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# Human recreation shapes the local scale impact of ungulates on the carbon pools of a temperate coniferous forest

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## ABSTRACT

Greenhouse gases accumulation constitutes one of the main problems of modern society. Forests, which are a main terrestrial carbon sink, could represent a great help to reduce carbon footprints. Recent studies show that animals play a big role in carbon dynamics, and while the impacts of animals such as ungulates are affected by human presence, these effects have not been considered in studies on carbon stocks. Here, we studied the impact of ungulates on different carbon pools of a temperate coniferous forest at the Veluwe area (Gelderland, the Netherlands), and incorporated the influence of humans on ungulates presence and vigilance at fine spatial scales. We selected 22 paired plots at 20 and 100 m distance from human trails, ensuring that all of them had comparable environmental conditions. We divided each plot in three subplots, and in each subplot, we collected a sample of aboveground vegetation, understory litter and soil. Using camera traps in the same plots, we related differences in presence and behaviour of ungulates with the above-mentioned carbon stocks measured in the same plots. We found consistently fewer ungulate visits per day at 20 m than at 100 m from human trails, while their vigilant level was not significantly different. The concentrations of carbon were substantially higher in all three measured carbon pools at 20 m than at 100 m distance from the human trails. Hence, our study suggests that ungulates not only have an impact on the carbon stocks of temperate forests, but moreover that this impact is affected by human presence through the proximity to human trails. We suggest that for a proper understanding of carbon dynamics in forests, not only the impact of animals should be considered, but also how this impact is influenced by human activities.

## 1. Introduction

Climate change represents a main challenge for modern society (Naustdalslid, 2011; Nunes et al., 2020). Scientists are focusing their attention on carbon cycling to find ways to store carbon more effectively and reduce global warming (Gorte, 2009; Sedjo, 1989; Singh, 2013; Turner et al., 2009; Withey et al., 2019). According to the Kyoto protocol (UNFCCC, 1997), terrestrial carbon sinks can be used to mitigate the effect of green-house gases. Since forests represent one of the main terrestrial carbon sinks (Gorte, 2009; Nunes et al., 2020; Pant and Tewari, 2020), a correct understanding of the carbon cycle in forest ecosystems plays a key role in finding a solution to climate change. While most carbon models focus on the role of primary producers, recent studies show that also animals have a big impact on carbon dynamics (Schmitz et al., 2018, 2014; Tanentzap and Coomes, 2012; Wilmers and Schmitz, 2016). At the

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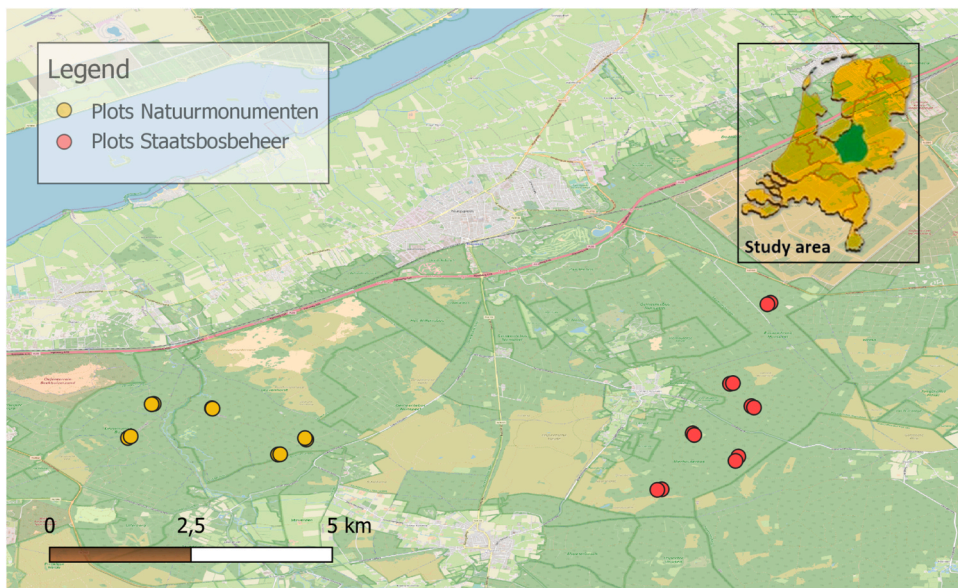
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same time, previous work indicates how humans largely influence the behaviour of animals in those systems (Bonnot et al., 2013; Ciuti et al., 2012; Mols et al., 2021; Möst et al., 2015; Proudman et al., 2021). Hence, it is very likely that the impacts of animals on carbon dynamics are affected by humans, but thus far very few studies have tested this idea. Studies on the influence of animals and humans on forests' carbon stocks might further improve model predictions of carbon fluxes.

Wild ungulates represent one of the main drivers of change in vegetation structure and composition in forest ecosystems (Bardgett and Wardle, 2003; Bressette and Beck, 2013; Chollet et al., 2021; Gerhardt et al., 2013; Gill, 2001; Putman, 1996; Ramirez et al., 2021) and so strongly affect forest regeneration and succession (Bressette et al., 2012; Bressette and Beck, 2013; Hirst, 2021; Ramirez et al., 2018). According to Tanentzap and Coomes (2012), herbivores reduce the carbon storage in worldwide temperate forests by  $40,000 \pm 60,000$  tonnes of carbon per year, by directly and indirectly affecting above- and below-ground carbon stocks (Bressette and Beck, 2013; Chollet et al., 2021; Hirst, 2021). For example, Wilmers and Schmitz (2016) show that selective browsing by moose (*Alces alces*) affects litter quality, thus reducing boreal forest productivity, whereas elk (*Cervus canadensis*) grazing is believed to increase Yellowstone's grasslands productivity; both species thus affect the carbon retention ability in their respective ecosystems. While several studies demonstrate the existence of direct effects of herbivores on above-ground carbon storage, e.g. via grazing and browsing, less is known about their impact on below-ground carbon stocks, e.g. via trampling and affecting litter quality and quantity, even though evidence suggest that it might be significant (Chollet et al., 2021; Hirst, 2021; Tanentzap and Coomes, 2012) and that above- and below- ground dynamics are strictly intertwined (Andriuzzi and Wall, 2017; Bardgett and Wardle, 2003). Ungulates can affect below-ground carbon content in various ways. For example, deer browsing removes biomass, which influences quantity and quality of litter, the main source of carbon in the soil (Hirst, 2021; Bardgett and Wardle, 2003; Harrison and Bardgett, 2003; Tanentzap and Coomes, 2012). This consequently affects soil fauna composition, and thus organic matter decomposition rates and carbon stabilisation in the ground (Allombert et al., 2005; Bardgett and Wardle, 2003; García-Palacios et al., 2013). Ungulates can also affect below-ground carbon content by trampling, which compacts the soil and changes its physical properties (Andriuzzi and Wall, 2017; Bardgett and Wardle, 2003; Chollet et al., 2021; García-Palacios et al., 2013; Hirst, 2021; Mohr et al., 2005; Ramirez et al., 2021). Forest ungulates like wild boar (*Sus scrofa*) can also have a great impact on soil mechanisms, aboveground vegetation growth and litter quantity (Genov et al., 2017; Liu et al., 2020; Mohr et al., 2005; Risch et al., 2010). Their bioturbation activities like trampling and grubbing significantly affect soil properties such as soil bulk density and moisture, and can alter soil fauna and microbe composition, thus potentially leading to an increase in soil CO<sub>2</sub> emissions (Bagchi et al., 2017; Cuevas et al., 2012; Liu et al., 2020; Risch et al., 2010). Soil fauna plays a key role in soil carbon dynamics and ungulates can affect it directly by consumption of plants and soil fauna (Cuevas et al., 2012; Mohr et al., 2005; Risch et al., 2010). Although evidence suggests that ungulates such as deer and wild boar can drastically affect forest carbon contents (Andriuzzi and Wall, 2017; Bardgett and Wardle, 2003; Chollet et al., 2021; Hirst, 2021; Tanentzap and Coomes, 2012), we still require better insight in the role of ungulates in carbon dynamics (Don et al., 2019; Liu et al., 2020), especially at finer spatial scales (<100 m).

