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RESEARCH ARTICLE

Direct and indirect effects of food, fear and management on crop damage by ungulates

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Abstract

1. Foraging on crops by wild ungulates may create human–wildlife conflicts through reducing crop production. Ungulates interact with and within complex socio-ecological systems, making the reduction of crop damage a challenging task. Aside from ungulate densities, crop damage is influenced by different drivers affecting ungulate foraging behaviour: food availability and food quality in the landscape (i.e. the foodscape) as well as fear from hunting and scaring actions (i.e. the landscape of fear) may together affect the degree of damage via both direct and indirect effects. A better understanding of the individual effects of these potential drivers behind crop damage is needed, as is an appreciation of whether the effects are dependent on ungulate density.
2. We investigated this by applying path analysis to test indirect and direct links between ungulate density, foodscape, landscape of fear and human management goals on crop damage of oats and grass, respectively.
3. Our results suggest that crop type is the major driver behind crop damage, with more damage to oats than to leys, implying that human decisions (i.e. changing crop type) influence the level of crop damage.
4. We found that management goals and actions influenced the foodscape and the landscape of fear, by affecting the amount of forage produced in the agricultural landscape and the amount of scaring actions. Additionally, we found that supplementary feeding influenced the local ungulate densities in the area.
5. Our results highlight the importance of including human actions on multiple levels when assessing drivers behind damage by ungulates in managed landscapes. We suggest that more studies using path analysis on multiple scales are needed in order to tackle complex issues, such as crop damage and other human–wildlife conflicts.

KEYWORDS
agriculture, crop damage, deer management, path analysis, ungulate

1 | INTRODUCTION

Wild ungulates interact with and within complex socio-ecological systems (Reimoser & Putman, 2011) and many of these systems are heavily influenced by multiple human interests and different types of land use (Dressel et al., 2018). While such ungulates (e.g. different deer species and wild boar) may benefit from certain human land use practices (e.g. agriculture and/or forestry) through increased foraging opportunities and shelter (Ferretti & Lovari, 2014; Presley et al., 2019), their foraging and trampling may also create human–wildlife conflicts, for example, through reducing crop production and increasing associated economic losses (Reimoser & Putman, 2011). The cost of grazing and browsing from wild ungulates can be extensive, varying widely among continents and countries, with Europe having the highest number of wildlife-damage compensation schemes and the highest amount of compensation paid (Ravenelle & Nyhus, 2017). However, the costs are often unclear since data on wildlife-related crop damage are unavailable or limited due to the lack of monitoring programs (Linnell et al., 2020; Reimoser & Putman, 2011). In some European countries, however, documented compensation payments for crop damage by wild ungulates reaches >10 million euro in certain years (Linnell et al., 2020).

High risk of crop damage can lead to farmers adjusting their crop choice to reduce grazing pressure by wild ungulates. For example, in areas with high ungulate densities in Sweden, farmers may switch to crops that are less attractive to ungulates and less prone to damage (Åberg, 2017; Statens Offentliga Utredningar, 2014). Thus, the risk of crop damage may be preventing farmers from choosing the most profitable crop, and from producing a mix of roughage (e.g. silage) and concentrates (e.g. cereals) necessary in raising livestock. With ungulates increasing both in numbers and distribution throughout Europe (Apollonio et al., 2010; Linnell et al., 2020; Thulin et al., 2015), there is a growing need to understand the drivers behind the damage they cause on farmland. Successful ways to reduce this damage will ultimately depend on a better understanding of the dynamic interactions between the use of agricultural lands by ungulates and farmers. In this article we developed and tested a detailed conceptual model of these interactions and the direct and indirect drivers of crop damage to address these knowledge gaps.

1.1 | Conceptual model of crop damage

Ungulate densities have been suggested to be an important direct driver in determining the intensity and distribution of crop damage (Bleier et al., 2012, 2016; Kupferschmid et al., 2020) (path d in Figure 1). However, behavioural responses of the ungulates may result in additional density independent damages, or alter the degree of density dependence. Thus, it is important to include factors that can influence ungulate behaviour and potentially act as indirect drivers of crop damage when aiming for mitigating damage.

The availability and quality of forage across the landscape, here referred to as the foodscape [Searle et al., 2007], are important drivers of foraging behaviour, influencing ungulate habitat selection and space use across spatial and temporal scales (Senft et al., 1987) as well as influencing densities, by determining the carrying capacity (Allen et al., 2017). Forage availability importantly influences how ungulates affect human land use, with lower damage levels in areas with high availability of natural forage (Herfindal et al., 2015; Jarnemo et al., 2014; Kupferschmid et al., 2020; Månsson, 2009; Pfeffer et al., 2021). Thus, the effect of the foodscape on variation in crop damage within a landscape can be: (1) direct—(i.e. density independent) the foodscape influences foraging behaviour by steering ungulates spatio-temporal use of the landscape, including crop fields (path c1 in Figure 1) and (2) indirect—through the foodscape influencing ungulate densities (i.e. density dependent; path b1 + d in Figure 1).

Moreover, animals also face trade-offs between finding food and reducing predation risk (Brown et al., 1999). Prey can respond to predation risk by altering their behaviour, including foraging in less risky habitats or changing time allocation to feeding (Bergerud et al., 1983; Blumstein & Daniel, 2002; Creel et al., 2005; Lima & Dill, 1990; Thaker et al., 2011). The term landscape of fear is used when prey respond to spatial variation in predation risk, for example, by adjusting their foraging-site selection (Laundré et al., 2010). Thus, fear-inducing practices to mitigate crop damage, such as hunting and scaring, may drive variation in animals' spatial and temporal use within the landscape as it influences their perception of predation risk (Gaynor et al., 2019). However, these practices may also influence ungulate densities across the landscape through reducing the total number of animals in the landscape via killing or scaring (path b2 + d in Figure 1). Fear has been shown to have strong community level effects and may influence population abundance and fecundity partly due to the consequences of the reduction in time spent foraging, resulting in fewer offspring (Zanette & Clinchy, 2020). Thus, we assume that the landscape of fear, similar to the foodscape, will have both a direct (i.e. density independent; path c2 in Figure 1) and an indirect effect (Path b2 + d in Figure 1) on crop damage.

