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► **To cite this version:**

Laurent Bergès, V. Pellissier, C. Avon, K. Verheyen, J.L. Dupouey. Unexpected long-range edge-to-forest interior environmental gradients. *Landscape Ecology*, 2013, 28 (3), p. 439 - p. 453. 10.1007/s10980-012-9841-1 . hal-00824329

HAL Id: hal-00824329

<https://hal.science/hal-00824329>

Submitted on 21 May 2013

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Version auteur corrigée

Unexpected long-range edge-to-forest interior environmental gradients

Laurent Bergès • Vincent Pellissier • Catherine Avon • Kris Verheyen • Jean-Luc Dupouey

L. Bergès (Corresponding author) • C. Avon

Irstea, UR EMAX, CS 40061, 13182 Aix-en-Provence Cedex 5, France

e-mail: laurent.berges@irstea.fr

phone: +33442669906/fax: +33442669923

V. Pellissier

UMR 7204 CERSP, MNHM/CNRS/UPMC, 61 rue Buffon, 75005 Paris

K. Verheyen

Ghent University, Laboratory of Forestry, Geraardsbergsesteenweg 267, 9090 Melle-

Gontrode, Belgium

J.L. Dupouey

INRA-Nancy University, Forest Ecology and Ecophysiology Unit, 54280 Champenoux,

France

Date of the manuscript revision: December 10, 2012

Manuscript word count (including text, references, tables, and captions): 8048

ABSTRACT

We examined the relationships between distance-to-edge and environmental factors inferred from mean plant indicator values across large distance-to-edge and patch size gradients. Floristic composition, landscape metrics and site variables (climate, soil and forest management) were collected on 19989 plots in 1801 forest patches in Northern France using the French National Forest Inventory. Statistical models were applied to mean plant indicator values (MIV) from Ellenberg and Ecoplant databases for soil pH, soil nitrogen (N), soil humidity (F), light (L) and air temperature (Ta) using distance-to-edge and forest patch size as predictors. The five mean indicator values significantly varied with distance-to-edge and MIV.pH, N and Ta decreased over distances in excess of 500 m. Consistent very long edge-to-interior gradients were also detected for site variables. The distance-to-edge effect remained significant after controlling for site differences, especially for MIV.pH and N. Significant edge-to-core gradients of MIV were detected over much larger ranges than previously recognised. Neither the presence of an ecological boundary between forest and the surrounding matrix, nor microclimate, soil or forest management heterogeneity within forest patches can fully explain this long edge-to-interior gradient observed in MIV. Two hypotheses are discussed for MIV.pH and N: (1) soil eutrophication, due to atmospheric N deposition, which could occur deeper into forest cores than previously acknowledged; (2) land-use legacies, as the periphery of ancient forests is more often occupied by recent forests where former agricultural practices have irreversibly modified topsoil properties. Land use history data would help identify the drivers underlying these long-range edge gradients.

Key words: landscape patterns; mean plant indicator value; depth-of-edge influence; patch size; land-use history; edge displacement; eutrophication.

INTRODUCTION

Edges have received considerable research attention in ecology, conservation biology and ecosystem management fields in the past few decades, since they play a central role in controlling interactions and ecosystem functions (Murcia 1995; Ries et al 2004). Forest edges are transition zones where forest habitat and the surrounding matrix interact. Adjacent ecosystems experience flows of energy, nutrients and species across their mutual boundary (Murcia 1995; Ries et al 2004), which can trigger changes in the species composition, structure and ecological processes of an ecosystem near the edge (Murcia 1995; Harper et al 2005). Forest patches are generally surrounded by a matrix of lower biomass and structural complexity, such as pasture, cropland or urban areas. The difference in microclimate between the two sides of the edge creates a temperature and moisture gradient that is perpendicular to the edge (Murcia 1995). During daytime, forest edges typically have lower air humidity, higher air temperature, higher soil temperature, higher solar radiation and lower soil moisture than the forest interior (Brothers and Spingarn 1992). The altered microclimate of forest edges may also lead to changes in nutrient mobilisation and rates of decomposition (Murcia 1995). Edges are also subjected to the inflow of chemical compounds from the atmosphere or via drift from adjacent land (Thimonier et al 1992; Wuyts et al 2008). This results in increased deposition of potentially acidifying and eutrophying ammonium, nitrate and sulphate depositions at the edge (Wuyts et al 2008). The microclimatic gradient and altered chemical inputs combined with more frequent disturbances at the edge (Godefroid and Koedam 2003) result in differences in topsoil properties and undergrowth plant species composition between forest edge and forest interior (Matlack 1994; Wuyts et al 2011).

The depth-of-edge influence (DEI) has been measured as the distance over which these changes significantly penetrate into the habitat (Harper et al 2005). However, edge effects are variable in space and time, and are influenced by several parameters (Murcia 1995, Ries et al

2004, Ewers and Didham 2006, Laurance et al 2007). Among them, patch size is of particular importance as patch size and distance-to-edge in landscape are generally correlated, since the density of edge habitat in a patch increases with decreasing patch size (Fletcher et al 2007). Potential synergies between edge and area effects have been highlighted (Ewers et al 2007), but rarely investigated in plants (Guirado et al 2006, Gonzalez et al 2010). Here, we hypothesized that patch size effect could modulate edge effects.

The depth-of-edge influence directly determines the forest-core area, which must be larger than a certain size to be considered suitable habitat and maintain a viable population of some threatened or endangered species (Murcia 1995; Laurance 2000). Depending on the abiotic variable-of-interest, the edge influence can extend into the forest for just a few metres or up to two hundred meters (Murcia 1995; Davies-Colley et al 2000; Honnay et al 2002; Harper et al 2005; Marchand and Houle 2006). However, most study designs on edge effects have been restricted to small spatial scales and thus capture edge effects over relatively small spatial scales of only 20-250 *m* (Ewers and Didham 2008). A few studies in Brazilian and New Zealand forests have suggested that edge effects on several ecological processes and species abundance might penetrate as far as 1 km into habitat patches (Laurance 2000, Laurance et al 2007, Ewers and Didham, 2008). A limited number of studies in Europe have addressed the spatial patterns of abiotic and biological components along longer distance-to-edge gradients, i.e. up to 800-1000 *m* (Thimonier et al 1992; De Schrijver et al 1998; Kennedy and Pitman 2004). Here, we considered that there is no single correct scale of analysis for studying ecological relationships between patterns and processes (Levin 1992; Saunders et al 1998), and hypothesised that other ecological or biological mechanisms unrelated to the usual “edge effect” might explain the presence of a generalized long-range edge-to-interior gradient in environmental variables. However, these long-distance gradients may be hindered by the heterogeneity resulting from the spatial distribution of site and disturbance conditions within

