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Research article

Intensive feeding modifies nutrient patterns in a strictly protected area

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ABSTRACT

Recovering deer populations are causing conflict across Europe, especially in the vicinity of protected areas where densities are generally higher. Consequently, a variety of management approaches, such as the provision of winter feeding, have been deployed to keep deer from foraging in undesired areas in an attempt to mitigate conflicts. However, as large ungulates play a key role in nutrient recycling and redistribution, management actions that affect their space use and introduce additional nutrients into a system may translate into changes in the biogeochemistry of protected areas. Yet, little is known about the implications of such deer-management strategies on nutrient patterns. Here, we tested the effects of intensive supplementary feeding in combination with winter enclosures on nutrient distribution in a strictly protected area in Central Europe, the Bavarian Forest National Park. We found significant effects of the current management approach on plant nutrients with elevated nutrient concentrations not only within, but, importantly, extending up to several hundred meters around the enclosures/feeding stations. The increased nutrient concentrations could have cascading consequences for soil microbial activity, plant community composition and other herbivores. Our results illustrate that management actions designed to solve a specific problem (mitigating human-wildlife conflict), may alter local landscape chemistry and influence broader ecosystem functions. Ultimately, this may compromise conservation success, highlighting the need to critically evaluate all potential consequences of common management approaches such as supplementary feeding.

1. Introduction

While many European species face population declines (European Environment Agency, 2020), some mammalian wildlife has made strong comebacks over the last decades (Ledger et al., 2022; Ritchie, 2022). The population of red deer (*Cervus elaphus*), for example, has increased by more than 300 % since 1960, due to natural recolonization, changes in hunting regulation, higher habitat quality and more available area, and the absence of large predators (Ledger et al., 2022; Linnell et al., 2020). Such changes in animal numbers can be expected to have a corresponding impact on ecosystem functioning, such as a reduction in plant biomass, changes in soil structure or an increase in heterogeneity of vegetation structure (Bakker et al., 2016; Harrison and Bardgett, 2004; Trepel et al., 2024a,b). However, these impacts are not equally welcomed by the different stakeholders (Gerner et al., 2011; Valente et al., 2020) and the recovery of deer has led to conflicts with farmers and foresters (Côté et al., 2004), particularly due to concerns about economic damage in the forest and agricultural sector (Ammer, 1996; Kuijper, 2011; Putman and Moore, 1998). As a result, red deer are often the target of severe management interventions such as large-scale annual culls (around 20 % of the population in Scotland (Ferraro and Hirst, 2024; The Deer Working Group, 2019)) or the mandatory hunting of any individual outside legally specified red deer areas in Germany (Kinser et al., 2010).

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The conflict between the economic interests of the forest sector and nature conservation can be particularly pronounced in the vicinity of protected areas, which are home to comparatively large wildlife populations. Although these areas are intended to actively conserve natural processes and dynamics, they are often too small to cover the range of the resident large mammal populations (Hurley et al., 2012; Janzen, 1983; van Beeck Calkoen et al., 2020) – especially if they exhibit seasonal migratory behavior (as is the case with red and roe [*Capreolus capreolus*] deer (Cagnacci et al., 2011; Mysterud et al., 2011; Peters et al., 2019)). National parks (NP) follow different management approaches to mitigate conflicts that arise when animals move outside NP boundaries. A common strategy is the provisioning of supplementary feeding to attract deer away from conflict areas (van Beeck Calkoen et al., 2020). The Bavarian Forest NP (BFNP) in south-eastern Germany, for example, attracts the majority of the local deer population into winter-enclosures, where they receive substantial amounts of supplementary fodder throughout the winter (~5–6 months). This is in an attempt to prevent the deer from bark peeling and browsing in forestry enterprises outside the national park. This strategy concentrates deer impact in the enclosures and the surrounding areas. Not all deer are enclosed but the highly social nature of red deer (Albery et al., 2022; Alves et al., 2013) in combination with baiting attracts remaining free-ranging deer to congregate in the areas surrounding the enclosures (Möst et al., 2015).

Such localized gathering of high numbers of deer can alter their ecological impact potentially affecting ecosystem functioning. One of the animal impacts less frequently talked about, but increasingly recognized, is the key role that animals play in recycling and redistributing nutrients (Hobbs, 1996; McInturf et al., 2019; Schmitz et al., 2018; Subalusky and Post, 2019). By eating in one place, and then excreting, egesting or dying elsewhere, animals can have pronounced effects on nutrient patterns and dynamics through the distribution of bioavailable nutrients. Large herbivores (i.e. > 100 kg) are thought to be particularly important for nutrient dynamics due to their high food consumption, their greater dispersal distances and their ability to access nutrients that are not available to smaller consumers (i.e. locked up in less digestible vegetation biomass) (Doughty et al., 2013; Hobbs, 1996; Wolf et al., 2013). Changes in nutrient regimes can influence ecosystem composition and functioning (Bobbink et al., 2010; Naiman, 1988), and yet little is known about how management actions - such as intensive supplementary feeding and the artificial concentration of animals into small areas for extended periods of time - affect the influence of animals on nutrient patterns and dynamics (Abraham et al., 2022; Trepel et al., 2024a,b). Therefore, we sought to investigate the influence of red deer population management (i.e., intensive supplementary feeding with associated elevation deer density) on soil and plant nutrients in the Bavarian Forest NP. Specifically, we expect that by providing large quantities of food and congregating the majority of the red deer population in and around enclosures, management indirectly elevates soil and plant nutrient concentrations locally. While we expect these impacts to be most pronounced closest to the enclosures, we also explore the spatial extent over which these impacts manifest.

