Journal of Vegetation Science **24** (2013) 9–24

Understorey plant species show long-range spatial patterns in forest patches according to distance-to-edge

Vincent Pellissier, Laurent Bergès, Théodora Nedeltcheva, Marie-Cécile Schmitt,
Catherine Avon, Catherine Cluzeau & Jean-Luc Dupouey

Keywords
Core species; Dispersal limitation; Edge effect; Landscape pattern; Land-use history; Patch size; Periphery-to-interior gradient; Plant traits

Nomenclature
French BDNFF flora nomenclature (Tela-Botanica 2009), European BDNBE bryophyte nomenclature (Tela-Botanica 2010)

Received 18 August 2011
Accepted 30 April 2012
Co-ordinating Editor: Otto Wildi

Pellissier, V. (vincent.pellissier@gmail.com), **Bergès, L.** (corresponding author, laurent.berges@irstea.fr) & **Avon, C.** (catherine.avon@irstea.fr): Irstea, UR EFNO, Domaine des Barres, 45290, Nogent-sur-Vernisson, France
Pellissier, V.: UMR 7204 CERSP, MNHM/CNRS/UPMC, 61 rue Buffon, 75005, Paris, France
Bergès, L. & **Avon, C.**: Irstea, UR EMAX, CS 40061, 13182, Aix-en-Provence Cedex 5, France
Nedeltcheva, T. (theodora.nedeltcheva@nievre.chambagri.fr): Inventaire Forestier National, 14 rue Girardet, CS 4216, 54042, Nancy Cedex, France
Schmitt, M.C. (marie-cecile.schmitt@onf.fr) & **Cluzeau, C.** (catherine.cluzeau@onf.fr): Office National des Forêts, 5 rue Girardet, CS 5219, 54052, Nancy, France
Dupouey, J.L. (dupouey@nancy.inra.fr): Forest Ecology and Ecophysiology Unit, INRA-Nancy University, 54280, Champenoux, France

Abstract

Questions: How does the presence of understorey plant species vary with distance-to-edge along very large periphery-to-interior and forest patch size gradients? Can forest core and periphery species profiles be identified? What life-history traits can discriminate between forest core and forest periphery species?

Location: Temperate forests in the northern half of France.

Methods: Local climate, soil, stand characteristics and landscape metrics were collected on 19 989 plots in 1801 forest patches using data from the French National Forest Inventory. Very large distance-to-edge (3–1096 m) and patch size gradients (327–100 000 ha) were explored. Four logistic regression models were compared to determine the response patterns of 214 species to distance-to-edge, while controlling for patch size and local habitat quality (soil, climate and stand). The maximum distance of correlation between species occurrence and distance-to-edge was assessed using response curve characteristics. The relationships between life-history traits (habitat preference, preference for ancient forests, reproduction mode, dispersal mode, life form and autecology) and species profile according to distance-to-edge were tested.

Results: Of the 214 species analysed, 40 had a core profile and 38 a periphery profile. The maximum distance of correlation was on average 748 m. Core species were more often species reproducing both by seed and vegetatively, ancient forest species, anemochores, bryophytes, pteridophytes, hemicryptophytes and acidophiles, whereas peripheral species were more often species reproducing by seed only, endozoochores, phanerophytes, thermophiles, basophiles, nitrogen-demanding and heliophiles.

Conclusions: Significant periphery-to-core patterns of distribution were detected over much larger ranges than hitherto recognized for common understorey plant species. Plant traits differentiated forest core from forest periphery species. This deep gradient cannot be solely explained by the usual edge-related biotic and abiotic factors. We hypothesized that it was due to edge displacement following general reforestation since ca. 1830. This edge shift created recent forests with new habitats on former agricultural lands where dispersal-limited core species had slowly expanded and forest edge species regressed at variable speeds. This long periphery-to-interior gradient of presence has important implications for forest plant species distribution, dynamics and conservation.

Introduction

Habitat loss and fragmentation are recognized as major threats to biodiversity (Tilman et al. 1994; Ewers & Didham 2006) and have become a central issue in conservation biology (Meffe & Carroll 1997). Several recent literature reviews on habitat fragmentation have focused on the creation of habitat boundaries and have proposed

Doi: 10.1111/j.1654-1103.2012.01435.x

conceptual frameworks for edge effects, with many examples in forest habitats (Cadenasso et al. 2003; Ries et al. 2004). Forest edges are transition zones where the forest habitat and the surrounding matrix interact. Ecological processes at the edge are directly affected through the alteration of biotic and abiotic flows (organisms, energy, water and nutrients), which leads to changes in site conditions and species interactions (Ries et al. 2004; Ewers & Didham 2006; Marchand & Houle 2006).

Many studies have quantified a depth-of-edge influence (DEI), operating over the distance from the edge to the adjacent habitat where there is a tangible edge influence (Harper et al. 2005). Depending on the variables considered (biotic or abiotic), this edge influence can extend into the forest for just a few metres or for as much as several hundred metres (Murcia 1995; Honnay et al. 2002; Harper et al. 2005; Gignac & Dale 2007; Gonzalez et al. 2009, 2010). Forest edges have generally higher plant species richness (Ranney et al. 1981; Fraver 1994; Gonzalez et al. 2010), and higher shrub richness and cover (Matlack 1994a; Gignac & Dale 2007), than the forest interior. Also, competitive, synanthropic and exotic species may replace stress-tolerant species at the forest edge (Honnay et al. 2002; Guirado et al. 2006), mainly due to specific microclimatic conditions (Honnay et al. 2002), higher agro-nutrient inputs (Thimonier et al. 1992; Gignac & Dale 2007) and more frequent disturbances (Godefroid & Koedam 2003).

The depth-of-edge influence up to 150 m is well-characterized and it is usually assumed that the area beyond this zone of influence, inside forest patches, does not display spatial patterns other than those related to local site conditions (soil, climate and stand type and structure).

Abundant grey literature on European forest plant communities points to species preference for edge habitats, and this knowledge has been included in regional/national species lists (e.g. Rameau et al. 1989; Schmidt et al. 2003) and plant trait databases (e.g. Biolflor, Kühn et al. 2004). The propensity of some species to prefer the habitat interior or avoid edges has often been discussed, but, as far as we know, is often based on expert knowledge rather than field observations (Grashof-Bokdam 1997; Hermy et al. 1999; Honnay et al. 1999a,b). In Europe, species preferences simply make a distinction between forest, edges, clearings and non-forest open habitats. These classifications can be based on several traits: shade tolerance, sensitivity to disturbance (Gonzalez et al. 2009) or preference for ancient forests (Hermy et al. 1999). The term 'forest interior' species is misleading since these classifications do not rely on a direct analysis of species frequency variation according to distance-to-edge (Grashof-Bokdam 1997; Honnay et al. 1999a,b; Schmidt et al. 2003). A more fitting name for such species would be 'closed' or 'true' forest species.

However, very few analyses of the spatial distribution of plant species along a very long distance-to-edge gradient, i.e. up to 1000 m, have been attempted, because such large-scale phenomena are inherently difficult to study (Laurance 2000). In tropical rain forest fragments, increased disturbance and exotic weeds could be detected up to 500 m from edges (Laurance 1991) and tree mortality up to 300 m (Laurance et al. 2002). Laurance (2000) cited several studies showing indirect edge effects on animal populations that operated over a distance of 2 km inside tropical forest reserves. Based on previous results on small forest fragments, we hypothesized that other ecological or biological mechanisms and processes unrelated to the usual 'edge effect', such as land-use history or forest edge displacement with time, might explain the spatial distribution of species according to edge proximity (Palik & Murphy 1990; Blois et al. 2001). Such mechanisms are likely to be driven by plant traits. Indeed, the spatial distribution of species can differ depending on specific biological attributes (Ries & Sisk 2004; Ewers & Didham 2006). A plant trait approach has proved useful to uncover generic patterns and processes underlying vegetation responses arising from various anthropogenic environmental changes, including fragmentation (Dupré & Ehrlén 2002; Kolb & Diekmann 2005), land-use change (Verheyen et al. 2003; De Frenne et al. 2011) and edge effects (Honnay et al. 2002; Guirado et al. 2006; Avon et al. 2010). In what follows, we use the term 'peripheral species' in place of 'edge species' to avoid confusion with the usual 'edge effect' (sensu Ries et al. 2004).

The spatial distribution of species in forest patches does not depend only on edge proximity but also on patch size. Distance-to-edge and patch size in landscapes tend to co-vary in their amount, since the density of periphery habitat in a patch, i.e. periphery-to-total-area ratio, increases as patch size decreases (Fletcher et al. 2007). Much of the literature investigating both edge and patch size across multiple taxa did not control for one potential effect while testing for the other, with many edge effects mistakenly presented as patch size effects (Fletcher et al. 2007). Only a limited number of studies on plants have taken into account both patch size and distance-from-edge effects in their approach (Guirado et al. 2006; Gignac & Dale 2007; Gonzalez et al. 2009). In this study, patch size was considered as a covariate, with no discussion of its influence, even though it is of primary importance in fragmented landscapes (Honnay et al. 1999a; Kolb & Diekmann 2005; Ewers et al. 2007)

The aims of the present work were to:

1. Analyse plant species distribution in forest patches according to distance-to-edge in a broad biogeographical context and detect core species profiles using a quantitative assessment;

Doi: 10.1111/j.1654-1103.2012.01435.x

2. Determine what life-history traits discriminated forest core from forest periphery species, among habitat preference, preference for ancient forests, reproduction and dispersal modes, life form and autecology (temperature, light, pH and humidity requirements).

