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Ungulates increase forest plant species richness to the benefit of non-forest specialists

Vincent Boulanger¹  | Jean-Luc Dupouey² | Frédéric Archaux³ | Vincent Badeau² | Christophe Baltzinger³ | Richard Chevalier³ | Emmanuel Corcket⁴ | Yann Dumas³ | Françoise Forgeard⁵ | Anders Mårell³ | Pierre Montpied² | Yoan Paillet³ | Jean-François Picard² | Sonia Saïd⁶ | Erwin Ulrich¹

¹Office National des Forêts, Département Recherche, Développement et Innovation, Fontainebleau, France

²INRA - Université de Lorraine, UMR 1137 Ecologie et Ecophysiologie Forestières, Champenoux, France

³Irstea, UR EFNO, Domaine des Barres, Nogent-sur-Vernisson, France

⁴Université de Bordeaux, UMR1202 BioGeCo, Allée Geoffroy St-Hilaire, Pessac Cedex, France

⁵Laboratoire d'Ecologie Végétale, Université de Rennes I, Rennes Cedex, France

⁶Office National de la Chasse et de la Faune sauvage, DRE Unité, Ongulés sauvages, Birieux, France

Correspondence

Vincent Boulanger, Office National des Forêts, Boulevard de Constance, Fontainebleau, France.
Email: vincent.boulanger@onf.fr

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Abstract

Large wild ungulates are a major biotic factor shaping plant communities. They influence species abundance and occurrence directly by herbivory and plant dispersal, or indirectly by modifying plant-plant interactions and through soil disturbance. In forest ecosystems, researchers' attention has been mainly focused on deer overabundance. Far less is known about the effects on understory plant dynamics and diversity of wild ungulates where their abundance is maintained at lower levels to mitigate impacts on tree regeneration. We used vegetation data collected over 10 years on 82 pairs of enclosure (excluding ungulates) and control plots located in a nation-wide forest monitoring network (Renecofor). We report the effects of ungulate exclusion on (i) plant species richness and ecological characteristics, (ii) and cover percentage of herbaceous and shrub layers. We also analyzed the response of these variables along gradients of ungulate abundance, based on hunting statistics, for wild boar (*Sus scrofa*), red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*). Outside the enclosures, forest ungulates maintained higher species richness in the herbaceous layer (+15%), while the shrub layer was 17% less rich, and the plant communities became more light-demanding. Inside the enclosures, shrub cover increased, often to the benefit of bramble (*Rubus fruticosus* agg.). Ungulates tend to favour ruderal, hemerobic, epizoochorous and non-forest species. Among plots, the magnitude of vegetation changes was proportional to deer abundance. We conclude that ungulates, through the control of the shrub layer, indirectly increase herbaceous plant species richness by increasing light reaching the ground. However, this increase is detrimental to the peculiarity of forest plant communities and contributes to a landscape-level biotic homogenization. Even at population density levels considered to be harmless for overall plant species richness, ungulates remain a conservation issue for plant community composition.

KEYWORDS

biodiversity, biotic homogenization, enclosure, large herbivores, species richness, temperate forest, vegetation cover, vegetation monitoring

1 | INTRODUCTION

Environmental drivers such as climate change, atmospheric deposition and land use changes have been causing rapid change in forest ecosystems in the last few decades. Although the impacts of ungulates on forest ecosystems have been widely studied, they receive less attention as a global driver of forest changes. Since the last glaciation, forest ecosystems in Europe have evolved in the presence of large ungulates (Bradshaw, Hannon, & Lister, 2003). After a low point estimated around the turn of the twentieth century, populations of wild ungulates have increased and recolonized large areas in Europe during the last decades (Putman, Apollonio, & Andersen, 2011) following a multicontinent phenomenon (Beguín, Tremblay, Thiffault, Pothier, & Côté, 2016). New hunting regulations and reintroduction programmes are recognized as the major causes of the recovery of wild large ungulate populations in numbers and their geographical range since the 1970s (Maillard et al., 2010 and Supplementary material S1), forest expansion being also a possible driver for these changes. Wild ungulates now occur in almost all forest areas, even at low densities, and consequently, contribute to recurrent pressure in forest ecosystems. Increasing ungulate populations are an issue for forest managers since the damages they may cause to trees and seedlings can jeopardize forest regeneration processes (Bradshaw & Waller, 2016). Many studies have been carried out under high densities of ungulate populations (Habeck & Schultz, 2015) obtained either experimentally (Bachand et al., 2014) or naturally (Martin, Stockton, Allombert, & Gaston, 2010), or resulting from local management choices (Baltzinger et al., 2016), or in areas where noticeable impacts had been a priori observed (Boulanger et al., 2015). The roles of ungulates as general drivers of changes in forest dynamics and biodiversity have been less investigated in standard conditions.

Herbivores affect overall plant species diversity by modifying local colonization and extinction dynamics in grasslands (Olf & Ritchie, 1998). In temperate forest ecosystems, large ungulates (mainly red and roe deer and wild boar in temperate lowlands of Europe) play a triggering role in dispersal processes (Boulanger et al., 2011). Furthermore, they generate small-scale disturbances through soil trampling that damages plant tissues, breaks shoots or uproots plants (Hester, Bergman, Iason, & Moen, 2006) and when scraping their bedding sites (Adrados, Baltzinger, Janeau, & Pépin, 2008). These microsite disturbances may favour germination and seedling establishment, similar to what has been found for grassland pastures (Borer et al., 2014). More specifically, deer forage selectively so that they affect local extinction processes, either directly through the consumption of palatable plant species that increases local death rate or indirectly by changing inter-specific competition (Hester et al., 2006). When at destructively high levels, deer populations lead

to local extirpations of native plant species (Rooney & Dress, 1997) and reduce local plant diversity (Stockton, Allombert, Gaston, & Martin, 2005), sometimes amounting to shifts in plant communities toward alternate stable states (Hidding, Tremblay, & Côté, 2013). Situations of deer overabundance favour the development of unpalatable or browse-tolerant plant species at the expense of more palatable or browse-intolerant species (Augustine & McNaughton, 1998), and cause biotic homogenization of plant communities (Rooney, Wiegmann, Rogers, & Waller, 2004).

