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Regular paper

Landownership is an unexplored determinant of forest understory plant composition in Northern France

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ABSTRACT

Few studies have investigated the influence of landownership on biodiversity. Therefore we analysed how the presence of forest understory plant species varied according to landownership in a broad geographical context and assessed which plant traits discriminated between species associated with state, other public or private forests. We also quantified the degree to which differences in soil type, forest management and landscape structure among ownership categories could explain the differences in species composition. Landownership, climate, soil, forest stand and landscape variables were collected on 38,751 plots located in temperate forests (5.1 Mha) in northern half of France using the French National Forest Inventory and GIS analyses. First, logistic regressions were used to determine species response to landownership after controlling for month of the plant survey and spatial autocorrelation. Relationships between plant traits and species association with landownership were then tested. Second, climate, soil, forest stand and landscape differences among ownerships were investigated. Third, species and trait responses to landownership were re-examined after controlling for month of the plant survey, spatial autocorrelation and climate, soil, forest stand and landscape variations.

Of the 276 species, 69 were associated with state forests, 38 with other public forests and 85 with private forests. Species associated with state and other public forests were more often urbanophobic, ancient-forest species, barochores and myrmecochores whereas private forest species were more often nutrient-, light-demanding, urbanophilic and endozoochorous species. Differences among landownerships were detected for all the soil, climate, forest management and landscape variables investigated. However, the ownership effect remained or became significant for 131 plants after controlling for environmental variability.

Landownership is not simply an administrative classification of land without ecological signification but was evidenced as a driver shaping understory plant community composition and plant traits in Northern France. These differences were partly explained by soil, management, edge and patch size effects, but land use history may help to explain the residual landownership effect. Our results have major implications on biodiversity monitoring and large-scaled conservation strategies. There is a need for deeper investigation into the impacts of land policy on biodiversity.

KEYWORDS

Landscape patterns, edge effect, past land use, plant traits, urbanity, dispersal mode.

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1. INTRODUCTION

Land-use change and ecosystem exploitation are considered the primary drivers of biodiversity loss (Foley *et al.*, 2005). Reports suggest an influence of forest landownership on forest management practices, landscape heterogeneity and land-use change over time (Crow *et al.*, 1999; Stanfield *et al.*, 2002; Wimberly and Ohmann, 2004; Ohmann *et al.*, 2007; Ko and He, 2011). However, few studies have considered the extent to which type of landownership is associated with differences in biodiversity (Lovett-Doust and Kuntz, 2001; Lovett-Doust *et al.*, 2003; Ohmann *et al.*, 2007). Two studies in Ontario reported differences among private, public and mixed-ownership sites in the number of vegetation community types, rare vascular plants, butterflies, mammals, and regionally- and locally-rare breeding birds, with higher numbers at public and mixed-ownership sites compared to privately-owned sites (Lovett-Doust and Kuntz, 2001; Lovett-Doust *et al.*, 2003).

However, many environmental and disturbance factors such as soil, climate, land use history, present and past management practices and landscape characteristics can also vary strongly among landownerships and could thus explain the differences in biodiversity at first sight attributed to landownership (Maltamo *et al.*, 1997; Lovett-Doust *et al.*, 2003; Zmihorski *et al.*, 2010; Riitters *et al.*, 2012).

Publicly-owned land has been found to occur more often at higher elevation and on soils less suitable for agricultural production, having been spurned by private ownership due to its lower value for agriculture and forestry and difficulties with access (Wright *et al.*, 2001). The same trend may have occurred in France, but the one study to address the issue only compared the distribution of soil types and soil chemical properties between forest and agricultural land; the authors found that cambisols, stagnic, gleyic luvisols, gleysols and podzols were more frequent in forested areas (Badeau *et al.*, 1999). Focusing on forest management and disturbance regime, it has been established that forest ownership is a relevant factor for variations in forest vegetation (Ohmann *et al.*, 2007) and forest structure (Maltamo *et al.*, 1997; Wimberly and Ohmann, 2004). A recent study in central Poland (Zmihorski *et al.*, 2010) showed that (i) private forests showed lower DBH and basal area than state forests, but (ii) state forests displayed higher proportions of non-native tree species (*Robinia pseudoaccacia*, *Acer negundo*, *Prunus serotina* and *Platanus* sp.). The differences in DBH and basal area could be partly explained by origin and age differences between state and private forests. First, a substantial proportion of the private forests could have originated from secondary succession and second, large connected patches were more often state-owned whereas small isolated patches were more often private (Zmihorski *et al.*, 2010). This suggests that past land use and landscape fragmentation could also be involved in the observed differences between public and private lands. However, the higher proportion of non-native tree species would tend to suggest different and maybe more intense management practices and timber harvesting in state-owned forests.

Lovett-Doust & Kuntz (2001) demonstrated that differences in biodiversity remained significant even after controlling for differences in landscape-level factors, which indicates a residual effect of landownership. This issue has yet to be explored in other geographical contexts and by controlling for a wider panel of environmental parameters (soil, climate and forest management). In this study, we focused on understory plants and basically assumed that plant species composition varied according to forest ownership (Fig. 1). However, we also hypothesised that the effect of forest ownership was actually attributable to a combination of environmental factors that differed among forest ownerships, i.e. abiotic conditions, forest management disturbances, landscape patterns and land-use history. Moreover, as species traits vary according to soil, climate, disturbance and landscape patterns, we assumed that plant traits also varied with forest ownership. We hypothesised that state forests were generally on less favourable site conditions than private lands, and thus would host species with lower nutrient requirements and indicator of wetter conditions. We also expected that private forest stands would be more intensively managed than public forests, and thus would be younger and have a lower stand basal area and volume and would host more disturbance-tolerant species, whereas public forests would host more disturbance-sensitive species. Finally, we expected a higher proportion of private forests to be recently afforested, smaller (Zmihorski *et al.*, 2010) and often disconnected from ancient forests or preferentially located at their periphery (Bossuyt *et al.*, 1999): thus, we hypothesised that fast-colonizing species would be more frequent in private forests while species with lower dispersal ability would be more frequent in state forests. In addition to these assumptions, we assumed that environmental conditions and plant trait responses in "other public" forests (run by local public, departmental or regional authorities or by public institutions) would be intermediate between state and private forests.

