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Ramirez Chiriboga, J.I.; Jansen, P.A.; Ouden, J.; Li, X.; Iacobelli, P. et al

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## Temperate forests respond in a non-linear way to a population gradient of wild deer

J. Ignacio Ramirez<sup>1,2</sup>, Patrick A. Jansen<sup>2,3</sup>, Jan den Ouden<sup>1</sup>, Xuqing Li<sup>1</sup>, Palma Iacobelli<sup>2</sup>, Natalie Herdoiza<sup>4</sup> and Lourens Poorter<sup>1</sup>

<sup>1</sup>Forest Ecology and Forest Management Group, Wageningen University & Research, PO Box 47, 6700 AA Wageningen, The Netherlands

<sup>2</sup>Wildlife Ecology and Conservation Group, Wageningen University & Research, PO Box 47, 6700 AA Wageningen, The Netherlands

<sup>3</sup>Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Balboa, Ancon, Panama

<sup>4</sup>Copernicus Institute of Sustainable Development, Utrecht University, Vening Meineszgebouw A, 3584 CB Utrecht, The Netherlands

\*Corresponding author: Tel: +46 761 12 78 09; E-mail: juanignacio.ramirez@icloud.com

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Wild deer exert strong top-down control on forest composition by browsing on palatable trees, and these effects are exacerbated as red, fallow, and roe deer populations increase in northern temperate forests. However, the relationship between deer abundance and plant recruitment remains poorly documented. Here, we combined camera trap and vegetation plot data to quantify the shape of the relationship between habitat utilization by deer (red, fallow and roe deer) with different components of the forest understory in ten sites distributed across a temperate mixed forest in the Veluwe, the Netherlands. The list of forest attributes included the density, richness and diversity of saplings, the proportion of conifers to broadleaves, the number of browsed broadleaves and conifers, the forest basal area, the understory cover of shrubs, moss and bare soil and the depth of the litter layer. When applying General Linear Mixed Models to those camera trap data, six of the eleven forest variables were related to the utilization level (UL) by deer. With increasing UL by fallow deer, there was a decrease in sapling species richness ( $\beta = -0.26$ ). With increasing UL by red deer, there was a decrease in litter depth ( $\beta = -0.14$ ) and an increase in browsed broadleaf stems ( $\beta = 0.40$ ). With increasing UL by roe deer, there was a decrease in species richness of sapling plants ( $\beta = -0.26$ ), Shannon diversity ( $\beta = -0.11$ ) and shrub cover ( $\beta = -0.36$ ), whereas there was an increase in stem density ( $\beta = 0.06$ ). When combining all deer species into one guild, a negative relation was found between UL by deer and sapling richness ( $\beta = -0.21$ ), diversity ( $\beta = -0.09$ ) and litter depth ( $\beta = -0.14$ ) and a positive relation with sampling density ( $\beta = 0.04$ ). The relationship between UL by deer and different forest attributes followed a linear  $\log_{10}$  shape. When back transforming, the response was curvilinear with large changes at a low UL and small changes when the UL was high. Yet, the exact shape of the curve varied according to (a) biotic factors specific to each study location. The conservation of temperate forests can benefit from limiting the size of deer populations and the time deer spend browsing in forest patches with high biodiversity value.

### Introduction

Wild deer affect ecosystems through various direct and indirect interactions with the vegetation community. Direct interactions include browsing, trampling, fraying, stripping and uprooting (Reimoser, 2003), while indirect interactions include seed dispersal, nutrient enrichment and modification of plant-plant interactions (Hobbs, 1996; Gill and Beardall, 2001). These interactions are known to shape the density, richness and diversity of saplings, the proportion of conifers to broadleaves, the number of browsed broadleaves and conifers, the forest basal area, the understory cover of shrubs, moss and bare soil and the depth of the litter layer. Thus, deer are considered keystone species as these interactions influence the entire structure and dynamics of woody ecosystems (Waller and Alvenson, 1997). The strength

of these interactions varies spatially and temporally, and the strongest interactions occur at high deer densities, for example  $>8$  deer  $\text{km}^{-2}$  (Alvenson *et al.*, 1988; Rooney and Waller, 2003). In systems with high primary productivity, deer probably have a weak impact on vegetation as plants can recover quickly thanks to a resource surplus, whereas in systems with low productivity, the impact might be especially strong because plants lack nutrients to mitigate browsing damage (Heckel *et al.*, 2010; Pellerin *et al.*, 2010).

In temperate forests of the Northern Hemisphere, deer populations are increasing (Clutton-Brock and Albon, 1992; Pellerin *et al.*, 2010). This increase is considered to be the result of rewilding projects; abandonment of agricultural land; reduced competition with domestic ungulates; absence of top predators; reduced hunting and improvement of habitat quality

(Côté *et al.*, 2004). In parallel, the fragmentation of natural forests by infrastructure, agricultural fields and forestry (Gordon and Prins, 2008) has led to the isolation of cervids in forest fragments and influenced their foraging behaviour (Kuiters *et al.*, 1996). Forest fragmentation has resulted in a large variation in deer density and species composition, and hence, a large variation in deer effects on the environment (Reimoser, 2003).

