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Recreation and hunting differentially affect deer behaviour and sapling performance

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Humans are increasingly acknowledged as apex predators that shape landscapes of fear to which herbivores adapt their behaviour. Here, we investigate how humans modify deer space-use and their effects on vegetation at two spatial scales; zones with different types of human use (largescale risk factor) and, nested within that, trails (fine-scale risk factor). In zones with three contrasting types of human activities: 1) no recreation, no hunting, 2) with recreation, no hunting and 3) with recreation and hunting, we linked deer space-use (dropping counts) to browsing intensity, relative growth and survival of planted saplings. Plots were located at two distances to trails (20 versus 100 m) to test how trails affect deer space-use and sapling performance. Additionally, plots were distributed over forest and heathland as risk effects are habitat-dependent. Deer space-use was highest in the zone without recreation or hunting, resulting in higher browsing levels and lower sapling growth and survival, but only in heathland. In contrast, deer space-use and sapling performance did not differ between zones with recreation only and zones with recreation and hunting. Deer dropping counts were lower near trails used for recreation, but this was not associated with browsing impact or sapling performance. Our results show that recreational use modifies deer space-use which is associated with browsing impact on woody vegetation, while seasonal hunting activities in zones with recreation did not have additive year-round effects. Yet, effects were only observed at the larger scale of recreation zones and not near trails. Furthermore, deer space-use was only associated with sapling performance in open heathland, where high visibility presumably increases avoidance behaviour because it increases detectability and decreases escape possibilities. This suggests that recreation creates behaviourally mediated cascading effects that influence vegetation development, yet these effects are context-dependent. We advocate incorporating human-induced fear effects in conservation, management and research.

Keywords: ecology of fear, human disturbance, hunting for fear, landscapes of fear, tree recruitment, ungulate browsing

Introduction

The fear of death by predation is a major driver of animal behaviour and can influence ecosystem structure and functioning (Ripple et al. 2014). Patterns of predator space-use and environmental characteristics may create a landscape of fear with varying levels of perceived predation risk for their prey (Laundré et al. 2001, 2010, Gaynor et al. 2019), which can respond by adapting their distribution and/or behaviour (Brown 1999, Brown et al. 1999). This can reduce effects of herbivores on vegetation in locations with high (perceived) predation risk and locally increase plant growth ('behaviourally mediated trophic cascades', BMTCs; Ripple et al. 2016). Such BMTCs have been documented in a variety of terrestrial and aquatic systems, with examples ranging from spiders that reduce grasshopper foraging and increase grass growth (Schmitz et al. 1997), to tiger sharks *Galeocerdo cuvier* that alter sea cow *Dugong dugon* and sea turtle *Chelonia mydas* feeding patterns, impacting sea grasses (Burkholder et al. 2013). By exerting these indirect effects, predators can act as keystone species as they can indirectly modify vegetation structure, which in turn may have knock-on effects on others species and thereby affect biodiversity and ecosystem structure and functions (Ripple et al. 2014, 2016).

Most of our knowledge of landscapes of fear and associated behaviourally-mediated trophic cascades comes from laboratory and mesocosm experiments, and the few studies in natural systems have shown ambiguous results. For example, a majority of our knowledge on the indirect effects of large carnivores on prey and the ecosystem comes from the well-studied interactions between wolves *Canis lupus* and elk *Cervus canadensis* in North America. Here, a wide array of studies (Ripple and Beschta 2012) have reported behavioural responses of elk to wolf predation risk, while others found no to weak effects of wolves on elk behaviour (Kauffman et al. 2010, Cusack et al. 2019). This has created a scientific and societal debate around landscapes of fear and associated behaviourally mediated trophic cascades (Creel et al. 2008, David Mech 2012, Winnie 2012, 2014, Allen et al. 2017, Creel 2018, Zanette and Clinchy 2019). It has become increasingly clear that the relative importance of nonlethal effects of predators on ecosystem structure and functioning is highly context-dependent (Gaynor et al. 2019).

In the Anthropocene, humans have increasingly taken over the role of top predators in regulating both prey numbers (Darimont et al. 2009, 2015) and behaviour in many areas worldwide (Oriol-Cotterill et al. 2015, Clinchy et al. 2016, Kuijper et al. 2016, Zanette and Clinchy 2019). Recent experimental studies have shown that humans, analogous to predators, can trigger antipredator responses and elicit cascading effects on lower trophic levels. In Suraci et al. (2019) it was demonstrated that the sound of humans was avoided by mountain lions *Puma concolor* and reduced medium-sized carnivore activity, which in turn released small mammals from predation pressure. This allowed the latter to spend more time foraging, ultimately likely increasing their abundance and resource consumption. Moreover, human effects on antipredator behaviour of prey can be stronger than those of other natural predators. For example, effects of human hunting and disturbance on the vigilance (Ciuti et al. 2012), movement rate and grouping patterns (Proffitt et al. 2009), circadian rhythm (Ensing et al. 2014) and stress levels (Zbyryt et al. 2018) of cervids (*Cervidae*) have overruled the effects of large carnivores such as wolves. Consequently, humans have vast behaviourally-mediated effects on wildlife communities (Kuijper et al. 2016, Gaynor et al. 2019, Suraci et al. 2019, Mendes et al. 2020). Perhaps the strongest behaviourally-mediated effects humans have on ecosystems is through influencing the foraging patterns of large herbivores such as deer.

Deer can have strong effects on vegetation development and ultimately ecosystem structure and functioning through foraging and trampling activities (Ramirez et al. 2018, 2020). Humans have strong effects on these processes as deer experience landscapes of fear created by spatial and temporal variation in human hunting and recreation activities (Möst et al. 2015). To navigate through this perceived risk landscape, deer apply antipredator strategies comparable to those applied in response to large carnivore risk, notably by changing spatial distribution and habitat selection (Frid and Dill 2002). In general, deer avoid areas with high human activity (Coppes et al. 2017) or human predation risk (Kilgo et al. 1998, Marchand et al. 2014, Morgantini and Hudson 2019). In response to perceived human risk, they select for more dense habitat types where they are difficult to detect, can easily escape, and where hunting pressure is low (Licoppe and De Crombrugghe 2003, Godvik et al. 2009, Cleveland et al. 2012, Bonnot et al. 2013). Recent work has also shown responses at fine spatial scales, where hiking and cycling activities on trails locally reduce deer space-use and browsing on tree saplings in the direct vicinity (< 100 m) of trails (Mathisen et al. 2018). Likewise, hunting can induce behavioural alterations on within home-range scales (Proffitt et al. 2009, Sullivan et al. 2018). For example, in Le Saout et al. (2014) it was demonstrated that hunting can reduce deer browsing levels on local scales by comparing 'risky' and control plots 600 m apart. These examples show how humans may shape large- and fine-scale browsing patterns and thereby influence other trophic levels (Ramirez 2021).