The three research questions addressed in this study were:

(1) to analyse plant species responses to forest ownership on a broad geographical scale and determine what plant traits discriminated preference for forest ownership among habitat requirements, dispersal mode and life form;

(2) to analyse landownership differences in climate, soil, forest management and landscape patterns;

(3) to re-examine both individual species and plant trait responses to forest ownership after controlling for climate, soil, forest management and landscape variations in order to test whether a residual landownership effect remains and, if so, to propose an ecological interpretation.

The use of the French National Forest Inventory dataset enabled us to explore very large gradients of environmental conditions and to properly disentangle the complex relationships among these factors.

2. METHODS

2.1 Materials

2.1.1 Study area and French National Forest Inventory data

In France, the total forest surface area (11.5 M*ha*) is 75% privately-owned, 10% (1.4 M*ha*) state-owned and 15% (2.4 M*ha*) "other public" (Anonymous, 2010). Moreover, private forest units are highly parcelled out (a forest unit is the forest land that belongs legally to a single landowner entity): average unit size is just 2.9 *ha* in private forest compared to 189 *ha* in other public forest and a massive 1282 *ha* in state forest (Anonymous, 2010).

The study area for this research covered the northern half of France with a surface area of 270,962 *km²* and a forest cover of 20.4%. Data came from the French National Forest Inventory (FNFI, http://inventaire-forestier.ign.fr/spip/) totalling 38751 plots distributed in 10131 forest patches (Fig. 2). Forest ownership (OWN) was composed of three classes: state forest (22%), other public forest (mainly communal forests, 22%) and private forest (56%). Plots were located within one of the 133 FNFI-defined "ecoregions", i.e. the division of the country into homogeneous areas in terms of geomorphology, regional climate and forest management.

2.1.2 Plant survey

Plant species composition was surveyed inside 700 *m²* circles at each plot throughout the year. Although the full study period was 1989-2009, 97% of the plots were sampled between 1990 and 2004. The data gathering process involved a total of 63 teams with a range of expertise in plant identification, which means random variation could be substantial due to observer effects, plant oversight and species misidentification (Archaux *et al.*, 2006). However, we considered that the species distribution model was reliable because all the forest types were equally sampled and total sample size was huge. Plant phenology is also an important factor as it affects the observed plant species composition, and so month of the plant survey was always included in our models as a covariate (MONTH). We did not control for year of survey. Nomenclature followed the French BDNFF flora nomenclature for vascular plants and the European BDNBE nomenclature for bryophytes (Tela-Botanica, 2011).

2.1.3 Climate, topography and soil data

These variables were recorded on-plot during field sampling or obtained from existing databases (Appendix A). Climate variables [mean annual precipitation (RAIN) and annual mean of monthly maximum temperatures (TMAX) from 1961 to 1990] were obtained using the AURELHY meteorological model built on a 1 km² grid (Bénichou and Le Breton, 1987). We determined topography in the field using a topographical index measuring the difference between lateral water inflow and outflow of the plot (TOPO). The TOPO index increases as difference in flow increases. Soil characteristics were mainly based on soil type using a standardised soil classification (IUSS-Working-Group-WRB, 2006): the 41 initial classes were collapsed into 14 soil classes (SOIL) based on class frequency and similarities. Some plots were deleted due to the low frequency of soil classes and the impossibility of grouping into close categories. Other pedological variables were: humus type (HUMUS), depth of HCl effervescence in the fine soil fraction (DHCl), soil water capacity (SWC) and depth of temporary waterlogging (DTW).

2.1.4 Forest stand variables

Forest stand characteristics were collected in 1964 *m²* circular plots and concerned total canopy cover (CCOV), stand age (AGE), stand basal area (BA), stand volume (VOL), dominant tree species of the overstory layer (TREE.SPECIES), forest stand structure (STRUC) and traces of felling or thinning (FELLING; Appendix A). The five most frequent tree species were: *Quercus petraea* (21%), *Q. robur* (19%), *Fagus sylvatica* (13%), *Pinus sylvestris* (6%) and *Picea abies* (5%). Stand structure was composed of even-aged high forest (56%), high forest with coppice (36%), and coppice (8%).

2.1.5 Landscape variables

Distance from the plot to the closest forest road (DIST.ROAD) was measured in the field using distance classes (Appendix A). Distance from the plot to the closest external edge of the forest patch (DIST.EDGE), size of the forest patch where the plot was located (FPS), forest surface area and number of forest patches within a 1000-*m* radius buffer around the plot (FA.1000 and NFP.1000) were calculated using GIS and FNFI forest maps (Appendix A).

2.1.6 Plant traits

Plant trait approach (Table 1) was mainly based on plant indicator values that have been extensively employed as indicators of abiotic conditions (Diekmann, 2003; Bergès *et al.*, 2013). Ellenberg *et al.* (1992) and more recently Gégout *et al.* (2005) defined a set of indicator values for plants across central Europe and France, respectively. These values estimate the ecological optima of species along a series of environmental gradients.

To test the assumption that private forests were on richer soils and on less constraining conditions for waterlogging, we used pH for soil pH from EcoPlant database (Gégout *et al.*, 2005), N for soil nitrogen and F for soil moisture from Ellenberg. We also used Ta for mean annual temperature from EcoPlant to detect large-scale vegetation variations among landownerships.

To test the assumption that private forests were more intensively managed and had lower basal area, we used L for light from Ellenberg and two indicator values of disturbance (hemeroby and urbanity) available in Bioflor database (Kühn *et al.*, 2004). These authors assigned a hemeroby

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level (degree of human impact) to most plants of the German flora. These levels were converted to a numerical index varying from 1 (ahemerobic or completely natural) to 7 (metahemerobic or completely artificial). Similarly, the urbanity index (i.e. tendency of the species to occur in urbanised areas) were rescaled in a 5-point scale ranging from 1 (urbanophobic) to 5 (urbanophilic).

To test the assumption that private forests were more recently afforested, of smaller size and often disconnected from ancient forests or preferentially located at their periphery, we used previous traits plus (i) preference for ancient forests (hereafter called ancient forest species: AFS) from a combination of the two lists provided by Hermy *et al.* (1999) for Europe and Dupouey *et al.* (2002) for France and (ii) eight dispersal modes from Julve (2011).