The role of ungulates in shaping natural ecosystems across the world has been a topic of much debate during the last decades (Cyr and Face, 1993; Augustine and Frelich, 1998; Gill and Morgan, 2010). Empirical studies in temperate forests maintain that deer exert strong top-down control on forest structure and dynamics through herbivory, which may negatively affect forest conservation goals (Pastor *et al.*, 1993). Alternatively, cervids can enhance species diversity and functioning in a non-linear way (Rooney and Waller, 2003) when herbivory levels are intermediate, in accordance with the intermediate disturbance hypothesis (Wilkinson, 1999; Ramirez *et al.*, 2018). For example, forests with intermediate deer densities may present greater forest structure and tree diversity (Gill and Morgan, 2010) because deer browsing promotes forest heterogeneity and reduces plant competition (Fuller and Gill, 2001) during advanced forest successional stages. Forests with few deer may have less tree diversity because there are fewer mechanisms – for example browsing, faeces deposition and seed dispersal – that promote a variety of niches in the forest understory and help distribute saplings (Reimoser and Putman, 2011). Forests with numerous deer may result in a low diversity understory because deer consume most of the forest regeneration (Ramirez *et al.*, 2019).

The exact relationship between deer abundance and different forest attributes varies with environmental conditions, vegetation type and the types and density of cervid species found in that system (Gill, 1992a; Reimoser and Putman, 2011). Another complication arises as past studies may have estimated the deer density with different methods, such as indirect and incomplete counts of animals (Pellerin *et al.*, 2010; Lucas *et al.*, 2013). To reconcile these seemingly contrasting findings, there is a need to study effects along a full gradient of deer density using a single and reliable method.

In this study, we assessed the relationship between deer abundance and different forest attributes in temperate forests in the Netherlands. We used a novel approach that involved arrays of camera traps paired with vegetation transects across 10 forest sites that varied widely in deer abundance, yet forest composition and structure were comparable. We predicted that an increase in deer abundance would lead to a non-linear (P1) increase in browsing and trampling (Rooney and Waller, 2003), which subsequently leads to the homogenization of the ecosystem by decreasing (P2) forest structure (Gill and Beardall, 2001), (P3) tree diversity (Côté *et al.*, 2004), (P4) understory cover (Gill, 1992b) and (P5) litter depth (Husheer *et al.*, 2005).

## Methods

### Study area

Fieldwork was conducted at the Veluwe, a 1200 km<sup>2</sup> ridge of hills forest-heathland complex, located in the central part of the Netherlands, with an elevation below 90 metres above sea

level. Average annual precipitation is 850 mm ·yr<sup>-1</sup> and the average annual temperature is 10.5°C. The main soil types are xeric humic podzols and brown earths (Kuiters and Slim, 2002). The Veluwe is covered by a mosaic of forests, agricultural land, drift sands and heathland, where forests take up two-thirds of the total area (1100 km<sup>2</sup>). The main conifer species are *Pinus sylvestris*, *Larix kaempferi* and *Pseudotsuga menziesii*, while the main broadleaved species are *Quercus robur*, *Fagus sylvatica* and *Betula pendula*. The deer guild varies across the Veluwe and include roe deer (*Capreolus capreolus* with an average body mass of 25 kg), fallow deer (*Dama dama*, 65 kg) and red deer (*Cervus elaphus*, 190 kg). In 2002, the combined average deer density was 11 individuals km<sup>-2</sup> (Kuiters and Slim, 2002). The study area is characterized by various wildlife management regimes, separated by fenced roads, leading to considerable spatial variation in cervid density caused by different hunting pressures (with an annual hunt density ranging between 0 and 10 ind·km<sup>-2</sup>·y<sup>-1</sup>, <http://www.verenigingwildbeheerveluwe.nl/>).

### Sampling design

Within the Veluwe, we selected 10 research sites that widely ranged in deer abundance (Figure 1 and Table 1) to relate local abundances to a set of forest attributes. The distance among sites with the closest proximity was on average 6 km apart and the farthest was 50 km. One contiguous square forest plot of 1 km<sup>2</sup> was established in each site. Within each plot, 21 random points were generated using ArcGIS with a minimum spacing of 100 metres between points. At each random point, we measured the UL by deer with camera traps and forest regeneration with vegetation plots.

### Deer utilization level

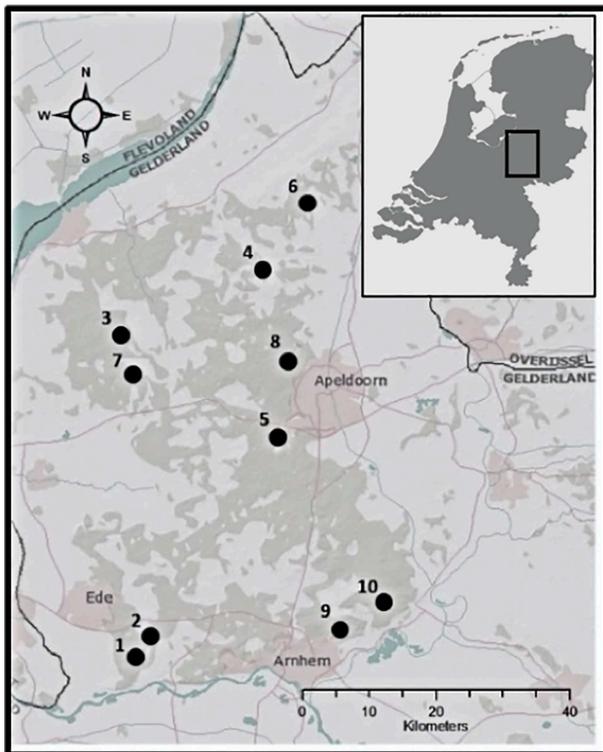
Between June and October 2017, we quantified deer UL with camera traps (Rowcliffe *et al.*, 2008; Kays *et al.*, 2009). Reconyx HyperFire HC500 cameras were mounted onto trees at 50-cm height in steel enclosures, facing north and aimed parallel to the ground. Cameras were then set to take 10 simultaneous images with no delay after being triggered. If necessary, understory vegetation directly in front of the camera was pruned one time below 50 cm to ensure a free view of the first 3 metres. The maximum detection distance of camera traps was determined at the time of placement by walking away from the camera until the sensor stopped detecting human movement. Linear detection distance was used to control UL because trees would often disrupt camera detection.

