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1 **Past landscape explains forest periphery-to-core gradient of understory plant**
2 **communities in a reforestation context**

3
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16

17 **Running headline:** History explains spatial patterns of plants.

18 **ABSTRACT**

19 **Aim.** To disentangle whether long-range periphery-to-core gradient of forest understory plants
20 could be attributed to past forest landscape and/or to current environmental filtering processes.
21 We investigated (i) whether species response to past land use (ancient *vs.* recent forest) was
22 consistent with species response to distance to present forest edge (core *vs.* periphery) (ii) what
23 life-history traits explained plant response to distance to present edge and past land use (iii)
24 whether distance to past forest edge explained current species distribution better than distance
25 to present forest edge.

26 **Location.** Temperate forests in the northern half of France (80,000 km²).

27 **Methods.** Local climate, soil and stand characteristics, past land use, and present and past
28 landscape metrics were collected on 11,936 plots using National Forest Inventory data and
29 historical maps from 1831. Logistic regressions were applied to determine the response patterns
30 of 181 species to present and past landscape, while controlling for local habitat quality (soil,
31 climate and stand).

32 **Results.** Species response to distance to present edge very well matched response to past land
33 use. Plant traits related to colonisation capacity explained species response to present edge and
34 past land use. The spatial distribution of 42 species was better explained by distance to forest
35 edge in 1831, 37 species were better explained by distance to present edge and 24 species were
36 better explained by distance to present edge and past land use.

37 **Main conclusions.** Two mechanisms were responsible for the long-range periphery-to-core
38 gradient: (i) past landscape and colonisation processes and (ii) present edge-related
39 mechanisms. This suggests that plant community differences between periphery and core zones
40 are thus related to dispersal limitation and not only to environmental filters. Our results
41 underline the need to combine landscape ecology and history and have important implications
42 for forest plant dynamics and conservation in the context of climate change.

43
44 **Keywords:** colonisation credit, edge effects, forest core species, land use history, periphery-to-
45 interior gradient, plant dispersal limitation.

46
47 **Abbreviations:** AF: ancient forest; RF: recent forest; PF: present forest; AFS: ancient forest
48 species; RFS: recent forest species; DEI: depth-of-edge influence; PLU: past land use;
49 DIST.PF.EDGE: distance to present forest edge; DIST.1831.EDGE: distance to forest edge in
50 1831.

51 INTRODUCTION

52 For centuries forest landscapes have been continuously modified by natural and human drivers
53 of land use change, resulting in successive periods of deforestation and reforestation (Kaplan *et*
54 *al.*, 2009; Rhemtulla *et al.*, 2009; Etienne *et al.*, 2013). Over the past twenty years the role of
55 history in ecology has been increasingly emphasised for both a fuller understanding of the
56 current structure and functioning of ecosystems, and the proper evaluation of conservation
57 goals (Foster *et al.* 2003; Rhemtulla *et al.*, 2009; Jackson and Hobbs, 2009; Vellend *et al.*,
58 2013), in particular in landscape ecology (Rhemtulla and Mladenoff, 2007).

59 Human development tends to fragment ecosystems, resulting in habitat loss, habitat isolation
60 and a relative or absolute increase in edge-to-core ratio (Jaeger *et al.*, 2011; Haddad *et al.*,
61 2015). Many studies have evidenced abiotic and biological gradients from habitat edge, and
62 proposed several underlying ecological processes (Ries *et al.*, 2004). The magnitude of these
63 gradients are often described in terms of depth-of-edge influence (DEI), *i.e.* the distance from
64 the edge to the habitat where there is a tangible edge influence on biophysical parameters
65 (Harper *et al.*, 2005). In forest ecosystems, estimated DEI range from a few meters to 250 m
66 (Davies-Colley *et al.*, 2000; Weathers *et al.*, 2001; Honnay *et al.*, 2002a; Gignac and Dale,
67 2007; Wuyts *et al.*, 2008; Gonzalez *et al.*, 2010).

68 However, a few studies in Brazilian and New Zealand forests have suggested that edge effects
69 might penetrate as far as 1 km into habitat patches (Laurance *et al.*, 2007, Ewers and Didham,
70 2008). A limited number of studies in Europe have explored the spatial patterns of abiotic and
71 biological components along long distance-to-edge gradients, *i.e.* up to 800–1100 m (Thimonier
72 *et al.*, 1992; De Schrijver *et al.*, 1998; Kennedy and Pitman, 2004; Hofmeister *et al.*, 2013;
73 Pellissier *et al.*, 2013). Some have reported periphery-to-core gradients for understory plant
74 species occurrence and mean indicator values for nitrogen and pH over much wider ranges than
75 previously recognized, *i.e.* up to 700–800 m (Bergès *et al.*, 2013; Hofmeister *et al.* 2013;
76 Pellissier *et al.*, 2013). This gradient in plant communities may be due to the penetration of
77 external pressures deeper into forest interior than recognized, *e.g.* eutrophication of terrestrial
78 ecosystems (Bernhardt-Romermann *et al.*, 2007; Wuyts *et al.*, 2008; Bergès *et al.*, 2013).

79 A complementary hypothesis, not formally tested so far, might be that this long-range DEI is
80 related to edge shift following reforestation (Pellissier *et al.*, 2013). Statistics on land cover
81 showed that forest cover in France increased from 9 to 16 million hectares between 1830 and
82 2009 (Anonymous, 2010), and similar land use changes occurred in many countries in Europe
83 (Mather *et al.*, 1999). For Northern France, this forest expansion roughly corresponds to a
84 theoretical edge shift of 440 m on average (Pellissier *et al.*, 2013). Past land use also lastingly

85 influences forest soil properties and understory vegetation, giving rise to the concept of ancient
86 forest (AF) and ancient forest species (AFS) (Hermy *et al.*, 1999; Hermy and Verheyen, 2007).
87 The association between forest temporal continuity and ancient forest species is related to their
88 low dispersal capacity and low recruitment success linked to soil changes arising from earlier
89 agricultural soil use (Flinn and Vellend, 2005). The role of history on the long DEI could be
90 explained as follows (Hofmeister *et al.*, 2013; Pellissier *et al.*, 2013): core species would be
91 slow colonisers and would fail to follow forest expansion and edge shift, producing what is
92 called a colonisation credit (Vellend, 2003; Jackson and Sax, 2010; Naaf and Kolk, 2015). This
93 delay would form a downward gradient of species occurrence from core to edge that would be
94 proportional to the forest expansion at the periphery of AF. Conversely, peripheral species
95 would be fast colonisers, poor competitors and shade intolerant; they would readily follow
96 forest expansion; they would also temporarily persist in recent forests following edge
97 movement, and would show a gradual regression from edge to core (Pellissier *et al.*, 2013).
98 However, these long-distance gradients in species patterns may be hindered by forest habitat
99 heterogeneity due to soil, disturbance regime and forest stand age and composition (Fortin *et al.*,
100 1996; Redding *et al.*, 2004; Kimberley *et al.*, 2014). Large datasets and replicated
101 landscapes are thus required to partition out the respective influence of these different
102 ecological factors (Avon *et al.*, 2015).

