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RESEARCH ARTICLE

From here to there: free-ranging large herbivores redistribute nutrients from grassland to forest soil

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Abstract

Context Large herbivores contribute to biogeochemical cycling across spatial scales. Nutrient transport by herbivores is often linked to their movements between habitats preferred for foraging (nutrient intake) and resting (nutrient excretion).

Objectives We investigated whether movement decisions of free-ranging red deer (*Cervus elaphus*) lead to changes in plant-available soil nutrients. We hypothesised that concentrations of soil phosphorus and potassium would increase in forest relative to grassland with increasing red deer use. Additionally, we tested whether soil nutrient concentrations are positively related to the intensity of deer resting behaviour.

Methods Our study was conducted in the Grafenwöhr military training area, Germany. We collected 200 soil samples from semi-natural grasslands and forests in three zones with varying red deer use. Using GPS telemetry and accelerometer data from 25 red deer, we classified their relocations into active

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(foraging, travelling) and passive (resting) and calculated a utilisation distribution for resting behaviour.

Results Phosphorus and potassium were significantly enriched in forest compared to grassland soil in the zone with the highest red deer use, and potassium also in the intermediate zone. Nutrient concentrations in forests, where red deer spent more passive than active time contrary to grasslands, increased with resting intensity. This suggests that the differences in nutrient concentrations between forest and grassland are related to deer resting behaviour in forest and associated excrement deposition.

Conclusion By combining data from soil tests, telemetry and activity sensors, we showed that movement decisions of wild ungulates result in nutrient transfer from grassland to forest, contributing to nutrient-poor conditions in grassland favourable to biodiversity. Ungulate effects in forests go beyond browsing as nutrient subsidies could increase forest soil fertility.

Keywords Activity sensors · Animal movement · *Cervus elaphus* · Telemetry · Wildlife management · Zoogeochemistry

Introduction

The important role of large mammalian herbivores in ecosystem functioning and biogeochemical cycling at local to global spatial scales is increasingly recognised (Malhi et al. 2016; Ellis-Soto et al. 2021; Pringle et al. 2023; Rizzuto et al. 2024). The removal of above-ground plant biomass by foraging can influence soil processes via changes in microclimate (Vaieretti et al. 2018), plant community composition (Augustine and McNaughton 1998), vegetation productivity (Olofsson et al. 2001) and litter quality (Pastor et al. 1993; Ramirez et al. 2021). However, the impacts of large herbivores go beyond herbivory: their movement is related to trampling (Schrama et al. 2013; Ramirez et al. 2021), and they deposit urine, dung and carcasses, affecting the physical and chemical properties and biota of soils, thereby influencing biogeochemical processes through multiple interacting pathways (Haynes and Williams 1993; Hobbs 1996; Bardgett and Wardle 2003; Sitters and Andriuzzi 2019; Balandier et al. 2022).

Free-ranging large herbivores regularly move between habitat types to meet different requirements, e.g., resting in forests and foraging in open areas (Ellis-Soto et al. 2021). When rates of nutrient removal and excretion differ between habitat types, the movement of herbivores between habitats turns them into vectors of nutrients (Jeltsch et al. 2013). Consequently, nutrients are depleted in habitat types primarily used for foraging, while habitat types mainly used for purposes other than foraging receive nutrient subsidies (Daufresne 2021; Rizzuto et al. 2024). In terms of local ecosystem functioning, this raises the question of how such nutrient dynamics mediated by animal movement affect soil nutrient availability to plants (rather than the total soil nutrient stocks). This question becomes particularly important for habitats of high conservation value, such as semi-natural grasslands, which require low soil nutrient availability, and are highly threatened in Europe (Habel et al. 2013; EEA 2020). Nutrient emissions from anthropogenic activities such as agriculture can lead to biomass accumulation and successive changes in vegetation composition, thus compromising plant diversity in these habitats (EEA 2020). Therefore, successful open habitat conservation and restoration often require counteracting nutrient enrichment (Helsen et al. 2014).

Extensive livestock grazing has been used successfully to maintain nutrient-poor soil conditions favourable to plant diversity in open habitats (Kooijman and Smit 2001; Uytvanck et al. 2010). Wild herbivores, particularly red deer (*Cervus elaphus*), can also support open habitat conservation and grassland plant diversity (Tschöpe et al. 2011; Riesch et al. 2019, 2020), and thus represent a useful alternative for conservation management, especially in areas where livestock grazing is not feasible (e.g., due to military training and access restrictions or in protected areas such as the core zones of national parks). Previous research has quantified the import and export fluxes of nitrogen (N) and phosphorus (P) by free-ranging red deer in grasslands and heathlands and reported that nutrient removal by grazing exceeds nutrient return via excreta in these habitat types (Riesch et al. 2022). Whether such a discrepancy in import and export nutrient fluxes translates into measurable

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changes in plant-available soil nutrient concentrations is still unclear.

Generally, our mechanistic understanding of the impacts of herbivores on nutrient cycling remains limited (Balandier et al. 2022; Monk and Schmitz 2022; Pringle et al. 2023). Considering information on animal movement and behaviour could be an important step towards improving our understanding of the mechanisms governing animal-vectored nutrient redistribution (Jeltsch et al. 2013; Earl and Zollner 2017; Ellis-Soto et al. 2021). Recent advances in animal tracking via satellite telemetry allow for the collection and analysis of high-resolution spatio-temporal data, which can elucidate animal movement and behaviour, especially when combined with additional data from animal-borne sensors (Kays et al. 2015; Nathan et al. 2022). While telemetry data have often been used to study bottom-up effects, i.e., how the movement and habitat use of wild herbivores relate to vegetation composition (Jaroszewicz et al. 2021) or forage quantity and quality (Balluffi-Fry et al. 2020), the top-down effects of wildlife on vegetation or soil have received less attention in telemetry studies to date. In systems grazed by livestock, attempts have been made to relate animal-mediated nutrient fluxes to soil nutrient concentrations (Bakker et al. 2004; Jewell et al. 2007; Schnyder et al. 2010; Koch et al. 2018; Castillo-Garcia et al. 2022), whereas studies on wildlife often measure fluxes (Seagle 2003; Abbas et al. 2012; Murray et al. 2014; Riesch et al. 2022) but rarely quantify soil nutrient levels in different habitat types used by wild herbivores (but see Schoenecker et al. 2004; Jensen et al. 2011). This might be related in part to the fact that soil chemical properties change slowly (Steffens et al. 2008; Mikha et al. 2015); therefore, herbivore habitat use patterns must be stable over time to produce detectable effects in the soil.

