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ARTICLE

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Effects of stand structure and ungulates on understory vegetation in managed and unmanaged forests

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Abstract

Conventional conservation policies in Europe notably rely on the passive restoration of natural forest dynamics by setting aside forest areas to preserve forest biodiversity. However, since forest reserves cover only a small proportion of the territory, conservation policies also require complementary conservation efforts in managed forests in order to achieve the biodiversity targets set up in the Convention on Biological Diversity. Conservation measures also raise the question of large herbivore management in and around set-asides, particularly regarding their impact on understory vegetation. Although many studies have separately analyzed the effects of forest management, management abandonment, and ungulate pressure on forest biodiversity, their joint effects have rarely been studied in a correlative framework. We studied 212 plots located in 15 strict forest reserves paired with adjacent managed forests in European France. We applied structural equation models to test the effects of management abandonment, stand structure, and ungulate pressure on the abundance, species richness, and diversity of herbaceous vascular plants and terricolous bryophytes. We showed that stand structure indices and plot-level browsing pressure had direct and opposite effects on herbaceous vascular plant species diversity; these effects were linked with the light tolerance of the different species groups. Increasing canopy cover had an overall negative effect on herbaceous vascular plant abundance and species diversity. The effect was two to three times greater in magnitude than the positive effects of browsing pressure on herbaceous plants diversity. On the other hand, a high stand density index had a positive effect on the species richness and diversity of bryophytes, while browsing had no effect. Forest management abandonment had few direct effects on understory plant communities, and mainly indirectly affected herbaceous vascular plant and bryophyte abundance and species richness and diversity through changes in vertical stand structure. Our results show that conservation biologists should rely on foresters and hunters to lead the preservation of understory vegetation communities in managed forests since,

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respectively, they manipulate stand structure and regulate ungulate pressure. Their management actions should be adapted to the taxa at stake, since bryophytes and vascular plants respond differently to stand and ungulate factors.

KEYWORDS
biodiversity, bryophytes, *Capreolus capreolus*, *Cervus elaphus*, conservation, large herbivores, old-growth forest, rewilding, set-aside, *Sus scrofa*, vascular plants

INTRODUCTION

In Europe, past and present forest management, harvesting, and deforestation have reduced the forest ecosystems undisturbed by human activities to a mere 2.4% of the surface area (Forest Europe, 2020), with primary forests accounting for <1% of the forested area (Sabatini et al., 2018). These unmanaged forests host rare and endangered forest specialists and consequently constitute crucial reservoirs for the preservation of forest biodiversity (Parviainen et al., 2000). Primary forest attributes can be restored by setting aside previously managed forests in so-called "strict forest reserves" (Parviainen et al., 2000). These conservation measures rely on ecological succession to restore the structural and functional complexity of forest stands and landscapes by allowing natural disturbance dynamics to occur; they are an example of passive rewilding (Perino et al., 2019). However, strict reserves alone are not sufficient to maintain the biodiversity and natural dynamics of European forests. Alternative integrated measures are needed to at least partially restore primary-forest structural and functional attributes in managed forests (Bollmann & Braunisch, 2013).

Compared to managed forests, unmanaged forests show higher amounts of lying and standing deadwood (Christensen et al., 2005) and large living trees (Paillet et al., 2015), and have a more complex spatial arrangement of these attributes (Burrascano et al., 2013), especially when they reach the old-growth stage. Unmanaged forests also have greater structural heterogeneity from small to large spatial scales (Podlaski et al., 2019; Stiers et al., 2018), which determines microclimate (Ehbrecht et al., 2017) and the availability of resources such as light, atmospheric moisture, and soil nutrients (Merino et al., 2008). These, in turn, modify the abundance, richness, and composition of vascular plants and terricolous bryophytes (Tinya et al., 2009; Virtanen et al., 2000). While some studies have documented lower levels of understory vascular plant species richness (Burrascano et al., 2008; Horvat, Biurrun, et al., 2017; Paillet et al., 2010) and terricolous bryophytes (Müller et al., 2019; Tullus et al., 2018) in unmanaged forests compared to managed forests in Europe, the response may vary according to the taxa studied (Paillet et al., 2010). Within a given taxon, these effects may also vary with ecological group (e.g., light-demanding vs. shade-tolerant species) due to differences in sensitivity to light or microclimate. For example, although considered to be forest species, only a limited number of shade-tolerant species persist and grow under closed dense canopies, while many more intermediate and light-demanding species, considered to be open-habitat specialist species, survive under open canopies with sparse trees (Barbier et al., 2008; Sabatini et al., 2014).

In temperate forests, large wild ungulates play a major role in ecosystem functions, dynamics, and structure, depending on their local densities (Bernes et al., 2018). Ungulates consume plants (grazing, browsing, and fruit feeding) and contribute to the dispersal of numerous species (epi- and endozoochory; Baltzinger et al., 2019), thereby directly affecting the abundance, composition, and richness of forest community assemblages from local to regional levels (Tanentzap et al., 2009; Tremblay et al., 2007). At the stand level and at intermediate densities, browsing by wild ungulates decreases the abundance and richness of palatable young trees and shrubs to the benefit of the abundance and richness of the herbaceous plants (Boulanger et al., 2018). However, high densities of ungulates generally lead to impoverished understory vegetation composed of only a few browsing-tolerant species (Nuttle et al., 2014). In extreme cases, heavy browsing could even shift the understory toward a diverse cover of terricolous bryophytes, which are unpalatable to large herbivores, and could flourish after the competitive vascular-plant field layer has been overbrowsed (Chollet et al., 2013).

Natural ungulate–plant interactions are altered in ecosystems influenced by human activities (e.g., wood harvesting, nature tourism, and hunting), which simultaneously affect ungulate population abundance and individual behavior (Faeth et al., 2005). Forest management and ungulate pressure are therefore interactive disturbances (Buma, 2015; Kleinman et al., 2019; Meier et al., 2017). By modifying understory vegetation, forest management alters ungulates' food resources and may cause subsequent changes in browsing pressure. For

example, Kuijper et al. (2009) found that ungulates respond positively to food resource availability and preferentially feed in forest gaps (<0.3 ha) rather than in a closed forest. In addition, forest management modifies the tolerance of regeneration seedlings to damage by ungulates (Reimoser, 2003). Indeed, some silvicultural techniques, such as clear cutting, would be more attractive to ungulates (Reimoser & Gossow, 1996), but their relative damage depends on both the amount of forage being produced and competition (Stokely & Betts, 2019). In more light-limiting environments, the effects on the understory can be much more dramatic, since browsing outweighs understory production (Royo et al., 2010). Habitat composition at the landscape scale affects the daily spatial occupation of shelter areas, potentially leading to uneven browsing pressure on understory vegetation (Godvik et al., 2009). However, these cascading effects involving forest conservation measures, stand structure, and ungulate populations have, to our knowledge, rarely been tested within a single correlative framework.

In this study, we compared 212 plots in 15 strict forest reserves and matched them with adjacent managed forests (Figure 1; Paillet et al., 2015) to simultaneously test the cascading effects of management abandonment (set-asides) and ungulate pressure (browsing) on understory vegetation (vascular herbaceous plants and terricolous bryophytes). We applied structural equation modeling analyses to answer the following questions (Figure 3): (1) How do forest management and ungulate pressure modify understory plant diversity? (2) Do these effects vary with taxa or ecological groups, especially in terms of light affinity? And (3) are these effects direct or mediated by stand structure? We hypothesized that the most important disturbance effect would be due to forest management, which modifies stand structure, as measured by the stand density index (SDI) and forest cover.

MATERIALS AND METHODS

Study area

We compared plots in 15 strict forest reserves distributed across France with matched adjacent managed plots with the same site conditions (Paillet et al., 2015; Figure 1). Generally speaking, in managed French forests, management types roughly correspond to harvesting recommendations, which, though they vary locally, can be summarized as follows: tree selection and felling occur generally every 5–10 years in the lowlands, and every 10–20 years in the mountains.

We restricted our study to native lowland oak–beech–hornbeam forests (*Quercus robur* L. and *Q. petraea* [Mattus.] Liebl., *Fagus sylvatica* L., and *Carpinus betulus* L., elevation ≤800 m) and mountain beech–fir–spruce forests (*Fagus sylvatica* L., *Abies alba* Mill., and *Picea abies* [L.] Karst., elevation >800 m; Figure 1). In lowlands, forests sites corresponded to a mix of acidophilous oakwood, oak–birch forest, pedunculated oak–hornbeam forest, sessile oak–hornbeam forest according to European forest types (EEA, 2006) for oak forests and Atlantic and sub-Atlantic lowland beech forest, more rarely, subalpine and mountainous spruce and mountainous mixed spruce–silver-fir forest, for beech forests (EEA, 2006). In mountains, forests sites corresponded to southwestern European mountainous beech forest according to European forest type (EEA, 2006) for beech forests and subalpine and mountainous spruce and mountainous mixed spruce–silver-fir according to European forest type for coniferous forests (EEA, 2006). All planted forests were excluded from the sampling.

At each of the 15 study sites, sampling locations were randomly preselected on a regular 100 × 100 m grid, then plots were selected according to site conditions observed in the field, as follows: edaphic conditions (soil texture, depth, hydromorphy, and reaction to HCl) and topography (elevation, aspect, and slope) were checked so that each plot within the forest reserve had a paired managed equivalent outside the reserve (Figure 2). The managed plots were selected within 5 km of the forest reserve boundaries and in stands composed exclusively of native tree species of the same forest type (oak–beech–hornbeam in lowlands, beech–fir–spruce in mountains). The majority of the plots were located in adult forests. Due to field constraints and posterior plot selection, the final sample comprised a total of 212 plots and was not fully balanced (Table 1).

