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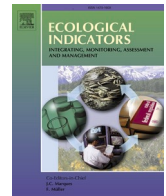
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Warning in the woods: Species-specific and functional responses of the understorey along a deer browsing intensity gradient in a mixed temperate forest in France

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ABSTRACT

Understanding and predicting responses of plant community diversity and ecosystem functioning to disturbance is essential to achieving forest conservation and management goals. In recent decades, the abundance and geographic distribution of wild ungulates have expanded in many parts of Europe due to, among other factors, land-use changes, hunting regulations and lack of predators. The study aims to explore the effects of deer browsing and grazing intensity, estimated through a browsing index on woody and semi-woody plants, on understorey vegetation composition, analysing both taxonomic and functional diversity. Specifically, we aim to test the intermediate disturbance hypothesis (IDH), which states that plant biodiversity peaks at intermediate levels of browsing intensity regarding plant species richness and functional groups. We also aim to identify species revealing different levels of browsing intensity, accounting for plant functional traits. Our results revealed that intermediate levels of browsing intensity, through species replacement, strongly and positively affected total species richness. This result is consistent with the IDH prediction, but distinct patterns varied across plant functional types. Moreover, increasing browsing intensity favoured disturbance-tolerant species by replacing functional traits. These species were characterised by ruderal traits, including high specific leaf area, low leaf dry matter content, small height and seed mass, annual and short lifespans. However, although browsing intensity increased functional richness and decreased functional redundancy, indicator species analysis revealed that high browsing intensity favoured highly competitive, browsing-tolerant perennial species. These results suggest that annual species may fail to colonise the understorey even if they are favoured by deer browsing, thereby affecting the functioning and the stability of ecosystem, with a potential homogenisation of understorey vegetation. Although confounding effects cannot be ruled out (e.g., local vegetation structure and diversity), our study highlights the need to consider functional diversity when assessing deer effects on vegetation to draw a complete picture of plant-large herbivore interactions.

1. Introduction

Understanding and predicting plant community diversity and ecosystem functioning responses to disturbance, such as wild ungulate grazing and browsing, are crucial to achieving sustainable ecosystem management objectives. In theory, plant species composition and diversity across the landscape follows the community assembly rules based on species traits, environmental filters and plant competition ability (Keddy, 1992). However, species pools may shift with site productivity, disturbance intensity and frequency (Herrero-Jáuregui and Oesterheld, 2018; Gao and Carmel, 2020a) and grazer identity (Tóth

et al., 2018). Among the various hypotheses that predict community assembly trajectories after disturbance, the intermediate disturbance hypothesis (IDH) argues that plant biodiversity peaks at intermediate levels of disturbance frequency or intensity (Grime, 1973; Connell, 1978; Milchunas et al., 1988), though recent studies showed that IDH mainly occurs in wet areas (Gao and Carmel, 2020b).

The original IDH was articulated regarding a trade-off between species competition and colonisation (i.e., disturbance-tolerant species) (Roxburgh et al., 2004). Consequently, within a mosaic of communities, that share the same species, changes in disturbance may favour species replacement (i.e. turnover) and increase spatial and temporal

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heterogeneity in species composition (i.e., beta-diversity, Whittaker, 1960) (Milchunas and Lauenroth, 1993; Adler et al., 2001). Species replacement may have an implication on functional diversity and thus on ecosystem functioning (Allan et al., 2011; Gonzalez et al., 2020), depending on the number of redundant species (i.e., species with similar functions) involved in the process (Pakeman et al., 2018). Indeed, functional redundancy can reinforce temporal stability while protecting the community against the loss of ecosystem functions (Biggs et al., 2020; de Bello et al., 2021b). Hence, maintaining a high level of functional diversity at a regional scale may favour multiple ecosystem functions and services (multifunctionality) (Hector and Bagchi, 2007; van der Plas et al., 2016; Gross et al., 2017) and improve ecosystem resilience, optimising the ecosystem's ability to cope with perturbations (Mori et al., 2013; Oliver et al., 2015).

Over the last decades, populations of wild ungulates, such as red deer (*Cervus elaphus* L.), roe deer (*Capreolus capreolus* L.) and wild boar (*Sus scrofa* L.) have exponentially increased in abundance and range in European temperate forests, mainly due to extirpation of large predators, hunting regulations and land-use changes (Côté et al., 2004; Apollonio et al., 2010; Massei et al., 2015). Besides increasing the risk of collision with vehicles and the spread of diseases to domestic animals, the overabundance of wild ungulates may have substantial effects on vegetation within agricultural and forestry systems (Boulanger et al., 2015; Carpio et al., 2020; Chevaux et al., 2022), with significant ecological and socio-economic consequences (Valente et al., 2020).

Through browsing, grazing and bark stripping, trampling, seed dispersal and rooting, wild ungulates modify the structure and composition of plant communities and regulate the dynamics of entire ecosystems (Albert et al., 2015; Habeck and Schultz, 2015; Sabo et al., 2017; Baltzinger and Mårell, 2022). As such, they can be seen as dominant species (sensu Power et al., 1996) and ecosystem engineers (sensu Jones et al., 1994), where the trajectory of vegetation dynamics primarily depends on the ungulate density, foraging selectivity and the plants' resistance and tolerance to disturbance. Wild ungulates may thus favour certain species (e.g., Perea et al., 2014), or growth forms, such as graminoids (Rooney, 2009; Sabo, 2019) or pteridophytes (Takatsuki, 2009), by altering plant-plant interactions (Côté et al., 2004). If IDH occurs, disturbance should diminish the competitive advantage of plant and open up space to new colonising species, tolerant and resistant to grazing, leading to an increase in biodiversity up to intermediate grazing intensity, for which competitors and colonisers coexist in the system. As grazing intensity increases, competitive exclusion results in the loss of species and thus a decrease in plant species richness and ultimately leads to a biotic homogenisation of plant communities (Rooney, 2009; Pakeman and Fielding, 2021), with potential local extinction of non-tolerant species (Frerker et al., 2014). These modifications in plant communities may affect ecosystem functioning by altering the assembly of plant traits. Variation in plant traits is related to plant resource use strategy (i.e., recovery of foliar investment and return of matter and energy), described by the worldwide leaf economics spectrum (Wright et al., 2004). For example, species with a slow ("conservative") strategy are associated with low specific leaf area (SLA) and high leaf dry matter content (LDMC), while species with a fast ("acquisitive") strategy are associated with high SLA and low LDMC. Ecosystem functions may thus change, as LDMC or SLA are respectively related to litter turnover and plant productivity (Poorter and De Jong, 1999; Fortunel et al., 2009). Therefore, interpreting vegetation changes in the interaction between ungulate populations and their habitat and defining the threshold of grazing intensity to achieve high levels of functionality and ecosystem services is crucial for forest conservation and management.

Another important point for managers is identifying how browsing and grazing alter plant biodiversity regarding species identity by integrating indicator species monitoring into their management plan. Indicator species are defined as species that reveal ecological changes because of their sensitive responses to these changes, giving early warning signals about ecosystem processes (Siddig et al., 2016).

Although indicator species are site-specific, determining which species are tolerant or sensitive to browsing and grazing, and knowing at what intensity these species may occur and dominate the plant community may be helpful for game management and preserve forest sustainability. Indicator species of a given herbivory or browsing disturbance intensity are commonly detected using parameters such as reduction in the size, reproduction, survival and density of palatable species (e.g., Koh et al., 2010; Lecomte et al., 2016; Blossey et al., 2019; Inatomi et al., 2022). Many approaches were developed for their detection based on their presence or on their abundance to a given disturbance intensity (e.g., Dufrière and Legendre, 1997; De Cáceres and Legendre, 2009; De Cáceres et al., 2010; Podani and Csányi, 2010). For example, Bachand et al. (2014) showed that species indicator analysis proved to be an effective tool for monitoring ecosystem recovery after reducing deer density on Anticosti Island (Canada). However, these methods do not consider the plant functional traits that, besides allowing the identification of larger sets of species and occurrences in distinct groups of species, may provide information on the role of indicator species on the structure and functioning of the ecosystems (Ricotta et al., 2015; Ricotta et al., 2020; Dalle Fratte et al., 2022).