Studies on the involvement of large herbivores in biogeochemical cycling have focused primarily on nitrogen (N) so far (Sitters and Olde Venterink 2015; Sitters and Andriuzzi 2019), presumably because N is regarded as the main limiting nutrient for plant growth in terrestrial systems (LeBauer and Treseder 2008) and an important driver of herbivore diet selection (Felton et al. 2018). Measuring plant-available N, however, is difficult because it is strongly influenced by plant traits and their interactions with microbes and minerals, which show significant temporal dynamics, and therefore cannot be assessed in a single measurement (Grandy et al. 2022). Like N, phosphorus (P) is also often limiting to aboveground plant production (Hou et al. 2020) and might affect herbivore diet selection (Dykes et al. 2018). Phosphorus translocation has received attention, especially in livestock systems (Jewell et al. 2007; Schnyder et al. 2010; Koch et al. 2018), and has to some extent also been addressed in wildlife studies (Schütz et al. 2006; Flueck 2009; Abbas et al. 2012). Still, increased efforts to collect data to elucidate herbivore-mediated cycling of P and other elements are recommended (Sitters and Olde Venterink 2015; Sitters and Andriuzzi 2019). Among the macronutrient cations, potassium (K) is the most important for plant productivity, and large herbivores can play an important role in K cycling (Whitehead 2000; Kayser and Isselstein 2005; Assmann et al. 2017); however, to our knowledge, this has rarely been considered in terms of wild ungulates (Jensen et al. 2011). In general, soil P and K concentrations have been recognised as suitable indicators for long-term nutrient transfer by grazing animals (Tonn et al. 2019).

The present study aimed to investigate whether the movement and behaviour of free-ranging red deer cause relative changes in plant-available soil nutrient concentrations between habitat types. We took advantage of a system with a long-term wildlife management strategy dedicated to encouraging open habitat use by red deer (Meißner et al. 2013; Richter et al. 2020). While red deer forage intensively in open habitats (Riesch et al. 2019), they rely on covered habitats as refuges from humans (Richter et al. 2020; Bojarska et al. 2024). As a result, they display regular daily movements between open and covered habitats—a common pattern in wild ungulates seeking to avoid predators (Ager et al. 2003; Leblond et al. 2010; Allen et al. 2014; Kohl et al. 2018; Monk and Schmitz 2022). Previous quantification of nutrient fluxes revealed net nutrient removal by red deer in open habitats (Riesch et al. 2022). As the largest share of nutrients ingested by grazers is returned via excreta (Haynes and Williams 1993; Whitehead 2000) and nutrient export from our study system through animal harvest is minor (Riesch et al. 2022), we expected to find evidence for nutrient translocation by red deer caused by their movement between open grassland and sheltered places preferred for resting, such as forests and dense shrubs (Seagle 2003; Schoenecker et al.

2004; Murray et al. 2014). Focusing on P (returned via dung (Whitehead 2000)) and K (returned via urine and dung (Whitehead 2000)), we hypothesised that (i) the concentrations of these nutrients increase in the soils of forests compared with those in open habitats with increasing red deer use, i.e., we expected a significant interaction between habitat type and intensity of habitat use by red deer. By contrast, in the case of soil characteristics that are mostly defined by bedrock, plant-soil or microbial interactions (Ehrenfeld et al. 2005; Philippot et al. 2024) or other processes unrelated to large herbivores (e.g., soil pH, total soil nitrogen (N_t), total soil carbon (C_t) and soil organic matter (SOM)), we did not expect an interaction between habitat type and the intensity of habitat use by red deer. To test this hypothesis, we collected 200 soil samples from forests and grasslands across a gradient of low to high red deer use. Additionally, we hypothesised that (ii) soil P and K concentrations increase with the probability that red deer have spent time resting at that location. We tested this hypothesis by combining soil sample data with telemetry and activity data recorded from 25 collared red deer individuals over six years.

Methods

Study area

The study took place in the Grafenwöhr military training area (GTA, 230 km^2, centred at 49° 40′ 56″ N, 11° 47′ 20″ E) in Bavaria, Germany (Fig. 1), which is located in the Upper Palatine-Upper Main Hills natural region at elevations of approximately 450 m (Raab et al. 2019). Annual long-term means (1991–2020) of temperature and precipitation are 9.0 °C and 769 mm, respectively (as calculated from data from four weather stations of the German Weather Service within a 35 km radius). Military training in GTA started at the beginning of the twentieth century. The western part of GTA, where we conducted our study, was added to the area in the 1930s. While a few ruins in the landscape tell of the former rural settlements, exceptionally low soil nutrient levels indicate that agricultural intensification has not affected this area (Riesch et al. 2018). Unauthorised persons are not permitted to enter the area, but it is not fenced. The land cover in GTA is dominated by coniferous forests (38%) and broad-leaved forests (16%), roughly forming a circle around the area, and open habitats mostly located in the centre of the area (30%), which are partially managed by annual mowing or mulching (Raab et al. 2019). A share of 8% of the land is covered by artificial surfaces and bare soil, 4% by moors and heathlands, 3% by transitional woodlands or shrubs,

