013. Can soil acidity and light help to explain tree species effects on forest herb layer
559 performance in post-agricultural forests? *Plant and Soil* 373: 183-199.
- 560 Thomaes, A., De Keersmaecker, L., Van Calster, H., De Schrijver, A., Vandekerckhove, K., Verstraeten,
561 G. & Verheyen, K. 2012. Diverging effects of two contrasting tree species on soil and herb layer
562 development in a chronosequence of post-agricultural forest. *Forest Ecology and Management* 278:
563 90-100.
- 564 Thomaes, A., De Keersmaecker, L., Verschelde, P., Vandekerckhove, K. & Verheyen, K. 2014. Tree
565 species determine the colonisation success of forest herbs in post-agricultural forests: Results from a
566 9 yr introduction experiment. *Biological Conservation* 169: 238-247.
- 567 Tullus, T., Tullus, A., Roosaluuste, E., Kaasik, A., Lutter, R. & Tullus, H. 2013. Understorey vegetation
568 in young naturally regenerated and planted birch (*Betula* spp.) stands on abandoned agricultural
569 land. *New Forests* 44: 591-611.
- 570 Van Nevel, L., Mertens, J., De Schrijver, A., De Neve, S. & Verheyen, K. 2014. Can shrub species with
571 higher litter quality mitigate soil acidification in pine and oak forests on poor sandy soils? *Forest
572 Ecology and Management* 330: 38-45.
- 573 Verheyen, K. & Hermy, M. 2001. An integrated analysis of the spatio-temporal colonization patterns of
574 forest plant species. *Journal of Vegetation Science* 12: 567-578.
- 575 Verheyen, K., Honnay, O., Motzkin, G., Hermy, M. & Foster, D.R. 2003. Response of forest plant
576 species to land-use change: a life-history trait-based approach. *Journal of Ecology* 91: 563-577.
- 577 Verstraeten, G., Baeten, L., De Frenne, P., Vanhellemont, M., Thomaes, A., Boonen, W., Muys, B. &
578 Verheyen, K. 2013. Understorey vegetation shifts following the conversion of temperate deciduous
579 forest to spruce plantation. *Forest Ecology and Management* 289: 363-370.
- 580 Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. 2007. Let the
581 concept of trait be functional! *Oikos* 116: 882-892.
- 582 WRB, I.W.G. 2015. World Reference Base for Soil Resources 2014, update 2015 - International soil
583 classification system for naming soils and creating legends for soil maps. In, pp. 191, Rome.
- 584 Wulf, M. & Heinken, T. 2008. Colonization of recent coniferous versus deciduous forest stands by
585 vascular plants at the local scale. *Applied Vegetation Science* 11: 307-316.
- 586 Wulf, M. & Naaf, T. 2009. Herb layer response to broadleaf tree species with different leaf litter quality
587 and canopy structure in temperate forests. *Journal of Vegetation Science* 20: 517-526.

589 **Supporting Information**

590 Additional supporting information may be found in the online version of this article.

591

592 Appendix S1. Detailed analysis of humus form, soil and stand variations among sites

593 Appendix S2. Plant trait data

594 Appendix S3. Set of hypotheses on the expected relationship between plant traits and ecological
595 gradients

596 Appendix S4. Detailed methodology to analyse the relationship between plant traits and forest
597 continuity and tree species

598 Appendix S5. Individual species response to forest continuity and tree species

599 Appendix S6. Detailed results of multiple logistic regression models applied to individual species

600 Appendix S7. Ordination of plant species in the first RLQ factorial map

601

602 **Table 1.** Definition of the six sampling units based on forest continuity (according to past land use maps
 603 of 1840 and aerial photographs taken in 1949) and tree species, and number of sampling points.

| Tree species composition | | | |
|-------------------------------------|--|--|-----------|
| | deciduous (<i>Q. petraea</i> / <i>Q. robur</i>) | coniferous (<i>Pinus sylvestris</i>) | Total |
| ancient forest (AF) | AF-DEC: deciduous ancient forest | AF-CON: plantation of pines between 1840 et 1949 on deciduous ancient forest | |
| | 15 | 12 | 27 |
| intermediate- age forest (IF) | IF-DEC: natural colonisation of deciduous tree species between 1840 and 1949 on former agricultural land | IF-CON: plantation of pines between 1840 and 1949 on former agricultural land | |
| | 16 | 13 | 29 |
| recent forest (RF) | RF-DEC: natural colonisation of deciduous tree species after 1949 on former agricultural land | RF-CON: plantation of pines after 1949 on former agricultural land | |
| | 8 | 16 | 24 |
| Total | 39 | 41 | 80 |