In this study, we aim to assess how wild ungulate (i.e., red deer and roe deer) intensity affects plant communities' taxonomic and functional diversity. Specifically, we aim 1) to evaluate how wild ungulate disturbance affects the taxonomic diversity of plant communities, testing for the IDH along an ungulate intensity gradient; 2) to understand how these effects translate into functional diversity; and 3) to identify indicator species of ungulate disturbance level (plant tolerant or sensitive to wild ungulate disturbance) based on their functional traits.

2. Methods

2.1. Study area

We used data collected in the Sologne Natural Region in the centre of France to assess the effects of deer on vegetation characteristics (Fig. 1). Sologne covers approximately 5000 km² and has a high forest cover and a flat topography. The soil is generally acidic (pH_{KCl} ranging between 3.3 and 4.8 at study plots), with a clay-sandy texture and a low nutrient availability. The climate is temperate Atlantic, with mean minimum and maximum annual temperatures of 7 °C and 16.3 °C, respectively, and mean annual precipitation of 635.5 mm (Orléans station for 1991–2020 long-term mean, source: <https://meteofrance.com>). Forests grow at relatively low tree densities, with deciduous species representing approximately 77 % of the forest cover (e.g., *Quercus robur*, *Quercus petraea*, *Castanea sativa* and *Betula pendula*), mixed with conifers, such as *Pinus sylvestris*, the most frequent species. A mixture of shrubs, ferns and herbaceous species characterize the understorey. No absolute density estimates of wild ungulates, i.e. red deer, roe deer and wild boar, were available for the study area, but hunting statistics for the three species are among the highest in France and remained steady between 2011 and 2017 (FDC41 (Fédération Départementale des Chasseurs du Loir et Cher), 2018). Hunting bags for the 2013/2014 hunting season in the region (corresponding to our vegetation sampling period) averaged 0.86 ± 0.96 (mean ± SD) and 1.95 ± 1.85 and 3.7 ± 3.7 individuals per km², for the three species respectively (source: French Office for Biodiversity, OFB). Deer species differ in body size and thus in browsing height with a maximum of 1.30 m for roe deer (Chianucci et al., 2015) and 2.0 m for red deer (Walters et al., 2020). Although wild boars were present in the study area, the observed rooting intensity was low during the study period, as 78 % of the plots experienced less than 5 % rooting of the subplot area. Thus, this species was not considered in this study. No large wild predators were present in the study area.

We limited the study sites to a geographically restricted area, with a low elevation range (70–180 m) and similar habitat (i.e., structure and composition of the canopy layer) and soil types to minimize possible confounding effects arising from herbivore preferences, contrasting with

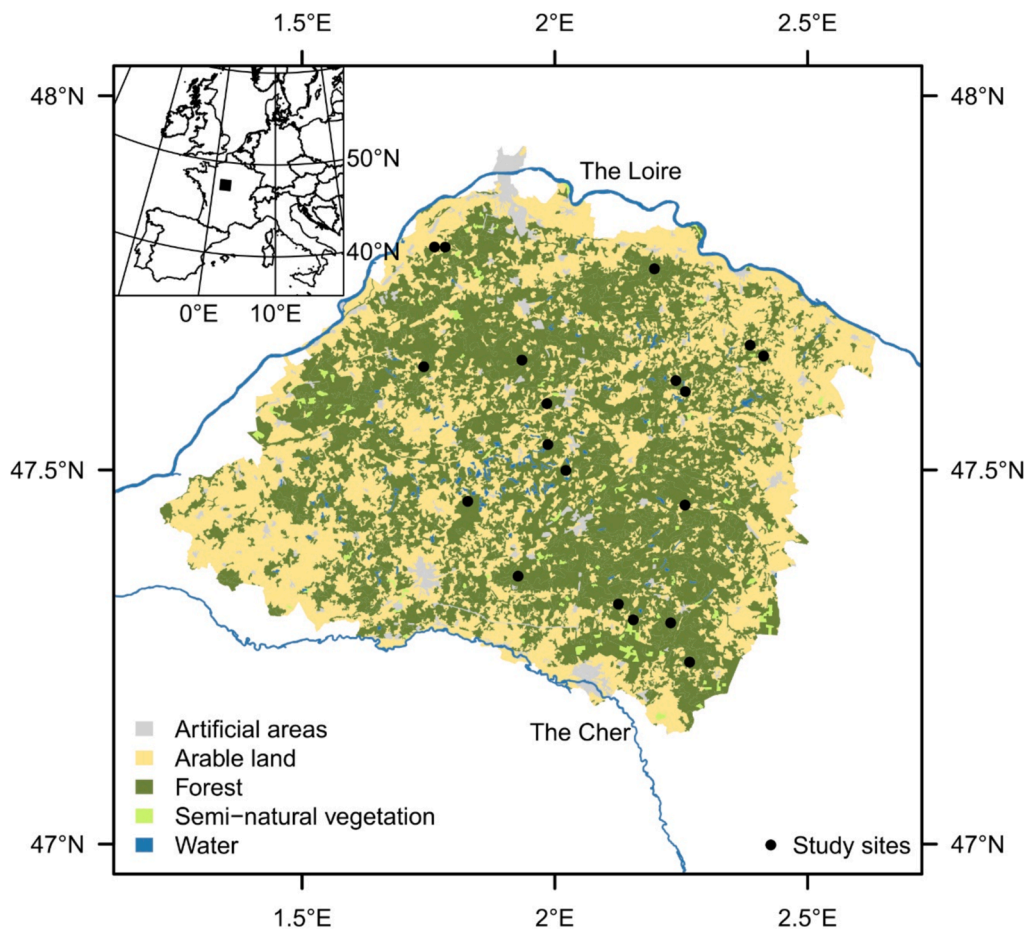


Fig. 1. Location of the study area (top left), the Sologne, a natural forest region in Centre-Val de Loire. Black dots indicate the geographical location of the sampled properties.

herbivory effects, or environmental factors. When studying herbivore effects along an intensity gradient, it is essential to avoid spurious/erroneous correlations (Landsberg and Crowley, 2004).

The study was conducted in 19 private properties with an area ranging between 120 and 879 ha. The properties were initially chosen according to a gradient of game species harvesting (i.e., hunting bag), for covering the extent of the available gradient. The mean forest cover was $80.38 \pm 2.58\%$ (mean \pm se) and the mean basal area was $18.6 \pm 0.47 \text{ m}^2/\text{ha}$ (mean \pm se), testifying to the relative canopy openness of the stands. The understorey was mainly composed of shrubs (e.g., *Calluna vulgaris*, *Rubus fruticosus*, *Hedera helix*), fern (e.g., *Pteridium aquilinum*, *Dryopteris* spp) and herbaceous species such as grasses (e.g., *Molinia caerulea*, *Deschampsia flexuosa*, *Carex pilulifera*) and forbs (e.g., *Fragaria vesca*, *Moehringia trinervia*, *Teucrium scorodonia*). Landowners managed the properties primarily for forestry and hunting purposes and no livestock grazing occurred at any of the study sites.

2.2. Sampling design

Plant community composition: We assessed the understorey plant composition in five 1000 m² circular plots per property ($n_{\text{tot}} = 95$). We estimated total plant diversity, by recording all vascular plant species in summer (June–July 2013) and visually assessed the cover of each species up to 2.0 m to account for the two deer species (see S1 for details). Sampling was carried out by five experienced botanists ($n_{\text{BotA}} = 75$, $n_{\text{BotB}} = 59$, $n_{\text{BotC}} = 26$, $n_{\text{BotD}} = 20$, $n_{\text{BotE}} = 10$) who formed mixed teams composed of two observers in order to minimise observer effects. A team was composed of either botanists A ($n = 36$) or B ($n = 20$) and any of the other botanists, or both of them ($n = 39$). In order to harmonise the

sampling effort among study plots, teams spent at least 30 min actively searching new species (Archaux et al., 2006), excluding extra time added for species identification problems and plant cover estimations. We used a relatively large sample plot size (1000 m²) as we were interested in capturing common and rare species while limiting the size in order to remain in a single forest habitat type. The relative abundance of each species was calculated in each plot from its cover (i.e., cover of individual species divided by the sum of the species cover, multiplied by 100).