Most of the studies report that ungulates decrease plant species richness (Côté, Rooney, Tremblay, Dussault, & Waller, 2004) but these conclusions are drawn from contexts of high population densities, rarely investigating a full gradient of ungulate impacts (Faison, DeStefano, Foster, Motzkin, & Rapp, 2016). Synthesizing 13 European and North American studies, Gill and Beardall (2001) showed that young tree species richness and cover decreased under browsing pressure, thereby increasing light penetration at ground level and suggested that this phenomenon should increase the biomass in lower strata. Further, Stewart, Bowyer, Kie, Dick, and Ruess (2009) found that low to moderate levels of North American elk population densities increased both net aboveground primary productivity and plant species diversity. Experimentally combining various disturbances with fencing, Royo, Collins, Adams, Kirschbaum, and Carson (2010) observed a higher plant species density in browsed versus fenced plots (5.6 vs. 2.9 species/m² respectively), these positive effects being attributed to moderate population levels. In an insular context, Hegland, Lilleeng, and Moe (2013) experimentally identified a humped-back shape curve linking deer browsing and plant species richness, suggesting that below a threshold level, deer abundance increases species richness.

Although a large number of individual studies have been conducted, experimental evaluation of the magnitude of the effects of ungulates on plant communities has rarely been done at large geographical scales as pointed out by Habeck and Schultz (2015) for white-tailed deer. In Northern America, studies conducted in the region of Wisconsin and Michigan are among the widest, both geographically and temporally, with a long precedence in vegetation surveys in a context of increasing deer populations (Frerker, Sabo, & Waller, 2014; Frerker, Sonnier, & Waller, 2013; Rooney et al., 2004). In Europe, based on a coarse grained evaluation of game populations in forests coupled with resampled vegetation plots, Bernhardt-Römermann et al. (2015) found negative correlations between game densities and plant species diversity indices. Fenced enclosure experiments are particularly effective at detecting the influence of browsing by ungulates on the dynamics of plant species and communities (Waller, 2014). Yet, such data are rarely available over large areas, notably because the maintenance of a spatially homogenous experimental design over long time periods is difficult to ensure. In this

study, the French network of forest ecosystem monitoring – Renecofor – allowed us to investigate the effects of wild ungulates on forest understory vegetation. Initially set up for the monitoring of long term effects of atmospheric deposition, it provides consistent monitoring of plant species composition inside and outside fenced exclosures over 10 years across productive forests of France, in context of standard forest and game management.

Here, we analyzed vegetation changes occurring in 82 mature forest stands of this network, focusing on the divergence of trajectories between exclosures and outside controls. We aimed to address the following questions. What is the effect of ungulate exclusion on plant species richness and cover? Do the different vegetation layers respond similarly? Does the magnitude of change correlate with ungulate abundance? What plant types benefit from the absence or presence of ungulates? We hypothesized that, through selective shrub consumption, ungulates should alleviate ground-level light limitation thereby favouring light-demanding plant species.

2 | MATERIALS AND METHODS

2.1 | Monitoring plots

The 102 permanent plots of the Renecofor network, established in 1993, are located in managed public forests. It is a stratified sample of productive forests in France. All plots (2 ha) were established in mature and predominantly even-aged and pure stands. Within each plot, a central area covering 0.5 ha was fenced off in 1993–1994 in order to protect scientific equipment and to exclude large mammals (2 m high wire mesh fencing). One local forest manager has been missioned to ensure the maintenance of each plot and regularly checked the fence all along the 10-year monitoring period. The management regimes follow standard regional silvicultural practices and are the same inside and outside the exclosures. Populations of red deer, roe deer and wild boar are regulated by traditional hunting practices, with culling quotas defined locally, in accordance between foresters and hunters. The network encompasses a large range of bioclimatic conditions (Lat. 42°51'N – 50°10'N; Long. 3°32'W – 7°08'E; Figure 1). Elevation ranges from 5 to 1,700 m above sea level.

We excluded 20 plots, either heavily impacted by storms in 1999, for which monitoring was temporarily suspended (17 plots) or disturbed by domestic cattle or pigs (3 plots). In the remaining 82 plots (Figure 1), dominant tree species are *Abies alba* Mill. (11 plots), *Fagus sylvatica* L. (15 plots), *Quercus petraea* (Matt.) Liebl. (18 plots), *Quercus robur* L. (9 plots), *Picea abies* (L.) H.Karst. (10 plots), *Pinus nigra* subsp. *laricio* Maire (1 plot), *Pinus pinaster* Aiton (4 plots), *Pinus sylvestris* L. (9 plots) and *Pseudotsuga menziesii* (Mirb.) Franco (5 plots).