forest patches (Fortin et al 1996; Redding et al 2004). Large datasets and replicate landscapes are thus required to partition out their respective influences. We first assumed that this hypothetical long-range gradient was not attributable to the external edge influence but partly to covariations between soil, climate and forest management on one side and distance-to-edge and patch size on the other. For example, differences in soil type proportions between the periphery and the interior of forest patches are likely to occur but have never been examined. Another hypothesis for soil nutrients would be that atmospheric deposition could occur deeper into forest cores than previously acknowledged, as suggested by the results of two studies detecting higher N up to 500 m into forest interior (Thimonier et al 1992; Kennedy and Pitman 2004). A third possible explanation results from three evidences (Pellissier et al 2013): edge displacement following reforestation creating ecological patterns in space and time (Matlack 1994), the persistent effect of past land use on forest soils and plant communities (Hermy and Verheyen 2007), and the more frequent location of recent forests at the periphery of ancient forest remnants (Bossuyt et al 1999).

Edge effects in forest ecosystems are often studied through direct microclimate and soil measurements (Davies-Colley et al 2000). Other studies use plant indicator values to gain indirect metrics of environmental conditions (Diekmann 2003). This method has a wide applicability in biomonitoring, as it yields information on several environmental factors, including estimated soil, light and climate conditions in various communities (Diekmann 1995; Hawkes et al 1997), changes resulting from vegetation succession or past land use (Verheyen et al 2012), and soil acidification and eutrophication in forests (Thimonier et al 1994; Diekmann and Dupré 1997; Hülber et al 2008). Mean plant indicator values (MIV) for soil acidity, nitrogen, moisture, light and air temperature have been demonstrated to be highly correlated with a series of abiotic parameters such as forest soil pH and nitrogen, C/N ratios in topsoil, relative light intensity in forests, mean spring and average annual groundwater levels,

and lowest soil moisture content in summer, in various ecosystems and several countries in Europe (Diekmann and Falkengren-Grerup 1998; Ertsen et al 1998; Schaffers and Sykora 2000; Diekmann 2003; Wamelink et al 2002; Gégout et al 2003; Tichy et al 2010).

The aims of this study were:

- (1) to analyze the effects of distance-to-edge and forest patch size on MIV for temperature requirement, light availability, soil pH, nitrogen availability, and humidity and to assess the depth-of-edge influence (*sensu* Harper et al 2005) for each MIV;
- (2) to analyze the distance-to-edge effect on MIV values after controlling for climate, soil and forest management differences, in order to test whether a residual distance-to-edge effect remains and, if so, to hypothesise which factors could account for it;
- (3) to analyze the variations in climate, soil and forest management according to distance-to-edge and forest patch size.

MATERIALS AND METHODS

French National Forest Inventory data

Data came from the French National Forest Inventory (NFI), an organisation entrusted with inventorying and monitoring forest resources throughout France (Pellissier et al 2013). Only plots in the northern half of France were analysed so as to limit the biogeographical gradient. The initial dataset comprised a total of 38751 plots in 10131 forest patches measuring at least 2.25 ha (Fig. 1). Plot density was one plot every 31.25 ha, and corresponded to a systematic rectangular grid of X(longitude)=500 m, and Y(latitude)=625 m, with slight regional variations.

#Fig. 1 approximately here#

Mean plant indicator values (MIV)

Plant species composition was surveyed in 700- m^2 circles. In all, 97% of the plots were sampled between 1990 and 2004. MIVs were used to separately assess climate, light and nutrient richness conditions. Ellenberg et al (1992) and Gégout et al (2005) have defined sets of indicator values for plants across central Europe and France, respectively. Each value estimates the position where each species achieves peak frequency or abundance (i.e. the indicator value) along a series of environmental gradients. The Ellenberg indicator values for N, L and F are integer values ranging from 1 to 9, with high values for N, L and F corresponding to nitrogen-, light- and moisture-demanding species, respectively. Following the method proposed by Ellenberg et al (1992), MIV were calculated for each plot as the mean of the indicator values of all the plant species present in the plot. We selected five indicator values representative of the main ecological gradients (Appendix S1) and that were as little correlated as possible ($|r| < 0.77$), i.e. nitrogen availability (N), light availability (L) and humidity (F) taken from Ellenberg and pH for soil acidity and Ta for mean annual temperature taken from the Ecoplant database (Gégout et al 2005).

A total of 63 teams with different levels of expertise in plant identification were involved in floristic data gathering, and as a result, random variation could be substantial due to observer effects, overlooking plants, and species misidentification (Archaux et al 2006). However, the MIV system is considered a robust bioindicator tool that is only weakly influenced by plant survey exhaustiveness and plot size (Ewald 2003; Archaux et al 2007). Moreover, the stability of the ecological behaviour of herbaceous forest species in terms of soil pH has been demonstrated for Northern France (Coudun and Gégout 2005).

Landscape data and plot selection

Both minimum distance from the plot to the external edge of the forest patch (DIST) and size

of the forest patch where the plot was located (FPS) were calculated using GIS and NFI forest maps. Four forest patches were larger than 100000 *ha* (227439, 230939, 313614 and 322527 *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 thus assigned a single surface area of 100000 *ha* to limit the statistical weight of such extremely large values. The initial dataset contained 7396 plots that were closer to an internal gap than to the external edge of the patch. Due to the equivocal nature of these gaps, we decided to remove these 7396 plots from the sample.

To properly dissociate patch-size from distance-to-edge effects (Fletcher et al 2007), we made every effort to minimise the correlation between these two variables ($r=0.62$) by selecting a subset where DIST and FPS were crossed in a quasi-complete, slightly unbalanced 2-way factorial design ($r=0.14$). The final sampling design contained 19989 plots in 1801 forest patches, where DIST ranged from 3 *m* to 1096 *m* and FPS ranged from 327 *ha* to 100000 *ha* (Appendix S1 and Fig. 1).

Local data

A set of climate, topography, soil and forest stand variables was selected to characterize plot habitat quality (Appendix S1). These variables were recorded on the plots during field sampling or obtained from climate databases.