Ungulate intensity gradient: We quantified winter deer browsing on the last year's shoots of woody and semi-woody plants (i.e., tree and shrub species) on three 40 m² circular subplots in late winter (March 2014), each situated 14 m from the centre of the study plot. This method has been shown to be an efficient and reliable method for estimating deer browsing pressure (Chevrier et al., 2012; Gaudry et al., 2022). We followed the modified Aldous method (Aldous, 1944) described in Morellet and Guibert (1999) in order to construct the browsing index to analyse the data along an intensity gradient. Plant cover (C, the horizontal projection of shoots, twigs and branches) and browsing intensity (B, the percentage of browsing marks) for each species were estimated visually, according to the percentage classes: 1: <1 %, 2: 1 %–5 %, 3: 5 %–20 %, 4: 20 %–50 %, 5: 50 %–75 %, 6: >75 %.

The browsing index (BI_{*j*}) (hereafter “deer intensity”) was calculated by weighting the intensity of browsing on each species by its relative cover according to the following formula:

$$BI_j = \frac{\sum_{i=1}^n C_{ij} * B_{ij}}{\sum_{i=1}^n C_{ij}}$$

where C_{ij} is the cover of plant species i at subplot j and B_{ij} is the percentage of available shoots browsed of plant species i at subplot j , for both deer species, i.e. up to 2 m height. Mid-point values of the classes were used for all calculations within each subplot and the mean values of the three subplots were used to estimate the overall deer browsing intensity. Finally, for specific analyses (see below), we defined four deer intensity groups: $\leq 7.5\%$, $7.5\text{--}15\%$, $15\text{--}25\%$ and $> 25\%$. We assumed that the observed browsing rates reflect the past browsing history as red and roe deer show high seasonal and yearly site fidelity (Richard et al., 2014).

2.3. Computing diversity indices

We calculated species richness, as the total number of species observed in each plot. We also calculated Shannon's evenness index. Evenness describes the pattern of relative species abundances in a community, a major component of functional plant diversity. A community with a more homogeneous distribution of species between functional groups should be less likely to lose complete functional traits following disturbances such as deer browsing (Fonseca and Ganade, 2001). Thus, a community with more functionally redundant species may be more resilient to the loss of function (Biggs et al., 2020). We assessed dissimilarity in species composition between plots by calculating the Bray-Curtis distance matrix (i.e., pairwise comparisons of community composition between plots based on species abundance). All the calculations were done using the package *vegan* (Oksanen et al., 2022), using the R computational environment, version 4.3.2 (R Core Team, 2023).

2.4. Trait selection and functional trait metrics

Plant functional traits are crucial for understanding responses to environmental disturbances, such as grazing and browsing, abiotic changes, such as soil water and nutrient availability, and for predicting overall plant community functioning (Petchey and Gaston, 2006; O'Gorman et al., 2011). Information about selected plant functional traits was retrieved from the TRY plant trait database, which computes information from an international collaborative research network (Kattge et al., 2020) (Table 1). We selected traits that were informative about different mechanisms by which ungulates disturb and interact with plant communities (e.g. herbivory, seed dispersal, soil disturbance). We used a single mean per species for each trait. When the species was not included in the database, we used the mean value of the nearest species found based on species morphological characteristics or the mean value for the genus (Table S1).

The community-weighted mean (CWM) for each trait was calculated for each plot corresponding to the average trait value of the plant community, weighted by the relative abundance of each species (Garnier et al., 2007; Lavorel et al., 2008). Log-transformation of some quantitative traits (i.e., seed dry mass and leaf area) was required to reduce the effects of extreme values. CWM is directly related to the biomass ratio hypothesis, which argues that ecosystem properties are influenced mainly by the characteristics of dominant plant species (Grime, 1998). As such, ecosystem function may equally depend on the dominant trait values of the communities. CWM was calculated using the `FD::functcomp` function (Laliberte and Legendre, 2010; Laliberte et al., 2014).

We calculated functional richness $FRic$ (i.e., the amount of functional space filled by the community) and functional redundancy $FRed$ (i.e., the ability of the community to maintain its function, inferred from multiple traits) to describe functional diversity. We first computed a multi-trait dissimilarity matrix between species traits using the *gawdis* package developed by de Bello et al. (2021a). This approach allowed us to deal with "fuzzy coded variables" and correlated variables, such as leaf traits and Grime's CSR strategies scores (Grime, 1974) to produce a more balanced contribution of traits. We then calculated the functional

Table 1

Selected functional traits and categories for the study (types, categories/units and main functional role in plant community functioning).

Trait	Type	Categories/units	Functional role
LEAF			
Specific Leaf Area (SLA)	Continuous	mm ² /mg	Competitive strength, Plant defence
Leaf Dry Matter Content (LDMC)	Continuous	g/g	Disturbance resistance
Leaf area	Continuous	mm ²	Competitive strength, Plant defence
VEGETATIVE			
Raunkier Plant life form	Categorical	Hemicytrophite Geophyte Chamaephyte Phanerophyte Therophyte	Competitive strength, Plant defence, Disturbance resistance (e.g., Light capture, above-ground competition, reproduction, seed dispersal)
Plant lifespan	Categorical	Annual (Annual + Bi-annual) Perennial (Short-, Medium- and Long-lived)	reproduction, seed dispersal
Plant functional type	Categorical	Graminoid Forb Shrub Tree Fern	
Plant height	Categorical	Small (0–1.2 m) Medium (1.2–2.0 m) Large (>2.0 m)	
Spinescence	Categorical	Yes/No	
REPRODUCTIVE			
Seed mass	Continuous	Mg	Disturbance resistance
Fruit type	Categorical	Dry Fleshy Spore	competitive strength (e.g., reproduction, seed dispersal)
PLANT STRATEGY and PREFERENCE			
Grime's CSR strategies	Continuous (unitless)	C-score (competitive) S-score (stress-tolerant) R-score (ruderal)	Disturbance resistance, competitive strength
Ellenberg indicator values	Ordinal (unitless)	Light (L) Nitrogen (N) Soil reaction (R)	

richness, using the function `FD::dbFD` and the functional redundancy, using the function `adiv::uniqueness` (Ricotta et al., 2016). These functions use the multi-trait dissimilarity matrix and the species abundance matrix as inputs.

2.5. Statistical analyses

To test the IDH, we investigated the relationship between plant species richness and the deer intensity gradient. We used generalised linear mixed effect models (GLMM), using the `lme4::glmer` function with a Poisson distribution (Bates et al., 2015). Due to the high number of zero values for the CWM of the fern plant functional type (i.e., 39 % of the plots), we applied a negative binomial, using the `lme4::glmer.nb` function (Bates et al., 2015). We added plots ($n = 95$) nested within the site ($n = 19$) as random factors in all analyses described hereafter to account for the hierarchical structure of the design (i.e. 5 replicates per study site) and thus avoid pseudoreplication (Zimmerman et al., 2021). We tested for a linear and unimodal relationships, by adding a quadratic component of deer intensity and compared models using partial F-test, checking AIC values and P value. We analysed total species richness and

richness per plant functional types as response variables. When the quadratic relationship performed better than the linear relationship, we tested the model against the null model to get the final significance of the model.