Besides their ecological importance, human-induced large- and fine-scale risk effects could be applied to alleviate human wildlife conflicts, most notably with large herbivores such as deer (Cromsigt et al. 2013, Apollonio et al. 2017). Globally increasing cervid densities cause ecological, economical and social concerns (Côté et al. 2004, Nugent et al. 2011, Ramirez et al. 2018). Specifically, limited tree recruitment as a result of high deer abundance is a common ecological and silvicultural problem (Rooney 2001, Russell et al. 2001, Klopcic et al. 2010, Salk et al. 2011, Bradshaw and Waller 2016, Churski et al. 2017). Undesired impacts of deer have traditionally been managed by regulating population size through hunting, but this has proven difficult as even intense hunting schemes cannot always prevent damage

(Tanentzap et al. 2011, Forsyth et al. 2013, Simard et al. 2013). This led to the development of the 'hunting for fear' concept (Cromsigt et al. 2013), which embraces the application of fear-related mechanisms to develop effective, non-lethal wildlife management practices to mitigate undesired impacts. A clear example of this, is a more directed spatial planning of hunting and recreation zones to steer herbivore space-use and their resulting impacts on the landscape, yet this idea largely remained to be empirically tested (Cromsigt et al. 2013, Apollonio et al. 2017).

Several comparative observational studies suggest that human activities can induce behavioural alterations in deer at larger (> ha, such as human use zones) and at finer scales (meters, such as near or far away from trails), with potential consequences for browsing patterns and vegetation structure and composition. However, to date, very few experimental studies exist that investigate human-induced behavioural responses and effects on the vegetation at both large and fine scales. Therefore, we incorporated two nested scales by conducting measurements on the scale of large-scale zonation in human recreation and hunting, and nested within that measurements at the finer scale of distance to trails. This allowed us to assess how human use affects deer space-use, browsing patterns and tree recruitment at different spatial scales. We conducted dropping counts over a period of two months to quantify the space-use of fallow *Dama dama* and red deer *Cervus elaphus* across large-scale zones with three different types of human use: 1) no recreation and no hunting (hereafter: 'reserve'), 2) with recreation and no hunting (hereafter: 'recreation only') and 3) with recreation and with hunting (hereafter: 'recreation and hunting') (Fig. 1). Counts were conducted on transects in a paired design close to (20 m) and further away from (100 m) trails to test the fine-scale effects of recreation. Plots closest to the trails (20 m) were expected to experience higher disturbance effects from recreation on the trails compared to the plots further from trails (100 m).

At the same locations, we planted 284 tree saplings of which we measured browsing levels and relative growth during four months, and survival over a period of over one year. All experimental plots were distributed over two dominant habitat types: open heathland and closed canopy *Pinus sylvestris* forest, as habitat selection plays an important role in human-induced antipredator behaviour through its effects on detection and escape possibilities (Brown et al. 1999, Godvik et al. 2009, Cleveland et al. 2012). We expect deer space-use, browsing pressure and impact on tree saplings to be lowest in zones with recreation and hunting, and highest in the reserve, with no recreation and no hunting. Deer are expected to avoid the vicinity of trails, locally reducing their impact on saplings. We hypothesise that this effect will be strongest in open habitat with low cover (heathland versus forest) in zones with more disturbance (i.e. recreation and/or hunting).

Material and methods

Study area

We conducted our study in Deelerwoud (DW) and National Park Veluwezoom (NPVZ), which are nature reserves situated in the Veluwe region of the province of Gelderland in the Netherlands (Fig. 1). DW is situated near the village Deelen (52°04'51.96''N, 05°53'51.72''°E) and covers 1230 ha. NPVZ is situated to the east of DW (52°02'48.84''°N, 06°00'43.92''°E) and covers an area of 5000 ha. DW and NPVZ are neighboring areas separated by the fenced highway A50, but connected with a well-used wildlife overpass (Van Wieren and Worm 2001, Renard et al. 2008). While both areas are almost entirely fenced, they are connected through wildlife corridors with the surrounding landscapes of the Veluwe area (Huysentruyt and Casaer 2015). Both areas are
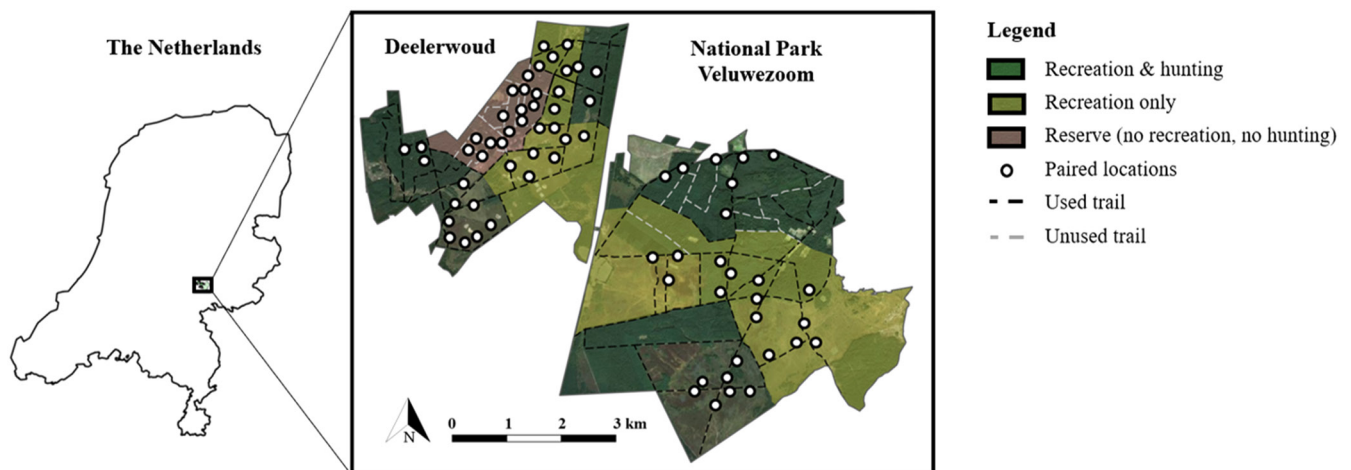