The foodscape and the landscape of fear are under constant influence by diverse human management practices and interests. Diverse, and sometimes conflicting, human interests determine the tolerated population densities of wildlife (Gordon et al., 2004; Menichetti et al., 2019), as wildlife deliver ecosystem services such as hunting and wildlife tourism, and limit others such as food production (Widemo et al., 2019). Landowners aiming for recreational hunting or ecotourism (Gordon et al., 2004; Menichetti et al., 2019) often maintain high ungulate densities by increasing food availability via supplementary feeding or habitat management (e.g. sowing dedicated game crops) (Cooper et al., 2006; Smith, 2001), thus intentionally changing the foodscape to benefit game. Likewise, landowners aiming for agricultural profit may manipulate the foodscape for increasing crop yield, crop performance and productivity (Nkurunziza et al., 2020). Human goals and management strategies, thus directly influence both forage availability and forage quality in agricultural fields and the surrounding landscape (path a1 in Figure 1). Similarly, land owners may intentionally or unintentionally

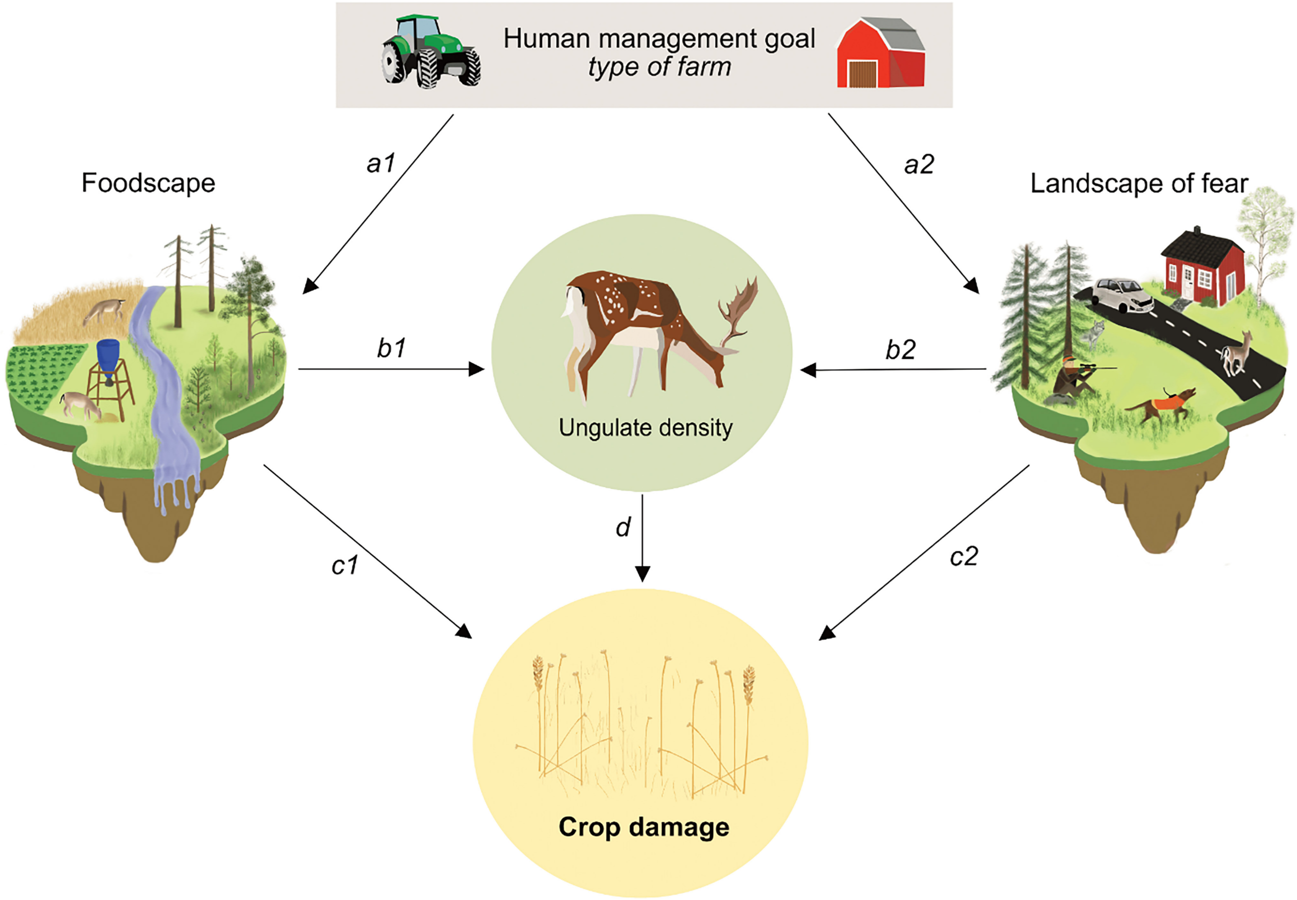

FIGURE 1 Conceptual model illustrating direct and indirect effects between human management goals, foodscape, landscape of fear and ungulate density on crop damage. Human management goals (the type of farm) can directly influence the foodscape and the landscape of fear (paths a1 and a2). The foodscape and landscape of fear can directly influence ungulate density (path b1 and b2) and also crop damage (path c1 and c2). Ungulate density can directly influence crop damage (path d), meaning that there is an indirect link from the foodscape and landscape of fear to crop damage via ungulate density (path b1 + d and b2 + d), as well as indirect links from management goal on crop damage via foodscape and landscape of fear (path a1 and a2 + c1 and c2), and ultimately from management goal via foodscape and landscape of fear, via ungulate density (path a1 and a2 + b1 and b2 + d).

shape the landscape of fear depending on their management goal and strategies. Specifically, farmers aiming for high crop yields often conduct different actions to reduce negative impact of wildlife by increasing the hunting pressure or using scaring practices to reduce damage on fields (Bonnot et al., 2013; Geisser & Reyer, 2004; Pęksa & Ciach, 2018; Setsaas et al., 2018; Vistnes & Nellemann, 2007). Hence, farmers' practices directly influence the landscape of fear depending on their management goals (path a2 in Figure 1).

A major limitation of previous studies is that they have not managed to disentangle individual effects of the drivers of crop damage, such as foodscape versus landscape of fear and whether the effects are density dependent or independent (i.e. direct or indirect) since many studies assess them separately (Corgatelli et al., 2019; DeVault et al., 2007; Naughton-Treves, 1998; Retamosa et al., 2008).

Moreover, we lack an understanding of the dynamic interaction between ungulate and human behaviour. In such dynamic interactions, ungulates respond to foodscapes and landscapes of fear that are (un)intentionally shaped by human land use, but human land use also responds to the behaviour of the ungulates. Understanding these interactions between human behaviour (in terms of their management goals and practices), and ungulate behaviour and their effects on crop damage calls for an alternative type of data collection as it deals with people's motivation as well as animal behaviour. In this study, we approach this challenge by applying an interdisciplinary approach that combines social survey data to quantify the human management goals and behaviours with ecological experimental field data on ungulate densities, foodscape and crop damage. We then use a path analysis to investigate direct and indirect effects on crop damage according to the above-described conceptual framework (Figure 1). Multivariate modelling approaches such as path analysis can provide useful insights in complex systems like these. They allow researchers to simultaneously test complex direct and indirect links between several dependent and independent variables and thereby identify if mediation occurs (Ahn, 2002; Lam & Maguire, 2012).