We used GLMM to test the effect of deer intensity on species evenness, using the `nlme::lme` function (Pinheiro et al., 2023). A permutational multivariate analysis of variance (PERMANOVA), with 9,999 permutations on the Bray-Curtis dissimilarities distance matrix, was also performed to test for the effect of deer intensity gradient on species community dissimilarity between plots, using `vegan::adonis2` function (Oksanen et al., 2022). We decomposed beta diversity into replacement (i.e., species turnover) and richness difference (i.e., nestedness) (Podani et al., 2013; Legendre, 2014) to assess the prevalent process involved in order to understand better how deer intensity affects the spatial dissimilarity in species composition among plots. Species replacement suggests that, along an ecological gradient, species tend to replace each other, while richness difference refers to the fact that one community includes a smaller or more extensive set of species than another. This analysis also used a matrix of dissimilarity in species composition between sites. It was performed based on presence/absence and abundance data (transformed to the arcsine of their square root prior to the analysis), using the `adespatial::beta.div.comp` function (Dray et al., 2023). For abundance data, Baselga (2013) defined species replacement as the balanced variation in abundance (i.e., a species is replaced by another species at the same magnitude of abundance) and richness difference as the abundance gradient (i.e., abundance of species increases or decreases equally between sites).

To visualise the effect of deer intensity on plant species composition (i.e., abundance data), we performed a non-metric multidimensional scaling ordination (NMDS) based on the Bray-Curtis distance measure between plots, using the function `vegan::metaMDS` (Oksanen et al., 2022). We used the function `vegan::ordisurf` to incorporate deer-intensity surfaces into the NMDS (Oksanen et al., 2022). This function uses the NMDS axes as predictors and runs a general additive model with the deer intensity data as the response variable. We performed both two-dimensional and three-dimensional NMDSs and retained the best fitting one based on the stress value (i.e., <0.2). Because we had a large set of species (i.e., 240 species in total), we used the function `goeveg::ordiselect` to select 20 % of the species that best fit the NMDS axes for representing the species distribution along the deer intensity gradient (von Lampe and Schellenberg, 2024). Finally, as few plots experienced high levels of deer intensity, and in order to display a more comprehensive graphical output, we also used the four groups defined for the index of deer intensity.

We used GLMM to test the effect of deer intensity on CWM of each trait and also on FRic and FRed, using the `nlme::lme` function (Pinheiro et al., 2023). As for the fern richness, we applied a negative binomial for the CWM of the fern plant functional type, using the `lme4::glmer.nb` function. Similarly, we assessed the relationship between FRic and species richness, using the `nlme::lme` function. When significant, we also tested for either a linear or unimodal relationship, by adding a quadratic component of the deer intensity, and compared models using AIC values and P value.

We decomposed functional beta diversity into trait replacement (i.e., dissimilarity due to the replacement of some traits by others) and trait richness difference (i.e. dissimilarity due to differences in functional richness among communities) using the function `BAT::beta` (Cardoso et al., 2013; Cardoso et al., 2014), after transforming our multi-trait dissimilarity matrix into a functional tree using `stats::hclust` function (R Core Team, 2023). We performed a PERMANOVA, with 9,999 permutations on the dissimilarity distance matrix obtained to test for the effect of deer intensity gradient.

Finally, to determine whether particular plant species were significantly associated with some of the four deer intensity index BI groups, we performed a species indicator analysis following the functional-based approach developed by Ricotta et al. (2020). This method

identifies the indicator species based on species abundance and functional traits by calculating the functional distance between the indicator species and the functional centroids of all plots in each group. A species indicates a given group when its mean functional distance from the plot centroid is significantly lower than expected by chance (Ricotta et al., 2015). We computed the positive functional association, ϕ , between each group and a given species j of plot k as the proportion of 999 permutation-derived values of ϕ_{jk} that is as high or higher than the actual value.

3. Results

3.1. Deer intensity and plant richness relationship

The deer intensity gradient ranged from 0.64 % to 79.74 %, presenting an unbalanced distribution with 63 % of the plots with a browsing intensity inferior to 20 %, 25 % with a browsing intensity between 20 and 40 % and only 12 % with a browsing intensity superior to 40 %. However, our plots were evenly distributed within the four groups of browsing intensity (i.e., ≤ 7.5 %, 7.5–15 %, 15–25 % and >25 %), with 22.1, 26.3, 25.3 and 26.3 % of the plots respectively.

Total species richness was highly variable among plots ranging from 8 to 60 species, for a total set of 240 species. The study revealed that deer intensity had a high and overall positive effect on the total species richness (mean \pm SD: 32 ± 14 species, $P < 0.001$), and the richness of graminoids (8 ± 5 species, $P < 0.001$) and forbs (8 ± 7 species, $P < 0.001$) (Fig. 2, Table S2) for which we observed a hump-shaped pattern, in agreement with the IDH. We also observed a positive and significant linear relationship between deer intensity and shrub richness (8 ± 3 species, $P = 0.019$). On the contrary, deer intensity did not affect the species richness of ferns (1 ± 1 species; $P = 0.055$) and trees (7 ± 2 species; $P = 0.967$).

Overall deer intensity did not affect species evenness ($t = -1.14$, $P = 0.259$). However, we found a significant negative effect on species evenness of graminoids ($t = -2.14$, $P = 0.035$), a significant positive effect on species evenness of forbs ($t = 2.24$, $P = 0.031$) and trees ($t = 3.19$, $P = 0.002$) and no effect on species evenness of shrubs ($t = -0.84$, $P = 0.408$) and ferns ($t = 1.81$, $P = 0.076$).

Deer intensity affected plant community composition. We found a significant effect on plant dissimilarity ($F = 3.7425$, $P < 0.001$), though it accounted for a relatively small amount of the variation in composition (3.9 %). For both presence/absence data and abundance data, we found that species dissimilarity between plots was due to species replacement rather than richness difference (Fig. 3). Species replacement accounted for 58.3 % of the total β -diversity when using presence/absence data but up to 80.6 % with abundance data. The three-dimensional NMDS ordination, with a final stress value of 0.16, revealed distinct patterns along the four groups of deer intensity (Fig. 4A). Species distribution, as shown in two dimensions for a better graphical representation, also showed a distinct pattern according to the deer intensity gradient (Fig. 4B). Ericaceous shrub species (e.g., *Erica cinerea*, *Calluna vulgaris*) and tree (e.g., *Pinus sylvestris*, *Pseudotsuga menziesii*, *Quercus ilicifolia*) species best fitted to the axes at low deer intensities. In contrast, higher proportions of graminoids and forbs species were associated with increasing deer intensities. Results also highlighted that rarer species, i.e. species that occurred in less than 5 % of the sampling plots (e.g., *Carex elongata*, *Elymus canina*, *Epilobium lanceolatum*, *Rumex conglomeratus*) appeared at deer intensities above 30 %.

3.2. Deer intensity and plant functional trait space

3.2.1. Species leaf traits

While deer intensity significantly increased CWM of specific leaf area ($P < 0.001$), showing a hump-shaped pattern with a maximum value at an intermediate level of intensity (Fig. 5A), CWM of leaf dry matter