Figure 1. Deelerwoud and National Park Veluwezoom situated in the Netherlands and with all paired sample locations (white dots) near used (black dashed line) or unused (grey dashed line) trails in different human use zones. Map created on PDOK aerial photo base layer 'Luchtfoto Actueel Ortho 25 cm RGB' in QGIS ver. 3.2.2-Bonn.

managed by the nature organisation 'Natuurmonumenten' for conservation purposes. Additionally, our seven southern-most plots were located on heathland ('Roosendaalse Veld') owned and managed by the city of Roosendaal, which connects to the southern part of NPVZ. The climate is temperate maritime, mean annual temperature is $10.51°C \pm 0.12$ SE and mean yearly precipitation is 850 mm $\pm$ 255 SE (30 year averages, 1990–2019; De Bilt, Royal Netherlands Meteorological Inst.).

The overall study area consists of open heathland and coniferous and mixed deciduous forests. The most common forest type is pine-bilberry, dominated by scots pine *Pinus sylvestris* with bilberry undergrowth *Vaccinium myrtillus* (Ekeris 2015). For the purposes of our study, we focused on this forest type and open *Calluna vulgaris* heathlands because these are the dominant habitat types in the area (Ekeris 2015).

The large herbivores in DW are European fallow deer *Dama dama* (28 ind. km^{-1}), red deer *Cervus elaphus* (7 ind. km^{-1}) and wild boar *Sus scrofa* (2 ind. km^{-1}) (data from bi-annual count on 12 April 2018, in which ungulates are counted on two consecutive nights by wildlife managers, covering the entire Veluwe region). Roe deer *Capreolus capreolus* have become very rare (or absent) in DW, possibly due to competition with the other cervid species (Huysentruyt and Casaer 2015). In the NPVZ overall ungulate density is lower with densities of 4, 2 and 3 ind. km^{-1} for fallow deer, red deer and wild boar respectively, and roe deer is still present in low densities (data from bi-annual count on 12 April 2018). Ungulates in DW and NPVZ are functionally part of one population, since the wildlife overpass that connects both areas is intensely used (Van Wieren and Worm 2001, Renard et al. 2008). Differences in density between the two areas are, therefore, largely driven by differences in management. Restricted parts of both areas are grazed by free-ranging, largely unmanaged Scottish Highland cattle (170 ind., pers. comm. A. ten Hoedt, area manager, April 2018). Mesocarnivores red fox *Vulpes vulpes* and European badger *Meles meles* occur in the area, but there were no top predators (e.g. wolves) that predate on deer during the time of study (<www.wolveninnederland.nl>; pers. comm. A. Ten Hoedt, area manager, April 2018). In this study we focused on fallow and red deer, since these species are hunted and the main species affecting the vegetation as most abundant browsers in the area (Gill and Beardall 2001).

The areas have an extensive trail network used during daylight hours by approximately 2 million hikers and cyclists per year (pers. comm. A. ten Hoedt, area manager, April 2018; Fig. 1). Off-trail recreation is prohibited and motorized traffic is limited to managers using the trails with 4WD vehicles with low frequency. House dogs are permitted when leashed, which is enforced by law. In 2019, approximately 13% of recreationalists were accompanied by a leashed dog in our study area (unpubl. data from our camera traps, 2019, subset of trails used in this study). In DW, there is a reserve with low disturbance as recreation and hunting are prohibited, but maintained trails are present which are occasionally used by managers and researchers (estimated 2–3 visits per week, pers. comm. A. Ten Hoedt, area manager, April 2018). The presence of infrequently used trails provided us with a natural experimental setting allowing us to test the effect of trails used and not used by recreationalists. Furthermore, the study area is divided in zones varying in hunting activities (Fig. 1). Deer in DW were not hunted from 2001 to 2014. From 2014 onwards, deer have been hunted in designated hunting zones. In 2014 a hunting-free zone was established in NPVZ, while in the rest of the area both fallow and red deer are hunted. In the designated hunting zones, trained nature managers hunt from high-seats and on foot across the area. Hunting is conducted between the 1 August and the 15 February, with decreasing intensity as the season progresses (Faunabeheereenheid Gelderland 2019). Managers minimize wildlife behavioural (fear) responses and association with people by using rifle sound suppressors and refraining from the use of dogs. The zonation plan creates areas with recreation, but without hunting activities ('recreation only') and areas with both recreation and hunting ('recreation and hunting'). Hunting is also not conducted in the reserve where recreation is prohibited. This created an ideal setting for us to test if hunting activities lead to effects on deer and their impact on tree recruitment that are additive to the effects of recreation.

Experimental design

We selected 72 plot pairs with one transect of the pair close to (20 m) and one far from (100 m) trails. These distances to trails were selected as earlier work had determined that trails influence deer browsing up to distances of 40–80 m from trails (van Woersem and Elders 2016, Mathisen et al. 2018, Brouwer 2020). With this design, we aimed at one of the paired locations to be stronger influenced by recreation on the trails, while the second of the pair experienced no or less disturbance from recreation. Additionally, locating plots at more than 100 m from trails was unfeasible due to high trail density in our study area. Pairs were at least 250 m apart (100 m between transect endings) and distributed over forest and heathland habitat to test the habitat-dependent effects (see the Supporting information for a schematic overview of the experimental setup and for tables of replication). We strived for a balanced design across the different human use zones in our study area. Yet since there was only one 'reserve' in our study area, the sample size for plots in the reserve was lower (n = 16, we placed 1 extra paired plot in heathland in the reserve compared to other human use zones) than of other human use zones (n = 28). This led to a design with three levels of human use: 1) no recreation and no hunting ('reserve'), 2) with recreation and no hunting ('recreation only') and 3) with recreation and with hunting ('recreation and hunting'); two levels of distance to trail: 1) 20 m and 2) 100 m; and two habitat levels: 1) forest and 2) heathland. For each of the combinations of these factors our design included 14 replicates (7 in DW and NPVZ each), except for combinations including the 'reserve', which is only found in DW