2. Methods and material

2.1. Study area

The Bavarian Forest NP is a strictly protected area (IUCN category II) in southeastern Germany, close to the German-Czech border (Fig. 1). It was established in 1970 and covers an area of ~250 km^2. The NP is located in the Bohemian Forest Ecosystem and is inhabited by many Central European large mammals (i.e., red deer, roe deer, wild boar [*Sus scrofa]*, wolves [*Canis lupus*] and lynx [*Lynx lynx*]). The elevation ranges from 600 to 1453 m above sea level, mean annual precipitation ranges

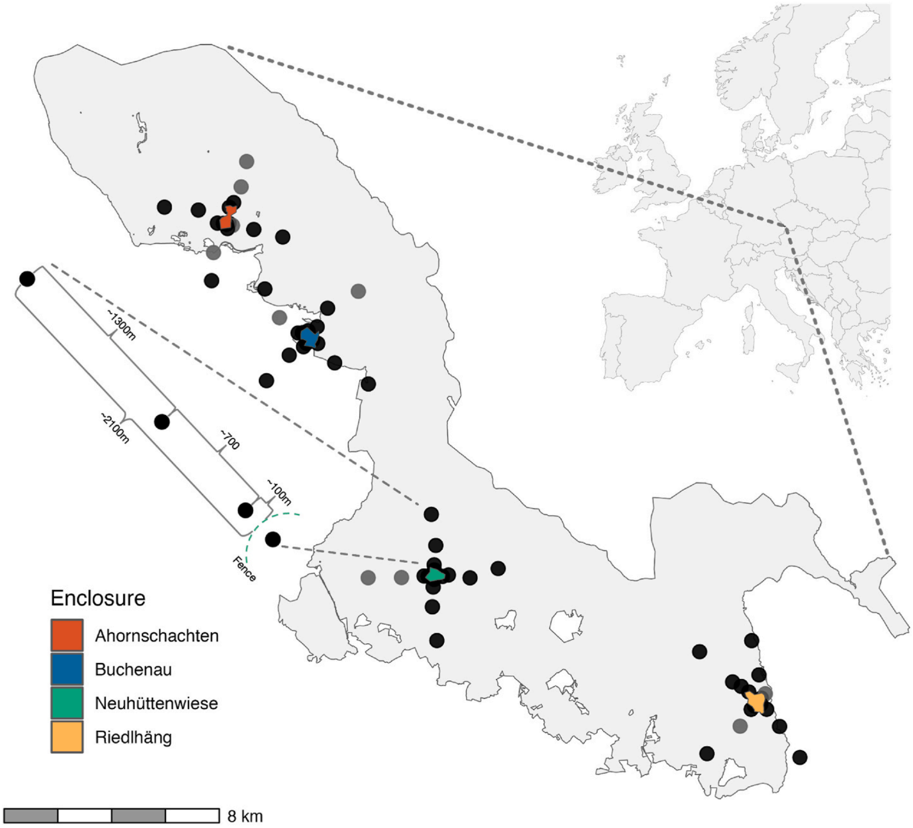

Fig. 1. Study site and plot **locations.** Black plots (n = 53) were included in the analysis while gray plots (n = 11) were excluded as they were either located on wet soil, directly next to a road or a fertilized meadow.

from 830 to 2280 mm and mean annual temperature ranges from 2.0 to 7.2 °C (Heurich et al., 2010a,b).

In the summer months, the deer in the NP have densities of ~2 deer/km^2 (Tourani et al., 2023) and occupy mainly the higher laying elevations, while they migrate towards lower elevations (outside the park) in winter. Following complaints by the surrounding landowners, the Bavarian Forest NP distributed four enclosures of varying sizes (22.5–39 ha) across the park from 1970 onwards. The management approach includes supplementary feeding to prevent bark peeling and browsing in forest enterprises and to compensate for the lack of winter habitat inside the NP. Rounding up the red deer population every winter also provides an opportunity for population control through culling. From the first snowfall, the main enclosures are closed, and late arriving animals are baited and trapped in a small pre-enclosure (less than 1 ha) attached to the main enclosure. Afterwards, the contained animals are either led into the main enclosure or culled. In the beginning of May, following the spring flush of vegetation, the enclosures are opened, and the animals can again range free in the park and its surroundings. We note that this particular culling approach as applied in the BFNP is likely not representative for other strictly protected areas. Nevertheless, hunting itself is a common management practice in European national parks (van Beeck Calkoen et al., 2020). Likewise, the provision of supplementary (winter) feeding is common practice in protected areas.

During their time in the enclosures, the deer get fed daily. For example, during winter 2023/24, a total of 97.2 t of a wildlife food mix ("AFS", consisting of apple pomace, carrot, corn-silage and hay), 64 t of apple pomace, 30 t of sugar beet, 25.6 t of silage and 10.2 t of hay were provided across all enclosures. Each enclosure hosts on average between 31 and 114 deer at densities between 110 and 510 individuals/km^2 (average from 2002 to 2020).