Ungulate behaviour is strongly influenced by humans. For example, human presence can increase vigilant behaviour of ungulates, and alter their space-use and food intake (Bonnot et al., 2013; Ciuti et al., 2012; Mols et al., 2021; Möst et al., 2015; Proudman et al., 2021). A recent study by Mols et al. (2021) in the Veluwe forest (the Netherlands) shows that ungulates are more abundant 100 m away from human trails than 20 m away, and that vegetation growth and survival respond to these distances. Mols et al. (2022) also found that the reduction of deer near (20 m) human trails led to reduced tick densities in the proximity of trails. Hence, from these studies it is



**Fig. 1.** Map of paired plot locations in our study area at the Veluwe (Gelderland, the Netherlands). Plots were all located in pine-bilberry forest in Leuvenumse bos, managed by Natuurmonumenten (yellow dots), and in Boswachterij Nunspeet, managed by Staatsbosbeheer (red dots).

clear that ungulates respond to the distance to trails and that their effects on the ecosystem (vegetation growth / tick abundance) are mediated by this. Hereby, recreation strongly affects ungulates behaviour and thereby ecosystem functioning (Kuijper et al., 2016; Ramirez et al., 2021; Suraci et al., 2019). However, to what degree these effects also cascade onto the carbon content of a forest ecosystem remains to be explored.

In this study we aim to understand the fine-scale impact of humans on the effects of ungulates on the carbon content of a temperate forest ecosystem. We expect to find that plots close to human trails have fewer, and more vigilant ungulates, resulting in higher concentration of carbon in the understory vegetation, litter, and soil carbon pools, than compared to plots further away from human trails. By incorporating the impacts of humans on ungulates, this study aims to increase our understanding of the dynamics of carbon stocks in forest ecosystems and shed light on the development of future research and possible conservation strategies to prevent further carbon losses.

2. Methods

2.1. Study area and study design

Our study system, the Veluwe area (Gelderland, the Netherlands, Fig. 1), is one of the largest connected natural areas of the Netherlands (Boonman-Berson et al., 2018). We focused on two nature reserves (Boswachterij Nunspeet, 2388 ha managed by Staatsbosbeheer; Leuvenumse bos, 837 ha managed by Natuurmonumenten) in the northern part of the area. They are located between three main human settlements Apeldoorn (52.2112° N, 5.9699° E) in the south-east, Nunspeet (52.3748° N, 5.7699° E) in the north and Ermelo (26.5124° S, 29.9856° E) in the west (Fig. 1). The climate of the region is temperate maritime, with mean annual temperatures of 10.5 °C ± 0.12 SE and mean annual precipitation of 850 mm ± 255 SE (30 years average, 1990–2019, De Bilt, Royal Netherlands Meteorological Inst.). The main soil types are brown podzols derived from Pleistocene loamy sand (Kuiters and Slim, 2002). The areas have a network of trails that is open to the public between sunrise and sunset and is used by tens to hundreds of hikers and cyclists daily and year-round (see recreation pressure in Appendix 3, table 3). Walking off-trails is prohibited, and only the area managers are allowed to use motorised vehicles on the trails.

The vegetation in the Veluwe area is dominated by deciduous, mixed-deciduous and coniferous forest alternating with heather (*Calluna vulgaris*) heathlands. Forests occupy two thirds of the Veluwe area and the main tree species are *Quercus robur*, *Pinus sylvestris*, *Betula pendula*, *Fagus sylvatica*, *Quercus rubra*, *Larix kaempferi*, *Pseudotsuga menziesii* and *Picea abies*. Our study plots were located exclusively in pine-bilberry forests, where Scots pine trees (*Pinus sylvestris*) and bilberry bushes (*Vaccinium myrtillus*) were the dominant species.

Ungulate composition in the area consists of red deer (*Cervus elaphus*), fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*), which use the entire area year-round without clear seasonal patterns in space-use. Exact densities of these ungulates at the study locations are not known, but Kuiters and Slim (2002) reported an average of 14 ungulates per km<sup>2</sup> in the Veluwe

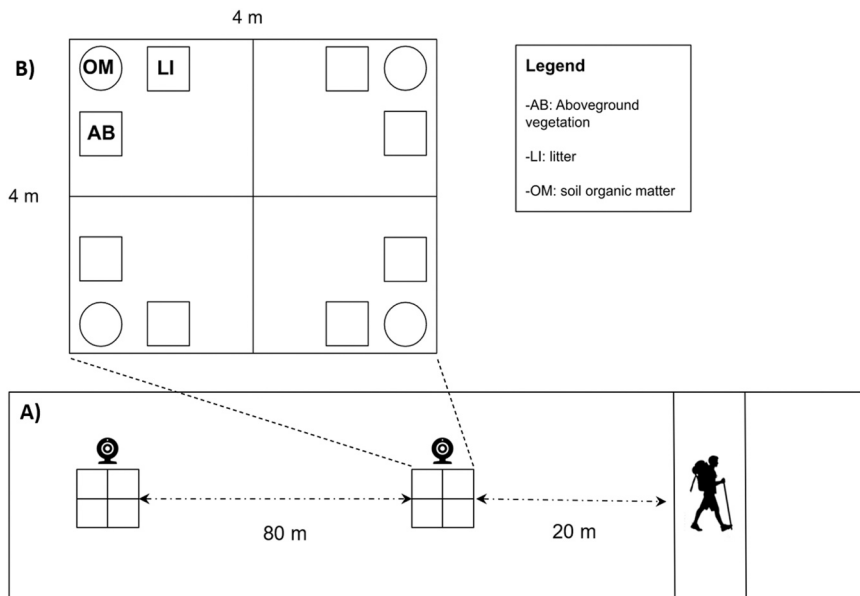


Fig. 2. paired plots set-up. A) On the right a human trail (with hiker) is depicted, the two squares represent the paired plots 20 and 100 m distance from the trail, where the videos were recorded (camera icon), and the carbon measurements taken. B) Each plot (4 × 4 m) is divided into four subplots (2 × 2 m). For each subplot we took samples of understory aboveground vegetation, litter, and soil organic matter. The data of each plot represents the mean of the measurements of each subplot.

area, and since then the numbers have kept rising (Ramirez et al., 2021). All ungulates are subject to culling in the hunting season (August – February), with a focus during late autumn-winter. In 2018, the first Dutch wolf pack established its core area (denning/rendez-vous sites) several kilometres away from our study areas and has annually reproduced since 2019.

We analysed a total of 22 plots (11 pairs) of which 12 plots were in Boswachterij Nunspeet and 10 in Leuvenumse Bos (Fig. 1). Each plot-pair consisted of one plot located at 20 m from the trail and the other 100 m away (Fig. 2). We ensured that paired plots had comparable environmental conditions (understory composition, canopy openness, tree composition and densities) and notably light availability and tree density, to ensure that differences in carbon content could be related to ungulate activity.

Previous studies in another area of the Veluwe forest demonstrated that ungulates tended to visit plots at 20 m from trails less often than those at 100 m from trails (Mols et al., 2021, 2022). Here, we assessed carbon stocks at different pools, namely the aboveground understory vegetation, the litter layer, and the soil in the 22 plots close (20 m) and away (100 m) from human frequented trails. We focused on these carbon pools because we expected that these could be strongly affected by ungulates in the short term of our data collection, and for this reason we did not incorporate the carbon pool of mature standing trees in this study. We used camera traps in the same locations where we assessed the carbon stocks to relate the carbon content to the presence and the behaviour of ungulates.