Unfortunately, the fact that agriculture in many areas, including our study area in southern Sweden, has been adapted to minimize ungulate damage by switching to less attractive crops, particularly in areas with high ungulate density, limits the potential to study the full extent of the foodscape (i.e. strong contrasts in crop quality) in existing agricultural landscape. Therefore, we manipulated the agricultural foodscape experimentally, by contracting farmers to sow crops (oat) they normally would have avoided due to the risk of high levels of crop damage. Thus, we created a strong experimental variation in the foodscape in the form of fields planted with crops that are very attractive to ungulates versus crops that are much less attractive. On top of this, we included a large number of farmers that varied widely in their main management goals (intensive crop production versus strong focus on wildlife use and situations in between) and, therefore, their potential management practices. Using questionnaires we collected detailed information about these management goals and practices. The combination of our interdisciplinary approach with experimentally manipulating the foodscape on a large scale, allowed us to investigate how human management goals and practices influence the foodscape and landscape of fear and ultimately ungulate densities, and crop damage on fields.

2 | MATERIALS AND METHODS

2.1 | Study area and study design

The study was performed in the county of Södermanland, in the hemiboreal climate zone of southern central Sweden (58.96° N, 17.15° E). The mean monthly temperature ranged between 5 and 20°C during the study period (April–August 2020) and mean monthly precipitation ranged between 25 and100 mm from April to August 2020 (Swedish Meteorological and Hydrological Institute [SMHI], 2021). The region is composed of a mix of boreal forests and agriculture with 20%–39% of the total land area being agricultural land (Jordbruksverket, 2020a). The agricultural land is comprised of leys (hereafter grass), cereals and rape seed (*Brassica napus*) as the three most common crop types. The three dominating cereal crops are wheat (*Triticum* spp.), barley (*Hordeum vulgare*) and oat (*Avena sativa*) (Jordbruksverket, 2020b). The average annual yields in 2020 in the county were 7240 ± 65 kg winter wheat/ha (mean ± SD), 4230 ± 140 kg barley/ha, 4510 ± 131 kg oats/ha, 2680 ± 383 kg grass/ha and 3470 ± 38 kg rape seed/ha (Jordbruksverket, 2020c). In addition to crop fields, the area consists of cattle farms and a relatively large number of estates where game management and hunting is an important part of the land use, including those who sell hunting opportunities. The diversity in land use and management is creating conflict in the area, where farmers are concerned about crop damage by the high population densities of wild ungulates (Åberg, 2017).

Moose (*Alces alces*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and wild boar (*Sus scrofa*) coexist in the study area. The populations of these ungulates are managed through regulated annual hunting, and harvest statistics can be seen as indices of relative abundance. During the hunting season 2019/2020, the following number of ungulates were harvested per 1000 ha in the study area: ~69 fallow deer, ~14 wild boar, ~5 roe deer, ~2 Moose and ~2 red deer (moose data: Länsstyrelserna (2021); other ungulates: Svenska Jägareförbundet (2021)). As an important objective of this study, we wanted to test how the type of crop, that is, quality or palatability to ungulates, affects crop damage. For this purpose, we selected oat as an attractive nutrient-dense crop (to ungulates) and grass as a less nutrient-dense crop (Felton et al., 2021). Due to the high densities of ungulates in the study area, most farmers had already switched to the production of grass at the time of our study, as they perceived high damage on oats (Åberg, 2017). We, therefore, specifically approached farmers and financially compensated them to grow oats. Our aim with this was to set up a balanced experimental design with a similar number of oat and grass fields, diversifying quality of crops and simulating a foodscape consisting of both attractive, nutrient dense (oat fields) areas and less attractive, less nutrient dense (grass fields) areas. However, we only managed to convince farmers to grow oats on 16 fields and thus ended up with 16 oat fields and 32 grass fields. The fields were spaced in a systematic manner with approximately 3 km between each other aiming for independent fields not being used by the same ungulate individual. Five of the fields had a shorter distance between each other due to logistical and natural circumstances, with a minimum distance of 1 km.

We measured crop damage by ungulates on these 48 agricultural fields (Figure 2b) by comparing crop biomass between 2.3 × 2.3 m fenced exclosure plots (with a 1.6 m tall metal net to prevent ungulate grazing) and unfenced paired grazed plots. Within each field, we placed three pairs of exclosures and grazed plots with 5 m distance between paired plots and each pair situated at the same distance to (i.e. parallel to) the field edge. Per field, we placed one pair in the centre of the field (furthest distance to any field edge), one pair 10 m from a forest edge and one pair 10 m from a non-forest edge (Figure 2c). Forest was mapped using the national ground cover data in QGIS (QGIS Development Team, 2021). In total, we thus had 144 pairs of exclosures and grazed plots on 48 agricultural fields. We erected the exclosures on all fields (oat and grass) around 20 April 2020, coinciding with the sowing of the oat fields.

2.2 | Ecological data collection

2.2.1 | Crop damage

To estimate biomass loss (crop damage) on fields caused by ungulates, we took biomass measurements manually by harvesting the exclosures and the grazed plots using electric scissors just before the farmer would harvest the field. A buffer zone of 0.65 m was applied in the control plots and the exclosures to account for potential edge effects, thus biomass was only collected from a 1 m^2 plot in each control and exclosure. In addition, in the fields with oats, we collected the panicles and the straws above 5 cm separately and weighed them. Samples were stored in paper bags and frozen. All samples were dried at 65°C in drying cabinets for 48 h. Farmers harvested all grass fields, except one, multiple times. On these fields,