For 196 out of the 212 study plots, the time since last harvesting was recorded from management plans or wood sales data. Stand age was generally not available. The mean time since last harvesting for the strict forest reserves was 48 years (46 ± 42 years in lowlands, and 50 ± 38 years in mountains; mean ± SD) and 9 years (7 ± 5 years in lowlands and 12 ± 10 years in mountains) for the managed forests. Twenty-five plots in the strict forest reserves had experienced harvesting during the last 20 years before designation, while five plots in the managed forests had not been harvested for more than 20 years. The mean surface area of strict forest reserves was 678 ± 792 ha (range 39–2636 ha). All but three plots were located in or within 30 m of ancient forests.

Silvicultural treatments were also recorded even though they were strongly biased by elevation: 78% of the

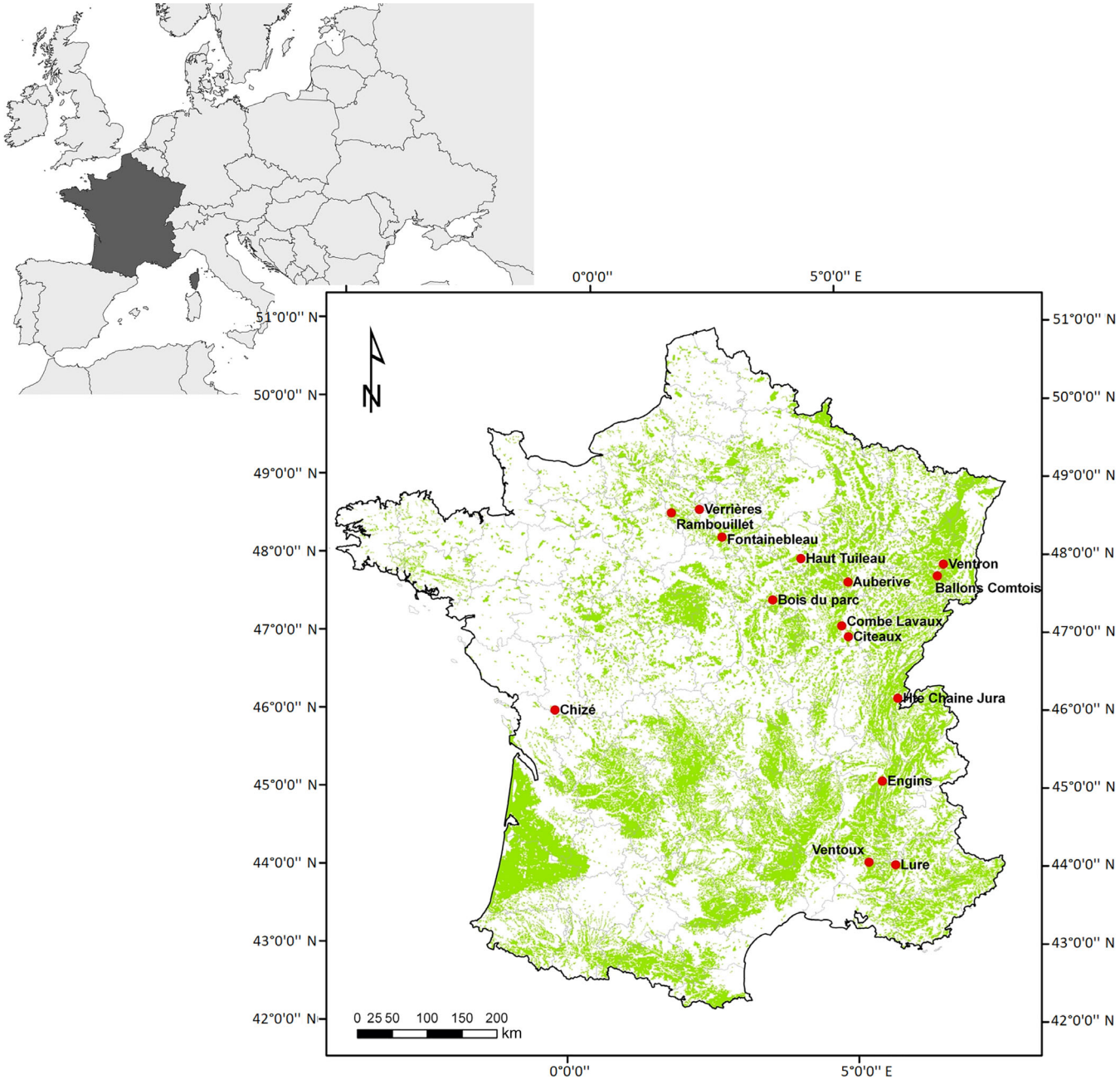


FIGURE 1 Location of the study sites

uneven-aged forests (continuous cover) were located in the mountain beech–fir–spruce forests whereas all the even-aged high forests (selective cutting followed by natural regeneration and final cut) were located in the lowland oak–beech–hornbeam-dominated forests. No other type of management (e.g., grazing by domestic animals) occurred on the plots. Furthermore, specific information about past harvesting operations, in both the protected and unprotected forests, was very scarce and heterogeneous. Consequently, we did not address silvicultural treatments or past harvesting intensity in our analyses but rather focused on forest-structure effects.

At most of the sites in both the strict forest reserves and in the surrounding managed forests, wild ungulates are hunted without strong differences in hunting methods; this is the case in many protected areas in Europe (van Beeck Calkoen et al., 2020). Most are driven hunts with hound packs and hunters located at the borders of the reserves or on internal tracks. Individual hunting occurs occasionally. Hunting pressure levels were available at the municipality

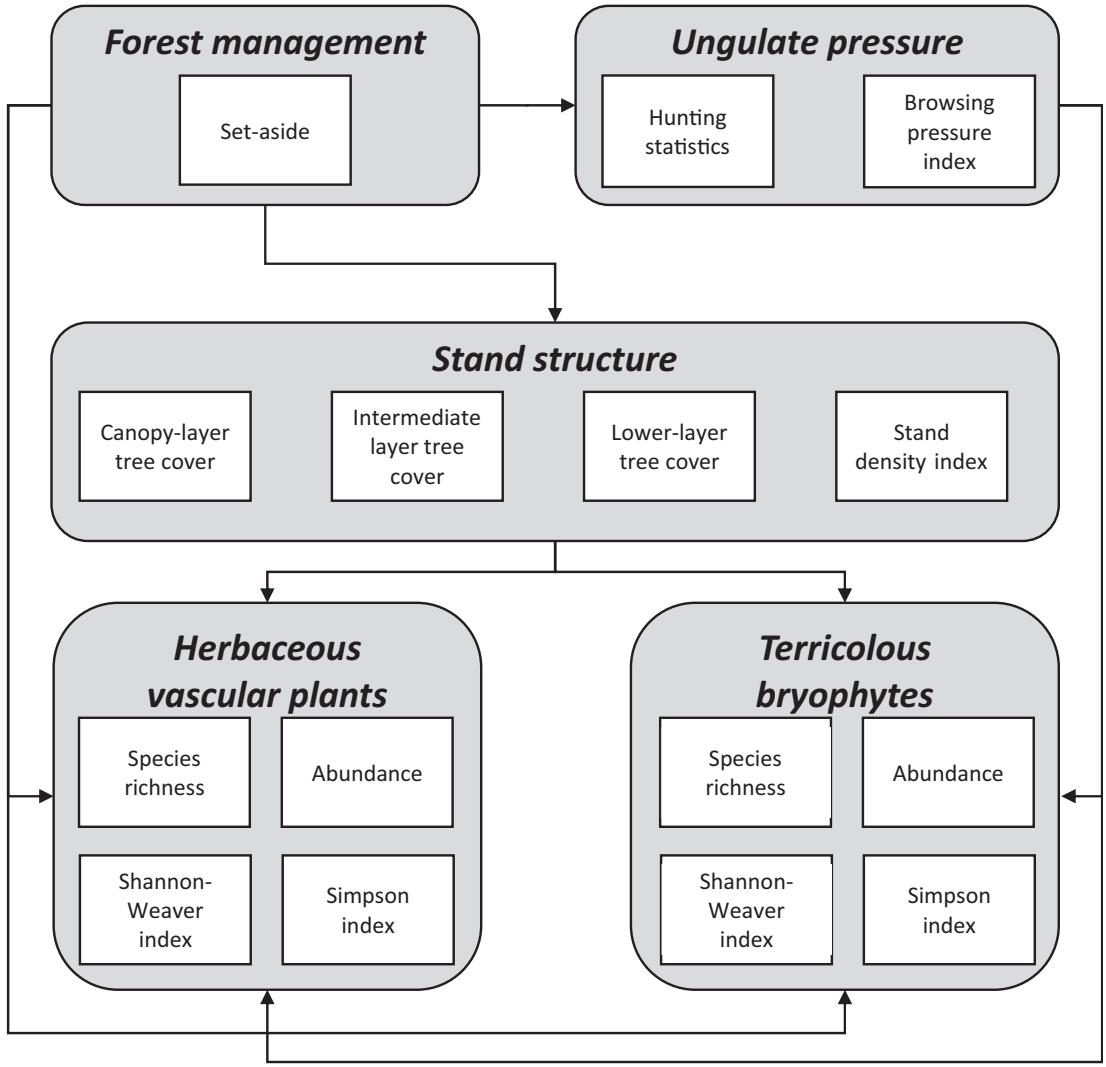


FIGURE 2 Simplified hypothesis diagram (Metamodel)

and management-unit scales, but not at the site scale; see the "*Hunting statistics*" section.