2.2 | Vegetation data

The plots were monitored for the first time in 1995, and then resampled in 2000 and 2005. Each sampling year, vegetation was

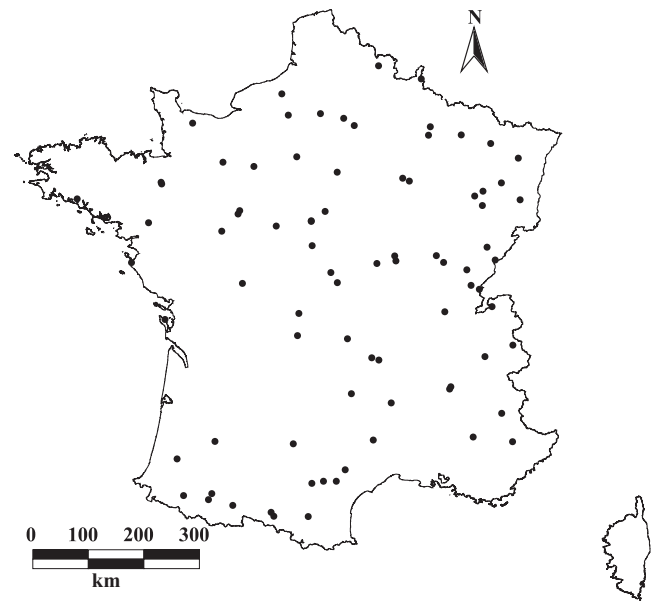


FIGURE 1 Location of the 82 study sites in France

inventoried twice, first in spring then in summer. In each plot, the vegetation sampling design consisted of eight subplots of 100 m² (50 m × 2 m): four inside the fenced area (exclosure) and four outside (control). Experienced botanists, most often working in pairs, recorded the abundance-dominance of all plant species (Supplementary material S2) and terricolous bryophytes (moss and hepatic species). Ligneous species were separately noted in four different vertical strata: tree layer (>7 m), high shrub layer (2–7 m), low shrub layer (0.3–2 m) and herbaceous layer (<0.3 m). We classified all herbaceous vascular species into the herbaceous layer, whatever their height. We attributed the terricolous bryophytes to a fifth specific layer. The percentage of bare soil (i.e. not covered by living vegetation) was visually estimated in 2000 and 2005 to the nearest 5%. A quality assurance programme, including calibration meetings the year before and the year of sampling, was applied to limit observer effects on plant censuses (Archaux et al., 2009). We aggregated vegetation data from spring and summer and retained the maximum abundance-dominance coefficient in order to constitute composite samples representing the overall non-seasonal plant community. Species names followed the *Flora Europaea* nomenclature (Tutin et al., 1968; –1980, 1993) for vascular species and Blockeel and Long (1998) for mosses and hepatic species.

Species traits were compiled from either Ellenberg et al. (1992) for ecological indicator values (light, temperature, soil moisture, acidity and nitrogen availability), Julve (2016) for Raunkiaer's life form and perennation, main dispersal mode and forest or non-forest specialist species, Bioflor (Kühn, Durka, & Klotz, 2004) for hemeroby index which is an indicator of the degree of preference of a species for artificialized habitats, and Hunt et al. (2004) for Grime plant CSR functional signature (competitiveness, stress tolerance and ruderality).

Details about data types and scales are provided in supplementary material (Tables S3 and S4).

2.3 | Changes in community diversity and structure

We analyzed changes in species richness and overall cover for each vegetation layer separately. Species richness was calculated at the subplot level (100 m², $n = 656$) and for each sampling year (1995, 2000 and 2005). We first converted the recorded abundance-dominance coefficients to cover percentages (see Table S2), then we computed a global cover index for each vegetation layer based on these cover percentages. This index was calculated at the subplot level for each sampling year following Fischer (2015); it ranges from 0 to 100%. This index was arcsine square root transformed before analysis. For each vegetation layer separately, we built a generalized linear mixed model (GLMM) with a Poisson error distribution and log-link to analyze the temporal changes in plant species richness and a linear mixed model (LMM) to analyze changes in cover index. We included three fixed effects: time (three levels: 1995, 2000 and 2005), fencing (two levels: control and enclosure) and the interaction between time and fencing, and subplot nested within plot as a random effect. Using contrasts, we tested the differences in cover index and species richness between enclosure and control subplots for each sampling year; p -values for pairwise comparisons were adjusted for multiplicity using a single-step method based on the joint normal distribution (Hothorn, Bretz, & Westfall, 2008).

Next, we examined the effect of enclosure on changes in community-aggregated species traits using linear mixed models, with time, fencing and their interaction as fixed effects and plot as random effect. Because of too many missing values, community averaged values could not be computed at the subplot level. Thus, we pooled the subplots into two aggregated relevés, one for the enclosure and one for the control plot (all subsequent analyses were conducted on these pooled plots). At each plot, for control and enclosure, we computed unweighted mean indicator values for quantitative species characteristics (Ellenberg indicator values, Grime CSR strategies converted to numerical values following Hunt et al. (2004) and hemeroby). For categorical plant characteristics, we computed the species richness in each category for enclosure and control plots (Gosselin, 2012). We analyzed species richness in each category separately, using generalized linear mixed models with a Poisson error distribution. Using contrasts, we tested the differences in community-aggregated species characteristics between enclosure and control plots for each sampling year.

2.4 | Role of variations in ungulate pressure among sites

We analyzed the relationship between variations in ungulate pressure among sites and the differences in vegetation richness and cover between enclosure and control plots, after 10 years of fencing. We used hunting bag statistics from the wild ungulates national

network to characterize the variations in ungulate abundance among plots. Statistics of animals killed were available at different spatial grains, depending on the species: municipalities (on average 1,200 ha of forested area) for wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*), and management units (on average 20,000 ha of forested area) for red deer (*Cervus elaphus*). Chamois (*Rupicapra rupicapra*) and mouflon (*Ovis orientalis*) could also occur at 19 out of 82 study plots, but no reliable hunting statistics were available.

Because the values were highly correlated among years, we only retained hunting statistics related to the last vegetation sampling (2005). For wild boar, we collected data available in 2004, 2005 and 2006 and retained the average over the 3 years as a reference for 2005. We did the same for roe deer but relying only on data available in 2002 and 2007 (data are reported every 5 years only).