In each of the 10 sites, three camera traps were deployed simultaneously for an average of 21 days at each random point. After 21 days, the same three camera traps were rotated to new random points within the same site, and this procedure was repeated seven times, until all 21 points had been sampled. We aimed for a minimum of 440 camera trap days per site, and if the camera was stolen, a new camera was deployed in a new random point. We assumed that seasonality had no effect on deer behaviour because all sites were sampled evenly over time.

Camera traps were checked every 21 days, and images were stored in a computer and annotated with Agouti software (<https://agouti.eu/>). The software automatically grouped the

**Table 1** Sampling effort and UL of deer. Data were collected across the 10 forest sites at the Veluwe, the Netherlands. UL represents the average time (in seconds) that animals (in metabolic kg) spent in front of the camera trap, and sampling effort is the total number of days that camera traps were deployed. Kruskal-Wallis test for UL total (chi-squared = 147.81, df = 9,  $P < 0.001$ ).

Site	Code	Sampling effort (d)	Pictures (#)	UL (kg <sup>0.75</sup> ·s·m <sup>-1</sup> ·d <sup>-1</sup> )			
				Red deer	Fallow deer	Roe deer	Total
Achterpark	ACH	467	6226	1	0	3	4
Buunderkamp	BUU	476	10 850	15	0	12	27
Dellen	DEL	472	20 855	9	0	5	14
Garderen	GAR	471	19 239	2	0	10	12
Oostereng	OOS	516	8227	0	0	276	276
Rozendaalse Bos	ROZ	456	13 701	601	0	169	770
Rheden	RHE	400	15 563	2602	94	1071	3767
Speulderbos	SPE	446	13 017	2799	32	6199	9030
Gortel	GOR	459	43 463	195 490	2355	8489	206 334
Hoenderloo	HOE	466	18 640	861 610	17 965	73 717	953 292



**Figure 1** Research sites in the Veluwe, the Netherlands. Numbers and black dots indicate research sites, and light gray areas indicate forest. 1 = Oostereng, 2 = Buunderkamp, 3 = Speulderbos, 4 = Gortel, 5 = Hoenderloo, 6 = Dellen, 7 = Garderen, 8 = Achterpark, 9 = Rozendaalse Bos and 10 = Rheden.

images into sequences that represented separate animal visits. For each sequence of images, we annotated information on species, number of individuals, deer behaviour (browsing, moving, resting) and the duration of the sequence. We then calculated UL (kg<sup>0.75</sup>·s·m<sup>-1</sup>·d<sup>-1</sup>) by deer as the time in metabolic (sec) that a deer – expressed as the species average metabolic

active tissue (species average kg<sup>0.75</sup>) (Kleiber, 1947) – spent in front of a camera trap in proportion to the maximum detection distance in metres (m<sup>-1</sup>) and the deployment duration in days (d<sup>-1</sup>). Metabolic weight allowed for the quantification of different deer species in one independent variable. UL was calculated as:

$$UL = \sum_{i=1}^n \frac{A \times B^{0.75} \times T}{D \times S},$$

where (A) is the number of different deer in the same image sequence and (B) is the total number of kilogrammes per species raised to the power of 0.75, (T) is the time an animal spends in front of a camera trap in seconds, (D) is the maximal detection distance of the camera in metres and (S) is the sampling effort in days.

### Forest attributes

To quantify forest responses across sites, 21 vegetation plots in each site were paired to the 21 cameras. Plots were positioned 3 m away from the camera to avoid the pruned area, had a width of 4 metres and a variable length to assure that 50 tree stems with a height above 10 cm but less than 250 cm were included. We used a 4 × 4-m plot, located 3 m from each camera trap, to measure the percentage cover of understorey vegetation. The size of plot is commonly used in temperate forests (Ramirez et al., 2019).

We quantified eleven response variables within each plot (Nuttle et al. 2014). To describe forest structure, we measured tree stem density and basal area (for detailed methods see below). To describe tree composition, we measured species richness, Shannon diversity and conifer proportion (Shannon, 1948; Eskelinen and Oksanen, 2006). We measured litter thickness as it indicates the amount of litter accumulated on the forest floor that serves as a food source for invertebrates (Facelli and Pickett, 1991). The litter layer also acts as a barrier for the establishment of species in the seedbank (Facelli and Pickett, 1991). To describe the direct

impact of deer on tree regeneration, we measured the percentages of browsed broadleaved and conifer species. Three variables were used to describe the understory cover: percent cover of moss, shrub and bare soil. Moss and shrubs directly compete with trees and bare soil might facilitate seed establishment and development. We measured light in the understory, soil pH and canopy composition to understand how forest structure and soil fertility shape tree recruitment.

Each sapling was identified and its height measured as the vertical distance between the forest floor and the apex. Browsing damage was quantified as the presence or absence of at least one damaged branch during the current growing season. Canopy cover, which determines the understory light availability, was measured with a densiometer by standing at the centre of the vegetation plot (Lemmon, 1956). The dominant trees from the canopy determined the type of canopy cover and the local seed rain. We identified the two species with the greatest abundance within the forest canopy by counting the number of adult trees in a radius of 20 metres centred on a random point within the plot. The basal area was estimated with the Bitterlich Prism-method, with a counting factor of 3 (Bruce, 1955). We estimated the understory vegetation cover by using a grid to determine the percentage cover of shrubs (*Rosaceae* and *Ericaceae*), up to 1.5 m height, moss (*Bryophyta*) and bare soil (rocks, dead wood and soil). We used a ruler to quantify litter depth as the average of two measurements at random locations within the plot. One soil sample was collected from the plot to determine soil pH in the laboratory, dissolving soil in 0.01 M KCl and measuring it with a inoLab pH Plus (Maes *et al.*, 2019).