The recently available French National Forest Inventory data sets enabled us to explore very large gradients of distance-to-edge, forest patch size and local site quality conditions and so reach a certain level of generalization.

Methods

French National Forest Inventory data

Data were obtained from the French National Forest Inventory (NFI), an organization entrusted with the inventory and monitoring of forest resources throughout France. To cover a homogeneous temperate climate zone, only plots in the northern half of France were analysed. The original data set comprised a total of 38 751 plots on 10 131 forest patches (Fig. 1). Plots were located within one of the 133 NFI-defined ecoregions, i.e. the division of the country into homogeneous areas in terms of geomorphology, regional climate and forest management.

Plant survey

Plant species composition was surveyed inside 700 m² circles at each plot throughout the year. Ninety-seven per cent of the plots were sampled between 1990 and 2004 (the full period was actually 1989–2009). A total of 63 teams with a range of expertise in plant identification were involved in data gathering. As a result, random variation could be substantial due to observer effects, plant oversight and species misidentification (Archaux et al. 2006). However, we considered that species presence was not likely to be biased because the sampling survey was quasi-systematic and the sample size was very large. Plant phenology is also an important factor as it affects the observed plant species composition; the month of the plant survey was therefore also included in our analysis as a covariate (MONTH). We did not control for the year of survey.

Landscape data

The distance from the plot to the closest external forest edge and the size of the forest patch where the plot was located (hereafter referred to as DIST and FPS, respectively) were calculated using GIS and NFI forest maps. Forest maps were drawn in the year preceding the field surveys. Four forest patches were larger than 100 000 ha (227 439, 230 939, 313 614 and 322 527 ha) and included 4302 plots. A log transform for FPS did not enable us to obtain a suitable FPS distribution. Each of these four forest patches was therefore assigned a single surface area of 100 000 ha to limit the statistical weight of such extremely large values. The initial data set contained 7396 plots that were closer to an internal gap than to the external edge of the patch. Because of the equivocal nature of these gaps, we removed these 7396 plots from the sample.

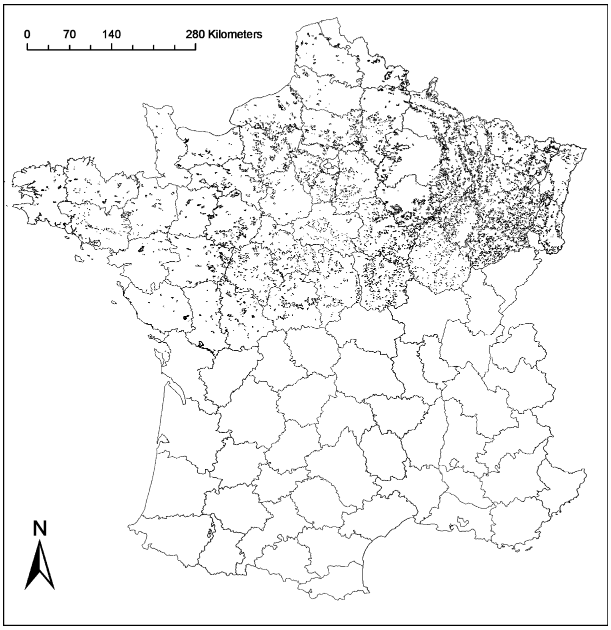

Fig. 1. Location of the 19 989 plots studied in the northern half of France.

To properly dissociate patch size from distance-to-edge effects, we largely reduced the correlation between these two variables by selecting a subset, where DIST and FPS were crossed in a quasi-complete, slightly unbalanced two-way factorial design (Fig. 2). The correlation after selection was reduced to $r = 0.16$, much lower than before ($r = 0.62$). The final sampling design contained 19 989 plots in 1801 forest patches, where DIST ranged from 3 m to 1096 m and FPS ranged from 327 ha to 100 000 ha (Table 1).

Local data

A set of climate, topography, soil, forest stand variables and mean plant indicator values were selected to characterize plot habitat quality (Table 1). These variables were recorded on the plots during field sampling or were obtained from climate databases.

We determined plot location within a topographical gradient (TOPO: index measuring the difference between lateral water inflow and outflow of the plot). The TOPO index increases as the difference in flow increases (Bergès & Balandier 2010). Climate variables (mean annual

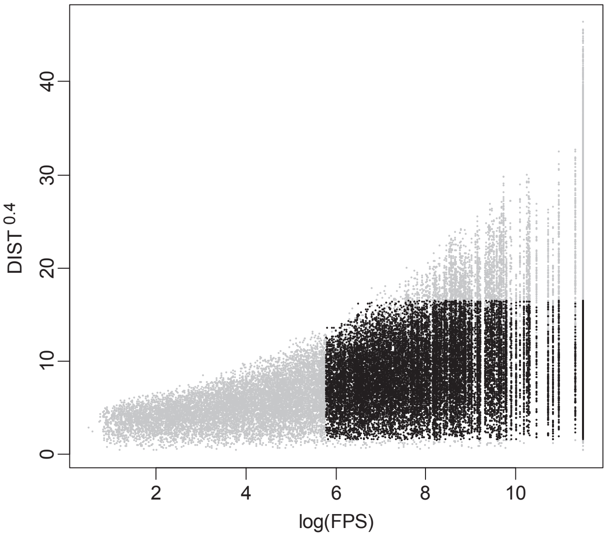

Fig. 2. Construction of a quasi-complete, two-way factorial design crossing distance-to-edge and forest patch size. The plots kept in the analyses are in black, removed plots are in grey. Distances are in $m^{0.4}$, forest patch size in ha in base-10 logarithm scale.

precipitation, annual mean of monthly maximum temperatures from 1971 to 2000) were obtained using the Aurelhy meteorological model (Bénichou & Le Breton 1987) built on a 1-km² grid.

Soil characteristics were essentially based on soil type using standardized soil classification (FAO soil group): 14 soil classes (SOIL) resulted from grouping the 41 initial classes based on class frequency and similarities. Some plots were also deleted due to low frequency of several soil classes and the impossibility of grouping with close categories. Other pedological variables were: humus type (HUMUS) following Ponge et al. (2002), depth of HCl effervescence in the fine soil fraction (DHCl) and depth of temporary waterlogging (DTW).

Forest stand characteristics were collected in 1964-m² circular plots and concerned total plot canopy cover (CCOV), tree species composition (COMP), forest structure type (STRUC) and landowner type (OWN).

We also used mean plant indicator values that have been extensively used as indicators of abiotic conditions (Diekmann 2003; Godefroid & Koedam 2003; Jacquemyn et al. 2003). Ellenberg et al. (1992) and Gégout et al. (2005), respectively, defined a set of indicator values for plants across Central Europe and France. These values estimate the ecological optima of species along a series of environmental gradients. Following the calibration method given in Ellenberg et al. (1992), mean indicator values (MIV) were calculated for each plot as the average of the indicator values of all the plant species present on the plot except for the species analysed. Hence, each species analysed was assigned a specific set of mean plant indicator values, preventing circularity (Boulanger et al. 2011). We selected N for soil nitrogen, F for soil moisture and L for light from Ellenberg et al. (1992), and Ta for mean annual temperature and pH for soil pH from the Ecoplant database (Gégout et al. 2005). We used Ecoplant pH and Ta instead of Ellenberg R or T because (1) Ecoplant indicator values have been calibrated for France and (2) there were fewer missing values in pH and Ta. Moreover, for N, F and L, we did not have to choose because there are no corresponding indicator values in Ecoplant.

Statistical analyses

Model selection for species

A multiple logistic regression was used to model the response of each species (i.e. probability of presence) to local and landscape variables:

$$\text{logit}(P_i) = \log\left(\frac{P_i}{1-P_i}\right) = \alpha + \beta_i.X_i + \varepsilon$$

To avoid over-parametrization (Coudun & Gégout 2006), species with fewer than 100 occurrences were excluded from the analysis. Thus 214 out of 645 species were retained for further analysis.

Since our sampling region was very large, the spatial distribution of species within the study area was not homogeneous and there was room for geographical bias. We therefore defined a subsample for each species by selecting all the plots of any ecoregion where the species occurred at least once. This approach created a rough spatial species envelope. The resulting species-specific sample size ranged from 551 to 19 377 plots.

The correlations between all predictors (month, local and landscape variables) were checked before analysis to avoid problems of multicollinearity. Then, we selected the best local model (M_{LOCAL}) using a forward step-wise procedure based on the *step* function of R (R Foundation for Statistical Computing, Vienna, AT) and considering the following list of local predictors: MONTH, TOPO, DTW, DHCl, SOIL, HUMUS, COMP, STRUC, OWN, TMAX, RAIN, CCOV, MIV.Ta, MIV.pH, MIV.N, MIV.F and MIV.L (Table 1). Continuous variables were always tested using a linear and a quadratic form. The *step* procedure used the Akaike information criteria (AIC) to progressively select and deselect the variable in the local model.

Once the local model was determined, three alternative models were fitted for species response to landscape variables: forest patch size (M_{FPS}), distance to edge (M_{DIST}) and

Table 1. Basic statistics for landscape, climate, soil and forest stand variables. Climate data are means over the period 1971–2000. Summary statistics are means ± SD [min-max] for continuous variables (C) and occurrences in each class for factors (F).