Stand-structure description

Based on a stand-structure description (Paillet et al., 2015), we calculated the SDI as a competition index between trees at the plot level defined as

$$\mathrm{SDI} = N \times \left(\frac{\mathrm{QMD}}{25.4}\right)^{1.605}$$

where N is the number of trees per hectare (density) and QMD is the quadratic mean diameter. This index is a relative measure of stand density and can be used as a measure of stocking density (Reineke, 1933). During data exploration, we found that basal area and SDI correlated positively; we therefore only used SDI in subsequent analyses since SDI integrates both stand density and tree size.

Finally, botanists visually assessed the tree cover (%) at each plot, with each time a moderator to limit observer effect. Tree cover is then analyzed in three different vertical layers: canopy (height > 16 m), intermediate (8 m < height < 16 m), and lower (2 m < height < 8 m) tree layers.

Ungulate pressure

Browsing pressure (plot level)

We used the modified Aldous method to assess browsing pressure (Morellet & Guibert, 1999). On each study plot, we recorded food resource availability and utilization on

TABLE 1 Summary statistics for study site plots in managed forests (MAN) and strict reserves (UNM)

	No. plots		ALT (m)		BA (m^2)		SDI (no./ha)		B (%)		BMR	Richness		Shannon	
Site	MAN	UNM	MAN	UNM	MAN	UNM	MAN	UNM	MAN	UNM	(kg)	MAN	UNM	MAN	UNM
Vascular plants															
Auberive	12	12	453 ± 30	451 ± 17	18 ± 4	18 ± 8	374 ± 79	382 ± 182	7 ± 2.3	9.4 ± 4.1	109	21.6 ± 9.6	25.4 ± 8.8	2.69 ± 0.5	2.98 ± 0.32
Ballons Comtois	8	8	1025 ± 40	1002 ± 77	30 ± 10	35 ± 13	512 ± 177	620 ± 248	10.5 ± 7.1	14.8 ± 9.1	34	12.6 ± 5	17.1 ± 6.8	2.27 ± 0.43	2.55 ± 0.52
Bois du Parc	5	5	210 ± 13	152 ± 6	20 ± 6	28 ± 2	472 ± 154	673 ± 70	5.5 ± 1.8	9.5 ± 1.9	38	14.6 ± 3.4	24.6 ± 4.2	2.44 ± 0.31	3.03 ± 0.14
Chizé	12	12	82 ± 11	76 ± 10	19 ± 10	19 ± 7	435 ± 217	445 ± 166	5.7 ± 2.8	13.6 ± 8.3	7	20.8 ± 5.1	23.8 ± 7.3	2.81 ± 0.26	2.89 ± 0.36
Citeaux	6	6	229 ± 9	237 ± 8	31 ± 4	37 ± 12	598 ± 121	603 ± 181	6.2 ± 2.1	7.4 ± 3.9	54	16.2 ± 8	13.7 ± 4.6	2.47 ± 0.74	2.45 ± 0.38
Combe-Lavaux	4	4	441 ± 61	421 ± 80	23 ± 5	21 ± 6	480 ± 82	425 ± 68	9.1 ± 5.9	2.2 ± 1.5	80	18.3 ± 18.9	14.5 ± 10.4	2.37 ± 1.06	2.28 ± 1.03
Engins	5	4	1595 ± 26	1571 ± 42	31 ± 3	37 ± 10	514 ± 78	674 ± 208	11.5 ± 7.5	6.2 ± 4.2	37	59.6 ± 18.4	58 ± 11	3.94 ± 0.3	3.9 ± 0.18
Fontainebleau	16	13	128 ± 15	137 ± 9	18 ± 10	21 ± 6	339 ± 189	395 ± 87	15.1 ± 15.2	13.2 ± 10.2	144	19.9 ± 10.6	16.4 ± 6.7	2.51 ± 0.69	2.4 ± 0.37
Hte-Chaine Jura	8	8	1036 ± 156	1116 ± 196	27 ± 7	30 ± 9	529 ± 97	580 ± 125	6.1 ± 6.5	3.1 ± 2.3	64	33.4 ± 13.9	30.1 ± 14.2	3.31 ± 0.51	3.22 ± 0.47
Haut Tuileau	7	7	164 ± 11	161 ± 5	25 ± 4	28 ± 8	484 ± 81	601 ± 188	17.2 ± 14.4	16.5 ± 9.1	320	21 ± 15	19 ± 8.3	2.64 ± 0.63	2.53 ± 0.84
Lure	4	4	1413 ± 65	1507 ± 56	30 ± 7	39 ± 8	617 ± 139	816 ± 183	9 ± 9.1	7.8 ± 9.7	97	13.3 ± 5.9	17.3 ± 8.2	2.32 ± 0.57	2.64 ± 0.51
Rambouillet	8	8	180 ± 13	158 ± 23	16 ± 7	25 ± 6	269 ± 103	468 ± 161	18 ± 13.7	16 ± 11.6	122	15.6 ± 7.5	14.3 ± 7	2.33 ± 0.59	2.2 ± 0.55
Ventron	4	4	898 ± 20	1007 ± 40	21 ± 5	33 ± 9	417 ± 91	561 ± 122	19.5 ± 8.3	9.3 ± 3	52	35.8 ± 14.7	22 ± 15.9	3.21 ± 0.46	2.71 ± 0.67
Verrières	4	4	171 ± 6	177 ± 1	26 ± 4	26 ± 7	521 ± 56	491 ± 130	21.6 ± 11.2	17.9 ± 5.4	8	16.3 ± 8.1	9.5 ± 4.4	2.45 ± 0.48	2.02 ± 0.51
Ventoux	5	5	1321 ± 52	1352 ± 112	34 ± 9	35 ± 12	713 ± 179	707 ± 227	2.7 ± 3.4	26.8 ± 20.2	99	9.4 ± 3	15 ± 3.8	2.07 ± 0.38	2.62 ± 0.23
Bryophytes															
Auberive	11	11	453 ± 31	452 ± 18	18 ± 4	20 ± 6	371 ± 82	417 ± 143	7 ± 2.4	9.3 ± 4.3	109	21.3 ± 10.1	24.2 ± 8.1	2.66 ± 0.51	2.93 ± 0.29
Ballons Comtois	7	8	1027 ± 43	1002 ± 77	31 ± 10	35 ± 13	536 ± 177	620 ± 248	11.8 ± 6.4	14.8 ± 9.1	34	12.3 ± 5.3	17.1 ± 6.8	2.23 ± 0.44	2.55 ± 0.52
Chizé	12	12	82 ± 11	76 ± 10	19 ± 10	19 ± 7	435 ± 217	445 ± 166	5.7 ± 2.8	13.6 ± 8.3	7	20.8 ± 5.1	23.8 ± 7.3	2.81 ± 0.26	2.89 ± 0.36
Citeaux	6	6	229 ± 9	237 ± 8	31 ± 4	37 ± 12	598 ± 121	603 ± 181	6.2 ± 2.1	7.4 ± 3.9	54	16.2 ± 8	13.7 ± 4.6	2.47 ± 0.74	2.45 ± 0.38
Combe-lavaux	4	4	441 ± 61	421 ± 80	23 ± 5	21 ± 6	480 ± 82	425 ± 68	9.1 ± 5.9	2.2 ± 1.5	80	18.3 ± 18.9	14.5 ± 10.4	2.37 ± 1.06	2.28 ± 1.03
Fontainebleau	14	13	132 ± 11	137 ± 9	17 ± 11	21 ± 6	325 ± 198	395 ± 87	16.9 ± 15.5	13.2 ± 10.2	144	19.5 ± 11	16.4 ± 6.7	2.47 ± 0.72	2.4 ± 0.37
The-Chaine Jura	5	2	1115 ± 58	1280 ± 11	28 ± 8	31 ± 4	534 ± 98	584 ± 105	8.7 ± 7.1	2.4 ± 0.4	64	39 ± 13.1	50 ± 14.1	3.52 ± 0.34	3.81 ± 0.31
Haut-Tuileau	5	7	167 ± 11	161 ± 5	27 ± 3	28 ± 8	492 ± 68	601 ± 188	15.3 ± 12.2	16.5 ± 9.1	320	14.4 ± 6.4	19 ± 8.3	2.4 ± 0.51	2.53 ± 0.84
Rambouillet	8	6	180 ± 13	165 ± 22	16 ± 7	24 ± 6	269 ± 103	438 ± 158	18 ± 13.7	11.1 ± 4.9	122	15.6 ± 7.5	16.5 ± 6.6	2.33 ± 0.59	2.35 ± 0.53
Ventron	4	4	898 ± 20	1007 ± 40	21 ± 5	33 ± 9	417 ± 91	561 ± 122	19.5 ± 8.3	9.3 ± 3	52	35.8 ± 14.7	22 ± 15.9	3.21 ± 0.46	2.71 ± 0.67
Verrières	2	3	170 ± 5	177 ± 0	27 ± 5	23 ± 3	553 ± 32	426 ± 23	19.1 ± 7.7	17.5 ± 6.5	8	22 ± 7.1	10 ± 5.2	2.8 ± 0.36	2.07 ± 0.62

Note: Environmental (ALT, altitude; BA, basal area; SDI, stand density index; B, browsing pressure; BMR, basal metabolic rate index) and response (species richness and Shannon diversity index) variables are mean ± SD values.

three circular subplots (40 m^2 each, maximum vegetation height of 2 m). We excluded herbaceous species because we could not differentiate ungulate browsing from lagomorph browsing. For woody and semi-woody species, we visually estimated plant cover (d_{ij}) and browsing rate (a_{ij}, proportion of shoots consumed by ungulates). We conducted the surveys at the end of the winter, just before the growing season began, to better observe browsing rates. At each subplot, j, plant cover and browsing rate per species, i, were estimated according to six classes (0%–1%, 1%–5%, 5%–20%, 20%–50%, 50%–75%, and 75%–100%). We replaced the class values by their respective class medians for the statistical analyses. We calculated the average plot browsing rate (B_j in %) by weighting the browsing rate for each species on the subplot by its cover index, according to the formula

$$B_j = \frac{\sum_{i=1}^{e} d_{ij} \times a_{ij}}{\sum_{i=1}^{e} d_{ij}}$$

We used the mean value for all three subplots per plot in the subsequent analyses as a proxy for browsing pressure at the plot level.