For wild boar and roe deer, we collected the hunting statistics available in all municipalities intercepted by a circular buffer zone around each plot (radius = 6 km). Then we computed, for each available year and each municipality, the density of animals killed as the ratio between the number of animals killed and the surface area of woodland within the municipality. We excluded data for municipalities with <10% of forest cover in order to avoid aberrant density values of animals killed. At each plot, for both species, we computed the average densities of animals killed over all surrounding municipalities weighted by intercepted forest area.

For red deer, which hunting statistics are available at the management unit, we collected the hunting statistics available in all management units intercepted by a circular buffer zone around each plot (radius = 6 km) in 2005. As for roe deer and wild boar, we estimated the density of red deer killed as the ratio between the number of animals killed and the surface area of woodland within the management unit. Then at each plot, we computed the average densities of red deer killed over all surrounding management units weighted by intercepted forest area.

Finally, we combined ungulate abundances of different species into composite indices based on allometric relationships between body weight and metabolic rate (White & Seymour, 2005). We transformed densities of killed ungulates to equivalents of basal metabolic rates (hereafter "BMR equivalents") using the following masses for each species: roe deer (23 kg), red deer (130 kg) and wild boar (80 kg). We also summed the BMR equivalents by functional guild: herbivore – roe and red deer – or omnivore – wild boar. Even though these hunting statistics are a coarse indirect indicator of ungulate pressure, they are spatially homogeneous and can be used to reveal differences in ungulate species abundances and guilds among sites at the national scale (Melis, Nilsen, Panzacchi, Linnell, & Odden, 2013). We calculated the Spearman rank correlations, for the 2005 campaign, between plot BMR equivalents and the differences between enclosure and control plot species richness, cover index for each vegetation layer and percentage of bare soil.

All statistical analyses were performed in R (version 3.4.0; R Core Team 2017) with the packages LME4 (functions lmer and glmer for LMM and GLMM respectively) and multcomp for contrast tests (function glht).

3 | RESULTS

We observed 761 plant species during the study period. Among the 645 species observed in the herbaceous layer, a higher number was found on control plots (presence of ungulates) than on enclosure plots (absence of ungulates): 593 and 544 species respectively (difference significant according to a chi-square test: $\chi^2 = 17.1$, $p < .001$). Conversely, for the low shrub layer, a higher number of species was found inside the enclosures: 118 versus 105 among a total of 123 species (chi-square test: $\chi^2 = 6.9$, $p < .01$). All vegetation layers pooled, the number of species occurring only inside enclosures (67 species out of 665) was lower than the number of species occurring only outside (96 species out of 694) (chi-square test, $\chi^2 = 4.2$, $n = 163$, $p < .05$). All the species found inside or outside only were rare (less than five occurrences for the three sampling periods and all study plots combined).

3.1 | Species richness

Total plant species richness at the subplot level (100 m²) was strongly affected by fencing and revealed opposite patterns among vegetation layers (Figure 2 and Table S5). No effect was observed for bryophytes (Table 1). For both the low and high shrub layers, species richness increased over time both inside and outside

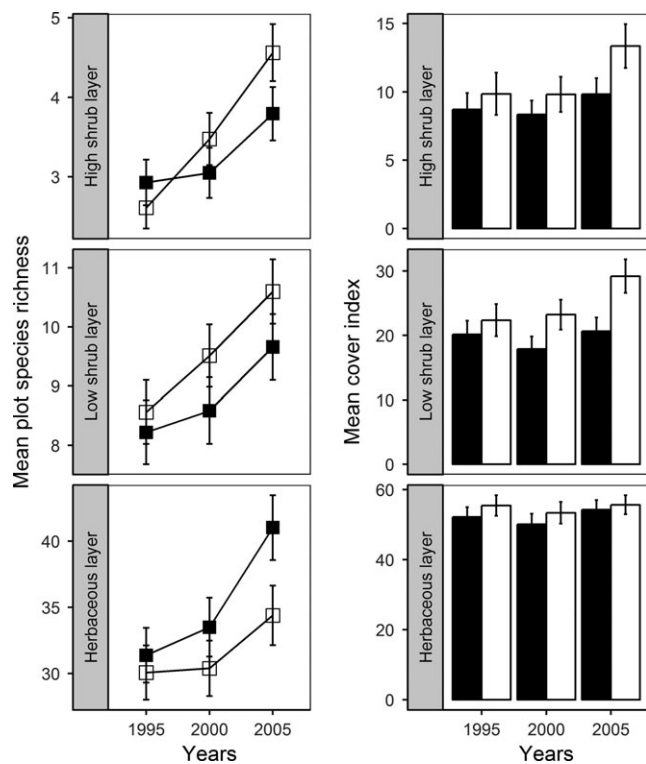


FIGURE 2 Mean species richness and cover index of high shrub (2–7 m), low shrub (0.3–2 m) and herbaceous (<0.3 m) layers in enclosure and control plots at the three sampling dates: 1995 (year of enclosure establishment), 2000 (5 years after ungulate exclusion) and 2005 (10 years after). Error bars represent the standard error of the mean. Black: control plots. White: enclosure plots

TABLE 1 Effects of fencing on plant species richness by layer and year of observation. Enclosure/Control is the ratio of species richness of enclosure to control, estimated according to a general linear mixed model (see methods). SE is the standard error of the ratio. Adjusted *p*-values: contrast test between control and enclosure species richness, adjusted for multiple comparisons within a layer. Bold: significant test ($p < .05$)

Layer	Year	Enclosure/ Control	SE	Z ratio	Adjusted <i>p</i> -values
High shrubs	1995	0.940	0.06	−0.95	.715
	2000	1.130	0.07	2.11	.101
	2005	1.210	0.06	3.68	<.001
Low shrubs	1995	1.080	0.04	2.08	.108
	2000	1.150	0.04	4.22	<.001
	2005	1.200	0.04	5.88	<.001
Herbaceous layer	1995	0.977	0.02	−1.04	.628
	2000	0.933	0.02	−3.13	<.001
	2005	0.858	0.02	−7.32	<.001
Bryophytes	1995	0.986	0.03	−0.39	.972
	2000	1.010	0.03	0.38	.974
	2005	0.997	0.03	−0.11	.999

enclosures, but the increase was greater inside enclosure plots than on the unfenced control plots (Figure 2). After 10 years of fencing, for the low and high shrub layers respectively, there were 20% and 21% more species in enclosures compared to control plots (Table 1). No changes were observed for the tree layer. For the herbaceous layer, species richness also increased over time but the greatest increase occurred on the control plots, not in the enclosures. Although there was no difference initially, after 10 years of fencing there were 14% fewer herbaceous species in enclosures than on control plots (Figure 2 and Table 1).