and included one extra pair, yielding eight replicates for each combination with the distance to trail and habitat. On each plot we conducted dropping counts along transects to measure deer space-use (54 paired plots as we did not conduct dropping counts in heathland in the reserve due to access restrictions). Furthermore, within each plot we planted tree saplings (n = 284, 4 plants, 2 at 20 m from trail and 2 at 100 m from trail on 71 paired locations) and measured sapling browsing intensity, relative growth and survival. Our design allowed us to assess large-scale effects of zonation in hunting and recreation, and fine-scale effects of trails, on deer space-use and their browsing impact. We selected unpaved sandy trails of 4–6 m in width and ensured trails in areas with recreation had comparable utilization by recreationalists using Strava Inc. Heat Map (based on heatmap color), which uses compiled spatial data of users of Strava, a hiking, running and cycling GPS tracking application (<http://labs.strava.com/heatmap>). The infrequently (2–3 timer per week) used trails in the reserve served as a control.

Dropping counts to quantify deer space-use

To quantify deer space-use we conducted dropping-group counts. This is a well-established proxy for deer space-use that has been proven to yield appropriate measures of deer space-use (Acevedo et al. 2010, Alves et al. 2013). Counts were conducted along 150 m long and 2 m wide transects parallel to a trail at 20 m and 100 m distance from the trail (see the Supporting information for schematic overview of experimental setup). Two researchers walked the transect side by side in one direction, each recording all dropping groups in a 1 m wide strip. Dropping groups (≥ 1 dropping) were considered a group when researchers estimated that droppings originated from the same defecation event based on color, shape and location of the droppings. We did not distinguish between deer species because this is prone to misidentifications (Spitzer et al. 2019). Counts were conducted between the 25 April and the 20 June 2018, and thus reflect deer densities and space use mainly during spring when hunting efforts had largely been completed (Faunabeheereenheid Gelderland 2019, main hunting period from 1 August to 15 February). Conducting the counts early in the growing season optimised dropping detectability and reduced bias between habitat types (Lioy et al. 2015). By recording the main (> 50% cover) vegetation type for each 5 m of transect we established that transects in forest were dominated by *Vaccinium myrtillus* (72% cover), *Deschampsia flexuosa* (24% cover) and open soil (4% cover). In heathland transects were dominated by *Calluna vulgaris* (55% cover), *Molinea caerulea* (37% cover) and open soil (8% cover).

Tree saplings

Between the 7th and the 24th of April 2018 we planted one pendunculated oak *Quercus robur* (hereafter: 'oak'; n = 142; mean height (cm) ± SEM = 93.08 ± 1.05; range

(cm) = 65–137) and one silver birch *Betula pendula* (hereafter: 'birch'; n = 142; mean height (cm) ± SEM = 129.94 ± 0.68; range (cm) = 110–158) sapling in 142 paired plots (71 pairs) in the center of our dropping count transects (Fig. 1, Supporting information; on one paired location planted trees were damaged and thus not included in the analysis). Initial sapling height did not differ between human use zones (Kruskal–Wallis rank sum test: Kruskal–Wallis χ^2 = 0.79, df = 2, p = 0.68) or distance to trails (Kruskal–Wallis rank sum test: Kruskal–Wallis χ^2 = 0.03, df = 1, p = 0.85). At each distance to the trail (20 m, 100 m), we planted one oak and one birch sapling 1.5 m apart. We selected planting locations where the surrounding (5 × 5 m) vegetation ground cover was dominated (> 95% cover) by bilberry *V. myrtillus* in the forest and by common heather *C. vulgaris* in open heathland, and other saplings were absent.

Sapling height, the total number of shoots (terminal buds), and the total number of shoots browsed (terminal buds damaged/disappeared) were measured and survival recorded (yes/no) when planting the saplings and during five visits every 7–11 days between the 17 April and 20 June 2018. Trees were considered dead when they had no leaves and were visibly dried out. In April 2019 we revisited all saplings and scored survival. Recording browsing levels and height in this final measuring round was not useful as many trees had died and thus did not provide meaningful data on browsing levels and growth (yet results did not differ, see the Supporting information). The percentage of shoots browsed was averaged over all measuring rounds in 2018 to provide 'browsing levels', which served as a proxy for browsing intensity. The response variable 'relative growth' (= height final measuring round − initial height/initial height) was used to analyze sapling growth. We used sapling survival (yes/no) in April 2019 for analysis.

Statistical analyses

All analyses were conducted using R, ver. 3.6.2 (<www.r-project.org>). To assess how human use zone, the distance to trails, and habitat type influenced deer dropping counts, browsing intensity and sapling performance (relative growth, survival), we used mixed models (linear mixed model, LMM; generalized linear mixed model, GLMM) with the *lmer* and *glmer* functions from the lme4 package (Bates et al. 2015). The effects on deer dropping counts were analysed using GLMM with the Poisson distribution. The analyses of browsing intensity and relative growth were conducted using linear mixed models. For analysing survival (1/0) we used GLMM with the binomial distribution.

Initial models contained the fixed factors human use zone ('zone': reserve, recreation only, recreation and hunting), the distance to trails ('distance': 20 m, 100 m), 'habitat' (forest, heathland) and tree species (birch, oak; for analysis of sapling data). We included all two-way interactions for which we had clear hypotheses within the scope of the main research objectives. Since we expected effects of human use zones and

trails on deer and saplings to depend on habitat and tree species, we included the interactions between 'distance' and 'habitat', between 'distance' and 'species', between 'distance' and 'zone', between 'zone' and 'habitat' and between 'zone' and 'species'. 'Paired plot ID' was included as a blocking factor to account for the paired design (20 m and 100 m from trails).

We performed model selection by automatically ranking models using Akaike's information criteria corrected for small sample sizes (AICc). Models were generated starting from the initial model including all hypothesised interactions using the 'dredge' function from the MuMIn package (Barton and Barton 2018). We considered all models with ΔAICc ≤ 2 to have empirical support and selected the most parsimonious model from this set as best model, except when more complex models with ΔAICc ≤ 2 contained significant interactions (Burnham and Anderson 2002). We assessed the importance and significance of predictor variables using Wald χ^2 tests (type III test; using the *Anova* function from the car package (Fox et al. 2020)). Additionally, we tested for significance between groups by conducting post hoc Tukey tests on significant factors ($p = 0.05$) in the best model using the emmeans package (Lenth et al. 2021). We assessed model fit through visual inspection of model residuals (Zuur et al. 2010). Dispersion was checked using the DHARMa package (Hartig and Lohse 2020).