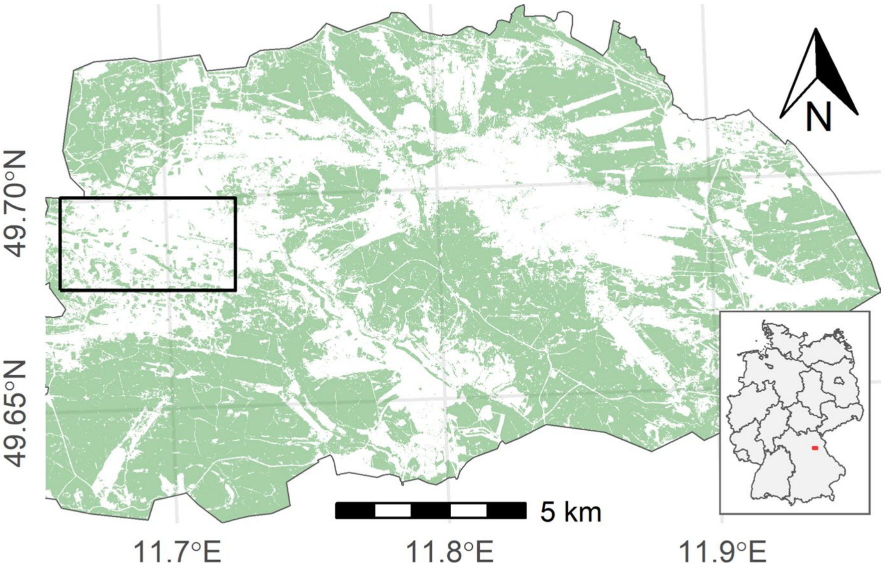

Fig. 1 Map of the Grafenwöhr military training area (GTA) with forest cover derived from multi-temporal Tasselled Cap RapidEye time-series (Raab et al. 2019) shown in green. The black frame indicates the sampling area within GTA, see Fig. 2. The inset map in the lower right corner shows the location of GTA (red rectangle) in northern Bavaria, Germany

and 1% by water (Raab et al. 2019). In addition to mechanical biomass removal, fires and disturbances due to military training as well as grazing by wild red deer contribute to maintaining open habitats in GTA (Riesch et al. 2019). Red deer are the most abundant game species (number of animals shot in GTA during the hunting period from April 2022 to April 2023: 1605 red deer, 588 roe deer (*Capreolus capreolus*), 464 wild boar (*Sus scrofa*)). The total red deer population was estimated to be approximately 6,000 individuals in the spring, i.e., 26 individuals km^{-1}, although their density varies spatially. The region is experiencing ongoing recolonisation by wolves (*Canis lupus*), with the first wolf recorded in GTA in 2016 (DBBW 2023). Data from wildlife camera traps and red deer telemetry (unpublished data) indicate that wolves had no detectable impact on red deer movement up to 2021, the year in which soil samples were collected for the present study.

Wildlife management in the military training area is executed by the Federal Forestry Administration (Bundesforst) of the German Institute for Federal Real Estate. For several decades, the management objective has been to reduce damage caused by bark-stripping and browsing in forests and encourage red deer to forage in open habitats. In the large forest areas that stretch along the inner margin of GTA, hunting therefore continues throughout the hunting season (red deer: June to January), whereas the open habitats in the centre of GTA are affected mostly by a few driven hunts in autumn/winter. Previous studies have shown that the red deer use the open habitats on GTA regularly and even during the day (Meißner et al. 2013; Richter et al. 2020), mostly for foraging (Riesch et al. 2019). Roe deer are rarely observed in the centre of GTA, likely due to their tendency to avoid red deer (Borkowski et al. 2021).

For the present study, we chose a sampling area of approx. 800 ha in the western central part of GTA (Fig. 1), which largely corresponds to the “Sommerhau” area (cf., Richter et al. 2020). The sampling area represents a heterogeneous mosaic landscape composed of mown and unmown grasslands (62.7% cover) intermingled with hedges, shrubs and mixed forest patches (16.7% forest cover and 10.7% shrub cover). The remaining land consisted of other cover classes including buildings, roads and water (Raab et al. 2019). The most common overstorey tree species in the forest patches were *Pinus sylvestris*, *Picea abies*, *Salix* sp., *Alnus incana*, *Fagus sylvatica* and *Quercus* sp. The shrub layer was composed mainly of *Crataegus* sp. and *Prunus spinosa*, but also *Rosa* sp., *Cornus sanguinea*, *Corylus avellana* and *Rubus* sp. occurred frequently. Grasslands can be characterised to some extent as EU Habitats Directive Annex I habitat type 6510, lowland hay meadows, and harbour high plant species richness (Riesch et al. 2018). The soils in this area are very heterogeneous and are mainly classified as varieties of brown earth, in some parts rendzina, on terra fusca and carbonate rock, or (calcareous) sandstone or (sand-) marlstone (LFU 2023). A large military road crosses the site, and open areas are partly used for training with artillery. Red deer in “Sommerhau” show a preference for open habitats during night hours, while spending more time in covered habitats during the day, presumably because they have adapted to frequent traffic and other human activities during daylight hours in this part of GTA (Richter et al. 2020).

The sampling area was unevenly frequented by red deer. This can be explained by higher military activity in the western part of the area, which presumably deters the red deer. Moreover, the south-eastern part of the area transitions to a large contiguous forest, where red deer were concentrated before the wildlife management by the Federal Forestry Administration began to promote open habitat use by red deer. We made use of this pattern in our analyses by dividing the sampling area into three zones with differing red deer habitat use (1—low, 2—intermediate, 3—high) on the basis of information from the local forester and telemetry data (Fig. 2a).

Soil sampling and laboratory analyses

To assess the potential effects of red deer on soil chemical parameters, we collected 200 soil samples from 32 linear transects running from grasslands to forest patches in November 2021 (Fig. 2). The locations of the transects were defined prior to sampling with the aim of covering the entire sampling area systematically while maintaining a minimum distance of at least 100 m between individual transects. As a result, the number of soil sampling transects differed between zones of red deer habitat use (low: n = 9, intermediate: n = 6, high: n = 17).

For 15 transects, we sampled soil at 4 m, 20 m and 50 m from the forest edge in both grasslands and