We determined plot location within a topographical gradient (TOPO: calculated index of the difference between lateral water inflow and outflow of the plot, based on a 50 x 50 *m* digital elevation model). The TOPO index increases as the difference in flow increases (Bergès and Balandier 2010). Climate normals (annual cumulative precipitation, annual mean of monthly maximum temperatures from 1971 to 2000) were obtained using the Aurelhy meteorological model (Bénichou and Le Breton 1987) built on a 1 *km*² grid.

Soil types (SOIL) were clustered into 14 classes according to the standardised FAO soil classification (IUSS-Working-Group-WRB, 2006). We also removed some plots due to the rarity of their soil type. Other pedological variables were: soil water capacity (SWC), depth of HCl effervescence in the fine soil fraction (DHCl) and depth of temporary waterlogging (DTW), all of which were characterized using field observations.

Forest stand characteristics were collected in 25 m-radius circular plots and concerned total plot canopy cover (CCOV), tree species composition (COMP) and forest structure (STRUC).

Statistical analyses

Effects of DIST and FPS on MIV

We preliminarily tested the influence of spatial autocorrelation. The comparison between generalized least squares regressions with and without spatial correlation error indicated that DIST and FPS effects were significant in both cases. Then, spatial autocorrelation was not controlled for in order to be able to apply variance partitioning. To simply depict the shape of MIV response to DIST and FPS, we applied locally-weighted polynomial regressions, using the lowess function of R and a variable smoothness parameter. Smoother span f in lowess function gives the proportion of points in the plot that influence smoothing at each value: larger values give more smoothness. After comparing several f values (0.1 to 0.8), regression curves were plotted using, for DIST, $f=0.2$ for MIV.pH and N, $f=0.3$ for F and Ta, and $f=0.5$ for L, and for FPS, $f=0.6$ for all five MIV.

Two-way ANOVA with interaction was applied to the five MIV using deciles of the distribution of DIST and FPS as categorical predictors. Residuals were checked for normality and homoscedasticity after fitting. Variance partitioning determined pure and joint effects of DIST and FPS.

Determination of the depth-of-edge influence

A first method defined the edge influence as extending from the edge to a point where the response value was 90% of the variation measured (or modelled) along the gradient considered (Redding et al 2004). A second method advocated using second derivative optima of the response curve (Ewers and Didham 2006). A third method applied tests of multiple comparisons of means to determine which distance-to-edge intervals were different (Honnay et al 2002). The first two approaches could be judged as more accurate, but the accuracy actually depends on response curve shape and model prediction quality. If the response curve is not asymptotic, the definition of the reference value is speculative. Model prediction quality should also be taken into account to assess DEI error. Otherwise, the third method is reproducible, even though it could be less powerful. So, we assessed DEI using Tukey multiple comparisons of means applied to the ANOVA model with a 95% family-wise confidence level and controlling for FPS differences. Clusters of deciles were identified by letters, and DEI was defined as the lower bound of the lowest decile belonging to the cluster including the highest decile [683-1096 m].

Test of the robustness of DIST and FPS effects

We checked whether the effects of DIST and FPS on MIV remained significant after controlling for local site quality (named SITE factors) using the following procedure. First, the correlations between all predictors (local and landscape variables) were checked before analysis to avoid problems of multicollinearity. No strong correlation occurred ($|r| < 0.5$ except for three pairs; see Appendix S2). Second, we selected the best SITE model (M_{SITE}) using a forward stepwise procedure based on the *step* function of R and considering the following list of ten potential SITE predictors: TMAX, RAIN, SWC, TOPO, SOIL, DTW, DHCl, CCOV, COMP and STRUC. Continuous variables (TMAX, RAIN and CCOV) were always tested

using linear and quadratic forms. The stepwise procedure used AIC to progressively select (and deselect) the variable in the SITE model. Thirdly, four alternative models were fitted and compared using AIC: (1) M_{DIST} : model with SITE + DIST, (2) M_{FPS} : model with SITE + FPS, (3) M_{ADD} : model with SITE + DIST + FPS, and (4) M_{INTER} : model with SITE + DIST x FPS. To observe the change in magnitude of DIST and FPS effects before and after SITE correction, we applied variance partitioning among the three predictors (SITE, DIST and FPS) to calculate seven non-overlapping fractions, apart from the unexplained variance, i.e. a: pure effect of SITE; b: pure effect of DIST; c: pure effect of FPS; d: joint effect of SITE and DIST; e: joint effect of SITE and FPS; f: joint effect of DIST and FPS; and g: joint effect of all three explanatory variables.

Relationships between DIST, FPS and soil, climate and stand

Multiple logistic regressions were applied to each class of the previous ten SITE factors using deciles of DIST and FPS as categorical predictors. Least-square regressions were applied to TMAX, RAIN, SWC and CCOV using the same predictors. Five models were compared using AIC: (1) null model, (2) model with DIST, (3) model with FPS, (4) model with DIST + FPS (additive), and (5) model with DIST x FPS (with interaction).

Data calculation and statistical analyses were carried out using the *lm* and *glm* functions of R software version 2.12.1 (R Development Core team 2011).

RESULTS

Response of MIV to distance-to-edge and forest patch size, and DEI assessment

MIV.pH, N, F and Ta significantly varied with distance-to-edge and FPS (Table 1 and Fig. 2).

MIV.L also varied, but less significantly. The interaction was significant for MIV.L and

MIV.Ta, although much less than for main effects. MIV.pH, N and Ta regularly decreased with distance-to-edge, whereas MIV.F increased. The decrease was low and less regular for MIV.L ($p < 0.001$). The differences between the first [3-37 m] and last [683-1096 m] decile of DIST were -0.74 for pH, -0.44 for N, -0.09 for L, +0.15 for F and -0.34°C for Ta.

The five MIV also varied with FPS, but less regularly (Fig. 2): MIV.pH, N and Ta decreased whereas MIV.F increased with decreasing patch size, with a marked increase or decrease above 16000 ha, which nearly corresponds to the two largest deciles of patch size ($\text{FPS} > 13566 \text{ ha}$). Variations were non-monotonic for MIV.L.

The percentage of total variation explained by DIST and FPS varied from 3.4% to 10.2%, and was negligible for L (Appendix S3). The statistical magnitude of the pure effect of DIST was higher than the magnitude of the pure effect of FPS for N, slightly lower for pH, much lower for Ta, and similar for F. Joint effect of DIST and FPS was always negligible.