Hunting statistics (site level)

We used hunting statistics for the ungulate species present at the study sites (provided by Réseau Ongulés Sauvages ONCFS/FNC/FDC, extraction dates 19 April 2018 and 6 January 2020) as a proxy for ungulate population pressure at the site level. Although hunting statistics

are generally considered a poor proxy for local population densities (Pettorelli et al., 2007), they have proven to be a reasonably good approximation for ungulate population densities over large areas (equivalent to the size of our study sites; Ueno et al., 2014). We used data from the hunting seasons occurring on the plots during the study years, or the seasons closest to the study period. Three species of wild ungulates were present at the study sites: red deer (*Cervus elaphus* L.), roe deer (*Capreolus capreolus* L.), and wild boar (*Sus scrofa* L.). For red deer, we collected data at the territorial management-unit level. For the other species (roe deer, wild boar), we recorded data from both the municipality where plots were located but also from the neighboring municipalities. We combined the ungulate hunting statistics for the three different species, i, into a composite index with allometric relationships to account for body mass, m_i, and metabolic rate (White & Seymour, 2003). We used the number of ungulates taken, n_i, to reflect densities and then transformed the densities into equivalents of basal metabolic rates (BMR) for each study site, s (Boulanger et al., 2018; Petersson et al., 2019)

$$\mathrm{BMR}_s = \sum_i \frac{n_i \times m_i^{0.75}}{A_s}$$

Where A_s is the surface area of the study site, s. We assumed the following live body mass values of adult individuals with equal proportions of males and females for each species: roe deer (23 kg), red deer (130 kg), and wild boar (80 kg).

No reliable estimates of ungulate population densities were available for the study sites, but hunting statistics suggest that overall population densities were low to moderate; no cases of overabundance were reported by managers for any of the study sites.

Herbaceous vascular plants

We recorded the abundance of all vascular plant species on 212 circular plots of 1000 m^2 (18-m radius) following the Braun-Blanquet method (1952), between 0 and 2 m in height corresponding respectively to the herbaceous and the low-shrub layers. Two experienced botanists conducted the surveys during a controlled census time of 35 min (±5 min) (Archaux et al., 2006). The pairs of botanists varied among sites but always included a moderator in charge of protocol application and a local botanist.

We used the cover class median value as an abundance estimate for each species as follows: 0.5% for one individual or rare, 3% for class 1, 15% for class 2, 37.5% for class 3, 62.5% for class 4, and 87.5% for class 5. Herbaceous, woody, and semi-woody species were recorded in the field but we only used herbaceous species as a response variable for biodiversity index calculations to avoid correlations between browsing pressure (i.e., Aldous estimations based on woody and semi-woody species) and understory biodiversity. We classified the species into ecological groups according to their light tolerance following Rameau et al. (Rameau et al., 1991, 1993): shade and semi-shade species were classified as shade tolerant, intermediate species were denoted as such, and semi-open and open species were combined as light demanding. We assumed that this national classification would better discriminate the species compared to other, more general, classifications (e.g., Ellenberg).

Terricolous bryophytes

On 154 plots, we recorded all terricolous bryophyte species (i.e., those growing on mineral soil, humus, and litter, and excluding those growing on wood, whether alive or dead, standing or lying) within three circular subplots of 2 m radius located 10 m from the plot center in three directions (0°, 120°, and 240°). Two experienced botanists conducted the field surveys at each site, and final species identification was carried out in a laboratory. Nomenclature follows the list established by Lemonnier (2010). Light requirements for bryophytes are only available from Ellenberg indicator values in BRYOATT database. We classified them into three ecological groups according to their light preference: shade-tolerant species (Ellenberg L value <3), intermediate species (between 3 and 6), and light-demanding species (>6).

Diversity indices

We calculated different indices at the plot level for both herbaceous vascular plants and terricolous bryophytes: species richness, abundance, and two additional diversity indices (Shannon-Weaver and Simpson).

The Shannon-Weaver index, H', gives more weight to rare species

$$H' = -\sum_{i=1}^{s} p_i \times \ln(p_i)$$

where p_i is the relative abundance of species i and s the total species richness at the plot level.

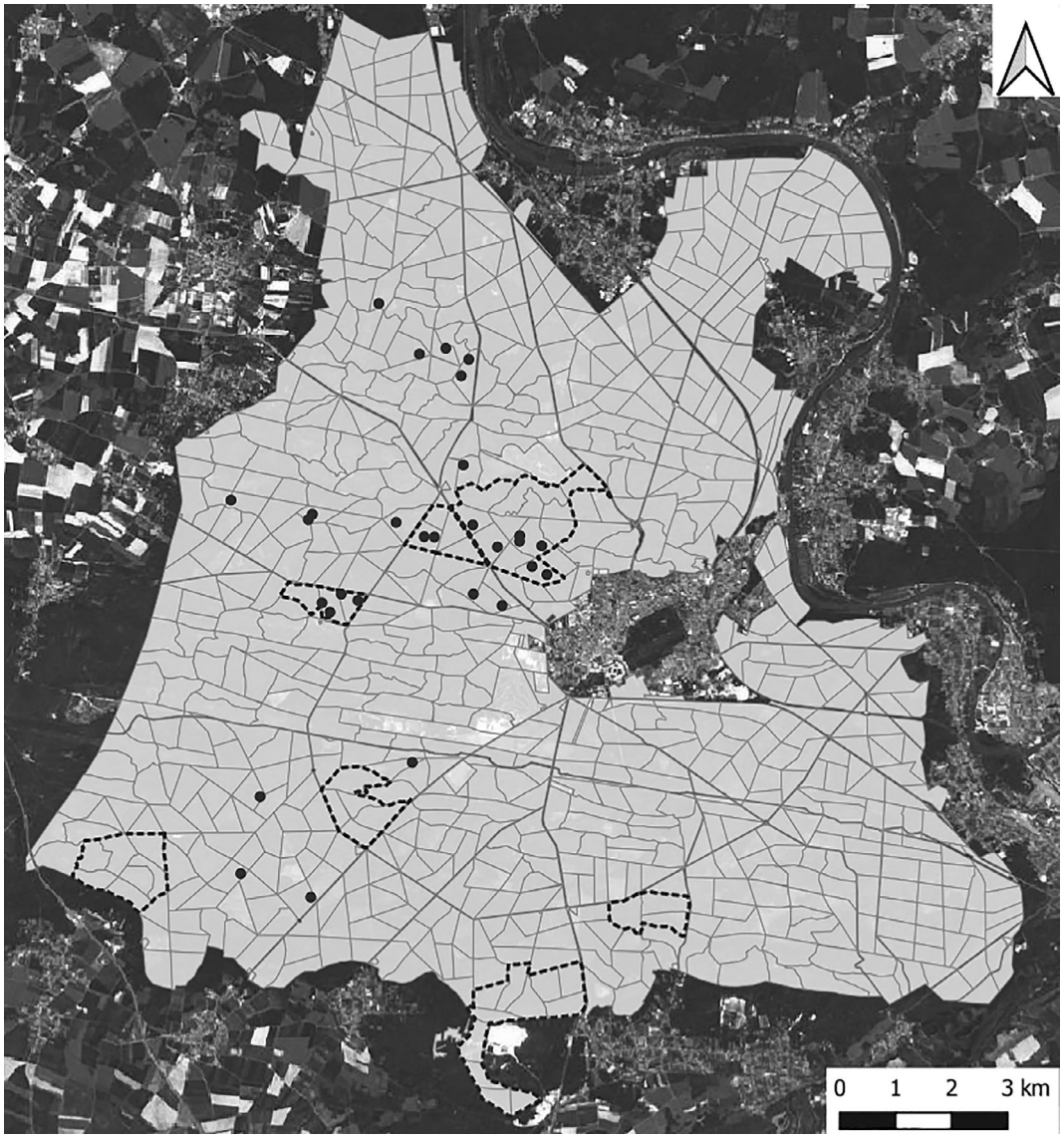


FIGURE 3 Map of an example of one of the forests studied: Fontainebleau. The plots monitored are represented by black dots. Set-asides boundaries are represented by a black dotted line

The Simpson index, D, gives more weight to dominant species

$$D = 1 - \sum_{i=1}^{s} (p_i)^2.$$

Species richness and abundance were also calculated for each ecological group and taxa separately.

Statistical analyses

All statistical analyses were performed on the R 3.6.1 statistical platform (R Core Team, 2019). Diversity indices were calculated with the *vegan* package (Oksanen et al., 2018). All models were processed with the *lme4* package (Bates et al., 2015).