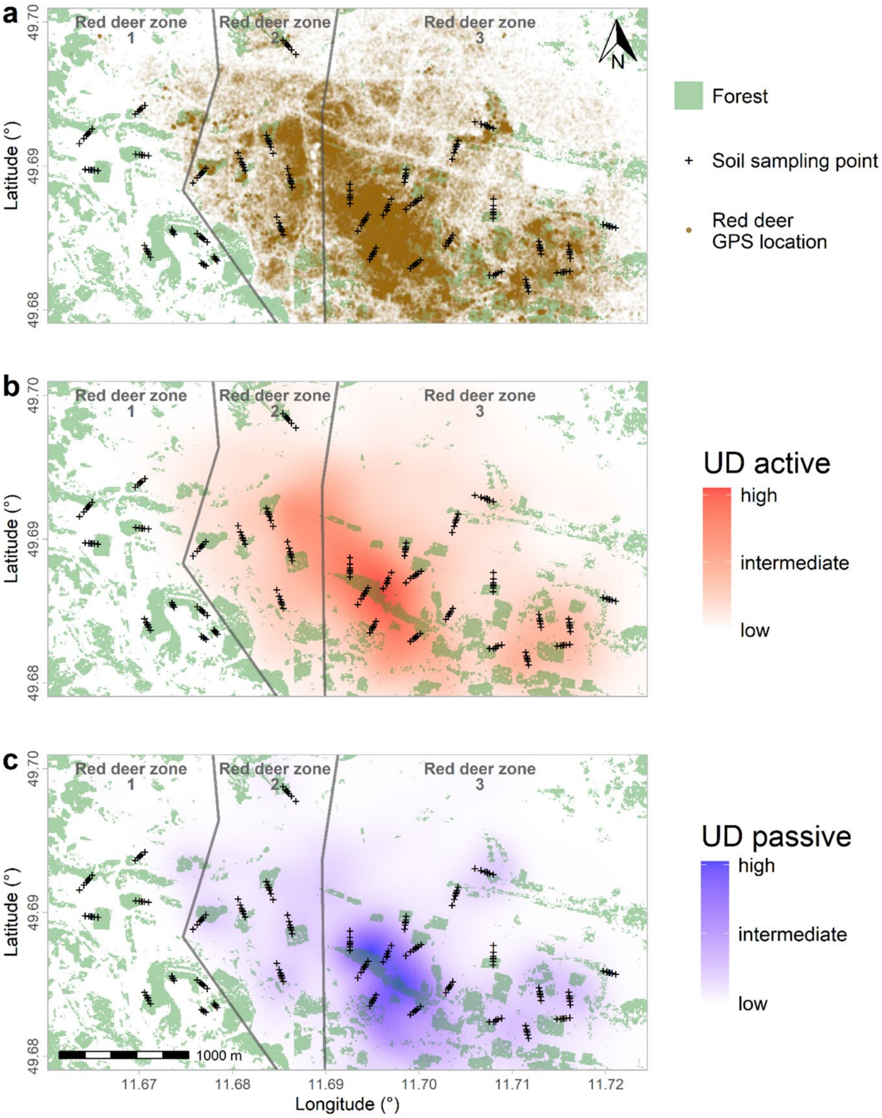

Fig. 2 Map of the sampling area with **a** GPS locations of collared red deer, **b** utilisation density (UD) of red deer in the active behavioural state and **c** UD of red deer in the passive behavioural state. The red deer zones 1–3 represent areas with low, intermediate, and high red deer use, respectively

forests, i.e., six soil sampling points per transect. The maximum distance was limited by the size of forest patches. For 14 transects, grassland size was large enough to collect an additional, seventh sample at a 100-m distance from the forest edge. For three transects where the grassland and forest patches were smaller, we collected samples only at the distances of 4 m and 20 m, i.e., four soil sampling points per transect. The sampling points were located in the field by a tablet with a dedicated GPS module. At each sampling point, we collected a soil sample by pushing a Pürckhauer soil corer 10 times into the mineral soil to a depth of 10 cm within an area of approximately 4 m^2.

The soil samples were split into two sub-samples. One sub-sample was used to measure soil pH, macronutrient cation concentrations and P. After freeing soil from roots using a 2-mm sieve, the pH of the fresh soil was measured in a 1 M KCl solution (pH$_{KCl}$). To determine the soil macronutrient cation concentrations, the soil was ground and dried at 70 °C for 48 h. The effective cation exchange capacity (in µmol g^{-1} dry soil) of K was assessed by inductively coupled plasma optical emission spectrometry (ICP-OES; iCAP7000, Thermo Fisher Scientific, MA, USA) after percolation with a 0.1 M BaCl$_2$ solution. To determine plant-available P, we used the resin-bag method (anion-exchange resin Dowex 1×8–50, cf.

Leuschner et al. (2014)). Soil nutrient concentrations of K and P are presented in mg kg^{-1}.

The second soil sub-sample served to determine the percentages of N_t and C_t. After drying at 30 °C for 72 h, the soil samples were sieved (2 mm) and ground in a ball mill. Subsequently, 0.10–0.20 mg soil from each sample was transferred into a tin capsule and analysed via an elemental analyser (Flash EA 1112, Thermo Fisher Scientific, Rodano, Milan, Italy). To correct N_t and C_t for residual moisture content, the dry matter of each sample was determined after drying at 105 °C for 24 h. Additionally, we determined the percentage of soil organic matter (SOM) via loss-on-ignition, i.e., incinerating each sample in a muffle furnace at 550 °C (Hoogsteen et al. 2018). One sample (taken in a forest, at 20-m distance to the edge) showed a suspiciously high SOM content (>30%) indicative of contamination with material from the organic layers (AG Boden 2005) and was therefore excluded from all analyses.

Red deer telemetry

The capturing and collaring of red deer was authorised by the authorities of Lower Franconia (animal experiment permit numbers 55.2-2532-2-14 and 55.2.2-2532.2-1092-17). The animals (females n = 17, males n = 8) were either captured in a corral or by a large drop net before being anaesthetised with a dart gun or blow pipe or anaesthetised with a dart gun from a high seat in 2016 to 2022. The GPS collars (Vectronics GPS Pro, Vectronics Aerospace GmbH, Berlin, Germany) recorded the locations of the animals once per hour. Additionally, a collar-integrated two-dimensional accelerometer recorded data on animal activity state (active/passive) every 8 s and stored a 5-min average, which was retrieved for analyses.

Data preparation and statistical analyses

For all data processing and statistical analyses we used R version 4.3.3 (R Core Team 2023). Red deer activity data were classified into two distinct states that reflect high and low activity (we labelled these states active and passive). To find individual-specific thresholds that separate active and passive observations, we used a hidden Markov model for each red deer individual to model the first norm of the two-dimensional activity data (i.e., their squared sum). To do so, we fitted a gamma distribution to each state, which was estimated with maximum likelihood state-specific scale and shape parameters following Leos-Barajas et al. (2017). We decoded the two hidden states (active or passive) with the Viterbi algorithm. For all the animals, we used the same starting values. For the shape parameter, we used the values 1 and 5 for the passive and the active state, respectively, and for the scale parameter, we used the values 5 and 10 for the passive and the active state, respectively. We set 90% and 10% as the starting values for the probabilities of being in the passive or active state. For each step (two consecutive GPS locations in time) of the hourly GPS data, we calculated the proportion of active and passive activity data points. For further analyses, we only used the GPS points (start points of a step) where ≥ 90% of the following activity data points were classified as either active or passive. Thus, we used only 56% of all the GPS points (26% active and 30% passive) in further analyses. For both sets of GPS points (active and passive), we quantified utilisation distributions for active behaviour (UDa, Fig. 2b) and passive behaviour (UDp, Fig. 2c) using kernel density estimates (with the AMT package, Signer et al. 2019), pooled across individuals and applying a reference bandwidth.