604
605

606 **Table 2.** The 15 plant traits analysed by ecological function: trait name, data sources, type, trait category
607 (continuous: C; ordinal: O; nominal: N) and code. Data sources: Catminat
608 (<http://philippe.julve.pagesperso-orange.fr/catminat.htm>), Ecoplant (Gégout et al. 2005), Ellenberg
609 indicator values (Ellenberg et al. 1992), LEDA (Kleyer et al. 2008), Biolflor (Kühn et al. 2004) and D³
610 (Hintze et al. 2013).

| Ecological function | Plant trait | Data source | Type | Category | Code |
|---------------------------|--------------------------------------|-----------------------------|---|--|-------------------------------|
| Ecological performance | Habitat preference: distance to edge | Pellissier et al. (2013) | N | Forest core species | HAB.core |
| | | | | Forest peripheral species | HAB.peripheral |
| | CSR strategy | Hunt et al. (2004) | C | C-coordinate S-coordinate R-coordinate | C.coord S.coord R.coord |
| Resource requirement | Ind. value for pH | Ecoplant | O | - | pH |
| | Ind. value for N | Ellenberg | O | - | N |
| | Ind. value for L | Ellenberg | O | - | L |
| Persistence | Specific leaf area | LEDA | C | - | SLA |
| | Leaf dry matter content | LEDA | C | - | LDMC |
| Regeneration | Plant life span + bryophytes | Catminat | N | annual or biennial | PLS.ann.bie |
| | | | | perennial herb | PLS.per.herb |
| | | | | shrub pr tree | PLS.shr.tree |
| | | | | bryophyte | PLS.bryo |
| | Reproduction type | Biolflor | N | s: by seed only | REPRO.s |
| | | | | ssv: mostly by seed, rarely vegetative | REPRO.ssv |
| | | | | sv: by seed and vegetatively; vvs: mostly vegetative, rarely by seed | REPRO.sv.vvs |
| Start of flowering | Catminat | C | - | beg.fl | |
| End of flowering | Catminat | C | - | end.fl | |
| Dispersion | Dispersal mode | Catminat | N | anemochory | DISP.anemo |
| | | | | barochory | DISP.baro |
| | | | | myrmecochory | DISP.myrmeco |
| | | | | zoochory | DISP.zoo |
| | Seed weight (mg) | D ³ and Biolflor | C | log transformed | log.SW |
| | Seed length (mm) | D ³ and Biolflor | C | log transformed | log.SL |
| Seed bank longevity index | LEDA | C | 0: transient; 0.5: short-term persistent; 1: long-term persistent | SBLI | |

611

612 **Table 3.** Trait responses to forest continuity, tree species and other environmental variables using RLQ:
 613 fourth-corner tests (Pearson correlation coefficient r) between the first two RLQ axes for plant traits
 614 (AxisQ1 and AxisQ2) and forest continuity, tree species and environmental variables. P values were
 615 adjusted for multiple comparisons using the FDR (false discovery rate) procedure. See also Fig. 3 for
 616 codes for environmental variables.

| Code | Variable description | AxisQ1 | | AxisQ2 | |
|---------------------------------------|-------------------------|--------|-----------|--------|-----------|
| | | r | P value | r | P value |
| AF | Ancient forest | -0.309 | *** | -0.068 | NS |
| IF | Intermediate-age forest | -0.141 | *** | 0.082 | * |
| RF | Recent forest | 0.433 | *** | -0.016 | NS |
| CON | Coniferous forest | 0.025 | NS | -0.152 | *** |
| DEC | Deciduous forest | -0.025 | NS | 0.152 | *** |
| Humus index | - | -0.430 | *** | -0.063 | NS |
| pH H ₂ O | - | 0.434 | *** | 0.006 | NS |
| log(P ₂ O ₅ +1) | - | 0.465 | *** | -0.048 | NS |
| CC 2-8 m | Canopy cover 2-8 m | 0.084 | NS | 0.148 | *** |
| CC > 8 m | Canopy cover > 8 m | -0.222 | *** | 0.085 | * |