## 2.2. Camera traps

Each of the 22 plots was provided with a camera trap attached at a height of 100–120 cm on a tree, pointing in the opposite direction of the human trails. The following two (similar) types of camera traps were used: Bushnell Trophy Cam HD Agressor 2017 No Glow and Bushnell Trophy Cam HD 2013 (for settings see Appendix 2, Table 1), and they were regularly rotated between paired plots. Camera traps recorded videos of 15 s every time they detected movement, both during day and night, and stopped when no more movements were detected. The camera trap sessions took place between May 2020 and September 2021, with the largest sampling efforts during spring and summer (see Appendix 2 table 2). The videos were analysed with the software Boris version 8.7 (Friard and Gamba, 2016). We assessed the number of visits per day and the species of ungulates (wild boar, red deer, roe deer and fallow deer). For all the species of deer we assessed their behaviour following an ethogram, with in total 17 types of behaviour (see Appendix 4, table 4). These different behaviour types were grouped into “vigilant” or “non-vigilant” behaviour and we registered their duration to calculate the total vigilance level. To assess the vigilance levels, we recorded the behaviour of only one individual per video. In videos with more than one individual, we chose the first one that appeared in sight of the camera. In videos where animals were already present, we recorded the behaviour of the individual in the centre of the video. We calculated vigilance levels as the percentage of the time spent on vigilant behaviour versus the total observation time. Vigilance levels were only considered for deer species since it was difficult to determine wild boar behaviour.

## 2.3. Carbon sampling

To minimise difference linked to different seasons, we conducted all the carbon sampling within one month and within the same day for each paired plot, between the 16th of March and the 17th of April 2022 in all 22 plots where camera traps had been installed. At 3 m distance from the trees where the camera traps were located, we placed squares of 4 × 4 m all characterised by the same vegetation type (pine-bilberry forest dominated by blueberry undergrowth). These 4 × 4 m plots were divided in 4 subplots of 2 × 2 m (Fig. 2) in each of which we took measurements of the understory aboveground vegetation, of the litter and of the soil. On the corner of each 2 × 2 m subplot, we placed a square of 0.5 m × 0.5 m, from which we cut and collected all the aboveground vegetation and litter. In addition, in each 2 × 2 m subplot we took a 25 cm deep soil sample using a soil auger (excluding litter). Hence, of each 4 × 4 m plot we collected 4 samples of understory aboveground vegetation, 4 litter samples and 4 soil samples, totalling up to 12 samples per plot, and 264 samples for the whole study. All the samples were stored at 4 °C until being analysed in the laboratory.

## 2.4. Laboratory analysis: soil organic matter (loss of ignition method)

We dried all soil samples at 105 °C for 24 h in an electric oven. Once the samples were dried, we took a well-mixed subsample of 8–12 g from each sample and measured the dry weight. All the subsamples were then placed in a muffle furnace at 420 °C for 8 h: 4 h to reach the temperature and 4 h at 420 °C. After 8 h in the muffle furnace all the subsamples were weighed again. The weight lost after the ignition is representative for the OM (organic matter) content of the subsample (Abella and Zimmer, 2007; Heiri et al., 2001; Hoogsteen et al., 2015), that we calculated as percentage of the weight of the subsample before the ignition. Finally, the total SOM % (soil organic matter) of each plot was calculated as the average SOM % of each subplot. We used SOM as a proxy for the carbon content in the soil, based on the assumption that ca. 58% of OM is carbon content (Manns et al., 2016; Navarro et al., 1993; Rutherford et al., 1992).

## 2.5. Laboratory analysis: litter and understory aboveground vegetation

We clipped all the litter and aboveground vegetation samples and placed them in a 70 °C oven inside half-open paper bags for 48–72 h until they were completely dried. Once dried, we measured the biomass of all the samples. Since different studies show that aboveground vegetation and litter contain large amounts of carbon (Chapungu et al., 2020; Frank et al., 2004; Johnson et al., 2017; Sierra et al., 2007; Smith et al., 2013), we used their biomass as a proxy of the carbon content of these carbon pools.

## 2.6. Statistical analysis

Data analysis was done with R 4.1.2 (R Core Team, 2021). Before working on the models, we transformed our data based on the raw distribution of the variables (Appendix 5, Fig. 2). “aboveground vegetation” and “visits per day” raw data distribution were both right skewed. We normalised their distribution by log transformation (Appendix 5, Fig. 3). “Soil organic matter” and “vigilance level” data were reported in percentages, and they presented an irregular distribution (Appendix 5, Fig. 2). We performed an arcsine square root transformation which homogenised their variance (Appendix 5, Fig. 3). “Litter” data were not transformed. Since we were assuming a Gaussian distribution and the different variables had different scales, we standardised all the continuous parameters of the model after the transformations using the dplyr package (Wickham et al., 2022).

Afterwards, we ran a linear mixed model with a Gaussian distribution for each of our five response variables (“visits per day”, “vigilance level”, “aboveground vegetation”, “litter” and “soil organic matter”) using the lme4 package (Bates et al., 2015). For each of the five models we used “distance to trails” as an explanatory variable. To account for the paired plot design (20 m and 100 m from human trails) we included “paired plot ID” as a random factor. The set of candidate models contained all the carbon stocks models representing a priori hypotheses, from which we selected the most parsimonious models using the Akaike’s information criteria (AIC) (Appendix 6, table 5). Based on that, in the model explaining differences in “soil organic matter” we included the factors “aboveground vegetation” and “litter” as explanatory variables.

We assessed the significance level based on the 95% confidence interval and used the Wald  $\chi^2$  tests to assess the significance of our variables (Anova function from the car package (Fox and Weisberg, 2019)). We checked for the fitness of the model by visual inspection of the residuals (Zuur et al., 2010) and for the dispersion by using the DHARMA package (Hartig, 2022).

## 3. Results

### 3.1. Presence and behaviour of ungulates

Number of ungulate visits per day significantly differed between 20 and 100 m distance from trails (Table 1). Plots at 20 m from trails had fewer ungulate visits per day ( $1.81 \pm 0.30$  SE) than plots at 100 m distance ( $5.46 \pm 1.32$  SE) (Fig. 3). Ungulate vigilance levels seemed higher at 20 m distance from trails ( $27.81 \pm 2.70$  SE % vigilance level) than at 100 m from trails ( $24.18 \pm 4.60$  SE % vigilance level) (Fig. 3), but this difference was not statistically significant (Table 1).

### 3.2. Carbon stocks

The carbon contents of all the analysed pools significantly differed between 20 m and 100 m distance from human trails (Table 1). Plots at 20 m distance from trails had higher content in aboveground vegetation, litter and soil organic matter than plots at 100 m distance from trails (Fig. 4, see Appendix 7, Table 6). Soil organic matter was positively related with aboveground vegetation and litter content (Table 1).

## 4. Discussion

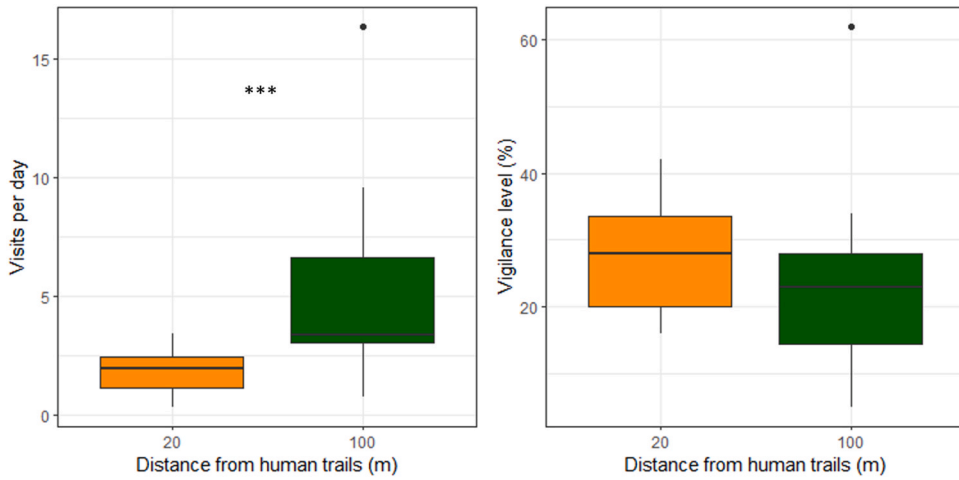
Overall, our study suggests that ungulates impact carbon stocks at fine spatial scales, and that this impact is mediated by humans. We found fewer ungulate visits close to (20 m) than further away (100 m) from human trails, and in line with this difference, carbon stocks differed significantly, with greater carbon pools close to than further away from human trails. This effect was stronger for the aboveground vegetation, followed by the understory litter and soil. Moreover, we found that the soil carbon pool was related to aboveground vegetation and litter content, suggesting that above- and below- ground dynamics are intertwined. We discuss the possible mechanisms behind these findings, highlighting the role of humans in shaping the impact of ungulates on carbon stocks.