2.2. Study design and data collection

First, to investigate deer spatial distribution in the NP and to test whether deer abundance is higher closer to the enclosures, we utilized a dataset from 139 cameras deployed from 15 October 2023 to 31 March 2024. Camera traps were equally spaced out across the entire BFNP (Fig. S1). Each camera was mounted at a height of 50 cm and configured to record three pictures per trigger, with no delay between photos or between triggers. The cameras were also set to record one photo per day independently of triggers to monitor potential malfunction. At the end of the study period, all cameras were retrieved, and all images were classified using the software DeepFaune (Rigoudy et al., 2023). Images that DeepFauna failed to classify accurately were visually inspected by BFNP staff. Only pictures of red deer were then selected for the analysis. A series of pictures was grouped into one event if an animal or group of animals was continuously present in front of the camera. A new event started whenever the time gap between two consecutive photos exceeded 5 min. For each event, the number of individuals recorded corresponded to the number of deer in the photo within the series that showed the highest count.

Second, we collected plant and soil samples to investigate how the intensive provisioning of introduced nutrients through feeding and the artificial concentration of high densities of red deer in and around winter enclosures affect the nutrient patterns of the NP. To do so, we established 4 transects at each enclosure. Each transect was approximately 2200 m, originated ~100m inside the enclosure and radiated outward in one of the cardinal directions (i.e., arranged in a cross pattern). Sampling points were placed at ~100m inside of the enclosure, and ~100 m, ~800 m and ~2100 m outside of the enclosures (Fig. 1). This results in 4 sampling plots at each distance level for each enclosure (n = 64 plots in total). At each plot, we collected grass and soil samples at three locations within a 5 radius and aggregated them into a composite sample per plot. Plant samples were collected as fully unfolded, adult leaves of *Calamagrostis villosa* (a widespread grass species in the area) and soil samples were taken from the top 5 cm (after removal of the organic layer). Samples were collected in May 2023.

Soil and grass samples were dried for 96 h at 60 °C. Grass samples were ground to a powder and homogenized, and soil samples were sieved at 2 mm pore size. All samples were analyzed for carbon (C) and nitrogen (N), using a "vario EL cube" C:N analyzer. Inductively Coupled Plasma analysis was used to measure the content of available phosphorus (P), calcium (Ca), potassium (K), sodium (Na) and Magnesium (Mg).

2.3. Data analysis

To evaluate the drivers of deer abundance, we used an N-mixture model based on the camera trap data, using the unmarked package (Fiske and Chandler, 2011; Kellner et al., 2023). N-mixture models estimate abundance using count data, while accounting for detection probability. To accurately estimate absolute abundance, N-mixture models assume no false positives. However, because individual deer could not be uniquely identified with our camera trap setup, we relaxed this assumption and interpreted the model output as an index of relative, rather than absolute, abundance — an approach adopted in multiple studies (Chaudhuri et al., 2022; Cunningham et al., 2020). To determine the optimal occasion length for dividing the study period, we ran three global models using 3-, 5-, and 7-day intervals (Can et al., 2020; Wang et al., 2019) Each global model included all ecological covariates considered relevant. For the detection part of the model, we included: sampling effort (number of camera trap days), vegetation density (derived from a 5 m resolution airborne laser scanning LIDAR data within a 10m buffer) and ruggedness (quantified using the Terrain Ruggedness Index). For the abundance part, we considered: land cover (categorical variable with five classes: mixed stand - coniferous stand - deciduous stand - open habitat - deadwood), elevation, ruggedness, vegetation density (derived from a 5 m resolution airborne laser scanning LIDAR data within a 35 m buffer) and distance from winter enclosure. We based our selection on the ĉ (c-hat) statistic (MacKenzie and Bailey, 2004), and selected a 3-day occasion length. After selecting the best occasion length, we performed model selection to identify the most parsimonious model. We compared a subset of models using the quasi Akaike Information Criterion corrected for small sample size (qAICc), which accounts for overdispersion in the model selection step (Ward et al., 2017). In the top-ranked model, detection probability was modeled as a function of sampling effort and vegetation density. For the abundance component, we included habitat type, canopy cover, vegetation density, elevation, and distance from winter enclosures. All continuous variables were scaled and centered before analysis. Model fit was assessed using the Nmix.gof.test() function from the unmarked package (Fiske and Chandler, 2011; Kellner et al., 2023) and by visual inspection of the residuals. As the ĉ value indicated moderate overdispersion ($\hat{c} = 2.69$), we adjusted standard errors and p-values using a quasi-likelihood approach (i.e., by dividing the standard error by the square root of the ĉ parameter (Mazerolle, 2009)).

We then used generalized additive mixed effect models (GAMMs) to investigate potential changes in soil and grass nutrient concentrations with increasing distance to the enclosures. GAMMs use splines - functions which are composed of simpler functions - to allow for non-linear relationships between response and predictor variables (Wood, 2000). As variables in the candidate models we used distance to the enclosure either as a linear or a smoothed (i.e., non-linear) term, the height above the nearest drainage (HAND), elevation, relative elevation (i.e., elevation relative to the first plot [which is in the enclosure] of each transect), literature derived soil type (Bayerisches Landesamt für Umwelt, 2017) , as well as a random effect of enclosure identity (random intercept). The elevation related variables were used as nutrient accumulation can be expected to be particularly pronounced at the bottom of slopes. Additionally, to account for potential effects of bark beetle outbreaks, a common phenomenon in the NP (Sommerfeld et al., 2021), we also included the year in which the tree layer at our plots turned into deadwood (Heurich et al., 2010a,b) as a direct effect in the model. The monitoring dates back to 1988. Thus, for every plot without information on the year when its tree layer changed to deadwood, we assumed no impact from bark beetle outbreaks and accordingly set the variable value to 1980. We generated all possible combinations of a maximum of four variables and excluded strongly correlated (cor >0.6) variables (Fig. S2). Moreover, we excluded variable combinations containing both the linear and the smoothed term of distance to enclosure. All numeric predictor variables were scaled and centered prior to modeling. We used soil and plant N, C, P, K, Ca, Mg, Na as well as the ratios of C:N and N:P as response variables.