We used structural equation modeling analyses (SEM) to assess the effects of forest management, stand structure, and ungulate pressure on understory (herbaceous vascular plants and bryophytes) richness, abundance, and diversity within a correlative framework. Piecewise SEM is a method that statistically evaluates a network of dependence relationships through the analysis of covariances (Lefcheck, 2016). Structural equations are probabilistic models with several variables that can be predictors or responses in the same correlative network. These models are often represented by path diagrams, with directional relationships between the observed variables. In the *piecewiseSEM* package, the path diagram consists of a set of linear (structured) equations, which are then evaluated individually (Lefcheck, 2016). SEMs use the Fisher d-separation test to assess potentially missing links in the diagram: when the test is not significant ($p > 0.05$), the SEM is considered validated without any missing paths. For

each species group and metric described, we fitted a SEM corresponding to the metamodel described in Figure 3. For each model, we included site as a random effect and altitude as a continuous covariable. We added correlated errors between explanatory variables. Correlated errors account for residual variance between two explanatory variables in the SEM (Lefcheck, 2016). When abundance, stand structure (SDI and forest cover), and ungulate pressure (browsing index, B_j, and hunting statistics, BMR_s) were response variables, we used generalized linear mixed-effects models (GLMM) with a gamma error distribution and log-link for continuous positive data (a negligible value was added to avoid null values and to comply with the assumptions of the gamma error distribution). For richness, we used a GLMM with a Poisson error distribution for count data. We added an observation random effect to account for over-dispersion whenever necessary. Finally, we used linear mixed-effects models for the diversity indices (Shannon and Simpson).

RESULTS

In all, we identified 363 herbaceous vascular plant species and 62 species of bryophytes (see Appendix S1: Table S1 for a more detailed description).

All SEMs were validated for the relationships presented in the metamodel (Figure 3) and no missing links were clearly identified (all d-sep test $p > 0.05$). Furthermore, for herbaceous vascular plants, correlated errors were added to SEM between SDI and canopy tree cover (standardized $\beta = 0.443$, $p < 0.0001$), SDI and browsing pressure (standardized $\beta = -0.057$, $p = 0.21$), as well as canopy tree cover and browsing pressure (standardized $\beta = 0.121$, $p = 0.04$). On the other hand, for bryophytes, correlated errors were added to the SEM between SDI and canopy tree cover (standardized $\beta = 0.533$, $p < 0.0001$), SDI and browsing pressure (standardized $\beta = -0.0064$, $p = 0.47$), canopy tree cover and browsing pressure (standardized $\beta = 0.120$, $p = 0.07$), SDI and BMR (standardized $\beta = -0.317$, $p < 0.0001$), canopy tree cover and BMR (standardized $\beta = -0.111$, $p = 0.08$), as well as BMR and browsing pressure (standardized $\beta = 0.180$, $p = 0.41$).

Stand structure

Herein, we will only report the results for vascular plants, the largest data set. For all standardized coefficients, see Appendix S1: Table S1. Management abandonment (set-asides) had a positive effect only on the lower tree layer (standardized estimates $\beta = 0.2445$, $p = 0.01$), while altitude had a positive effect on SDI ($\beta = 0.003$, $p = 0.01$) and a negative effect on the intermediate tree layer ($\beta = -0.008$, $p < 0.0001$; Figure 3). There was no effect of management abandonment or altitude on the other variables.

Canopy-layer had a negative effect on the intermediate ($\beta = -0.0127$, $p < 0.0001$) and the lower tree ($\beta = -0.0124$, $p < 0.0001$) layers (Figure 4). Likewise, increasing intermediate-layer tree cover had a negative effect on the lower-layer tree cover ($\beta = -0.0065$, $p < 0.02$; Figure 4). Conversely, the SDI had a positive effect on tree cover in the intermediate layer ($\beta = 0.0018$, $p < 0.0001$; Figure 3).

Among the correlated errors, only SDI and canopy cover ($p < 0.0001$), SDI and site-level browsing pressure ($p = 0.002$), and local browsing pressure and canopy cover ($p = 0.03$) were significantly correlated.

Herbaceous vascular plant diversity

Canopy-layer tree cover and browsing pressure had opposite effects on the herbaceous vascular plant community (Figure 6), except for the shade-tolerant species (Table 2). Indeed, canopy tree cover had a negative effect on overall herbaceous vascular plant diversity (species richness, abundance, Shannon and Simpson indices) as well as on the species richness and abundance of intermediate and open-habitat species, while browsing pressure had positive effects (Figure 4 and Table 2). Conversely, canopy-layer tree cover had a positive effect on species richness for the shade-tolerant species. In general, canopy-layer tree cover had a stronger effect on the herbaceous vascular plant richness and diversity than did browsing pressure (Table 2). For example, in absolute values, an increase of one standard deviation in canopy-layer tree cover had, respectively, 1.7 and 2.0 times greater impact on total species richness and abundance of herbaceous vascular plants than an equivalent increase of one standard deviation in browsing pressure (cf. standardized coefficients, Table 2). A simultaneous increase of one standard deviation in canopy-layer tree cover and browsing pressure had antagonistic effects on light-demanding species richness and abundance, respectively 3.1 and 3.4 times greater for canopy-layer tree cover than for browsing pressure (Table 2). However, the effects of browsing pressure and canopy-layer tree cover on overall species diversity (Shannon and Simpson diversity indices) and on shade-tolerant species richness were of equal magnitude (Table 2). In addition, intermediate-layer tree cover had negative effects on both species richness and abundance for intermediate and light-demanding herbaceous vascular plant species (Table 2). Forest management abandonment, lower-layer tree cover, and SDI had no direct effect on overall herbaceous vascular plant abundance, species richness, or diversity, while altitude had a positive effect on total (vascular plants and bryophytes) species richness (Figure 4, Table 2).

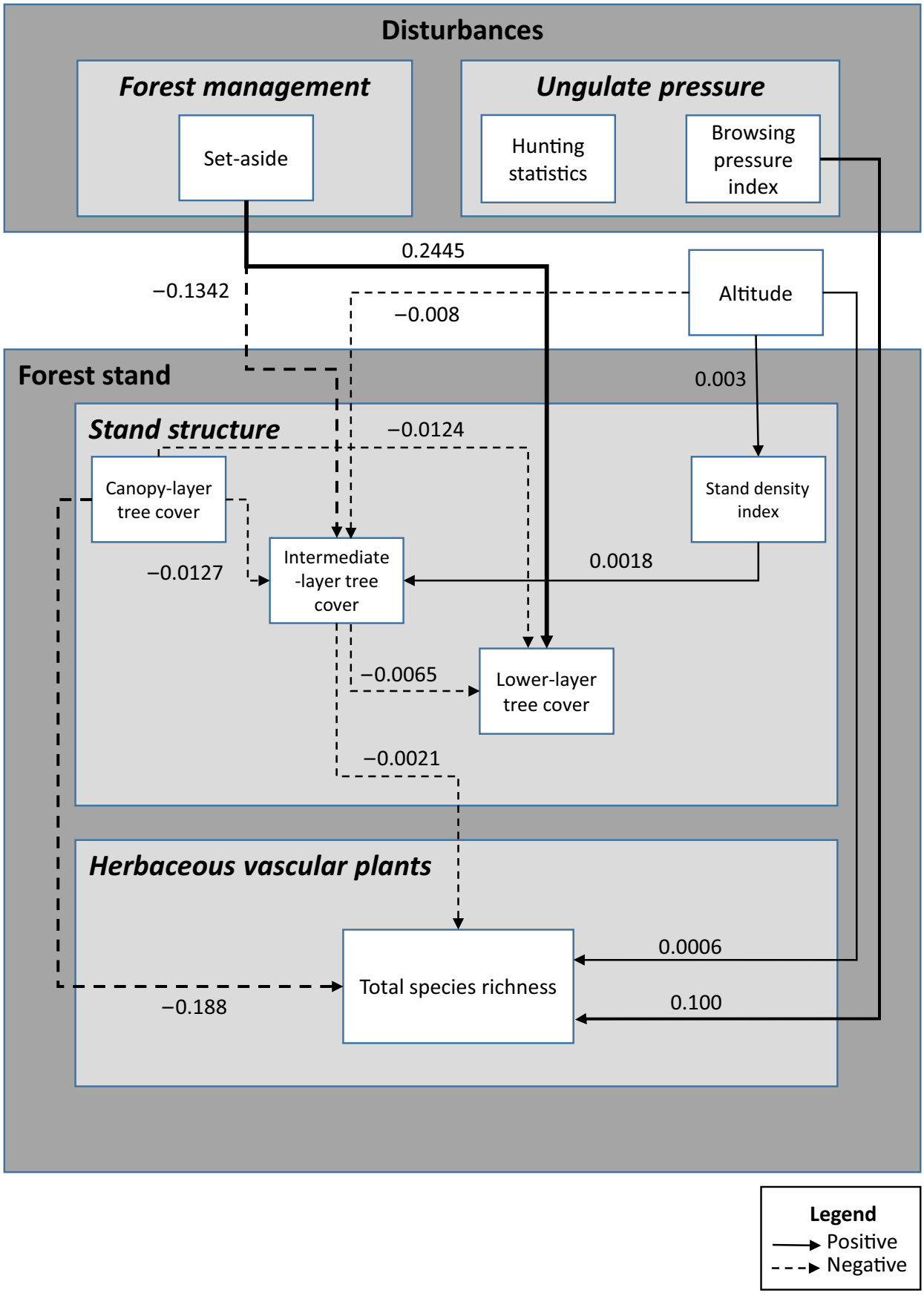


FIGURE 4 Summary of the structural equation model results for vascular plants. Here, the response variable is species richness of vascular plants. Only significant results with associated beta values are shown, with solid lines for positive and dashed lines for negative effects. Line thickness indicates the relative magnitude of the results

TABLE 2 Summary of the results from the structural equation models (SEM) for vascular plant species for the overall community (Total) and for the three ecological groups (shade-tolerant, intermediate, and light-demanding species)