For all the soil chemical parameters (P, K, pH, C_t, N_t, SOM), we tested the effects of habitat type (forest/open), red deer zone (three levels) and distance to the forest edge (three levels) as well as all the interactions of these factors in separate linear mixed effects (LME) models using the nlme package (Pinheiro et al. 2015). The distance to the forest edge was included to account for potential changes in red deer behaviour due to variation in forage availability or risk perception with distance to the habitat edge (Hernández and Laundré 2005; Alves et al. 2014). As the 100-m distance was only sampled in grasslands, we pooled these samples with the 50-m distance samples after confirming that there was no significant difference between these distance levels for any of the response variables via boxplots and Wilcoxon tests. The transect ID served as a random factor in all the models. To ameliorate the normality of residuals, the percentages of soil C_t and soil N_t were logit-transformed, and soil P and soil K concentrations were log-transformed. To account for variance heterogeneity between factor levels, we added a variance structure function to the models for soil pH, C_t,

N_t, and SOM. For each dependent variable, we successively simplified the global model using likelihood ratio tests (Tredennick et al. 2021) to select the minimum adequate model (MAM). We checked for spatial autocorrelation in the residuals of all our models via Moran's I. We first looked for all nearest neighbours for each point within a distance of 1 to 500 m. Next, we calculated spatial weights, and a randomised version of Moran's I test as implemented in the spdep package (Bivand 2022). The test statistics were not significant for the residuals of any model, indicating that spatial autocorrelation did not affect our results.

For the MAMs that retained the red deer zone as a significant explanatory factor ($p < 0.05$), we repeated the analysis replacing the factor red deer zone with the intensity of use by red deer in the passive behavioural state derived from the UDp for each soil sampling point as a continuous predictor (i.e., resting intensity). The extracted UDp values were scaled to zero mean and unit variance before being entered into the model. For all MAMs, we computed estimated marginal means or trends of significant explanatory variables using the emmeans package (Lenth 2021). All figures were created using the ggplot2 package (Wickham 2016).

Results

The hypothesised interaction effect of red deer zone with habitat type was significant ($p < 0.01$) for the MAMs of soil P and K but not for any other soil chemical parameter (Table 1; Fig. 3). The estimated marginal mean of soil P concentration was significantly higher in forests (28.81 mg P kg^{-1}) than in grasslands (13.60 mg P kg^{-1}) in the zone where red deer habitat use was high ($p < 0.001$; Online Resource 1, Table S1). The soil K concentration was significantly higher in forests than in grasslands in the zones with intermediate (245.45 mg K kg^{-1} vs. 104.58 mg K kg^{-1}, $p < 0.001$) and high red deer use (369.80 mg K kg^{-1} vs. 119.01 mg K kg^{-1}, $p < 0.001$; Online Resource 1, Table S1). Both soil P and soil K were affected by distance from the forest edge in interaction with habitat type, but this effect was consistent across red deer zones (Table 1).

Soil pH ranged between 4.82 and 7.90, with an overall estimated mean (±SE) of 6.48 ± 0.13, as all explanatory variables had been removed from the MAM (Table 1). Soil N_t ranged between 0.14% and 0.80% with a slightly but significantly higher estimated marginal mean in forests (0.36 ± 0.20%) than in grasslands (0.33 ± 0.17%). Soil C_t ranged widely between 1.67 and 16.32% and was on average significantly higher in forests (5.13 ± 0.41%) than in grasslands (4.09 ± 0.32%). Similarly, SOM, ranging from 3.87% to 23.63%, was significantly higher in forests (10.85 ± 0.45%) than in grasslands (8.78 ± 0.41%).

Our telemetry dataset comprised 25 red deer with an average of 13,413 ± 6,796 GPS relocations (mean ± SD) per individual. The accelerometer data showed that the animals dedicated most of their time in the forest to resting (mean ± SE proportion of passive time: 0.78 ± 0.015 across individuals), whereas in the open grassland, they were mostly active (mean ± SE proportion of passive time: 0.40 ± 0.015 across individuals).

The differences in soil P and K concentrations between grassland and forest increased with increasing red deer resting intensity (Fig. 4; Table 1; Online Resource 1, Table S2). The slope of the relationship between resting intensity and soil P or soil K concentration differed significantly from zero in the forest (P: estimate 0.36, SE = 0.11, t-ratio = 3.16, $p = 0.002$, K: estimate 0.30, SE = 0.08, t-ratio = 3.67, $p = < 0.001$) but not in the grassland (P: estimate 0.13, SE = 0.12, t-ratio = 1.06, $p = 0.291$, K: estimate 0.02, SE = 0.08, t-ratio = 0.19, $p = 0.849$).