Based on Tukey multiple comparisons of means, DEI reached 683 m for MIV.Ta, 489 m for pH and N, and 286 m for F, and was not easily definable for MIV.L as the two most contrasted mean clusters largely overlapped (Appendix S4).

#Table 1 and Fig. 2 approximately here#

Robustness of distance-to-edge and forest patch size effects

All the SITE variables were predictors of the five MIV except DHCl for MIV.L (Appendix S5). Best predictors were SOIL for MIV.pH, N and F, COMP for L, and TMAX for Ta.

Continuous variables (see Appendix S1) always entered the model with a quadratic form. The effects of DIST and FPS remained significant after controlling for SITE differences (Table 2).

M_{INTER} was never better than M_{ADD} , meaning no interaction between DIST and FPS. SITE explained 35.9% to 48.6% of the variance in MIV (Appendix S6). A large share of the pure

effect of DIST in the first analysis was captured by the joint effect of DIST and SITE. Pure effect of DIST represented 1.6% and 2.0% for MIV.pH and N, respectively, and was low or negligible for the three other parameters. Locally-weighted regressions showed that the long-range DEI was still present, but the range of variation decreased (Appendix S7). For FPS, an even larger part of the pure effect of FPS in the first analysis was captured by the joint effect of FPS and SITE, especially for pH and Ta (Appendix S6). Pure effect of FPS accounted for 1.1% for MIV.Ta and was negligible for the other MIV.

Variation in local site quality with distance-to-edge and forest patch size

Model comparisons by AIC are presented in Appendix S8 and illustrated by Fig. 3 for soil and forest stand types.

Soil type (SOIL) varied with DIST (Fig. 3a): the proportion of ochreous brunisols, podzolic soils, podzols, waterlogged podzols, planosols, pelosols and pseudogleys increased with increasing DIST, whereas the proportion of calcarisols, rendzinas and calcosols decreased.

Depth of HCl effervescence in the fine soil fraction (DHCl) displayed a similar trend: the proportion of soils with CaCO₃ above 10 cm in depth (DHCl 0-1) decreased while the proportion of soils without CaCO₃ (DHCl absence) increased with increasing DIST.

The fraction of soils with temporary waterlogging above 10 cm in depth (DTW 0-1) increased while the fraction of soils with no temporary waterlogging (DTW absence) decreased with increasing DIST.

The proportion of positive and negative topographical positions (TOPO) decreased whereas the share of neutral topographical positions increased with increasing DIST. Soil water capacity (SWC) increased and annual maximum temperature (TMAX) decreased with increasing DIST. Precipitation (RAIN) and canopy cover (CCOV) did not significantly vary with DIST.

Concerning stand types, proportion of coniferous stands increased (8 to 11%) whereas proportion of deciduous stands tended to slightly decrease (not significant) with increasing DIST (Fig. 3b). Proportion of even-aged high forest stands increased (9 to 11%) while proportion of coppice and high forest with coppice decreased (18 to 6% and 11 to 9%, respectively; Fig. 3c) with increasing DIST.

SITE factors varied significantly with FPS (Appendix S8). In contrast with DIST, we did not detect a linear trend with increasing FPS but rather a strong gap between the largest or the two largest deciles and the other deciles.

#Table 2 and Fig. 3 approximately here#

DISCUSSION

Edge-to-core gradients of mean plant indicator values

Using mean plant indicator values, we observed that plant communities indicated less acidic, nutrient-richer (N), drier (F), more shade-intolerant (L) and warmer (Ta) conditions at the edge. In terms of direction, the edge effects we observed are largely in agreement with the general patterns observed in other forests for soil and air temperature, seasonal stand transpiration, photosynthetic active radiation and litter moisture (Gehlhausen et al 2000; Honnay et al 2002; Marchand and Houle 2006; Herbst et al 2007).

However, most of the literature on DEI has reported a rather short distance for edge-related ecological gradients (see Murcia 1995 for a review): from 7 to 240 *m* for air temperature and moisture (Davies-Colley et al 2000; Gehlhausen et al 2000; Honnay et al 2002), 5 *m* for soil pH (Honnay et al 2002), 50 *m* for several chemical substances including organic matter, available phosphorous, ammonium, nitrate and potassium (Hester and Hobbs 1992), and from 25 to 180 *m* for N and S atmospheric depositions coming from agricultural land, industry and

transport (De Schrijver et al 1998; Wuyts et al 2008). Here, we detected very long-range gradients, since DEI varied up to 500-700 *m* for MIV, pH and Ta. Using the same dataset and in total concordance with these results, significant edge-to-core patterns of distribution for common understory plant species were detected over much larger ranges than previously recognised (Pellissier et al 2013). Two reasons could explain the long-range edge gradients detected: (1) previous studies explored a small distance-to-edge gradient (Murcia 1995, Davies-Colley et al 2000; Gehlhausen et al 2000; Honnay et al 2002) and (2) they were based on small sample sizes, meaning less statistical power. Indeed, variance partitioning underlined that the long-distance edge signal is blurred by small-scale habitat quality heterogeneity within forest patches. The detection of such a low magnitude signal is statistically improbable without large datasets.

Patch size effects on MIV and interaction with distance-to-edge

Plant communities indicated less-acidic, nutrient-richer (N), drier (F) and warmer (Ta) conditions in small forest patches compared to large patches, and FPS magnitude was high, especially for Ta. However, FPS effect was largely due to the largest patches and was not gradual as for DIST. We suspect that FPS effect was linked to the specificity of these seven largest patches, i.e. climate, soil and location within the study area. Our results also indicated that edge effect was not modulated by patch size, i.e. the slope of the edge effect was not altered in fragments of different sizes, in contradiction with Ewers et al (2007). The lack of interaction could be due to the absence of very small fragments in our sampling: the smallest patches were larger than 327 *ha* whereas other studies have generally considered much smaller patches (e.g. Ewers et al 2007). This probably prevents us from assessing the role played by multiple edge effects in the edge-related change with decreasing fragment area (Ewers et al 2007; Fletcher et al 2007).

