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

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Running headline: History explains spatial patterns of plants.

ABSTRACT

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

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

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

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

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

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

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

INTRODUCTION

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

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

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

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

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

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

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

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

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

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

METHODS

Materials

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

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

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

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

Statistical analyses

Model selection

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Plant trait approach (Q2)

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

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

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

The procedure is detailed in Appendix S9.

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

RESULTS

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

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

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

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

Pteridophytes and hemicryptophytes displayed higher proportions in the pool of forest core species, while phanerophytes and endozoochorous species had higher proportions in the pool of forest periphery species (Fig. 2a). On average, forest core species had lower seed mass, seed size and indicator values for urbanity, pH and N than forest periphery species (Fig. 3). Species previously classified as ancient forest species, hemicryptophytes and myrmecochorous species displayed higher proportions in our pool of AFS while phanerophytes and endozoochorous species had higher proportions in our pool of RFS (Fig. 2b). Species from our AFS pool had higher CCI, lower seed size and lower indicator values for urbanity, pH, N and L than species from our RFS pool (Fig. 4).

Species response to distance to the nearest forest edge in 1831

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

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

DISCUSSION

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

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

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

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

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

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

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

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

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

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

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

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

inside ancient forests using old forest maps from two periods: 1775 and 1904-1931 (De Keersmaecker *et al.*, 2014): AFS number decreased with increasing distance to the nearest past edge in RF and increased with increasing distance from the nearest past edge inside AF. Even if true edge effects inside ancient forest could be invoked, additional elements could explain the shape of species response to distance to edge in 1831. First, the status of ‘ancient forest’ is based on a single historical map (1818-1844), whereas the patch could have been deforested before or after this date (and then reforested). It has been recently pointed out that the proportion of AF strongly depends on the number of intermediate maps available (De Keersmaecker *et al.*, 2015). Second, RF patch age varied widely, because reforestation in France occurred in successive waves from 1831 onwards (Mather *et al.*, 1999). The ecological information contained in historical land use maps is relevant because the date of mapping (around 1830) corresponds most probably to the lowest minimum forest cover experienced by the French temperate forests in the past 2000 years (Mather *et al.*, 2000). However, the remaining gradient for some AFS inside AF patches suggests that earlier waves of deforestation could have occurred in our study area, as suggested by De Keersmaecker *et al.* (2014) in Flanders and documented by Georges-Leroy *et al.* (2011) in North-eastern France.

Plant response to environmental processes related to present edge effects

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

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

The different underlying mechanisms are difficult to disentangle

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

CONCLUSION

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

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BIOSKETCH

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

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

SUPPORTING INFORMATION

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

Appendix S1. Protocol for historical data collection

Figure S2. Study area map

Figure S3. Specific spatial distribution of AF and RF patches

Appendix S4. Forest cover variation between 1831 to 2002

Appendix S5. Detailed Material

Appendix S6. Preliminary analyses to select local habitat quality variables

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

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

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

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

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

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)

Table 2. Relative importance of the local variables used in the local model (M_{LOCAL}) for the 181 species. The table gives, for each predictor and for each rank, the number of times the predictor entered the model at this rank (see Appendix S5 for variable description). Continuous 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

