

Zoogeochemistry of a protected area: Driven by anthropogenic impacts and animal behavior

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Abstract

Anthropogenic eutrophication of ecosystems is an important driver of biodiversity loss. Even protected areas (PAs) may be impacted by anthropogenic nutrients, for example, from atmospheric deposition or the provision of supplementary feeding. However, the resultant nutrient patterns, and the role of local wildlife in shaping them, remain poorly understood. We investigated anthropogenic influences on the role that red deer (*Cervus elaphus*) play in the nutrient balance of a PA in Denmark. We used habitat selection modeling and theoretical scenarios where we varied the proportion of energy the deer obtained from supplementary versus natural forage and compared it with the nutrients removed due to hunting. We show that the movement and distribution of the red deer population within the PA are very heterogeneous and likely influenced by the need for shelter. Moreover, depending on their reliance on supplementary feeding, deer can potentially import large amounts of nutrients to the PA, and concentrate them in localized hotspots. However, we also explore the potential for nutrient loss due to hunting activities. Such indirect anthropogenic impacts on nutrient landscapes may counteract restoration and conservation efforts. We therefore recommend incorporating anthropogenic influences on zoogeochemistry and the animal-mediated connectivity between PAs and anthropogenically dominated landscapes into future management plans.

KEY WORDS

anthropogenic impact, conservation biology, deer, eutrophication, large herbivores, management, nature conservation, nutrients, protected areas, zoogeochemistry

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INTRODUCTION

Anthropogenic activities have a pervasive and profound effect on nutrient cycles (e.g., global nitrogen [N] and phosphorus [P] cycles) (Vitousek, Aber, et al., 1997; Vitousek, Mooney, et al., 1997). One of the primary mechanisms through which humans alter elemental cycles is the direct release and transfer of elements into ecosystems, for example, via burning fossil fuels or the application of fertilizers (Vitousek, Aber, et al., 1997). These impacts have important consequences for ecosystems, including shaping plant composition (Duprey et al., 2016; Hautier et al., 2009; Wang et al., 2021) and changing ecosystem functioning (Doughty et al., 2013, 2016; Hautier et al., 2014). Moreover, ecosystems are connected through reciprocal flows of energy and matter (Loreau et al., 2003). For example, artificial nutrient enrichment in one area (e.g., fertilizer application on arable fields) has been shown to affect the nutrient budgets of neighboring systems (e.g., forests) (Abbas et al., 2012). Yet, many indirect human influences on nutrient cycles such as alterations to the abundance and movement of large herbivores remain poorly quantified.

Animals are agents of nutrient transfer (McInturf et al., 2019) and recycling (Hobbs, 1996), and mediate landscape nutrient heterogeneity (Ferraro et al., 2022). Megafauna in particular (i.e., large mammals >45 kg) are considered to be disproportionately important for nutrient movement (Wolf et al., 2013) due to their higher food consumption rate, longer digesting times, and longer traveling distances compared to smaller animals. Additionally, they are able to access nutrients which would be otherwise locked away for years or decades in stems, branches or other less digestible biomass (Doughty et al., 2013; Hobbs, 1996; Wolf et al., 2013). While most wild large animals have been extirpated from Europe, populations of several deer species have experienced significant population increases over the past decades (Burbaitė & Csányi, 2010), partly due to a lack of natural predators, targeted winter feeding, and increased food availability due to agricultural intensification. These deer populations often occupy heavily modified, human-dominated landscapes, where they may act as a vector of nutrients between fertilized agricultural fields and more natural surrounding vegetation.

In many parts of Europe, protected areas (PAs) are small (and thus with high edge-to-interior ratios) and embedded in a matrix of agricultural land and production landscapes. At the same time, many PAs contain nutrient-poor habitats that may be particularly vulnerable to nutrient spillover from adjacent, intensively used production landscapes. This aspect deserves particular attention as PAs in Europe are already affected by

increased atmospheric nutrient inputs from intensive agriculture (Kelleghan et al., 2020). In addition, PAs are usually unfenced, allowing deer to move freely between the PA and any surrounding crop fields, thereby facilitating animal-mediated nutrient transfer.

Animals feed selectively across a landscape (Felton et al., 2018). As a result, they are likely to react to anthropogenically created nutrient patterns (McInturf et al., 2019) such as fertilized crop fields and supplementary feeding stations, features that are known to attract animals (Jerina, 2012). Moreover, the spatial distribution of any animal impact is strongly influenced by human hunting (Benítez-López et al., 2017; Harrison et al., 2016). Deer, for example, tend to use PAs as a refuge from hunting that occurs in the surrounding landscape (Grignolio et al., 2011). Hunting can also directly impact population sizes within PAs (Rija et al., 2020) and thereby have a density-mediated influence on animal nutrient transfer potential. Relatedly, the removal of (hunted) carcasses can result in a net loss of nutrients from ecosystems where the nutrients contained in animal biomass were originally sourced from the PA and then removed off-site (Abraham et al., 2021; Brodie & McIntyre, 2019; Flueck, 2009).

Soil nutrient availability can influence a variety of ecosystem properties, including vegetation structure and species composition (Bobbink et al., 2010), and can affect a variety of ecosystem properties. Thus, understanding anthropogenic effects on zogeochemistry (how animals influence the spatial distribution and cycling of nutrients; *sensu* Schmitz et al., 2018; Schmitz & Leroux, 2020) is crucial for successful conservation and restoration efforts (Abraham et al., 2022). However, evidence for these effects from PAs is scarce. To address this, we investigated animal-driven nutrient transfer in a PA in Denmark that is dominated by nutrient-poor heathland and inhabited by a free-roaming population of red deer (*Cervus elaphus*). Specifically, we aim to answer the following questions:

1. What drives the space use of the red deer in the PA?
2. What is the potential range of impact of the deer population on the influx/efflux of nutrients to/from the PA under different feeding scenarios?
3. Do the deer create measurable changes in the nutrient landscape (i.e., spatial distribution of nutrients) of the PA?

MATERIALS AND METHODS

Study site

Ovstrup Hede is a 486 ha heathland-dominated PA in western Denmark (56.244008°N; 8.932489°E) (Figure 1,