Plots which were located on either wet soil and close to potential other sources of nutrient introduction such as roads and fertilized meadows were excluded (n = 11; Fig. 1). Specifically, we excluded plots when they were located closer than 25 m to a fertilized meadow, less than 5 m next to a frequently driven road, directly on a forest road, on areas which have been recently impacted by heavy machinery and in areas with wet soil. We fitted models using the "gam" function of the "mgcv" package (Wood, 2000) and selected the best-fitting model, considering model complexity, according to the AICc. The k value (number of basis functions) was set to 3 to account for the limited number of distance classes to the enclosure. Model performance was assessed using the "gam.check" function (Wood, 2000) and diagnostic plots for concurvity (Fig. S3), observed vs predicted values (Fig. S4) and residual distribution (Fig. S5) can be found in the supplement.

All data analysis and processing was done in R version 4.5.0 (R Core Team, 2025)

3. Results

3.1. *Drivers of deer abundance*

We found that relative deer abundance in winter was significantly elevated close to the enclosures (Fig. 2; Table S1). Moreover, we found that deer preferred open and coniferous habitat types and avoided higher elevation during the winter as well as dense vegetation and canopy cover (Fig. 2; Table S1).

3.2. *Effect of winter enclosures on nutrient concentrations*

We found that the current management approach of containment and feeding of deer in winter enclosures, and the resulting seasonally elevated deer densities in the surrounds of these enclosures had a significant impact on the surrounding nutrient concentrations. The concentration of a variety of leaf-nutrients (N, P, K, and Mg) decreased with distance from the enclosure up to several hundred meters beyond the fence (Figs. 3a and 4, Table 1). Although retained in the best model, the distance to the enclosures had no significant relationship with plant Na concentration. Consistent with the decrease in N and the lack of strong effect in C, the leaf C:N ratio increased with increasing distance from the enclosures (Fig. 3a). The N:P ratio of leaves did not change significantly at greater distances from the enclosures.

Soil N appeared elevated in and adjacent to the enclosures as it significantly decreased up to 800m away. However, soil N again significantly increased at 2100m, to concentrations comparable or higher to those found in the enclosures (Fig. 3b). Overall, the trend in soil nutrient concentration was comparatively less pronounced than those found in vegetation (Fig. 3b–Table 1).

Interestingly, we observe lower plant nutrient concentrations at plots which have been recently affected by bark beetle outbreaks for N, P and K while C concentrations appear to be slightly higher the more recent the impact (Fig. S6a). Additionally, Soil P was significantly lower in areas with more recent tree diebacks (Fig. S6b).

4. Discussion

The current management approach was associated with significantly altered nutrient patterns in a strictly protected area, the Bavarian Forest NP. Especially plant nutrient concentrations were elevated within and in direct proximity to the winter enclosures and decreased gradually to a distance of several hundred meters.

The large amounts of supplementary feeding does not only provide energy for the deer but also introduces large quantities of external nutrients into a small area. Throughout the winter enclosed period, deer would merely recycle these exogenous nutrients within the enclosure, yet several pathways could cause these nutrients to eventually be transported beyond the enclosure boundaries. First, lateral subsurface flow through the upper layers of soil can carry nutrients to the surroundings, particularly in sloped areas. Second, deer accumulate nutrients in their bodies and may release them outside of the enclosures upon their death. Third, elevated deer densities around the feeding stations could cause elevated nutrient concentrations in close proximity to enclosures. We did not perform pellet counts to quantify deer nutrient inputs directly (Limpens et al., 2020), but instead utilized a large camera trap survey across the park to quantify relative deer abundance. In line with our expectations, we found that deer abundance in winter is indeed higher closer to the enclosures. This is also in agreement with parkwide surveys of browsing signs showing that winter feeding has a strong influence on the space use behavior of the red deer population as a whole, attracting them every winter to the enclosure locations where many individuals congregate in the enclosure surrounds, either to be let in later or not at all (Möst et al., 2015). This is consistent with evidence

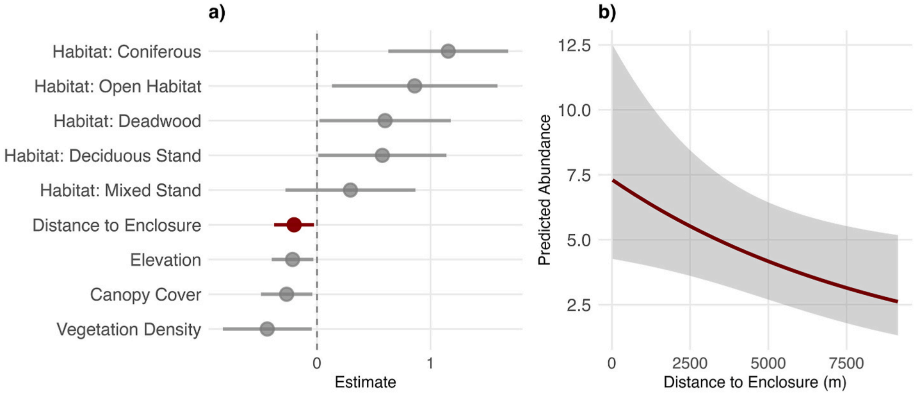

Fig. 2. Drivers of deer abundance **in winter**. a) Estimates (±95 % confidence intervals) from the n-mixture model. Distance to enclosure is highlighted in dark red; b) predicted deer abundance in the National Park Bavarian Forest depending on distance to the winter enclosure. Predictions were made by holding all variables but distance to enclosure constant (continuous variables at their median, categorical at their mode). Confidence intervals were adjusted using a quasi-likelihood approach.