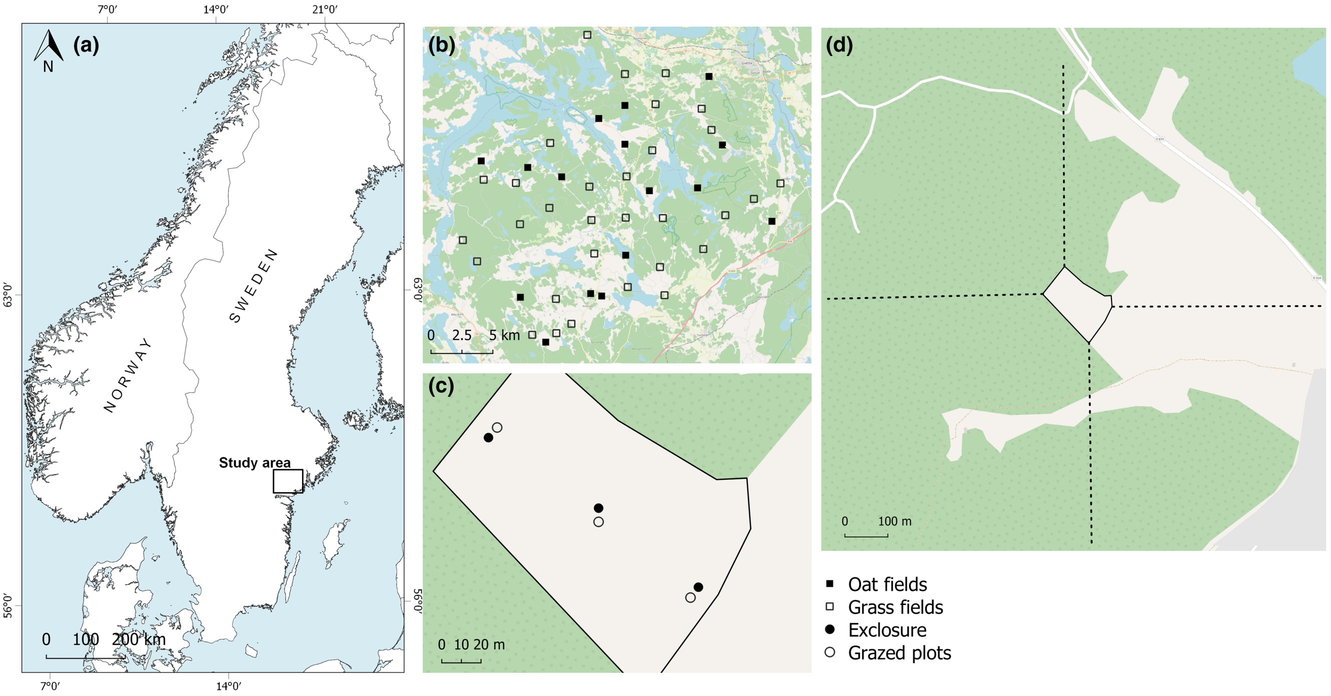

FIGURE 2 (a) Location of the study area within Sweden, (b) map of the study area with distribution of experimental fields (oat fields as black squares, grass fields as white squares, green colour indicates forest and white/cream colour represents non forest), (c) the placement of pairs of exclosures (black circles) and grazed (white circles) plots and (d) the distribution of the four 500 m transects in each cardinal direction from the field edge.

we took biomass measurements both before the first harvest in late May to early June 2020, and after the second harvest by the end of July to early August 2020. For grass fields, the exclosures were removed prior to harvest and replaced immediately after each harvest at the exact same position using the already existing holes from the poles.

Based on the biomass measurements in dry weight, we calculated difference in biomass between exclosure and grazed plots, which was later calculated into % biomass loss. The precision of the balance measured to the nearest 0.1 g. An average of the three exclosures and three grazed plots per field was used in the analyses.

2.2.2 | Biomass production on fields

To get an estimate of how much biomass the field would have produced without ungulate grazing, as part of the foodscape, we calculated biomass produced per field. For this, biomass in dry weight inside the exclosures was converted into biomass in gram per m^2 and further into biomass in gram per field. The area of the field was estimated using the function $area in the field calculator in QGIS.

2.2.3 | Alternative forage availability

We measured alternative forage availability surrounding the fields along 500 m transects in each cardinal direction from the field edge in July 2020 (Figure 2d). We used a modification of the step-point method (Evans & Love, 1957). The step-point method allows for quantification of food items (vegetation) at different foraging heights. For this we used a 3 m wooden pole (3 m representing the maximum browsing height for the largest ungulate, moose) (Spitzer et al., 2021). We took measurements every fifth metre along the transects (see Appendix for species list) resulting in 100 measurements per transect, 400 per field. At every fifth metre, the pole was placed at the tip of the boot and all species that touched the pole were recorded as present in each of the height classes. Based on the forage availability data and on previous work on diet use of the ungulates in this system (Spitzer et al., 2020), we identified five key forage groups comprising food items being important for all four ungulate species; Ericaceous shrubs: (bilberry (*Vaccinium myrtillus*), cowberry (*Vaccinium vitis-idaea*) and heather (*Calluna vulgaris*)), birch: (downy birch (*Betula pubescens*) and silver birch (*Betula pendula*)), other deciduous trees: (oak (*Quercus robur*), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and willow (*Salix* spp.)), graminoids and forbs. Based on this, we calculated the proportion of the key forage species groups per transect. An average of the four transects was calculated to give us one alternative forage availability index per field.

2.2.4 | Ungulate density

To get an estimation of ungulate density of the surrounding area, we conducted a pellet count survey in June 2020 during the early growing season. We were not able to measure pellet counts on the fields due to high vegetation and thus used the pellet counts in the surrounding area as a proxy for ungulate density in the local area, including the fields. We measured pellets as number of pellet groups in 100 m^2 circular plots distributed at 0, 100, 200, 300, 400 and 500 m along the above-mentioned transects starting from the field edge (Figure 2d) making 24 pellet count plots per field. Pellet groups were defined as a group, if consisting of ≥20 pellets for moose and ≥10 pellets for all other ungulates. Moose and red deer were estimated within a 5.64 m radius (100 m^2), fallow and roe within a 1.78 m radius (10 m^2). We counted only pellet groups that had been deposited after the leaf-fall of the previous autumn; that is, pellet groups that were deposited above the leaf litter and not heavily decomposed. Because we were interested in the overall influence of ungulate species on crop damage, and not species specific effects on crop damage, we combined the pellet counts into one ungulate index. Another reason for combining pellet counts of individual species into one index is that pellets of several of the species in our study area (specifically roe, fallow and red deer) are very difficult to differentiate (Spitzer et al., 2019). We divided the number of pellet groups along transects by the total area sampled for all transects (around the field), thus only considering the actual area sampled. We thus ended up with one ungulate index per field.

2.3 | Social data collection

We developed a questionnaire to collect information on management goals and practices conducted at three different levels: the whole farm, the surrounding area (500 m area surrounding the field) and on the specific field included in the study. To identify the human management goal on each farm (farm level), we asked respondents to specify 'what is the dominant land use type on your farm' giving them six answer alternatives (crop production, meat productions, dairy production, equine husbandry, hunting/game keeping and forestry). With respect to management practices on field level, respondents were asked 'which of the following management options did you carry out on your field in order to decrease damage', giving them nine answers alternatives (supplementary feeding, fencing, extended hunting during regular hunting season, protective hunting outside regular hunting season, fear-inducing measures using: scarecrow, sound, human presence or dog; and none of the above). Each response option also included three alternatives related to the frequency of implementation: sporadic implementation throughout the growing season, implementation for half of the growing season or implementation for the entire growing season.

Note that a 'Yes' answer for supplementary feeding could imply that supplementary feeding was conducted on the field or in close vicinity of the field, that is, field edge. Furthermore, with respect to management practices conducted in the surrounding area, a map of the field with a marked area of 500 m surrounding the field was attached to the survey. Respondents were asked 'which of the following management options were carried out inside the marked area', given the same nine answer alternatives stated above.