We found that fewer ungulates frequent areas closer to human trails, which is in accordance with the results of Mols et al. (2021) in the Veluwe forest and with other studies around the globe which found that ungulates spatially avoid human activity and infrastructure (Bonnot et al., 2013; Proffitt et al., 2009; Scholten et al., 2018; Mathisen et al., 2018). These results suggest that humans impact the space use of ungulates and that ungulates tend to avoid areas closer to humans. This can be considered as a fear response in

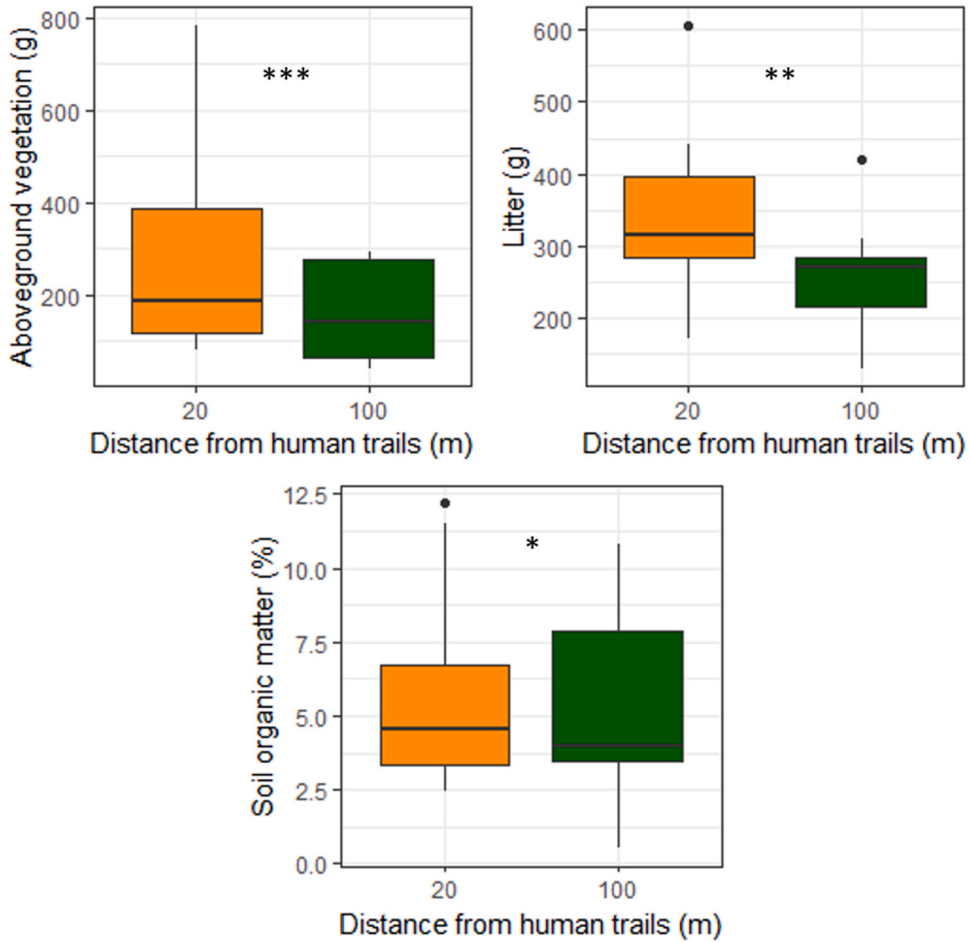
**Table 1**

Wald  $\chi^2$  and significance test of the five models of the study (df = degree of freedom; C.I. = confidence interval; p = p-value). Predictors change only for the model of “soil organic matter” where we included “litter” and “aboveground vegetation” as explanatory variables. Significant values are illustrated in bold.

Response	Predictor	Wald $\chi^2$	df	C.I.	p
Visits per day	<b>Distance to trail</b>	<b>28.55</b>	<b>1</b>	<b>[- 1.56; - 0.70]</b>	<b>&lt; 0.001</b>
Vigilance level	Distance to trail	0.53	1	[- 0.53; 1.16]	0.470
Aboveground vegetation	<b>Distance to trail</b>	<b>16.51</b>	<b>1</b>	<b>[0.31; 0.94]</b>	<b>&lt; 0.001</b>
Litter	<b>Distance to trail</b>	<b>9.84</b>	<b>1</b>	<b>[0.26; 1.24]</b>	<b>0.002</b>
Soil organic matter	<b>Distance to trail</b>	<b>4.54</b>	<b>1</b>	<b>[- 1.29; - 0.09]</b>	<b>0.033</b>
	<b>Litter</b>	<b>14.69</b>	<b>1</b>	<b>[0.39; 0.96]</b>	<b>&lt; 0.001</b>
	<b>Aboveground vegetation</b>	<b>19.32</b>	<b>1</b>	<b>[0.31; 0.89]</b>	<b>&lt; 0.001</b>



**Fig. 3.** Boxplots showing the visits per day by deer and wild boar (left) and the vigilance levels of deer (right) at 20 m (orange) and 100 m (green) distance from human trails. Asterisks indicate significance (\* =  $p < .05$ ; \*\* =  $p < .01$ ; \*\*\* =  $p < .001$ ).



**Fig. 4.** Boxplots showing the average “aboveground vegetation” (top-left), “litter” (top-right) and “soil organic matter” (bottom) at 20 (orange) and 100 m (green) distance from human trails. “Aboveground vegetation” and “litter” are expressed in grams per sample unit ( $0.25 \text{ m}^2$ ), while “soil organic matter” is expressed in percentages per sample unit ( $7.4^{-5} \text{ m}^3$ ). Asterisks indicate significance (\* =  $p < .05$ ; \*\* =  $p < .01$ ; \*\*\* =  $p < .001$ ).

ungulates, where the (likelihood of) presence of humans gets associated with a potential danger (Bonnot et al., 2013; Ciuti et al., 2012; Mols et al., 2021; Proffitt et al., 2009; Proudman et al., 2021). Ungulate vigilance levels were not significantly affected by the distance to trails in our study. Proudman et al. (2021) also did not find higher vigilance levels in deer when closer to human settlements, and they explain that by the ability of deer to distinguish between risky and non-risky human behaviours. These results are in contrast with other studies that show a vigilant response of ungulates to the presence of humans, yet this was mainly related to humans walking off-trails (Miller et al., 2006; Stankovich, 2008; Taylor and Knight, 2003), which in the Veluwe forest is strictly forbidden. Stankovich (2008) also suggested that the response of ungulates to humans is related to the natural history of the territory and to the level of accustomization of the local population towards human presence. The high predictability of human movements in the Veluwe forest, namely restricted to trails, might explain why deer do not change their vigilant behaviour but simply avoid staying close to human trails. Our results show that deer in our study area manage the risk landscape by adapting their space use rather than their vigilance levels. Wolves are present close to our study area and are known to use trails, possibly increasing the (perceived) risk posed by trails for recreation (Musiani et al., 1998). Our study does not allow us to assess the possible impact of wolf presence on our results, yet we emphasise that similar effects of trails have been found near our study area before wolf colonisation (Mols et al., 2021; 2022).