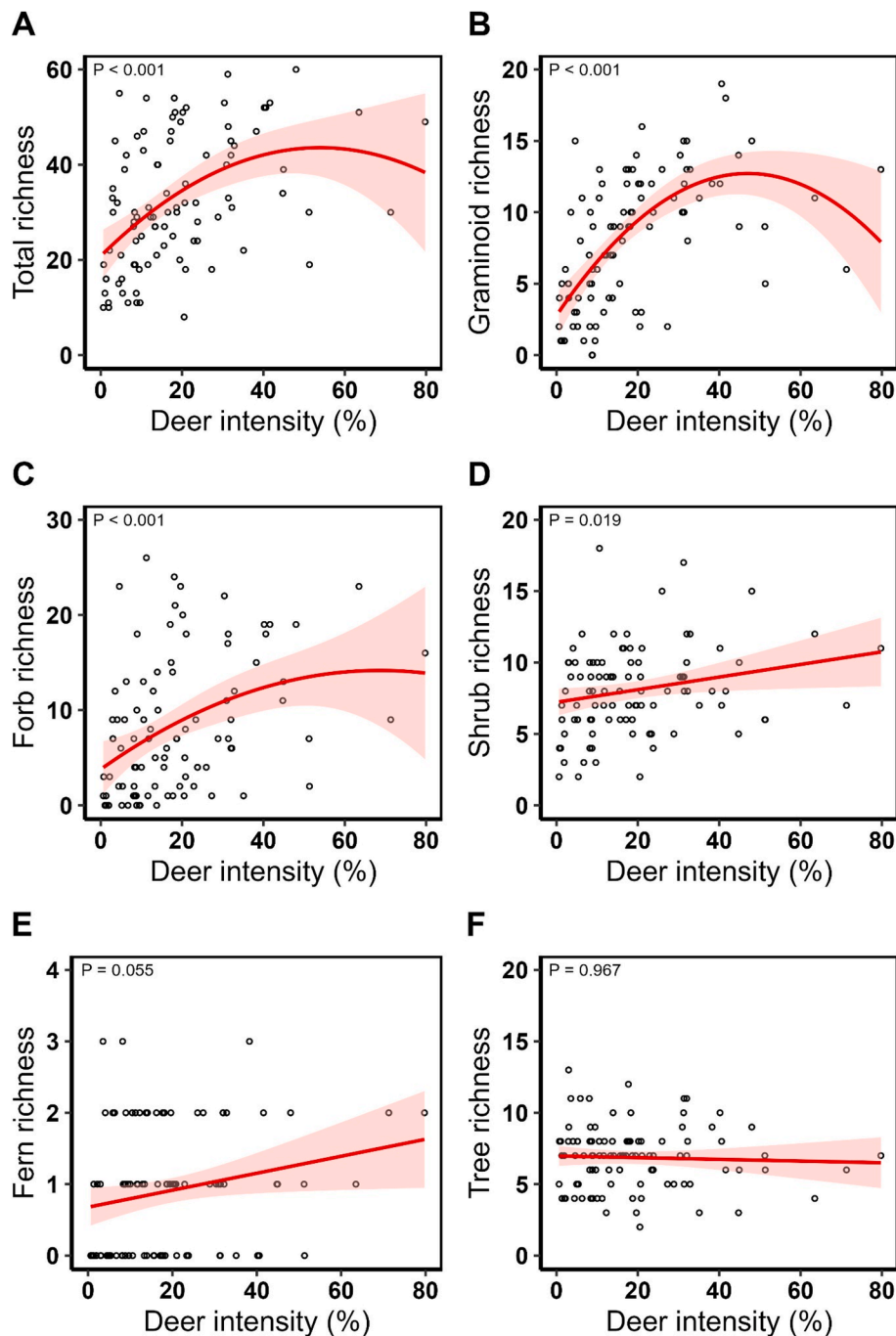


Fig. 2. Relationship between deer intensity and total species richness (A) and species richness for plant functional type (B-F) of the forest understory in the Sologne Natural Region in the centre of France. Red lines are shown for the selected models (linear vs quadratic), taking into account random effects (i.e., plots within each site) from the mixed effects modelling (at 95% confidence interval). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

content exhibited a decreasing trend with deer intensity ($P < 0.001$), with a slight inverse hump-shape curve. We found no effect on CWM of the leaf area ($t = 0.24$; $P = 0.812$).

3.2.2. Vegetative traits

Raunkier's plant life forms. Deer intensity had a significant, positive and linear effect on CWM of geophytes ($t = 2.17$, $P = 0.034$) and therophytes ($t = 2.02$, $P = 0.047$). We also observed a significant and positive effect on hemicryptophytes (i.e., trees and tall shrubs) ($P < 0.001$), showing a hump-shaped pattern with maximum value at intermediate levels of disturbance (Fig. 5B). Moreover, deer intensity had a

significant, negative and linear effect on CWM of phanerophytes ($t = -4.89$, $P < 0.001$). We found no effect on CWM of chamaephytes ($t = -1.37$, $P = 0.17$).

Plant lifespan. While we found a significant, positive and linear effect of deer intensity on CWM of annuals ($t = 2.72$, $P = 0.008$) and short-lived ($t = 4.18$, $P < 0.001$) perennials, we found no effect on CWM of medium-lived species but a significant, negative and linear effect on the CWM of long-lived perennials ($t = -3.33$, $P = 0.001$).

Plant functional types. Deer intensity had a positive significant effect on CWM of graminoids, which peaked at intermediate intensity levels ($P < 0.001$). On the contrary, deer intensity had a significant

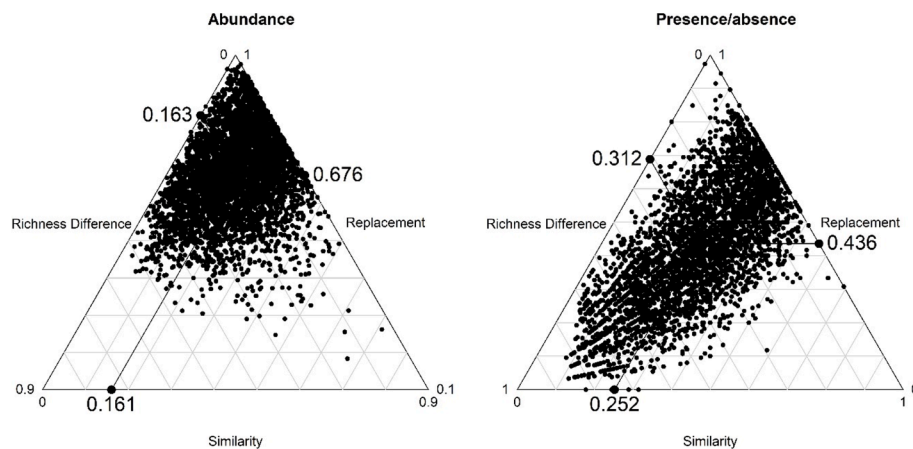


Fig. 3. Simplex ternary plots of beta-diversity partitioning of taxonomic diversity for the survey sites in the Sologne Natural Region in the centre of France. Each black dot represents a pair of sites. The noted values represent the values for the similarity, the difference and the replacement components. (A) With the Ružička dissimilarity coefficients for abundance data, and (B) the Jaccard dissimilarity coefficients for Presence/Absence data, both from the Podani coefficient family.

negative effect on CWM of trees, with a slight inverse hump-shaped curve ($P < 0.001$) (Fig. 5C). In contrast, we found no effect on CWM of shrubs ($t = -1.11$, $P = 0.27$), forbs ($t = 1.59$, $P = 0.12$) and ferns ($z = 1.48$, $P = 0.14$).

Plant height. While deer intensity had a significant, positive and linear effect on CWM of small-size plant species ($t = 4.91$, $P < 0.001$), we observed a significant, negative and linear effect on CWM of large-size species ($t = -3.56$, $P < 0.001$) (Fig. 5D). We found no effect on CWM of medium-size species ($t = 0.005$, $P = 0.99$).

Plant defence strategies. Deer intensity did not significantly affect CWM of plant defence strategies (i.e., Spiny species) ($t = -0.31$, $P = 0.76$).

3.2.3. Reproductive traits

Deer intensity had a strong and significant effect on CWM of dry seed mass ($t = -2.65$, $P = 0.009$), showing a negative linear trend (Fig. 5E). However, we found no effect on CWM for fruit type (i.e., dry ($t = 0.56$, $P = 0.58$), fleshy ($t = -0.61$, $P = 0.54$) or spore ($t = 1.09$, $P = 0.27$).

3.2.4. Plant strategy and preference

Deer intensity had a significant, positive and linear effect on CWM of ruderal species ($t = 5.46$, $P < 0.001$) but a significant, negative and linear effect on CWM of stress-tolerant species ($t = -3.61$, $P < 0.001$) (Fig. 5F). We found no effect on CWM of competitive species ($t = 0.74$, $P = 0.46$), or for L ($t = 0.31$, $P = 0.75$), N ($t = 1.37$, $P = 0.18$) and R ($t = 0.07$, $P = 0.94$) Ellenberg values.

3.2.5. Functional diversity indices

Functional richness was strongly correlated with species richness through a quadratic relationship ($r^2 = 0.79$; $P < 0.001$, Fig. 6A). Deer intensity had a significant, positive and linear effect on functional richness ($t = 3.72$, $P < 0.001$) (Fig. 6B) and a significant, negative and linear effect on functional redundancy ($t = -2.45$, $P = 0.017$) (Fig. 6C).