We sent the questionnaire to all involved farmers in our study. Several of the 48 fields were used by the same farmer and, as a result, the survey was sent to a total of 35 respondents. Of those, 31 farmers representing 44 fields responded, which corresponds to a response rate of 88%. Due to restriction in the number of variables that could be used in the analysis, based on sample size, we could not include management practices on both the field level and in the surrounding area in the model. Because of our ultimate question being what influences crop damage on the fields, and because uncertainty increases in answers on the surrounding area (e.g. the respondent might not own all of the land in the 500 m surrounding area), we chose to include management practices on field level for further analysis. However, to better estimate the direct impact from hunting on ungulate density, we included answers about hunting in the surrounding area in the analysis, but this variable was not linked with human management goal due to the above-mentioned uncertainty. Management practices in order to decrease damage at the field level were grouped into three separate variables: hunting (including extended hunting during regular hunting season and/or protective hunting outside regular hunting season), the answers were assigned scores ranging from 0 to 3. A score of 0 indicated no hunting conducted, a score of 1 represented sporadic hunting during the growing season, a score of 2 indicated hunting during half the growing season and a score of 3 represented hunting during the entire growing season. The scores were then summed, and the resulting sum was utilized in subsequent analyses. Fear-inducing actions/scaring (including presence of scarecrows, use of sounds, human presence, and/or dog presence, the answers assigned scores ranging from 0 to 3. A score of 0 indicated no scaring conducted, a score of 1 represented sporadic scaring during the growing season, a score of 2 indicated scaring during half the growing season and a score of 3 represented scaring during the entire growing season. The scores were then summed, and the resulting sum was utilized in subsequent analyses) and supplementary feeding where the answers similarly were assigned scores ranging from 0 to 3. A score of 0 indicated no supplementary feeding conducted, a score of 1 represented sporadic supplementary feeding during the growing season, a score of 2 indicated supplementary feeding during half the growing season and a score of 3 represented supplementary feeding during the entire growing season. The scores were then summed, and the resulting sum was utilized in subsequent analyses. Fencing was excluded in the analysis since none of the landowners used this method. Management goal at the farm level was pooled into one variable and labelled '−1' for hunting/game keeping, '1' for agriculture and '0' for both, with agriculture being comprised of crop production, meat production and equine husbandry. Forestry was excluded from the analysis due to low sample size, that is, very few landowners had forestry as their main goal.

2.4 | Statistical analysis—PLS application

We used partial least squares (PLS) path analysis to investigate indirect and direct effects of ungulate density, foodscape, landscape of fear and human management goal on crop damage and to test the hypothesized conceptual model shown in Figure 1. PLS is a specialized form of path analysis that tries to maximize the explained variance in the model (Eriksson et al., 2006; Vinzi et al., 2010). PLS path models, in contrast to normal path analysis, are less conservative regarding sample sizes, residual distribution and measurements scales (Mateos-Aparicio, 2011) while still allowing for a complex model for relatively small number of independent observations. Analysis was conducted in the program SmartPLS3 (Ringle et al., 2015). Before fitting the model, all variables were checked for multicollinearity (Pearson's *r* ≥+0.7 or ≤−0.7). We used language of evidence according to Muff et al. (2022), using the *p*-values as cut-off values accordingly: little or no evidence of effect, $p=1–0.1$; weak evidence, $p=0.1–0.05$; moderate evidence, $p=0.05–0.01$; strong evidence, $p=0.01–0.001$; and very strong evidence $p=0.001–0.0001$ (Muff et al., 2022).

3 | RESULTS

Twenty-seven percent of the total variation in crop damage (i.e. percentage reduction in yield in controls as compared to exclosures) was explained by all predictors together (Figure 3). The average biomass on fields was 1349.7 kg (SE: 306.83, min: 112.48 kg, max: 12,510 kg). The biomass loss on fields caused by grazing ungulates (i.e. crop damage) averaged 41% (SE: 0.04) with a maximum of 99% and min of 0. The average alternative forage availability surrounding fields represented as an average proportion of four transects per field was 36% (SE: 0.02, min: 0, max: 76%). The average ungulate density represented as pellets per square meter was 0.08 (SE: 0.01, min: 0, max: 0.53). Thirty-one percent of the total variation in ungulate density was explained by variables representing the foodscape, landscape of fear and human management goals (Figure 3).

3.1 | Variables (other than management goal) influencing crop damage

We found strong evidence for the choice of crop type influencing crop damage ($\beta=-0.886$, $p=0.008$; $f2=0.207$, Figure 2), with higher biomass loss on oats (54% on average and standard error of 9%) than on grass fields (34% on average and standard error of 4%). We found no evidence for any other direct effect between foodscape or landscape of fear variables and crop damage.

3.2 | Variables (other than management goal) influencing ungulate density in the landscape

We found moderate evidence that supplementary feeding had a positive effect on ungulate density ($\beta=0.406$, $p=0.044$; $f2=0.205$, Figure 2). The mean ungulate density on fields with supplementary feeding was 0.14 pellets/m^2 (SE: 0.05), while mean ungulate density

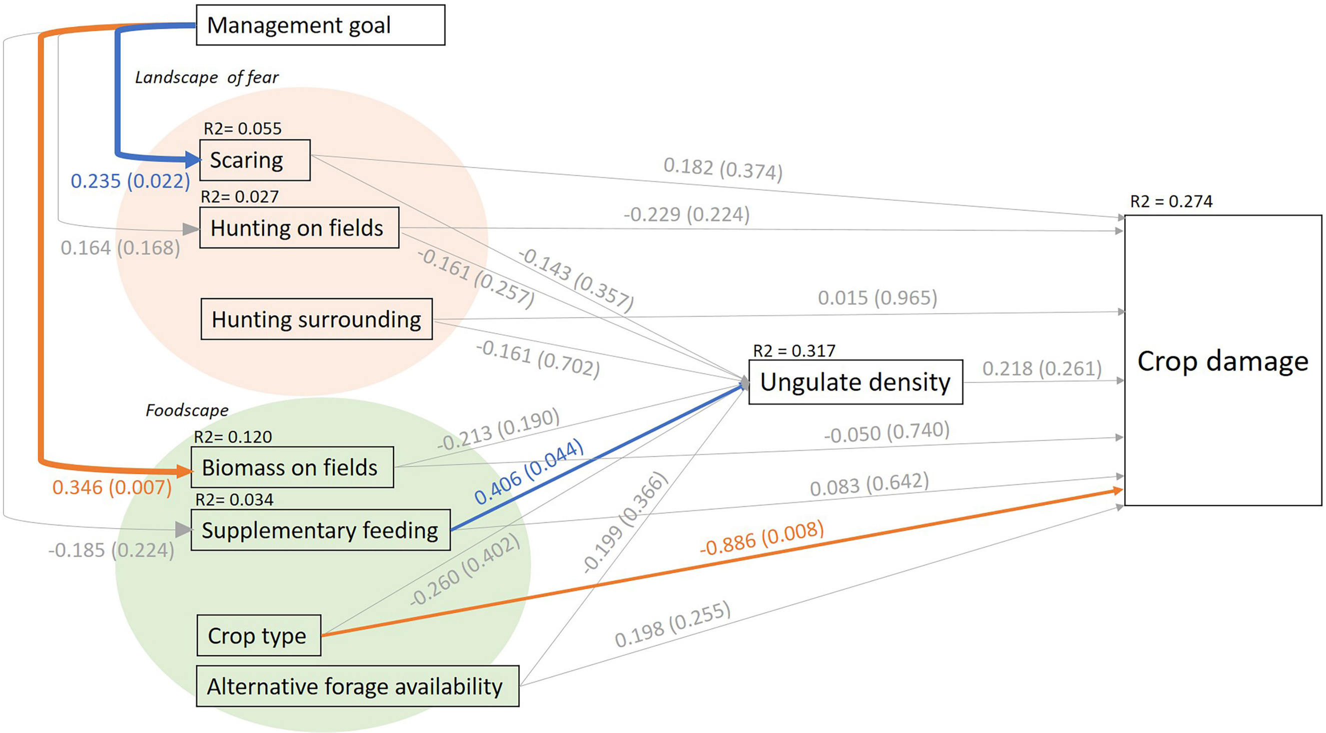

FIGURE 3 Path analysis/PLS results showing direct effects of foodscape, landscape of fear, human management goals and ungulate index on crop damage. Values in the figure are path coefficients (direct effects) and *p*-values. Positive path coefficients from the management goal box implies positive effect from farms with agricultural goal. Colours of arrows represents the strength of evidence based on *p*-value. Orange = strong evidence of effect ($p=0.01–0.001$). Blue = moderate evidence of effect ($p=0.05–0.01$), according to Muff et al. (2022).

on fields without supplementary feeding was 0.06 pellets/m^2 (SE: 0.008). Besides that, none of the other foodscape and landscape of fear-related variables had a direct effect on ungulate density.