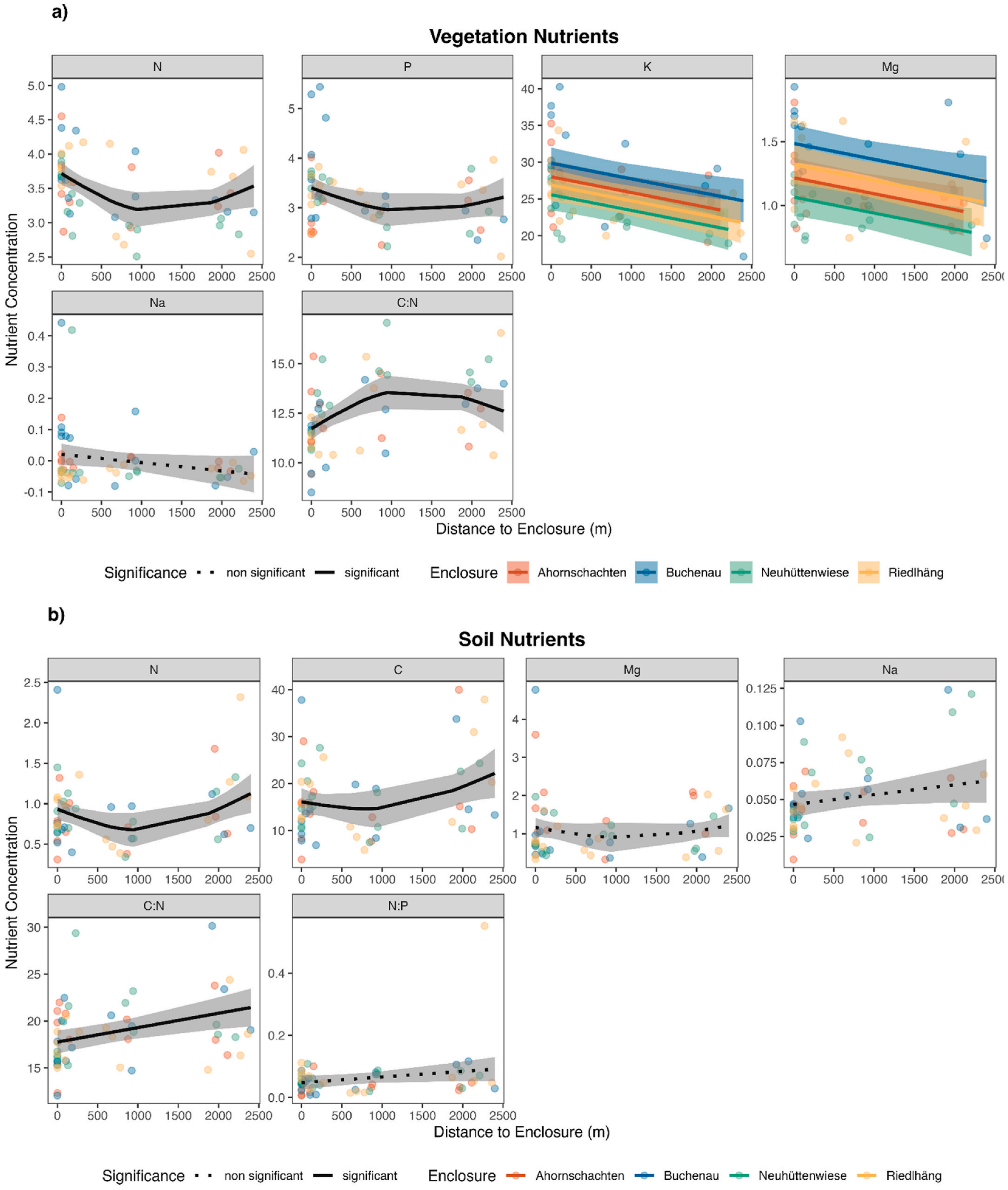

Fig. 3. Model results for the distance to the **enclosure.** Included are the predictions from all responses which included the distance to the enclosure as independent term in the best model (Table 1). a) Vegetation nutrients; b) Soil nutrients. Units are mg/g. Black lines indicate that there was no random effect of enclosure.