Forest type was measured using an index of broadleaf canopy dominance, which quantifies the mono dominance of the forest stand. When a stand was dominated by a single coniferous species, it was coded as zero; when it was dominated by a single broadleaved species, it was coded as one; while mixed stands had intermediate values (Ramirez, *et al.*, 2019). Seedlings and saplings were counted within each plot, and the density was calculated as the total number of individuals per ha. We did not group the stems by height because individuals between 10 and 150 cm were within the browsing height of red deer. Sapling species richness was quantified as the total number of woody species per 50 stems present in the transect. Shannon diversity of trees was calculated based on species abundance (Shannon, 1948). The proportion of conifers was calculated as the number of conifer saplings relative to the total of conifer and broadleaf saplings.

## Statistical analyses

All analyses were conducted not only at species level (red, roe and fallow deer) but also at a guild level (cervid = all deer species). To normalize data, we  $\log_{10}$ -transformed UL. To verify that fixed factors (UL of deer, light, soil pH, and broadleaf canopy dominance) were not collinear, an unconstrained principal component analysis (PCA) and a Pearson correlation test were performed; the results showed no collinearity (Dormann *et al.*, 2013). Generalized Additive Mix Models (GAMM) were used to assess the shape of the relationship between the UL of deer and the eleven forest attributes (Wood *et al.* 2017). For this analysis, forest attributes were the dependent variables; UL of deer, light, soil pH and

broadleaf canopy dominance were explanatory variables and the ten forest sites were grouped as a random factor. GAMM is a model that uses a smoothing function to test if relationships are linear or non-linear (Shadish *et al.*, 2014). We identified the best models as those with the lowest Akaike information criteria value and linearity was determined by the effective degree of freedom (edf) (Shadish *et al.*, 2014). The results suggested a strong linearity (edf = 1) and thus, we proceeded with generalized mixed linear models (GLMM). The alpha was set to zero as this is the default setting in GLMM. We focused the reporting of results on those variables from UL of cervid that influenced the expression of the forest attributes. For all statistical analysis, we used 'R, version 3.4.0' and the 'vegan', 'nlme' and 'gamm4' packages (Oksanen *et al.*, 2013; R Core Team, 2017; Wood *et al.*, 2017; Pinheiro *et al.*, 2018).

## Results

### Sampling effort, UL and Covariates

The sampling effort was on average 462 camera days per site (range 400–516, Table 1), yielding on average 16 978 photographs per site (range 6226–43 463). UL ranged more than five orders of magnitude across sites (4–953 292  $\text{kg}^{0.75} \cdot \text{s} \cdot \text{m}^{-1} \cdot \text{d}^{-1}$ ). Camera trapping showed a large variation in deer abundance and composition (Appendix A1), with the main species being red deer (90.6 per cent of the observations), roe deer (7.7 per cent) and fallow deer (1.7 per cent).

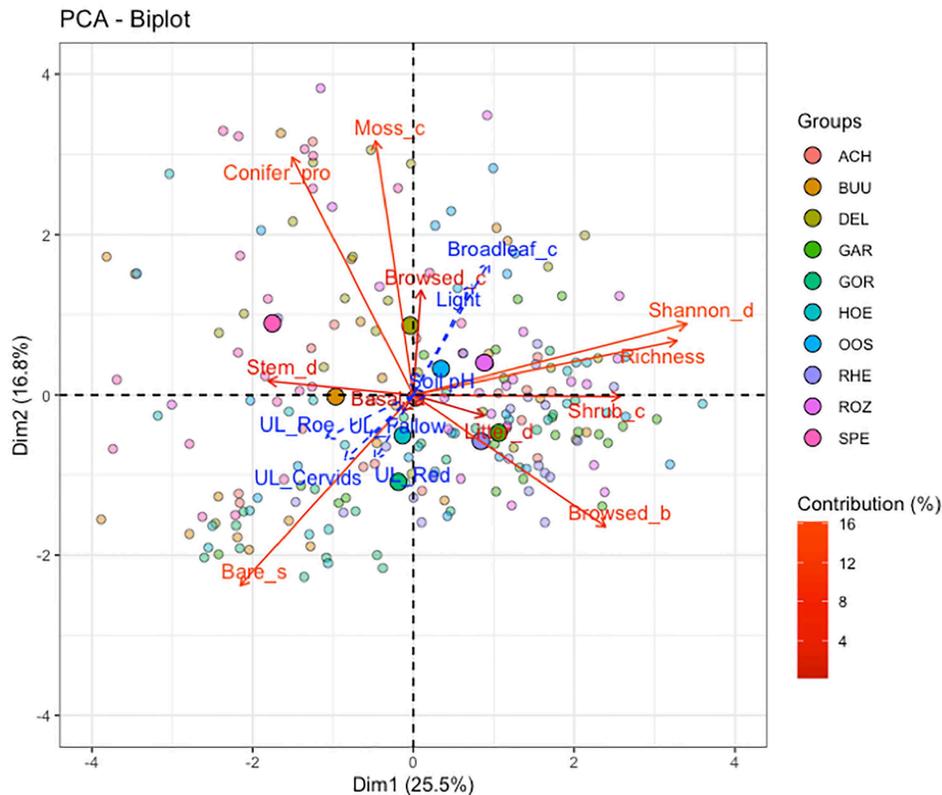
The PCA, which included all response variables, presented a clear association among variables (Figure 2). Principal component one (PC1) explained 25.5 per cent of the variation and was associated with sapling diversity, richness, shrub cover, litter depth and levels of browsed broadleaves on the right side and with stem density on the left side. PC2 explained 16.8 per cent of the variation and was associated with levels of browsed conifers, moss cover and conifer proportion on the upper section; and bare soil cover and basal area on the lower section. The associated fixed factors (as superimposed variables in blue-dashed arrows), cervids, roe, red and fallow deer UL were positively associated with bare soil and negatively associated with broadleaf canopy dominance, light, soil pH, browsed conifer sapling, diversity, richness and shrub cover.