MIV variations falsely attributed to edge and forest patch-size effects

It could be argued that the long-distance trend in MIV reported here may be partly explained by concomitant long-distance climate, soil and forest management variations. Our results highlighted for the first time that soil type, tree species composition and stand structure also displayed unexpected long-range distance-to-edge gradients. First, the frequency of nutrient-rich soils (rendzinas, calcarisols, calcosols and calcisols) decreased from the periphery to the interior of the forest patches, whereas nutrient-poor soils (ochreous brunisols, podzolic soils and podzols) increased. This was also confirmed by analysis of the depth of HCl effervescence in fine soil fraction. These soil gradients could thus explain the decrease in MIV.pH and N with distance-to-edge. Secondly, the frequency of soils that were temporarily waterlogged close to the soil surface increased with distance-to-edge (pseudogleys, waterlogged podzols, pelosols and planosols) whereas the frequency of shallow soils decreased (rendzinas and calcarisols). This was also confirmed by the patterns of temporary waterlogging depth and soil water capacity. These soil gradients could explain why MIV.F increased with distance-to-edge. Thirdly, maximum temperature decreased with increasing DIST, which could explain the decreasing pattern of MIV.Ta.

Concerning stand characteristics, we found that there were more coniferous and even-aged high forests in the forest interior and more high forest with coppice and coppice stands near the edge. Differences have been reported between coniferous and broadleaved species in terms of soil acidity, soil moisture, light transmittance and LAI (Augusto et al 2003; Barbier et al 2008). Indeed, conifers are reported to produce more acidic topsoils than hardwoods (Augusto et al 2003; Barbier et al 2008). Changes in pH, nitrogen, soil moisture and light have also been emphasized during forest conversion from coppice-with-standards to even-aged high forest (Van Calster et al 2007).

Consequently, MIV variations with distance-to-edge partly reflected parallel climate, site and stand type variations, and the occurrence of parallel biotic and abiotic gradients explains why the pure effect of distance-to-edge in the first analysis was partly absorbed by the joint effect of site factors and distance-to-edge in the second analysis, especially for MIV.pH, N and F. However, a significant part of variance in MIV remained explained by distance-to-edge, especially for pH and N. Similarly, MIV variations according to patch size were shown to be also attributable to covariations in site factors. These differences mainly concerned the largest patches and thus explained why the pure effect of patch size in the first analysis was almost totally absorbed by the joint effect of site factors and patch size in the second one, especially for MIV.pH, N and Ta.

Explaining the residual long-range gradient in mean plant indicator values

Two hypotheses could explain the residual edge-to-interior gradient for MIV pH and N: (1) atmospheric depositions deeper inside forest interior, and (2) edge displacement following reforestation since the early 19th century combined with land use legacies.

Nitrogen and sulphur emissions, like other nutrient pollutions, have risen since the 1940s due to increasing fossil fuel consumption and agriculture intensification (Bobbink et al 2010).

Forest edges affect the inflow of chemical compounds from the atmosphere (Harper et al 2005). Forest edges are exposed to high atmospheric ion deposition (H^+ , NH_4^+ , NO_3^- , SO_4^{2-}) because they disturb the vertical wind profile and cause air turbulence (Weathers et al 2001; Wuyts et al 2008).

The literature reports up to a four-fold increase in atmospheric N and S deposition at forest edges compared to forest interiors (De Schrijver et al 2007). This edge effect generally decreases exponentially with increasing distance from the edge until it reaches a more or less interior forest level at 8 to 180 *m* from the edge (Spangenberg and Kölling 2004;

Devlaeminck et al 2005; De Schrijver et al 2007; Wuyts et al 2008). However, these observational or experimental studies were also limited in terms of the maximum distance-to-edge prospected or number of replications, and few studies have explored long-range gradients (700 to 800 m). For example, Wuyts et al (2008) and Devlaeminck et al (2005) covered a 200-m gradient from the edge. Bernhardt-Römmerman et al (2007) analysed changes in spatial distribution of vegetation types over four decades in a 24-ha isolated plot, which corresponds to a maximum edge distance of 277 m. Some studies have used Ellenberg's indicator values for nitrogen as a vegetation bioindicator to study atmospheric N deposition (Diekmann and Dupré 1997; Brunet et al 1998) and two have detected higher N up to 500 m into forest interior (Thimonier et al 1992; Kennedy and Pitman 2004). The decreasing MIV.N with distance-to-edge observed here is thus consistent with the parallel decreasing gradient of atmospheric N deposition from the edge.

However, the excess of acid throughfall deposition at the edge (Devlaeminck et al 2005; Wuyts et al 2008) should also lead to soil and vegetation acidification at the edge, as reported by several historical analyses or spatial comparisons (Thimonier et al 1994; Brunet et al 1998; De Schrijver et al 1998). The opposite trend in MIV.pH observed here is therefore difficult to explain. Our result is based on mean plant indicator values, and the pattern could be obscured by the positive correlation between MIV.pH and MIV.N, which is common when large environmental gradients are sampled (Diekmann and Dupré 1997; Dupré et al 2010), thus making it difficult to disentangle eutrophication from acidification (Verheyen et al 2012). Nevertheless, soil pH and buffer capacity largely determine response to N and S deposition, and a differential effect of eutrophication and acidification has often been documented for understory vegetation, with nutrient-rich sites remaining relatively unaffected by acidifying deposition (Thimonier et al 1994; Diekmann and Dupré 1997; Hülber et al 2008). Moreover, eutrophication is also reported to have a stronger effect on vegetation than acidification

(Dupré et al 2010). Consequently, more research is needed to determine the potential role of atmospheric deposition to explain the observed long-range gradients.

A second hypothesis could result from edge dynamics following reforestation. First, the total forest area in France rose from 9 million *ha* in 1840 to 15 million *ha* in the late 1990s (+66% increase, Mather et al 1999). Considering this increase, potential forest edge displacement ranges from 187 *m* to 3274 *m*. Second, past land use has a long-lasting effect on forest soils and plant communities (Falkengren-Grerup et al 2006; Dambrine et al 2007; Hermy and Verheyen 2007; Sciama et al 2009), which allows the differentiation between recent and ancient forests, particularly in Europe and North America. Soils in recent forests generally have higher pH, nutrient concentrations and nitrification rates, and lower C/N ratio and soil porosity than soils under ancient forests (Bossuyt et al 1999; Verheyen et al 1999; Falkengren-Grerup et al 2006). Third, if we assume that recent forests are more frequently located at the periphery of the ancient forest remnants (Bossuyt et al 1999), the differences in soil properties between recent and ancient forests could be responsible for the residual decrease in MIV.pH and N from the edge. Our hypothesis was also supported by the much higher proportion of ancient forest species among the 40 species more frequently found in forest interior (Pellissier et al 2013).