We found differences in all the assessed carbon pools between plots close to and further from trails. Due to the study design, we feel confident in relating these differences to the activity of ungulates. Other factors affecting carbon pools are unlikely as we ensured all plots had comparable environmental conditions, notably light availability and species composition. To this end, we located our plots 'near trails' at 20 m from the trail to minimise edge effects caused by the trails. Previous work with a similar design has already shown fine-scale effects of trails on deer and the vegetation (Mols et al., 2021, 2022). Furthermore, earlier work in the Veluwe forest showed that canopy openness, and thus tree density and light availability, did not relate with the distance to trails (from 20 to 240 m; Mols et al., 2022). Therefore, the differences in carbon pools discussed in this study can likely be contributed to the effect of trails on ungulate visitation rate.

The difference in carbon pool between 20 and 100 m distance from trails was the largest for the understory aboveground vegetation. We found higher concentrations of aboveground vegetation biomass close to human trails where we also found the lowest ungulate visitation frequency. These findings are in line with other studies from different ecosystems that also show a negative impact of ungulates on aboveground vegetation and sapling performance (Haffey and Gorchov, 2019; Gill, 2001; Mols et al., 2021; Pant et al., 2014; Putman, 1996; Tanentzap and Coomes, 2012) that are primarily related to the direct impacts of browsing on the vegetation (Gill, 2001). Thus, in areas closer to humans, where less ungulates are present, the understory vegetation height and biomass are less affected by browsing, which allows for more carbon storage in the pool.

Litter carbon pools were greater close to human trails than further away. This could be the consequence of higher ungulate activity further away from trails, which can negatively affect litter quantity. This has been shown by studies demonstrating how deer exclusion increases litter biomass and thus carbon content in the litter carbon pool (Bressette et al., 2012; Haffey and Gorchov, 2019; Ramirez et al., 2021). According to Bressette (2012), trampling activities increase litter decomposition rate, and Johnson (1995) shows that when the foraging is scarce, deer consume leaf matter which also lowers litter quantity. In addition, grubbing by wild boars also is likely to reduce litter biomass (Barrios-Garcia et al., 2014, 2022) and may have contributed to our results, although we did not explicitly quantify wild boar grubbing in our plots at 20 and 100 m from the trails.

Soil organic matter content was also higher close to than further away from trails where less ungulates were present, suggesting an effect of ungulates on soil organic matter. Based on the assumption that ca. 58% of organic matter is carbon content (Manns et al., 2016; Navarro et al., 1993; Rutherford et al., 1992), this result indicates an impact of ungulates on soil carbon content. In addition, soil organic matter was considerably related to aboveground vegetation and litter content. This is in line with the idea that litter biomass is a key factor linking above- and below- ground compartments (Bressette et al., 2012; Andriuzzi and Wall, 2017; Bardgett and Wardle, 2003). While this result could indicate an effect of vegetation and litter on soil organic matter, it can also suggest an indirect effect of ungulates on soil organic matter by affecting aboveground vegetation and litter content. The indirect effects of ungulates on soil carbon stock have been attributed to their negative impact on litter quality and quantity that reduces the amount of nutrients reaching the soil and thus the soil carbon content (Bardgett and Wardle, 2003; Chollet et al., 2021; Harrison and Bardgett, 2003; Hirst, 2021; Tanentzap and Coomes, 2012). Ungulates can also indirectly affect soil carbon by reducing the quantity of soil fauna (Allombert et al., 2005; Andriuzzi and Wall, 2017; Cuevas et al., 2012; Mohr et al., 2005; Ramirez et al., 2021; Risch et al., 2010) which has a key role in soil carbon dynamics. Moreover, bioturbation activities such as trampling and grubbing significantly affect soil properties, such as soil bulk density and moisture, potentially leading to an increase in soil CO<sub>2</sub> emissions (Cuevas et al., 2012; Liu et al., 2020; Risch et al., 2010), as was for example shown for wild boar grubbing that significantly increases soil carbon emission rates in Swiss hardwood forests (Risch et al., 2010).

The results of our study can be interpreted by recent extensions on the ecology of fear theory. According to this theory, in presence of a threat, herbivores will change their space-use and increase vigilance at the cost of foraging, and this can trigger cascading effects on vegetation structure and composition (Bonnot et al., 2013; Brown, 1999; Laundre et al., 2010; Ripple and Beschta, 2004; Strickland et al., 2013; Zanette and Clinchy, 2019). While this theory used to be specifically applied to fear responses to wild predators, recent studies show that ungulate behaviour is also strongly influenced by fear responses to humans (Bonnot et al., 2013; Ciuti et al., 2012; Mols et al., 2021; Proffitt et al., 2009; Proudman et al., 2021), and that behaviourally mediated trophic cascades triggered by humans might even overrule those induced by predators (Ciuti et al., 2012; Proffitt et al., 2009). For example, Proffitt et al. (2009) show that ungulates such as elk respond to human disturbance even stronger than to predator disturbance, supporting the idea that humans are seen as apex predators by most animals. Our results support the hypothesis that the fear of ungulates for humans can trigger a trophic cascade: ungulates were less present in plots close to human trails and, probably as a result of long-term reduced browsing and trampling, their impact on the different carbon stocks was reduced in comparison with plots further away from trails. In our case study,



rather than adapting their vigilance levels, ungulates seemed to manage the risk landscape through adaptations in space-use. Thus, our results indicate that the behaviourally mediated trophic cascade triggered by humans does not stop at the vegetation structure and composition but continues by influencing the carbon stocks in the soil.

High population density of ungulates is a common phenomenon in many temperate forests around the world, often related to the loss of natural predators (Kuipers et al., 1996; Pellerin et al., 2010; Ramirez et al., 2019; Rooney, 2001), and in many of these forests human recreational activities such as hiking also influence ungulate space-use (Salvatori et al., 2023). This makes our findings relevant for other temperate forests worldwide, where humans may have similar fine-scale effects on ungulate visitation rate and carbon stocks. While different studies show services and disservices that come with outdoor recreation (Salvatori et al., 2023; Tucker et al., 2018; Suraci et al., 2019; Larson et al., 2016; Cooper et al., 2015; McCurdy et al., 2010; Bushell et al., 2007), our work does not allow us to draw definite conclusions about this topic. Our results may suggest a positive outcome of recreation, with humans reducing the impact of ungulates and thus increasing C stocks. However, we did not test whether recreation activities, while reducing the impact of ungulates close to the trails, increase it further away from them. Future research should assess the larger scale impact of the trophic cascade analysed in this study and quantify the extent of the effect. As we did not differentiate between day and night activities, we believe it could also be relevant for future studies to test whether temporal avoidance represents a strategy used by ungulates in the Veluwe forest to respond to human recreational activities, as it is in other ecosystems (Salvatori et al., 2023). Another possible future direction of this study could be testing how soil fauna abundance changes with the distance from human trails, and how such differences are related to the carbon stocks. This because soil fauna has a key role in soil carbon dynamics (Fahey et al., 2013; Filser et al., 2016; Fox et al., 2006; García-Palacios et al., 2013; Vetter et al., 2004) and its abundance can be mediated by the presence of ungulates (Allombert et al., 2005; Andriuzzi and Wall, 2017; Cuevas et al., 2012; Mohr et al., 2005; Ramirez et al., 2021; Risch et al., 2010). Furthermore, many temperate forest ecosystems in Europe and the United States are witnessing a comeback of large carnivores (Chapron et al., 2014) that are also able to trigger a trophic cascade. Including large carnivores in a study of this kind would allow to test whether their presence increases the effect of trails on prey space-use. Additionally, such research allows for the investigation of the relative importance of human-induced fear vs. carnivore-induced fear in trophic cascades, and to what degree large carnivores are affected by fear for humans (Smith et al., 2017; Suraci et al., 2019; Zanette and Clinchy, 2019). Ultimately, one could test how ungulates adapt their space use and behaviour to both humans and large carnivores and how this affects carbon pools (Proudman et al., 2021).

In conclusion, the results of this study suggest that human recreation activities influence the fine-scale space use of ungulates, triggering a trophic cascade which leads to changes in the carbon pools content in different areas. We showed that deer and wild boar tend to avoid areas closer to human trails, without significantly changing their behaviour. This suggests that the spatial adaptation seems to be enough for ungulates to overcome the threat represented by humans in the Veluwe forest. Ultimately, we found that these human-mediated changes in habitat utilisation led to an impact on local carbon stocks, with greater carbon pools in areas closer to the trails where less ungulates are present. Hence, for improved predictions of dynamics of carbon stocks in forest ecosystems, it is important to not only include animals but also the influence of human activities on animal behaviour.