We found that the functional dissimilarities between plots were due to trait replacement rather than trait difference (Fig. 6D), accounting for 76.89 % of the total β functional diversity. Functional dissimilarity was significantly associated with deer intensity (PERMANOVA test: $F = 8.3245$, $P < 0.001$), though it accounted for a relatively small amount of the variation in composition (8.2 %).

3.3. Species indicator analysis

We identified 24 species as indicator species (Table S3). Two shrub species, *Erica cinerea* and *Ilex aquifolium* and one tree species *Pinus sylvestris*, were only associated with the first group of plots showing the

lowest deer intensity (BI < 7.5 %). The graminoid *Agrostis canina*, the shrub species *Crataegus monogyna* and the tree species *Betula pubescens* were strictly associated with the third group with plots at medium levels of deer intensity ($15 < BI \leq 25$ %). Two graminoid species, *Poa nemoralis* and *Holcus lanatus* and one tree species *Quercus rubra* were only associated with the fourth group, including plots with the highest deer intensities (BI > 25 %). We found no species only linked to the second group of deer intensity ($7.5 < BI \leq 15$ %).

We observed three species associated with the four deer intensity groups: one graminoid species, *Deschampsia flexuosa*, and two shrub species, *Lonicera periclymenum* and *Rubus fruticosus*. Excluding these three species, the first group was represented by only shrub and tree indicator species. We observed an increase in the proportion of graminoids as deer intensity increased, from the second to the fourth group, with 2, 4 and 5 species, respectively. Finally, bracken fern, *Pteridium aquilinum*, was associated with the second, third and fourth groups of deer intensity but not with the first group. In contrast, ivy *Hedera helix* was associated with the first three groups but not the fourth one.

4. Discussion

Deer browsing affects plant understorey communities but few studies have explored the IDH in forest ecosystems, as in temperate (Suzuki et al., 2013) or boreal ecosystems (Suominen et al., 2008). Indeed, most studies used deer enclosure experimental design (e.g., Perrin et al., 2011; Nishizawa et al., 2016; Chollet et al., 2021), which usually does not allow to establish multiple levels of deer intensity and define a threshold to maximise plant biodiversity (Hester et al., 2000; but see Tremblay et al. (2006) on Anticosti Island). Our study showed that deer intensity affected species communities. Although our deer intensity gradient was truncated and did not reach 100 % and that few plots experienced browsing rates higher than 60 %, we found, as expected, support for IDH in terms of taxonomic richness. We revealed this pattern for total species richness with a maximum reached around 55 % deer intensity, followed by a decrease of richness. At higher browsing intensity, this may eventually cause an overall reduction in species richness, as showed in previous studies (e.g., Suzuki et al., 2013; Begley-Miller et al., 2014). At the plant functional type level, species richness of graminoids peaked at around 45 % and forbs at 70 % deer intensity. These two groups fitted the IDH closely and explained much of the overall pattern for total species richness. On the other hand, the species richness of ferns and shrubs increased linearly, while tree species richness decreased along the deer intensity gradient. Hegland et al. (2013) also showed that forbs agreed with the IDH, but they found that graminoid species richness increased linearly along the red deer intensity gradient in a boreal old-