### Relationships discriminated by species

The GLMM analysis (Table 2) that was conducted per species indicated that roe deer UL had a significant positive relationship with stem density (absolute regression coefficient  $\beta = 0.06$ , Figure 3A) and a negative relationship with sapling richness ( $\beta = -0.26$ , Figure 3D), Shannon diversity ( $\beta = -0.11$ , Figure 3F) and shrub cover ( $\beta = -0.36$ , Figure 3I). Red deer UL had a positive relationship with browsed broadleaves ( $\beta = -0.40$ , Figure 3H) and a negative relationship with litter depth ( $\beta = -0.14$ , Figure 3J). Fallow deer only had a negative relationship with sapling richness ( $\beta = -0.26$ , Figure 3C).

### The relationships for the entire browsing guild

The GLMM results indicated a significant relationship of cervid UL with 4 of the 11 forest response variables (Table 2 and Figure 3).



**Figure 2** Variation in forest attributes across the study sites at the Veluwe, the Netherlands. PCA for the vegetation response variables (in red arrows) and (a) biotic explanatory variables (as superimposed variables in blue arrows) that are used in the GLMM presented in Table 2. Each small circle represents a random point ( $N=212$ ) and colour indicates the forest site where the camera trap was placed. Each large circle represents the site average. Forests were coded as in Table 1. Superimposed variables with no effect on the PCA were coded as UL\_Cervids=utilization level cervids, UL\_Red=utilization level red deer, UL\_Roe=utilization level roe deer, UL\_Fallow=utilization level fallow deer, Light=light, Soil pH=soil pH, Broadleaf\_c=broadleaf canopy dominance. Response variables were coded as Stem\_d=stem density, Basal\_a=basal area, Richness=sapling richness, Shannon\_d=sapling Shannon diversity, Conifer\_pro=seedling conifer, Browsed\_b=browsed broadleaves, Browsed\_c=browsed conifers, Shrub\_c=shrub cover, Moss\_c=moss cover, Bare\_s=bare soil, Litter\_d=litter depth. Pearson correlation test suggested that there is no collinearity among fixed factors (UL – broadleaf canopy dominance =  $-0.22$ , UL – soil pH =  $0.07$ , UL – total light =  $-0.14$ , soil pH – total light =  $0.03$ , soil pH – broadleaf canopy dominance =  $-0.04$ , broadleaf canopy dominance – total light =  $0.38$ ).

Cervid UL had a negative relationship with tree species richness ( $\beta = -0.21$ , Figure 3E), Shannon diversity ( $\beta = -0.09$ , Figure 3G) and litter depth ( $\beta = -0.14$ , Figure 3K) and a positive relationship with stem density ( $\beta = 0.04$ , Figure 3B). Although cervid UL did not explain a significant amount of variation in the percentage of browsed conifers and broadleaves, a Mann-Whitney U test indicated that broadleaf saplings (median 26 per cent) were browsed significantly more than conifer saplings (median 0 per cent,  $W=41\ 150$ ,  $P < 0.001$ , Figure 4). Broadleaf canopy dominance had a significant positive relationship with sapling richness ( $\beta = 2.61$ ), diversity ( $\beta = 1.64$ ), conifer proportion in the understory ( $\beta = 0.46$ ) and moss cover ( $\beta = -0.88$ ), and a negative relationship with bare land cover ( $\beta = -0.64$ ). Soil pH had a positive relationship with browsed conifers ( $\beta = 0.02$ ) and a negative relationship with basal area ( $\beta = -8.48$ ). Light on the understory had a positive relationship with shrub cover ( $\beta = 0.69$ ) and a negative relationship with bare land cover ( $\beta = -0.74$ ) and litter depth ( $\beta = -0.02$ ). Finally, browsing incidence on average was greater for broadleaved species than for conifers (Figure 4) and red deer

accounted for more browsing incidences than roe and fallow deer, respectively (Figure 5).

## Discussion

In this study, we evaluated the shape of the relationships between the UL by deer and forest attributes along an extensive deer abundance gradient. UL is the proportion of time that a deer, expressed in metabolic weight units, spent in front of a camera trap in proportion to the deployment duration of the camera. Deer UL was associated with a reduced sapling richness and diversity, shrub cover and litter depth, as well as with an increase in sapling density and browsed broadleaves. Due to the log transformation of the variables for complying with normality, the relationships followed a  $\log_{10}$  linear response; however, when back transforming, the relationship followed a reverse asymptote. For didactical purposes, from here onwards, shape will be considered as curvilinear.