103 In sum, two main processes could explain current long range periphery-to-core gradient in
104 forest plant species distribution, but their respective role remains to be explored: (i) spatio-
105 temporal processes related to past land use and edge shift through time and (ii) edge effect, *i.e.*
106 ecological processes related to the presence of an ecological boundary between forest habitat
107 and the surrounding matrix. Our aim was to investigate in a broad geographical context whether
108 this long-range periphery-to-core gradient could be attributed to past forest landscape in
109 addition to other ecological processes, after controlling for climate, soil and forest stand
110 variations. Using land use maps from 1818–1844 (Carte d'État-Major, Dupouey *et al.*, 2007)
111 that cover 30% of the study area of our earlier work (Pellissier *et al.*, 2013), our approach takes
112 the view that landscape ecology and historical ecology should not be investigated
113 independently (Avon *et al.*, 2015). Specifically, we asked the following three questions:

114 Q1: Is species response to past land use (AF *vs.* RF) consistent with species response to
115 distance to present forest edge, *i.e.* preference for forest core *vs.* forest periphery?

116 Q2: What life-history traits explain plant species response to distance to present edge and past
117 land use among colonisation capacity, dispersal mode, life form and habitat requirements?

118 Q3: Can distance to the nearest past forest edge explain species distribution better than distance
119 to the nearest present forest edge?

120 Our hypotheses were: (1) core species prefer ancient forests and peripheral species prefer recent
121 forests (Fig. 1a, b) (2) species distribution patterns along forest periphery-to-core gradients are
122 mainly explained by traits related to plant colonisation capacity (3) distance to the nearest past
123 forest edge would better explain species distribution pattern (De Keersmaeker *et al.*, 2014),
124 which can be illustrated as follows (Fig. 1c): for species preferring AF and slowly colonising
125 RF, species occurrence should not vary in AF, and decrease with increasing distance from the
126 edge in 1818-1844 in recent forest (RF). For species preferring RF, occurrence should decrease
127 with increasing distance from present forest edge in RF and should not vary in AF.

128

129 **METHODS**

130 **Materials**

131 Past forest cover was based on historical maps (Carte d'État-Major) drawn between 1818 and
132 1844 (mean: 1831). Forest patches were georeferenced using ArcGIS version 10.0, and patch
133 boundaries were vectorised using a precise protocol (Appendix S1, Favre *et al.*, 2013) in three
134 distinct zones located in the northern half of France (Fig. S2). Present forest cover maps dated
135 from 1999 to 2004 (mean: 2002) and came from the French National Forest Inventory (NFI).

136 Past and present forest cover maps were intersected using ArcGIS to identify three types of
137 forests (Fig. S3): ancient forests (AF: patches present in 1831 and in 2002), recent forest (RF:
138 patches absent in 1831 and present in 2002), and deforested patches (DEF: patches present in
139 1831 but not in 2002). AF and RF patches formed the present forest patches (PF). Preliminary
140 analyses explored how RF and AF were spatially distributed in PF patches (Appendix S4) and
141 showed that distance to present edge was on average lower in RF than in AF.

142 Floristic and ecological data came from the NFI network and comprised a total of 11,936 plots
143 (Fig. S2). Past and present maps were used to determine past land use (PLU) for each NFI plot:
144 AF or RF. Distances from NFI plot to the edge of the nearest PF patch (DIST.PF.EDGE) and to
145 the edge of the nearest forest patch in 1831 (DIST.1831.EDGE) were calculated for each plot
146 using ArcGIS and present and past forest cover maps, respectively.

147 Plant species presence/absence was surveyed at each NFI plot inside 700 m² circles throughout
148 the year. To take plant phenology into account, the month of the plant survey (MONTH) was
149 always included in our models as a covariate and using a quadratic form. Plant traits are
150 detailed in Table 1. Climate, soil and stand variables were recorded on-plot during field
151 sampling or obtained from existing databases (see Appendix S5).

152

153 **Statistical analyses**154 Model selection

155 We performed preliminary analyses (Appendix S6) to select a short list of important habitat
 156 quality variables: annual mean of monthly maximum temperatures (TMAX), soil type (SOIL),
 157 canopy cover (CCOV), stand age (AGE) and dominant tree species of the overstory layer
 158 (TREE.SPECIES). We also explored correlations between PLU, DIST.PF.EDGE and
 159 DIST.1831.EDGE (Appendix S7) and variations in environmental conditions with
 160 DIST.PF.EDGE and PLU (Appendix S8).

161 Then, a multiple logistic regression was used to model the response of each species (*i.e.*
 162 probability of presence) to month, habitat quality and landscape variables:

$$\text{logit}(p_i) = \log\left(\frac{p_i}{1-p_i}\right) = \alpha + \beta \cdot X_i + \varepsilon$$

163

164 We controlled for habitat quality differences before looking at landscape and historical factors:
 165 we fitted species response to the six predictors mentioned above using a stepwise procedure
 166 based on the *step* function of R (M_{LOCAL}), following a parsimonious approach to start the model
 167 with a short list of major predictors, as acknowledged by Harrell (2001). Continuous variables
 168 were always tested using a linear and a quadratic form.

169 Once the local model was determined, four alternative models were fitted using distance to
 170 present edge ($M_{\text{DIST.PF.EDGE}}$), past land use (M_{PLU}), distance to present edge plus past land use
 171 ($M_{\text{DIST.PF.EDGE+PLU}}$) and distance to edge in 1831 ($M_{\text{DIST.1831.EDGE:PLU}}$). DIST.PF.EDGE and
 172 DIST.1831.EDGE were always included using a linear function of their logarithm. For
 173 $M_{\text{DIST.1831.EDGE:PLU}}$, we hypothesised that response would vary on either side of the edge in 1831
 174 but with a common intercept (see Fig. 1c): thus we only tested the interaction term
 175 "log(DIST.1831.EDGE+1):PLU".

$$176 \quad \text{logit}(p_i) = \omega + \varepsilon \quad (M_{\text{LOCAL}})$$

$$177 \quad \text{logit}(p_i) = \omega + \log(\text{DIST.PF.EDGE}+1) + \varepsilon \quad (M_{\text{DIST.PF.EDGE}})$$

$$178 \quad \text{logit}(p_i) = \omega + \text{PLU} + \varepsilon \quad (M_{\text{PLU}})$$

$$179 \quad \text{logit}(p_i) = \omega + \log(\text{DIST.PF.EDGE}+1) + \text{PLU} + \varepsilon \quad (M_{\text{DIST.PF.EDGE+PLU}})$$

$$180 \quad \text{logit}(p_i) = \omega + \log(\text{DIST.1831.EDGE}+1) : \text{PLU} + \varepsilon \quad (M_{\text{DIST.1831.EDGE:PLU}})$$

181 where ω corresponds to the combination of variables selected in the local model.

182

183 Comparison between species response to distance to present edge and past land use (Q1)

184 M_{PLU} and $M_{\text{DIST.PF.EDGE}}$ were compared with M_{LOCAL} using AIC and selected only if they had an
 185 AIC value five points lower than that of M_{LOCAL} . We analysed species response to
 186 DIST.PF.EDGE and to PLU to determine species profiles (core vs. periphery, AFS vs. RFS)
 187 using model equation coefficients. In our models, positive values indicate an increase in
 188 incidence with increasing DIST.PF.EDGE or a higher incidence in RF than in AF (by
 189 convention, AF was used as the baseline for testing the effect of PLU). Species not influenced
 190 by DIST.PF.EDGE or PLU were classified as "NS".

191 The two species classifications (core/peripheral, AFS/RFS) were then crossed to test whether
 192 core species preferred AF and peripheral species RF. We also applied a Spearman's correlation
 193 test to analyse the relationship between the coefficient for DIST.PF.EDGE in model
 194 $M_{\text{DIST.PF.EDGE}}$ and the coefficient for PLU in model M_{PLU} including all the 181 species, whether
 195 or not they responded significantly to distance-to-edge or PLU (Dupré and Ehrlen, 2002).