3.3 | Influence of human management goal on crop damage and ungulate density

The management goal of the farm had significant influence on the management practices performed. We found moderate evidence that the management goal determined scaring practices ($\beta=0.235$, $p=0.022$, $f2=0.058$). Expectedly, landowners having agriculture as their main goal were more likely to scare ungulates than landowners having hunting/game keeping as their main goal. We found that strong evidence suggested that landowners with agriculture as their main management goal had significantly higher biomass on their fields compared to landowners with a hunting/game keeping goal ($\beta=0.346$, $p=0.007$, $f2=0.136$). We found no evidence of management goal affecting the presence of supplementary feeding on fields ($\beta=-0.185$, $p=0.224$, $f2=0.035$) or hunting on fields ($\beta=0.164$, $p=0.168$, $f2=0.028$). We found moderate evidence for a negative total indirect effect of management goal on ungulate density ($\beta=-0.209$, $p=0.011$, Table S1), meaning the results of all indirect effects of management goal on ungulate density (via supplementary feeding, scaring, hunting on fields and biomass on fields). This implies that practices conducted by agricultural farms led to lower ungulate densities. Estimates for all indirect and total effects can be found in Table S1.

4 | DISCUSSION

We found that management goals such as agriculture and game keeping directly influenced the foodscape and the landscape of fear for ungulates, by influencing the production biomass on fields, and by influencing the amount of scaring practices conducted on the fields. The crop type influenced crop damage, with higher levels of damage on oats compared to leys, showing the importance of the food quality. Overall, we show that a simple decision such as crop choice can greatly influence ungulates' impact on agriculture, and that none of the other foodscape and landscape of fear measures came even close to having this direct effect.

One reason for the strong effect of crop type and the lack of influence from the other variables may be due to a frequency-dependent selection, that is, that selectivity of a food item will increase if its availability is low at landscape level (Greenwood & Elton, 1979). High ungulate densities in the study area (fallow deer in particular) have led to farmers adapting their management by growing less attractive crops, in order to decrease ungulate damage. Therefore, nutrient-dense palatable cereal crops like oats are relatively rare in the area. The fact that we increased the number of cereal fields in a landscape, where these fields are rare, might have led to a strong selection of oat fields, and thus potentially overshadowing the effects of surrounding foodscape and landscape of fear. This frequency-dependent selection has been seen also in forest ecosystems where a higher number of available stems of the highly selected food item, the scots pine (*Pinus sylvestris*), results in a lower relative level of browsing damage on pine due to a dilution effect (Bergqvist et al., 2014; Díaz-Yáñez et al., 2017; Pfeffer et al., 2021). Furthermore, as in the agricultural landscape (with farmers switching to less palatable grass fields instead of cereals), forest owners are taking action in order to decrease browsing damage, currently regenerating forests with less palatable spruce on sites more suitable for pine (Felton et al., 2020; Lodin et al., 2017). Moreover, similar actions in the agricultural landscape will thus most likely lead to increased grazing on the remaining fields of palatable crops, possibly influencing damage patterns in the landscape in opposite direction of what is desired. However, we can only speculate as to why the strong selection for oat would lead to a lack of strong influence from the other landscape variables. This is because our sample size limited our possibilities of investigating the relative effect of the explanatory variables on crop damage on the two different crops separately.

Surprisingly, we did not find any evidence for an effect of ungulate density on crop damage, something that has been suggested to be an important variable explaining crop damage in other studies (Bleier et al., 2012; Corgatelli et al., 2019). One explanation may be that the ungulate densities in our study area are generally high everywhere and even the relatively low densities within our study area are high compared to densities elsewhere. As a result, even comparatively low densities (for our area) likely caused high levels of damage. Furthermore, since we were not able to measure pellet counts on the fields due to high vegetation, the pellet counts we performed in the surrounding landscape potentially underestimated field use and actual grazing pressure on the fields. However, it is reasonable to believe that ungulate density in the close vicinity of the field reflects the use of the field as well. We thus assumed that a high ungulate density in the area surrounding the field also means a high use of the fields. Furthermore, studies have showed that the effect of ungulate density can be overshadowed by other factors in the surrounding landscape (Felton et al., 2022; Jarnemo et al., 2014). For example, food availability can show higher significance than ungulate density in explaining damage (Felton et al., 2022; Jarnemo et al., 2014). Our results show a similar pattern, since the effects of features of the foodscape (i.e. crop type) show a stronger influence on crop damage than ungulate density. Supplementary feeding had a positive influence on ungulate density. This implies that in the areas with frequent supplementary feeding, local ungulate density is higher. The manipulation of the foodscape seems not only to have an influence on crop damage (by crop type), but also on ungulate density. Moreover, our result shows that the major influence of supplementary feeding is on ungulate density and not on crop damage on fields.

4.1 | Influence of human management

Both the foodscape and the landscape of fear were influenced by the human management goal and the resulting management practices. Biomass on fields, being a proxy of forage productivity on the fields, was higher on farms with an agricultural goal compared to farms with a game keeping/hunting goal, implying that important features of the foodscape are driven by how the farm is managed. This is further supported by Nkurunziza et al. (2020) who found that the productivity on crop fields was largely driven by differences in farming practices guided by the category of farm. Thus, depending on how landowners decide to manage their farm, ungulates navigating in that landscape will experience differences in the foodscape. Furthermore, our study shows that scaring practices were more often conducted on farms with an agricultural goal. This makes sense since farmers that aim for high agricultural yields and production (i.e. agricultural management goal) have a greater need to invest in scaring practices to reduce negative impacts by wildlife, that is, directly influencing the landscape of fear. Therefore, human management goals direct what management practices will take place in a particular area, which in turn influences different features of the foodscape and landscape of fear. Moreover, when comparing the standardized ß coefficients, we can conclude that human management goals have a stronger effect on the foodscape than the landscape of fear, with a higher ß coefficient for biomass (0.392) than for scaring (0.149). Furthermore, the fact that we found strong evidence for a total indirect effect of human management goal on ungulate density implies that the actions conducted depending on the type of farm not only influence the landscape ungulates navigate in but also the ungulate density in the landscape. However, more studies are needed in order to disentangle specific indirect effects of human management goal on ungulate density.