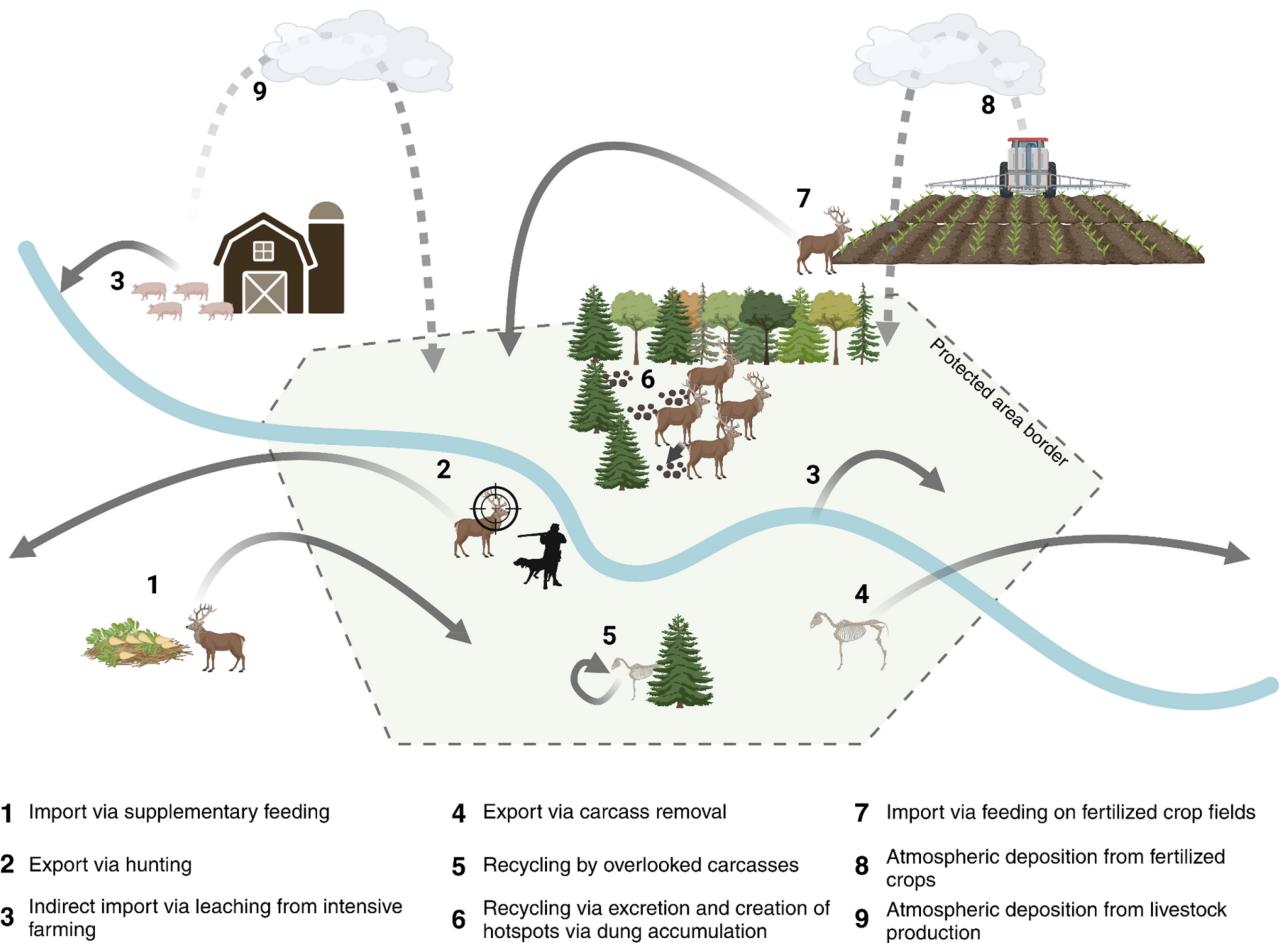


FIGURE 1 Potential anthropogenically driven zoogeochimical impacts in and around a protected area (PA). Animals can influence biogeochemical patterns and processes in a variety of ways with profound effects on ecosystems (McInturf et al., 2019; Subalusky & Post, 2019). Humans already changed global nutrient cycles and altered animal-mediated nutrient transfer (Doughty et al., 2016; Vitousek, Aber, et al., 1997) and the potential pathways in which they impact these processes in PA are diverse. These include (1) the direct transfer of nutrients via supplementary feeding outside of the PA that gets consumed by animals who may transport them back into the PA, (2) a direct export of nutrients by culling/hunting animals and thus removing the nutrients stored in their bodies, (3) nutrient leaching in streams from intensive agriculture and farming in the surroundings, (4) export of nutrients through carcass removal programs aimed at reducing the risk of disease spread (5) and thus potentially reducing nutrient heterogeneity in the landscape. By aggregating in small areas (e.g., to seek refuge from human disturbance or to avoid hunting pressure), animals may create nutrient hotspots via excretion (6), and further nutrients may get introduced into the system by animals feeding on fertilized crops and transporting them back into the PA (7). Additionally, nutrients are distributed across the landscape (including the PA) via atmospheric deposition from traffic and industry, crop fertilization (8) and livestock production (9). These alterations of nutrient patterns and pathways have important and cascading consequences for the whole ecosystem (Abraham et al., 2021, 2022, 2023; Brodie & McIntyre, 2019; McInturf et al., 2019; Schmitz et al., 2018; Schmitz & Leroux, 2020). The displayed mechanisms are broadly applicable to northern temperate systems, but we recognize there may be other location-specific mechanisms. This figure was created with BioRender.com.

Figure S1) and is owned by the private Aage V. Jensen Nature Foundation (AVJNF). The area has been protected since 1968 and was later included in the Natura 2000 network. The designation of Ovstrup Hede (Habitat area 249) is based on wet and dry heathland (habitat types 4010 and 4030), watercourse (3260), meadow (6410), lake (3160), and other habitat types (6230, 7140, 7230, 7220), as well as otter (*Lutra lutra*), brook lamprey (*Lampetra planeri*), and green club-tailed dragonfly (*Ophiogomphus cecilia*).

Moreover, the foundation has a strong management focus on red deer and fallow deer conservation and nature restoration. The vegetation diversity in plantation areas within the PA is gradually being increased through natural regeneration or, where deemed necessary, through the planting of native trees and shrubs. The PA is surrounded by agricultural fields, forests, and plantations, partly used as hunting grounds. In March 2022, a drone-based census covering Ovstrup

Hede and the surrounding areas (3760 ha), revealed 1015 red deer (27 red deer km^{-2}) and 32 fallow deer (0.85 fallow deer km^{-2}) (P. Sunde and L. Haugaard, unpublished data). There are at least 16 active supplementary feeding stations surrounding the PA (Kjær, 2021). These stations are used to attract deer for hunting or to divert them from crop fields (“diversionary feeding”). Since 2015 several exclosures of varying sizes (i.e., 1390–5950 m^2 ; fence height $\sim 2 \text{ m}$) have been established inside the PA, mainly in heathland, to monitor the impact of red deer on vegetation. Smaller animals (e.g., rodents, hares, and foxes) still have access to the exclosures.

Red deer habitat use

We used movement data from Global Positioning System (GPS)-tracking and habitat selection modeling to investigate what is driving the habitat use of red deer (our first question). Between 2019 and 2023, 12 red deer (11 females and 1 male) were equipped with Vectronic Vertex Plus GPS collars for 2 years, collecting location data every hour (on average 4965 [range: 563–9434] observations per individual). We used this movement data to estimate the time deer spend outside of the PA and to map deer habitat use within the PA. To check if the location data of the 12 deer were indicative of the habitat use of the whole population, we also walked a total of 48.4 km in transects of 2 m width across the PA, recording the location of each observed red deer fecal pellet pile (Figure S2). The transects were walked on January 22 and 23 and February 25, 2023.