Variable name	Code	Type	Summary statistics
Distance to edge (m)	DIST	C	292 ± 254 [3–1096]
Forest patch size (ha)	FPS	C	*$13.8 \cdot 10^4$ ± $26.8 \cdot 10^4$ [327–1.10^5] **1970 ± 4789
Month of survey (month number)	MONTH	C	1–12
Mean annual maximum temperature (°C)	TMAX	C	14.5 ± 1.0 [9.3–17.2]
Mean annual precipitation (mm)	RAIN	C	861 ± 200 [380–2356]
Topography	TOPO	F	0–9
Soil type	SOIL	F	Calcarisols/Rendzinas (n = 197)
			Calcisols (n = 904)
			endzinas/Calcosols (n = 377)
			Brunisols/Colluviosols (n = 3554)
			Brunisols/Luvisols (n = 582)
			Acid luvisols/Waterlogged luvisols (n = 608)
			Acid brunisols (n = 2403)
			Ochreous brunisols (n = 318)
			Podzolic soils/Podzols/Waterlogged podzols (n = 1441)
			Arenosols/Rankosols/Lithosols (n = 315)
			Waterlogged brunisols (n = 1931)
			Gleysols/Stagnosols (n = 191)
			Pseudogleys (n = 5520)
			Planosols/Pelosols (n = 520)
Depth of temporary waterlogging (dm)	DTW	C	0–10
Depth of HCl effervescence (dm)	DHCl	C	0–10
Humus form	HUMUS	F	Carbonated mull (n = 615)
			Thick carbonated mull or moder (n = 484)
			Eumull (n = 1879)
			Mesomull (n = 5669)
			Oligomull (n = 2386)
			Dysmull (n = 1760)
			Hemimoder (n = 1610)
			Eumoder (n = 2039)
			Dysmoder (n = 1732)
			Mor (n = 101)
			Hydromull (n = 871)
			Hydromoder (n = 296)
Canopy cover (%)	CCOV	C	0–100
Tree species composition	COMP	F	1: deciduous forest (n = 14 969)
			2: mixed stands (n = 1550)
			3: coniferous forest (n = 3470)
Canopy cover (%)	CCOV	C	0–100
Forest structure	STRUC	F	1: even-aged high forest (n = 11 453)
			2: high forest and coppice (n = 7422)
			3: coppice (n = 1085)
Landowner type	OWN	F	1: state forest (n = 5251)
			2: city forest (n = 5239)
			3: private forest (n = 9499)
Mean indicator value for Ta (Ecoplant)	MIV.Ta	C	9.84 ± 1.03 [3.8–15.7]
Mean indicator value for pH (Ecoplant)	MIV.pH	C	5.25 ± 1.07 [3.0–8.5]
Mean indicator value for N (Ellenberg)	MIV.N	C	4.74 ± 0.69 [1–7]
Mean indicator value for L (Ellenberg)	MIV.L	C	5.35 ± 0.54 [3–8]
Mean indicator value for F (Ellenberg)	MIV.F	C	5.45 ± 0.38 [2–8.09]

*Mean patch size calculated at plot scale (19 989 plots).

**Mean patch size calculated at patch scale (1801 patches).

both variables (M_{ADD}). Landscape variables were always included using a linear form; FPS was log-transformed and DIST transformed to the exponent 0.4 before fitting. We do not report on our results for patch size because we focused on the relationships between species occurrence and distance-to-edge.

$$\mathrm{logit}(P_i) = \omega + \varepsilon \qquad (M_{\mathrm{LOCAL}})$$

$$\mathrm{logit}(P_i) = \log(\mathrm{FPS}) + \omega + \varepsilon \qquad (M_{\mathrm{FPS}})$$

$$\mathrm{logit}(P_i) = \mathrm{DIST}^{0.4} + \omega + \varepsilon \qquad (M_{\mathrm{DIST}})$$

$$\mathrm{logit}(P_i) = \mathrm{DIST}^{0.4} + \log(\mathrm{FPS}) + \omega + \varepsilon \quad (M_{\mathrm{ADD}})$$

where ω corresponds to the local model equation.

The four models were cross-compared using the AIC (Burnham & Anderson 2002). The most parsimonious model was chosen under the following rules: the model with the lowest AIC was chosen, unless a simpler nested model had an AIC less than 5 points higher. M_{ADD} was selected only if M_{FPS} or M_{DIST} had an AIC 5 points lower than M_{LOCAL}. If M_{FPS} and M_{DIST} were both better than M_{LOCAL} (AIC 5 points lower) then the better model was selected. This meant that model M_{FPS} was often selected while model M_{DIST} was significantly better than M_{LOCAL}. Each species was assigned a response group for distance-to-edge effect according to the sign of the parameter of the DIST variable: core (positive), peripheral (negative) or neutral response (non-significant).

Determining the maximum distance of correlation between species occurrence and distance-to-edge

In order to avoid confusion with the usual edge effect, we used the term 'maximum distance of correlation' (MDC) instead of 'depth-of-edge influence' to characterize the threshold distance beyond which species occurrence no longer varied with distance-to-edge. In previous attempts to determine the extent of edge influence, Chen et al. (1992) and Hylander (2005) proposed defining the edge influence as extending from the edge to a point where the response value was, respectively, 67% and 90% of the variation measured (or predicted) along the gradient considered. Such values are rather arbitrary and Ewers & Didham (2006) suggested using second derivative optima. However, after fitting response curves on our data, we noted that the second derivative never reached an optimum. We finally applied the approach based on the point where the response value was 90% of the predicted variation along the distance gradient.

Plant trait approach

Species were classified according to the following life-history traits: preference for forest, forest edge or non-forest habitats, after simplification of the detailed classification provided by Julve (2009), preference for ancient forests, a combination of the two lists provided by Hermy et al. (1999) and Dupouey et al. (2002), reproduction mode (by seed or vegetatively) from the Biolflor database (Kühn et al. 2004), eight dispersal modes from Julve (2009), seven life forms following Raunkiaer (1934), and finally, ecological preference for temperature, soil pH, soil nitrogen, light and soil moisture. We ran Fisher's exact tests on the contingency tables, crossing each of the 29 life traits and species preference for forest periphery or interior.

In addition, to test the robustness of the plant trait approach, we analysed the relationship between the regression coefficient for distance-to-edge derived from the single species models (M_{DIST} or M_{ADD}) and the same previous traits including all the 214 species, whether or not they significantly responded to distance-to-edge (Dupré & Ehrlén 2002). The logistic regression coefficient denotes the change in the logit of presence for a unit change in the predictor variable. Large positive values indicate a large increase in incidence with increasing distance-to-edge. Differences in coefficient between classes for nominal variables (habitat preference, preference for ancient forests, reproduction mode, dispersal mode and life form) were examined with one-way ANOVA followed by a Tukey HSD test for unequal sample size. The relationships between the coefficient and indicator values for Ta, pH, N, L and F were examined using linear regressions.

Data calculation and statistical analyses were carried out using the R software, version 2.12.2 (R Foundation for Statistical Computing, Vienna, AT).

Results

Species response to site quality predictors

The local model (M_{LOCAL}) included between six and 17 predictors, with an average of 12 (Table 2). Among the list of potential predictors, MIV.pH and MIV.L with a quadratic form were the most frequent (they were predictors in 92% and 85% of the species models, respectively), followed by MONTH, MIV.N (quad), OWN, MIV.F (quad), COMP and SOIL. Also, MIV.pH (quad) was the most frequent first and second predictor (74 and 37 times, respectively), indicating the superiority of MIV.pH as a local site quality variable. Comparatively, SOIL or HUMUS had much lower ranks in the list of local predictors (eighth and 14th positions, respectively).

Species spatial pattern according to periphery-to-interior gradient and forest patch size

Of the 214 species available in the data set, 94 showed a neutral response to distance-to-edge and forest patch size (i.e. the best model for these species was M_{LOCAL}), 42 responded to patch size only and 44 to distance-to-edge only. A total of 34 species showed a significant response to

Table 2. Synthesis of the equation of the local model (M_{LOCAL}) for the 214 species. The table gives, for each predictor and for each rank, the number of times the predictor entered the model at this rank (see Table 1 for predictor description).

Predictor	Predictor rank no.																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
MIV.pH (quad)	74	37	24	17	19	6	9	4	1		2		2	1		1		197
MIV.L (quad)	12	33	31	29	23	12	14	9	7	1	6	3	2	1				183
MONTH	19	20	19	23	16	15	12	9	8	6	7	7	2	5	3			171
MIV.N (quad)	28	11	15	18	14	10	11	14	9	7	6	6	1	4			1	155
OWN	1	6	6	11	11	21	13	16	13	15	17	10	5	3	2	1		151
MIV.F (quad)	9	12	28	10	11	16	10	12	13	11	7	2	4	2	4			151
COMP	9	5	5	7	17	18	12	8	13	12	11	16	6	7	1		1	148
SOIL	9	17	25	22	15	14	11	14	8	3	3		1	1				143
TMAX (quad)	6	15	15	14	10	8	12	9	14	8	10	8	3	3			1	136
MIV.Ta (quad)	13	26	8	14	7	10	11	9	11	5	6	3	7	1	2			133
RAIN (quad)	7	5	11	12	21	14	12	13	11	9	4	3	6	1		2		131
STRUC		1	4	5	9	10	12	13	14	18	12	9	12	1	7	3		130
TOPO			2	1	4	5	6	13	9	16	13	9	10	8	7	3		106
HUMUS	10	4	8	8	4	15	14	8	6	7	2	8	6	2		1		103
DHCl	1	1		2	1	5	9	10	8	11	15	9	7	6	6	3	1	95
CCOV (quad)	3	6	2	7	6	2	6	7	7	7	4	5	6	1	4	3		76
DTW		1		1	1	4	3	6	9	10	9	7	9	7	4	2	2	75
CCOV				2	4	3	11	11	7	8	6	5	6	8	4			75
Ta	3	4		4	6	6	6	4	10		3	3	1	2		1		53
RAIN	2	1	1	1	5	5	6	6	2	6	1	3	4	2	1			46
TMAX		3	5	2		9	5	2	7	5	1	3	1			1		44
MIV.F	1		2	1	2	3	3	3	2	7	1	3	2	3				33
MIV.N	5	4			6	3	4	1		1	2	2	1	1				30
MIV.L		1	1	2			1	1	1	1	3	1	1			1		14
MIV.pH	2	1	2	1	2			2		2		1	1					14

both distance-to-edge and patch size. Among the species studied, 40 were core species and 38 were peripheral species (Fig. 3). For the core species, the MDC ranged from 741 and 892 m and averaged 824 m. For the peripheral group, MDC varied between 318 and 794 m and averaged 668 m. Species preference for forest periphery or interior and MDC estimates are reported in Appendices S1 and S2. Neutral species are listed in Appendix S3.