196

197 Plant trait approach (Q2)

198 We analysed and compared which plant traits explained species response to PLU and
 199 DIST.PF.EDGE: for nominal traits, we ran Chi-squared tests on the contingency tables crossing
 200 each trait and species profile (AFS/RFS or core/periphery). For continuous traits, we ran
 201 ANOVA using plant trait as dependent variable and species profile as predictor. In both cases,
 202 we also included non-significant species as a third group.

203

204 Comparison between species response to distance to past and present edge (Q3)

205 To test whether distance to forest edge in 1831 was a better predictor of species distribution, we
 206 compared the five models M_{LOCAL} , $M_{\text{DIST.PF.EDGE}}$, M_{PLU} , $M_{\text{DIST.PF.EDGE+PLU}}$ and $M_{\text{DIST.1831.EDGE:PLU}}$
 207 to determine which model was the most likely one, based on AIC differences between models.

208 The procedure is detailed in Appendix S9.

209

210 Statistical analyses were performed using R software, version 3.1.2 (R Development Core
 211 Team, Vienna, AT).

212

213 **RESULTS**

214 **Consistency between plant species response to distance to present edge and past land use**

215 The model M_{LOCAL} was always significant and contained between 1 and 6 predictors with an
 216 average of 4.9 (Table 2): the variable SOIL, TREE.SPECIES, TMAX, MONTH, AGE and
 217 CCOV occurred 164, 162, 160, 149, 140 and 120 times respectively in M_{LOCAL} . The part of

218 deviance explained by M_{LOCAL} (Nagelkerke's R^2) varied between 5.1% and 53.8% and averaged
 219 19.9% (Table S10). Among the 181 species analysed, 62 species significantly responded to
 220 DIST.PF.EDGE and PLU, 31 to DIST.PF.EDGE only, 31 species to PLU only and 57 did not
 221 respond to any variable (Table 3). Of the 62 species that significantly responded to
 222 DIST.PF.EDGE and PLU, 37 species preferred forest core and AF, 21 species preferred forest
 223 periphery and RF, three (*Hyacinthoides non-scripta*, *Polygonatum multiflorum* and *Rubus*
 224 *fruticosus*) preferred forest periphery but AF, and one (*Brachypodium sylvaticum*) preferred
 225 forest core but RF (Table 3). The part of deviance explained by PLU (when PLU was a
 226 significant predictor) varied between 0.1% and 6.7% and averaged 1.4%. The part of deviance
 227 explained by DIST.PF.EDGE (when DIST.PF.EDGE was a significant predictor) varied
 228 between 0.1% and 6.4% and averaged 1.4%. The regression coefficients associated with
 229 distance to PF edge and PLU were correlated ($R=-0.65$, $t=-11.5$, $df=179$, $p<0.0001$, Fig. S11).
 230 On removing the 62 species that significantly responded to the two effects, the correlation
 231 coefficient decreased but remained significant ($R=-0.29$, $t=-3.2$, $df=117$, $p=0.0015$).

232

233 **Plant trait response to distance to present forest edge and past land use**

234 Pteridophytes and hemicryptophytes displayed higher proportions in the pool of forest core
 235 species, while phanerophytes and endozoochorous species had higher proportions in the pool of
 236 forest periphery species (Fig. 2a). On average, forest core species had lower seed mass, seed
 237 size and indicator values for urbanity, pH and N than forest periphery species (Fig. 3).

238 Species previously classified as ancient forest species, hemicryptophytes and myrmecochorous
 239 species displayed higher proportions in our pool of AFS while phanerophytes and
 240 endozoochorous species had higher proportions in our pool of RFS (Fig. 2b). Species from our
 241 AFS pool had higher CCI, lower seed size and lower indicator values for urbanity, pH, N and L
 242 than species from our RFS pool (Fig. 4).

243

244 **Species response to distance to the nearest forest edge in 1831**

245 The comparison of the five models M_{LOCAL} , $M_{DIST.PF.EDGE}$, M_{PLU} , $M_{DIST.PF.EDGE+PLU}$ and
 246 $M_{DIST.1831.EDGE:PLU}$ using AIC provided the following seven categories (Table S10): among the
 247 181 species analysed, M_{LOCAL} was the best model for 52 species, $M_{DIST.PF.EDGE}$ was the best
 248 model for 37 species, M_{PLU} was the best model for 17 species, the two models $M_{DIST.PF.EDGE}$ and
 249 M_{PLU} were equivalent for two species, $M_{DIST.PF.EDGE+PLU}$ was the best model for 24 species,
 250 $M_{DIST.1831.EDGE:PLU}$ was the best model for 42 species, and the two models $M_{DIST.PF.EDGE+PLU}$ and
 251 $M_{DIST.1831.EDGE:PLU}$ were equivalent for seven species. Consequently, species can be classified in

252 three groups: a first group better explained by past land use and past landscape ($n=42+17=59$);
 253 a second group better explained by distance to present edge only ($n=37$); and a third group
 254 where the two effects were difficult to separate or added up ($n=2+7+24=33$). As a result of the
 255 modelling, we illustrated the response of six species for which $M_{DIST.1831.EDGE:PLU}$ was the best
 256 model and two for which M_{PLU} was the best model (*Stellaria holostea* and *Vinca minor*), with
 257 different shapes of response curve (Fig. 5): the presence probability of *S. holostea* and *V. minor*
 258 sharply decreased with increasing distance from past edge in RF, while it was rather flat inside
 259 AF. The presence probability of *Convallaria majalis* and *Euphorbia amygdaloides* showed the
 260 same pattern in RF as the two previous plants but it increased with distance to past edge in AF,
 261 rather than being flat. The predicted response for RFS also displayed variable shapes with a
 262 more or less flat curve in AF.

263

264 DISCUSSION

265 Through a large-scale approach, we found evidence that past forest landscape, plant dispersal
 266 capacity and ecological processes related to present edge effects were responsible for the long-
 267 range periphery-to-core gradient of many forest understory plant species in Northern France.
 268 Our results thus support the assertion that "*history matters in landscape ecology*" (Rhemtulla
 269 and Mladenoff, 2007). The historical landscape signal we detected in the distribution patterns
 270 of forest plants was supported by three results: (i) core plant species preferred ancient forests
 271 and peripheral species recent forests, (ii) plant traits related to species colonisation capacity
 272 explained species response to present edge and past land use and (iii) past land use and distance
 273 to the nearest forest edge in 1831 better explained plant distribution patterns for 23% of the
 274 species analysed.

275

276 **Periphery-to-interior gradient of plant species is related to forest temporal continuity**

277 Given that preliminary analysis revealed that recent forests were on average closer to the
 278 present forest edge than ancient forests (Appendix S4), we expected that species response to
 279 past land use and distance to the present forest edge would very well match. Indeed; 37 core
 280 species (63%) preferred AF and 21 peripheral species (60%) preferred RF, thus confirming our
 281 first hypothesis: recent forest species displayed a peripheral profile, while ancient forest species
 282 exhibited a core profile (Hofmeister *et al.*, 2013). Consequently, the "edge effect" usually
 283 invoked to explain spatial variations related to environmental filters on both sides of the edges

284 (Ries *et al.*, 2004) is not the only process accounting for this long-distance gradient (Pellissier
285 *et al.*, 2013).