617

618

619 **Table 4.** Trait responses to forest continuity, tree species composition and environmental variables
 620 using RLQ: fourth-corner tests (Pearson correlation coefficient r) between the first two RLQ axes for
 621 environmental gradients (AxisR1 and AxisR2) and plant traits. P values were adjusted for multiple
 622 comparisons using the FDR (false discovery rate) procedure. Codes for species traits are explained in
 623 Table 2.

| | | AxisR1 | | AxisR2 | |
|----------------|--|--------|-----------|--------|-----------|
| | | r | P value | r | P value |
| HAB.core | forest core species | -0.236 | *** | 0.020 | NS |
| HAB.peripheral | peripheral species | 0.094 | NS | 0.057 | NS |
| C.coord | coordinate for competition | -0.113 | * | -0.018 | NS |
| S.coord | coordinate for stress-tolerance | -0.148 | ** | 0.064 | NS |
| R.coord | coordinate for ruderality | 0.266 | *** | -0.046 | NS |
| pH | indicator value for soil pH | 0.441 | *** | 0.106 | NS |
| N | indicator value for soil nitrogen | 0.240 | *** | 0.039 | NS |
| L | indicator value for light | 0.039 | NS | -0.096 | ** |
| SLA | specific leaf area | 0.225 | *** | 0.014 | NS |
| LDMC | leaf dry matter content | -0.232 | *** | 0.028 | NS |
| PLS.ann.bie | annual/biennial | 0.247 | *** | -0.054 | NS |
| PLS.bryo | bryophyte | -0.183 | *** | 0.001 | NS |
| PLS.per.herb | perennial herb | 0.157 | ** | -0.026 | NS |
| PLS.shr.tree | shrub/tree | -0.076 | NS | 0.044 | NS |
| REPRO.s | reproduction by seed | 0.038 | NS | -0.027 | NS |
| REPRO.ssv | reproduction mostly by seed, rarely vegetative | -0.058 | NS | 0.019 | NS |
| REPRO.sv.vvs | reproduction by seed and vegetative | 0.158 | ** | 0.020 | NS |
| beg.fl | start of flowering | -0.015 | NS | -0.097 | ** |
| end.fl | end of flowering | 0.045 | NS | -0.124 | *** |
| DISP.anemo | anemochory | -0.026 | NS | -0.122 | *** |
| DISP.baro | barochory | 0.104 | * | -0.053 | NS |
| DISP.myrmeco | myrmecochory | 0.009 | NS | 0.083 | ** |
| DISP.zoo | zoochory | 0.108 | * | 0.095 | ** |
| log.SW | seed weight (log) | -0.009 | NS | 0.109 | ** |
| log.SL | seed length (log) | -0.107 | * | 0.084 | ** |
| SBLI | seed bank longevity index | -0.007 | NS | -0.084 | ** |

624

625

626 **Table 5.** Fourth-corner tests for bivariate associations between plant traits and environmental variables. The link is measured by a Pearson correlation
627 coefficient for two quantitative variables (trait and environmental variable), by a Pearson Chi^2 and G statistic for two qualitative variables and by a Pseudo-F
628 and Pearson r for one quantitative variable and one qualitative variable (significant associations are in bold). P values were adjusted for multiple comparisons
629 using the FDR (false discovery rate) procedure. Same legend as Tables 3 and 4.