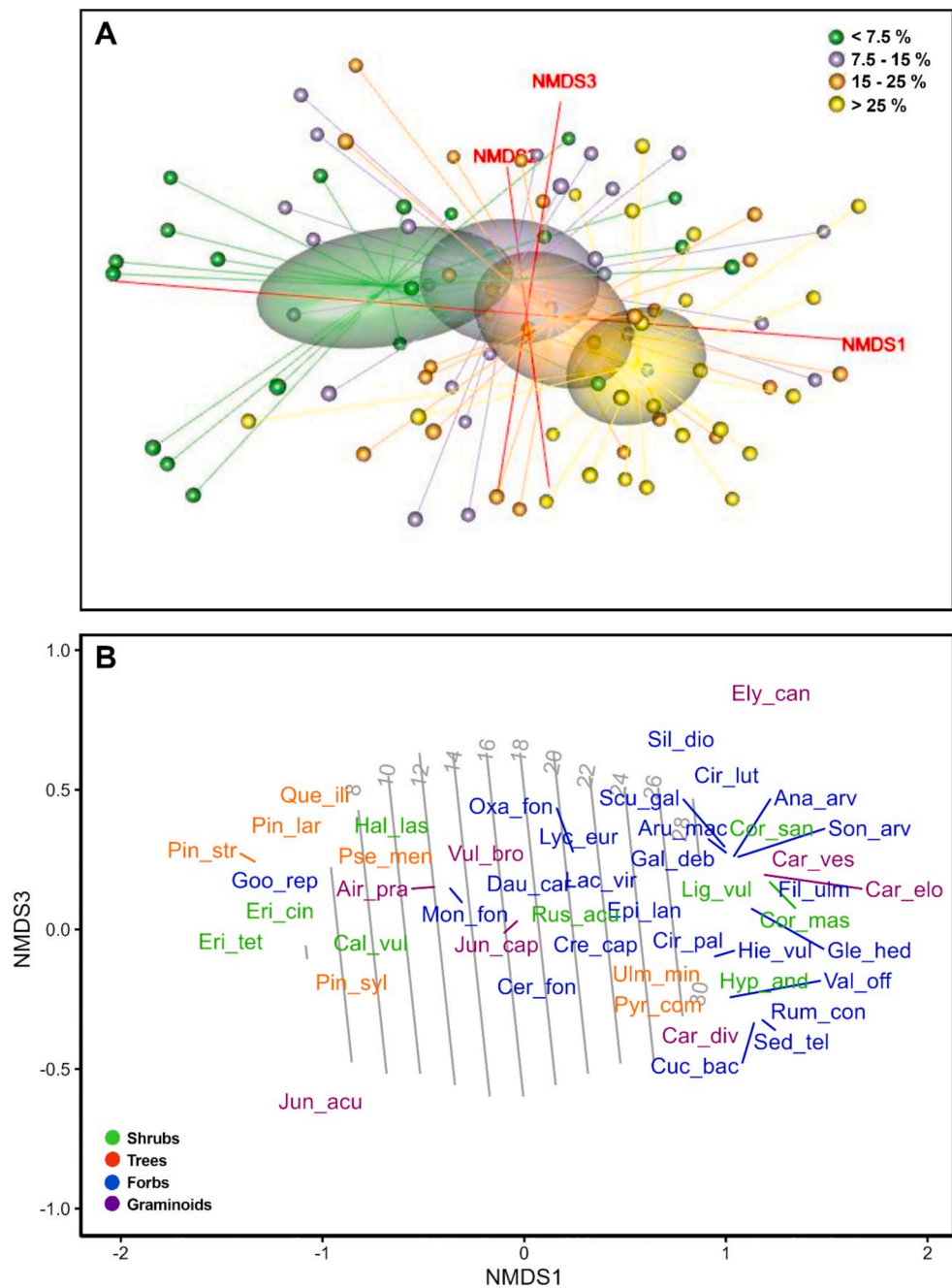


Fig. 4. Non-metric multidimensional scaling (NMDS) based on species abundance. (A) 3D representation of the dispersion of the plots according to the four groups of deer intensity (with 95% confidence). (B) 2D representation of the species distribution along the deer intensity gradient. 20% of the species with the best fit to the axes are represented (Species selected using the function ordiselect. Air_pra: *Aira praecox* (G), Ana_arv: *Anagallis arvensis* (F), Aru_mac: *Arum maculatum* (F), Cal_vul: *Calluna vulgaris* (S), Car_div: *Carex divulsa* (G), Car_elo: *Carex elongata* (G), Car_ves: *Carex vesicaria* (G), Cer_fon: *Cerastium fontanum* (F), Cir_lut: *Circaea lutetiana* (F), Cir_pal: *Cirsium palustre* (F), Cor_mas: *Cornus mas* (S), Cor_san: *Cornus sanguinea* (S), Cre_cap: *Crepis capillaris* (F), Cuc_bac: *Cucubalus baccifer* (F), Dau_car: *Daucus carota* (F), Ely_can: *Elymus caninus* (G), Epi_lan: *Epilobium lanceolatum* (F), Eri_cin: *Erica cinerea* (S), Eri_tet: *Erica tetralix* (S), Fil_ult: *Filipendula ulmaria* (F), Gal_deb: *Galium debile* (F), Gle_hed: *Glechoma hederacea* (F), Goo_rep: *Goodyera repens* (F), Hal_las: *Halimium lasianthum* (S), Hie_vul: *Hieracium vulgatum* (F), Hyp_and: *Hypericum androsaemum* (S), Jun_acu: *Juncus acutiflorus* (G), Jun_cap: *Juncus capitatus* (G), Lac_vir: *Lactuca communis* (F), Lig_vul: *Ligustrum vulgare* (S), Lyc_eur: *Lycopus europaeus* (F), Mon_fon: *Montia fontana* (F), Oxa_fon: *Oxalis fontana* (F), Pin_lar: *Pinus laricio* (T), Pin_str: *Pinus strobus* (T), Pin_syl: *Pinus sylvestris* (T), Pse_men: *Pseudotsuga menziesii* (T), Pyr_com: *Pyrus communis* (T), Que_ili: *Quercus ilicifolia* (T), Rum_con: *Rumex conglomeratus* (F), Rus_acu: *Ruscus aculeatus* (S), Scu_gal: *Scutellaria galericulata* (F), Sed_tel: *Sedum telephium* (F), Sil_dio: *Silene dioica* (F), Son_arv: *Sonchus arvensis* (F), Ulm_min: *Ulmus minor* (T), Val_off: *Valeriana officinalis* (F), Vul_bro: *Vulpia bromoides* (G)). The functional type is shown in brackets and the species are written in a different colour for each group: G (Graminoid in purple), F (Forb in blue), S (Shrub in green) and T (Tree in orange). The intensity gradient is represented by the vertical grey lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

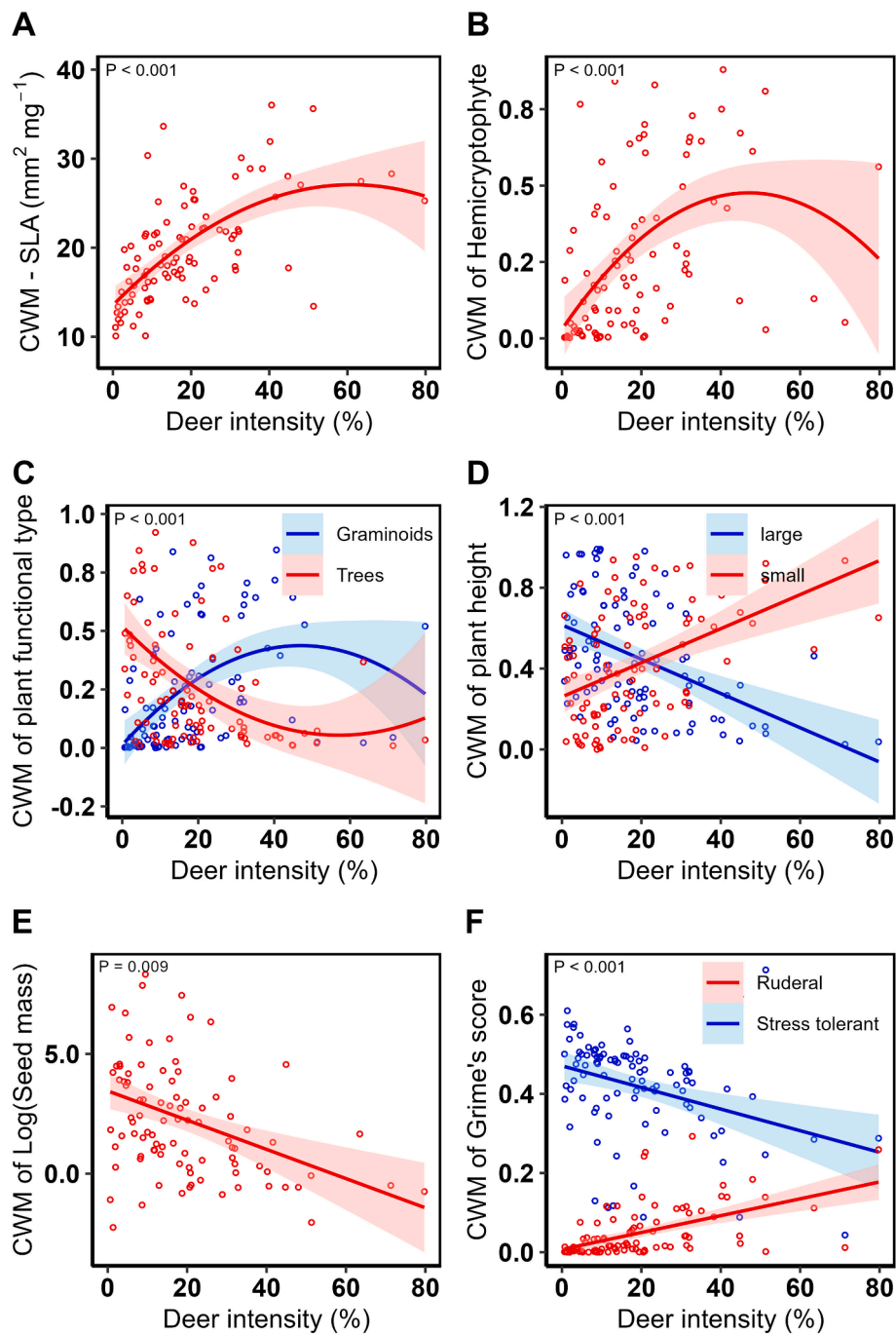


Fig. 5. Relationship between deer intensity and community weight mean (CWM) of plant functional traits: (A) Specific Leaf Area (SLA), (B) hemicryptophyte, (C) graminoid and tree functional types, (D) ferns, (E) seed dry mass and (F) Grime's S-score (Stress-tolerant species) and R-score (Ruderal species). Lines are shown for the selected models (linear vs quadratic), taking into account the random effects (i.e., plots within each site) from the mixed effects modelling (at 95% confidence interval).

growth forest, dominated by pine. In contrast, they found a linear decrease in shrub species richness. These results highlight how context-dependent these interactions are, making their generalisation risky (Hawkes and Sullivan 2001; Speed et al., 2014). Indeed, the deer intensity value at which e.g. species richness peaks (according to the IDH) may depend on the plant species composition, herbivore species and their feeding preferences, and local abiotic factors.

Besides species richness, analysis of plant functional traits may determine how ecosystems respond to disturbance in terms of functioning and stability (de Bello et al., 2021b). For instance, looking at how our plant functional traits responded to deer intensity, we did not

find any effect on the CWM of shrubs. This may be explained by species replacement within the same functional type, as Lilleeng et al. (2016) observed. Palatable shrub species may have been gradually replaced by less palatable species, thus increasing species richness but without changing the overall proportion of shrub species within the plant community. As stated above, it is worth noting that our deer intensity gradient does not cover the full gradient. For example, Arcese et al. (2014) showed that, at extreme deer intensity, even unpalatable shrubs were consumed, leading to an overall decline in both shrub species richness and cover. The same pattern may have also occurred with perennials forbs, as their CWM did not vary along the deer intensity