286 In addition, 62 species were influenced by distance to present edge only or past land use only
287 (Table 3). Here, we suspect that most of these species were not classified as significant for the
288 other predictor because we adopted a strict AIC threshold ($\Delta AIC > 5$ between M_{LOCAL} and M_{PLU}
289 or $M_{DIST.PF.EDGE}$). This was confirmed by the high correlation obtained between coefficients
290 associated with distance to present edge and past land use (Fig. S11): this graph shows that the
291 181 species were well structured along the second bisector (with few exceptions), even for
292 species that only significantly responded to one of the two variables.

293

294 **Consistency between plant trait response to distance to present edge and past land use**

295 In accordance with species response to distance to present edge and past land use, several traits
296 related to plant dispersal capacity similarly discriminated response to distance to present edge
297 and past land use, which confirms our second hypothesis. AFS had significantly higher CCI
298 than RFS (47.1 ± 8.0 vs. -28.4 ± 14.7) and core species displayed the same trend ($p=0.085$); core
299 species and AFS were more often hemicryptophytes and myrmecochores; and peripheral
300 species and RFS were more often endozoochores and phanerophytes. These differences in life
301 form and dispersal mode were previously observed between recent and ancient forests (Sciama
302 *et al.*, 2009). Indeed, endozoochorous species are often considered to be better colonizers than
303 the other groups (Bellemare *et al.*, 2002), even though the relationship between dispersal mode
304 and colonization ability is largely debated (Hermy and Verheyen 2007). Results on seed mass
305 and size were largely redundant with results on life form since phanerophyte seeds were much
306 heavier and longer than the other life forms. In addition, AFS and core species displayed higher
307 indicator values for pH and N, even after controlling for soil, tree species composition, stand
308 age and canopy cover differences among plots. This certainly results from higher topsoil pH,
309 nutrient concentrations and nitrification rates in soils under recent forests than under ancient
310 forests due to soil modifications by former agricultural use (Hermy and Verheyen, 2007).

311 We proposed an update list of AFS for northern half of France (Appendix S10), however
312 diverging from that of Hermy *et al.* (1999) and Dupouey *et al.* (2002): when we crossed the 59
313 AFS of our study and the 73 species of Hermy and Dupouey, we only found 34 shared species.
314 This confirms that there is not a unique list of AFS, as reported in other studies (Verheyen *et al.*
315 *et al.*, 2003; Schmidt *et al.*, 2014): regional variations remain and differences in land use history
316 and forest fragmentation must be considered (De Frenne *et al.*, 2011). The role of past land use
317 on plant communities is related to long-term soil modifications due to former agriculture and

318 dispersal limitation due to slow dispersal capacity of AFS. The variability in the list of AFS
 319 among studies suggests that past land use effect results from a complex combination of plant
 320 traits and study context, including characteristics of the regional species pool, forest
 321 fragmentation, age of the reforestation and abiotic differences between ancient and post-
 322 agricultural forests.

323

324 **Periphery-to-core gradient of plant species is related to past landscape**

325 Our analysis went further as we showed that distance to forest edge in 1831 was the best
 326 predictor of the distribution of 42 species, which is consistent with our third hypothesis. This
 327 means for these species that previous land use plus plot location relative to the forest edge in
 328 1831 ($M_{\text{DIST.1831.EDGE:PLU}}$) brought more information than previous land use only (M_{PLU}), plot
 329 location relative to present forest edge ($M_{\text{DIST.PF.EDGE}}$) or previous land use plus plot location
 330 relative to present forest edge ($M_{\text{DIST.PF.EDGE+PLU}}$). Moreover, AFS profile was much more
 331 common than RFS profile among these 42 species ($n=26$ vs. $n=7$, Table S10). Based on these
 332 results, we can conclude that many AFS followed the forest colonisation front with delay and
 333 became rarer with increasing distance from AF sources, *i.e.* from distance to the nearest
 334 population source (Flinn and Vellend, 2005). Their colonisation process into RF depends on: (i)
 335 the potential habitat quality between present and past edge position (do habitat conditions in RF
 336 correspond to the ecological niche of the species?), (ii) time elapsed since the reforestation
 337 (how much time did the species have to disperse and colonise the new habitat?) and (iii) plant
 338 colonisation capacity and establishment success, two species attributes that modulate
 339 colonisation process into post-agricultural forest (Hermy and Verheyen, 2007). Conversely,
 340 fast-colonising species quickly settled in newly forested areas and displayed a gradual pattern
 341 from periphery to core. All this creates a particular pattern of species distribution in present
 342 forest patches, with colonisation credit occurring for AFS in RF patches and extinction debt for
 343 RFS as forest continuously expands (Jackson and Sax, 2010; Naaf and Kolk, 2015).

344 Another aspect of our third hypothesis assumed that for AFS slowly colonising post-
 345 agricultural forests, species occurrence would be independent from distance to the edge in 1831
 346 in AF but decrease with increasing distance to that edge in RF (Fig. 1c). This expected response
 347 pattern was found for eight AFS: *Lonicera periclymenum*, *Melica uniflora*, *Q. petraea*, *Sorbus*
 348 *torminalis*, *S. holostea*, *Tilia cordata*, *V. minor* and *Viola reichenbachiana*. However, for other
 349 AFS species (*e.g.* *C. majalis* or *E. amygdaloides*), frequency still increased over several
 350 hundreds of metres inside ancient forest interior (Fig. 5). This result deserves attention because,
 351 as far as we know, only one study on understory plant species in Belgium found edge effects

352 inside ancient forests using old forest maps from two periods: 1775 and 1904-1931 (De
 353 Keersmaecker *et al.*, 2014): AFS number decreased with increasing distance to the nearest past
 354 edge in RF and increased with increasing distance from the nearest past edge inside AF.

355 Even if true edge effects inside ancient forest could be invoked, additional elements could
 356 explain the shape of species response to distance to edge in 1831. First, the status of ‘ancient
 357 forest’ is based on a single historical map (1818-1844), whereas the patch could have been
 358 deforested before or after this date (and then reforested). It has been recently pointed out that
 359 the proportion of AF strongly depends on the number of intermediate maps available (De
 360 Keersmaecker *et al.*, 2015). Second, RF patch age varied widely, because reforestation in France
 361 occurred in successive waves from 1831 onwards (Mather *et al.*, 1999). The ecological
 362 information contained in historical land use maps is relevant because the date of mapping
 363 (around 1830) corresponds most probably to the lowest minimum forest cover experienced by
 364 the French temperate forests in the past 2000 years (Mather *et al.*, 2000). However, the
 365 remaining gradient for some AFS inside AF patches suggests that earlier waves of deforestation
 366 could have occurred in our study area, as suggested by De Keersmaecker *et al.* (2014) in
 367 Flanders and documented by Georges-Leroy *et al.* (2011) in North-eastern France.