Results

Deer dropping counts

On average we counted 0.092 ± 0.013 (mean ± SEM) deer dropping groups per m^2 (n = 54). Dropping counts significantly differed between habitat types, human use zones and the distance to trails (Table 1, Supporting information). In the heathland habitat, deer dropping counts were significantly higher (mean ± SEM dropping groups per $m^2 = 0.152 \pm 0.023$) than in the forest (mean ± SEM dropping groups per $m^2 = 0.043 \pm 0.010$). Human use zonation affected deer space-use in forest habitat (significant Zone:Habitat interaction, Table 1), as dropping counts were 6- and 16-fold higher in the forest in the reserve (mean ± SEM dropping groups per $m^2 = 0.298 \pm 0.062$) than in forests in the recreation only (mean ± SEM dropping groups per $m^2 = 0.051 \pm 0.016$) and recreation and hunting (mean ± SEM dropping groups per $m^2 = 0.019 \pm 0.005$) zones respectively (Fig. 2). Both in forest and heathland, dropping counts in forest did not significantly differ between recreation only and recreation and hunting zones. For heathland, we could not confirm the difference in deer dropping counts we observed between the reserve and other zones in forests, since we did not conduct dropping counts on heathland in the reserve. At finer scales, deer dropping counts were consistently lower close to trails than further away, yet this trend was not significant in the heathland in the zone with recreation only. Near the infrequently used trails in the reserve, there was no such trend

observed (only tested for forest) as dropping counts did not differ between plots near and further from trails.

Saplings

Browsing intensity

Saplings in our study area experienced considerable browsing levels, as averaged over our measuring rounds, 28% (± 1.6 SEM) of tree shoots were browsed. During the final measuring round in June 2018, on average (mean (± SEM) 50% (± 1.6)) of the shoots of tree saplings were browsed.

Sapling browsing intensity differed between habitat types and human use zones, but not between the two distances to trails (Table 1, Supporting information). Overall, average browsing intensity was consistently higher in heathland (41 ± 2.5%) than in the forest (15 ± 1.0%). Human use affected browsing intensity in heathland but not forest (significant Zone:Habitat interaction, Fig. 2C, Table 1). In heathland, browsing intensity was higher in the reserve than in recreation only and recreation and hunting, while it did not differ between recreation only and recreation and hunting zones. Browsing levels were significantly higher for birch than for oak (Table 1), yet the effects of human use zonation and habitats were similar for both species (Table 1, Supporting information).

Tree sapling performance: relative growth and survival

Overall, sapling relative growth was lower in heathland than in forest. Also here, the effect of human use zonation depended on habitat type, as human use zonation only affected relative growth in heathland (Fig. 2C, Table 1, Supporting

Table 1. Wald's χ^2 values and significance tests for candidate predictors (human use zonation (zone), habitat, distance to trails (distance) and their interactions) included in the selected models predicting deer dropping numbers and sapling browsing levels, relative growth and survival. Significant factors and interactions are depicted in bold. See the Supporting information for model selection table.

| Response	Predictor	Wald's χ^2	df	p
Deer dropping counts				
	Zone	**18.82**	**2**	**0.001**
	Habitat	**33.60**	**1**	**< 0.001**
	Distance	**25.67**	**1**	**< 0.001**
	Zone × Distance	**17.06**	**2**	**< 0.001**
	Habitat × Distance	**5.84**	**1**	**0.016**
Browsing levels				
	Zone	**28.83**	**2**	**< 0.001**
	Habitat	**43.18**	**1**	**< 0.001**
	Species	**15.93**	**1**	**< 0.001**
	Zone × Habitat	**11.44**	**2**	**0.003**
Relative growth				
	Zone	**23.56**	**2**	**< 0.001**
	Habitat	**23.17**	**1**	**< 0.001**
	Species	**9.10**	**1**	**0.003**
Survival				
	Zone	4.63	2	0.099
	Habitat	**9.69**	**1**	**0.002**
	Zone × Habitat	**8.15**	**2**	**0.017**
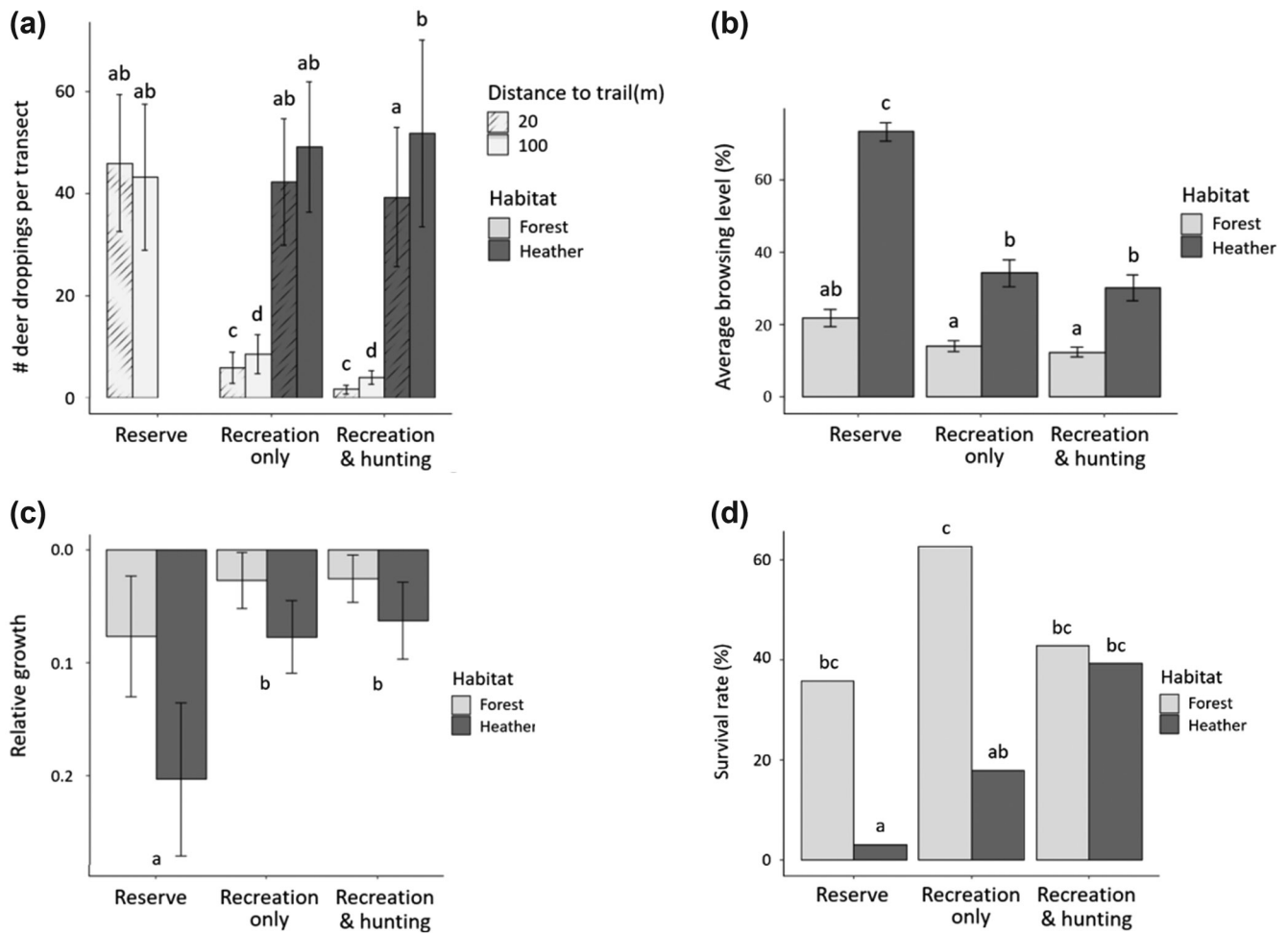
Figure 2. Deer dropping counts (a), average sapling browsing intensity (b), relative growth (c) and survival (d) in the three human use zones (reserve, recreation only, and recreation and hunting) and two habitat types (forest and heathland). Bar heights represent means ± SEM across zones and habitats (a–c) or sapling survival rate (%) after one year (d). Significant differences between groups are indicated with letters (a–d). In (c) significant differences are only shown between human use zones, as the factor human use zonation did not significantly interact with the factor habitat (but the factor was included in the third model that was within ΔAIC < 2). Only deer droppings numbers were influenced by the distance to trails.