630

631

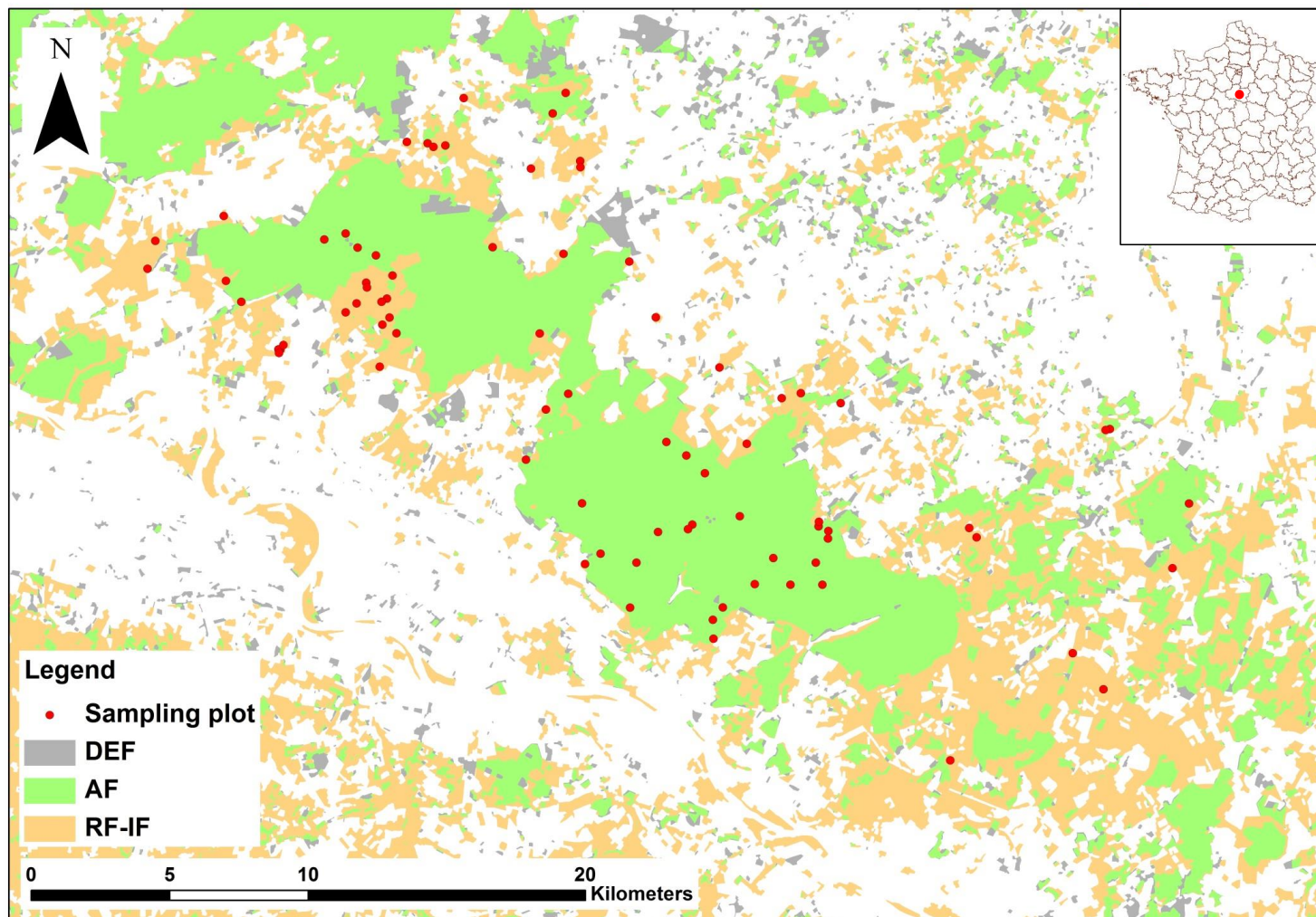
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634 See file "Table 5.xlsx"

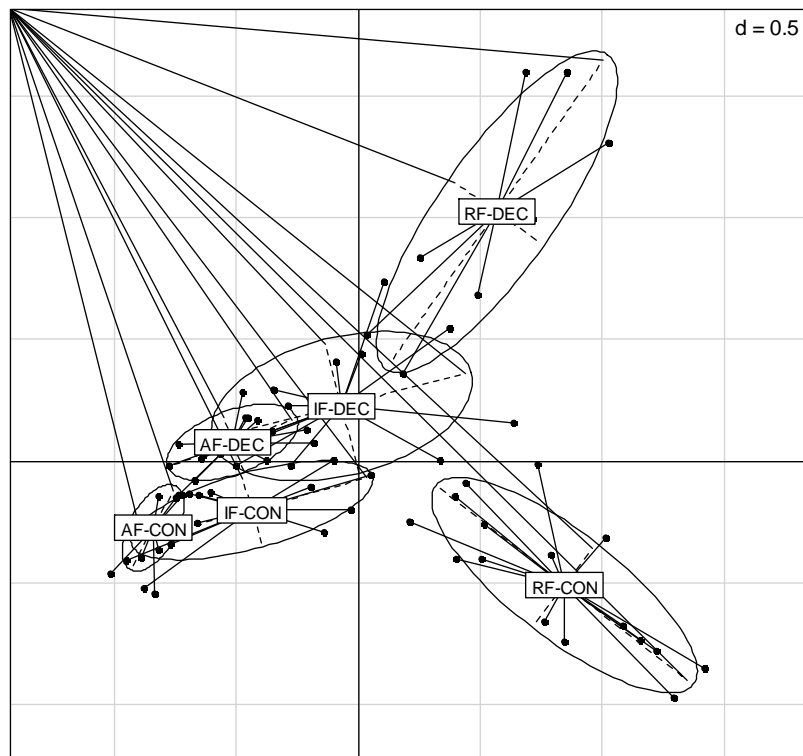
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637

638 **Fig. 1.** Location of the 80 sampling points in the forest of Orléans (Loiret, France); AF: ancient forest (present in 1840 and 2006); RF/IF: recent or
639 intermediate age forest (absent in 1840 and present after this date); DEF: deforestation (present in 1840 and absent in 2006).