368

369 **Plant response to environmental processes related to present edge effects**

370 Our results also indicated that, for other species, the long-range periphery-to-core gradient of
 371 plant distribution was better explained by ecological processes related to present edge effects
 372 than by past landscape. First, we identified 20 core and 11 peripheral species that did not
 373 respond significantly to past land use and 4 species with core/RF or peripheral/AF profile
 374 (Table 3). Second, the comparison of the five alternative models indicated that the best model
 375 for 37 species included distance to present forest edge only. Third, we identified plant traits that
 376 better discriminated between core *vs.* peripheral profile than between AFS *vs.* RFS profile:
 377 pteridophytes were lacking in the peripheral species pool (Fig. 2a) and distance to present edge
 378 explained a higher part of variance in indicator value for urbanity and N compared to past land
 379 use (Fig. 3 and Fig. 4). Peripheral species were much more nitrogen-demanding, had higher pH
 380 indicator values and were more urbanophilic than core species. This is fully consistent with the
 381 usual edge effect found in the literature (Weathers *et al.*, 2001; Honnay *et al.*, 2002a; Gonzalez
 382 *et al.*, 2010): pioneer, ruderal, competitive, nutrient-demanding and synanthropic species are
 383 more frequent close to forest edge (Honnay *et al.*, 2002a; Guirado *et al.*, 2006), due to specific
 384 microclimatic conditions, higher agro-chemical inputs (Thimonier *et al.*, 1992) and more
 385 frequent disturbances (Godefroid and Koedam, 2003). However, we detected periphery-to-core

386 gradients with much longer DEI than previously recognised, which suggests underlying
 387 processes other than the usual short range edge effect, such as atmospheric deposition,
 388 browsing pressure or seed pressure. Atmospheric N and S depositions are reported to decrease
 389 exponentially with increasing distance from the edge up to 8-180 m into forest interior (De
 390 Schrijver *et al.*, 2007; Wuyts *et al.*, 2008), because forest edges disturb the vertical wind profile
 391 and cause air turbulence (Weathers *et al.*, 2001). Using the same NFI plot network and covering
 392 a larger area than the present study, Bergès *et al.* (2013) showed that Ellenberg mean indicator
 393 value for N (MIV N) significantly decreased over distance-to-edge in excess of 500 m and this
 394 DEI remained significant after controlling for climate, soil and stand differences. They
 395 hypothesized that the long range gradients could be explained by atmospheric nitrogen
 396 deposition deeper inside forest interior, in accordance with previous investigations that detected
 397 DEI over 500 m into forest interior for MIV N (Thimonier *et al.*, 1992; Kennedy and Pitman
 398 2004). Other ecological processes are linked to ungulate movements between forest habitats
 399 and crops for feeding across forest edges (Bleier *et al.*, 2012) and their role in seed dispersal
 400 (endo- and epi-zoochory, Albert *et al.*, 2015) and browsing pressure (Boulanger *et al.*, 2015) in
 401 temperate landscapes.

402

403 **The different underlying mechanisms are difficult to disentangle**

404 The best model was $M_{\text{DIST.PF.EDGE+PLU}}$ for 24 species and the two models $M_{\text{DIST.PF.EDGE+PLU}}$ and
 405 $M_{\text{DIST.1831.EDGE:PLU}}$ were equivalent for seven species. It was also difficult to determine what
 406 traits were exclusively related to past land use effect or distance to present edge effect.
 407 Consequently, the separation of the respective influence of present edge effect and past
 408 landscape was not always feasible. One reason for this is certainly the additive effects of drivers
 409 on environmental variables, as evidenced by topsoil nutrient content: first, past deforestations
 410 occurred more frequently on nutrient-richer soils (Wulf, 2003; Flinn and Vellend, 2005;
 411 Brudvig *et al.*, 2013), thus reforestation tend to occupy soils with higher nutrient content
 412 (Appendix S8). Second, agricultural practises (*i.e.* fertilisation) enriched topsoil in carbon,
 413 nitrogen and mineral elements and these changes persist after reforestation (Hermy and
 414 Verheyen, 2007). Third, atmospheric nitrogen depositions display a decreasing gradient from
 415 forest edge to interior (Wuyts *et al.*, 2008; Bergès *et al.*, 2013). These three processes combine
 416 to modify topsoil nutrient content in the same direction, which could explain why plant
 417 communities had higher indicators values for pH and N at forest periphery but also in recent
 418 forests, even after controlling for soil differences.

419

420 **CONCLUSION**

421 Two complementary mechanisms explained long range periphery-to-core gradient in forest
 422 understory species: (i) past landscape and colonisation processes and (ii) mechanisms related to
 423 present forest edge. For several species, the two mechanisms are difficult to separate.
 424 Concerning the role of history, similar gradients of plant distribution might occur in other parts
 425 of the world because the same land use history occurred in many European countries, eastern
 426 USA and south-eastern Canada (Rudel *et al.* 2005). Nevertheless, our conclusion should be
 427 restricted to areas where a phase of net deforestation occurred in the past followed by a period
 428 of net reforestation, but cannot be transposed to landscapes dominated by continuous forest
 429 habitat loss and fragmentation, such as tropical or equatorial forests (Laurance *et al.*, 2007;
 430 Broadbent *et al.*, 2008; Haddad *et al.*, 2015). Our results underline the need to combine
 431 landscape ecology and historical ecology to properly understand the current structure and
 432 functioning of ecosystems (Rhemtulla and Mladenoff, 2007; Vellend *et al.*, 2013). Plant species
 433 composition differed between ancient and recent forests, recent forests were closer to present
 434 forest edge than ancient forests, and so biodiversity conservation policies should take into
 435 account the spatial distribution of ancient forests. Ancient forest species have great difficulty
 436 colonising newly established forest patches, especially when those patches are spatially isolated
 437 (Jacquemyn *et al.*, 2003). These slow-colonising plant species will thus be unable to follow
 438 climate change, and their survival will depend on their environmental tolerance and landscape
 439 connectivity (Honnay *et al.*, 2002b; Hodgson *et al.*, 2009).

440

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449

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643

644 **BIOSKETCH**

645 **Laurent Bergès** is a forest plant ecologist. His areas of research include the role of natural and
 646 human disturbances on forest plant biodiversity dynamics at different spatial and temporal
 647 scales. His current research focuses on the role of the surrounding landscape structure and
 648 composition on plant communities: impact of habitat fragmentation, linear infrastructure, and
 649 the potential benefit of ecological corridors.

650 **Author contributions:** LB, CA, SC and JLD conceived the ideas; LA and SC calculated the
651 spatial data. LB, CA, FA and JLD contributed to obtain past forest maps; LA, CA, JLD and LB
652 analysed the data, LB led the writing.

653

654 **SUPPORTING INFORMATION**

655

656 Additional Supporting Information may be found in the online version of this article:

657

658 **Appendix S1.** Protocol for historical data collection

659 **Figure S2.** Study area map

660 **Figure S3.** Specific spatial distribution of AF and RF patches

661 **Appendix S4.** Forest cover variation between 1831 to 2002

662 **Appendix S5.** Detailed Material

663 **Appendix S6.** Preliminary analyses to select local habitat quality variables

664 **Appendix S7.** Relationships between DIST.PF.EDGE, PLU and DIST.1831.EDGE

665 **Appendix S8.** Variations in environmental conditions with DIST.PF.EDGE and PLU

666 **Appendix S9.** Procedure to identify the best model among the five fitted models

667 **Table S10.** Detailed results of the five models for the 181 species analysed

668 **Figure S11.** Biplot of the regression coefficients associated with DIST.PF.EDGE and PLU

669

670 **Table 1.** Overview of the plant traits analysed.