To estimate space use from dung pellet distribution, we divided the area into 1 ha grid cells ($100 \text{ m} \times 100 \text{ m}$), calculated the area covered by the transects within each cell, and subsequently extrapolated the observed pellet groups on the transect to get an estimate of pellet groups per 1 ha grid cell. We excluded cells that contained less than 20 m of transect. Similarly, we recorded the number of deer GPS locations within each grid cell. We then used Spearman correlation to see if these two measures of localized deer abundance were correlated. Moreover, we fitted a linear model with the distribution of feces as response and the distribution of GPS locations as explanatory variable (distribution of feces \sim distribution of GPS locations) and compared it to an intercept-only model (distribution of feces ~ 1).

To investigate the drivers of deer habitat use, we used habitat selection modeling with the number of GPS locations per grid cell as a response variable (Nielson & Sawyer, 2013; Paton & Matthiopoulos, 2016). From the centroid of each cell, we calculated the distance to four

landscape features of the PA using the `st_distance` function from the “sf” package (Pebesma & Bivand, 2023). The features of interest were roads, forests, heathland, and parking lot (as a proxy for the area with the highest human activity) as these mark the main characteristics of the area.

We employed generalized boosted regression models, also known as gradient boosting machine (GBM), to identify the influence and direction of the variables on red deer habitat use. Inference from GBMs is little sensitive to multicollinearity, and GBMs do not make any assumptions about data distribution or the relationship between predictor and response variables (Finnegan et al., 2015). We fitted the GBMs using the “gbm” package (Greenwell et al., 2022) and used the “caret” package (Kuhn, 2008) for model training and identification of the most suitable hyperparameters (Figure S3). To account for spatial autocorrelation of the location data (as knowing the location of one point increases the likelihood of knowing the location of the next point) (Moran’s $I = .015$, $p = 0$), we added a spatial predictor to the model. Here, we used the centroid coordinates of each grid cell to calculate a distance matrix—specifically we used Moran’s Eigenvector Maps (i.e., the eigenvectors of a distance matrix, weighted by the degree they maximize autocorrelation) (Dray et al., 2006). These spatial predictors represent the effect of spatial proximity among records and can be directly used as explanatory variables in regression models (Dray et al., 2006). Including a spatial predictor successfully reduced the spatial autocorrelation in the data (Moran’s $I = .003$, $p = .07$).

To optimize model parameters and avoid overfitting, we used 10-fold cross-validation, meaning that the dataset was randomly split into 10 equal-sized subsamples from which nine subsamples were used as training data, and one was retained as validation data for testing the model. This process was repeated until each of the subsamples was used once as a validation set ($n = 10$). The final model was selected based on the smallest root mean squared error (RMSE). Model performance was estimated using R^2 and RMSE. The hyperparameters used for the final model were as follows: a learning rate (shrinkage) of 0.01, a minimum of 12 observations per node, and an interaction depth of 9 and 6150 trees (Figure S3).

Evaluating nutrient transfer potential

To evaluate the potential range of impact of the deer population on the influx/efflux of nutrients to/from the PA (our second question), we explored different theoretical scenarios. Given that there were no data on red deer diet available from the area, we established six different

TABLE 1 Assumptions used for calculations.

Variable	S1	S2	S3	S4	S5	S6	Abbreviation	Source
Percentage of energy covered by heathland vegetation (HV)	100	80	60	40	20	0	PHV	
Percentage of energy covered by supplementary feeding (SF)	0	20	40	60	80	100	PSF	
Population size	1015						PS	a
Individual energy demand (kcal/day)	7648						ED	(Mulley, 2002)
Red deer body mass (kg)	180						BM	(Flueck, 2009)
Food in PA energy content (kcal/g)	3						EC _{HV}	(Blaxter, 1964; Moss & Parkinson, 1972)
Food in PA N content (mg/g)	9.4						NC _{HV}	(Robertson & Davies, 1965)
Food in PA P content (mg/g)	0.8						PC _{HV}	(Robertson & Davies, 1965)
Food in PA Ca content (mg/g)	2.4						CaC _{HV}	(Robertson & Davies, 1965)
Food in SF energy content (kcal/g)	3.5						EC _{SF}	(Thomas et al., 1969; van der Honing et al., 1973), b
Food in SF N content (mg/g)	12.6						NC _{SF}	(Julliand et al., 2019; Thomas et al., 1969), b
Food in PA P content (mg/g)	1.9						PC _{SF}	(Julliand et al., 2019; Thomas et al., 1969), b
Food in PA Ca content (mg/g)	3.2						CaC _{SF}	(Julliand et al., 2019; Thomas et al., 1969), b
Number of female carcasses	133						Fc	a
Number of male carcasses	89						Mc	a
Number of unknown sex carcasses	111						Uc	a

Note: The energy content of the nutrition from inside the protected area (HV) was assumed to be the mean of heather and grass energy content. The energy content of SF was estimated as an average of the energy content of beet, hay, and silage which are most often in supplementary feeding in the area (Camilla Kjær, personal communication). We further assumed the average body weight of red deer to be 180 kg (Flueck, 2009) and each individual to be an adult.

Abbreviations: a, AVJNF, unpublished data; b, www.fdc.nal.usda.gov; S, scenario.

scenarios in which we varied the amount of energy demand covered by either supplementary feeding (SF) (i.e., provided by hunters or farmers to attract deer toward hunting grounds or away from agricultural fields) or by natural heathland vegetation (HV) (Table 1). We assumed that the proportion of GPS locations mirrored the amount of time deer spent either within the PA or in the surrounding landscape and we assumed that fecal input is proportional to where red deer spend their time, for example, if the deer spent 40% of their time in the surrounding landscape, then 40% of that feces would be deposited in the surrounding landscape.

To calculate nutrient intake, we estimated that each red deer individual requires 2,791,520 kcal per year (Mulley, 2002) and will satisfy that demand either through supplementary feeding or natural heathland vegetation or both. We used the average energy and nutrient content of sugar beet, hay, and silage for the supplementary feeding category, as these are the most frequent fodder types used in the area (Camilla Kjær, personal communication). Data on energy and nutrient content of

these crops were obtained from Thomas et al. (1969), van der Honing et al. (1973), and www.fdc.nal.usda.gov. Supplemental feeding happens only outside of the PA (Kjær, 2021). Although heather (*Calluna vulgaris*) is suggested to make up 25% of red deer's diet (Jensen, 1967), we assumed the average of heather (*Calluna vulgaris*) (Moss & Parkinson, 1972) and grass (average value of six commonly occurring species in Europe, namely *Festuca rubra*, *Lolium perenne*, *Poa trivialis*, *Arrhenatherum elatius*, and *Festuca arundinacea* [Hunt, 1966]) for the energy and nutrient content of the heathland vegetation. This was done to account for the disproportionately higher abundance of heather compared to grasses in the PA (own observation). We used the average nutrient values measured in different European heathlands (Robertson & Davies, 1965) as nutrient content for heathland vegetation. We then considered six different scenarios wherein we varied the proportional dietary split between supplementary feed and natural vegetation (see Table 1) to obtain a range of spatially explicit estimates of nutrient intake (i.e., either originating from supplementary feeding

or natural forage). For each scenario, we calculated the amount of nitrogen (N), phosphorus (P), and calcium (Ca) consumed by the deer population from supplementary and natural forage. We decided to focus on these nutrients because of their ecological importance for plant productivity and animal health, and because calcium and phosphorus accumulate in animal skeletons in contrast with background availability. As such, their loss through carcass removal will be particularly pronounced.