4.2 | Limitations of study and future research needs

In this study, we were restricted to a fairly low sample size (for this type of complex system), reducing the statistical power of the model and making it difficult to disentangle relative impacts. One possible reason for the lack of relatively strong effect sizes in our model is also that our measurement of crop damage may have been insufficient in capturing the possible variation in damage caused by our explanatory variables. We were restricted to biomass measurements from three exclosures and three grazed plots per field (three pairs). Thus, only investigating grazing impacts in a relatively small area of the field.

In our study, we examined a complex system characterized by multiple factors that influence ungulate density and impact. It is important to acknowledge that we may have inadvertently overlooked and excluded variables that likely play an important role in determining ungulate density and their landscape impact. This may be an important explanation for the fact that our model only explained 27% of the variation in crop damage. For instance, landscape features such as the proportion of surrounding forest and the distance to forest cover, which provide safe shelter, have been recognized as important determinants of ungulate landscape use (Bleier et al., 2012, 2016; DeVault et al., 2007). Similarly, other variables representing the landscape of fear, such as settlements, roads hiking trails and human presence, are known to influence how ungulates distribute across the landscape (Menichetti et al., 2019; Pęksa & Ciach, 2018). However, due to the limitations of our sample size, we were constrained in the number of variables we could include in our model. Therefore, future research should consider incorporating these additional features to gain a better understanding of the factors that determine crop damage. Moreover, possible scaling issues and spatial resolution could have impacted the power of our model. The effects of management actions on ungulate density and crop damage might vary across different scales, including within-fields, between-fields and in the larger landscape. However, due to logistical reasons, we were limited in measured the potential response at various scales. Consequently, we may not have adequately accounted for the influence management actions on ungulate density and crop damage. All together, these factors likely contributed to the relatively low explanatory power of our model and may also explain why some management actions did not yield the expected results (e.g. the lack of effect of hunting on ungulate density). By taking these limitations into account, future studies may provide a more comprehensive picture of the underlying factors influencing ungulate impact.

5 | CONCLUSIONS

To conclude, crop damage by ungulates is part of a complex web of multiple influencing factors with indirect and direct relationships across several spatial levels. By tackling this complex system using a novel interdisciplinary approach, and incorporating ecological drivers as well as human practices, we were able to show that depending on how humans manage their land, they will directly influence the landscape ungulates navigate in by modifying the foodscape and the landscape of fear, consequently influencing ungulate density in the area and the impact ungulates have on the landscape. Moreover, we can conclude that crop type was the strongest driver of crop damage. Implying that farmers can influence damage levels by adapting choice of crop, as indicated in our study area with the reduced levels of cereal crops as a result of high ungulate levels. This pattern may in the long run influence damage patterns in the landscape in opposite direction of what is desired, with high levels of damage on remaining cereal fields, something that of course is of high societal relevance knowing the large economic impact crop damage may have.

Furthermore, the understanding that crop type plays an important role in determining crop damage can offer valuable insights for management recommendations aimed at influencing animal behaviour and mitigating negative impacts. For example, by strategically providing attractive forage in specific locations and designating these areas for ungulate grazing, it may be possible to influence damage patterns in the landscape by diverting animals away from areas where their impacts are unwanted. However, it is important to consider that the intensity of ungulate use will likely be higher in the close proximity of such sacrificial areas, potentially resulting in increased impact in such nearby areas (Gundersen et al., 2004; Månsson, 2009; van Beest et al., 2010).

There is a need for a management approach that involves the foodscape on a larger scale, beyond property borders of land owners and a need for collective action in order to decrease individual risk. We suggest that more studies are needed using this type of path analysis on larger scales and using larger sample sizes, to tackle complex issues such as wildlife damage to crop production and human–wildlife conflicts. Our findings highlight that it is important to incorporate human actions on multiple levels when assessing the potential drivers behind damage caused by free-ranging ungulates in managed landscapes.

AUTHOR CONTRIBUTIONS

Anna Widén, Fredrik Widemo, Joris P. G. M. Cromsigt, Annika M. Felton, Sabrina Dressel and Navinder Singh conceived the idea and designed the study; Anna Widén collected the data; Anna Widén analysed the data with contributions from Sabrina Dressel, who especially contributed with knowledge on path analysis methodology as well as collecting and treating social data. Anna Widén led the writing of the manuscript, but all authors contributed to drafts and approved the manuscript.

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CONFLICT OF INTEREST STATEMENT

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.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.nk98sf7xw (Widén et al., 2023).

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REFERENCES

Åberg, M. (2017). *The impact of Swedish game species on livestock feed production*. Avancerad nivå, A1E. SLU, Institutionen för husdjurens utfodring och vård (HUV).

Ahn, J. (2002). Beyond single equation regression analysis: Path analysis and multi-stage regression analysis. *American Journal of Pharmaceutical Education*, *66*(1), 37–42.

Allen, A. M., Dorey, A., Malmsten, J., Edenius, L., Ericsson, G., & Singh, N. J. (2017). Habitat–performance relationships of a large mammal on a predator-free island dominated by humans. *Ecology and Evolution*, *7*(1), 305–319. https://doi.org/10.1002/ece3.2594

Apollonio, M., Andersen, R., & Putman, R. (2010). *European ungulates and their management in the 21st century*. Cambridge University Press.

Bergerud, A. T., Wyett, W., & Snider, B. (1983). The role of wolf predation in limiting a moose population. *Journal of Wildlife Management*, *47*(4), 977–988.

Bergqvist, G., Bergström, R., & Wallgren, M. (2014). Recent browsing damage by moose on scots pine, birch and aspen in young commercial forests—Effects of forage availability, moose population density and site productivity. *Silva Fennica*, *48*(1). https://doi.org/10.14214/sf.1077

Bleier, N., Kovács, I., Schally, G., Szemethy, L., & Csányi, S. (2016). Spatial and temporal characteristics of the damage caused by wild ungulates in maize (*Zea mays* L.) crops. *International Journal of Pest Management*, *63*(1), 92–100.

Bleier, N., Lehoczki, R., Újváry, D., Szemethy, L., & Csányi, S. (2012). Relationships between wild ungulates density and crop damage in Hungary. *Acta Theriologica*, *57*(4), 351–359.

Blumstein, D. T., & Daniel, J. C. (2002). Isolation from mammalian predators differentially affects two congeners. *Behavioral Ecology*, *13*(5), 657–663.

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. *European Journal of Wildlife Research*, *59*(2), 185–193.

Brown, J. S., Laundré, J. W., & Gurung, M. (1999). The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, *80*(2), 385–399. https://doi.org/10.2307/1383287

Cooper, S. M., Owens, M. K., Cooper, R. M., & Ginnett, T. F. (2006). Effect of supplemental feeding on spatial distribution and browse utilization by white-tailed deer in semi-arid rangeland. *Journal of Arid Environments*, *66*(4), 716–726.