**Table 2** Relationship results between deer utilization and forests. GLMM for the relationship of forest variables with UL ( $\text{kg}0.75\text{-s}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$ ) in 10 forest sites across the Veluwe, the Netherlands. The model consists of  $\log_{10}\text{UL}$  (discriminated by species: red, fallow, roe deer and the UL of the entire browsing guild), understory light, soil pH and broadleaf canopy dominance as fixed factors, 10 forest sites and camera location were included as random effects. Models are accompanied by their units, absolute regression coefficients of the predictor variables, and significance is presented with asterisks (\*). All models were tested independently; however, light, soil pH and broadleaf canopy dominance are provided only for UL Cervids.

Variable	Units	Coefficients						
		UL red deer	UL fallow deer	UL roe deer	UL cervids	Light	Soil pH	Broadleaf
<b>F. regeneration</b>								
Stem density	$\text{ind}\cdot\text{ha}^{-1}$	-0.01	-0.01	0.06**	0.04*	0.01	-0.11	-0.13
Basal area	$\text{m}^2\cdot\text{ha}^{-1}$	0.10	0.47	-0.58	-0.39	n/a	-8.48***	5.35
Richness	#	-0.10	-0.26*	-0.26**	-0.21**	0.01	0.55	2.61**
Shannon Div.	h-index	-0.01	-0.11	-0.11*	-0.09*	0.01	0.31	1.64***
Conifer pro.	$\alpha$	0.21	0.17	0.36	0.23	0.26	-0.30	0.46*
<b>F. Browsing</b>								
Broadleaves	%	0.40*	0.11	0.06	0.28	0.28	-0.14	-0.13
Conifers	%	-0.01	-0.01	-0.01	-0.01	-0.01	0.02***	0.01
<b>F. Understory</b>								
Shrub	%	-0.24	-5.37	-0.36*	-0.26	0.69***	0.10	0.12
Moss	%	-0.55	-0.20	-0.24	-0.40	0.08	-0.20	0.88**
Bare cover	%	-0.04	0.13	0.31	0.19	-0.74***	0.01	-0.64**
Litter depth	cm	-0.14***	-0.09	-0.10	-0.14**	-0.02***	0.08	0.71

Significance levels: \*\*\* ( $P < 0.001$ ), \*\* ( $P < 0.01$ ) and \* ( $P < 0.05$ ).

### Deer and forest response relationships

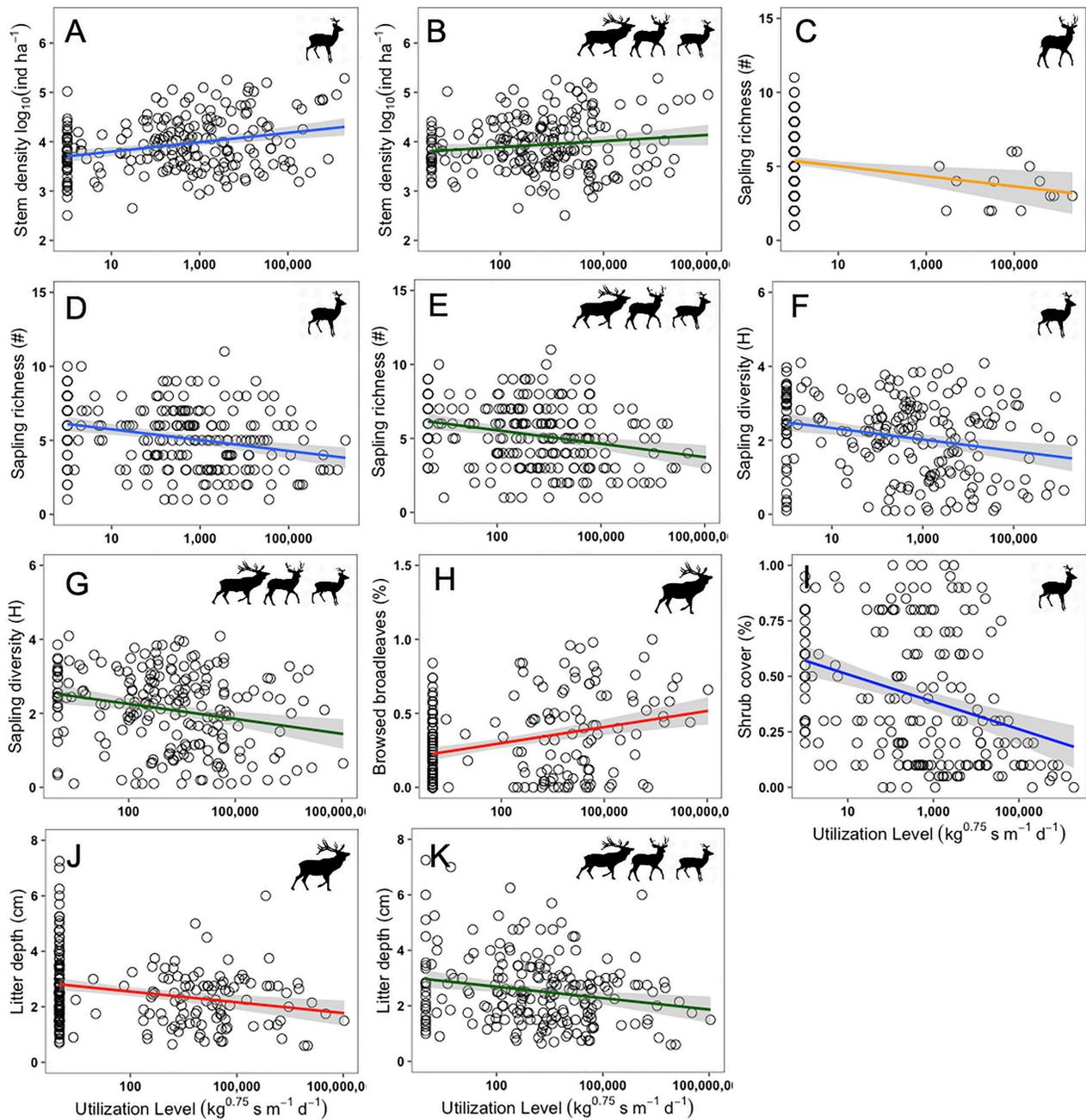
We predicted (P1) and found that browsing of broadleaf seedling increased with deer UL (Table 2), yet this relationship was only evident for red deer. A plausible explanation is that fallow and roe deer tend to browse in specific spots making it more difficult to quantify their damage to the vegetation compared with red deer (Gill, 1992a). From all 2370 feeding events registered by our camera traps, red deer dominated, which reflected their high metabolic weight and high UL at our sites (Figure 5). Soil pH had a positive relation with the percentage of browsed conifers (Table 2) plausibly because better soil conditions favour the development (Smilde, 1973), hence the higher attractiveness to deer.