Response according to life-history traits

The proportion of edge species taken from Julve (2009) was higher in our peripheral pool than in the interior pool (53% vs 25%; Table 3). No relationship was detected with Julve's forest or non-forest species. The proportions of ancient forest species, hemicryptophytes and acidophilous species (with an indicator value for $\text{pH} < 4$) were significantly higher in our core pool than in our peripheral pool. Myrmecochorous and anemochorous species were more frequent among our core pool, and bryophytes were only present in this group, but the differences were not significant. Conversely, proportions of species reproducing by seed only, endozoochores, phanerophytes, thermophiles ($\text{Ta} > 12$ °C), basophiles ($\text{pH} > 6.5$), nitrogen-demanding ($N > 6$) and light-demanding ($L > 6$) species were significantly higher in our peripheral pool. Therophytes were present only in this group, but the difference was not significant.

Variations in the regression coefficient for distance-to-edge were significantly explained by the same plant traits (preference for ancient forests, reproduction mode, dispersal mode, life form, Ta, pH and L), except for habitat preference and N (Figs 4, 5). For dispersal mode, anemochory and autochory had positive regression coefficients for distance-to-edge and were opposed to endozoochory, which had a negative regression coefficient, but there were very few autochorous species ($n = 3$). For life form, bryophytes, pteridophytes and hemicryptophytes preferred the interior, in contrast to phanerophytes that preferred the periphery.

Discussion

Large-scale spatial distribution of forest plants with interior and peripheral profiles

Our study scale (spanning the northern half of France and almost 20 000 plots) enabled us to identify a list of 40 forest core species and 38 peripheral species. The high number of

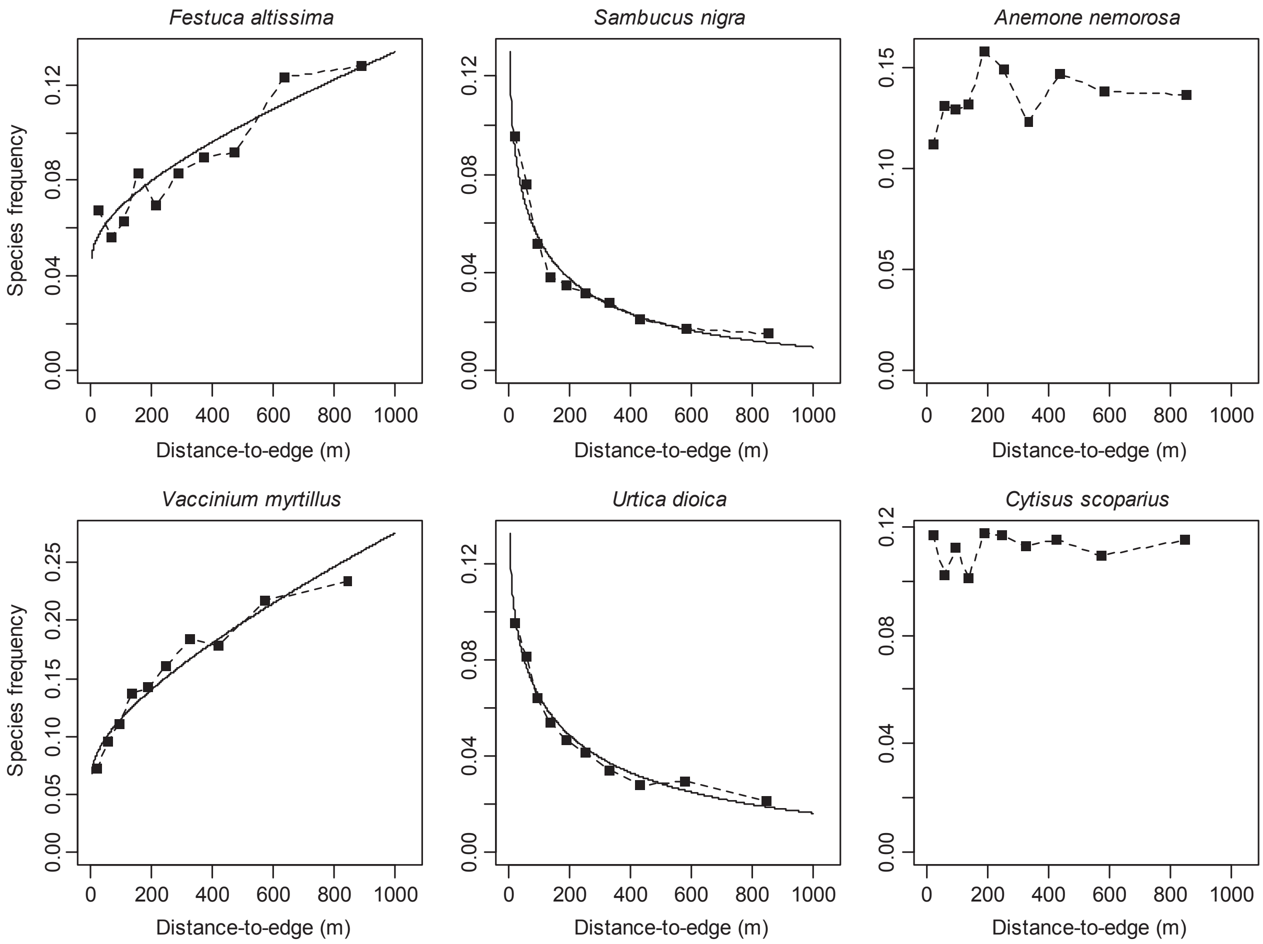

Fig. 3. Observed species frequency according to distance-to-edge and corresponding predicted curve for two core (*Festuca altissima*, *Vaccinium myrtillus*), peripheral (*Sambucus nigra*, *Urtica dioica*) and neutral species (*Anemone nemorosa*, *Cytisus scoparius*). The distance-to-edge plotted for the observed data is the average distance of the corresponding decile.

core species confirms the importance of forest interior areas for forest plant biodiversity conservation, as assessed by Dzwonko & Loster (1988, 1989) in forest remnants. We suspect that the same patterns may apply to less frequent species with higher conservation value. Nevertheless, we detected species preference for forest interior or forest periphery but not strict specialization, all 78 species being always present along the entire distance gradient.

Godefroid & Koedam (2003) found no forest species occurring only in the interior zone they studied, located at least 1 km from an urban area. Our results were in accordance with the findings of Gonzalez et al. (2009) and Honnay et al. (2002): *Fagus sylvatica, Carpinus betulus, Quercus petraea* and *Convallaria majalis* were also identified as core species in these studies whereas *Fraxinus excelsior, Quercus robur, Galium aparine, Hedera helix, Sambucus nigra* and *Urtica dioica* displayed edge profile. However, our results point to a much higher distance of correlation than those detected in the previous studies.

Concerning species habitat preference, only edge species according to Julve (2009) were more frequent in our peripheral pool (see Table 3). The proportion of forest species according to Julve (2009) did not differ in our core and peripheral pool, meaning that a clear distinction should be made between forest species and forest core species. In agreement with our results, Vockenhuber et al. (2011) did not find consistent results concerning the variation of the proportion of true forest species according to distance-to-edge within a large range of distance-to-edge (up to 830 m) in the largest deciduous forest of Germany: the proportion of true forest species increased at one location but decreased at the other. Discrepancies between species profile and the expected behaviour according to Julve were found in our quantitative analysis. For example, classifying *Pteridium aquilinum* or *Vaccinium myrtillus* as forest core species is surprising because they are known to occur frequently in open habitats, such as heathlands or grasslands, across Europe. However, we only sampled forests

Doi: 10.1111/j.1654-1103.2012.01435.x

Table 3. Number of species for each life-history trait category (habitat preference according to Julve (2009), preference for ancient forests, reproduction mode, dispersal mode, life form and autecology) in our core and peripheral groups. Percentages show the proportion of species having a given life-history trait among the total number of core or peripheral species. The Fisher exact test of the odds ratio indicates whether there is a significant difference in proportion between the core and peripheral species pool for the plant trait.