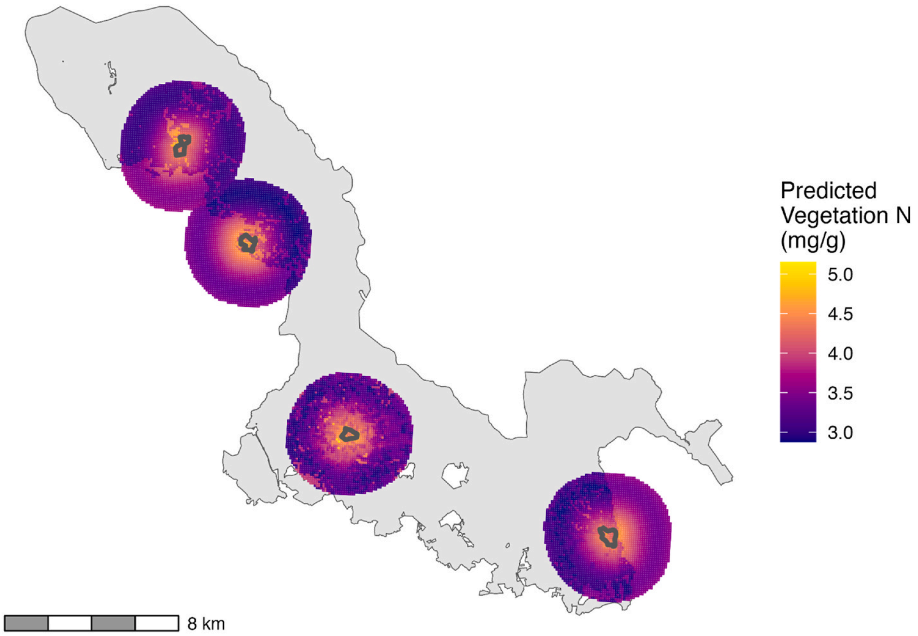

Fig. 4. Predicted plant nitrogen concentration in a radius of 2500m around the enclosures/feed**ing sites.** Shown is the predicted N concentration in *Calamagrostis villosa* leaves, using the best fitting model (Table 1) and under consideration of bark beetle impacts (i.e., deadwood) and distance to the enclosure (i.e., the best model for plant N). The dark gray polygons indicate enclosure locations.

from other areas where supplementary feeding has also been shown to change the space use and browsing behavior of ungulates (Gundersen et al., 2004; Jerina, 2012; van Beest et al., 2010). The deer attracted into the vicinity of the feeding stations are then thought to browse on the remaining vegetation (Möst et al., 2015), thereby potentially freeing up otherwise locked away nutrients. However, we did not quantify the specific pathway of nutrient accumulation around the exclosures, leaving some uncertainty about the exact mechanism behind the elevated nutrient concentrations. Nevertheless, elevated deer densities as driver would be in line with former work who also showed the fertilization potential of large herbivores (Barbero-Palacios et al., 2023; Ferraro et al., 2022; McInturf et al., 2019; Schmitz et al., 2018; Trepel et al., 2024a,b; Trepel et al., 2024a,b).

Interestingly, despite a clear signal in plant nutrient elevation, we found a considerably weaker effect on soil nutrient stocks. One potential reason for this may be the temporal difference between time of nutrient introduction outside of the fences (early winter) and sampling (peak growing season). While soil nutrient concentrations may have been elevated following nutrient input via deer excreta or other pathways, the plants could have already taken up the additional nutrients by the time of sampling. This aligns with the timing of nutrient inputs during winter, which could then be taken up by the plants during the spring flush and thus be captured by our sampling period in June. We even found slightly higher (although insignificant) soil C concentrations further away from the enclosures. A possible explanation could be if nutrient addition stimulated more activity in soil biota and thus greater respiration (Nguyen and Marschner, 2016, 2017) which would have resulted in a loss of carbon to the atmosphere.

The increased nutrient availability could potentially have a variety of downstream consequences such as changes in soil microbial composition and activity (Knelman et al., 2014; Zhou et al., 2017) and changes in the plant community composition (Biederman et al., 2017; Goldberg and Miller, 1990; Koerner et al., 2016). Rare species are often adapted to low nutrient availability thus especially affected by nutrient addition (Stevens et al., 2004; Wassen et al., 2005), raising concerns about potential undesired outcomes - particularly when considering that protected areas often have a mandate to conserve rare species. Moreover, the higher abundance of deer in and around the enclosures could further shift the plant community towards less palatable and/or faster growing species (Atkinson et al., 2024) such as nettles. Higher plant nutrients itself may further have important consequences for insect herbivores (Wetzel et al., 2016) which could have downstream effects for ecological processes such as decomposition (Chapman et al., 2003). However, we note that these potential consequences are merely speculative and strongly recommend that future studies evaluate such possible changes in soil and plant community composition and insect herbivory with relation to distance from the winter enclosures.

Another interesting pattern emerging from our results was the effect of bark beetle outbreaks. We found that plant nutrient concentrations were consistently lower at plots that were more recently affected by bark beetles (and highest at plots where trees (mostly spruce [*Picea abies*]) have not been transformed into deadwood), except for C, which showed the opposite pattern. This goes against theoretical expectations which suggests that bark beetle infestations should rather increase nutrient concentrations due to a reduction in nutrient uptake from trees and increased nutrient inputs from decaying tree biomass (Mikkelson et al., 2013). However, our findings may be explained by an increase of carbon (i.e. more structural material) resulting from increased photosynthetic activity due to the higher light availability which subsequently dilutes nutrient concentration in the plant tissue (Kaspari and Welti, 2024). Another potential explanation may be increased competition for nutrients due to fast growing pioneer species which results in lower nutrient concentrations of *Calamagrostis villosa* (our sampled species). However, results from both a neighboring NP (Šumava NP) and the Bavarian Forest NP itself indicate that bark beetle outbreaks do not necessarily lead to a long-term shift of species communities (Jonášová and Prach, 2008; Zeppenfeld et al., 2015). Alternatively, given that large herbivores tend to affect soil and plant nutrient concentrations (Trepel et al., 2024a, b), increased nutrient concentrations with increasing duration since canopy dieback could be explained by the long-term preference of deer for these disturbed areas (Oeser et al., 2021). Nevertheless, more work is required to disentangle the relationship between bark beetle outbreaks and nutrient patterns.