We predicted (P2) that an increase in deer UL would promote browsing and trampling of forest regeneration and therefore result in decreased stem density and plot basal area (Klopčič *et al.*, 2010; Salk *et al.*, 2011). Yet, roe deer UL had a positive relation with stem density (Figure 3A). A plausible explanation is that browsing reduced the cover of the competing shrub layer (Figure 3I), which probably enhances the amount of light reaching the forest floor, thus releasing tree seedlings from shade suppression (Whitmore, 1989). UL had no significant relationship with tree basal area, meaning that trees develop regardless of high ungulate presence. Soil pH had a negative relation to the stand basal area (Table 2), given that trees are probably not prone to develop to their full potential on poor sandy soils, typically characterized by an average pH of 3.44 (Smilde, 1973).

We predicted (P3) that increased deer UL would promote an increase in the proportion of conifers in the vegetation and reduce tree sapling diversity because deer preferentially browse on palatable broadleaved individuals, thus favouring conifers through competitive release (Rooney and Waller, 2003).

We indeed found that broadleaved saplings were browsed more frequently (26 per cent) than conifer (0 per cent, Figure 4), but there was no significant relationship of UL with the proportion of conifer species in the sapling layer. Alternatively, we found evidence that UL decreased sapling richness and diversity and this relationship might strengthen over time as shown in a previous long-term study (Ramirez *et al.*, 2019) with the possibility of cascading effects to other trophic levels (McShea and Rappole, 2000; Ramirez *et al.*, 2020). However, broadleaf canopy dominance strongly mediated these relations (Table 2) because a broadleaved forest allows for different sapling species to coexist, whereas a conifer forest, through allelopathy, inhibits other sapling species (Kuiters and Sarink, 1986). Light had no relationship with the sapling composition, perhaps because half of the dominant conifer species at the Veluwe consisted of light-demanding species (*P. sylvestris* and *L. kaempferi*) and the other half of shade-tolerant species (*P. menziesi* and *Picea abies*).

We predicted (P4) that deer would decrease the understory shrub cover by browsing and trampling, and indirectly decrease moss cover because of increased understory light availability. Our results partially supported our prediction because roe deer UL proved to have a negative relationship with shrub cover (Figure 3) but no relationship with moss cover (Table 2). We also found that light in the understory had a positive relationship with shrub cover and that broadleaf canopy dominance had a negative relationship with bare land cover and a positive relationship with moss cover (Table 2). Our results are aligned with the literature because broadleaf trees, such as *F. sylvatica*, form a thick recalcitrant litter layer that helps maintain humidity and control light in the understory, which are beneficial for moss establishment (Mills and Macdonald, 2004).

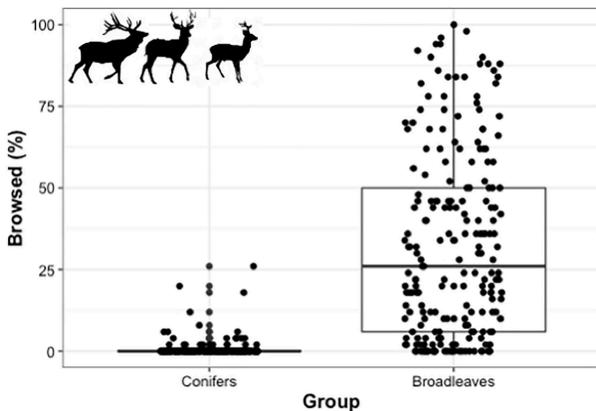


**Figure 3** Relationships of forest attributes with deer UL in forests across the Veluwe, the Netherlands. GLMM fits for different forest attributes, for deer species (red deer = H and J, fallow deer = C, roe deer = A, D, F and I) and the entire browsing guild (B, E, G and K). The regression lines were calculated based on the results of GLMM presented in Table 2. All relationships shown are statistically significant at an alpha level of 0.05.

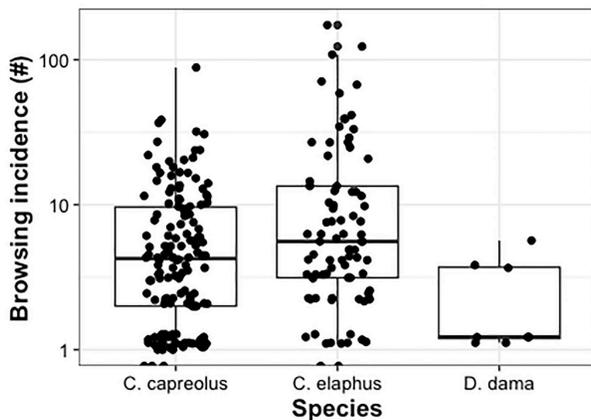
We predicted (P5) and found that deer reduced litter thickness on the forest floor (Table 2, Figure 3) because trampling can either compact litter, or mix litter with the soil (Hobbs, 1996). A reduction in litter thickness can have cascading effects on other trophic levels as it reduces food availability for invertebrates and exposes the soil to increased irradiance and temperature, leading

to desiccation and erosion (Allombert *et al.*, 2005; Ramirez *et al.*, 2020).