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

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

Figure Captions

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

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

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

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

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

Fig. 1

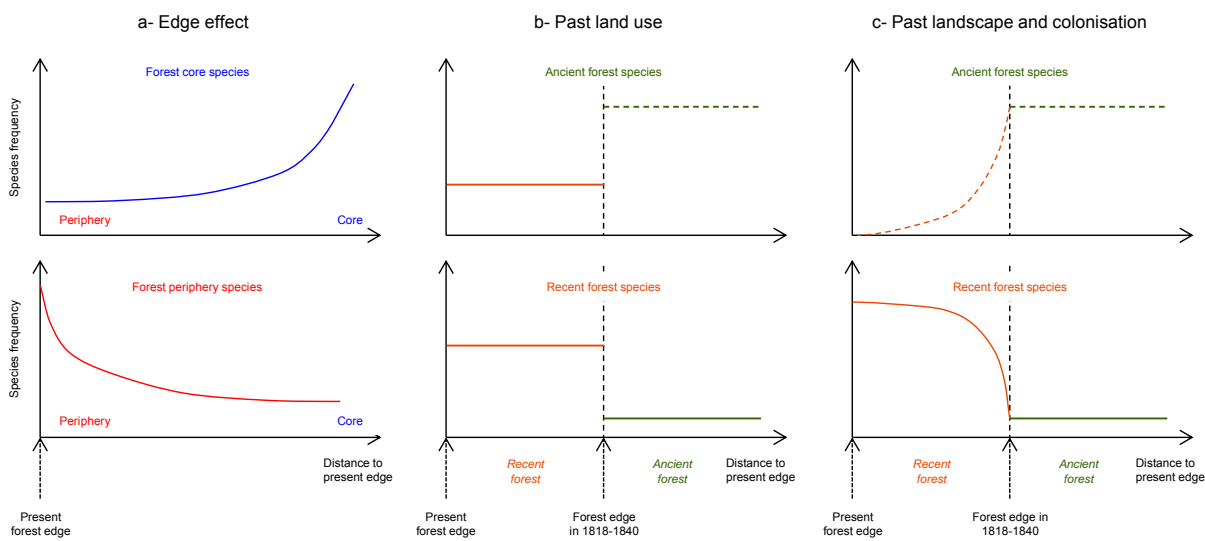
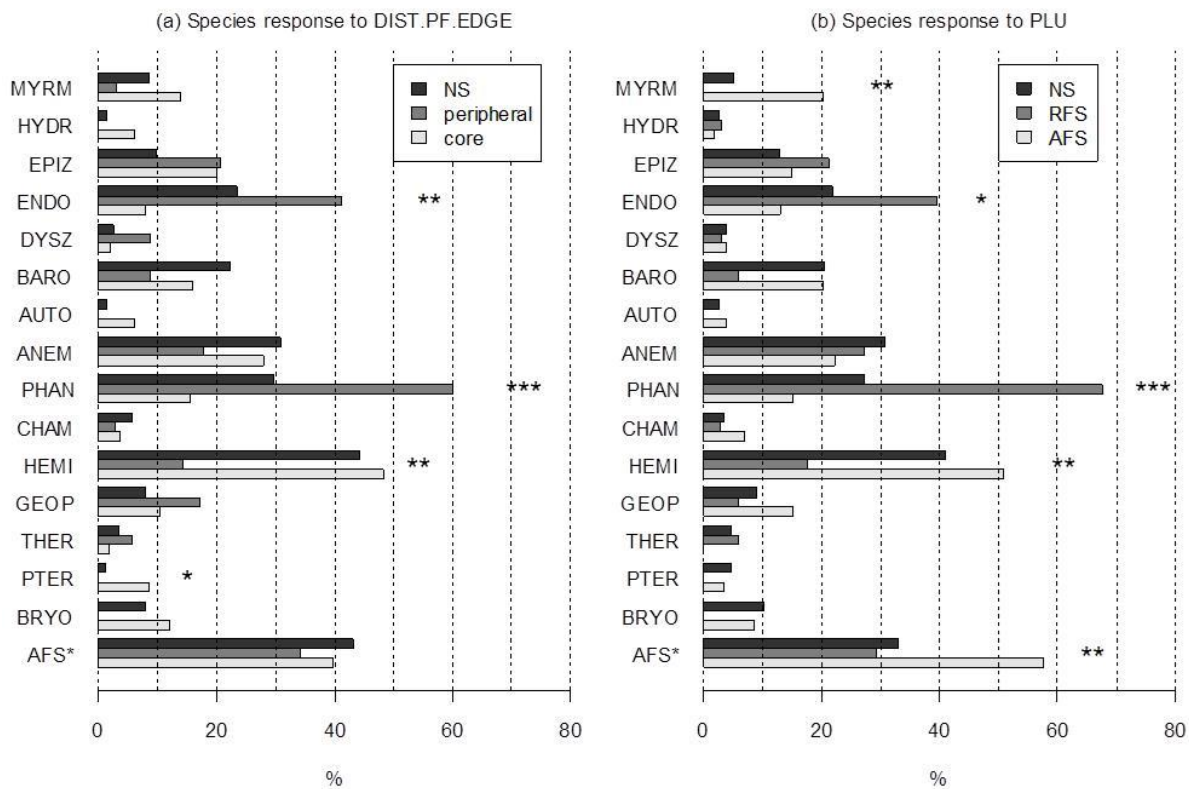
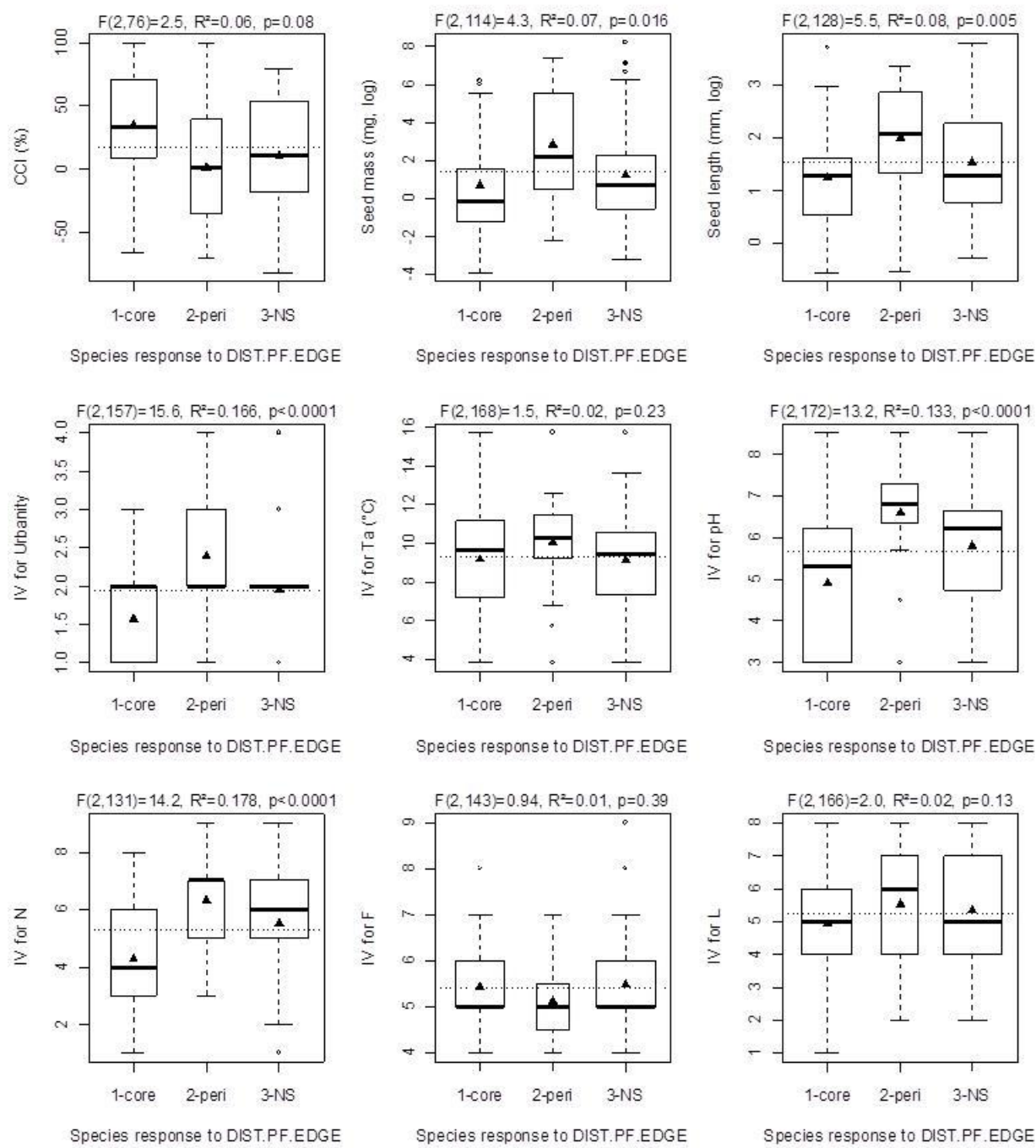