2.2 Statistical analyses

2.2.1 Species response to landownership

To avoid overparameterisation (Pellissier *et al.*, 2013), species with fewer than 70 occurrences were excluded from the analysis. Thus 276 out of 645 species were retained for further analysis. Since our sampling area was very large, the statistical analysis should be adapted to the geographical distribution of the species within the study area to reduce uninformative absences. We therefore defined a sub-sample for each species by selecting all the plots of any ecoregion where the species occurred at least once. This approach created a spatial envelope for the species. The resulting species-specific sample size ranged from 1886 to 35520 plots while occurrences ranged from 70 to 19690.

A multiple logistic regression model was used to determine response of each species (*i.e.* probability of presence) to landownership (OWN) while controlling for the period of the relevé (MONTH) and spatial structure. Following Borcard *et al.* (1992), the spatial structure was modelled with the nine terms for a cubic trend surface analysis [centred geographical coordinates (x, y) of the grid squares, and the higher and cross-product terms (x^2, y^2, x^3, y^3, xy, x^2y and xy^2)]. The best model $M_{SPATIAL}$ was selected using a forward stepwise procedure based on the *step* function of the R *stats* package and considering MONTH with a quadratic term and cubic trend surface as predictors. Once $M_{SPATIAL}$ was determined, landownership was added as a new predictor ($M_{SPATIAL+OWN}$). This model was tested using AIC, and OWN was considered a significant predictor if the AIC difference between $M_{SPATIAL}$ and $M_{SPATIAL+OWN}$ was greater than 5 (which corresponds to $p < 0.01$). Each species was assigned a response group for OWN according to the regression parameters associated to OWN effect: association with state forest, other public forest, private forest, or neutral response (non-significant).

2.2.2 Variations in environmental factors among landownerships

For nominal variables, we ran Chi-squared tests on the contingency tables crossing OWN with SOIL, HUMUS, DHCl, TOPO, DTW, TREE.SPECIES, STRUC, FELLING and DIST.ROAD. For continuous variables, we applied ANOVA to TMAX, RAIN, SWC, CCOV, AGE, BA, VOL, FPS, DIST.EDGE, FA.1000 and NFP.1000 using OWN as factor.

2.2.3 Test of the species response to landownership after environmental correction

We tested whether the effect of landownership on species presence remained significant after controlling for climate, soil, forest management and landscape differences. The correlations among all predictors were first checked before analysis to avoid problems of multicollinearity. We removed HUMUS, DTW, DHCl, SWC, VOL, FPS and FA.1000 because they all displayed correlations above 0.54. We kept PLUVIO and TMAX in the model despite correlations above 0.57 as it was too crude to model species ecological niche with only one climatic variable. We selected the best model $M_{SPATIAL+ENVIR}$ using a forward stepwise procedure as above considering $M_{SPATIAL}$ as the lower model and the following list of additional predictors: TOPO,

SOIL, TREE.SPECIES, STRUC, TMAX, RAIN, CCOV, AGE, DIST.EDGE and NFP.1000. Continuous variables were always tested using a linear and a quadratic term, except for DIST.EDGE and NFP.1000 because we expected linear response to these landscape parameters. Once $M_{SPATIAL+ENVIR}$ was determined, landownership was added as a new predictor ($M_{SPATIAL+ENVIR+OWN}$) and tested using the same criterion as above. Each species was re-assigned a response group for OWN effect according to the value of the re-adjusted parameter associated to OWN effect.

2.2.4 Plant trait approach

We ran Chi-squared tests on the contingency tables crossing each category of plant traits and species preference for landownership, before and after ENVIR correction.

All data calculations and statistical analyses were carried out using R software version 2.12.2 (R Foundation for Statistical Computing, Vienna, AT).

3. RESULTS

3.1 Species and plant trait responses to landownership

The model $M_{SPATIAL}$ was always significant and included between 1 and 10 components with an average of 6.5. The most frequent components were MONTH, x, y, x^3 and x^2.
Of the 276 species analysed, 192 significantly responded to OWN, among which 69 were associated with state forests, 38 with other public forests and 85 with private forests. Twelve categories of plant traits (out of 18) showed significantly different proportions among the three types of landownership (Fig. 3). There were higher proportions of acidophiles ($pH < 4$), urbanophobes ($urbanity \leq 1$) and barochores in the pool of state forest species. There were lower proportions of hygrophilous species ($F > 6$) and higher proportions of AFS and myrmecochores in the pool of other public forest species. There were higher proportions of basophiles ($pH > 7$), nitrogen-demanding ($N > 6$), light-demanding species ($L \geq 6$), urbanophiles ($urbanity > 3$), hemerobic species ($hemeroby > 3$) and endozoochores in the pool of private forest species.

3.2 Soil, climate, forest stand and landscape pattern variations among landowner types

All the ENVIR variables significantly varied among landowner types (Table 2). The following analysis only considers the variables for which the share of variance explained by ownership was above 1%. For soil type (Fig. 4a), nutrient-poor soils and waterlogged soils were more frequent in state forests, whereas nutrient-rich soils were more frequent in private forests. For humus form, moder, dysmoder and mor were more frequent in state forests whereas eumull, carbonated mull and thick carbonated mull were more frequent in private forests. This trend was confirmed by the depth of a carbonated horizon, which was more often close to the soil surface in private forests and more often absent in state forests. TOPO and DTW showed weaker trends, but DTW displayed a higher share of superficially waterlogged soils in state forest compared to private forest. For climate, TMAX increased from other public to state then private forests, while RAIN followed the reverse gradient (Appendix B).
Stand characteristics also varied with landownership: AGE, VOL and FELLING all increased from private to other public then state forests, while DIST.ROAD was lowest in state forests (Fig. 4b, Appendix B). Concerning tree species composition, stands dominated by shade-tolerant species (*F. sylvatica* and *Abies alba*) were less frequent while those dominated by pioneer species (*Alnus* sp., *Betula* sp., *Populus* sp., *Robinia pseudoacacia* and *Salix* sp.) were more frequent in private forests (Fig. 4c). Stands dominated by *Q. petraea* were more frequent in state forests whereas those dominated by *Q. robur* were more frequent in private forests. The

proportion of "even-aged high forest" was higher in state forests; the proportion of "high forest with coppice" was higher in other public forests and the proportion of "coppice" was much higher in private forests (Fig. 4d).

Concerning landscape patterns, DIST.EDGE, FPS and FA.1000 increased from private to other public forests then state forests, whereas NPF.1000 showed the opposite trend (Fig. 5). These trends were also clearly visible in Fig. 2.