	Core ($n = 40$)	Peripheral ($n = 38$)	Odds ratio	*P* values
Forest species (Julve 2009)	19	14	1.54	0.370
Edge species (Julve 2009)	10 (25%)	20 (53%)	0.305	0.019
Non-forest species (Julve 2009)	3	3	0.95	1.000
Ancient forest species	22 (50%)	9 (24%)	3.87	0.006
Reproduction by seed only (s)	9 (22%)	23 (61%)	0.216	0.002
Reproduction mostly by seed, rarely vegetative (ssv)	7	2	4.29	0.081
Reproduction by seed and vegetatively (sv)	17	11	2.21	0.147
Reproduction mostly vegetative, rarely by seed (vvs)	2	1	2.16	0.609
Anemochores	9	3	3.34	0.12
Autochores	1	0	∞	1.00
Barochores	5	4	1.21	1.00
Hydrochores	1	0	∞	1.00
Myrmecochores	6	3	2.04	0.48
Epizoochores	7	7	0.94	1.00
Endozoochores	5 (12%)	19 (50%)	0.147	0.0005
Dyszoochores	2	2	0.95	1.00
Bryophytes	4	0	∞	0.12
Pteridophytes	1	0	∞	1.00
Therophytes	0	3	0	0.11
Geophytes	5	4	1.21	1.00
Hemicryptophytes	20 (50%)	4 (11%)	8.26	<0.0001
Chamaephytes	2	3	0.62	0.67
Phanerophytes	8 (20%)	24 (63%)	0.15	0.0002
Indicator value for Ta > 12 *	2 (5%)	10 (27%)	0.15	0.011
Indicator value for pH < 4 *	11 (27%)	3 (8%)	4.22	0.038
Indicator value for pH > 6.5 *	11 (27%)	20 (54%)	0.33	0.021
Indicator value for N > 6 *	2 (10%)	11 (41%)	0.10	0.003
Indicator value for L > 6 *	9 (22%)	16 (46%)	0.35	0.049
Indicator value for F ≤ 5 *	28	23	0.764	0.76

*Number of species with missing values: Ta: 1; pH: 1; N: 20; L: 3; F: 14.

and not other ecosystems. In addition, these two species have been repeatedly recognized as ancient forest species (Bossuyt et al. 1999; Hermy et al. 1999; Sciama et al. 2009).

Edge-induced abiotic changes alone cannot explain the long periphery-to-interior gradient

Even though we rigorously controlled for local site quality differences (soil, climate and stand), species traits still differed between core and peripheral species pools: peripheral species had higher temperature and pH indicator values, and were much more nitrogen-demanding and light-demanding than core species. These ecological preferences are fully consistent with the usual edge effect found in the literature (Palik & Murphy 1990; Weathers et al. 2001; Honnay et al. 2002; Gonzalez et al. 2009, 2010).

We detected that the frequency of the 78 core and peripheral species varied, on average, until 748 m from the forest edge. This is an original finding for temperate forests: the usual MDC on abiotic variables reported in the literature is rather short and so does not suffice to fully explain the large gradient identified here for forest plants: 7–240 m for air temperature and moisture (Matlack 1993; Burke & Nol 1998; Davies-Colley et al. 2000; Gehlhausen et al. 2000; Honnay et al. 2002), from 25–180 m for nitrogen and sulphur atmospheric deposition from agricultural land, industry and transport (Weathers et al. 2001; Wuyts et al. 2008) and 5 m for soil pH (Honnay et al. 2002). It is noteworthy that high soil nitrogen values can occur as far as 500 m into the forest interior (Thimonier et al. 1992; Kennedy & Pitman 2004).

In addition, almost all the studies that have analysed species composition change or species profile from the edge into the forest interior have reported a gradient shorter than 100 m (Whitney & Runkle 1981; Palik & Murphy 1990; Fraver 1994; Burke & Nol 1998; Gehlhausen et al. 2000; Euskirchen et al. 2001; Honnay et al.

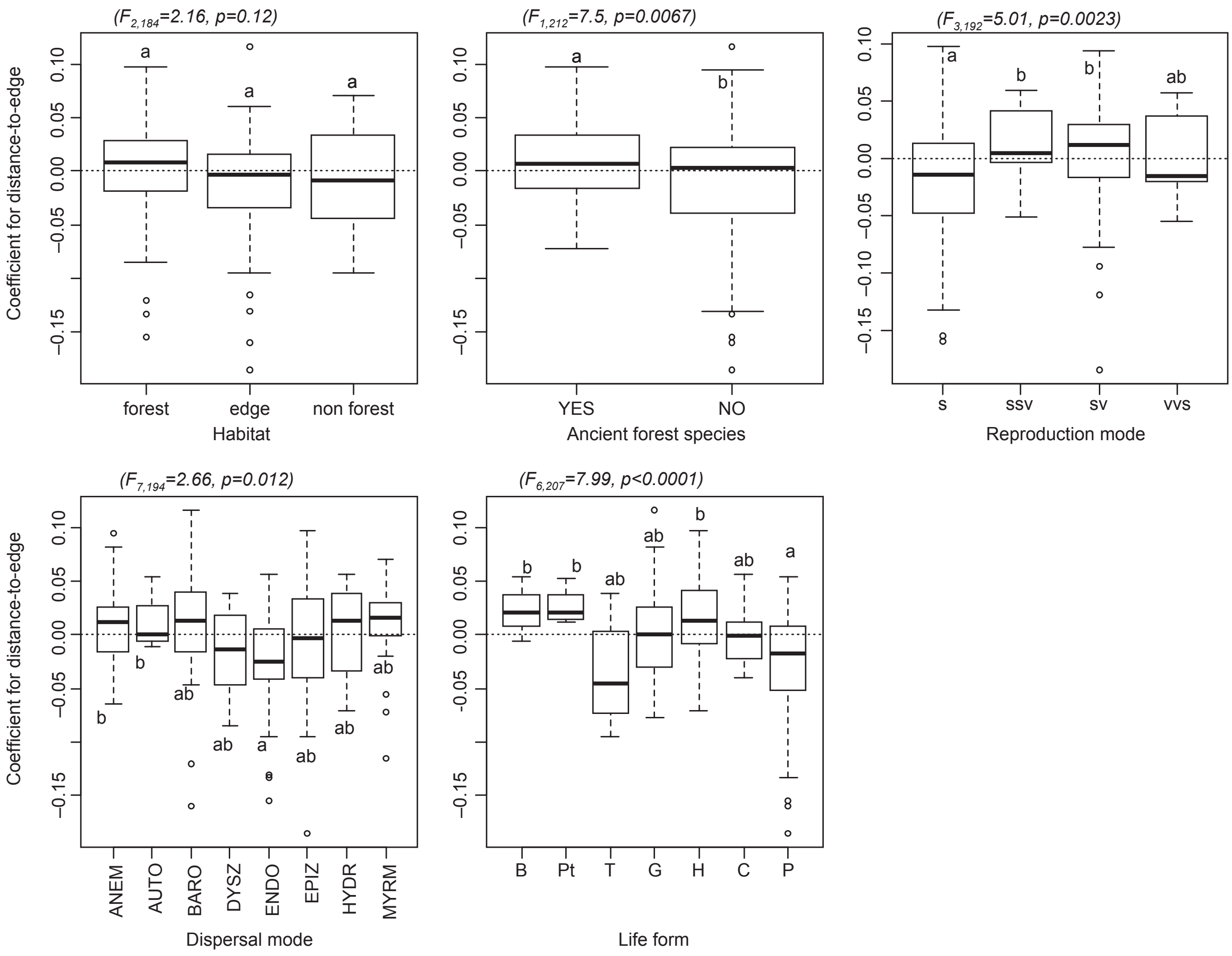

Fig. 4. Differences in the regression coefficient for distance-to-edge between categories of five life-history traits, tested with one-way ANOVA followed by a Tukey HSD test for unequal sample size; means without common letters differ at $P < 0.05$. For ancient forest species: YES = classified as ancient forest species; NO = not classified as ancient forest species; for reproduction mode: s = by seed only; ssv = mostly by seed, rarely vegetatively; sv = by seed and vegetatively; vvs = mostly vegetative, rarely by seed; for seed dispersal: ANEM = anemochorous; AUTO = autochorous; BARO = barochorous; DYSZ = dyszoochorous; ENDO = endozoochorous; EPIZ = epizoochorous; HYDR = hydrochorous; MYRM = myrmecochorous; for life form: B = bryophyte; Pt = pteridophyte; T = therophyte; G = geophyte; H = hemicryptophyte; C = chamaephyte; P = phanerophyte.

2002; Gignac & Dale 2007; Gonzalez et al. 2009, 2010). Only Ewers & Didham (2006) measured a longer gradient, up to 387 m. However, most work has mainly focused on a limited gradient of edge distance and is based on small sample sizes, even though some studies have advocated exploring longer gradients (Laurance 2000). In contrast, we explored an exceptionally long periphery-to-interior gradient and used a large sample size, enabling us to detect spatial variations in species occurrences that are usually masked by habitat quality heterogeneity.

It could be argued that the long-distance plant trend reported here may be at least partly explained by concomitant long-distance soil and forest management variations. However, our statistical models always controlled for climate, soil and stand type, making it unlikely that passive habitat selection alone could explain the periphery-to-interior gradient. In addition, we used mean indicator values that were much better predictors than abiotic variables in our local models (Table 2), but the species analysed was carefully excluded from the computation of the mean indicator values, which prevents circular analysis (Boulanger et al. 2011).

Periphery-to-interior gradient as a result of land-use history?