To calculate nutrient removal through hunting/carcass removal, we assigned a loss of 9.6 kg N, 4.22 kg P, and 7 kg Ca for every hunted male, 4.8 kg N, 1.76 kg P, and 2.9 kg Ca for every hunted female (all individuals were assumed to be adults; values obtained from Ferraro et al., 2022; Flueck, 2009; Hobbs et al., 1982; McCull-

scenarios of proportional dietary split (Table 1, Equation 1, AVJNF, unpublished data). We then used the spatially explicit (1) estimates of nutrient intake, (2) estimates of fecal return, and (3) estimates of carcass nutrient removal to estimate a total nutrient balance for the system (Equation 2). Next, we estimated the import/export of nutrients to/from the PA under each feeding scenario (Equations 3 and 4), where P_{tPA} and P_{tSL} are the proportion of time spent (based on GPS locations) in the PA (P_{tPA}) or the surrounding landscape (P_{tSL}), P_{HV} is the proportional dietary contribution from heathland, EC_{HV} and EC_{SF} is the energy content (kcal) in heathland vegetation and supplementary feed, respectively, and NRC is the nutrient removal via carcasses obtained in Equation (1).

$$\text{Nutrient removal via carcasses(NRC)} = (\text{Fc} \times \text{carcasses nutrient content}) + (\text{Mc} \times \text{carcasses nutrient content}) + (\text{Uc} \times \text{carcasses nutrient content}) \quad (1)$$

$$\text{Nutrient turnover} = ([P_{HV} \times EC_{HV} \times \text{nutrient content HV}] + [P_{SF} \times EC_{SF} \times \text{nutrient content SF}]) - \text{NRC} \quad (2)$$

lough & Ullrey, 1983), and used the average values for carcasses of unknown sex. In total, 333 deer were hunted in 2022. We considered the nutrients that made up each carcass to have originated from either supplementary feeding or heathland vegetation based on the six

By subtracting the nutrients exported via carcasses from the nutrients imported into the PA, we estimated the net import/export between the PA and the surroundings (Equation 5). Hence, nutrient import/export here refers to the movement of nutrients into or out of the PA.

$$\text{Nutrients exported from the PA} = P_{tSL} \times (([P_{HV} \times EC_{HV} \times \text{nutrient content HV}] - (P_{HV} \times \text{NRC})) \quad (3)$$

$$\text{Nutrients imported to the PA} = P_{tPA} \times (([P_{SF} \times EC_{SF} \times \text{nutrient content SF}] - (P_{SF} \times \text{NRC})) \quad (4)$$

$$\text{Nutrient import/export PA} = \text{Nutrient imported to the PA} - \text{Nutrient exported from the PA} \quad (5)$$

To obtain a mean balance of nutrients in kg/ha/year of the whole area, we calculated the home range of the deer using 95% kernel density estimated via the `hr_kde` function and estimated the area via the `hr_area` function from the “amt” package (Signer et al., 2019). Moreover, as the deer are not using the area homogeneously, we estimated the nutrient balance of the most used 5% and 10% of the PA to show how high the balance can be in intensively used areas.

To get an estimate of the fecal nutrient content, we collected 20 fresh individual fecal samples along our transects in January and February 2023 and analyzed these for nutrient content. To minimize the risk that the fecal pellets were from the same individual we kept a minimum distance of 10 m between collected fecal samples. Samples were stored in paper bags and frozen until analysis. Fecal samples were dried for 96 h at 60°C, weighed to get an estimate of the average dry mass of a pellet group in the area, ground to a powder, and homogenized. All samples were analyzed for carbon (C) and N, using a “vario EL cube” C:N analyzer and for available P and Ca, using inductively coupled plasma analysis.

Evaluation of nutrient content inside and outside of the enclosures

To answer our third question (whether the deer create measurable changes in the nutrient landscape of the PA), four exclosures within the PA (established from 2015 onwards) were selected, and soil and plant material were sampled from three plots in and outside of each enclosure in April 2023 (Figure S1). Plots had a radius of 3 m and were placed spaced out in the exclosures to maximize the distance between the plots. We collected fully unfolded, adult leaves of *Deschampsia flexuosa* and took soil samples from the top 5 cm (after removal of the organic layer) on three locations within each plot and merged them into one composite sample (Figure S1). Overall, we collected 24 soil and 24 grass samples.

Soil and plant samples were dried for 96 h at 60°C. Plant 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 N, using a “vario EL cube” C:N analyzer. Furthermore, Inductively Coupled Plasma analysis was used to measure the content of available P and Ca.

We used general linear mixed effect models (GLMMs) to investigate potential differences between the soil and grass nutrient content inside and outside of the exclosures. Given that there may be some site-specific dependencies in nutrient values between the different exclosures (e.g., because of land use history) we included

exclosure identity as random effect. Fixed-effect variables included the exclosure treatment (i.e., inside or outside of the exclosure) and one of two deer density variables i.e., the number of GPS observations within a radius of 100 m or the number of counted fecal pellets groups within a radius of 100 m around each plot. The exclosure treatment variable and a proxy for localized deer impact (number of GPS points or feces) were included additively and as an interaction (see Table S1 for the list of compared models). We fitted models via the `glmmTMB` function from the “glmmTMB” package (Brooks et al., 2017) and selected the best-fitting model, considering model complexity, according to the AICc.

All data analyses were conducted in R version 4.2.2 (R Core Team, 2022).

RESULTS

The distribution of the GPS location data correlated significantly with the distribution of red deer fecal counts ($\text{Rho} = 0.47, p = <.001$; Figure 2). Moreover, our linear model for the distribution of feces significantly improved by adding the distribution of GPS locations as a predictor ($p = <.0001$, adjusted $R^2 = 0.23$, $\text{deltaAIC} = -87.6$). Therefore, we considered the GPS locations to be a reasonable estimate of the habitat use of the whole population.

Drivers of red deer habitat use

Tagged individuals (predominantly female) spent 25% ($\text{SD} = 10\%$) of their time in the PA and 75% ($\text{SD} = 10\%$) in the surrounding area. The best-performing generalized boosted regression model (GBM) had an R^2 of 0.68 and was, on average, 7 location points per grid cell off from the observations ($\text{RMSE} = 6.6$). The habitat use of the deer (Question 1) was mostly explained by distance to forest (relative variable importance: 29%), with higher deer presence closer to forests (Figure 3).

Nutrient balance of the PA

The mean fecal nutrient concentration was 2.00% ($\pm \text{SD}: 0.57$) N, 0.45% (± 0.20) P and 0.47% (± 0.15) Ca. During the study period (March 13, 2019 to December 31, 2022), the 12 GPS-tagged deer roamed a total area (95 kernel density) of 3374 ha.