3.3 Species and plant trait responses to landownership after controlling for ENVIR

All species responded to at least one ENVIR factor since the $M_{SPATIAL+ENVIR}$ model included between 2 and 10 environmental predictors (with an average of 7.1). SOIL and TREE.SPECIES were the most frequent predictors, showing that these two factors strongly determined the ecological niche of plant species in our study area.

Of the 276 species analysed, 126 significantly responded to OWN before and after ENVIR correction, while 66 responded to OWN before correction but not after. Five responded to OWN solely after ENVIR correction. Among the 131 species for which $M_{SPATIAL+ENVIR+OWN}$ was the best model, 64 were associated with state forests, 26 with other public forests and 41 with private forests. The remaining 145 species showed a neutral response to landownership.

Plants with indicator value for $pH < 4$ became non-significant after controlling for ENVIR variations (Appendix C). Conversely, two plant traits became significant after ENVIR correction: epizoochores (higher proportion in state forest species pool) and plants with indicator value for $Ta > 10°C$ (higher proportion in private forest species pool).

4. DISCUSSION

4.1 Effect of landownership

In total, 70% of the plants significantly responded to landownership while controlling for month of the plant survey and spatial structure, which confirmed our first assumption and underlined landownership as a driver of understory plant species distribution at a large geographical scale. Plant traits very often exhibited extreme proportions in state *versus* private forests, while other public forests presented intermediate values.

Thirty-four percent of the species that significantly responded to ownership became non-significant after controlling for soil, climate, forest management and landscape, which confirms our second assumption that many environmental factors related to landownership could partly explain plant response to landownership. Nevertheless, 66% of the species that significantly responded to ownership remained significant and most plant traits remained or became significant after environmental correction. Taken together, these results highlight that forest ownership had a residual effect on forest plant composition, in agreement with previous investigations (Lovett-Doust and Kuntz, 2001; Lovett-Doust *et al.*, 2003). Our approach suggests that this residual effect of landownership should be related to other environmental factors not included in our models.

4.2 Differences in abiotic conditions

In accordance with our assumption, private forests were more often located on nutrient-rich soils than public forests (soil, humus form). Similarly, temporary waterlogging was observed at a lower depth in state forests, thus confirming wetter soil conditions in state forests. These soil differences corroborated that severe site conditions were less desirable for private ownership due to their lower suitability for agriculture (Wright *et al.*, 2001). In addition, a substantial proportion of the private forested lands were likely to result from agricultural set-aside (Zmihorski *et al.*, 2010). The European forest soil survey also revealed that forest soils in France were more acidic and superficially waterlogged than agricultural soils (Badeau *et al.*,

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1999). However, after controlling for ENVIR variations, plant traits for pH and N still varied among landownerships (Appendix C), which means that ownership-related soil differences remained. Concerning climatic differences among ownerships (TMAX, RAIN), they mainly resulted from their spatial distribution within our study area: other public forests were more present in the eastern part of the study area, where climate is colder and wetter, while private forests were slightly more frequent in the south-centre part of the study area, where climate is warmer and drier. State forests were in average in an intermediate latitudinal position and more frequent at the north.

4.3 Differences in forest management practises

Forest management practises varied among ownership types: private forest stands were younger, had lower stand volume and were more often composed of pioneer tree species than state forests, whereas state and other public forests were more often composed of shade-tolerant species. Conversely, private forests displayed lower felling/thinning frequency and a larger distance to the closest forest road. As a result, it was difficult to conclude on the most intensively managed type of ownership: younger age and lower volume in private forests rather suggest shorter rotation length and thus more intensive silviculture, but this conclusion is contradicted by the lower felling/thinning frequency and longer distance to the closest road in private and other public forests. However, stand age and volume could be spurious indicators of management intensity, since they are also dependent on silvicultural treatment and tree species composition. A deeper investigation showed that silvicultural systems were not uniformly distributed among forest ownerships, as indicated by the higher proportion of even-aged high forest stands and the lower proportion of high forest with coppice in state forests. Either way, management practises are highly variable in privately-owned forests and vary according to forest unit size: large private forests (unit > 25 *ha*) representing about half of the private forest area tend to be more intensively managed since owners' main objective is timber production, whereas the other half of private forest area tends to be less intensively managed as the forest owners have multiple objectives such as firewood, recreation, hunting or heritage. Owners are not concerned in managing their small forests due to the high level of fragmentation observed of these privately-owned stands. In addition, economical studies indicates that in Western Europe, private owners are no more active farmers and are largely urbanised; thus they are not so interested in the economic value of their forests (Ziegenspeck *et al.*, 2004). Conversely, state forest resources are likely to be more exploited as the market for biomass energy develops (Lattimore *et al.*, 2009). Private forest owners in Western, Central and Eastern Europe are typically non-industrial private owners (Zmihorski *et al.*, 2010). The context largely differs from Scandinavia or North America where the big private forest owners are industrial private owners (Maltamo *et al.*, 1997; Ohmann *et al.*, 2007).

Our results corroborate the hypothesis that private forests hosted more species associated to early-successional phases and disturbance-tolerant or disturbance-favoured species. Indeed, numbers of light- and nutrient-demanding species decrease with time since the last major disturbance, i.e. clearfelling, regeneration felling or plantation (Brunet *et al.*, 1996; Zenner and Berger, 2008). Furthermore, other differences in silvicultural systems (Decocq *et al.*, 2004; Gartner and Reif, 2005; Van Calster *et al.*, 2007) and tree species composition (Augusto *et al.*, 2003; Barbier *et al.*, 2009 ;Wulf and Naaf, 2009) not related to forest succession could contribute to explain differences in plant composition and traits among ownerships.

4.4 Differences in landscape patterns

Landscape patterns displayed the highest correlations with landownership among the group of ENVIR factors (Table 2): private forests were closer to the external forest edge, in smaller forest patches and in more fragmented landscapes than public forests, consistently with our initial assumption (Zmihorski *et al.*, 2010; Riitters *et al.*, 2012). This suggests private forest is more prone to the influence of the surrounding matrix, in relation to processes occurring at the forest edge (Harper *et al.*, 2005). Plant community composition generally indicated higher soil pH, nitrogen availability and light availability at the forest edge than in the forest interior (Marchand and Houle, 2006; Vallet *et al.*, 2010). Pioneer, ruderal, competitive, synanthropic and non-indigenous species were also more frequent at the forest edge (Honnay *et al.*, 2002; Guirado *et al.*, 2006), mainly due to the specific microclimatic conditions, higher agro-chemical inputs (Thimonier *et al.*, 1992) and more frequent disturbances (Godefroid and Koedam, 2003a). Previous investigations on the same study area identified long depth-of-edge influence on understory plant species and traits (Pellissier *et al.*, 2013): we crossed the two classifications [species association with OWN (3 classes) *versus* species preference according to distance-to-edge (forest interior or forest edge)] and noted that 58% of forest-interior species preferred state forests while 66% of forest-edge species preferred private forests ($Chi^2 = 52.3$, $df = 6$, $p < 0.0001$).