	Tree cover																				
	Canopy (>16 m)			Intermediate (8–16 m)			Lower (2–8 m)			SDI			B			BMR			Management (UNM)		
	β	SE	*p*	*β*	SE	*p*	*β*	SE	*p*	*β*	SE	*p*	*β*	SE	*p*	*β*	SE	*p*	*β*	SE	*p*
Total																					
S	**−0.188**	**0.048**	**<0.0001**	−0.051	0.045	0.262	−0.037	0.038	0.339	0.0003	0.044	0.994	**0.100**	**0.034**	**0.003**	0.026	0.099	0.791	−0.034	0.067	0.615
A	**−0.234**	**0.054**	**<0.0001**	−0.037	0.052	0.477	−0.071	0.043	0.099	−0.025	0.049	0.601	**0.113**	**0.039**	**0.003**	0.054	0.155	0.729	−0.0177	0.073	0.808
H	**−0.073**	**0.024**	**0.002**	−0.008	0.023	0.721	−0.010	0.019	0.621	−0.002	0.022	0.919	**0.048**	**0.017**	**0.005**	0.009	0.052	0.867	−0.0054	0.034	0.871
D	**−0.019**	**0.008**	**0.014**	−0.003	0.007	0.705	−0.001	0.006	0.844	0.0003	0.007	0.966	**0.015**	**0.006**	**0.009**	−0.0015	0.010	0.887	0.0002	0.011	0.984
Shade-tolerant species																					
S	**0.138**	**0.060**	**0.021**	0.093	0.053	0.079	0.079	0.046	0.085	0.018	0.050	0.723	0.073	0.047	0.120	−0.084	0.186	0.651	−0.040	0.078	0.617
A	0.166	0.269	0.537	0.184	0.250	0.463	0.163	0.212	0.443	0.136	0.224	0.547	0.331	0.188	0.081	−0.199	0.685	0.776	−0.482	0.356	0.178
Intermediate species																					
S	**−0.209**	**0.031**	**<0.0001**	**−0.056**	**0.028**	**0.046**	−0.043	0.024	0.072	0.023	0.027	0.387	**0.1035**	**0.020**	**<0.0001**	0.080	0.112	0.475	−0.046	0.041	0.269
A	**−2.399**	**0.496**	**<0.0001**	**−0.854**	**0.473**	**0.072**	**−0.855**	**0.407**	**0.037**	−0.310	0.456	0.498	**0.749**	**0.360**	**0.039**	0.651	1.499	0.672	−0.102	0.689	0.882
Light-demanding species																					
S	**−0.397**	**0.104**	**0.0001**	**−0.217**	**0.101**	**0.031**	−0.103	0.079	0.193	−0.060	0.101	0.552	**0.152**	**0.062**	**0.014**	0.300	0.291	0.302	−0.159	0.145	0.272
A	**−0.654**	**0.167**	**0.0001**	**−0.663**	**0.168**	**0.001**	**−0.579**	**0.149**	**0.0002**	−0.140	0.169	0.408	0.099	0.128	0.437	0.042	0.195	0.833	0.054	0.256	0.832

Note: Only models directly linking biodiversity indices as both response variables and explanatory variables are represented here. *β*, standardized estimates; SDI, stand density index; B, browsing index; BMR, basic metabolic rate index; UNM, unmanaged forest (strict reserve); S, species richness; A, abundance; H, Shannon diversity index; D, Simpson diversity index. Values in boldface type identify significant effects ($p \leq 0.05$).

TABLE 3 Summary of the results from the structural equation models (SEM) for terricolous bryophytes for the overall community (Total) and for the three ecological groups (shade-tolerant, intermediate, and light-demanding species)

	Tree cover																				
	Canopy (>16 m)			Intermediate (8–16 m)			Lower (2–8 m)			SDI			B			BMR			Management (UNM)		
	β	SE	*p*	*β*	SE	*p*	*β*	SE	*p*	*β*	SE	*p*	*β*	SE	*p*	*β*	SE	*p*	*β*	SE	*p*
Total																					
S	−0.095	0.059	0.11	0.055	0.052	0.29	0.043	0.056	0.44	**0.13**	**0.056**	**0.016**	0.028	0.044	0.53	0.15	0.079	0.07	−0.0133	0.0887	0.881
A	−0.0989	0.118	0.40	0.134	0.114	0.24	0.116	0.117	0.32	0.0138	0.119	0.908	0.0285	0.0913	0.76	0.165	0.441	0.71	0.188	0.179	0.295
H	−0.081	0.055	0.14	0.053	0.050	0.30	0.038	0.049	0.44	**0.10**	**0.052**	**0.047**	0.034	0.042	0.41	0.16	0.14	0.26	−0.0357	0.0783	0.649
D	−0.030	0.029	0.31	0.015	0.027	0.58	0.025	0.026	0.35	**0.069**	**0.027**	**0.013**	0.018	0.022	0.43	0.030	0.050	0.56	−0.0656	0.0421	0.121
Shade-tolerant species																					
S	0.32	0.36	0.38	0.18	0.30	0.54	0.15	0.33	0.64	**0.53**	**0.24**	**0.027**	−0.37	0.34	0.29	−0.15	0.33	0.64	0.116	0.463	0.802
A	−0.005	0.152	0.98	0.0714	0.137	0.60	−0.219	0.157	0.163	**0.51**	**0.147**	**0.0005**	−0.132	0.115	0.25	−0.309	0.333	0.35	0.167	0.228	0.464
Intermediate species																					
S	−0.091	0.062	0.14	0.078	0.055	0.16	0.057	0.059	0.34	0.096	0.059	0.10	0.030	0.047	0.52	**0.18**	**0.090**	**0.049**	0.0805	0.0951	0.397
A	−0.0728	0.124	0.556	0.223	0.12	0.064	**0.369**	**0.131**	**0.0049**	−0.0522	0.128	0.68	0.0867	0.0973	0.37	0.302	0.436	0.49	0.371	0.194	0.056
Light-demanding species																					
S	−0.21	0.23	0.36	−0.35	0.22	0.12	−0.19	0.25	0.46	0.31	0.22	0.17	0.072	0.16	0.66	−0.005	0.25	0.99	**−0.87**	**0.398**	**0.029**
A	**−0.713**	**0.174**	**<0.0001**	**−0.404**	**0.153**	**0.008**	−0.262	0.165	0.112	**0.5**	**0.154**	**0.0011**	0.0283	0.107	0.79	0.188	0.28	0.50	**−0.667**	**0.269**	**0.013**

Note: Only models directly linking biodiversity indices as response variables and explanatory variables are represented here. *β*, standardized estimates; SDI, stand density index; B, browsing index; BMR, basic metabolic rate index; UNM, unmanaged forest (strict reserve); S, species richness; A, abundance; H, Shannon diversity index; D, Simpson diversity index. Values in boldface type identify significant effects ($p < 0.05$).

Terricolous bryophyte diversity

Increasing canopy- and intermediate-layer tree cover had a negative effect only on the abundance of light-demanding species (Table 3). SDI had a positive effect on overall species richness and diversity (Shannon and Simpson diversity indices), as well as on shade-tolerant species richness and, surprisingly, on light-demanding species abundance (Table 3).