Discussion

Our study links telemetry and animal activity data with field data on soil chemical parameters, in response to calls for enhanced data collection to better understand the mechanisms by which free-ranging herbivores redistribute nutrients (Sitters and Andriuzzi 2019; Ellis-Soto et al. 2021). We investigated whether wild red deer transport nutrients while moving between grasslands and forests, thereby influencing the concentrations of plant-available nutrients in the soil. Among the soil characteristics analysed, only the nutrients P and K, which are returned in considerable proportions via dung and urine (Whitehead 2000), were significantly related to red deer zone in interaction with habitat type: forest soils were enriched with P and K compared to grassland soils

Table 1 Effects of habitat type (forest, grassland), distance to the forest edge (three levels) and red deer zone (three levels) on different soil chemical parameters (soil phosphorus (P), soil potassium (K), pH, total soil carbon (C_t), total soil nitrogen (N_t), soil organic matter (SOM)). Results were obtained from marginal Wald tests of the most parsimonious linear mixed effects model for each response variable. Degrees of freedom are given for the nominator [$df_{(num)}$] and denominator [$df_{(den)}$]. Soil P and K, which were significantly affected by red deer zone, were additionally analysed using the intensity of use by red deer in the passive state (i.e., resting intensity) as an alternative continuous explanatory variable replacing the factor red deer zone. The conditional and marginal coefficients of determination (Nakagawa et al. 2017) express the variance explained only by fixed effects [$R^2_{(m)}$] and the variance explained by fixed and random effects combined [$R^2_{(c)}$].Significant effects ($p < 0.05$) are displayed in bold font

Response	Model term	$df_{(num)}$	$df_{(den)}$	F-value	*p*-value	$R^2_{(m)}$	$R^2_{(c)}$
Models including red deer zone as factorial variable of habitat use							
Soil pH	–	–	–	–	–	0.00	0.76
Soil C_t	**Habitat type**	**1**	**166**	**47.70**	**< 0.001**	0.05	0.74
Soil N_t	**Habitat type**	**1**	**166**	**8.68**	**0.004**	0.02	0.64
SOM	**Habitat type**	**1**	**166**	**61.74**	**< 0.001**	0.04	0.23
Soil P	**Habitat type**	**1**	**160**	**17.40**	**< 0.001**	0.26	0.62
	Red deer zone	**2**	**29**	**5.43**	**0.010**		
	Distance	2	160	2.54	0.082		
	Habitat type: red deer zone	**2**	**160**	**5.69**	**0.004**		
	Habitat type: distance	**2**	**160**	**4.57**	**0.012**		
Soil K	**Habitat type**	**1**	**160**	**103.20**	**< 0.001**	0.44	0.68
	Red deer zone	2	29	2.20	0.129		
	Distance	2	160	0.56	0.571		
	Habitat type: red deer zone	**2**	**160**	**10.73**	**< 0.001**		
	Habitat type: distance	**2**	**160**	**7.39**	**0.001**		
Models including red deer resting intensity							
Soil P	**Habitat type**	**1**	**160**	**32.99**	**< 0.001**	0.18	0.61
	Resting intensity	**1**	**160**	**5.01**	**0.027**		
	Distance	2	160	2.74	0.067		
	Habitat type: resting intensity	**1**	**160**	**7.73**	**0.006**		
	Habitat type: distance	**2**	**160**	**4.34**	**0.014**		
Soil K	**Habitat type**	**1**	**160**	**143.43**	**< 0.001**	0.39	0.62
	Resting intensity	**1**	**160**	**4.42**	**0.037**		
	Distance	2	160	0.37	0.695		
	Habitat type: resting intensity	**1**	**160**	**15.54**	**< 0.001**		
	Habitat type: distance	**2**	**160**	**6.79**	**0.002**		

in areas more intensively used by red deer. Moreover, red deer spent more time resting in forests than in grasslands, and the soil P and K concentrations in forests increased with increasing red deer resting intensity. This finding supports the hypothesis that the observed pattern in soil nutrient concentrations results from red deer movement and behaviour. Our findings enhance our understanding of the biogeochemical roles of large herbivores and the consequences of their movement decisions. This is important, as the zoogeochemical impacts of wildlife are increasingly recognised for their potential to support ecological restoration (Ellis-Soto et al. 2021; Monk and Schmitz 2022; Abraham et al. 2023) and even mitigate climate change (Schmitz et al. 2023; Kaštovská et al. 2024). In particular, our results have practical implications for habitat conservation, wildlife management, and forestry.

Plausibility and magnitude of effects

Although the importance of large ungulates as vectors of nutrients is well acknowledged, their net effects on soil nutrient concentrations have rarely been quantified

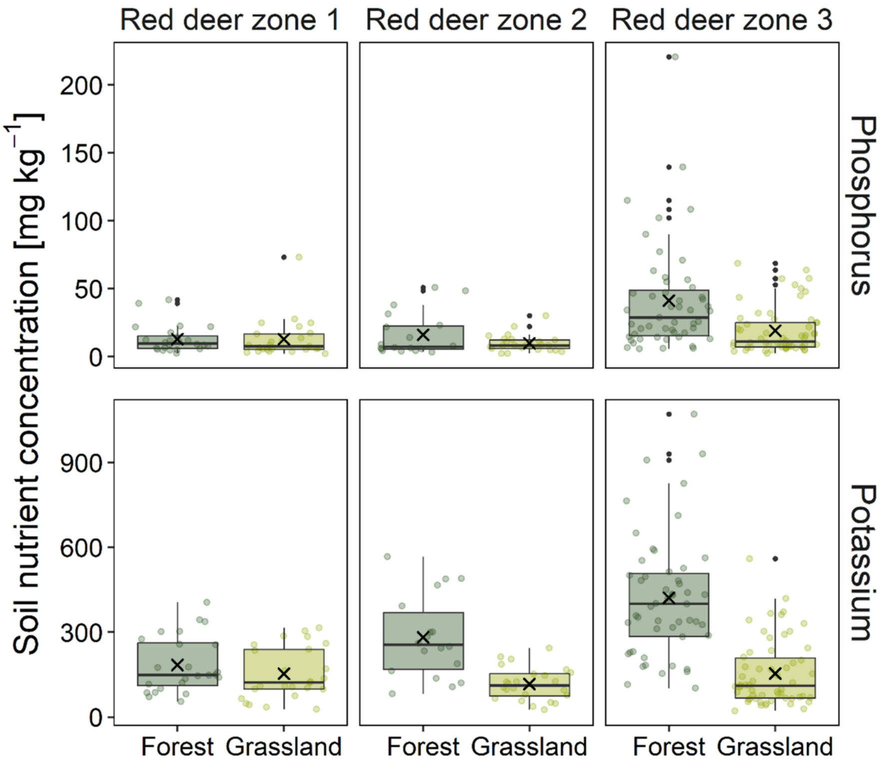

Fig. 3 Concentrations (mg kg^{-1}) of phosphorus (P) and potassium (K) in forest and grassland soil samples from zones with 1—low (n = 48), 2—intermediate (n = 42), and 3—high red deer use (n = 109) in the Grafenwöhr military training area, Germany. The × symbol shows the arithmetic mean