information). In heathland, relative growth was drastically lower in the *reserve* than in zones with recreation only and with recreation and hunting (Fig. 2C). However, relative growth did not differ between zones with recreation only and recreation and hunting zones. Sapling relative growth did not differ between the two distances to trails (Table 1, Supporting information). Oak saplings had lower relative growth than birch, but both species showed similar relative growth patterns across zones (Table 1, Supporting information).

In April 2019, approximately one year after planting, 37% of 284 saplings (39% of birch, 35% of oaks) survived. Significantly more trees survived in forest habitat (49%) than in heathland (24%). Human use zonation affected survival in heathland only, which was significantly lower in the *reserve* than elsewhere (Table 1, Fig. 2D). However, survival did not differ between recreation only and recreation and hunting

zones. The distance to trails did not affect sapling survival and survival did not differ between sapling species (Table 1, Supporting information).

Discussion

We conducted deer dropping counts and planted tree saplings across zones with different human use at 20 m and 100 m from trails in contrasting forest and heathland habitat. Our experiment demonstrated that human use zonation is associated with deer space-use and browsing patterns to such an extent that it affects tree recruitment and that recreation may have stronger effects than zonation of hunting activities. However, we also demonstrated that these effects are scale- (zones versus trails) and habitat-dependent (forest versus

heathland), indicating the high level of context-dependency that is increasingly highlighted by other studies on behaviourally mediated trophic cascades. We discuss our results in the light of the increased anthropogenic pressures on our ecosystems via human-induced behaviourally mediated effects (Corlett 2015), and we highlight the potential and context-dependency of such human-induced effects for applications in wildlife management, as current effects may contrast management goals (Cromsigt et al. 2013).

Effects of human activities on deer space-use

In our study, human use zonation influenced deer space-use, as indicated by much higher dropping counts in forest plots in the reserve than in the areas with recreation. Interestingly, dropping density did not differ between zones with hunting and non-hunting zones with recreation. Additionally, dropping counts were lower in the vicinity of forest trails than further away, but only when they were open for recreation. Dropping counts are a well-established proxy for deer space-use (Acevedo et al. 2010, Alves et al. 2013, Marcon et al. 2019) that allowed us to record long-term deer space-use on fine spatial scales over a large area. However, this method does not provide information on deer (foraging) behaviour or absolute density. Furthermore, habitat-dependent effects such as exposure to the elements or decomposers may influence dropping decay rates, biasing dropping counts between habitat types. However, in this study we did not attempt to compare absolute dropping density between habitats, but we were rather interested in the relative differences in deer space-use patterns across human use zones and different distances to trails within habitats, for which dropping counts are suitable. Furthermore, deer dropping counts and intensity of deer use may not directly relate and be biased to certain behaviour types such as resting or foraging when deer tend to defecate more. As these behavioural types are unlikely to be largely different between the human use zones and two distance classes we studied, for the purposes of this study this method was suitable as it provided us with relative measures of deer space-use over human use zones and distances to trails. The differences in deer density we documented are likely due to behaviourally-mediated effects, i.e. avoidance, as density-mediated differences between our relatively small zones (smaller than red deer home range (Reinecke et al. 2013, van Woersem and Elders 2016) are unlikely. This large- and fine-scale avoidance of recreation by deer, which may be either reactive or proactive, indicates that humans create clear risk effects even when not directly threatening the animal's life (Frid and Dill 2002). These results are in line with recent studies showing similar avoidance of anthropogenic disturbance in a variety of terrestrial and aquatic fauna (Tucker et al. 2018), but this was only recently recognised as an antipredator effect (Darimont et al. 2015, Gaynor et al. 2019, Suraci et al. 2019, Zanette and Clinchy 2019). Also cervids are known to adjust their space-use in response to human disturbance, as they avoid areas with human activities and infrastructure in the wider landscape (Nellemann et al.