3.2 | Vegetation cover

Ungulate exclusion affected the cover of herbaceous and shrub layers differently than it did species richness. As for species richness, we found a significant effect of the interaction between time and fencing on both low and high shrub layers ($p < .05$ and $p < .001$ respectively, see Table S5). For both these layers, the overall pattern was an increase in cover over time with a more marked increase inside enclosure than outside (Figure 2). While there was initially no significant difference, low shrub cover was significantly higher inside 5 years after fencing, though high shrub cover was not. Ten years after fencing, both low and high shrub cover were significantly higher inside the enclosure plots (Table 2). Herbaceous layer cover index also increased significantly over time in control plots ($p < .001$, Table S5) but, contrasting with low and high shrub layers, it was initially significantly higher in enclosure than in control plots (Figure 2). Between 2000 and 2005 this difference decreased and was no longer significant in 2005 (Table 2). No effects were observed for the tree layer or the bryophytes.

TABLE 2 Effects of fencing on vegetation cover by layer and year of observation. Enclosure-control is the estimate of the difference between enclosure and control cover indices (arcsine square root transformed). These contrasts were calculated according to a general linear mixed model (see methods). SE is the standard error of the contrast. Adjusted *p*-values: contrast test of the difference between enclosure and control cover index, adjusted for multiple comparisons within a layer. Bold: significant test ($p < .05$)

Layer	Year	Enclosure-Control	SE	t Ratio	Corrected <i>p</i> -values
High shrubs	1995	0.011	0.012	0.904	.737
	2000	0.026	0.012	2.178	.084
	2005	0.052	0.012	4.361	<.001
Low shrubs	1995	0.030	0.014	2.063	.0589
	2000	0.076	0.014	5.305	<.001
	2005	0.12	0.014	8.072	<.001
Herbaceous layer	1995	0.040	0.012	3.142	.005
	2000	0.039	0.012	3.094	.006
	2005	0.015	0.012	1.175	.555
Bryophytes	1995	0.023	0.012	1.921	.154
	2000	0.016	0.012	0.321	.456
	2005	0.023	0.012	2.911	.157

3.3 | Effects on composition of the herbaceous layer

For almost all Ellenberg indicators (light, temperature, soil moisture, pH and nitrogen), mean values were similar between enclosure and control plots in 1995 and 2000 (Tables S6 and S7). In 2005, mean indicator values for light were significantly higher outside than inside the enclosures (Figure 3). This change was due to both a decrease in shade tolerant species and an increase in light-demanding species outside enclosures whereas the balance between these two groups did not change inside the fences. In 2005, mean indicator value for nitrogen was marginally higher outside the fences ($p = .05$). In 1995, life form types were not different between enclosure and control plots. In 2000 and 2005, the number of hemicryptophyte species was significantly (respectively $p < .05$ and $p < .001$) higher outside the enclosures than inside (Figure 3, Tables S6 and S7). The number of therophyte species was also higher outside than inside the enclosures in 2005 ($p < .05$, Figure 3). When grouped together, the proportion of annual or biennial species was significantly higher outside than inside the enclosures ($p < .01$, Table S6). Dispersal modes of the species were similar between enclosure and control plots in 1995. In 2005, the number of anemochorous, barochorous and epizoochorous species were higher outside the enclosures ($p < .001$ for both). Regarding Grime strategies, plant communities became more ruderal outside the enclosures from 2000 to 2005 (Figure 3, Tables S6 and S7, $p < .05$ both in 2000 and 2005). In 2005, the mean hemeroby index also tended to be higher for plant communities outside than inside the enclosures (difference marginally significant, $p = .059$). The number of non-forest specialist species was

initially similar between outside and inside enclosures, became significantly higher outside the enclosures in 2000 ($p < .05$) and this difference increased by 2005 ($p < .001$). The number of forest-specialist species did not change in the first 5 years between enclosure and control plots (1995–2000), and became marginally higher outside the enclosure in 2005 (Figure 3, Tables S6 and S7).

3.4 | Effects of variations in ungulate abundance among sites

At the lowest red and roe deer population abundances (index <10), we did not detect any difference in species richness for herbaceous and high shrub layer between inside and outside enclosures (Figure 4a), whereas higher population abundances correlated with richer herbaceous and poorer high shrub layers outside enclosure plots. This effect was more pronounced when red and roe deer populations were combined (Table 3). The difference in low shrub species richness between enclosures and control plots showed no correlation with any ungulate population density index (Table 3). Wild boar densities had no effect on species richness for any vegetation layer.

Low and high shrub covers were similar inside and outside enclosures at the lowest deer abundances, while higher abundances were related to sparser shrub layer in control plots (Figure 4b). The difference in proportion of bare soil between enclosure and control plots was negatively correlated with wild boar density (Table 3). At the lowest wild boar population densities (index <10), there was no difference in the proportion of bare soil between enclosures and control plots, whereas at higher population densities, bare soil developed outside the enclosures (Figure 4c).