We suspect that the long periphery-to-interior gradient we observed could result from edge displacement following reforestation, creating vegetation patterns in space and successional time, as documented by Matlack (1994b) and

Doi: 10.1111/j.1654-1103.2012.01435.x

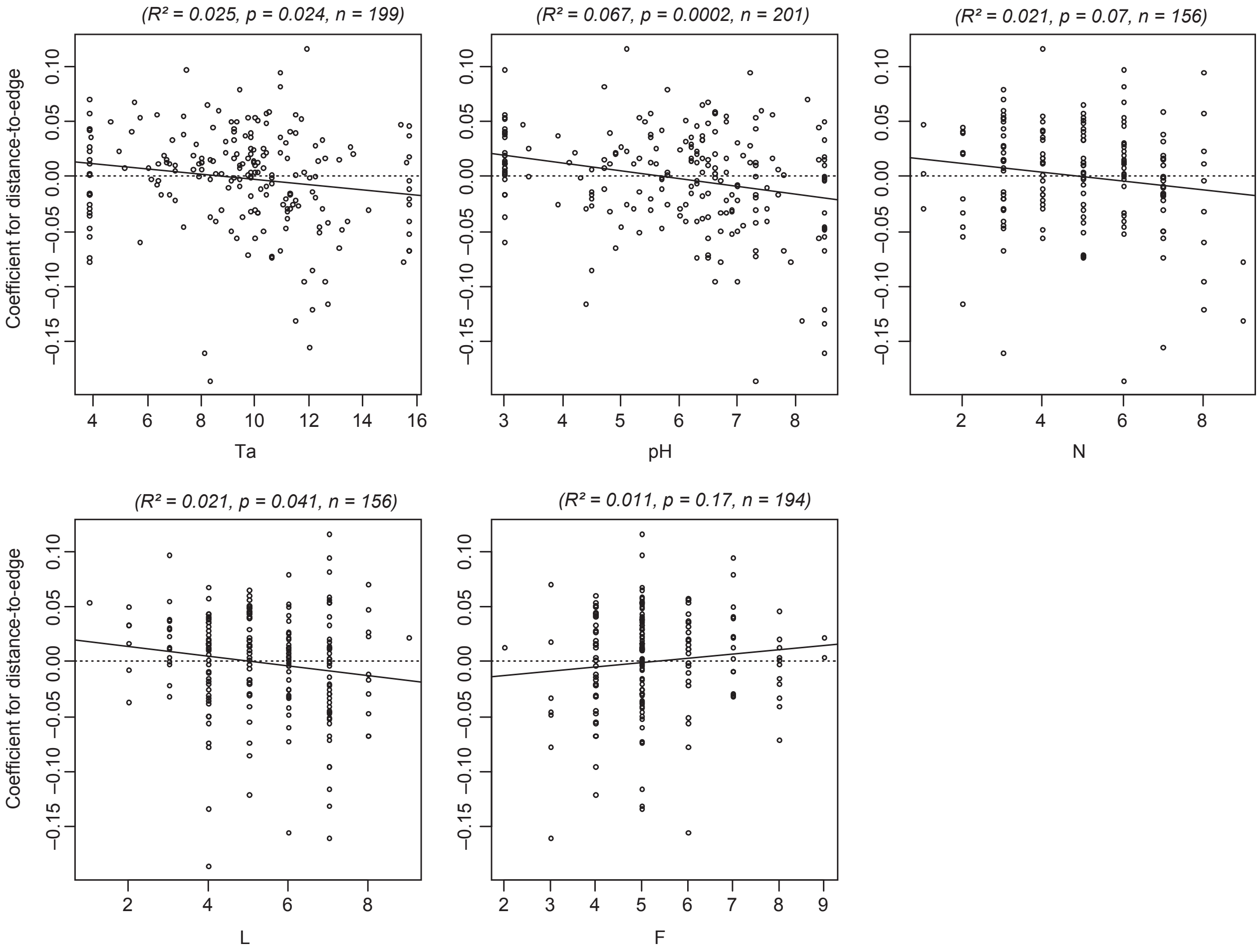

Fig. 5. Regression coefficient of distance-to-edge in the logistic model correlated with species indicator values for air temperature (Ta), soil pH (pH), soil nitrogen (N), light (L) and soil moisture (F). Each point represents a species. R² values are given and tested (above each graph).

De Blois et al. (2001). First, the total forest area in France has increased by 66% since the middle of the 19th century, rising from 9 million ha in 1840 to 15 million ha in the late 1990s (Mather et al. 1999). Second, preliminary results on a 7000-km² region located in the eastern part of our study area and based on a historical map dating back to 1830 show that reforestation on abandoned agricultural or pastoral lands occurred essentially through expansion of existing forest fragments (90%) and only marginally by creation of new forest patches disconnected from existing forest fragments (10%). Consequently, if we assume theoretical circular forest patches from 327 ha to 100 000 ha and a uniform 50% increase in total surface area, the forest edge displacement ranges from 187 m to 3274 m. For an average patch size of 1970 ha, it could reach 440 m. These figures are only rough estimates as most of the patches are probably far from circularity with uniform surface increases. Thus, edge displacement could have occurred over larger distances. Our rough estimates nonetheless underline the potential extent of past edge displacement due to forest expansion.

The third indication in favour of a historical interpretation is that many studies in temperate ecosystems have shown that land-use history has a long-lasting residual effect on forest soils and plant communities (e.g. Honnay et al. 1999b; De Blois et al. 2001; Bellemare et al. 2002; Verheyen et al. 1999, 2003; Graae et al. 2004; Flinn & Vellend 2005; Dambrine et al. 2007; Hermy & Verheyen 2007; Sciama et al. 2009; Svenning et al. 2009). The traits associated with core and peripheral species could also be explained by the remnant effect of former agricultural land use. In our study, even though we controlled for pH and N differences using mean plant indicator values, we still observed that the peripheral plant pool displayed higher average indicator values for pH and N. In addition to being more often ancient forest species, core species were more often hemicryptophytes, whereas peripheral species were more often endozoochores and phanerophytes. Moreover,

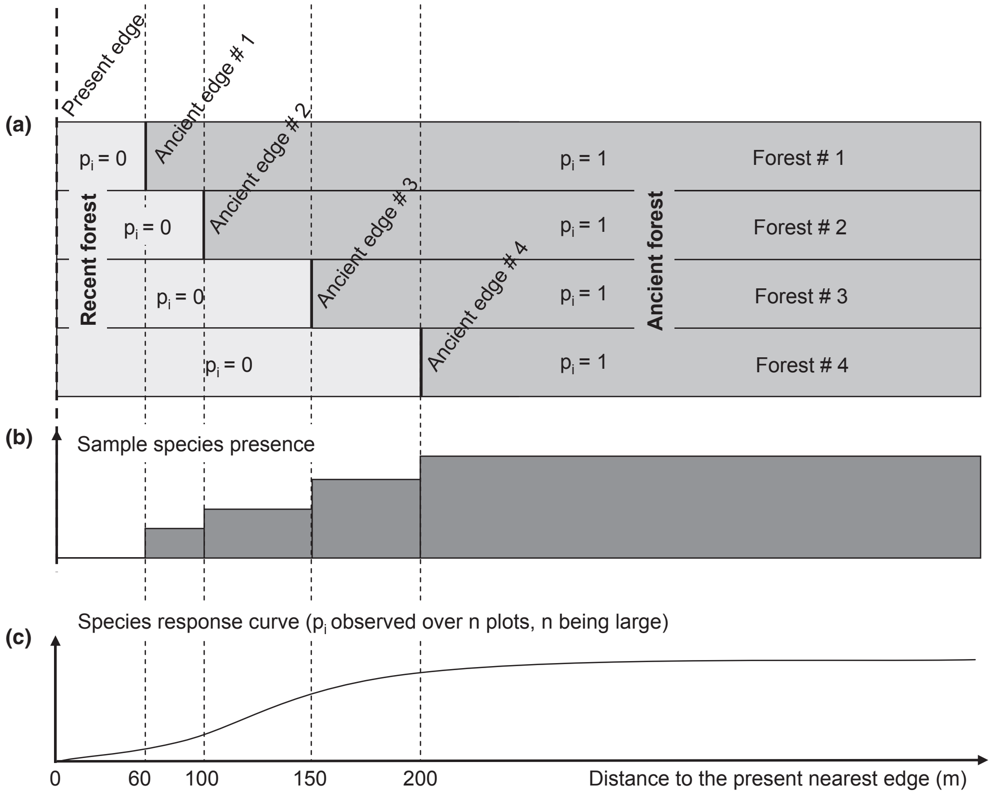

Fig. 6. Possible interpretation of the very long distance of correlation for core forest species. Four values of edge displacement between 1830 and the present day are represented: 60, 100, 150 and 200 m (part **a**). To simplify, we assumed that the species was always present in the ancient part of the forest patch (p_i = 1) and absent in the recent part (p_i = 0). The presence probability observed in the total sample (part **b**) results in an increasing stair-step curve along the distance-to-edge gradient (p_i varies from 0.25 to 1). Under the hypothesis of a large variability of edge movement in the 1801 forest patches sampled across the northern half of France (part **c**), the probability for the species forms a regular increasing response curve associated with a long MDC.

myrmecochrous species had positive regression coefficients, indicating core profile, whereas therophytes had negative coefficients, indicating a peripheral one. The same differences in life form and dispersal mode between recent and ancient forest plant communities were found in Sciama et al. (2009).

Dispersal limitation in time and space, recruitment limitation and low competitive ability are the main reasons why ancient forest species fail to colonize recent or secondary forests (Matlack 1994a; Hermy et al. 1999; Brunet et al. 2000; Verheyen & Hermy 2004). Colonization rate estimates fall between 0.30 and 0.50 $m \cdot y^{-1}$ on average (Bossuyt et al. 1999; Brunet et al. 2000; Dzwonko 2001). Two of our core species (*Carex pendula* and *Hypericum pulchrum*) have the lowest colonizing capacity indices according to Hermy & Verheyen (2007). This colonization rate is much lower than the afforestation rate, thus creating a colonization gradient from the ancient forest borderline (former edge) to the recent forest edge, as previously documented in Ehrlén & Eriksson (2000), Jacquemyn et al. (2001), Flinn & Vellend (2005) and Brunet (2007). Core species cannot spread fast enough to follow the edge displacement, which is consistent with the higher MDC of core species compared to peripheral species.