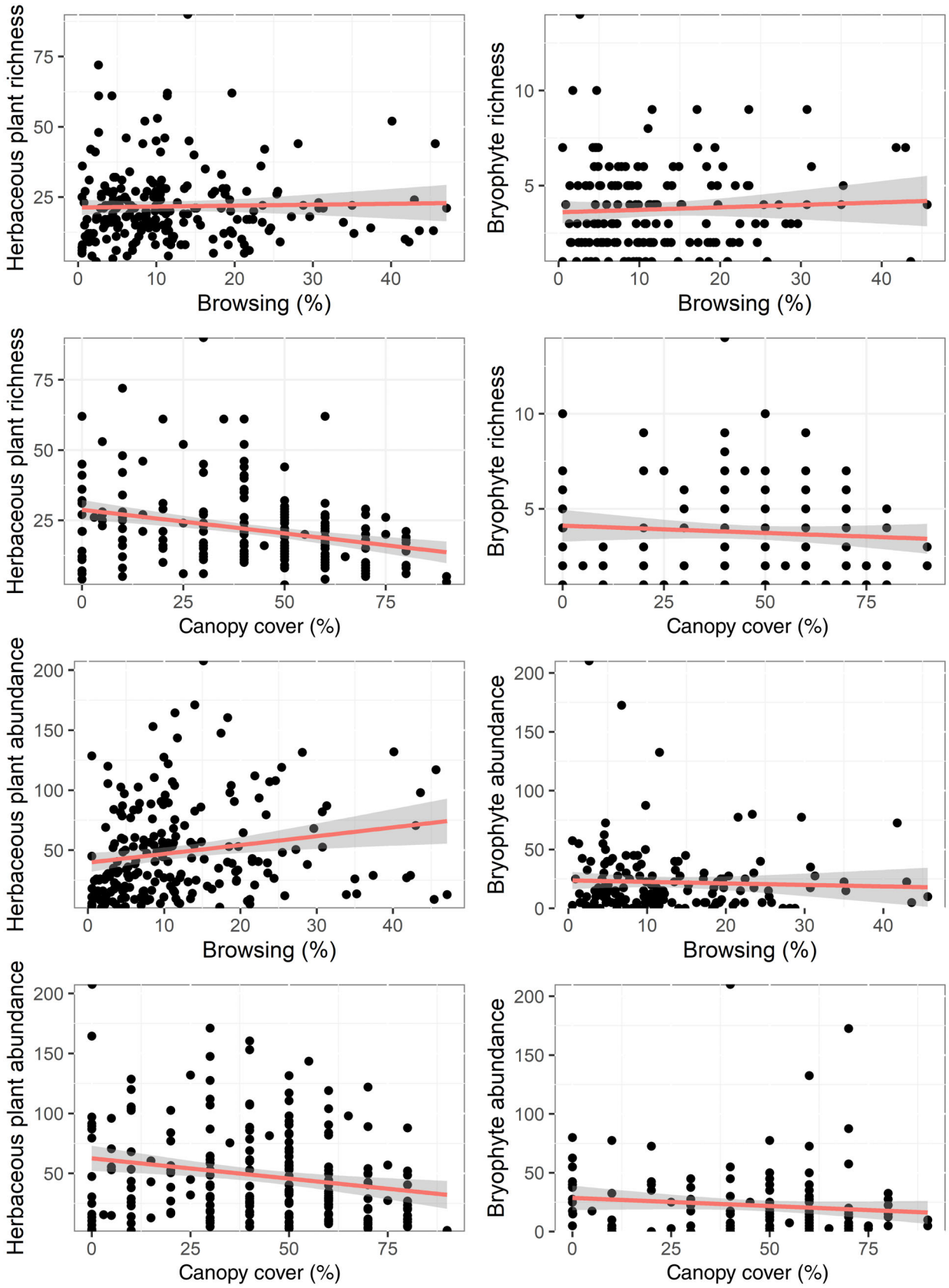


FIGURE 5 Scatter plots of the variations in total species richness and abundance for vascular plant species and bryophytes as a function of browsing and canopy cover. The black dots represent raw values. The red lines are from generalized models (see section "*Statistical analyses*"), while the gray ribbons represent the 95% confidence intervals

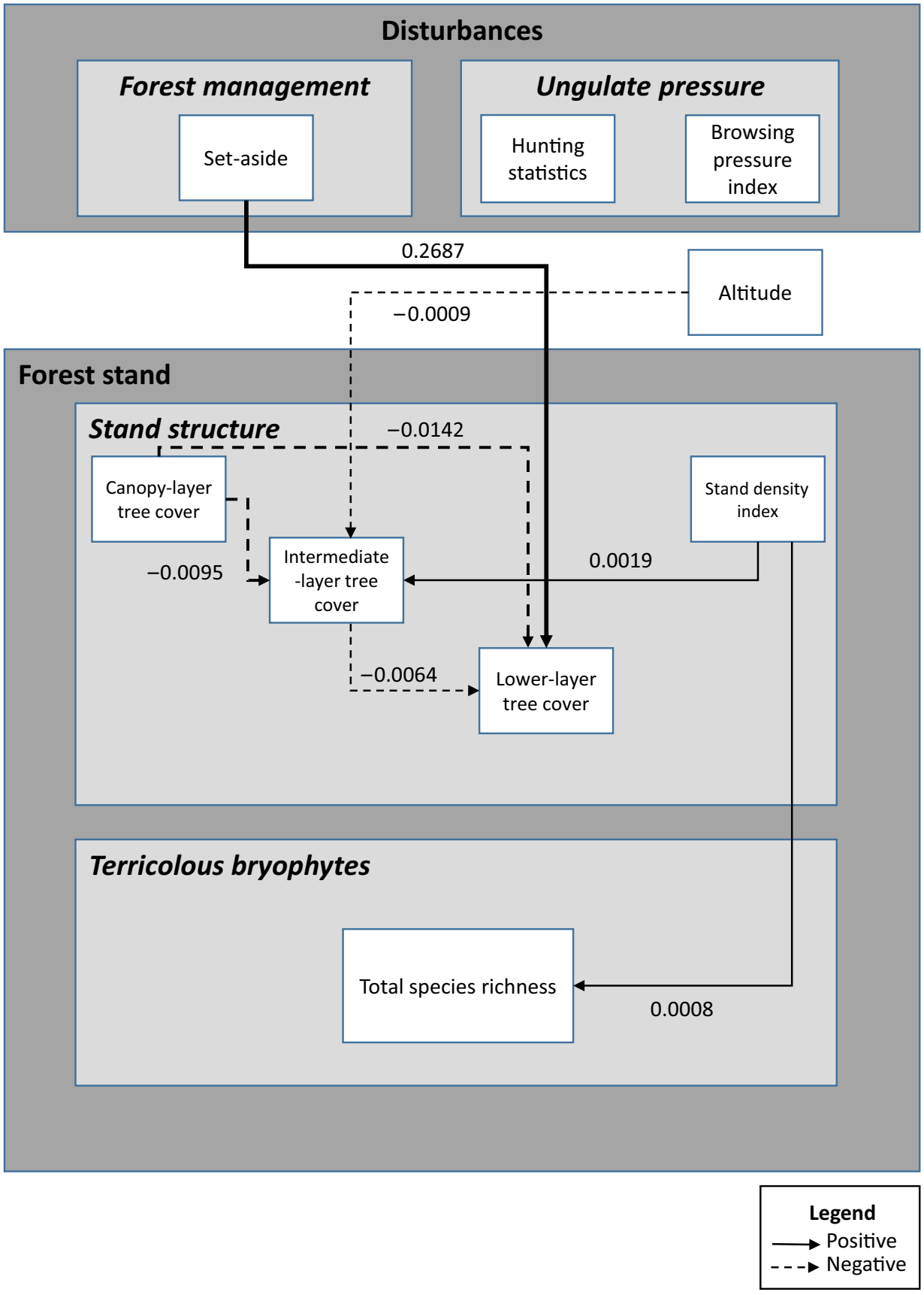


FIGURE 6 Summary of the Structural Equation Model results for terricolous bryophytes. Here, the response variable is species richness of terricolous bryophytes. Only significant results with associated beta values are shown, with solid lines for positive and dashed lines for negative effects. Line thickness indicates the relative magnitude of the results

There was also a positive effect of increasing the BMR index on the species richness of intermediate bryophyte species, while forest management abandonment had a negative effect on light-demanding bryophyte species richness and abundance (Figure 6, Table 3). Local browsing pressure had no significant effect on the bryophyte community (Figures 5 and 6, Table 3).

DISCUSSION

By comparing plots in managed forests and strict reserves with different levels of browsing pressure within a correlative framework, we revealed the direct antagonistic effects of cover indices (mostly canopy cover) and local browsing pressure on herbaceous vascular plants. Overall, bryophytes positively responded only to stand structure indices (mostly SDI). In terms of magnitude, we show that stand structure indices had a greater effect than did browsing pressure and even overrode the effects of forest management abandonment for vascular plants. We mainly attribute these strong effects of stand structure to different responses to understory light conditions, with positive effects of increased canopy cover and stand density on shade-tolerant species, and parallel negative effects on light-demanding species. Finally, stand structure effects were stronger on herbaceous vascular plants than on bryophytes, and usually had opposite directions. However, we found no effect of management abandonment on browsing pressure. These results may be useful for forest management planning and the preservation of understory biodiversity.

Herbaceous vascular plant diversity decreases with increasing canopy cover but bryophyte diversity increases with increasing stand density

Canopy cover was the strongest driver of understory vegetation in our study. Canopy cover determines access to light for understory vegetation (Gilliam, 2007; Laurent et al., 2017), resulting in a strong asymmetric competition between understory vegetation and canopy trees. In addition, for example, in stands with high vertical heterogeneity, overstory competition leads to the exclusion of less shade-tolerant plant species (Gravel et al., 2010). First, unsurprisingly, we found that the total species richness and abundance of herbaceous vascular plants decreased with increasing canopy-layer tree cover. Likewise, several studies in temperate forests have shown lower herbaceous species richness with increasing canopy cover (Hedwall et al., 2019; Kelemen et al., 2012; Naaf & Wulf, 2007; Tinya et al., 2009). Light transmittance reduced by canopy closure constitutes a limiting factor for the development of herbaceous vascular plant diversity (Tinya & Ódor, 2016), but this effect varies among ecological groups. We observed a gradual response of vascular plants to forest cover according to light tolerance: light-demanding plant species are more sensitive to light availability, while shade-tolerant plant species may respond to other factors limiting resources such as nutrients or soil moisture content (Härdtle et al., 2003; Tinya et al., 2009). This also likely explains why light-demanding and intermediate species responded negatively to increasing intermediate-layer tree cover, while we did not find any effect of the intermediate-layer tree cover on the richness and abundance of shade-tolerant species. Therefore, our results are consistent with the hypothesis that light constitutes a major limiting resource and determines functional understory composition (Barbier et al., 2008; Gilliam, 2007).

The effects on terricolous bryophytes were less pronounced than those on herbaceous vascular plants. Unlike for herbaceous vascular plants, neither canopy cover nor browsing pressure influenced overall abundance, species richness or diversity for bryophytes, with only non-significant trends for diversity and abundance indices. We only showed a significant negative effect of canopy- and intermediate-layer tree cover on the abundance of light-demanding species (Table 3). Instead, species richness and other diversity indices for bryophytes responded more significantly, and positively, to the SDI. Likewise, Evans et al. (2012) found a positive relationship between SDI and species richness for the ground floor bryophyte community, which the authors attributed to indirect effects of stand density on leaf litter through modifications in the shrub layer. Indeed, increasing SDI had a strong negative effect on shrub cover, which could lead to a decrease in the leaf litter layer. Other studies have shown that litter accumulation negatively influences bryophyte abundance and species richness by acting like a mechanical barrier, or through allelopathic effects (Dzwonko & Gawroński, 2002; Márialigeti et al., 2009; Startsev et al., 2008). In our case, the terricolous bryophytes could just as well have been influenced by microclimatic conditions induced by stand structure (Kovács et al., 2017; Von Arx et al., 2013): dense stands might promote higher bryophyte species richness because of the slightly higher below-canopy moisture conditions (Merinero et al., 2020). Contrary to what was found in other studies (Tinya et al., 2009), the terricolous bryophytes on our plots did not fully respond to changes in light availability since only the light-demanding species responded negatively to canopy cover, as did the

light-demanding herbaceous vascular plants. However, previous studies did not find any relationship between terricolous bryophyte species richness and light availability (Mills & Macdonald, 2004) or basal area (Barbier et al., 2008), which suggests that other factors play an important role.