CONCLUSIONS

This study detected significant edge-to-core gradients of mean plant indicator values for temperature, light, soil pH, nitrogen and humidity over much larger ranges than previously recognized. Even if the direction of these gradients was consistent with the microclimatic edge-effect and the consequence of across-edge movement of chemical compounds, very few scientific studies had so far reported long depth-of-edge influence. Furthermore, deep edge-to-core gradients in soil type, measured soil water availability, measured air temperature and

forest stand characteristics were also identified for the first time. We verified that these gradients explained a large part of edge effect magnitude, but the edge effect remained significant after controlling for forest site variability, particularly for MIV.pH and MIV.N. We hypothesized that the long-range gradient in MIV.pH and N could be the result of atmospheric deposition deeper inside forest interior. We also interpreted it as the result of the edge displacement and long-term persistence of past land use on pH, nitrogen content, and plant communities. Data on past land use in 1840 and distance to the ancient forest edge would help to corroborate this hypothesis. This long-range gradient has important conservation implications, and challenges the real extent of the forest core area. Further research is required, in particular direct soil chemical measurements (pH, N), in order to definitively unravel the drivers shaping this large spatial pattern of forest ground vegetation.

Table 1 ANOVA table applied to MIV for pH, N (nitrogen availability), L (light availability), F (humidity) and Ta (temperature requirement) using deciles of distance-to-edge (DIST) and forest patch size (FPS) as nominal predictors. The decile points for DIST were 2.7, 37, 73, 113, 160, 216, 286, 374, 489, 683 and 1096 *m*. The decile points for FPS were 327, 575, 889, 1374, 2215, 3293, 5057, 7315, 13566, 45734 and 100000 *ha*.

Variable	Predictors	Df	Sum of Sq.	Mean Sq.	F Value	P
MIV.pH	DIST	9	918	102.02	97.34	<2e-16
	FPS	9	1170	129.97	124.01	<2e-16
	DIST x FPS	81	78	0.96	0.92	0.69
	Residuals	19884	20840	1.05		
MIV.N	DIST	9	341	37.87	84.45	<2e-16
	FPS	9	211	23.48	52.35	<2e-16
	DIST x FPS	81	38	0.47	1.04	0.38
	Residuals	19884	8917	0.45		
MIV.L	DIST	9	9	1.02	3.49	0.00025
	FPS	9	21	2.29	7.87	1e-11
	DIST x FPS	81	33	0.41	1.41	0.009
	Residuals	19884	5790	0.29		
MIV.F	DIST	9	43	4.82	35.27	< 2e-16
	FPS	9	52	5.77	42.23	< 2e-16
	DIST x FPS	81	14	0.17	1.23	0.08
	Residuals	19884	2719	0.14		
MIV.Ta	DIST	9	89	9.88	10.38	4e-16
	FPS	9	1998	222.04	233.38	< 2e-16
	DIST x FPS	81	122	1.50	1.58	0.0007
	Residuals	19884	18918	0.95		

Table 2 Results of the five alternative models on mean indicator values (MIV) for pH, N (nitrogen availability), L (light availability), F (humidity) and Ta (temperature requirement) using SITE, DIST and FPS as predictors. M_{SITE} : SITE; M_{DIST} : SITE + DIST; M_{FPS} : SITE + FPS; M_{ADD} : SITE + FPS + DIST; M_{INTER} : SITE + FPS x DIST. The table gives the AIC for M_{SITE} and then the AIC difference between M_{DIST} , M_{FPS} , M_{ADD} or M_{INTER} , and M_{SITE} .

	M_{SITE}	M_{DIST}	M_{FPS}	M_{ADD}	M_{INTER}
MIV.pH	40742.94	-755.6	-373.7	-1072.5	-1006.2
MIV.N	28715.49	-744.3	-214.7	-892.2	-828.2
MIV.L	19578.78	-33.6	-68.2	-94.1	-61.1
MIV.F	6744.933	-168.4	-59.7	-228.5	-168.8
MIV.Ta	41479.86	-131.1	-466.2	-547.1	-483.6

Fig. 1 Location of the 19989 plots in the northern half of France with a regional focus to illustrate plot and forest patch structure. Plots kept in the final sample are in black, and discarded plots are in red. Plots were discarded for three reasons (see numbered circles): (1) distance to the external forest edge $> 1096\text{ m}$; (2) forest patch size $< 327\text{ ha}$; (3) plot closer to an internal gap than to the external forest edge.

Fig. 2 Curve of locally-weighted polynomial regressions applied to MIV for pH, N (nitrogen availability) L (light availability), F (soil humidity) and Ta (temperature requirement) according to distance-to-edge (left column) and forest patch size (right column).

Fig. 3 Proportions of (a) soil type, (b) deciduous, mixed and coniferous forests, and (c) even-aged high forest, high forest with coppice and coppice according to distance-to-edge deciles (D1: edge; D10: core). Proportions are relative to the total number of plots in each class of SITE variable. Significant relationships are flagged with an asterisk.