### CRedit authorship contribution statement

**Walter Di Nicola:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing (joint first author), Visualization, Project administration. **Bjorn Mols:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – review & editing (joint first author), Supervision, Project administration, Funding acquisitions. **Chris Smit:** Conceptualization, Validation, Resources, Writing – review & editing, Supervision, Project administration (lead), Funding acquisitions (lead).

### Declaration of Competing Interest

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

### Data availability

Data will be made available on request.

### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02574](https://doi.org/10.1016/j.gecco.2023.e02574).

### References

Abella, S.R., Zimmer, B.W., 2007. Estimating organic carbon from loss-on-ignition in Northern Arizona forest soils. *Soil Sci. Soc. Am. J.* 71, 545–550. <https://doi.org/10.2136/sssaj2006.0136>.

- Allombert, S., Stockton, S., Martin, J.-L., 2005. A natural experiment on the impact of overabundant deer on forest invertebrates. *Conserv. Biol.* 19, 1917–1929. <https://doi.org/10.1111/j.1523-1739.2005.00280.x>.
- Andriuzzi, W.S., Wall, D.H., 2017. Responses of belowground communities to large aboveground herbivores: Meta-analysis reveals biome-dependent patterns and critical research gaps. *Glob. Change Biol.* 23, 3857–3868. <https://doi.org/10.1111/gcb.13675>.
- Bagchi, S., Roy, S., Maitra, A., Sran, R.S., 2017. Herbivores suppress soil microbes to influence carbon sequestration in the grazing ecosystem of the Trans-Himalaya. *Agric., Ecosystem Environ.* 239, 199–206. <https://doi.org/10.1016/j.agee.2017.01.033>.
- Bardgett, R.D., Wardle, D.A., 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84, 2258–2268. <https://doi.org/10.1890/02-0274>.
- Barrios-García, M.N., Classen, T.A., Simberloff, D., 2014. Disparate responses of above- and belowground properties to soil disturbance by an invasive mammal. *Ecosphere* 5 (4), 44. <https://doi.org/10.1890/ES13-00290.1>.
- Barrios-García, M.N., Gonzalez-Polo, M., Simberloff, D., Classen, T.A., 2022. Wild boar rooting impacts soil function differently in different plant community types. *Biol. Invasions*. <https://doi.org/10.1007/s10530-022-02936-x>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67. <https://doi.org/10.18637/jss.v067.i01>.
- Bonnot, N., Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F., Hewison, A.J.M., 2013. Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. *Eur. J. Wildl. Res.* 59, 185–193. <https://doi.org/10.1007/s10344-012-0665-8>.
- Boonman-Berson, S., Driessen, C., Turnhout, E., 2018. Managing wild minds: From control by numbers to a multinatural approach in wild boar management in the Veluwe, the Netherlands. *Trans. Inst. Br. Geogr.* 44, 2–15. <https://doi.org/10.1111/tran.12269>.
- Bressette, J.W., Beck, H., 2013. The effect of high deer density on forest regeneration and carbon sequestration. *Environ. Res. J.* 7, 1.
- Bressette, J.W., Beck, H., Beauchamp, V.B., 2012. Beyond the browse line: complex cascade effects mediated by white-tailed deer. *Oikos* 121, 1749–1760. <https://doi.org/10.1111/j.1600-0706.2011.20305.x>.
- Brown, J.S., 1999. *Vigil, patch Use Habitat Sel.: Foraging predation risk 24*.
- Bushell, R., Staiff, R., Eagles, P.F.J., 2007. Tourism and protected areas: benefits beyond boundaries; the Vth IUCN World Park Congress. CABI, <https://doi.org/10.1017/9780851990224.000>.
- Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedó, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Buřka, L., Bunikyte, R., Ciucci, P., Dutosov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kotal, M., Liberg, O., Majčić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbínsek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajce, A., Tsingarska-Sedefcheva, E., Vána, M., Veevoja, R., Wabakken, P., Wölfel, M., Wölfel, S., Zimmermann, F., Zlatanova, D., Boitani, L., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346, 1517–1519. <https://doi.org/10.1126/science.1257553>.
- Chapungu, L., Nhamo, L., Gatti, R.C., 2020. Estimating biomass of savanna grasslands as a proxy of carbon stock using multispectral remote sensing. *Remote Sens. Appl.: Soc. Environ.* 17, 100275. <https://doi.org/10.1016/j.rsase.2019.100275>.
- Chollet, S., Maillard, M., Schörghuber, J., Grayston, S.J., Martin, J., 2021. Deer slow down litter decomposition by reducing litter quality in a temperate forest. *Ecology* 102. <https://doi.org/10.1002/ecy.3235>.
- Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A., Boyce, M.S., 2012. Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear. *PLoS ONE* 7, e50611. <https://doi.org/10.1371/journal.pone.0050611>.
- Cooper, C., Larson, L., Daye, A., Stedman, R., Decker, D., 2015. Are wildlife recreationists conservationists? Linking hunting, birdwatching, and pro-environmental behavior. *J. Wildl. Manag.* 79 (3), 446–457. <https://doi.org/10.1002/jwmg.855>.
- R. Core Team, 2021. *R: A Language and Environment for Statistical Computing*.
- Cuevas, M.F., Mastrantonio, L., Ojeda, R.A., Jaksic, F.M., 2012. Effects of wild boar disturbance on vegetation and soil properties in the Monte Desert, Argentina. *Mamm. Biol.* 77, 299–306. <https://doi.org/10.1016/j.mambio.2012.02.003>.
- Don, A., Hagen, C., Grüneberg, E., Vos, C., 2019. Bioturbation by wild boar increases the stability of forest soil carbon. (Prepr. ). *Biogeochem.: Soils*. <https://doi.org/10.5194/bg-2019-113>.
- Fahey, T.J., Yavitt, J.B., Sherman, R.E., Maerz, J.C., Groffman, P.M., Fisk, M.C., Bohlen, P.J., 2013. Earthworms, litter and soil carbon in a northern hardwood forest. *Biogeochemistry* 114, 269–280. <https://doi.org/10.1007/s10533-012-9808-y>.
- Filser, J., Faber, J.H., Tiunov, A.V., Brussaard, L., Frouz, J., De Seyn, G., Uvarov, A.V., Berg, M.P., Lavelle, P., Loreau, M., Wall, D.H., Querner, P., Eijsackers, H., Jiménez, J.J., 2016. Soil fauna: key to new carbon models. *SOIL* 2, 565–582. <https://doi.org/10.5194/soil-2-565-2016>.
- Fox, O., Vetter, S., Ekschmitt, K., Wolters, V., 2006. Soil fauna modifies the recalcitrance-persistence relationship of soil carbon pools. *Soil Biol. Biochem.* 38, 1353–1363. <https://doi.org/10.1016/j.soilbio.2005.10.014>.
- Frank, A.B., Berdahl, J.D., Hanson, J.D., Liebig, M.A., Johnson, H.A., 2004. Biomass and Carbon Partitioning in Switchgrass. *Crop Sci.* 44, 1391–1396. <https://doi.org/10.2135/cropsci2004.1391>.
- Friard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol. Evol.* 7 (11), 1325–1330.
- García-Palacios, P., Maestre, F.T., Kattge, J., Wall, D.H., 2013. Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. *Ecol. Lett.* 16, 1045–1053. <https://doi.org/10.1111/ele.12137>.
- Genov, P.V., Focardi, S., Morimando, F., Scillitani, L., Ahmed, A., 2017. Ecological Impact of Wild Boar in Natural Ecosystems. In: Melletti, M., Meijaard, E. (Eds.), *Ecology, Conservation and Management of Wild Pigs and Peccaries*. Cambridge University Press, pp. 404–419. <https://doi.org/10.1017/9781316941232.038>.
- Gerhardt, P., Arnold, J.M., Hackländer, K., Hochbichler, E., 2013. Determinants of deer impact in European forests – A systematic literature analysis. *For. Ecol. Manag.* 310, 173–186. <https://doi.org/10.1016/j.foreco.2013.08.030>.
- Gill, R.M.A., 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry* 74, 209–218. <https://doi.org/10.1093/forestry/74.3.209>.
- Gorte, R.W., 2009. *Carbon Sequestration For.* 26.
- Haffey, C.M., Gorchov, D.L., 2019. The effects of deer and an invasive shrub, *Lonicera maackii*, on forest understory plant composition. *Écoscience* 26, 237–247. <https://doi.org/10.1080/11956860.2019.1582195>.
- Harrison, K.A., Bardgett, R.D., 2003. How browsing by red deer impacts on litter decomposition in a native regenerating woodland in the Highlands of Scotland. *Biol. Fertil. Soils* 38, 393–399. <https://doi.org/10.1007/s00374-003-0667-5>.
- Florian Hartig, 2022. *DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models*.
- Heiri, O., Lotter, A.F., Lemcke, G., 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *J. Paleolimnol.* 25, 101–110.
- Hirst, C., 2021. deer a Chang. *Clim. – how do wild deer Affect Carbon sequestration Scott. Woodl. ?* <https://doi.org/10.7488/ERA/977>.
- Hoogsteen, M.J.J., Lantinga, E.A., Bakker, E.J., Groot, J.C.J., Titttonell, P.A., 2015. Estimating soil organic carbon through loss on ignition: effects of ignition conditions and structural water loss: Refining the loss on ignition method. *Eur. J. Soil Sci.* 66, 320–328. <https://doi.org/10.1111/ejss.12224>.
- Johnson, K.D., Domke, G.M., Russell, M.B., Walters, B., Hom, J., Peduzzi, A., Birdsey, R., Dolan, K., Huang, W., 2017. Estimating aboveground live understory vegetation carbon in the United States. *Environ. Res. Lett.* 12, 125010. <https://doi.org/10.1088/1748-9326/a8f8db>.
- Kuiters, A.T., Slim, P.A., 2002. Regeneration of mixed deciduous forest in a Dutch forest-heathland, following a reduction of ungulate densities. *Biol. Conserv.* 105, 65–74. [https://doi.org/10.1016/S0006-3207\(01\)00204-X](https://doi.org/10.1016/S0006-3207(01)00204-X).
- Kuiters, A.T., Mohren, G.M.J., Van Wieren, S.E., 1996. Ungulates in temperate forest ecosystems. *For. Ecol. Manag.* 88, 1–5. [https://doi.org/10.1016/S0378-1127\(96\)03876-5](https://doi.org/10.1016/S0378-1127(96)03876-5).