Traits	Description and range	Scale	Number (and %) of species with trait data available	Data source
Ancient forest sp.	2 classes: species previously classified as AFS (73 species) or not	Nominal	181 (100%)	Hermý <i>et al.</i> (1999), Dupouey <i>et al.</i> (2002)
Life form	7 classes: bryophyte, pteridophyte, therophyte, geophyte, hemicryptophyte, chamaephyte, phanerophyte	Nominal	181 (100%)	Julve (2011)
Dispersal mode	8 classes: anemochory, autochory (bryophytes), barochory, hydrochory, myrmecochory, epizoochory, endozoochory, dyszoochory	Nominal	165 (91%)	Julve (2011)
CCI	Colonisation capacity index: from 100: slow colonising species to -100: fast-colonising species	-	79 (44%)	Verheyen <i>et al.</i> (2003)
Seed mass	Mean seed mass	mg	117 (65%)	Kühn <i>et al.</i> (2004)
Seed size	Mean seed length	mm	131 (72%)	Kühn <i>et al.</i> (2004)
pH	soil pH [3 – 8.5]	pH Unit	175 (97%)	Gégout <i>et al.</i> (2005)
N	soil nitrogen: from 1 to 9 (nitrogen-demanding)	Ordinal	134 (74%)	Ellenberg <i>et al.</i> (1992)
F	soil humidity: from 1 to 9 (moisture-demanding)	Ordinal	146 (81%)	Ellenberg <i>et al.</i> (1992)
Ta	mean annual air temperature [3.8 – 15.7]	°C	171 (94%)	Gégout <i>et al.</i> (2005)
L	light: from 1 to 9 (light-demanding)	Ordinal	169 (93%)	Ellenberg <i>et al.</i> (1992)
Urbanity	5 classes: from 1: urbanophobic to 5: urbanophilic	Ordinal	160 (88%)	Kühn <i>et al.</i> (2004)

671 **Table 2.** Relative importance of the local variables used in the local model (M_{LOCAL}) for the
 672 181 species. The table gives, for each predictor and for each rank, the number of times the
 673 predictor entered the model at this rank (see Appendix S5 for variable description). Continuous
 674 local predictors were tested using a linear and a quadratic form (quad).

Predictor	Predictor rank no.						Total
	1	2	3	4	5	6	
SOIL	5	77	56	19	6	1	164
TREE.SPECIES	17	64	55	17	9	0	162
MONTH-quad	149	0	0	0	0	0	149
TMAX-quad	4	8	26	39	28	6	111
AGE-quad	1	11	13	35	29	15	104
CCOV-quad	3	7	12	18	13	15	68
CCOV	0	1	3	16	20	12	52
TMAX	1	8	6	17	16	1	49
AGE	1	4	7	7	9	8	36

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677 **Table 3.** Distribution of the 181 understory plant species analysed according to their response
 678 to distance to present forest edge and past land use.

		Species response to distance to present forest edge				
		Core	Periphery	NS	Total	
Species response to past land use	AF	37	3	19	59	93
	RF	1	21	12	34	
	NS	20	11	57	88	
	Total	58	35	88	181	
		93				

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681 **Figure Captions**

682 **Fig. 1.** Illustration of the three alternative hypotheses whereby the long distance periphery-to-
 683 core gradient of plant species frequency would be related to: (a) edge effects, (b) past land use
 684 or (c) past landscape and colonisation processes. See text for details.

685
 686 **Fig. 2.** Nominal plant trait variation according to (a) species response to distance to present
 687 forest edge (core, peripheral, NS) and (b) species response to past land use (AFS, RFS, NS).
 688 Percentage of species for each trait category according to species profile: AFS*: AFS according
 689 to previous publications; BRYO: bryophyte; PTER: pteridophyte; THER: therophyte; GEOP:
 690 geophyte; HEMI: hemicryptophyte; CHAM: chamaephyte; PHAN: phanerophyte; ANEM:
 691 anemochory; AUTO: autochory; BARO: barochory; DYSZ: dyszoochory; ENDO:
 692 endozoochory; EPIZ: epizoochory; HYDR: hydrochory; MYRM: myrmecochory. Percentages
 693 show the proportion of species having a given trait among the total number of core, peripheral
 694 or non-significant species (or along the total number of AFS, RFS or NS species). The usual
 695 flags indicate the significance level of the Chi-squared for testing difference in proportion
 696 among the three species pools: *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

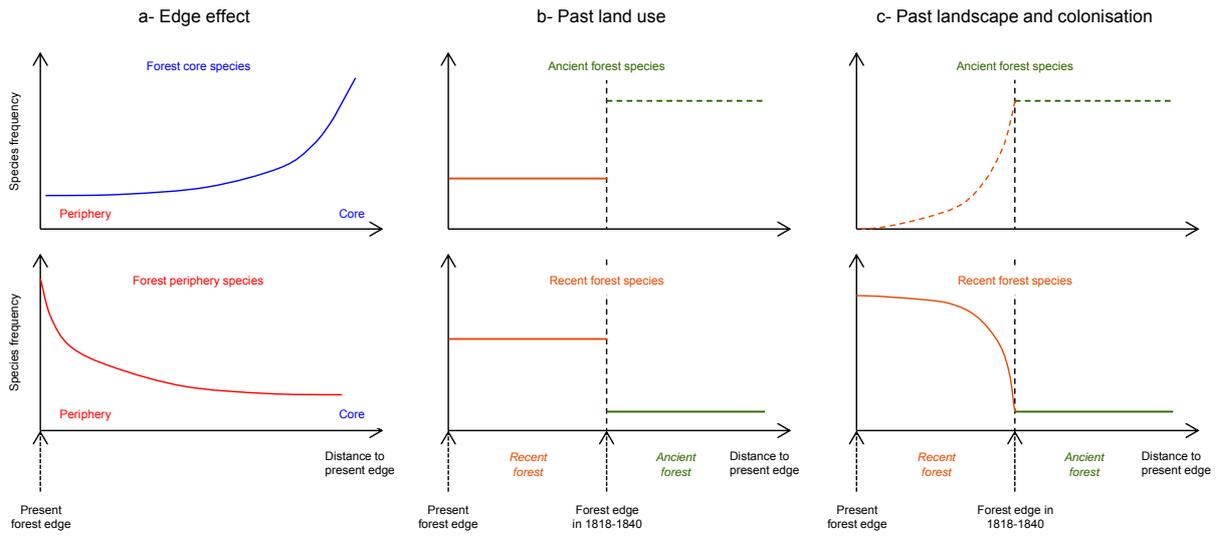
697
 698 **Fig. 3.** Differences in continuous species traits among core, peripheral and non-significant
 699 species (NS). The graph uses the box-and-whisker representation with the extreme of the lower
 700 whisker, the lower 'hinge', the median, the upper 'hinge' and the extreme of the upper whisker.
 701 Black triangles are mean values.

702
 703 **Fig. 4.** Differences in continuous species traits among AFS, RFS and non-significant species
 704 (NS). Same legend as Fig. 3.

705
 706 **Fig. 5.** Plant species presence probability according to distance to edge in 1831 as predicted by
 707 model $M_{\text{DIST.1831.EDGE:PLU}}$ (model including the interaction between distance to edge in 1831 and
 708 PLU as predictors) for four plants preferring AF: *Convallaria majalis*, *Euphorbia*
 709 *amygdaloides*, *Stellaria holostea* and *Vinca minor*; and four plants preferring RF:
 710 *Brachypodium pinnatum*, *Cornus sanguinea*, *Crataegus monogyna* and *Listera ovata*. For
 711 convenience, negative values for distance to edge in 1831 correspond to RF plots and positive
 712 to AF plots. The best model was M_{PLU} for *Stellaria holostea* and *Vinca minor* and
 713 $M_{\text{DIST.1831.EDGE:PLU}}$ for the six other species (see Table S10).