Forest patch size reduction and isolation also impact forest plant communities. Patch isolation is reported to negatively affect AFS richness (Petit *et al.*, 2004). Due to their closer proximity to potential sources (grasslands, arable fields or urban areas), plant communities in small forest patches are often characterized by more synanthropic and nutrient-demanding species but fewer AFS compared to communities in larger patches (Godefroid and Koedam, 2003b; Guirado *et al.*, 2006).

The trait indicating human disturbance or naturalness (e.g. urbanity and hemeroby) very well discriminated plant response to ownership. Among the seven species qualified as "moderately urbanophilic" (urbanity = 4) in Biolflor (*Aesculus hippocastanum*, *Hyacinthoides non-scripta*, *Laburnum anagyroides*, *Pyrus communis*, *Ribes uva-crispa*, *Rubus ulmifolius* and *Sorbus domestica*), all except *H. non-scripta* were significantly more frequent in private forests. This suggests that these two traits, which have developed for and tested in urban contexts (Hill *et al.*, 2002), are equally reliable indicators of anthropogenic influence on a much broader environmental context. Including the quantity of urban, peri-urban and rural matrix in the surrounding landscape of the plots as additional landscape-level predictors of plant community composition would allow a deeper analysis of patterns of plant urbanity and hemeroby.

4.5 Differences in past land use

A significant share of variation in species distribution remained attached to landownership after correction for many environmental differences. We suspect that the residual effect of landownership could result from contrasted land use history between public and private lands (Zmihorski *et al.*, 2010). The total forest surface area increased from 9.9 M*ha* to 15.6 M*ha* (+57%) in France between 1908 and 2009, and this increase was divided into a small increase in state and other public forests and a huge increase in private forest ownership (+0.2, +0.1 and +5.4 M*ha*, respectively; Dupouey *et al.*, unpublished). Moreover, preliminary results on a 7000 km^2 region in the eastern part of our study area based on historical maps dating back to 1830 showed that the proportion of ancient forests was much higher in present-day state forests (90%) and other public forests (88%) than in private land (49%), as also found in Eastern Europe (Zmihorski *et al.*, 2010). Another argument that supports this historical interpretation is the legacy of past land use on forest soils and plant communities (*e.g.* Hermy and Verheyen, 2007; Plue *et al.*, 2008).

Plant trait variations were largely consistent with the suspected remnant effect of former land use. The main evidence was the higher proportion of AFS in the public forest species pool (Fig. 3b and Appendix C). Moreover, species associated with state forests were also more often barochores and myrmecochores, whereas species associated with private forests were more often endozoochores. These plant community differences in dispersal mode were previously observed between recent and ancient forests (Sciama *et al.*, 2009). In addition, the private forest species pool showed higher indicator values for pH and N, even after controlling for soil differences (Appendix C). This is probably because soils in recent forests generally have higher pH, nutrient concentrations and nitrification rates than soils under ancient forests (Verheyen *et al.*, 1999).

6. CONCLUSIONS

Landownership was evidenced as a driver shaping understory plant community composition and plant traits in Northern France. Thus, ownership is not an administrative classification of land without any ecological meaning. Forest land tenure results from a complex history where several drivers (soil, forest management, landscape and probably land use history differences) interact at large temporal and spatial scales. Our results have major implications on biodiversity monitoring and large-scaled conservation strategies, such as networks of protected areas. First, land ownership is easily available and synthesise several present and past disturbance factors that are more difficult to collect. Land ownership may thus be a useful indicator for forest biodiversity conservation policies. Second, governments in many regions concentrate conservation efforts on protected areas in public forests because this is more acceptable for the public. This strategy is actually rationale as the conservation value of public forests was higher due to their higher rate of ancient forest species and slow-colonising species, whereas private forests hosted more ruderal and synanthropic species. However, this strategy is incomplete because public forests only represent 25% of the forested land in France. Moreover, important variations occur within private forests, concerning forest unit size, management intensity, forest fragmentation and land use history. All this means only a subset of environmental conditions and biodiversity is protected and particular attention might also be paid to privately-owned ancient forests. Moreover, major land use and ownership changes have occurred in Western Europe during the last two centuries (Eriksson *et al.*, 2010). More recently, the growing challenge on forest bioenergy (including fuelwood) might further intensify forest management in public forests and large privately-owned forest units (shortening of forestry cycle duration, conversion of forests into short-rotation coppices, development of forest roads and access routes, increase in old tree harvesting) and thus might negatively impact biodiversity and ecosystem functioning (Lattimore *et al.*, 2009 ; Bouget *et al.*, 2012). Our findings underline that landownership policies can have major biodiversity impacts that we can no longer ignore.

7. ACKNOWLEDGMENTS

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Table 1. Overview of the plant traits analysed.

Traits	Description and range	Scale	Number (and %) of species with trait data available	Main data source
pH	soil pH [3 – 8.5]	pH Unit	256 (93%)	Gégout *et al.* (2005)
N	soil nitrogen: from 1 to 9 (nitrogen-demanding)	Ordinal	205 (74%)	Ellenberg *et al.* (1992)
F	soil humidity: from 1 to 9 (moisture-demanding)	Ordinal	224 (81%)	Ellenberg *et al.* (1992)
Ta	mean annual air temperature [3.8 – 15.7]	*°C*	244 (88%)	Gégout *et al.* (2005)
L	light: from 1 to 9 (light-demanding)	Ordinal	250 (91%)	Ellenberg *et al.* (1992)
Urbanity	5 classes: from 1, urbanophobic to 5, urbanophilic	Ordinal	236 (86%)	Kühn *et al.* (2004)
Hemeroby	7 classes: 1, ahemerobic; 2, oligohemerobic; 3, mesohemerobic; 4, beta-euhemerobic; 5, alpha-euhemerobic; 6, polyhemerobic"; 7, metahemerobic	Ordinal	237 (86%)	Kühn *et al.* (2004)
Ancient forest species	2 classes: species classified as AFS or not	Nominal	276 (100%)	Hermy et al. (1999) and Dupouey et al. (2002)
Dispersal mode	8 classes: anemochory, autochory (bryophytes), barochory, hydrochory, myrmecochory, epizoochory, endozoochory, dyszoochory	Nominal	256 (93%)	Julve (2011)