Fig. 1

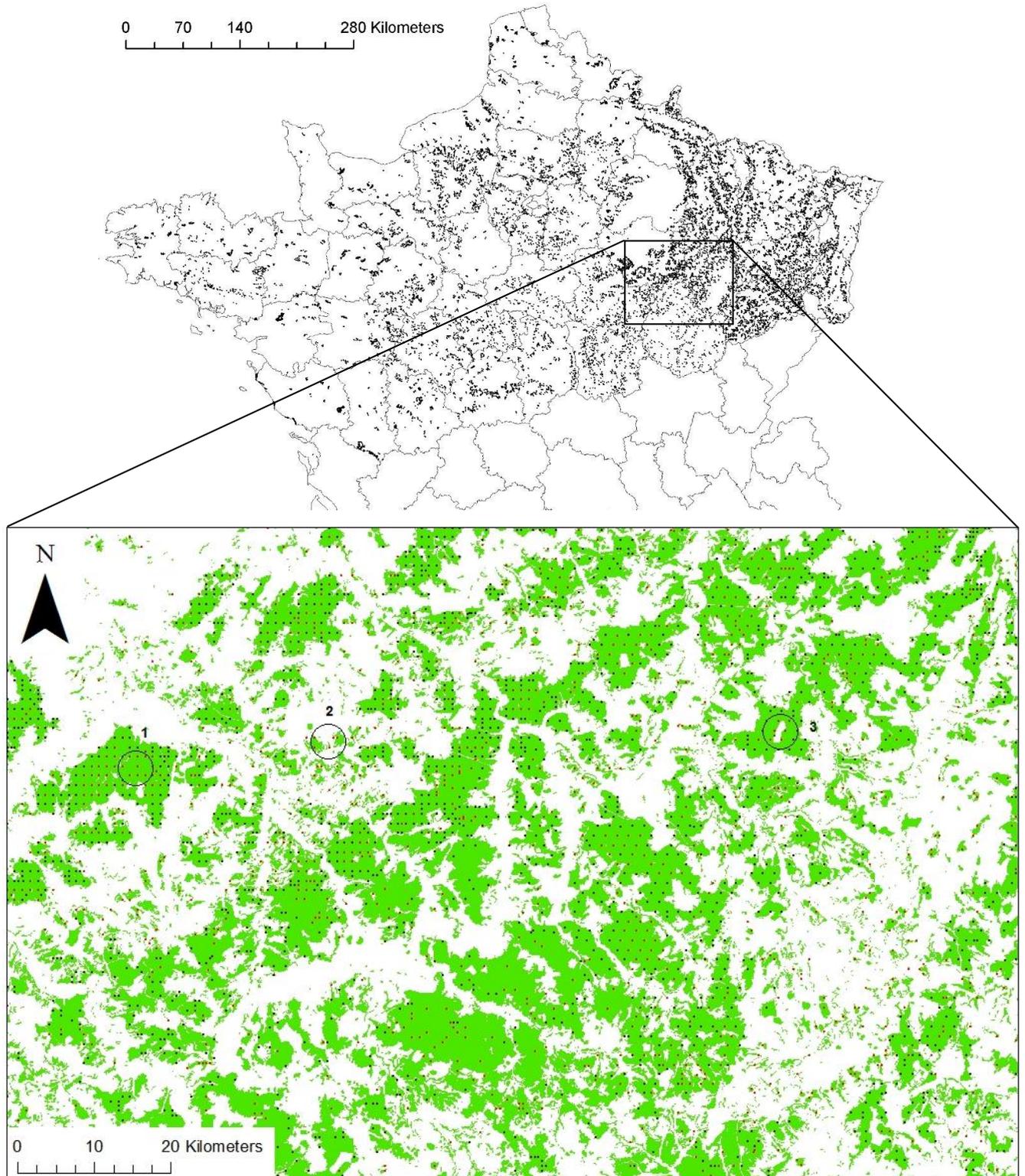


Fig. 2

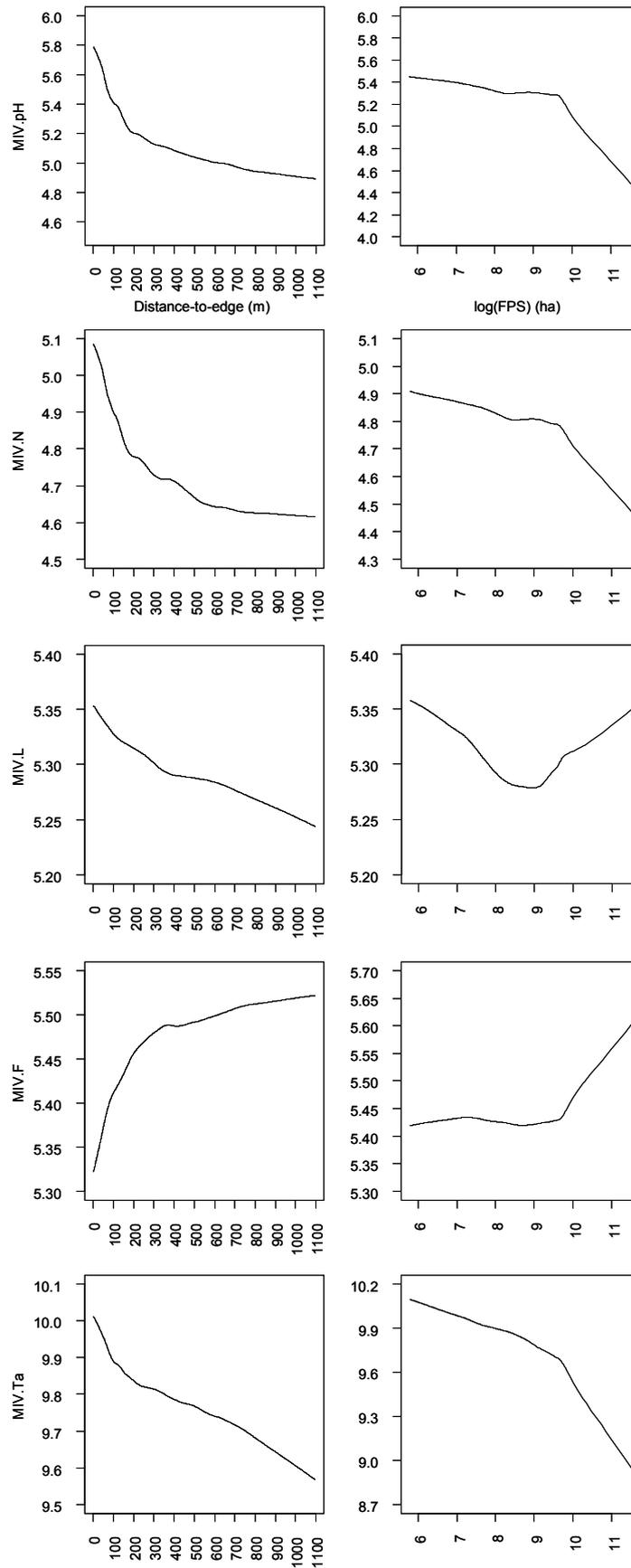
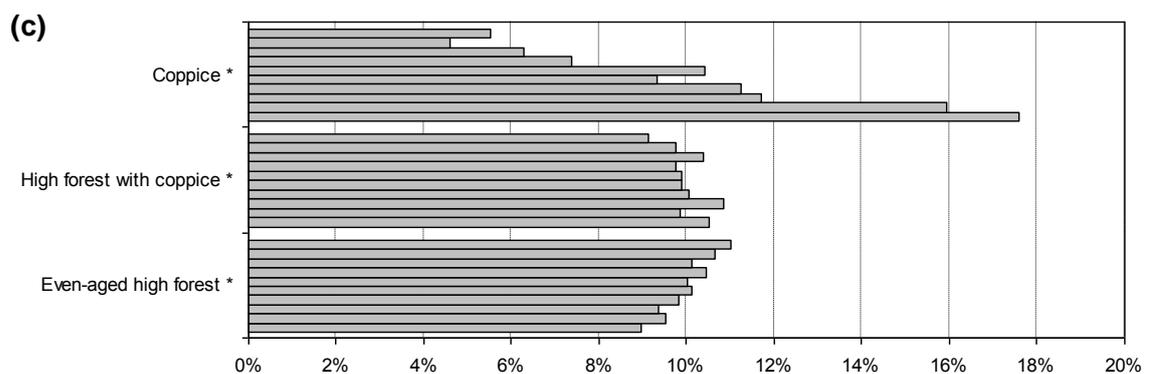
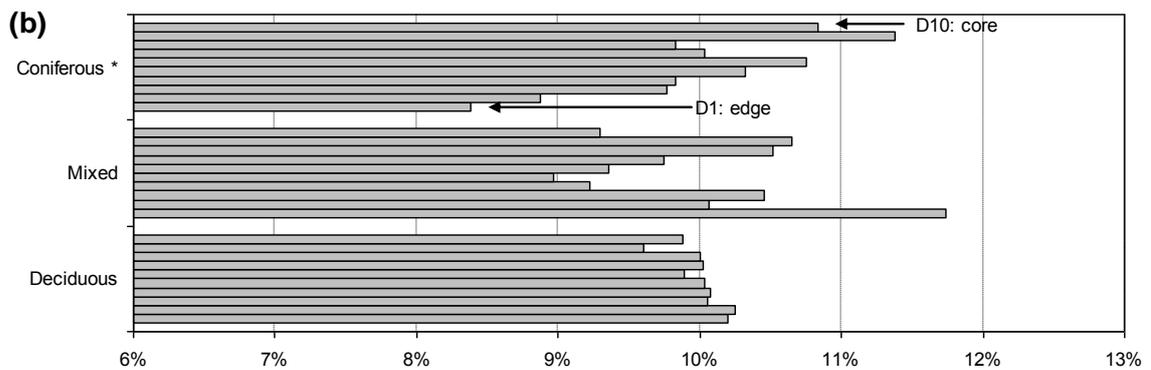
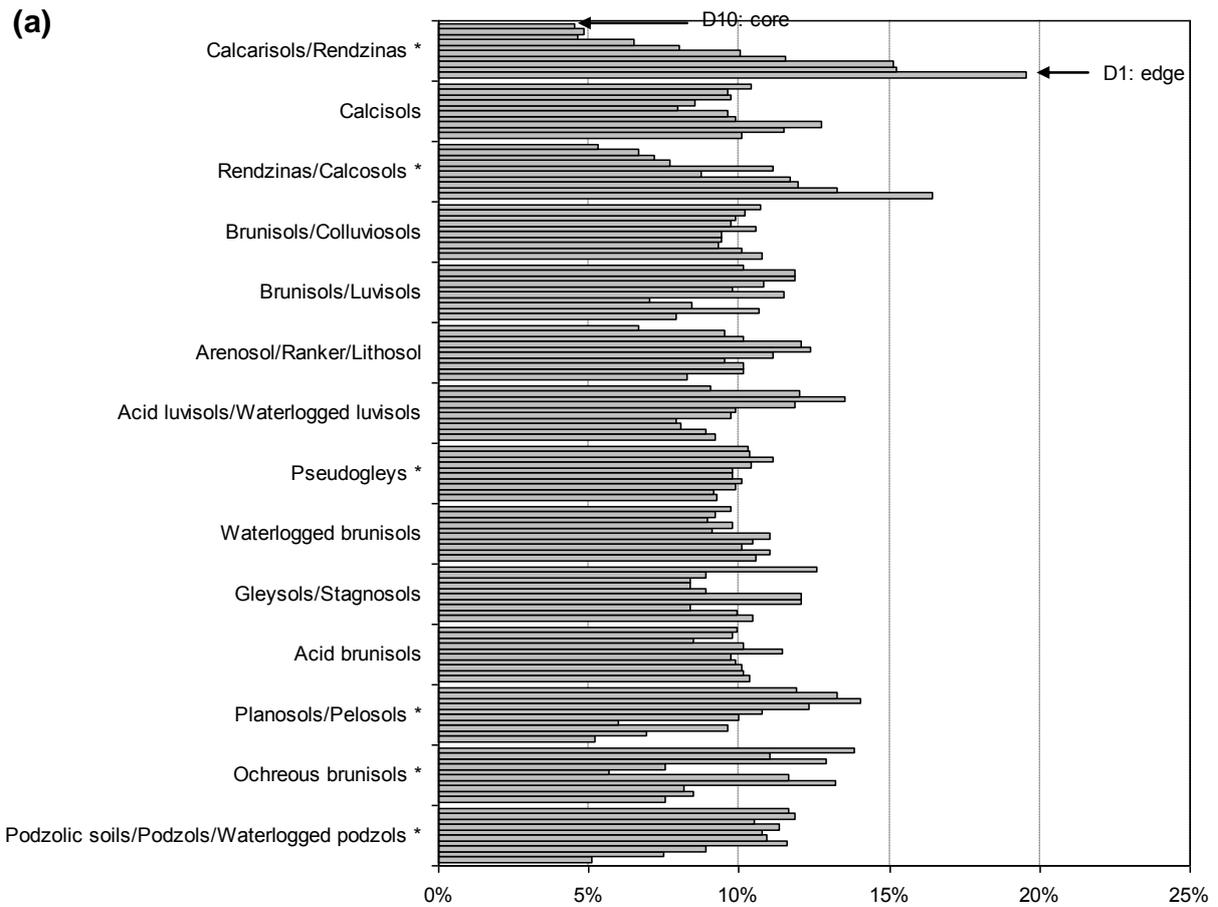


Fig. 3



ACKNOWLEDGMENTS

We wish to thank Theodora Nedeltcheva, Marianne Duprez and Catherine Cluzeau from the French National Forest Inventory (IFN) for their help on landscape parameter calculations and forest map database management. We also thank two anonymous reviewers for their thoughtful reviews of the manuscript. This study was partly funded by the French Ministry for the Environment research program "Biodiversité et Gestion Forestière" (BGF) through the Ecofor public interest group.

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