The potential range of deer impact on nutrient transfer in the area (Question 2) depends on where the nutrients are sourced. We found that the nutrient balance

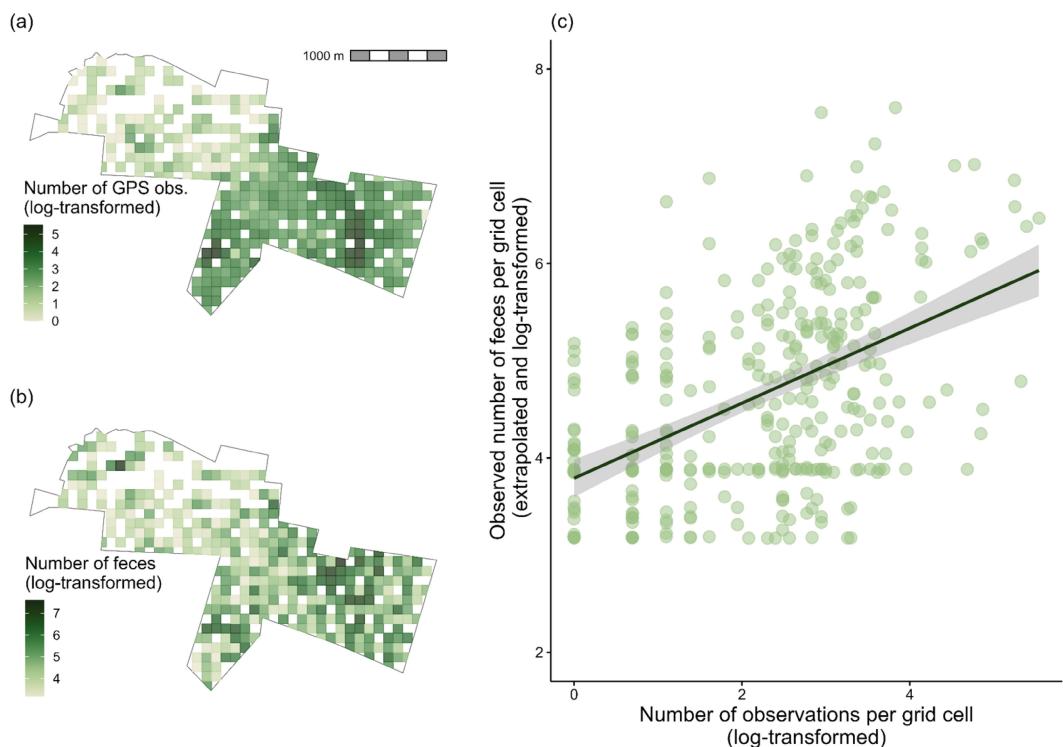


FIGURE 2 Correlation of GPS locations and observed pellet groups. (a) The number of red deer GPS locations per grid cell (relocation interval of 1 h), and (b) the extrapolated number of feces found in each grid cell for the Danish protected area “Ovstrup Hede.” For panels (a) and (b), white cells do not contain walked transects and are consequently omitted from the comparison. (c) The relationship between the number of GPS locations per grid cell and the number of feces per grid cell is significantly correlated ($\rho = 0.47$, $p < .001$). The regression line represents a linear model ($p = <.0001$, adjusted $R^2 = 0.23$) and the gray shade indicates the 95% confidence interval.

(estimate of nutrients consumed minus nutrients removed in carcasses, calculated from Equation 2) of the area as a whole is higher in theoretical scenarios where a greater proportion of deer diet was obtained from supplementary feeding (Figure 4a, Table S2). Moreover, scenarios assuming that deer obtain over 70% of their energy from supplementary feeding, predict an import of N and Ca into the PA (Figure 4b). Lastly, we estimated a notably higher localized nutrient input to the areas of the PA with the highest deer densities (i.e., most used 5% and 10% of the PA) than for the whole area average (Figure 4c,d).

Changes in nutrient distribution

We did not find evidence that the deer create measurable changes in the nutrient landscape of the PA (Question 3). Both soil and plant nutrients did not significantly differ between the exclosures and grazed paired plots (Table S3, Figure 5). Similarly, no significant differences were found in soil and plant stoichiometry between the exclosures and grazed paired plots (Table S3, Figure S4).

DISCUSSION

Our scenarios suggest that anthropogenic impacts on animal-driven nutrient movement could potentially have strong localized effects on the nutrient import/export balance of PAs. Anthropogenic activities that influence how deer shape the nutrient landscape of the PA include the direct supply of externally sourced nutrients and the indirect impact on deer distributions and movement. We have shown here that if deer were to feed preferably from natural heathland vegetation, hunting activities would lead to the export of nutrients (e.g., N and Ca; Figure 4) from the PA. Conversely, if these deer were to obtain 70% or more of their forage from supplementary feeding (a scenario that is not unlikely given deer's propensity for feeding selectively [Felton et al., 2018]), the movement of the deer in and out of the PA would lead to animal-mediated nutrient inputs to the PA. How long it takes for such nutrient shifts to become ecologically meaningful is still uncertain.

Previous studies have shown that deer select for feeding stations in close proximity to this PA, especially in winter (Kjær, 2021). The presence of feeding stations is