Table 2. Results of Chi-square tests or ANOVA (R^2) on the relationship between i) soil, climate, forest stand, landscape patterns and ii) landownership. For continuous variables, the mean of the ownership class was ranked numerically in increasing order, based on multiple comparisons of means (lowercase letters indicate significant ownership differences). Even if significant, results were not detailed for R^2 values below 0.01. Significance is flagged as: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Nominal variable	Chi-square	df	p-value
SOIL	1958.6	26	***
HUMUS	1589.2	24	***
DHCl	570.1	10	***
TOPO	113.3	6	***
DTW	292.2	10	***
TREE.SPECIES	4425.0	36	***
STRUC	2820.7	4	***
FELLING	856.8	2	***
DIST.ROAD	316.1	6	***

Continuous variable	R^2	p-value	Ownership rank		
			State	Other public	Private
TMAX	0.075	***	2b	1a	3c
RAIN	0.056	***	2b	3c	1a
SWC	<0.01	*	-	-	-
CCOV	<0.01	***	-	-	-
AGE	0.019	***	3c	2b	1a
BA	<0.01	***	-	-	-
VOL	0.013	***	3c	2b	1a
DIST.EDGE	0.124	***	3c	2b	1a
FPS	0.114	***	3c	2b	1a
FA.1000	0.176	***	3c	2b	1a
NFP.1000	0.090	***	1a	2b	3c

Figure Captions

Fig. 1. Conceptual framework of the relationships among the environmental drivers and understory plant response.

Fig. 2. Location of the 38,751 plots studied in the northern half of France with a regional focus to illustrate the specific spatial pattern of landownership.

Fig. 3. Percentage of species for each plant trait category according to species association with landownership: (a) indicator values (IV) for soil pH (pH), soil nitrogen availability (N), soil humidity (F), air temperature (Ta), light availability (L), urbanity and hemeroby; (b) preference for ancient forests (AFS) and dispersal mode. Percentages show the proportion of species having a given trait among the total number of species associated with state, other public, or private forests. The Chi-squared test indicates whether there is a significant difference in proportion among landownerships. Species with neutral response to landownership and species with missing values for plant traits were not included in the test. Number of missing values: pH: 6; N: 45; F: 39; Ta: 14; L: 15; urbanity: 23; hemeroby: 21; dispersal mode: 11.

Fig. 4. (a) Proportions of soil types according to landownership. Proportions are relative to the total number of plots in each type of landownership. Soil types are ranked in ascending order of soil pH. (b) Proportion of plots with distance to the closest forest road > 500 *m* and proportion of plots with traces of felling/thinning according to landownership. (c) Proportions of dominant tree species according to landownership. Tree species are grouped according to their response profile. (d) Proportions of even-aged high forest, high forest with coppice, and coppice according to landownership.

Fig. 5. Boxplot of distance-to-edge (DIST.EDGE, *m*, log scale), forest patch size (FPS, *ha*, log scale), forest surface area and number of forest patches within a 1000-*m* radius buffer around the plot (FA.1000, *ha* and NFP.1000) according to landownership. All the relationships were highly significant ($p < 0.0001$). The horizontal dotted lines correspond to grand mean values. "OTH.PUB.": other public forests.

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Fig. 1.

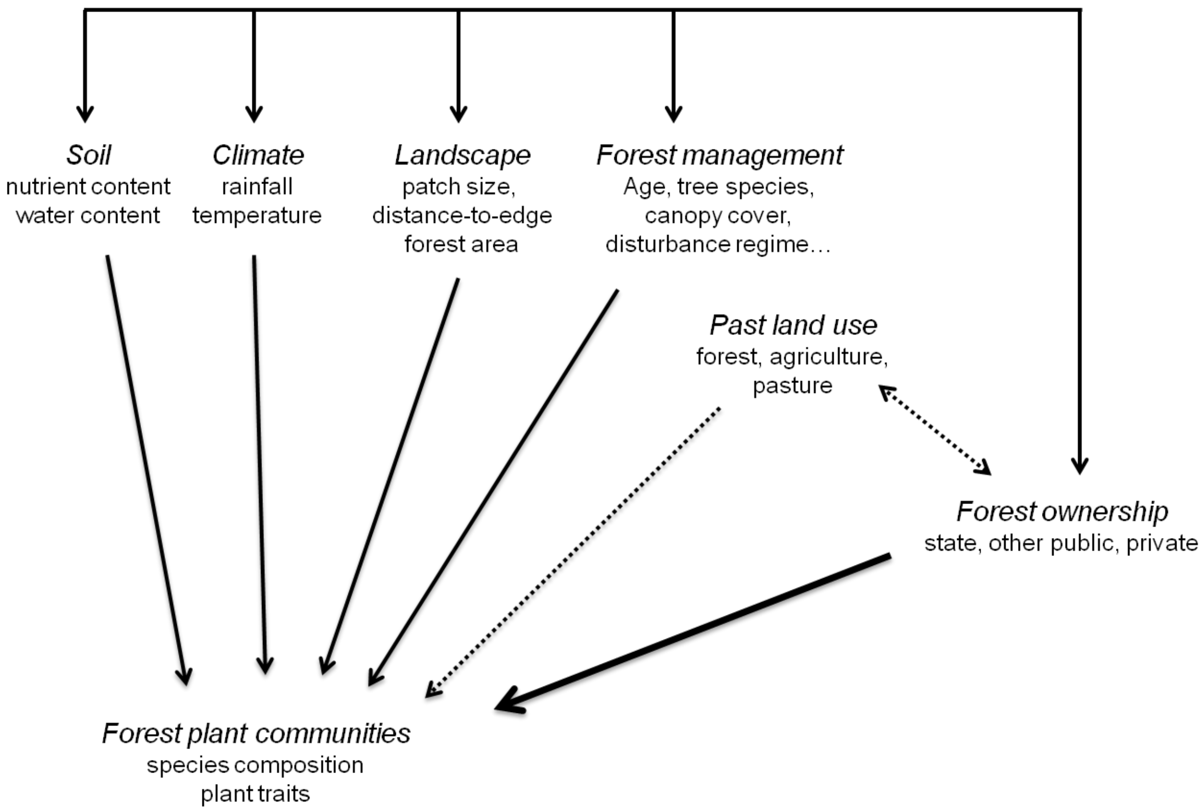

Fig. 2.