The main species driving the different forest attributes in this system was roe deer. This result can be explained by the fact that roe deer had a wider distribution across sites, relative to red and fallow deer (Table 1). Another reason for this result is that roe



**Figure 4** Boxplot for the percentage of browsed conifer and broadleaf stems by the entire browsing guild (red, fallow and roe deer). The difference is significant (Mann-Whitney U test:  $W = 41\ 150$ ,  $P < 0.001$ ).



**Figure 5** Boxplot showing browsing incidence discriminated by deer species captured by a camera network installed in the Veluwe, the Netherlands.

deer is a forest species, while red deer spends its time inside and outside forests and thus the time and strength in which these two species interact with forest, differs.

### Browsing guild shaping temperate forests

Temperate forests are complex systems, which not only harbour a single deer species but actually several deer species that interact at different spatial and temporal scales with the plant community. Therefore, it is necessary not only to analyse the relationship of a single species with its environment but also to understand the relationships of a complete browsing guild. Our results indicated that when the three deer species were combined, these browsers had a positive relationship with stem density (Figure 3B) and a negative relationship with litter depth (Figure 3K), sapling richness (Figure 3E) and diversity (Figure 3G). However, the relationship was weaker when compared with the individual deer species, indicating that not all deer species are forest specialists or strict browsers (Gill 1992a).

By measuring the maximal detection distance of our camera trap network, we took an important step to control the variation in how individual camera traps function and the heterogeneity of the forest understory. However, we did not model the detection rate based on habitat attributes, which is a potential source for bias in our results.

### A non-linear relationship

Our findings suggest that tree species richness and diversity respond to UL in a curvilinear fashion, where initial changes are largely followed by small changes at a higher UL. This tendency is in agreement with Rooney and Waller (2003), who reasoned that deer density has a negative exponential relationship with tree diversity. Similarly, a global literature review showed that deer density has a non-linear relation with regeneration diversity (Ramirez *et al.*, 2018); however, the shape of the curve in that review was negatively sigmoidal where small increases in deer density led to large decreases in tree diversity. Local studies in lowland Britain and Canada indeed showed such a negative exponential relationship with seedling density (Gill and Morgan, 2010) and aboveground tree biomass (Tremblay *et al.*, 2006). In contrast, two North American studies and one Czech study showed that vegetation responds linearly with an increase in deer density (Horsley *et al.*, 2003; Kamler *et al.*, 2010; Nuttle *et al.*, 2014). Other studies suggest that forest attributes should show a hump-shaped relationship with deer density (Rooney and Waller, 2003); we found no evidence for such a shape for any of the forest attributes. Perhaps because primary productivity was low in the Veluwe and trees cannot cope with browsing damage (Lieth and Whittaker, 2012) or because a landscape of fear was not established due to the lack of predators and hence, forest patches with high sapling diversity are not formed (Brown *et al.*, 1999; Kuijper *et al.*, 2013).

We found that the extent of the deer abundance gradient played a major role in the shape of the relationship. Earlier studies found different relationships but also used distinct deer gradients: from 0 to 30 deer  $\text{km}^{-2}$  (Nuttle *et al.*, 2014), from 0 to 60 deer  $\text{km}^{-2}$  (Gill and Morgan, 2010) and from 15 to 56 deer  $\text{km}^{-2}$  (Kamler *et al.*, 2010). Also, the method for measuring the density of deer (Gill, 1992a; Rooney and Waller, 2003) affects the shape of the relationship. Past studies estimated deer abundance with a range of methods, such as indirect and incomplete counts of animals. Typical inherent constraints related to indirect and incomplete counts involve the accumulation or decay of signs or prints left behind by animals over time (i.e. damage plants, faeces, frayed and stripped tree trunks), animals hiding from human sight, and a single animal reflecting the behaviour of the entire population (Koster and Hart, 1988). By pairing camera traps to regeneration plots, we quantified the relationship with a higher accuracy than in past studies because our network of camera traps monitored wildlife over a wide territory, 24 h a day and had fixed detection distances.

### Conclusion

Using a network of camera traps, we closely assessed the relationship between deer UL and forest regeneration at small spatial

scales. We found that deer had a moderate relationship with understory attributes of mixed forests on poor sandy soils. Deer decreased tree species richness and diversity and the depth of the litter layer while increasing sapling density and browsed broadleaf stems. Deer relationship with forest attributes followed a curvilinear relationship, with large changes followed by small changes at high UL. We made an important first step by monitoring vegetation and wildlife during summer and autumn, yet for future studies, annual monitoring repeated over the years should be implemented because animal populations can fluctuate for a variety of reasons. The conservation of temperate forests can benefit from limiting the size of deer populations and the time deer spend browsing in forest patches with high biodiversity value.

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## Data availability statement

The data from this research will be shared following a reasonable request to the corresponding author.

## Appendix

Appendix A1 Boxplots for the Utilization Level by cervids (red, roe and fallow deer) in each of the 10 research sites at the Veluwe, the Netherlands. Sites are coded as in Table 1 and black dots indicate the utilization level for each camera trap.

## Conflict of interest statement

None declared.

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