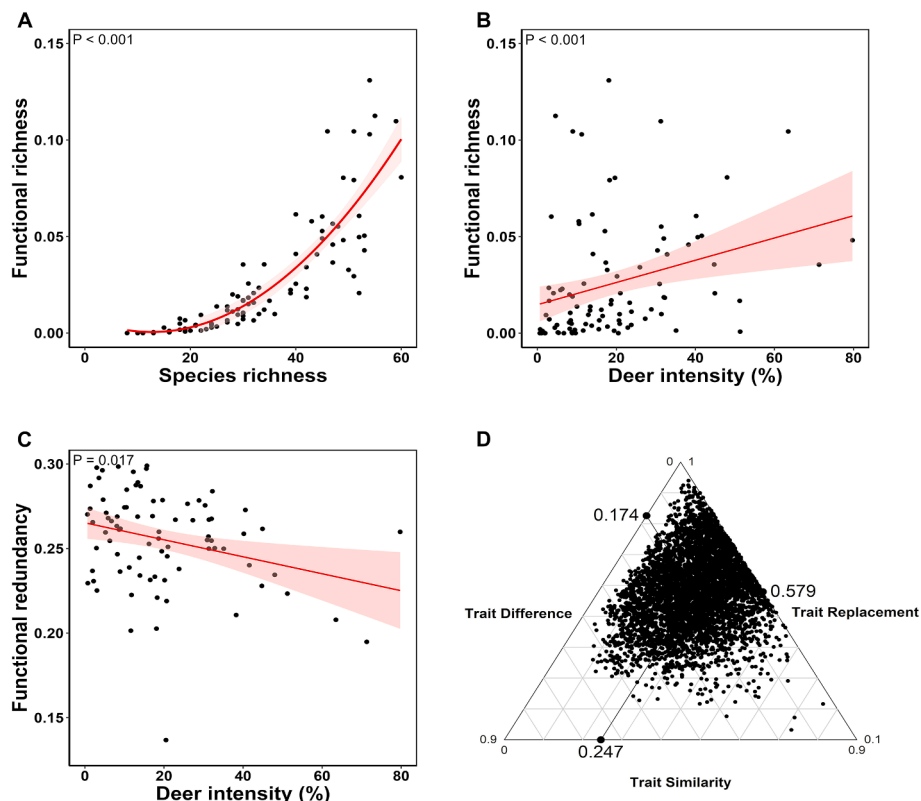


Fig. 6. A) Relationship between species richness and functional richness (at 95% confidence interval), B) Relationship between deer intensity and functional richness, C) relationship between deer intensity and functional redundancy and D) Simplex ternary plots of beta-diversity partitioning of functional diversity. The noted values represent the values for the similarity, the difference and the replacement components.

gradient. Contradictory to Hegland et al. (2013), we showed that deer intensity did not affect tree species richness. However, deer intensity negatively affected the CWM of the tree type, similar to the effects on CWM of phanerophytes. This means that, even if the number of species remained unchanged along the gradient, deer intensity decreased the overall proportion of tree species within the communities. This decrease, in turn, opened up gaps in the understory and reduced competition, allowing herbaceous species to colonise the understory (Boulanger et al., 2018; Davis et al., 2000). Moreover, tree evenness increased along the gradient, suggesting that deer may have browsed more competitive and palatable species, allowing newcomers of other functional types to colonise the understory. Finally, we observed increased CWM of the fern type, as shown by others (e.g., Horsley et al., 2003; Nuttle et al., 2014).

Overall, analyses of CWM trait values revealed that increased deer intensity favoured species indicative of moderate to heavily disturbed environments, specifically displaying ruderal traits including high SLA, low LDMC, short, annual or biannual lifespans (e.g., therophytes), short height and small seed mass, as found by others. For example, Boulanger et al. (2018) also found that ruderal species were favoured by wild ungulates along a stratified sample of 102 permanent plots in French managed forests. This may indicate a fast recovery of foliar investment and return of matter and energy, a typical resource use strategy, developed by ruderal species (Wright et al., 2004; Gorné and Dias, 2022; Wingler and Sandel, 2023). We observed increased ruderal plant strategies along our deer intensity gradient consistent with a trade-off with stress-tolerant plant strategies (i.e., indicative of low disturbance) associated with longer life-spans, likely due to deer feeding preferences (Busch et al., 2019). Moreover, we did not find any effect on the CWM of competitive species, especially for light that could be expected if forest specialist of late successional forest stage and shade tolerant species are browsed and replaced by light-demanding species (Boulanger et al.,

2018). This may be explained because of the relatively open tree canopy layer and the restricted geographical range of the study sites, limiting competition for light and abiotic resources. This was also supported by the non-significant effects on the CWM of the different Ellenberg values. Nonetheless, we observed a decrease in some competitive traits, such as tall plant height and long-lived life forms (i.e., tree functional type and phanerophytes). The shift observed in functional trait composition aligns with previous findings concerning grazing intensity (Wiegmann and Waller, 2006; Díaz et al., 2007).

Our indicator species analysis revealed patterns similar to those of species distribution along our deer intensity gradient. We identified three browsing-tolerant species, that do not indicate a given browsing intensity. Indeed, *Deschampsia flexuosa*, *Lonicera periclymenum* and *Rubus fruticosus* which were associated with the four levels of deer intensity, are commonly browsed by deer (Groot Bruinderink and Hazebroek, 1995; Morellet et al., 2001). A “sit and wait” strategy may also explain their persistence, waiting for opportunities for proliferate such as disturbance release. For example, Laurent et al. (2017) showed that *Rubus* spp. fastly regrew after deer exclusion, while Ladwig and Meiners (2010) showed that lianas, as *Lonicera* spp. increased in cover after agricultural activities abandonment. Such strategy may also explain the presence of *Hedera helix* within the three first levels of deer intensity and its absence in the plots most subject to animal pressure could be considered as a delayed indicator of disturbance. Except for the perennial graminoid *D. flexuosa*, only shrub and tree species emerged from the indicator species analysis under very light deer intensity, with species known to be browsing sensitive, such as *Pinus sylvestris* and *Quercus petraea* (Palmer and Truscott, 2003; Mårell et al., 2018). Graminoid indicator species abundance increased with deer intensity, as showed by others (e.g., Horsley et al., 2003; Côté et al., 2004; Begley-Miller et al., 2014). Graminoids are considered browse tolerant species, able to regrow due to the presence of basal meristems (Coughenour 1985).

However, these species were neither annual nor biannual, suggesting that short-lived species fail to maintain sufficient abundance to fulfil the criteria of an indicator species, as also attested by the negative relationship between graminoids evenness and deer intensity gradient. Thus, highly competitive, perennial and less palatable species, such as *Molinia caerulea*, *Holcus lanatus* and *Agrostis capillaris* may dominate the plant communities, thereby suppressing other less competitive species (Kirby, 2001; Gaertner et al., 2010). *Quercus rubra*, an exotic competitive species, was only associated with plots that experienced the highest level of deer intensity. Although this species is known to be browsed by deer, deCalesta et al. (2016) showed that trees from the white oak group, such as *Q. petraea*, are generally selected over those of the red oak group, such as *Q. rubra*.

Beside species replacement, as observed in our study, functional traits play a greater role in ecosystem functionality and stability. The system may be able to buffer the effects of disturbance to plant community by the replacement of species by others with similar traits, as stated by the “Insurance hypothesis” (Yachi and Loreau, 1999). Different taxonomic species may thus perform similar function and contribute to ecosystem resistance to disturbance (Oliver et al., 2015). These response traits require that species exhibit some redundancy in their traits allowing similar contribution to ecosystem processes (Hooper et al., 2005). In our study, although we showed an increase in functional richness, which increased with total species richness along the deer intensity gradient, we also showed a decrease in functional redundancy. Species were gradually replaced by others bearing different traits. Over time, this may eventually induce biotic homogenization by favouring more competitive and browsing- and disturbance-tolerant species (Wiegmann and Waller, 2006). This has implications for ecosystem functioning by increasing ecosystem vulnerability to future disturbances (Laliberte et al., 2010; de Bello et al., 2021b). Because our study was conducted at sites with similar abiotic characteristics (e.g., soil, climate and forest cover), we showed that deer significantly drive the plant community assembly, by altering plant species identity and functional traits, acting as a biotic filter (Begley-Miller et al., 2014, Chollet et al., 2021). Our results also highlighted that functional variability among species may play a higher role than taxonomic richness alone when defining ecosystem diversity (Cadotte et al., 2011). More research is needed, especially along a broader deer spatial or temporal intensity gradient, to understand the long-term effect of deer on ecosystem functioning and stability.

CRedit authorship contribution statement

Xavier Lecomte: Writing – review & editing, Writing – original draft, Formal analysis. **Christophe Baltzinger:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Anders Mårell:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2024.112766>.

Data availability

I have shared the link to my data at the attach file step

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