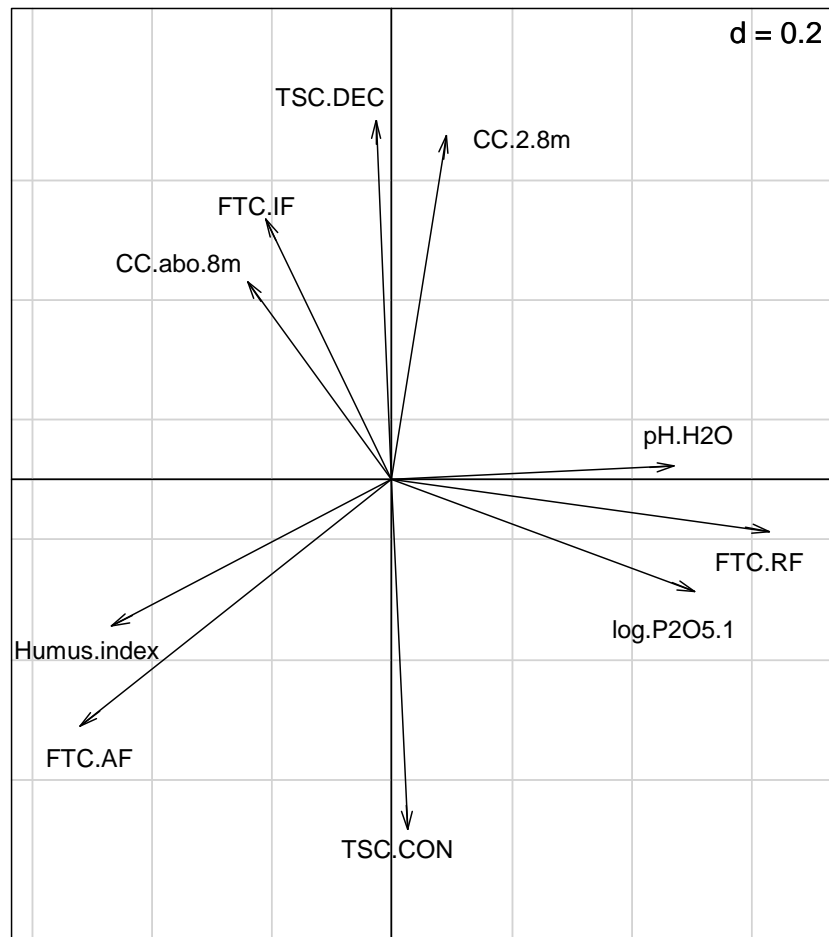
640

641 **Fig. 2.** Biplot of the sampling points in the first factorial map of the CCA applied to the matrix of 80
642 sampling sites and 197 species using forest continuity and tree species as predictors. The value of d
643 gives the grid size. The plots are grouped according to stand type: AF: ancient forests; IF: intermediate-
644 age forests; RF: recent forests; tree species: DEC: deciduous; CON: coniferous. The ellipses comprised
645 67% of the points on the hypothesis that the scatter is a simple random sample following a bivariate
646 normal distribution.