2010, Skarin and Alam 2017, Bojarska et al. 2020). Our results are corroborated by studies in nature areas with high visitor numbers, which show that for example red deer avoid zones with higher human activity (Coppes et al. 2017). This locally reduces deer space-use, but it remained unclear that this affects vegetation development (Coppes et al. 2017), which we clarified in this study.

Earlier studies showed that both paved and unpaved roads (Prokopenko et al. 2017, Borowski et al. 2021) can affect deer space use, even when traffic volume is relatively low. For example, elk *Cervus canadensis* have been shown to avoid roads with traffic rates of more than 1 vehicle per hour, while they do not avoid unused roads (Rowland et al. 2000, Wisdom et al. 2018). Such effects of roads leading to reduced deer visitation of up to several hundreds of meters distance from roads, have been widely documented (Rowland et al. 2000). What has received less attention are the fine-scale effects of recreational trails on cervids. In our study we found strong differences in deer space use between plots at 20 m and 100 m from trails. These results are corroborated by recent studies that documented how small forest roads and mountain biking trails reduced deer densities, but only in their close proximity of for example < 40 m (Licoppe and De Crombrugghe 2003, Mathisen et al. 2018, Scholten et al. 2018). Such fine-scale behavioural adaptations of deer to human recreation may be more prominent in areas where visitor numbers and trail density are relatively high, such as our study area which receives an estimated two million visitors per year. Here, intense human disturbance may force deer to apply behavioural alterations on fine spatial scales. Similarly, fine-scale behavioural responses to carnivore presence have been identified as important antipredator strategies potentially leading to cascading effects on lower trophic levels (Mech et al. 2015, Gaynor et al. 2019). For example, deer avoid the direct vicinity of downed tree logs as they impede predator detection and escape possibilities (Halofsky and Ripple 2008, Kuijper et al. 2015), with effects stronger in the core of wolf territories than outside (van Ginkel et al. 2018). Here, we show how also human recreation activities elicit fine-scale risk effects in deer, in combination with larger scale spatial avoidance. Our results suggest that recreational activities (in our study area mainly hiking with/without dogs and cycling) induce fear effects in deer. However, our study was not specifically designed to separate behavioural effects of these different types of recreation. Other studies showed that hikers with dogs could elicit stronger fear responses in deer compared to hikers without dogs, as for example flight initiation distances can be much larger in the former (Miller et al. 2001, but see Kloppers et al. 2005). Similarly, cycling can induce larger flight initiation distances compared to hiking (Gander and Ingold 1997, but see Taylor and Knight 2003). Future research could incorporate how these different types of recreational activities impact ungulate behaviour and effects in our study area.

The effect of trails on deer space use in our study was habitat-dependent as deer avoided forest trails, while heathland trails had weaker effects. While deer's avoidance of roads has

been documented in both open and closed habitat types, previous studies have documented how flight initiation distances of deer to recreationalists can be larger in open habitat with high visibility (Stankowich 2008). This could create a larger 'area of influence' around trails (Scholten et al. 2018), which may potentially have reduced the difference between our plots located at 20 m and 100 m from trails. Furthermore, habitat openness plays a pivotal role in deer's spatio–temporal space-use, likely explaining the lack of effects of trails in heathland on deer space use in our study. Heathlands are often preferred foraging grounds for deer due to high resource quantity and quality (Godvik et al. 2009), but deer avoid this open terrain and seek shelter in lower quality forest in response to both predator- and human-induced perceived predation risk (Creel et al. 2005, Bonnot et al. 2013, Lone et al. 2014, Martin et al. 2018). Therefore, deer in zones with recreation in our study area likely avoid open heathland during the day when humans are present and spend time in forest habitat to seek cover, while at night they select for heathland. This means deer spend most time on heathland during the night, when humans are absent and trails are not used, rendering avoidance of trails futile (Licoppe and De Crombrugghe 2003, Godvik et al. 2009, Coppes et al. 2017).

While deer avoided recreation in our study, the addition of hunting activities in zones with recreation did not affect deer space-use. Deer dropping counts did not significantly differ between recreation and hunting and recreation only zones. This contrasts a variety of studies that documented how hunting can elicit antipredator responses in deer on spatial scales comparable to the hunting zones in our study area (Le Saout et al. 2014, Sullivan et al. 2018). This suggests that deer in our study area do not adjust their patterns of space-use in response to hunting zones outside of the hunting season. Most studies that reported effects of hunting zones on deer space-use focused on effects during the hunting season or during periods of intense hunting, making it unclear whether effects persist throughout the year (Cromsigt et al. 2013). Moreover, earlier studies assessing both immediate as well as year-round effects have documented no effects of hunting zones and argued that other human activities can be the main driver of deer spatial behaviour (Kays et al. 2017, Schuttler et al. 2017, Osterhaus et al. 2020). For example, Fattebert et al. (2019) corroborated our results as they documented weak effects of the hunting season on red deer habitat selection, while non-lethal human disturbance was the main driver of deer habitat choice. Our study did not investigate the effect of hunting periods, but results do show a lack of effects of zonation in hunting activities year-round. This may be contributed to the restricted timing of hunting activities and current hunting methods (Cromsigt et al. 2013). In contrast to the daily and year-round recreation activities, hunting is very limited in time, also in our study area (Faunabeheereenheid Gelderland 2019). Hunting practices are restricted to seasons and limited to certain weekdays, concentrated during crepuscular periods and prohibited during the night. This creates risk effects in restricted timeframes, likely allowing deer to exploit hunting zones when hunting does not occur (Lima

and Dill 1990, Cromsigt et al. 2013). Zonation of hunting activities would likely have stronger effects when hunting is conducted in less restricted seasonal and daily timeframes. Additionally, responses of deer to hunting may be low as current hunting practices are aimed at minimising fear responses in deer by inconspicuous hunting from for example high seats while using rifle sound suppressors, leaving deer with little response cues (Proffitt et al. 2009, Forssman and Root-Bernstein 2018). Using more intrusive hunting methods such as hunting on foot, with dogs, and hunting all age-classes and sexes in a population may be required to provoke fear effects strong enough to induce lasting changes in deer spatial distribution and impact (Cromsigt et al. 2013). Alternatively, zonation of hunting activities may not have effects in our study because all deer in our study are subject to hunting and may therefore be unable to distinguish between zones with and without hunting and respond similarly to the presence of recreationists and hunters. However, we expect this is unlikely as hunting is conducted in across designated hunting zones, and never outside them while studies from other areas indicated that deer are then very able to distinguish between hunting and non-hunting zones (Le Saout et al. 2014, Proffitt et al. 2009).