under free-ranging conditions (Ellis-Soto et al. 2021). Our results from a military training area in Germany with abundant red deer show that the concentrations of soil P and K were similar in forests and grasslands in areas with low red deer use but increased by 110% and 210% in forests compared with grasslands in areas most frequently used by red deer. As the soil P and K concentrations did not change significantly with increasing red deer use in grasslands, the hypothesized interaction between habitat type and intensity of red deer use was confirmed. For other soil characteristics (i.e., pH, C_t, N_t, and SOM) that depend more on bedrock, plant-soil interactions (Ehrenfeld et al. 2005; Philippot et al. 2024) or other site conditions than on nutrient fluxes mediated by large herbivores, we found no effects (pH) or only the main effect of habitat type, reflecting typical differences between forest and grassland (Gajić 2013; Burst et al. 2020). While mowing in grasslands (which affected 68%, 29% and 60% of our grassland sampling points in the low, intermediate and high deer use zone, respectively) can reduce soil P and K concentrations (Mládková et al. 2015), this cannot explain the observed increase in nutrient concentrations in forest relative to grassland at higher levels of red deer use. Therefore, it seems unlikely that an unconsidered environmental factor, and not the red deer, is responsible for our results. Nutrient fluxes mediated by other wildlife species could be a confounding factor, but red deer are by far the most abundant species, so that any impact is likely to be small. In addition, substituting the ’red deer zone’ factor in the models of soil P and K by a continuous predictor of use intensity by red deer in the passive state, derived from telemetry and activity data, yielded similar model fit and results. This finding supports our second hypothesis that soil P and K concentrations increase with increasing red deer resting intensity in the forest. Consequently, our study provides evidence that lateral transport of nutrients by large herbivores can lead to sizable differences in plant-available soil nutrients between habitat types resulting from different habitat preferences for active behaviour, such as foraging, and resting behaviour, which is associated with more excreta deposition (Schoenecker et al. 2004).

Previous work on nutrient fluxes in our study area found that red deer grazing in grasslands removed 3.3 kg P ha^{-1} a^{-1} (Riesch et al. 2022) and 12.2 kg K ha^{-1} a^{-1} (unpublished data) on a net basis.

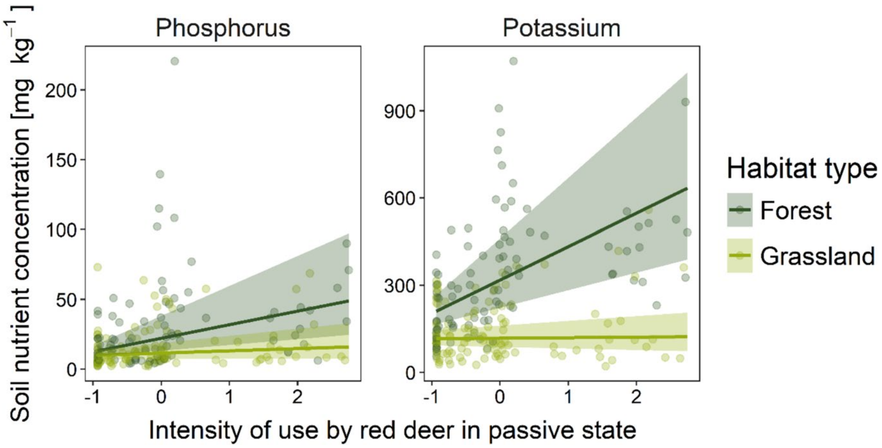

Fig. 4 Relationship between the intensity of use by red deer in a passive state (i.e., resting) at soil sampling points as a continuous variable derived from telemetry and accelerometer data and soil phosphorus and potassium concentrations (mg kg^{-1}). The x-axis is scaled in standard deviations from the mean centred at zero. Points are raw data; lines indicate the model-estimated trends with 95% confidence intervals

For a rough estimation of whether it is conceivable that the difference in soil nutrient concentrations found in the present study stems from red deer activities, we may assume, for simplicity, that all nutrients removed from grasslands were redistributed to forests. Further assuming that 90% of the P and K ingested are returned via excreta (Haynes and Williams 1993; Whitehead 2000) and completely retrieved in the extractable fraction of soil nutrients and that the soil bulk density is 0.73 kg l^{-1} in the 0–10 cm top forest soil layer (Panagos et al. 2024), it would have taken 4 years (P) or 17 years (K) for the observed differences to emerge. Red deer in GTA have been managed according to a stable strategy encouraging open habitat use by hunting restrictions for more than 30 years. Therefore, the magnitude of the effects observed in our study appears plausible.

We observed a more pronounced effect for K, being higher in forest soils than in grassland soils also in the zone with intermediate red deer use intensity, which might be associated with a greater quantity of K than P cycling in the system, since higher absolute amounts of K are excreted than of P (Haynes and Williams 1993). Moreover, the share of nutrients deposited via excreta that are recovered in the extractable fraction of soil nutrients differs between elements (Haynes and Williams 1993). In addition, spatial patterns of urination, making up the largest part of K returns, might not be identical to defecation patterns, which drive P returns (Haynes and Williams 1993; Auerswald et al. 2010), although this has not yet been studied in red deer.

Interestingly, the soil P and K concentrations increased with increasing resting intensity only in forests, and not in grasslands. While the collar-integrated accelerometers record a passive state, we do not know whether actual animal behaviour might differ between habitat types, potentially resulting in fewer excretion events in grasslands than in forests. For example, red deer may be more likely to defecate and/or urinate after a longer period of rest, which is consistent with the fact that the resting bouts of our collared animals were shorter in grasslands (mean ± SE: 57.5 ± 0.53 min) than in forests (80.9 ± 0.28 min). Direct animal observations, camera trap studies, or innovative animal-borne sensors (Marsden et al. 2021; Shorten and Welten 2022) might shed further light on such details in wildlife movement and behaviour. In addition, we found that the UDp and UDa values at the locations of our sampling points were strongly positively correlated in the zones with low or high red deer use (Online Resource 1, Fig. S1). This suggests that at intermediate red deer densities, animal activity data, in addition to information on movement and habitat use, are most important for explaining their role in biogeochemical cycling.