Fig. 2



722 **Fig. 3**



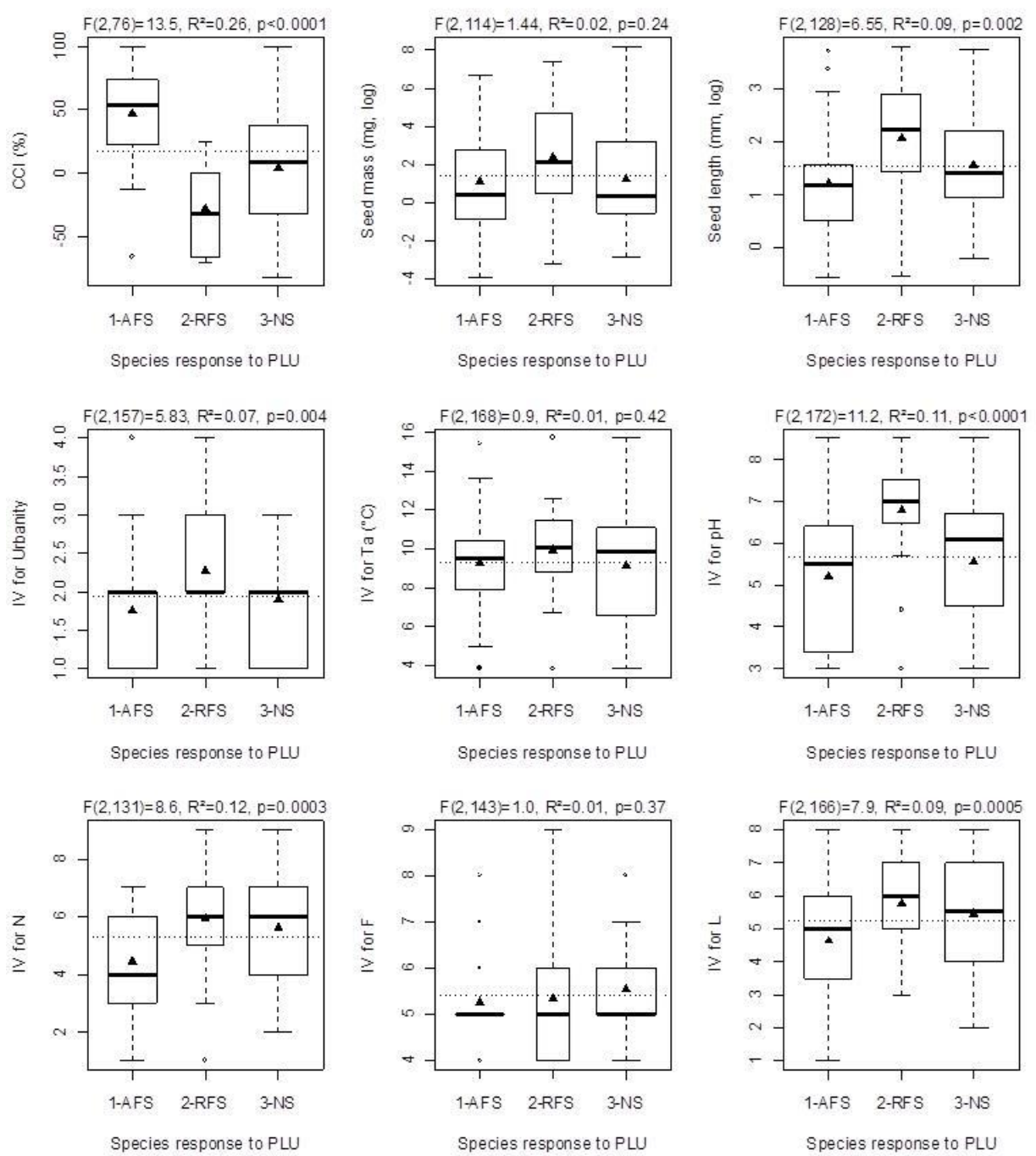
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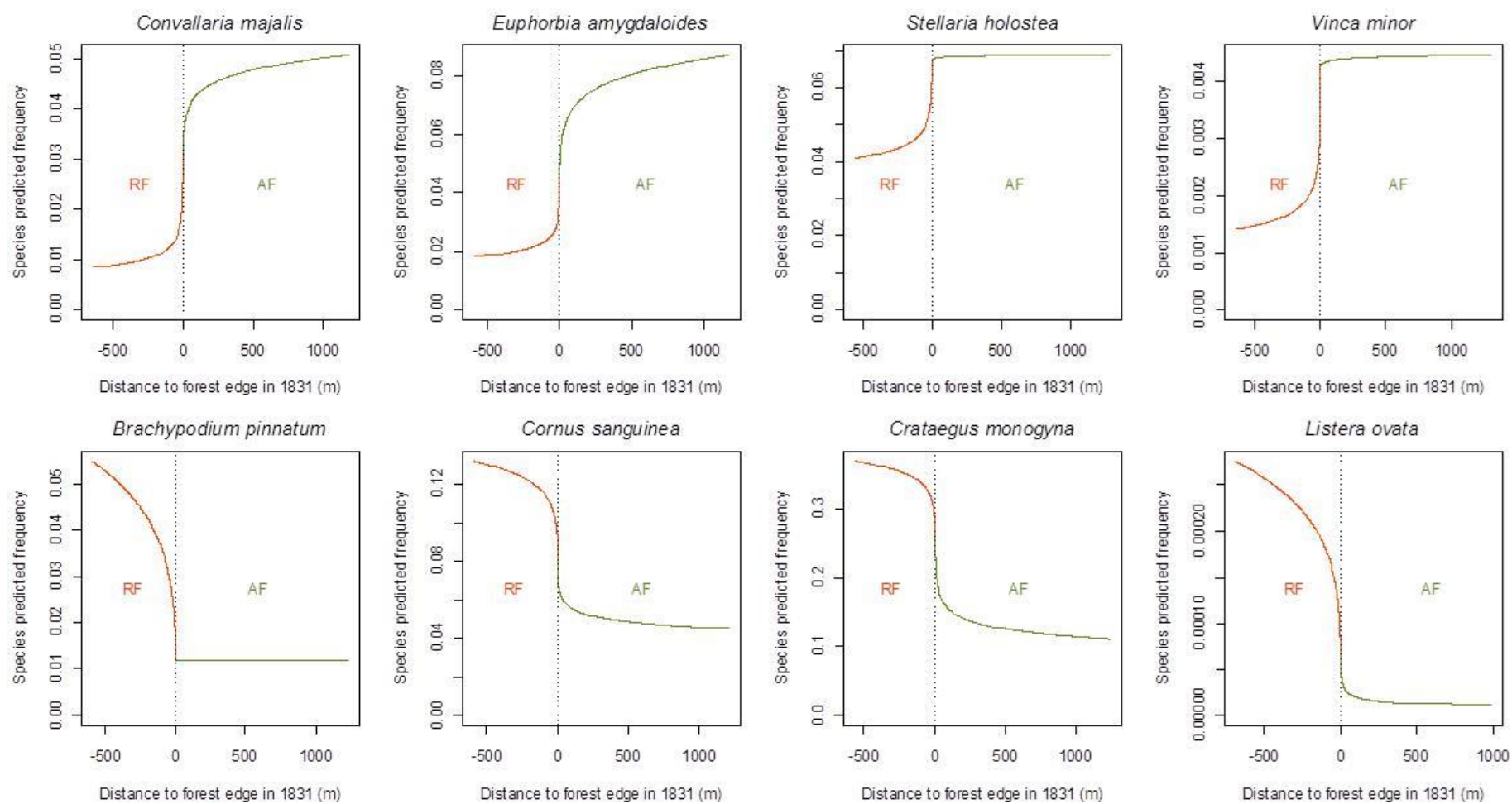
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726 **Fig. 4**



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729 **Fig. 5**



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