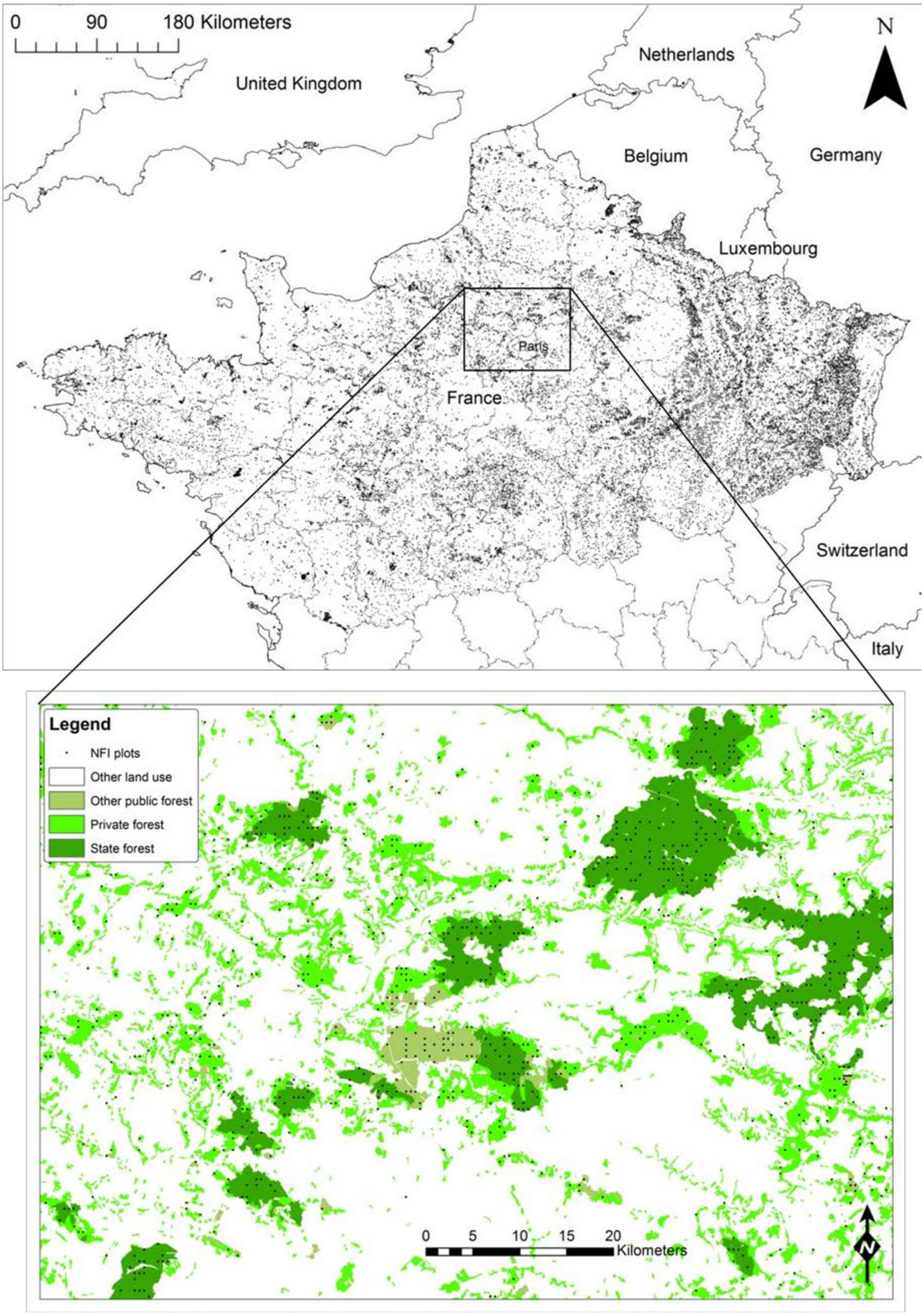
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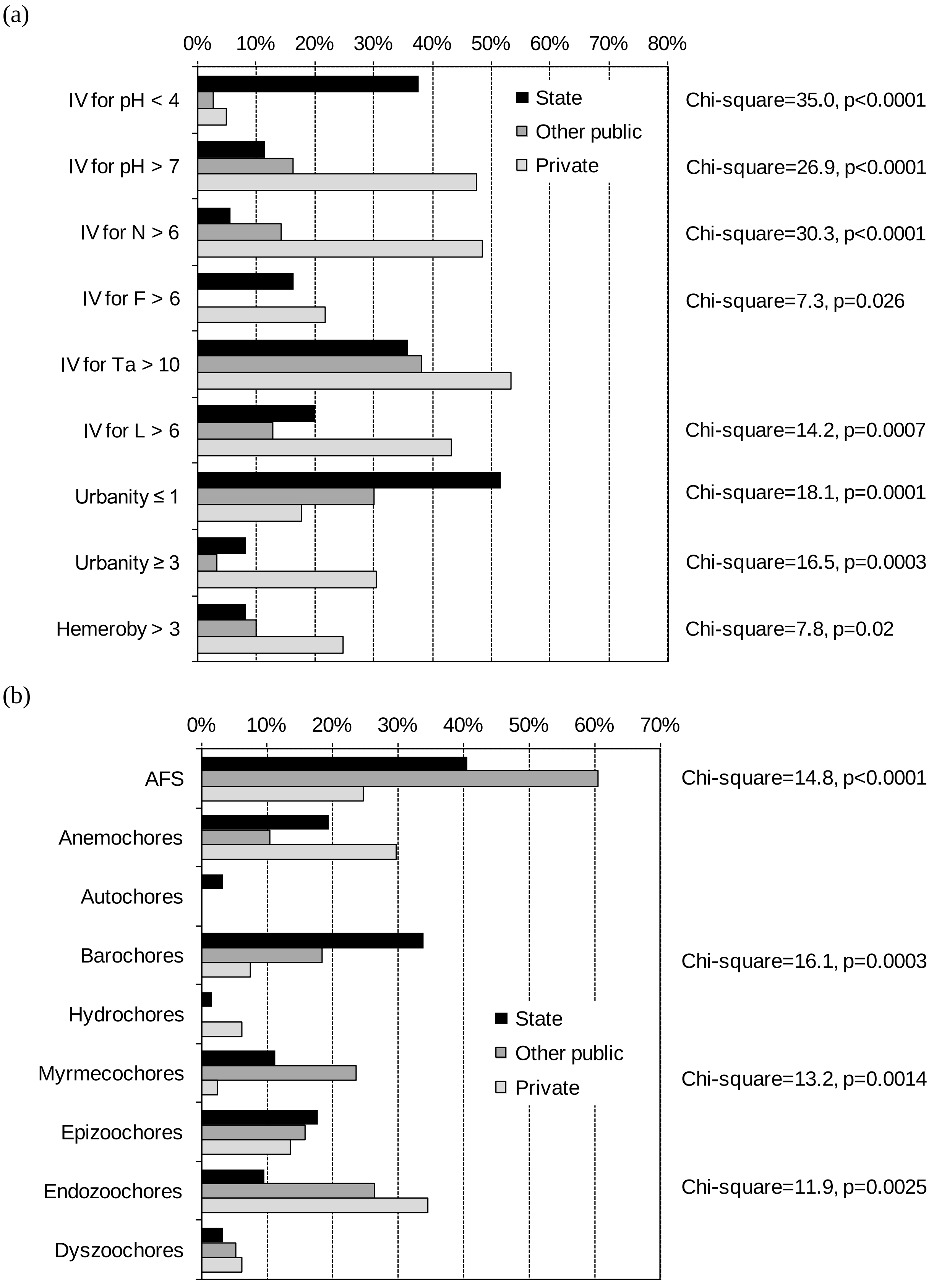
Fig. 3.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IV for pH < 4
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IV for F > 6
IV for Ta > 10
IV for L > 6
Urbanity ≤ 1
Urbanity ≥ 3
Hemeroby > 3
■ State
▨ Other public
☐ Private
Chi-square=35.0, p<0.0001
Chi-square=26.9, p<0.0001
Chi-square=30.3, p<0.0001
Chi-square=7.3, p=0.026
Chi-square=14.2, p=0.0007
Chi-square=18.1, p=0.0001
Chi-square=16.5, p=0.0003
Chi-square=7.8, p=0.02
(b)
0%
10%
20%
30%
40%
50%
60%
70%
AFS
Anemochores
Autochores
Barochores
Hydrochores
Myrmecochores
Epizoochores
Endozoochores
Dyszoochores
■ State
▨ Other public
☐ Private
Chi-square=14.8, p<0.0001
Chi-square=16.1, p=0.0003
Chi-square=13.2, p=0.0014
Chi-square=11.9, p=0.0025