Browsing pressure mostly benefits herbaceous vascular plants

Browsing pressure was the second driver for herbaceous vascular plants. Ungulate browsing mainly mediates interspecific competition between dominant and subordinate plants within the understory layer (Beguin et al., 2011; Koerner et al., 2018; Laurent et al., 2017). As discussed in the Intermediate Disturbance Hypothesis, an intermediate intensity disturbance can increase diversity (Wilkinson, 1999). In accordance, the presence of ungulates, not considered overabundant in this study (Nuttle et al., 2014), increases the herbaceous diversity of understory vegetation. Depending on the palatability of the dominant species, forest ungulates are likely to modify herbaceous plant diversity by controlling their abundance, as shown for grassland ecosystems (Koerner et al., 2018). In line with other studies (Boulanger et al., 2018), we found that local browsing pressure favored the species richness and diversity of the herbaceous vascular plant community, consequent to light-demanding and intermediate species increase. This effect may be due to reduced competition for resources (light and nutrients), linked with the decrease in cover percentage of potentially strong competitors that are more palatable and browsing sensitive, such as tree saplings and shrubs (Laurent et al., 2017; Perrin et al., 2011; Royo et al., 2010). However, we cannot confirm this hypothesis since, in our study, understory woody species (shrubs and trees) were used to assess herbivory pressure and were therefore excluded as a response variable (Boulanger et al., 2015). We did find, however, that the abundance and species richness of both intermediate and light-demanding species increased with increasing browsing pressure. Beyond the direct competitive effects among plants, ungulates may also favor herbaceous vascular plants by creating spatiotemporal environmental variations and by reducing niche overlap among plant species. For instance, Murray et al. (2013) found that ungulates increased the spatial heterogeneity of soil nutrients, and that this environmental variability explained the abundance and diversity of the herbaceous field layer better than understory light availability did.

Overall, ungulate pressure, whether assessed at the plot or at the site level, had a very limited impact on bryophyte diversity in our study. Only intermediate species positively responded at the site level (BMR index). Generally, bryophytes are not consumed by ungulates (Chollet et al., 2013) and any effects of ungulates on bryophytes might be more related to fluctuating resources (Davis et al., 2000), ungulate-mediated diaspore dispersal (Heinken et al., 2001) and success in diaspore development by suppressing mechanical barriers (e.g., trampling by animals stripping away the forest litter).

Stand structure overrides the direct effects of forest management abandonment on understory vegetation

Forest management abandonment changes forest structure most notably by restoring old-growth attributes (Paillet et al., 2015). We focused on three tree cover layers and showed that management abandonment also increased lower-layer (2–8 m) tree cover, with few direct effects on vascular plant and bryophyte communities. In other words, stand structure (namely canopy- and intermediate-layer cover for vascular plants and SDI for bryophytes) better explained the variations in vascular plant and bryophyte communities than did forest management abandonment per se. However, most of the reserves included in our data set were still in a relatively young development stage (set-aside >20 years but mean time since last harvesting of only about 40–50 years), and may still have been in a relatively homogeneous biomass-accumulation phase, characterized by increasing cover (Paillet et al., 2015). Several meta-analyses have shown that herbaceous diversity is generally higher in managed than in unmanaged forests (Chaudhary et al., 2016; Paillet et al., 2010). However, there are large variations in the response of vascular plants to management abandonment, and this seems to indicate a link with either the management type previously applied (von Oheimb & Härdtle, 2009), the management history before abandonment, the development stage of the newly unmanaged forest (Burrascano et al., 2009), or a combination of these factors. For example, other studies comparing managed and unmanaged forests have observed a decrease in vascular plant species richness in abandoned plots, ranging from 40% in a recently abandoned fir–beech forest located in the western Pyrenees (Horvat, Heras, et al., 2017), to 20%–30% in German beech forests (Schmidt, 2005; von Oheimb & Härdtle, 2009). Conversely, Burrascano et al. (2009) showed a 30% higher species richness in old-growth stands than in managed forests in the central Apennines in Italy. These differences suggest non-equivocal responses of vascular plants

to management abandonment combined with nonlinear dynamics.

Most of the studies comparing bryophytes in managed and unmanaged forests focus on corticolous and epixylic, rather than ground-dwelling, species. Indeed, the effects of management abandonment for terricolous bryophytes may be lower or nonsignificant compared to wood-associated bryophyte groups. Furthermore, the studies on terricolous bryophytes show variable responses to management abandonment. For example, Horvat, Heras, et al. (2017) observed no relation between forest management intensity and terricolous bryophyte richness in Pyrenean silver-fir–beech forests. Lesica et al. (1991) observed higher, although marginally significant ($p = 0.09$), richness of terricolous bryophytes in coniferous old-growth than second growth stands. Conversely, Müller et al. (2019) observed higher numbers of terricolous bryophytes in managed than in unmanaged forests dominated by European beech (*Fagus sylvatica*). Finally, Uotila et al. (2005) observed a higher abundance of mosses in managed Scots pine (*Pinus sylvestris*) boreal forests. In view of these results, it is likely that terricolous bryophyte responses should be contextualized with, for example, stand composition or soil properties.

No set-aside effect on ungulate pressure

We did not find any effect of forest management abandonment through reserve establishment on ungulate pressure, either at the plot level (browsing pressure) or at the site level (BMR index based on hunting statistics). In other words, there was no difference in ungulate pressure between managed forests and strict forest reserves. This is most likely due to the fact that, at our study sites, hunting differed only very marginally inside and outside the reserves. Consequently, strict forest reserves in France may not act as refuge areas for ungulates as they do elsewhere in Europe (Borkowski et al., 2019; Grignolio et al., 2011; Meisingset et al., 2018; van Beeck Calkoen et al., 2020), notably because the reserves are much smaller than the area occupied by ungulate populations. The small size of our strict forest reserves might also create a strong edge effect and hunting in nearby reserves could increase mortality, thereby counteracting a potential refuge effect (Tolon et al., 2012). In addition, managed and unmanaged sites are relatively close with an average distance of 1.63 km, largely exceeded by 48-h path length (average distance travelled in 48 h) of the three studied ungulates (i.e., ranging from 6.3 to 9.6 km, see table 1 in Pellerin et al., 2016).

Although we did not find any effect of forest management abandonment on ungulate pressure, we did find some correlations between stand attributes and ungulate pressure, at both the plot (browsing pressure) and site (BMR index) levels. These correlations could likely be explained by modifications in resource availability and use. Indeed, as shown above, stand structure affects the species composition and abundance of understory vegetation, thereby modifying the quality and quantity of the food resource for ungulates, which in turn modifies resource use and leads to higher browsing pressure in patches with high-quality food resources and less browsing pressure in poorer food patches (Kuijper et al., 2009; Moser et al., 2006; Naaf & Wulf, 2007). However, this relationship needs to be assessed at larger scales. We assumed unidirectional relationships between ungulate pressure and the food resource (herbaceous vascular plants) and this might have introduced a bias in our correlative framework. However, we believe that we avoided most of the circular feedback by excluding from our analyses all woody and semi-woody species (height < 2 m), on which we measured local browsing pressure.

CONCLUSIONS

We show that the recent setting aside of forest reserves has had few direct effects on herbaceous vascular plant and terricolous bryophyte communities. Instead, our results highlight the role of vertical stand structure and ungulate pressure in shaping understory plant diversity. From a management point of view, foresters can control stand attributes such as cover in the different vertical forest layers by applying alternative silvicultural treatments. Likewise, ungulate population densities can be controlled by applying carefully designed hunting management plans. Thus, our study underlines the importance of cooperation between foresters and hunters to manage stand attributes and ungulate pressure in favor of understory diversity, and more generally, overall ecosystem functions in managed forests. As already experienced, cooperation between several actors, such as hunters, can reduce the negative effects of ungulates on regeneration while increasing the herbaceous plant diversity (Stout et al., 2013). For example, if forest managers work toward forest stands with sparse tree canopies while hunters aim for moderate ungulate pressure, this should favor light-demanding and intermediate species at the same time and overall species diversity is likely to increase. On the other hand, if foresters and hunters favor dense canopy cover and low ungulate pressure, shade-tolerant species are likely to thrive at the expense of more light-demanding species, resulting in less rich plant communities. For conservation needs, as forest attributes are manipulated at the stand level, it is possible to elaborate forest management plans that favor independently or simultaneously the three ecological groups, within the

forest landscape matrix. On the other hand, ungulate pressure is more easily manipulated at the site level. Site-level ungulate pressure should therefore be cautiously monitored in accordance with the overall conservation goals for the site, especially regarding forest regeneration dynamics. We therefore suggest that conservation biologists adopt a more proactive conservation strategy in cooperation with foresters and hunters, including both passive set-asides and integrated conservation strategies (Bollmann & Braunisch, 2013). In addition, the passive rewilding of vast landscape mosaics hosting large ungulates and their natural predators could contribute to higher spatiotemporal habitat heterogeneity, restore natural disturbance dynamics and promote successional processes (Pereira & Navarro, 2015).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Chevaux, 2021) are available on the Portail Data INRAE repository at: https://doi.org/10.15454/EB8YXF.

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