Table 1

Best models. Terms wrapped in: "s(…)" are smoothed (i.e., non-linear). The expression "(1 | enclosure ID)" allows for a random intercept for the different enclosures. "Hand" = height above nearest drainage. Delta AICc gives the difference between the AICc of the respective intercept only model and the best model (i.e., all best models had a lower AICc than their respective intercept only model).

Nutrient	Variables	Delta AICc	R^2	Distance to enclosure included	Sphere
N	s(Distance to enclosure) + Deadwood year	15.5	0.3	significant	Vegetation
C	Deadwood year	1.5	0.05	not included	Vegetation
P	s(Distance to enclosure) + Deadwood year	5.5	0.16	significant	Vegetation
K	Distance to enclosure + Deadwood year + (1 | Enclosure ID)	18.6	0.38	significant	Vegetation
Mg	Distance to enclosure + (1 | Enclosure ID)	17.0	0.34	significant	Vegetation
Ca	Elevation + Deadwood year	4.66	0.12	not included	Vegetation
Na	Distance to enclosure	0.53	0.03	non-significant	Vegetation
C:N	s(Distance to enclosure) + Deadwood year	19.2	0.35	significant	Vegetation
N:P	Hand + (1 | Enclosure ID)	1.7	0.13	not included	Vegetation
N	s(Distance to enclosure) + Elevation	6.5	0.18	significant	Soil
C	s(Distance to enclosure) + Hand	3.7	0.13	significant	Soil
P	Elevation + Deadwood year	1.0	0.06	not included	Soil
K	1	0.0	0.0	not included	Soil
Mg	s(Distance to enclosure) + (1 | Enclosure ID)	0.8	0.02	non-significant	Soil
Ca	(1 | Enclosure ID)	3.3	0.13	not included	Soil
Na	s(Distance to enclosure) + Hand + (1 | Enclosure ID)	0.6	0.03	non-significant	Soil
C:N	Distance to enclosure + Soil type	10.9	0.3	significant	Soil
N:P	Elevation + (Distance to enclosure | Enclosure ID)	13.1	0.25	non-significant	Soil

4.1. Management implications

Our study highlights a management dilemma where the attempt to fix one problem (human-wildlife conflict) could potentially lead to unintended and unwanted consequences (changes in the nutrient landscape of a strictly protected area). While accommodating potentially diverging interests of conservationists and surrounding landowners can be difficult (Gerner et al., 2012), neglecting changes in biogeochemistry may lead to a variety of unintended consequences for species composition and ecosystem function and potentially go against the mandate of protection. We therefore suggest explicitly including changes in biogeochemistry that result from management interventions into a more holistic monitoring protocol, facilitating data-driven decision making in the management approach. Quantifying the elements introduced through winter feed and those exported through culled carcasses, will enable the design of more precise and targeted interventions to mitigate management impact. Such quantification should be the primary management action that will form the basis for additional mitigation strategies, outlined in Table 2.

Among the potential long-term solutions could be continuing the feeding but dropping the fences to the enclosure and eventually incorporating the migratory movement of large herbivores into the conservation focus and enabling them by removing feeding stations and enclosures completely. However, key to the success of such an approach is cooperation from the surrounding landowners (Gerner et al., 2011, 2012; Ludwig et al., 2012). Unfortunately, in the case of the Bavarian Forest NP repeated approaches to increase acceptance for changes in the winter enclosure management have been unsuccessful (Gerner et al., 2011, 2012; Ludwig et al., 2012). Over 90 % of the participants in an interview campaign of surrounding stakeholders supported the enclosures as a measure to prevent deer impacts outside of the park and 75 % were opposed to a removal of the enclosures (Gerner et al., 2012). One possible way to mitigate conflict arising from concerns about economic damages could be the establishment of a compensation program for browsing damages in forest enterprises. The required financial resources to compensate surrounding landowners for deer damages could be at least partially covered by savings on the costs of large quantities of fodder and the maintenance of feeding stations and fences. Ideally this would be in conjunction with educational campaigns (but see (Gerner et al., 2011, 2012; Ludwig et al., 2012) for unsuccessful examples of educational campaigns in the Bavarian Forest NP) specifically focused on clarifying the direct and hidden cost of such interventions (e.g., costs associated with feeding, manpower and maintenance and the costs associated with elevated herbivore population growth rates and the associated need for artificial population control). Transparent representation of the true costs (direct and indirect) of certain management strategies would simplify comparisons with the costs of compensation schemes, enabling a more accurate assessment of economic viability.

Overall, to avoid management impacts on the biogeochemistry of protected areas, a change of the current approach is needed. However, finding alternative measures is challenging and potentially associated with further trade-offs (Table 2). The approach which is likely to be most beneficial for conservation success - allowing migration of large herbivores and avoiding supplementary feeding - is only feasible when consensus with the surrounding landowners is reached.