4 | DISCUSSION

4.1 | Deer browsing moderates the development of the shrub layer which reverberates on the herbaceous layer

Excluding ungulates for 10 years resulted in higher cover and species richness of low and high shrub layers inside the enclosure. The increasing species richness of the shrub layers inside enclosures, relative to outside, suggests that deer browsing limits the growth of woody and semi-woody species, thus slowing their recruitment in higher layers (Kuijper et al., 2010; Murray, Webster, Jenkins, Saunders, & Haulton, 2016; Tanentzap et al., 2009). Our results also indicated a delayed response of the two shrub layers, the effect of enclosure on both vegetation cover and species richness being significant after 5 years for the low shrub layer, then after 10 years for the high shrub layer. Inside the enclosures, this indicates a rapid initiation of recovery of the low shrub layer, later propagating to the high shrub layer.

Within the herbaceous layer, plant communities inside and outside showed a clear divergence over 10 years that resulted in higher species richness to the benefit of light-demanding species outside the enclosures. Indeed, light availability, through solar radiation and

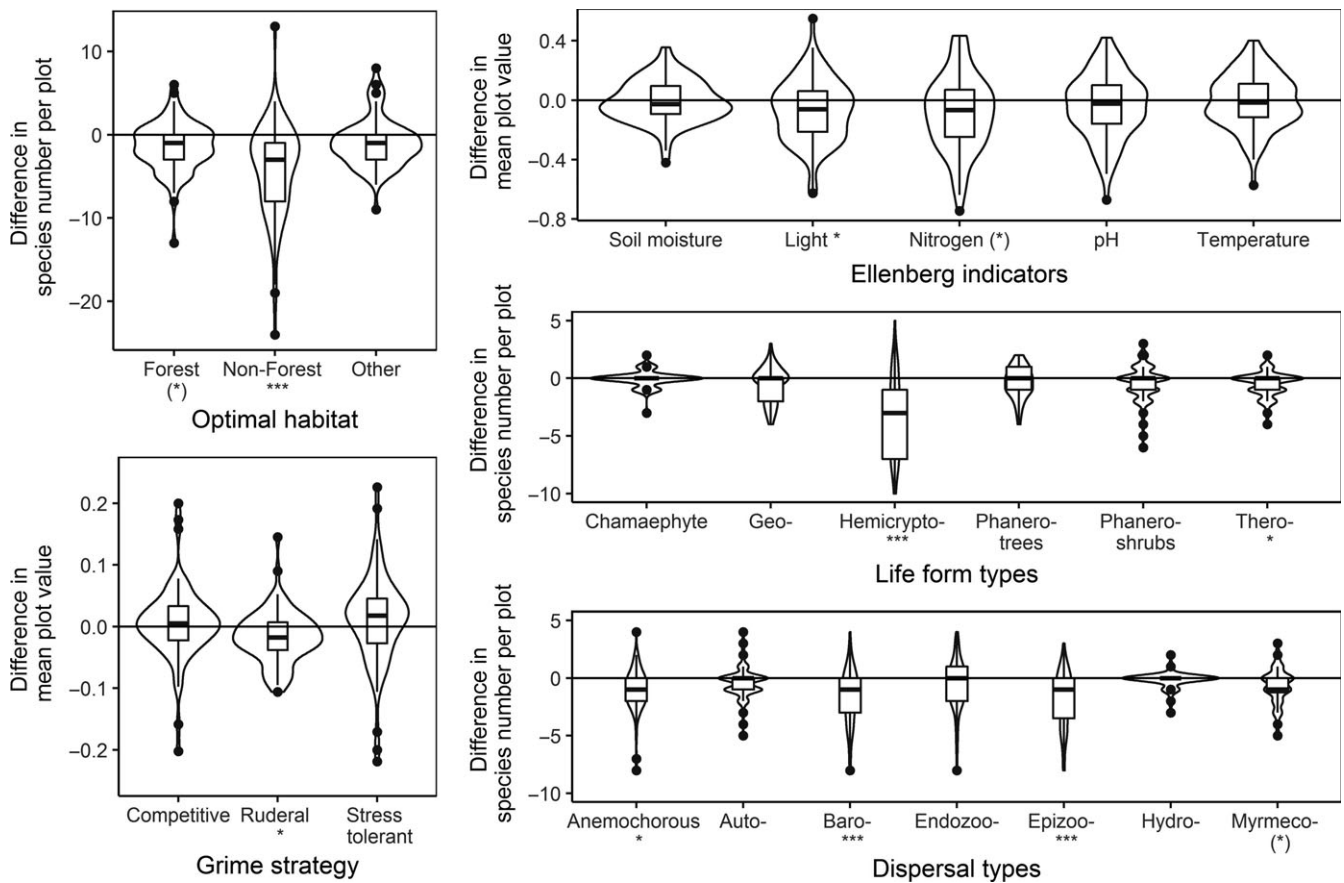


FIGURE 3 Boxplots and distribution of the differences (exclosure – control) in 2005 in mean Ellenberg values, mean Grime strategy indices, number of species per life form type, dispersal type and optimal habitat