Conversely, peripheral species, more often being edge species, endozoochores, phanerophytes and reproducing only by seed, were less dispersal-limited and thus better able to follow the edge shift. Endozoochorous species are often considered to be better colonizers than the other groups (Matlack 1994a; Bellemare et al. 2002), even though the link between dispersal mode and colonization ability is not yet fully proven (Hermy & Verheyen 2007). However, our results went further, since we identified peripheral species with very long MDC (up to 794 m). The usual edge effect is not sufficient to explain this response pattern. Our first interpretation is that these species, previously abundant at the former forest edge, progressively declined over time due to habitat change (increasing soil moisture and litter depth, and fewer disturbances) and competitive exclusion, but they were more resistant to habitat changes than the typical 'edge' species. Edge shift created an artificially long MDC for these species. This

Doi: 10.1111/j.1654-1103.2012.01435.x

could explain the higher percentage of phanerophytes in the peripheral species group: due to its longevity, this life form offers more resistance to change, once established, than other life forms.

However, even if we suspect that the MDC can reflect land-use change and edge displacement, the low colonization rate of ancient forest species alone cannot explain why some MDCs can reach nearly 900 m. A colonization rate of 0.3–0.5 or even 1.0 $m \cdot y^{-1}$ means a maximum species progression of 60–200 m since 1830. We suspect that the very long MDCs can also result from spatial heterogeneity in the extent of the edge displacement throughout our study area; colonization and extinction dynamics being only of secondary importance. This interpretation relies on two hypotheses and is illustrated in detail in Fig. 6: (1) recent and ancient forests are two distinct habitat types, with species present only in recent or ancient forests, and (2) a large variability in the edge displacement occurred, resulting from spatial heterogeneity in forest expansion over time within our study area. Consequently, if the frequency of a species preferring ancient forest is averaged over a very large sample size along the distance to present edge, a regular increase in species frequency with distance-to-edge is obtained and a very long periphery-to-interior gradient is likely to occur.

Conclusions

Significant periphery-to-core gradients of plant presence were detected in the northern half of France over much larger ranges than previously recognized for common understorey plant species. Preference for ancient forests, reproduction and dispersal mode, life form, temperature, soil pH, soil nitrogen and light requirements discriminate between core and peripheral species profiles. Because flora and long-term forest historical patterns are similar in western temperate Europe (Mather et al. 1998), the same patterns are likely to be observed in other European forests. We suspect that this deep gradient is the result of edge displacement and the long-term persistence of land-use history. This interpretation remains to be validated with historical data.

The temporal aspect of the peripheral effects in forest patches should henceforth be taken into account, and further research should explicitly focus on the role these ‘ghost edges’, i.e. the past successive locations of the external forest edge during forest expansion, play in present-day plant diversity. In terms of biodiversity conservation, provided that our historical assumption is valid, it would be more appropriate to protect ancient forest zones (using historical maps) than forest core zones based on the maximum width of the usual edge effect.

Acknowledgements

The authors thank Marianne Duprez from the French National Forest Inventory (IFN) for her help during landscape parameter calculations and forest map database management. The authors thank two anonymous reviewers for their valuable comments on the manuscript. This study was partly funded by the Research Program ‘Biodiversité et Gestion Forestière’ (BGF) of the French Ministry of Environment through the GIP Ecofor. Vincent Pellissier was supported by Irstea (postdoctoral fellowship).

References

Archaux, F., Gosselin, F., Bergès, L. & Chevalier, R. 2006. Effects of sampling time, quadrat richness and observer on exhaustiveness of plant censuses. *Journal of Vegetation Science* 17: 299–306.

Avon, C., Bergès, L., Dumas, Y. & Dupouey, J.L. 2010. Does the effect of forest roads extend a few meters or more into adjacent forest? A study on understory plant diversity in managed oak stands. *Forest Ecology and Management* 259: 1546–1555.

Bellemare, J., Motzkin, G. & Foster, D.R. 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. *Journal of Biogeography* 29: 1401–1420.

Bénichou, P. & Le Breton, O. 1987. Prise en compte de la topographie pour la cartographie des champs pluviométriques statistiques. *La Météorologie* 7: 23–34.

Bergès, L. & Balandier, P. 2010. Revisiting the use of soil water budget assessment to predict site productivity of sessile oak (*Quercus petraea* Liebl.) in the perspective of climate change. *European Journal of Forest Research* 129: 199–208.

De Blois, S., Domon, G. & Bouchard, A. 2001. Environmental, historical, and contextual determinants of vegetation cover: a landscape perspective. *Landscape Ecology* 16: 421–436.

Bossuyt, B., Hermy, M. & Deckers, J. 1999. Migration of herbaceous plant species across ancient–recent forest ecotones in central Belgium. *Journal of Ecology* 87: 628–638.

Boulanger, V., Baltzinger, C., Saïd, S., Ballon, P., Ningre, F., Picard, J.F. & Dupouey, J.L. 2011. Deer-mediated expansion of a rare plant species. *Plant Ecology* 212: 307–314.

Brunet, J. 2007. Plant colonization in heterogeneous landscapes: an 80-year perspective on restoration of broadleaved forest vegetation. *Journal of Applied Ecology* 44: 563–572.

Brunet, J., von Oheimb, G. & Diekmann, M. 2000. Factors influencing vegetation gradients across ancient–recent woodland borderlines in southern Sweden. *Journal of Vegetation Science* 11: 515–524.

Burke, D.M. & Nol, E. 1998. Edge and fragment size effects on the vegetation of deciduous forests in Ontario, Canada. *Natural Areas Journal* 18: 45–53.

Burnham, K.P. & Anderson, D.R. 2002. *Model selection and multimodel inference: a practical information theoretic approach*. Springer, New York, NY, US.

Cadenasso, M.L., Pickett, S.T., Weathers, K.C. & Jones, C.G. 2003. A framework for a theory of ecological boundaries. *BioScience* 53: 750–758.

Chen, J., Franklin, J.F. & Spies, T.A. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecological Applications* 2: 387–396.

Coudun, C. & Gégout, J.-C. 2006. The derivation of species response curves with Gaussian logistic regression is sensitive to sampling intensity and curve characteristics. *Ecological Modelling* 199: 164–175.

Dambrine, E., Dupouey, J.-L., Laüt, L., Humbert, L., Thinon, M., Beaufils, T. & Richard, H. 2007. Present forest biodiversity patterns in France related to former Roman agriculture. *Ecology* 88: 1430–1439.

Davies-Colley, R.J., Payne, G.W. & van Elswijk, M. 2000. Microclimate gradients across a forest edge. *New Zealand Journal of Ecology* 24: 111–121.

De Frenne, P., Baeten, L., Graae, B.J., Brunet, J., Wulf, M., Orczewska, A., Kolb, A., Jansen, I., Jamoneau, A., Jacquemyn, H., Hermy, M., Diekmann, M., De Schrijver, A., De Sanctis, M., Decocq, G., Cousins, S.A.O. & Verheyen, K. 2011. Interregional variation in the floristic recovery of post-agricultural forests. *Journal of Ecology* 99: 600–609.

Diekmann, M. 2003. Species indicator values as an important tool in applied plant ecology – a review. *Basic and Applied Ecology* 4: 493–506.

Dupouey, J.L., Sciama, D., Dambrine, E. & Rameau, J.C. 2002. La végétation des forêts anciennes. *Revue Forestière Française* 54: 521–532.

Dupré, C. & Ehrlén, J. 2002. Habitat configuration, species traits and plant distributions. *Journal of Ecology* 90: 796–805.

Dzwonko, Z. 2001. Effect of proximity to ancient deciduous woodland on restoration of the field layer vegetation in a pine plantation. *Ecography* 24: 198–204.

Dzwonko, Z. & Loster, S. 1988. Species richness of small woodlands on the Western Carpathian Foothills. *Vegetatio* 76: 15–27.

Dzwonko, Z. & Loster, S. 1989. Distribution of vascular plant-species in small woodlands on the Western Carpathian Foothills. *Oikos* 56: 77–86.

Ehrlén, J. & Eriksson, O. 2000. Dispersal limitation and patch occupancy in forest herbs. *Ecology* 81: 1667–1674.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Pauliflen, D. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta geobotanica* 18: 1–258.

Euskirchen, E.S., Chen, J.Q. & Bi, R.C. 2001. Effects of edges on plant communities in a managed landscape in northern Wisconsin. *Forest Ecology and Management* 148: 93–108.

Ewers, R.M. & Didham, R.K. 2006. Continuous response functions for quantifying the strength of edge effects. *Journal of Applied Ecology* 43: 527–536.

Ewers, R.M., Thorpe, S. & Didham, R.K. 2007. Synergistic interactions between edge and area effects in a heavily fragmented landscape. *Ecology* 88: 96–106.

Fletcher, R.J., Ries, L., Battin, J. & Chalfoun, A. 2007. The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? *Canadian Journal of Zoology* 85: 1017–1030.

Flinn, K.M. & Vellend, M. 2005. Recovery of forest plant communities in post-agricultural landscapes. *Frontiers in Ecology and Environment* 3: 243–250.

Fraver, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River basin, North Carolina. *Conservation Biology* 8: 822–832.

Gégout, J.C., Coudun, C., Bailly, G. & Jabiol, B. 2005. EcoPlant: a forest site database linking floristic data with soil and climate variables. *Journal of Vegetation Science* 16: 257–260.

Gehlhausen, S.M., Schwartz, M.W. & Augspurger, C.K. 2000. Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. *Plant Ecology* 147: 21–35.