5. Conclusion

Our study demonstrates that the current management approach consisting of intensive feeding in winter enclosures and the resultant deer aggregation significantly impacts the biogeochemistry of protected areas - extending up to several hundred meters beyond the feeding sites. The introduction of large quantities of nutrients and the concentration of the impact of the deer population to a restricted area of the park is therefore likely to change ecosystem functioning and composition. As this is in conflict with one of the main objectives of National Parks - the protection of ecological processes (Dudley, 2008) - we suggest that such impacts should be rigorously quantified in order to critically evaluate such practices, and where necessary, reduce, stop, or mitigate unintended management impact.

CRediT authorship contribution statement

Jonas Trepel: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Andrew J. Abraham:** Writing – review & editing, Methodology, Conceptualization. **Walter Di Nicola:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Uriel Gélin:** Writing – review & editing. **Martin Gahbauer:** Investigation. **Marco Heurich:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Elizabeth le Roux:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Table 2
Potential ways to decrease undesired impacts on the biogeochemistry of the NP.

Option	Description	Feasibility & Cost
Switch to feed that mimic natural forage nutrient concentrations more closely	Replacing the currently used nutrient rich feed with lower quality hay will more closely match natural low quality winter forage and will minimize the nutrient import into the protected area.	***Feasibility:*** high ***Cost:*** low ***Ecological risk:*** low ***Conflict potential:*** low ***Trade-off:*** Continued nutrient import at lower levels and would require careful monitoring of deer health to ensure animal welfare.
Continue feeding but remove fences	Continue to provide supplementary feeding in the winter but remove the fences to allow the deer to distribute further and enable easy access to feed for individuals arriving after the gates have been closed.	***Feasibility:*** medium ***Cost:*** low ***Ecological risk:*** low ***Conflict potential:*** intermediate-high ***Trade-off:*** Will likely lead to a less concentrated deer impact but may not prevent them from migrating further outside of the protected areas.
Move enclosures and feeding locations regularly	Enclosures could become less permanent structures that could be moved with minimal effort to a new location every few years. However, finding suitable spots can be difficult and additional challenges arise in areas with high snow cover (such as the BFNP)	***Feasibility:*** low ***Cost:*** very high ***Ecological risk:*** high ***Conflict potential:*** high ***Trade-off:*** Manpower, potentially higher costs, continued biogeochemical impact - but more evenly spread. Unfeasible in areas with high snow cover in winter such as the BFNP.
Increase hunting quotas in areas of high human-wildlife conflict and stop feeding	In areas where there is a high risk of crop or forest damage, hunting quotas could be increased, with schemes that compensate damage through hunting. Such an intervention could make these areas more risky to deer and potentially create a landscape of fear that may lower local deer densities through indirect means. However, as predator numbers are increasing in the park, deer may be trapped between two dangerous areas (predators inside the NP and hunting outside). Moreover, low forage availability, increased cost for locomotion and higher predation risk due to high snow cover in the NP in winter will continue to force deer to migrate to risky areas outside the NP.	***Feasibility:*** low ***Cost:*** low ***Ecological risk:*** high ***Conflict potential:*** high ***Trade-off:*** Deer numbers could be decreased to a level where their ecological impact in the NP itself would be reduced – with cascading consequences for the ecosystem. Unfeasible in areas with high snow cover in winter such as the BFNP.
Move enclosures to less ecologically valuable areas of the protected area	Enclosures could be erected in areas where the number of rare species and species of conservation concern is low. In case of the BFNP, three out of the four enclosures are already placed in the buffer zone of the park while finding an alternative location for the fourth enclosure has been unsuccessful.	***Feasibility:*** low ***Cost:*** high ***Ecological risk:*** intermediate ***Conflict potential:*** high ***Trade-off:*** Continued nutrient import at high levels, finding alternative locations can be challenging and lead to further conflicts.
Fencing in of the NP boundary	Build a fence around the NP to prevent deer from migrating in areas where deer impact is less welcome.	***Feasibility:*** very low ***Cost:*** very high ***Ecological risk:*** very high ***Conflict potential:*** very high ***Trade-off:*** Potential further loss in ecological connectivity. May not prevent deer congregating against the fence in search of winter forage and may not necessarily exempt from feeding.
Fencing in of valuable crop and forest areas	Build fences around agricultural or forestry areas in close proximity to the NP to prevent deer from entering.	***Feasibility:*** low ***Cost:*** very high ***Ecological risk:*** low ***Conflict potential:*** very high ***Trade-off:*** As deer migrate out of the NP borders due to a lack of winter food availability, chances are that they keep moving until they find food in an unfenced area.
Stopping enclosures and winter feeding all together and allowing migration with compensation for damages	Incorporating migratory movement of large herbivores into the conservation focus and enabling them by removing feeding stations and enclosures. However, key to the success of such an approach is cooperation from the surrounding landowners which can potentially be enhanced by establishing compensation schemes. Unfortunately, attempts to work together with landowners to increase acceptance have been unsuccessful in case of the BFNP.	***Feasibility:*** very low ***Cost:*** intermediate ***Ecological risk:*** low ***Conflict potential:*** very high ***Trade-off:*** Would minimize undesired impacts on biogeochemistry in the NP but could increase conflict with surrounding landowners. Compensation schemes could be misused.

Declaration of competing interest

We declare no conflict of interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.126572.

Data availability

All data and code used for the analysis are available at: https://github.com/JonasTrepel/BFNPEnclosureFeedingProject.

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