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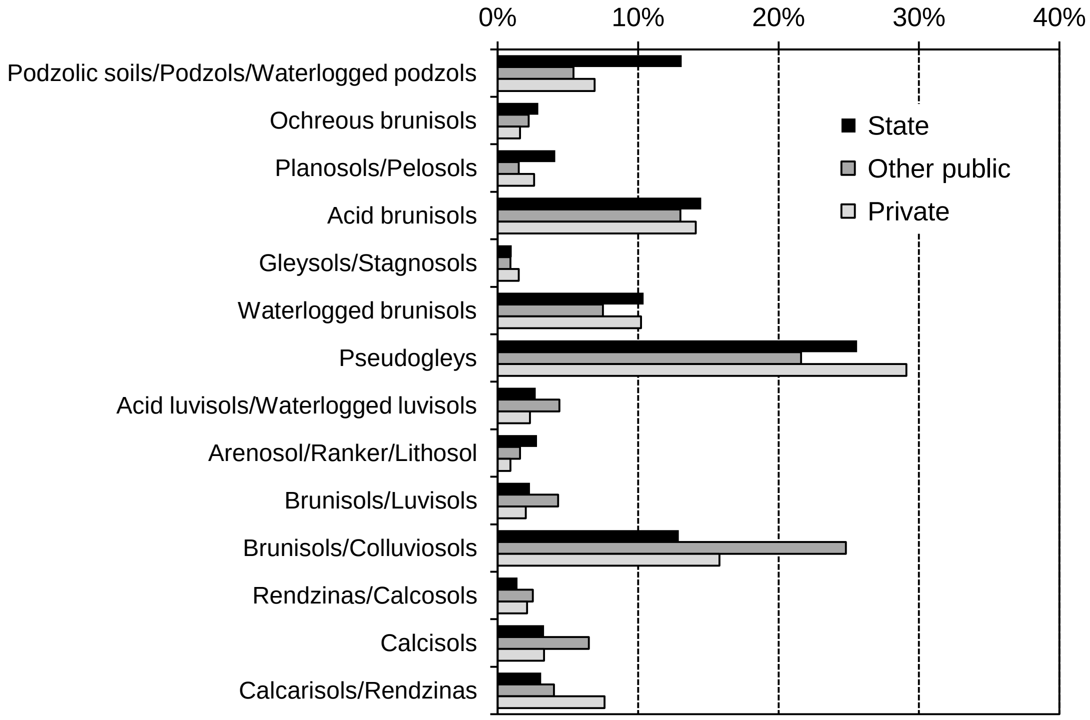
Fig. 4.

(a)



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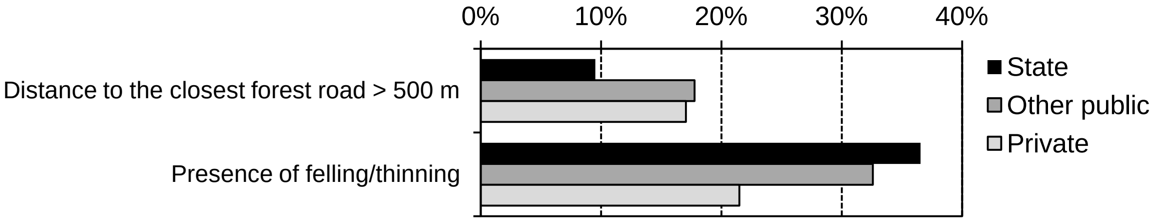

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Fig. 5.