- Larson, C.L., Reed, S.E., Merenlender, A., Crooks, K. R. M., 2016. Effects of recreation on animals revealed as widespread through a global systematic review. *PLOS One* 11 (12), e0167259. <https://doi.org/10.1371/journal.pone.0167259>.
- Laundre, J.W., Hernandez, L., Ripple, W.J., 2010. The Landscape of Fear: Ecological Implications of Being Afraid~!2009-09-09~!2009-11-16~!2010-02-02~!. *TOECOLJ* 3, 1–7. <https://doi.org/10.2174/1874213001003030001>.
- Liu, Y., Liu, X., Yang, Z., Li, G., Liu, S., 2020. Wild boar grubbing causes organic carbon loss from both top- and sub-soil in an oak forest in central China. *For. Ecol. Manag.* 464, 118059 <https://doi.org/10.1016/j.foreco.2020.118059>.
- Manns, H.R., Parkin, G.W., Martin, R.C., 2016. Evidence of a union between organic carbon and water content in soil. *Can. J. Soil. Sci.* 96, 305–316. <https://doi.org/10.1139/cjss-2015-0084>.
- Mathisen, K.M., et al., 2018. Effects of forest roads on oak trees via cervid habitat use and browsing. *Ecol. Manag.* 424, 378–386. <https://doi.org/10.1016/j.foreco.2018.04.057>.
- McCurdy, L.E., Phil, M., Winterbottom, K.E., Mehta, S.S., Roberts, J.R., 2010. Using nature outdoor activity to improve children's health. *Curr. Probl. Pedia Adolesc. Health Care* 2010 (40), 102–117. <https://doi.org/10.1016/j.cpped.2010.02.003>.
- Miller, S.G., Knight, R.L., Miller, C.K., 2006. Wildlife Responses to Pedestrians and Dogs. *Wildlife Society Bulletin* (1973–2006) 29, 124–132.
- Mohr, D., Cohnstaedt, L., Topp, W., 2005. Wild boar and red deer affect soil nutrients and soil biota in steep oak stands of the Eifel. *Soil Biol. Biochem.* 37, 693–700. <https://doi.org/10.1016/j.soilbio.2004.10.002>.
- Mols, B., Lambers, E., Cromsigt, J.P.G.M., Kuijper, D.P.J., Smit, C., 2021. Recreation and hunting differentially affect deer behaviour and sapling performance. *Oikos* 127, 884–894. <https://doi.org/10.1111/oik.08448>.
- Möst, L., Hothorn, T., Müller, J., Heurich, M., 2015. Creating a landscape of management: Unintended effects on the variation of browsing pressure in a national park. *For. Ecol. Manag.* 338, 46–56. <https://doi.org/10.1016/j.foreco.2014.11.015>.
- Musiani, M., Okarma, H., Jędrzejewski, W., 1998. 'Speed and actual distances travelled by radiocollared wolves in Białowieża Primeval Forest (Poland)'. *Acta Theriol.* 43 (4), 409–416. <https://doi.org/10.4098/AT.arch.98-51>.
- Naustdalslid, J., 2011. Climate change – the challenge of translating scientific knowledge into action. *Int. J. Sustain. Dev. World Ecol.* 18, 243–252. <https://doi.org/10.1080/13504509.2011.572303>.
- Navarro, A.F., Cegarra, J., Roig, A., Garcia, D., 1993. Relationships between organic matter and carbon contents of organic wastes. *Bioresour. Technol.* 44, 203–207. [https://doi.org/10.1016/0960-8524\(93\)90153-3](https://doi.org/10.1016/0960-8524(93)90153-3).
- Nunes, L.J.R., Meireles, C.I.R., Pinto Gomes, C.J., Almeida Ribeiro, N.M.C., 2020. Forest Contribution to Climate Change Mitigation: Management Oriented to Carbon Capture and Storage. *Climate* 8, 21. <https://doi.org/10.3390/cli8020021>.
- Pant, H., Tewari, A., 2014. Carbon sequestration in Chir-Pine (*Pinus roxburghii* Sarg.) forests under various disturbance levels in Kumaun Central Himalaya. *J. For. Res.* 25, 401–405. <https://doi.org/10.1007/s11676-013-0424-z>.
- Pant, H., Tewari, A., 2020. Green sequestration potential of Chir pine forests located in Kumaun Himalaya. *For. Prod. J.* 70 (1), 64–71. <https://doi.org/10.13073/FPJ-D-19-00016>.
- Pellerin, M., Said, S., Richard, E., Hamann, J.-L., Dubois-Coli, C., Hum, P., 2010. Impact of deer on temperate forest vegetation and woody debris as protection of forest regeneration against browsing. *For. Ecol. Manag.* 260, 429–437. <https://doi.org/10.1016/j.foreco.2010.04.031>.
- Proffitt, K.M., Grigg, J.L., Hamlin, K.L., Garrott, R.A., 2009. Contrasting Effects of Wolves and Human Hunters on Elk Behavioral Responses to Predation Risk. *J. Wildl. Manag.* 73, 345–356. <https://doi.org/10.2193/2008-210>.
- Proudman, N.J., Churski, M., Bubnicki, J.W., Nilsson, J.-Å., Kuijper, D.P.J., 2021. Red deer allocate vigilance differently in response to spatio-temporal patterns of risk from human hunters and wolves. *Wildl. Res.* 48, 163. <https://doi.org/10.1071/WR20059>.
- Putman, R.J., 1996. Ungulates in temperate forest ecosystems: perspectives and recommendations for future research. *For. Ecol. Manag.* 88, 205–214. [https://doi.org/10.1016/S0378-1127\(96\)03878-9](https://doi.org/10.1016/S0378-1127(96)03878-9).
- Ramirez, J.I., Jansen, P.A., Poorter, L., 2018. Effects of wild ungulates on the regeneration, structure and functioning of temperate forests: A semi-quantitative review. *For. Ecol. Manag.* 424, 406–419. <https://doi.org/10.1016/j.foreco.2018.05.016>.
- Ramirez, J.I., Jansen, P.A., den Ouden, J., Goudzwaard, L., Poorter, L., 2019. Long-term effects of wild ungulates on the structure, composition and succession of temperate forests. *For. Ecol. Manag.* 432, 478–488. <https://doi.org/10.1016/j.foreco.2018.09.049>.
- Ramirez, J.I., Jansen, P.A., den Ouden, J., Moktan, L., Herdoiza, N., Poorter, L., 2021. Above- and Below-ground Cascading Effects of Wild Ungulates in Temperate Forests. *Ecosystems* 24, 153–167. <https://doi.org/10.1007/s10021-020-00509-4>.
- Ripple, W.J., Beschta, R.L., 2004. Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems. *BioScience* 54, 755. [https://doi.org/10.1641/0006-3568\(2004\)054\[0755:WATEOF\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0755:WATEOF]2.0.CO;2).
- Risch, A.C., Wirthner, S., Busse, M.D., Pöge-Dumroese, D.S., Schütz, M., 2010. Grubbing by wild boars (*Sus scrofa* L.) and its impact on hardwood forest soil carbon dioxide emissions in Switzerland. *Oecologia* 164, 773–784. <https://doi.org/10.1007/s00442-010-1665-6>.
- Rooney, T.P., 2001. Deer impacts on forest ecosystems: a North American perspective. *Forestry* 74, 201–208. <https://doi.org/10.1093/forestry/74.3.201>.
- Rutherford, D.W., Chiou, C.T., Kile, D.E., 1992. Influence of soil organic matter composition on the partition of organic compounds. *Environ. Sci. Technol.* 26, 336–340. <https://doi.org/10.1021/es00026a014>.
- Salvatori, M., Oberosler, V., Rinaldi, M., Franceschini, A., Truschi, S., Pedrini, P., Rovero, F., 2023. Crowded mountains: Long-term effects of human outdoor recreation on a community of wild mammals monitored with systematic camera trapping. *Ambio* 52, 1085–1097. <https://doi.org/10.1007/s13280-022-01825-w>.
- Schmitz, O.J., Raymond, P.A., Estes, J.A., Kurz, W.A., Holtgrieve, G.W., Ritchie, M.E., Schindler, D.E., Spivak, A.C., Wilson, R.W., Bradford, M.A., Christensen, V., Deegan, L., Smetacek, V., Vanni, M.J., Wilmers, C.C., 2014. Animating the Carbon Cycle. *Ecosystems* 17, 344–359. <https://doi.org/10.1007/s10021-013-9715-7>.
- Schmitz, O.J., Wilmers, C.C., Leroux, S.J., Doughty, C.E., Atwood, T.B., Galetti, M., Davies, A.B., Goetz, S.J., 2018. Animals and the zoogeochemistry of the carbon cycle. *Sci.* 362, eaar3213. <https://doi.org/10.1126/science.aar3213>.
- Scholten, J., et al., 2018. Red deer *Cervus elaphus* avoid mountain biking trails. – *Eur. J. Wildl. Res.* 64, 8. DOI: 10.1007/s10344-018-1169-y.
- Sedjo, R.A., 1989. Forests: A tool to moderate global warming? *Environ.: Sci. Policy Sustain. Dev.* 31, 14–20. <https://doi.org/10.1080/00139157.1989.9929929>.
- Sierra, C.A., del Valle, J.I., Orrego, S.A., Moreno, F.H., Harmon, M.E., Zapata, M., Colorado, G.J., Herrera, M.A., Lara, W., Restrepo, D.E., Berrouet, L.M., Loaiza, L.M., Benjumea, J.F., 2007. Total carbon stocks in a tropical forest landscape of the Porc region, Colombia. *For. Ecol. Manag.* 243, 299–309. <https://doi.org/10.1016/j.foreco.2007.03.026>.
- Singh, 2013. Carbon capture and storage: an effective way to mitigate global warming. *Curr. Sci.* 105, 10.
- Smith, J.A., Suraci, J.P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L.Y., Wilmers, C.C., 2017. Fear of the human 'super predator' reduces feeding time in large carnivores. *Proc. R. Soc. B.* 284, 20170433. <https://doi.org/10.1098/rspb.2017.0433>.
- Smith, J.E., Heath, L.S., Hoover, C.M., 2013. Carbon factors and models for forest carbon estimates for the 2005–2011 National Greenhouse Gas Inventories of the United States. *For. Ecol. Manag.* 307, 7–19. <https://doi.org/10.1016/j.foreco.2013.06.061>.
- Stankowich, T., 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. *Biol. Conserv.* 141, 2159–2173. <https://doi.org/10.1016/j.biocon.2008.06.026>.
- Strickland, M.S., Hawlena, D., Reese, A., Bradford, M.A., Schmitz, O.J., 2013. Trophic cascade alters ecosystem carbon exchange. *Proc. Natl. Acad. Sci. U.S.A.* 110, 11035–11038. <https://doi.org/10.1073/pnas.1305191110>.
- Suraci, J.P., Zanette, L.Y., Wilmers, C.C., 2019. Fear Hum. apex Predat. Has. Landsc. Impacts Mt. lions mice 9.
- Tanentzap, A.J., Coomes, D.A., 2012. Carbon storage in terrestrial ecosystems: do browsing and grazing herbivores matter. *Biol. Rev.* 87, 72–94. <https://doi.org/10.1111/j.1469-185X.2011.00185.x>.
- Taylor, A.R., Knight, R.L., 2003. Wildlife responses to recreation and associated visitor perceptions. *Ecol. Appl.* 13, 951–963. [https://doi.org/10.1890/1051-0761\(2003\)13\[951:WRTRAA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2003)13[951:WRTRAA]2.0.CO;2).
- Tucker, M.A., et al., 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science* 359, 466–469. <https://doi.org/10.1126/science.aam9712>.