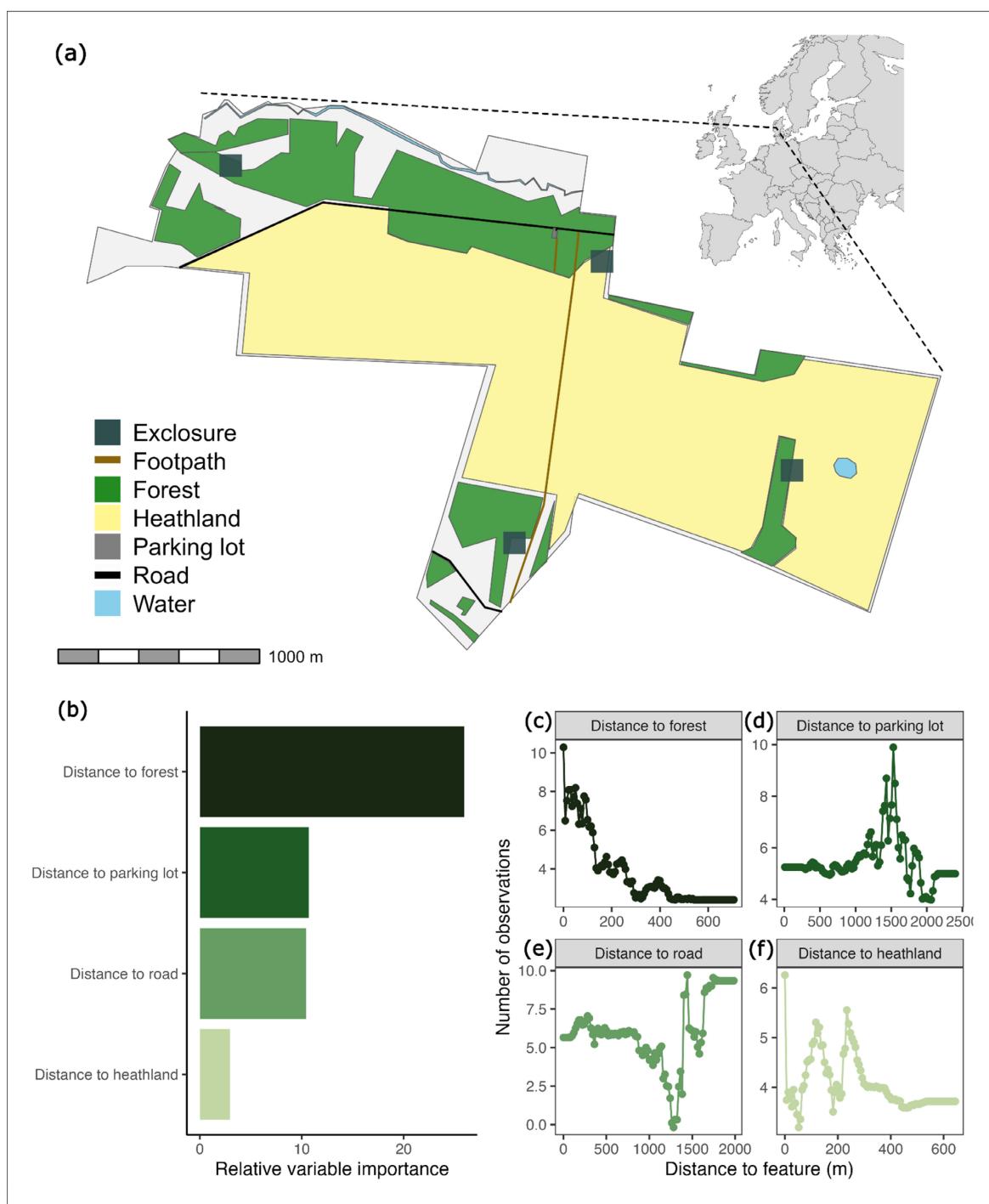


FIGURE 3 Study area, landscape features, and GBM results. (a) The PA (“Ovstrup Hede”) is located in western Jutland in Denmark. The 486 ha area is mainly dominated by heathland but also contains some forest patches, roads, and walking paths. The square symbols indicate the locations of the exclosures but not their actual shape. Panel (b) shows the relative variable importance and panels (c-f) show the predicted values from the boosted regression trees. The most important variable explaining red deer habitat use in the PA was the distance to the forest (b, c) followed by the distance to the parking lot (b, d), distance to road (b, e) and, as least important variable, distance to heathland (b, f).

known to lead to smaller home ranges of red deer (Reinecke et al., 2014), making it more likely that the population congregates around the stations. Moreover, an import of nutrients into a PA already affected by

atmospheric nutrient deposition, could compromise conservation of naturally nutrient-poor habitat types, such as heathlands, meadows, and rich fens and the persistence of nutrient-sensitive species such as heather (Bobbink

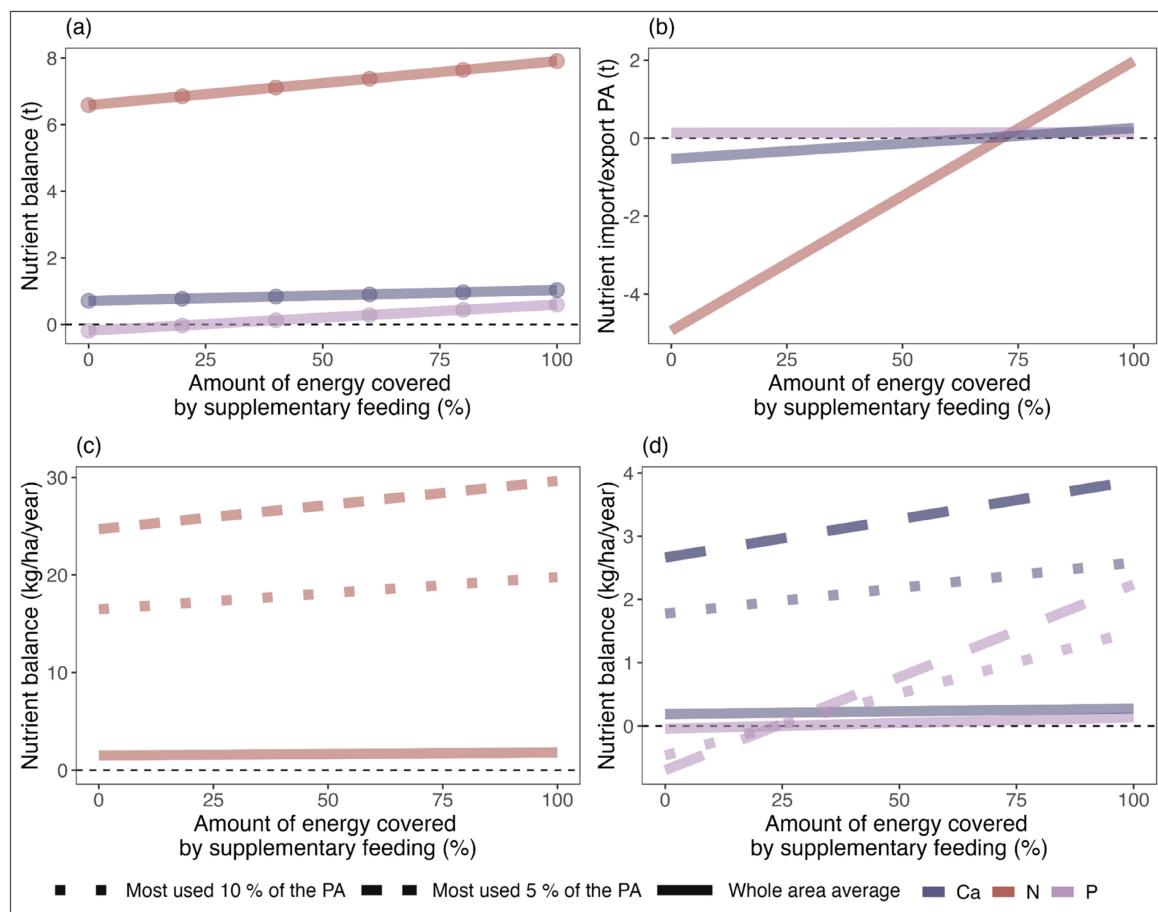


FIGURE 4 Nutrient balance according to the different theoretical scenarios. Nutrient balance here refers to the total nutrient turnover per year (the amount of nutrients contained in the amount of food that is required to cover the energy demand of the population minus the amount of nutrients removed from the system via carcasses). (a) the total yearly nutrient balance in the entire home range of the deer (PA and surrounds) under the different theoretical scenarios (scenarios depicted by bullet points); (b) the net annual amount of nutrients that get imported to or exported from the PA (reported in total tonnes for the entire PA); (c) the N balance in kg/ha/year for both the whole area (PA and surroundings; solid line), the most used 10% of the PA (dotted line) and most used 5% of the PA (dashed line); (d) similar to (c) but for P and Ca.

et al., 2003). Atmospheric N deposition in the area is estimated to be approximately 13.4 kg/ha/year (www.arealinformation.miljoeportalen.dk) and therefore within the empirical critical loads for the effect of excess nitrogen on heathland (10–20 kg N/ha/year) (Bobbink et al., 2003), providing a potential stressor for the ecosystem even without the potentially additional nutrients imported by deer. In our analyses of the different theoretical scenarios, whether the deer indeed import nutrients to the PA depends critically on how much of their dietary nutrients are obtained from supplementary feeding. Yet, even in our most conservative theoretical scenario, the critical loads of nitrogen for heathland can be exceeded in the parts of the PA most intensively used by red deer. Such heterogeneous habitat use may lead to localized nutrient hotspots (Ferraro et al., 2022) which can persist

and influence an area for millennia (Marshall et al., 2018).