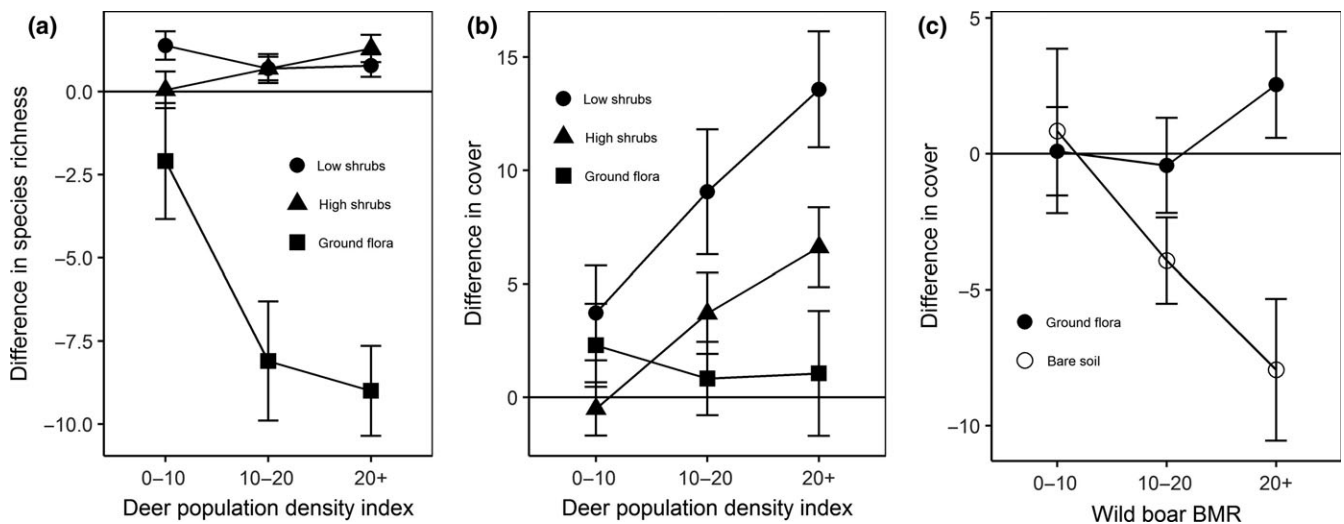


FIGURE 4 Differences between paired exclosure-control plots (inside minus outside exclosure) after 10 years of ungulate exclusion for species richness (a) and cover (b) of herbaceous layer, low shrubs and high shrubs in relation to indices of deer population densities based on hunting statistics transformed as equivalents of basal metabolic rates of the number of red and roe deer killed per 100 ha. (c) Differences between paired exclosure-control plots (inside minus outside exclosure) after 10 years of ungulate exclusion for cover of herbaceous layer and proportion of bare soil in relation to wild boar BMR

energy provision, is a critical determinant of herb-layer species richness (Borer et al., 2014). Comparing islands with and without deer, Judziwicz and Koch (1993) found that browsing eliminates Canada yew (*Taxus canadensis*), a species that tends to grow so densely that

it prevents the growth of most herbs, and notably native species (Mudrak, Johnson, & Waller, 2009). Browsing decreases the level of competition, particularly for light, imposed by shrubs on herbaceous species, and thus indirectly favours light-demanding species within

		BMR wild boar (omnivore)		BMR roe deer		BMR red deer		BMR herbivores	
		ρ	<i>p</i> -Value	ρ	<i>p</i> -Value	ρ	<i>p</i> -Value	ρ	<i>p</i> -Value
Species richness	High shrubs	0.058	.608	0.066	.564	0.142	.202	0.222	.048
	Low shrubs	0.167	.141	−0.043	.702	−0.087	.436	−0.165	.143
	Herbaceous	−0.029	.801	−0.241	.031	−0.101	.367	−0.311	<.01
Cover	High shrubs	0.006	.958	0.174	.122	0.120	.284	0.278	.012
	Low shrubs	0.245	.030	0.309	.005	0.076	.499	0.319	.039
	Herbaceous	0.165	.146	−0.247	.027	0.139	.212	−0.035	.760
Percentage of bare soil		−0.212	.064	0.144	.208	0.028	.808	0.069	.551

TABLE 3 Spearman's rank correlations between the differences in species richness and cover (inside minus outside the enclosure) in 2005, according to the vegetation layers (in lines) and indices of ungulate densities (basal metabolic rate, in columns). Bold: significant test ($p < .05$). Italics: marginally significant test ($p < .1$).

the herbaceous layer. The number of hemicryptophyte species also strongly increased outside the enclosures. In these species, buds are protected from herbivores by their location close to the ground. This life form could provide them a competitive advantage over plants with aerial buds more accessible to deer. Our results from a large geographical scale monitoring network extend previous local observations (Hegland et al., 2013) and experimental findings (Royo et al., 2010). They provide an example of indirect facilitation (Levine, 1999) of herbaceous layer species by deer through the suppression of shrub competitors and support the competitive hierarchy model in forest plant communities (Ewald, 2008; Shipley & Keddy, 1994).

These ungulate-induced modifications of plant-plant interactions may involve particular species, namely by reducing the dominance of palatable species with high competitive abilities and, in turn, enhancing plant species richness (Nishizawa, Tatsumi, Kitagawa, & Mori, 2016). Among the recovering plant species, bramble (*Rubus fruticosus agg.*) showed by far the strongest and widest recovery inside enclosures, in both the low shrub and herbaceous layers (Supplementary material S8). It is striking that deer emerged as a moderator for the plant cover of this species group, not only in other parts of Europe (Kirby & Thomas, 2000; Perrin, Mitchell, & Kelly, 2011), but also for *Rubus* spp. species in the United States (Faison et al., 2016; Horsley, Stout, & deCalesta, 2003; Murray et al., 2016; Royo et al., 2010). Experimental results by Van Uytvanck and Hoffmann (2009) showed that dense thickets of *R. fruticosus agg.* had a negative impact on the performance of certain plant species of the herbaceous layer due to the competition for light. The global trends we report here show that *Rubus* spp. plays a key role in forest ecosystems, mediating the interaction between deer and vegetation.

4.2 | Enclosure effects increase with ungulate abundances

Beyond a binary comparison of vegetation trajectories with and without ungulates, our results provide evidence for gradual effects of ungulate abundances on forest vegetation. Indeed, the extreme contrast created in enclosure experiments is often pointed as a major shortcoming (Waller, 2014). At the national scale, we showed that

the effects of fencing on forest vegetation increased with roe deer abundance inferred from hunting statistics; enhanced correlations when adding red deer populations indicate an additive effect of the two ungulates as reported experimentally by Faison et al. (2016). The increase in the percent cover of bare soil with wild boar density, along with the progression of therophyte species outside enclosures, suggests that soil disturbance might be another cause for the increasing herbaceous species richness outside the enclosure. Soil micro-disturbances due to trampling and rooting offer space and modify environmental conditions, favouring the colonization by new species or the recruitment from the soil seed bank (Bueno, Reiné, Alados, & Gómez-García, 2011).