714

715 **Fig. 1**

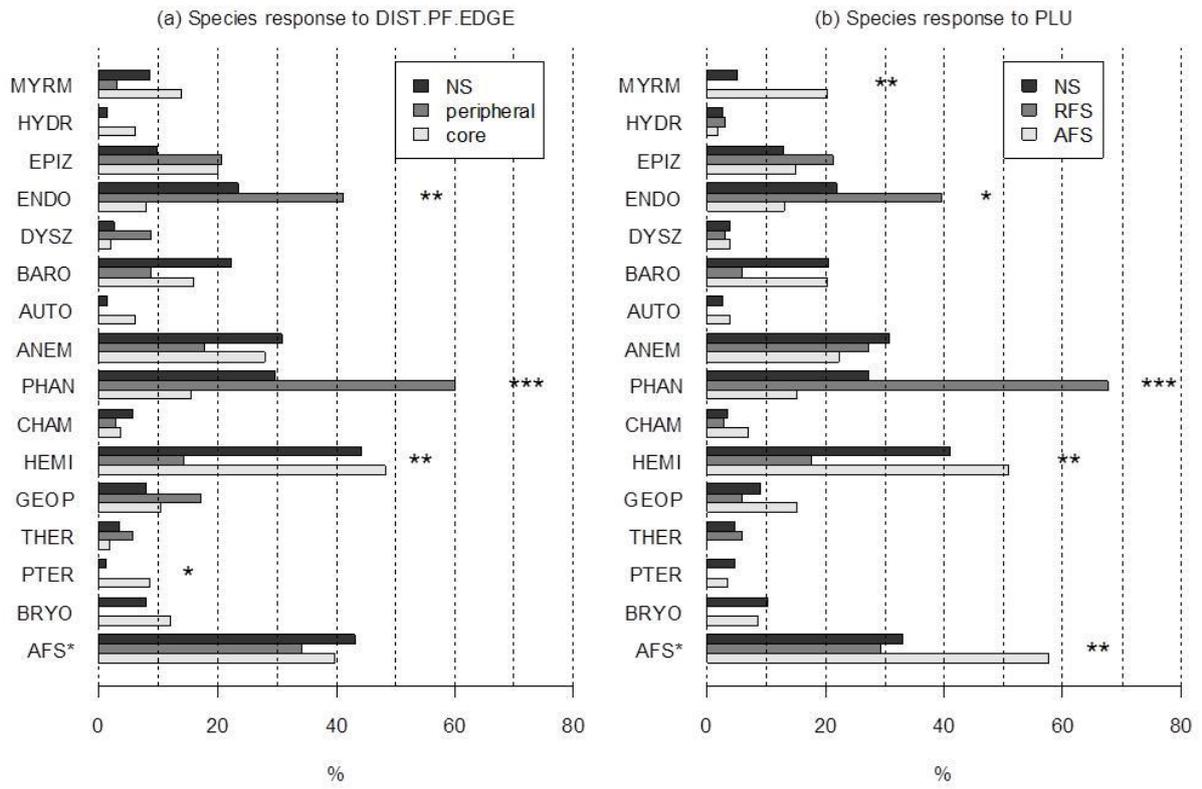


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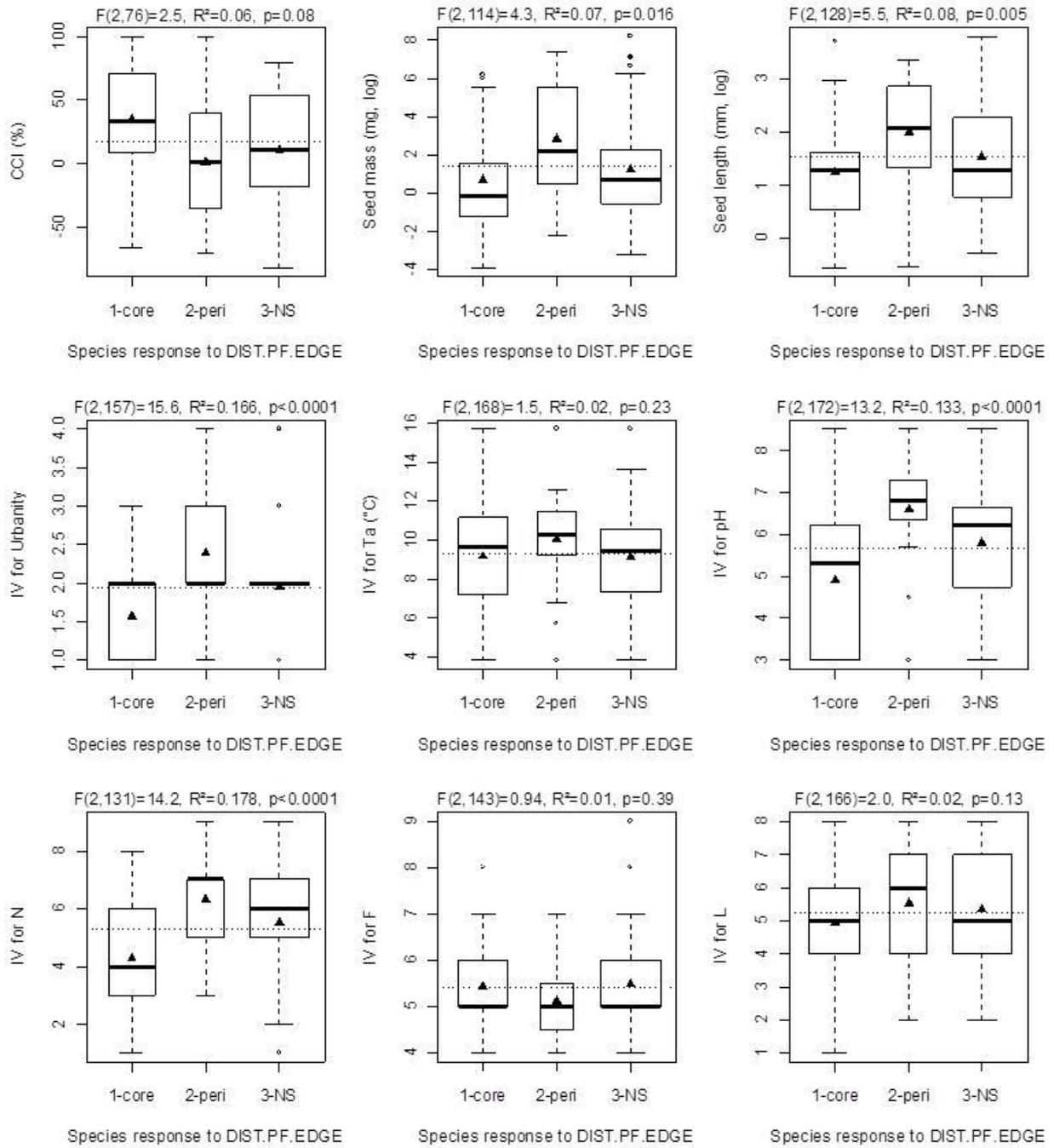
719 **Fig. 2**