Red deer preferentially used areas close to forests (as predicted from the predominantly female collared individuals). Given that hunting is known to impact deer behavior (Jayakody et al., 2008) and shift habitat use to more sheltered and/or less disturbed areas (Laguna et al., 2021; Lone et al., 2015; Sunde et al., 2009) and that deer tend to avoid areas with high human activity (e.g., well-used paths) (Bobrowski et al., 2020; Fattebert et al., 2019) we suggest that deer seek shelter in the PA. This is supported by the managers and neighbors of the PA reporting that the deer actively used the PA (with considerably lower hunting pressure than the surroundings) as sanctuary, especially during the hunting season (P. Sunde, unpublished data).

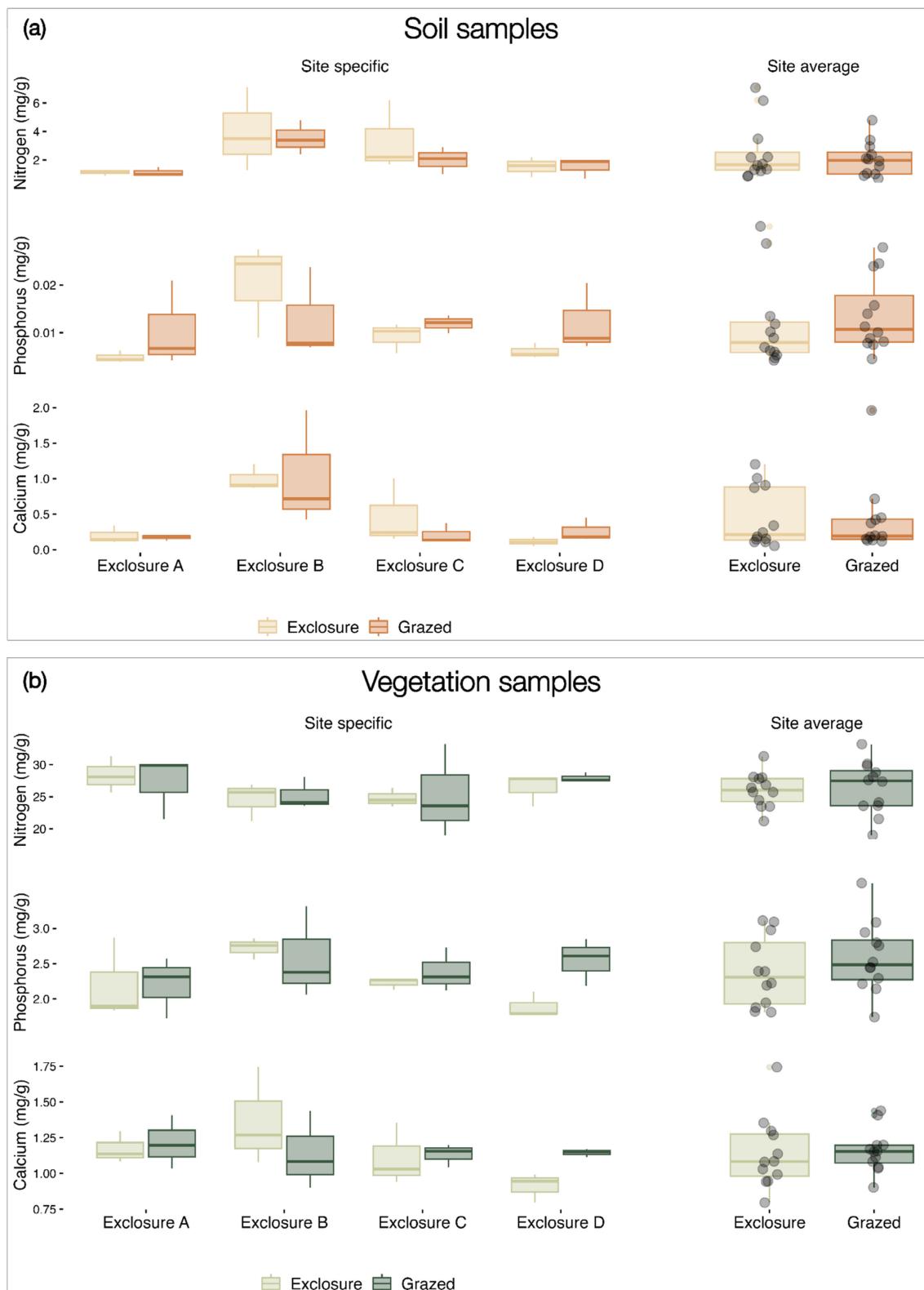


FIGURE 5 Nutrient content in and outside of the exclosures (raw data). The site-specific boxplots on the left show the comparison between specific grazed plots and the respective control (e.g., exclosure vs. grazed) while the site average boxplots show the difference between all grazed and all exclosure plots. The black points indicate individual measurements. (a) soil nutrient content; (b) plant nutrient content.

The intensively used parts of the PA are unlikely to provide the heathland vegetation dry mass per year necessary to maintain a population of this size (944 t heathland vegetation per year according to our calculations). Thus we contend that the limited space in the intensively used parts of the PA is largely selected for shelter, wherein the deer can rest and ruminate, while the feeding stations and surrounding agriculture are used for supplemental feeding. This assertion is further corroborated by the fact that fecal nutrient concentrations in Ovstrup Hede are comparatively high in winter. Here, we found concentrations of 2.0% N and 0.4% P, which is slightly higher than those found in a PA in southern Germany (1.9% N and 0.24% P) (Riesch et al., 2022) and in natural grazing sites in Oostvaardersplassen in the Netherlands (1.6 %N and 0.3 %P) (Valdés-Correcher et al., 2019) and Montana, USA (1.5% N) (Christianson & Creel, 2007). The average fecal nitrogen concentration of deer in winter in a comparable, but fenced PA in Denmark (Klelund Dyrehave) dominated by coniferous forest and heathland, but with supplementary feeding in winter was found to be 1.7% (Fløggaard et al., 2016). As fecal nutrients were slightly higher in our study compared to both natural feeding populations and those with access to supplementary feeding, we suggest that an ecologically reasonable expectation is that supplementary feeding and feeding on nutrient-rich winter crops play a considerable role as nutrient source of the deer.