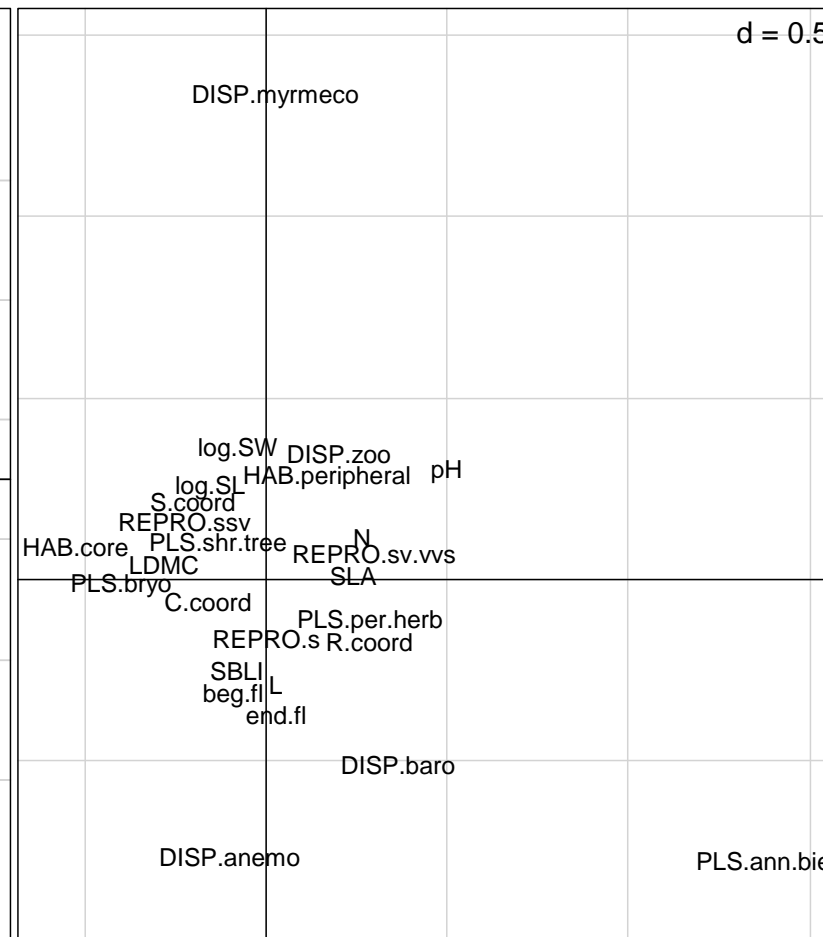
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(a)

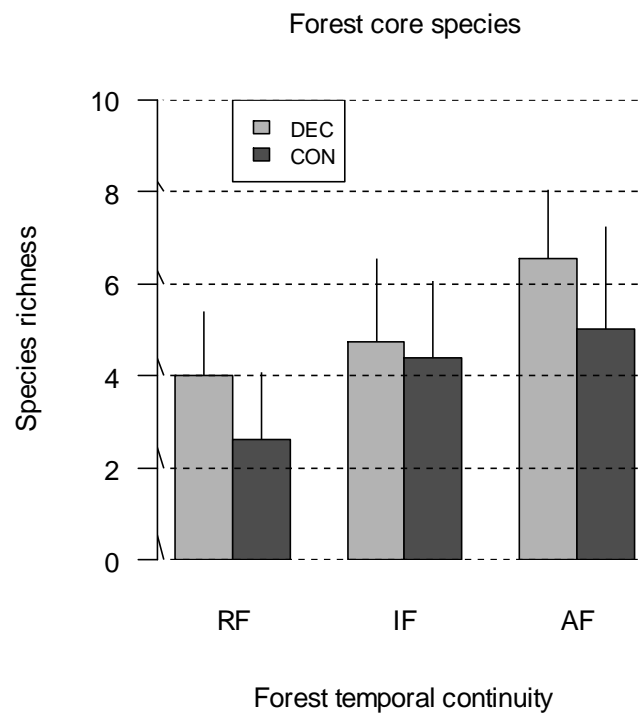


(b)



649

650 **Fig. 3.** Simultaneous ordination of (a) forest continuity, tree species and environmental variables and (b) species traits in the first RLQ factorial map. The
 651 value of d gives the grid size. Codes for environmental variables: AF: ancient forest; IF: intermediate-age forest; RF: recent forest; CON: coniferous; DEC:
 652 deciduous; CC >8 m: canopy cover above 8 m; CC 2-8 m: canopy cover 2–8 m (see text and Appendix S1 for details). See Table 2 for trait category code and
 653 Appendix S6 for plant name code.



654

655 **Fig. 4.** Species richness of forest core plants [*sensu* Pellissier et al. (2013)] as a function of forest
656 continuity and tree species. The graph gives mean and standard deviation. AF: ancient forest; IF:
657 intermediate-age forest; RF: recent forest; CON: coniferous; DEC: deciduous. Model results: forest
658 continuity effect: $P < 0.0001$; tree species effect: $P = 0.008$; interaction: $P = 0.39$; *adjusted-R*² = 0.324.