Sapling performance

In this study we show how the responses of deer to human activities are associated with saplings performance, which was strongly influenced by human use zonation. In turn, effects on saplings may ultimately cascade down the food chain and affect other species and forest structure and functioning (Ramirez et al. 2018, 2021). As discussed above, deer space-use was lower in the zones with recreation than in the reserve which was associated with a strong release of browsing pressure and higher growth of oak and birch saplings in the reserve than in the recreational zones. Similarly, survival of oak and birch saplings was higher in zones with recreation and hunting than in the reserve. These associations, however, were apparent in the heathland habitat but not in the forest. Our results suggest that the human-induced reductions in deer space-use we documented led to increased sapling performance in heathland areas with recreation.

The reduction in browsing pressure on saplings was only found in heathland and not in forest habitat. Effects on open heathland with high visibility were expected as human disturbance drives deer to select for denser habitat types (Licoppe and De Crombrugghe 2003, Godvik et al. 2009, Bonnot et al. 2013, Lone et al. 2014, Martin et al. 2018). This means that in areas with recreation, the fear of humans inhibits deer to use the heathland and drives them into the forest or reserve areas, reducing their impact on saplings in heathland. In contrast, we found lower deer dropping counts in forest in zones with recreation than in the reserve, while there were no differences in sapling performance in forest between zones. This suggests that while deer spend more time in the forest reserve than in other forest zones, this does not affect the vegetation. This could be explained by deer using

the forest reserve mainly for resting and meanwhile allocate relatively little time to foraging. This is in line with theory as deer select the most secure habitat while inactive, in this case the reserve's forest, and focus on foraging while venturing into more disturbed terrain (Bose et al. 2018). This may explain the discrepancy in effects of human use zones on deer space-use and sapling performance in forest.

The habitat-dependency of human-induced risk effects and resulting effects has implications for management. Human use zonation affected sapling performance in heathland, while the fate of saplings in forest did not differ between zones. Recreation on heathland halved browsing intensities on oak and birch saplings and increased survival rates with up to a factor 5 (Fig. 2) relative to heathland on the reserve without recreation. Since management aims to keep heathlands open, excluding recreation on certain heathlands may be important to promote deer browsing and reduce woody recruitment on heathlands. In the forest habitat, managers have the opposite goal and aim for reducing browsing pressure. Here, in our system, even intense recreation did not release browsing pressure and increase sapling performance in the forest habitat. Recreational zonation may thus be effective to steer desired deer impacts on heathland but not in forest habitat due to possible reasons we have explained further above.

While we documented fine-scale avoidance of forest trails by deer, saplings near these trails were not released from browsing pressure, as sapling browsing, relative growth or survival did not differ between our plots at 20 m and 100 m distance from trails. While the difference in deer dropping numbers we documented indicates lower deer space-use near trails, deer can easily access the vicinity of trails during the night when humans are absent (Coppes et al. 2017). During their night-time use of these areas, deer may compensate for missed foraging opportunities and offset effects on the vegetation. Such exploitation of resources by venturing into dangerous terrain in safe times (Dröge et al. 2017) has been documented in for example elk *Cervus canadensis*, who select for areas with high wolf predation risk during wolf absence (Kohl et al. 2018). Coppes et al. (2017) documented similar patterns in response to human predation risk as they demonstrated that red deer preferred refuge zones and areas far from trails during the day, while they selected for these places at night. This mechanism may be responsible for the lack of effects on saplings near trails we documented. Few studies have investigated the fine-scale effects of trail avoidance on sapling performance, yet in Mathisen et al. (2018) it was shown that in Poland, oak browsing damage decreased at distances lower than 40 m from forest trails. Yet this study area is inhabited by wolves, whose nightly use of trails makes the vicinity of trails dangerous, also at night (Musiani et al. 1998). This presumably makes night-time compensation less feasible than in our study system where large predators were absent during the study and human recreation is prohibited during the night, allowing deer to compensate at night. Additionally, other factors such as recreation pressure, herbivore density, forage availability, habituation, the presence of dogs and more may explain the difference between studies. Night-time activities such as torch-walks or nocturnal animal spotting, or predator recolonization, could make trails in our study area effective in mitigating deer impact on the vegetation at fine spatial scales, also at night and on open heathlands.

Conclusions

In this study, we demonstrate how human recreational activities can effectively influence deer space-use and increase sapling performance. Hereby, our results suggest that besides the well documented behavioural effects created by large predators (Ripple et al. 2014, Suraci et al. 2016), also human recreation creates landscapes of fear that can cause pervasive anthropogenic behaviourally-mediated trophic cascades (Suraci et al. 2019). However, we emphasize that risk effects and resulting effects on the vegetation are context-dependent, as they depended on the type of human disturbance (recreation versus hunting), scale (zones versus trails) and habitat (heathland versus forest). This corroborates a recent body of literature emphasising the complexity and context-dependence of fear-driven predator–prey interactions (Moll et al. 2017, Gaynor et al. 2019, Montgomery et al. 2019). For management, this means that recreational zonation may be applied to steer desired deer impacts on heathland but not in forest habitat, and that the installment of trails does not always release saplings from browsing pressure. As we stress how these pervasive human-induced fear effects are habitat- and scale-dependent, we advocate integrating the fear of humans as an ecological factor in research, nature conservation and management.

Author contributions

Dries P. J. Kuijper and **Christian Smit** contributed equally to this publication. **Bjorn Mols**: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Funding acquisition (supporting); Investigation (lead); Methodology (equal); Project administration (lead); Resources (supporting); Software (supporting); Supervision (equal); Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Evert Lambers**: Conceptualization (supporting); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Joris P. G. M. Cromsigt**:

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.j9kd51cdk> (Mols et al. 2021).

Supporting information

The supporting information associated with this article is available from the online version.

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