- Turner, W.R., Oppenheimer, M., Wilcove, D.S., 2009. A force to fight global warming. *Nature* 462, 278–279. <https://doi.org/10.1038/462278a>.
- UNFCCC, 1997, [https://unfccc.int/kyoto\\_protocol](https://unfccc.int/kyoto_protocol).
- Vetter, S., Fox, O., Ekschmitt, K., Wolters, V., 2004. Limitations of faunal effects on soil carbon flow: density dependence, biotic regulation and mutual inhibition. *Soil Biol. Biochem.* 36, 387–397. <https://doi.org/10.1016/j.soilbio.2003.10.012>.
- Wickham H., Romain François, Lionel Henry, Kirill Müller, 2022, dplyr: A Grammar of Data Manipulation.
- Wilmers, C.C., Schmitz, O.J., 2016. Effects of gray wolf-induced trophic cascades on ecosystem carbon cycling. *Ecosphere* 7. <https://doi.org/10.1002/ecs2.1501>.
- Withey, P., Johnston, C., Guo, J., 2019. Quantifying the global warming potential of carbon dioxide emissions from bioenergy with carbon capture and storage. *Renew. Sustain. Energy Rev.* 115, 109408 <https://doi.org/10.1016/j.rser.2019.109408>.
- Zanette, L.Y., Clinchy, M., 2019. Ecology of fear. *Curr. Biol.* 29, R309–R313. <https://doi.org/10.1016/j.cub.2019.02.042>.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems: *Data exploration*. *Methods Ecol. Evol.* 1, 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.