Moreover, increasing the energy covered by supplementary feeding leads to subsequent increases in the nutrient balance as a whole (i.e., more nutrients being imported to the system). Consequently, high amounts of supplementary feeding may contribute to increasing nutrient input into the area and might further threaten the current semi-natural ecosystem (Bobbink et al., 2003, 2010). Apart from these allochthonous nutrient provisioning, supplementary feeding is also likely to contribute to increased nutrient transfer by directly increasing population sizes (Milner et al., 2014) and supporting higher deer densities.

For the reasons stated above (i.e., comparatively high fecal nutrient content, likely insufficient amount of natural feeding opportunities in intensively used areas, and a known preference for supplementary feeding in that area in winter [Kjaer, 2021]), we consider the scenarios where deer meet most of their energy requirements in winter from supplementary feeding, to be a likely scenario. However, in the scenarios where most of the deer diet consists of natural heathland vegetation, even the potential losses of nutrients from the PA may be of concern to site managers. There are significant stoichiometric (i.e., the ratio between elements) mismatches between plant and animal tissue, with animal bodies containing

elements in very different ratios to those supplied by natural vegetation (Sitters et al., 2017; Sterner & Elser, 2002). For example, animal skeletons consist largely of Ca and P (Carter et al., 2007) and thus the removal of carcasses may be particularly consequential for the loss of these elements (Abraham et al., 2021; Brodie & McIntyre, 2019).

Regardless, we did not find a significant difference in soil and plant nutrients between deer exclosures and the surrounding landscapes where deer had access. There are several possible reasons for this lack of a significant effect. First, the time since enclosure establishment is relatively short given that, for example, 8–25 year exclosures show no or only little effects of ungulates on soil nutrients (Allen et al., 2023; Kolstad et al., 2018; Swain et al., 2023) while exclosures older than 40 years show strong effects (Pastor et al., 1993). Alternatively, shifts in the nutrient balance could change plant community composition instead of within-species nutrient content or increase turnover rates instead of nutrient concentrations—likely ecosystem responses that we did not measure here. It is also possible that the high atmospheric deposition of N and Ca (for Denmark, the Ca-deposition is estimated to be around 5 kg/ha/year [Michel et al., 2021]) may overshadow any effects of deer. Furthermore, the effect of fecal imports could well be mitigated by carcass export which would lead to a net effect of zero. Overall, the ways in which the ecosystem may respond to changes in zoogleochemistry, mediated by megafauna, are highly diverse and potentially interacting. More studies are needed to deepen our understanding of these complex processes so that we can take them into account when designing PAs and management strategies.

While our models provide preliminary insights in the potential for deer-mediated nutrient transfer, future studies should also include feeding observations so that the nutrient source location and the exact nutrient composition of the diet can be accurately estimated. Moreover, since we assumed a constant defecation rate, investigating whether defecation occurs preferentially in certain environments (i.e., is not perfectly linked to space use) can further improve these calculations. While our study highlights the potential extent of such impacts, the above-mentioned parameters will be crucial to quantify such nutrient movements exactly.

In addition, we recommend that other ways in which animals are connected to the nutrient landscape be investigated in more detail. This ranges from the physical influence on soil properties through trampling or the promotion of bare soil (Trepel et al., 2024) to localized inputs (e.g., calving and the associated release of large amounts of nutrients via the natal fluid in a very small area [Ferraro et al., 2023]). All these impacts can be altered by

anthropogenic factors (i.e. restrictions on habitat use, antler collection, etc.) and are therefore necessary to consider for nature conservation.

Management implications

Our study suggests that the zoogeochemistry of PAs can be substantially altered by anthropogenic factors, such as the transfer of allochthonous (originated elsewhere) nutrients via supplementary feeding, hunting, and disturbance impacts on animal movement and behavior and the removal of carcasses from the system. This likely has consequences for a variety of dynamics and processes within the system. Our results support the meta-ecosystem framework (Loreau et al., 2003) and highlight that ecosystems (including PAs) do not exist independent from each other but are always influenced by their surroundings (Ellis-Soto et al., 2021). We thus recommend incorporating impacts on zoogeochemistry to the management plans of PAs. One approach to minimize undesired nutrient influx would be to avoid feeding in proximity to PAs, or if feeding is unavoidable, to monitor nutrient levels periodically. Even though the intention of supplemental feeding stations is often to provide alternative food resources to attract deer away from valuable crop fields, evidence for the success of this approach is limited (Milner et al., 2014). In the study area, as in the rest of Denmark, feeding primarily takes place during the hunting season (September–January) (Kjær, 2021) where crops are least vulnerable for grazing and trampling. The mitigation effect of feeding during the cold season on crop damage is therefore minimal while it most likely reduces grazing intensity on PAs. Hence, by providing red deer with an easily accessible high-quality forage during the non-growing season (most food mounds last throughout the winter), artificial feeding may at the same time increase the population density of wild ungulates through altered carrying capacity yet reducing their ecological function through reduced foraging on natural vegetation (Abraham et al., 2023).

On a more general note, it is important to consider the protection goal of the area (i.e., if a particular species' population should be maintained or if instead the aim is to restore natural dynamics, as is the aim in rewilding approaches; Carver et al., 2021) as this will determine to what extent these nutrient movements are of concern or not. Moreover, monitoring the impacts on zoogeochemistry and its consequences (i.e., by establishing a network of long-term exclosures with regular sampling intervals) will help to recognize and react to potentially unwanted consequences in time.

Finally, the size of the PA is crucial for successful conservation efforts and should be at least equal to the mean home range of the inhabiting species to restore or preserve natural dynamics. Given that we show dependencies between the ecological dynamics (such as zoogeochemistry) and the management choices made in the landscape matrix, increased PA area size would likely increase conservation efficiency and restoration potential. Concomitantly, in areas where PAs are smaller than the home ranges of the grazers they contain, the unwanted nutrient flows from cultivated to PAs are unlikely to be entirely solved, although some mitigation is possible through carefully considered management action, such as (i) the removal/reduction of artificial feeding stations in close proximity to PAs, (ii) avoidance of excessive hunting disturbance that leads to animal congregations in areas of safety and (iii) the decision of whether or not to export carcasses.

AUTHOR CONTRIBUTIONS

Study conception and design: JT, AJA, EJL, and EIR. *Fieldwork and data collection:* JT, EIR, AJA, EJL, RØP, MT, PS, LH, CF, and KF. *Methodology:* JT, EIR, MT, AJA, and EJL. *Data analysis:* JT. *Co-supervision:* AJA, EJL, and JK. *Main supervision:* EIR. *Writing original draft:* JT, AJA, KF, CF, EJL, JK, PS, MT, and EIR. *Writing revision:* JT, AJA, EIR, KF, CF, and JK.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

All data and code are available on Figshare: https://figshare.com/projects/Data_and_scripts_for_manuscript_Zoogeochemistry_of_a_protected_heathland_driven_by_anthropogenic_impacts_and_animal_behaviour_178614.

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SUPPORTING INFORMATION

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