The classic grazing response curve, based on the intermediate disturbance hypothesis, predicting an increase in plant species richness from low to moderate browsing pressure, has been already locally documented (Faison et al., 2016; Murray et al., 2016; Nishizawa et al., 2016; Perrin et al., 2011). After 10 years of fencing, the lower species richness of the herbaceous layer inside the enclosures of our 82-site network, along with the gradual response to deer abundances provide a large-scale support for this grazing curve. However, it has to be refined according to vegetation layers and life forms. Along the gradient of deer abundance, we observed that deer deplete both the cover and species richness of the shrub layers as in most previous studies, although some others report positive effects of deer browsing on woody species and shrub layers (Faison et al., 2016). This advocates for the segregation of the vegetation layers in the analysis of deer effects on forest understory. The humped-back shape of the grazing curve is likely to be similar but the position of the tipping point will fluctuate according to the vegetation layer. The level of disturbance corresponding to the maximum species richness should be lower for shrub layers and woody species than for ground flora.

4.3 | An increase in species richness among all vegetation layers

Over 10 years of monitoring of forest vegetation, we observed a constant increase in species richness, at the plot level, among all vegetation layers. This contrasts with the conclusions of several

meta-analyses which revealed no net change in local scale plant species richness, especially in Europe and within forest habitats (Bernhardt-Römermann et al., 2015; Vellend et al., 2013; Verheyen et al., 2012). The quality assurance programme associated with the Renecofor network shed light on the sensitivity of plant censuses to observer effects (Archaux et al., 2009). The resampling of the plots by the same teams of observers, having previous relevés at their disposal, may have induced a training effect, increasing the probability of observing new species, and decreasing the over-looking rate. This training effect might have caused the conspicuous increase in species richness, but is not likely to have induced any bias regarding the comparisons between paired samples, inside and outside enclosure plots, conducted on the same day by the same team.

4.4 | Beyond increasing species richness: shifts in species composition

Plant species richness is a common indicator of plant diversity. Its analysis is, therefore, meaningful for understanding the mechanisms underlying species coexistence but compositional shifts are of greater ecological significance (Noss, 1990). Indeed, plant species richness is clearly increasing with management-related disturbances and is not a suitable indicator for the conservation status of the forests (Boch et al., 2013). Since our national scale monitoring network covers a wide diversity of ecological contexts, the composition of plant communities was highly variable so that the identification of winner and loser species is likely to be biased towards generalist species due to a low redundancy between plant communities (see Supplementary material S8). Thus, species traits appeared more appropriate to investigate the response of plant communities (Rooney & Waller, 2003). Our trait-based analyses revealed divergences in species composition between enclosure and control plots. The increasing number of epizoochorous species outside the enclosures confirms the role of deer and wild boar as dispersal agents for such plant species, locally enriching plant communities through increasing species immigration (Albert et al., 2015; Heinken & Raudnitschka, 2002). Even though Heinken, Lees, Raudnitschka, and Runge (2001) showed that roe deer and wild boar could play a significant and underestimated role in the dispersal of bryophytes, or Chollet, Baltzinger, Saout, and Martin (2013) identified indirect and positive effects of deer on bryophytes, mediated through reduced competition with vascular plants, we did not detect any significant response in bryophyte overall species richness or abundance.

The conservation issues associated with deer in forests are usually related to the depletion of the overall vegetation in overabundance contexts (Côté et al., 2004) and the cascading effects on other groups of species (Martin et al., 2010), to their ability to facilitate exotic species establishment (Shen, Bourg, McShea, & Turner, 2016; Wiegmann & Waller, 2006) or to biotic homogenization to the benefit of browse-tolerant species and detriment of browse-intolerant species (Rooney, 2009). From a conservation point of view, the most salient results in our study are the increasing indices of ruderality and hemeroby, and the increasing number of non-forest species outside

the enclosures, where ungulates are present. Ungulates maintain conditions that are favourable to non-forest species, that is higher levels of light and nitrogen, and soil disturbance by trampling or rooting. Moreover, they are known to disperse non-forest species more than forest species (Picard & Baltzinger, 2012). Thereby, ungulates tend to homogenize plant communities between forest and non-forest habitats by favouring the immigration of non-forest species within forest habitats. Nevertheless, it was not accompanied by a decrease in forest-specialist species richness.

Over a large monitoring network, covering a broad range of temperate forest ecosystems, we observed that the presence of wild ungulates enhanced species richness of the herbaceous layer. In line with Sabo, Frerker, Waller, and Kruger (2017), our results show that ungulate impacts on forest understory vegetation are a consequence of their effects on environmental factors but also bring to light their critical role on plant species dispersal and plant-plant interactions. More specifically, by reducing the cover of shrub layers and dominant and palatable plant species, deer maintain an openness that enhances ground flora diversity. Thus, according to the intermediate disturbance hypothesis, current levels of population densities, managed to limit damages to forest regeneration, would be considered below the detrimental level for species richness. However, this high species richness is maintained at the expense of the peculiarity of forest plant communities: ungulates promote ruderal and non-forest species. Hence, even in contexts where ungulates are maintained at intermediate densities, with no negative effect on total plant species richness, they are still a biodiversity management issue because they strongly affect the composition of communities.

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ORCID

Vincent Boulanger  <http://orcid.org/0000-0001-6103-5029>

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SUPPORTING INFORMATION

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