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722 **Fig. 3**

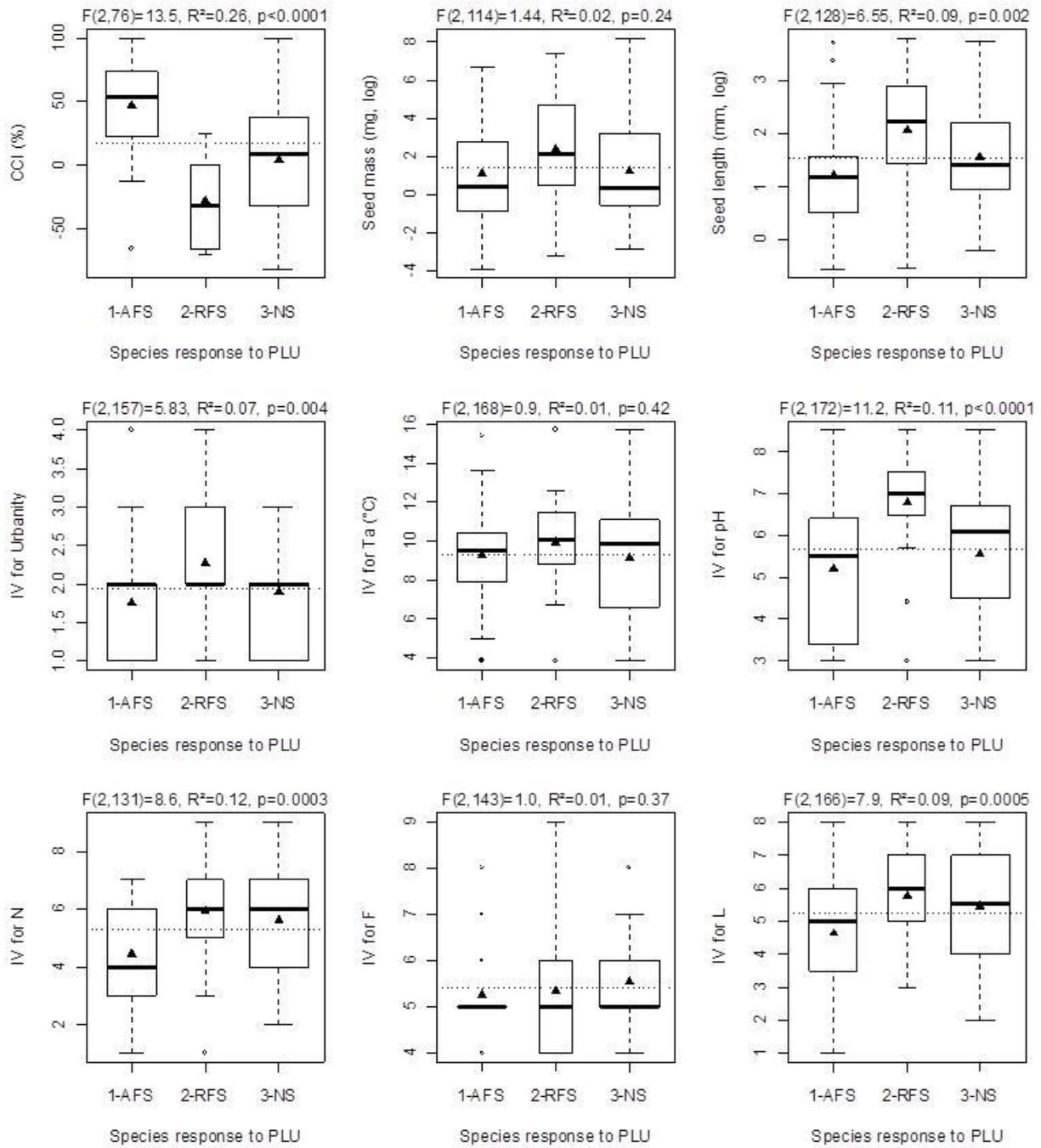


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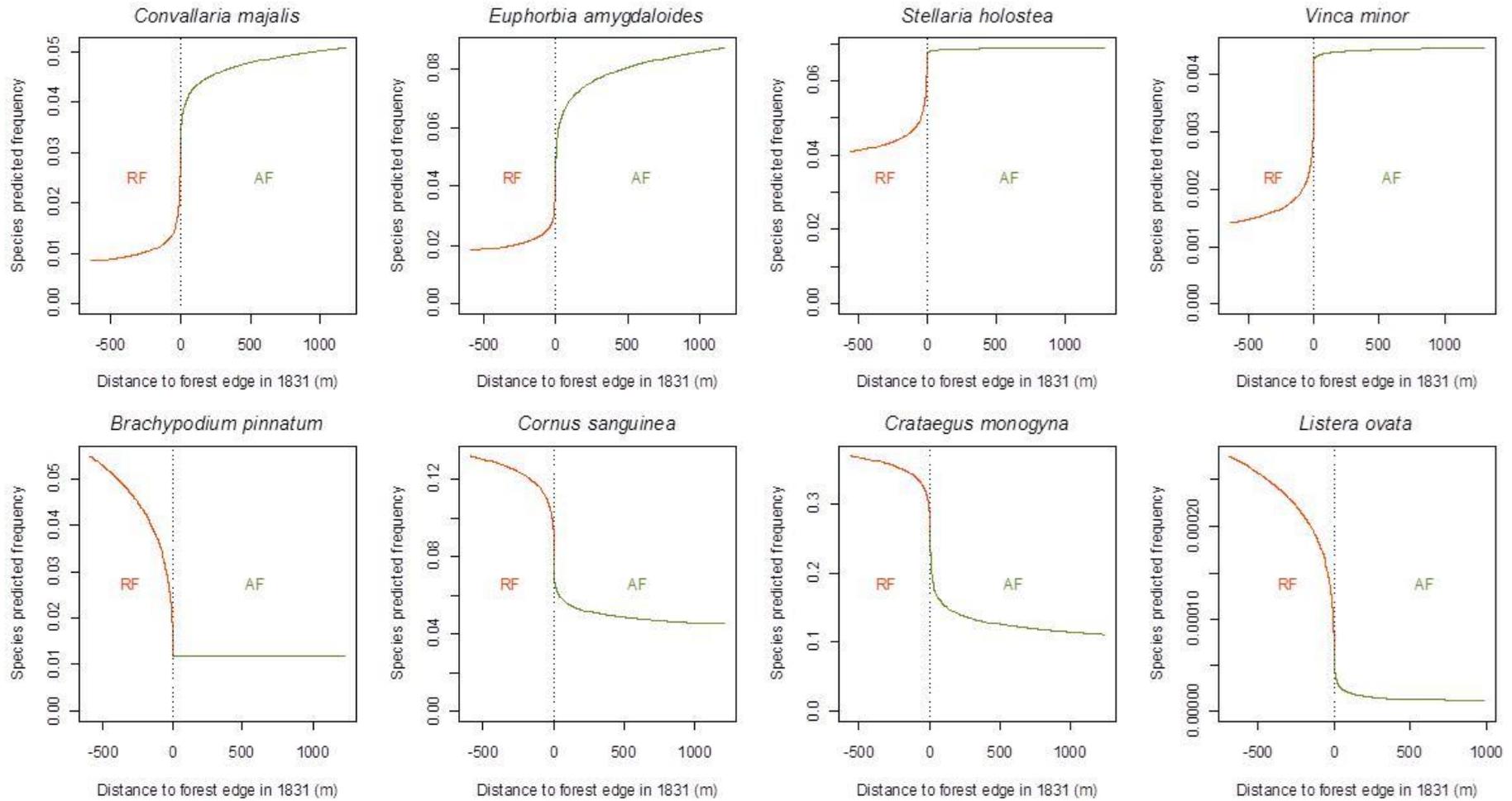
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726 **Fig. 4**



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729 **Fig. 5**



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