Gignac, L.D. & Dale, M. 2007. Effects of size, shape, and edge on vegetation in remnants of the upland boreal mixed-wood forest in agro-environments of Alberta, Canada. *Canadian Journal of Botany* 85: 273–284.

Godefroid, S. & Koedam, N. 2003. Distribution pattern of the flora in a peri-urban forest: an effect of the city–forest ecotone. *Landscape and Urban Planning* 65: 169–185.

Gonzalez, M., Deconchat, M. & Balent, G. 2009. Woody plant composition of forest layers: the importance of environmental conditions and spatial configuration. *Plant Ecology* 201: 305–318.

Gonzalez, M., Ladet, S., Deconchat, M., Cabanettes, A., Alard, D. & Balent, G. 2010. Relative contribution of edge and interior zones to patch size effect on species richness: an example for woody plants. *Forest Ecology and Management* 259: 266–274.

Graae, B.J., Okland, R., Petersen, P.M., Jensen, K. & Fritzboger, B. 2004. Influence of historical, geographical and environmental variables on understorey composition and richness in Danish forests. *Journal of Vegetation Science* 15: 465–474.

Grashof-Bokdam, C. 1997. Forest species in an agricultural landscape in the Netherlands: effects of habitat fragmentation. *Journal of Vegetation Science* 8: 21–28.

Guirado, M., Pino, J. & Roda, F. 2006. Understorey plant species richness and composition in metropolitan forest archipelagos: effects of forest size, adjacent land use and distance to the edge. *Global Ecology and Biogeography* 15: 50–62.

Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J.Q., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S. & Esseen, P.A. 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* 19: 768–782.

Hermy, M. & Verheyen, K. 2007. Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. *Ecological Research* 22: 361–371.

Hermy, M., Honnay, O., Firbank, L., Grashof-Bokdam, C. & Lawesson, J.E. 1999. An ecological comparison between

Doi: 10.1111/j.1654-1103.2012.01435.x

ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation* 91: 9–22.

Honnay, O., Hermy, M. & Coppin, P. 1999a. Effects of area, age and diversity of forest patches in Belgium on plant species richness, and implications for conservation and reforestation. *Biological Conservation* 87: 73–84.

Honnay, O., Hermy, M. & Coppin, P. 1999b. Impact of habitat quality on forest plant species colonization. *Forest Ecology and Management* 115: 157–170.

Honnay, O., Verheyen, K. & Hermy, M. 2002. Permeability of ancient forest edges for weedy plant species invasion. *Forest Ecology and Management* 161: 109–122.

Hylander, K. 2005. Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. *Journal of Applied Ecology* 42: 518–525.

Jacquemyn, H., Butaye, J. & Hermy, M. 2001. Forest plant species richness in small, fragmented mixed deciduous forest patches: the role of area, time and dispersal limitation. *Journal of Biogeography* 28: 801–812.

Jacquemyn, H., Butaye, J. & Hermy, M. 2003. Influence of environmental and spatial variables on regional distribution of forest plant species in a fragmented and changing landscape. *Ecography* 26: 768–776.

Julve, P. (2009). Baseflor. Available at http://philippe.julve.pagesperso-orange.fr/catminat.htm. Accessed March, 2009.

Kennedy, F. & Pitman, R. 2004. Factors affecting the nitrogen status of soils and ground flora in beech woodlands. *Forest Ecology and Management* 198: 1–14.

Kolb, A. & Diekmann, M. 2005. Effects of life-history traits on responses of plant species to forest fragmentation. *Conservation Biology* 19: 929–938.

Kühn, I., Durka, W. & Klotz, S. 2004. BiolFlor – a new plant-trait database as a tool for plant invasion ecology. *Diversity and Distribution* 10: 363–365.

Laurance, W.F. 1991. Edge effects in tropical forest fragments: application of a model for the design of nature-reserves. *Biological Conservation* 57: 205–219.

Laurance, W.F. 2000. Do edge effects occur over large spatial scales? *Trends in Ecology and Evolution* 15: 134–135.

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G. & Sampaio, E. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* 16: 605–618.

Marchand, P. & Houle, G. 2006. Spatial patterns of plant species richness along a forest edge: what are their determinants? *Forest Ecology and Management* 223: 113–124.

Mather, A.S., Needle, C.L. & Fairbairn, J. 1998. The human drivers of global land cover change: the case of forests. *Hydrological Processes* 12: 1983–1994.

Mather, A.S., Fairbairn, J. & Needle, C.L. 1999. The course and drivers of the forest transition: the case of France. *Journal of Rural Studies* 15: 65–90.

Matlack, G.R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation* 66: 185–194.

Matlack, G.R. 1994a. Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* 75: 1491–1502.

Matlack, G.R. 1994b. Vegetation dynamics of the forest edge – trends in space and successional time. *Journal of Ecology* 82: 113–123.

Meffe, G.K. & Carroll, C.R. 1997. *Principles of conservation biology*. Sinauer Associates, Sunderland, MA, USA.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10: 58–62.

Palik, B.J. & Murphy, P.G. 1990. Disturbance versus edge effects in sugar-maple–beech forest fragments. *Forest Ecology and Management* 32: 187–202.

Ponge, J.F., Chevalier, R. & Loussot, P. 2002. Humus index: an integrated tool for the assessment of forest floor and topsoil properties. *Soil Science Society of America Journal* 66: 1996–2001.

Rameau, J.C., Mansion, D. & Dumé, G. 1989. *Flore forestière française – Guide écologique illustré, Tome 1: Plaines et collines*. IDF, FR.

Ranney, J.W., Bruner, M.C. & Levenson, J.B. 1981. The importance of edge in the structure and dynamics of forest islands. In: Burgess, R.L. & Sharpe, D.M. (eds.) *Forest island dynamics in man-dominated landscapes*. pp. 67–95. Springer, New York, NY, USA.

Raunkiaer, C. 1934. *The life form of plants and statistical plant geography*. Clarendon Press, Oxford, UK.

Ries, L. & Sisk, T.D. 2004. A predictive model of edge effects. *Ecology* 85: 2917–2926.

Ries, L., Fletcher, R.J. Jr, Battin, J. & Sisk, T.D. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution and Systematics* 35: 491–522.

Schmidt, M., Ewald, J., Fischer, A., von Oheimb, G., Kriebitzsch, W.U., Schmidt, W. & Ellenberg, H. 2003. Liste der in Deutschland typischen Waldgefäßpflanzen. *Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft* 212: 1–35.

Sciama, D., Augusto, L., Dupouey, J., Gonzalez, M. & Domínguez, C. 2009. Floristic and ecological differences between recent and ancient forests growing on non-acidic soils. *Forest Ecology and Management* 258: 600–608.

Svenning, J.C., Baktoft, K.H. & Balslev, H. 2009. Land-use history affects understorey plant species distributions in a large temperate-forest complex, Denmark. *Plant Ecology* 201: 221–234.

Tela-Botanica 2009. Base de Donnees Nomenclaturale de la Flore de France (BDNFF, V4.02). Available at http://www.tela-botanica.org/ Accessed March, 2009.

Tela-Botanica 2010. Base de Donnees Nomenclaturale des Bryophytes d'Europe (BDNBE, V 1.00). Available at http://www.tela-botanica.org/ Accessed May, 2010.

Thimonier, A., Dupouey, J.L. & Timbal, J. 1992. Floristic changes in the herb-layer vegetation of a deciduous forest in the Lorraine Plain under the influence of atmospheric deposition. *Forest Ecology and Management* 55: 149–167.

Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. 1994. Habitat destruction and the extinction debt. *Nature* 371: 65–66.

Verheyen, K. & Hermy, M. 2004. Recruitment and growth of herb-layer species with different colonizing capacities in ancient and recent forests. *Journal of Vegetation Science* 15: 125–134.

Verheyen, K., Bossuyt, B., Hermy, M. & Tack, G. 1999. The land use history (1278–1990) of a mixed hardwood forest in western Belgium and its relationship with chemical soil characteristics. *Journal of Biogeography* 26: 1115–1128.

Verheyen, K., Guntenspergen, G.R., Biesbrouck, B. & Hermy, M. 2003. An integrated analysis of the effects of past land use on forest herb colonization at the landscape scale. *Journal of Ecology* 91: 731–742.

Vockenhuber, E.A., Scherber, C., Langenbruch, C., Meissner, M., Seidel, D. & Tscharntke, T. 2011. Tree diversity and environmental context predict herb species richness and cover in Germany's largest connected deciduous forest. *Perspectives in Plant Ecology, Evolution and Systematics* 13: 111–119.

Weathers, K.C., Cadenasso, M.L. & Pickett, S. 2001. Forest edges as nutrient and pollutant concentrators: potential synergisms between fragmentation, forest canopies, and the atmosphere. *Conservation Biology* 15: 1506–1514.

Whitney, G.G. & Runkle, J.R. 1981. Edge versus age effects in the development of a Beech–Maple forest. *Oikos* 37: 377–381.

Wuyts, K., De Schrijver, A., Staelens, J., Gielis, L., Vandenbruwane, J. & Verheyen, K. 2008. Comparison of forest edge effects on throughfall deposition in different forest types. *Environmental Pollution* 156: 854–861.

Supporting Information

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

Appendix S1. List of core species: number of plots analysed, occurrence of the species, the MDC, the minimum and maximum frequency as modelised by the logistic regression.

Appendix S2. List of peripheral species: number of plots analysed, occurrence of the species, the MDC, the minimum and maximum frequency as modelised by the logistic regression.

Appendix S3. List of neutral species: number of plots analysed, occurrence of the species, the MDC, the minimum and maximum frequency as modelised by the logistic regression.

Doi: 10.1111/j.1654-1103.2012.01435.x