Nutrient translocation by large herbivores in different systems

Similarly to our results, a study on white-tailed deer (*Odocoileus virginianus*) in northern temperate forests near Lake Superior, USA, found that the soil nutrient composition varied along a gradient of deer use, and that the soil K concentration was significantly higher in areas with high counts of deer pellet groups than in areas with low pellet counts (Jensen et al. 2011). In terms of P translocation by red deer within grasslands in the Swiss Alps, Schütz et al. (2006) reported that the spatial pattern of P input through dung was similar to that of P removal through grazing and was positively related to short-grass cover and the soil P pool. This highlights that it is important to consider the spatial scale, habitat types, and animal behaviours when inferring the ecosystem effects of free-ranging herbivores (Daufresne 2021; Rizzuto et al. 2024). Generally, the effects of wild ungulates on soil properties and nutrient availability are context-dependent and have been shown to vary along gradients of soil texture and moisture (Dodge et al. 2020).

In pastures grazed by livestock, effects of differential behavioural and movement patterns on soil nutrient concentrations have been supported by many studies showing that nutrients are removed from areas preferred for feeding and enriched in areas preferred for resting, such as flat areas within hilly pastures (Jewell et al. 2007; Schnyder et al. 2010; Koch et al. 2018; Svensk et al. 2023). Free-ranging ungulates are not restricted to a defined pasture area, so they have the potential to redistribute nutrients on a much larger scale and between more different habitat types. However, their habitat choice, movement, and other behaviours are restricted by risk trade-offs, primarily involving the avoidance of humans in the anthropogenic landscapes of Europe (Gaynor et al. 2019). In our study area, human influence on wildlife movement and behaviour is less profound than in the ordinary landscape because military training activities are spatially and temporally scheduled, and hunting in open areas, including our sampling area, is strictly limited (Richter et al. 2020; Bojarska et al. 2024). Nevertheless, red deer in other parts of Europe are known to feed on agricultural meadows and crops (Månsson et al. 2021; Jarnemo et al. 2022; Trdan et al. 2024), which might intensify the flow of nutrients from open to covered areas due to higher diet quality (Abbas et al. 2012). On the other hand, red deer abundance in our study area is high compared with common red deer management targets, contributing to the magnitude of effects observed in our study. Moreover, the relative amount of forest and open areas and their spatial configuration (Seagle 2003; Abbas et al. 2012) as well as supplementary feeding (Trepel et al. 2024) can strongly affect the flow of nutrients. In GTA, haylage produced from grass cut exclusively within the area is offered in open areas in winter. In this way, supplementary feeding contributes to diverting red deer from browsing in the forest.

Implications for forestry, conservation and wildlife management

Our results are in line with other studies from various ecosystems (e.g., Murray et al. 2014; Bump 2018; Veldhuis et al. 2018) that found evidence for changes in plant-available soil nutrient concentrations related to large herbivore-mediated nutrient transport. Such changes in nutrient availability can have far-reaching effects at the plant level. In North American temperate forests, heterogeneity in ground-layer vegetation community composition and relative soil nutrient variability increased with winter deer use, suggesting that indirect nutrient-mediated effects contrast with the direct effects of deer herbivory through defoliation (Jensen et al. 2011; Murray et al. 2014). However, research disentangling the interactive effects of large herbivores on forest plant communities through multiple above- and belowground pathways under different climate and soil conditions is still rare (Balandier et al. 2022). Regarding the overstorey, it has been shown that nutrient subsidies by deer that increase the concentration of plant-available nutrients in forest soil can enhance the growth of mature trees (Lucas et al. 2013). This can be interpreted as a benefit from a forestry perspective (Abbas et al. 2012). In the face of growing concerns about nutrient deficiencies in trees resulting from nutrient dilution effects of globally increasing CO_2 levels and atmospheric N deposition (Jonard et al. 2015; Penuelas et al. 2020) and high soil nutrient losses due to tree harvesting, especially when not only timber but also residues are removed (Egnell and Ulvcrona 2015; Knust et al. 2016; Špulák and Kacálek 2020), nutrient subsidies by wild herbivores might become increasingly relevant.

Our finding that red deer habitat use did not increase soil nutrient concentrations in grasslands is important in terms of conservation because nutrient inputs can quickly lead to plant species loss and changes in community composition, deteriorating the conservation value of grassland habitats (Ceulemans et al. 2013; Helsen et al. 2014). In our study area, grassland plant species richness was found to decrease with increasing soil P despite the overall low soil P concentrations (Riesch et al. 2018). Accordingly, the present study provides one more piece of evidence that free-ranging red deer can be regarded as efficient agents in the conservation of open habitats (Tschöpe et al. 2011; Iravani et al. 2011; Riesch et al. 2019, 2020, 2022). Future studies are needed to assess how various human impacts on landscapes and wildlife affect nutrient redistribution by wild herbivores to inform wildlife management strategies that contribute to ecosystem conservation and restoration (Abraham et al. 2023). Equally interesting is the question of how the return of large carnivores, such as wolves in Europe, affects these zoogeochemical processes (Bump et al. 2009; Monk and Schmitz 2022).

Conclusion

Combining data from soil tests, telemetry, and activity sensors enabled us to show that the movement and behaviour of free-ranging red deer translate into measurable changes in plant-available soil nutrient concentrations between habitat types, with increasing soil P and K concentrations in forests relative to grasslands with increasing use by red deer. While game foraging on meadows and crops might cause conflicts in agricultural landscapes, wild ungulates commuting between open and covered habitats for foraging and resting in areas designated for open habitat conservation can contribute to maintaining nutrient conditions that are favourable to open habitat biodiversity. In addition, foresters should be aware that ungulate effects go beyond browsing, as nutrient subsidies to forests could increase soil fertility and enhance tree growth.

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Author contributions FR designed the study with input from NG and BT. Soil data collection was performed by FR. The capture of red deer for telemetry was performed mainly by MM with support from MZ, JB, CR, NG, FR, NB, and SH. JS and FR analysed the data. Resources were provided by JI and NB, and supervision was provided by JS, JI and NB. Funding acquisition, development and conceptual design of the overarching project by MM, FR and SH. FR wrote the first draft of the manuscript with support from JS. All the authors commented on a previous version of the manuscript and approved the final manuscript.

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Data availability The data analysed in this study are openly available in the Zenodo digital repository at https://doi.org/10.5281/zenodo.15287871.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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