Corgatelli, G., Mattiello, S., Colombini, S., & Crovetto, G. M. (2019). Impact of red deer (*Cervus elaphus*) on forage crops in a protected area. *Agricultural Systems*, *169*, 41–48.

Creel, S., Winnie, J., Maxwell, B., Hamlin, K., & Creel, M. (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology*, *86*(12), 3387–3397.

DeVault, T. L., Beasley, J. C., Humberg, L. A., MacGowan, B. J., Retamosa, M. I., & Rhodes, O. E., Jr. (2007). Intrafield patterns of wildlife damage to corn and soybeans in northern Indiana. *Human-Wildlife Conflicts*, *1*(2), 205–213.

Díaz-Yáñez, O., Mola-Yudego, B., & González-Olabarria, J. R. (2017). What variables make a forest stand vulnerable to browsing damage occurrence? *Silva Fennica*, *51*(2), 1693. https://doi.org/10.14214/sf.1693

Dressel, S., Ericsson, G., & Sandström, C. (2018). Mapping social-ecological systems to understand the challenges underlying wildlife management. *Environmental Science & Policy*, *84*, 105–112.

Eriksson, L., Kettaneh-Wold, N., & Trygg, J. (2006). *Multi- and megavariate data analysis. Part I: Basic principles and Applications* (Vol. *425*). Umetrics.

Evans, R. A., & Love, R. M. (1957). The step-point method of sampling—A practical tool in range research. *Rangeland Ecology & Management/Journal of Range Management Archives*, *10*(5), 208–212.

Felton, A., Petersson, L., Nilsson, O., Witzell, J., Cleary, M., Felton, A. M., Bjorkman, C., Sang, A. O., Jonsell, M., Holmstrom, E., Nilsson, U., Ronnberg, J., Kalen, C., & Lindbladh, M. (2020). The tree species matters: Biodiversity and ecosystem service implications of replacing scots pine production stands with Norway spruce. *Ambio*, *49*(5), 1035–1049.

Felton, A. M., Hedwall, P.-O., Felton, A., Widemo, F., Wallgren, M., Holmström, E., Löfmarck, E., Malmsten, J., & Karine Wam, H. (2022). Forage availability, supplementary feed and ungulate density: Associations with ungulate damage in pine production forests. *Forest Ecology and Management*, *513*, 120187. https://doi.org/10.1016/j.foreco.2022.120187

Felton, A. M., Wam, H. K., Felton, A., Simpson, S. J., Stolter, C., Hedwall, P. O., Malmsten, J., Eriksson, T., Tigabo, M., & Raubenheimer, D. (2021). Macronutrient balancing in free-ranging populations of moose. *Ecology and Evolution*, *11*(16), 11223–11240.

Ferretti, F., & Lovari, S. (2014). Introducing aliens: Problems associated with invasive exotics. In R. Putman & M. Apollonio (Eds.), *Behaviour and management of European ungulates* (pp. 78–109). Whittles Publishing.

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019). Landscapes of fear: Spatial patterns of risk perception and response. *Trends in Ecology & Evolution*, *34*(4), 355–368.

Geisser, H., & Reyer, H. U. (2004). Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. *Journal of Wildlife Management*, *68*(4), 939–946.

Gordon, I. J., Hester, A. J., & Festa-Bianchet, M. (2004). The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology*, *41*(6), 1021–1031. https://doi.org/10.1111/j.0021-8901.2004.00985.x

Greenwood, J. J. D., & Elton, R. A. (1979). Analyzing experiments on frequency-dependent selection by predators. *Journal of Animal Ecology*, *48*(3), 721–737.

Gundersen, H., Andreassen, H. P., & Storaas, T. S. (2004). Supplemental feeding of migratory moose *Alces alces*: Forest damage at two spatial scales. *Wildlife Biology*, *10*(3), 213–223.

Herfindal, I., Tremblay, J.-P., Hester, A. J., Lande, U. S., & Wam, H. K. (2015). Associational relationships at multiple spatial scales affect forest damage by moose. *Forest Ecology and Management*, *348*, 97–107.

Jarnemo, A., Minderman, J., Bunnefeld, N., Zidar, J., & Månsson, J. (2014). Managing landscapes for multiple objectives: Alternative forage can reduce the conflict between deer and forestry. *Ecosphere*, *5*(8), 1–14. https://doi.org/10.1890/ES14-00106.1

Jordbruksverket. (2020a). Jordbruksmarkens användning (2020). Slutlig statistik. JO0104.

Jordbruksverket. (2020b). Jordbruksmarkens användning (2020). Sveriges officiella statistik. JO10SM 2011.

Jordbruksverket. (2020c). Skörd av spannmål, trindsäd, oljevaäxter, potatis och slåttervall. (2020). Slutlig statistik. JO0601. https://statistik.sjv.se/PXWeb/pxweb/sv/Jordbruksverkets%20statistikdatabas/Jordbruksverkets%20statistikdatabas__Skordar/JO0601J01.px/

Kupferschmid, A. D., Bütikofer, L., Hothorn, T., Schwyzer, A., & Brang, P. (2020). Ungulate species and abundance as well as environmental factors determine the probability of terminal shoot browsing on temperate Forest trees. *Forests*, *11*(7), 764.

Lam, T. Y., & Maguire, D. A. (2012). Structural equation modeling: Theory and applications in forest management. *International Journal of Forestry Research*, *2012*, 1–16.

Länsstyrelserna. (2021). Statistik älgdata. https://algdata-apps.lansstyrelsen.se/algdata-apps-stat

Laundré, J. W., Hernández, L., & Ripple, W. J. (2010). The landscape of fear: Ecological implications of being afraid. *The Open Ecology Journal*, *3*(1), 1–7.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation—A review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640. https://doi.org/10.1139/z90-092

Linnell, J. D. C., Cretois, B., Nilsen, E. B., Rolandsen, C. M., Solberg, E. J., Veiberg, V., Kaczensky, P., Van Moorter, B., Panzacchi, M., Rauset, G. R., & Kaltenborn, B. (2020). The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene. *Biological Conservation*, *244*, 108500.

Lodin, I., Brukas, V., & Wallin, I. (2017). Spruce or not? Contextual and attitudinal drivers behind the choice of tree species in southern Sweden. *Forest Policy and Economics*, *83*, 191–198.

Månsson, J. (2009). Environmental variation and moose *Alces alces* density as determinants of spatio-temporal heterogeneity in browsing. *Ecography*, *32*(4), 601–612.

Mateos-Aparicio, G. (2011). Partial least squares (PLS) methods: Origins, evolution, and application to social sciences. *Communications in Statistics—Theory and Methods*, *40*(13), 2305–2317.

Menichetti, L., Touzot, L., Elofsson, K., Hyvonen, R., Katterer, T., & Kjellander, P. (2019). Interactions between a population of fallow deer (*Dama dama*), humans and crops in a managed composite temperate landscape in southern Sweden: Conflict or opportunity? *PLoS ONE*, *14*(4), e0215594. https://doi.org/10.1371/journal.pone.0215594

Muff, S., Nilsen, E. B., O'Hara, R. B., & Nater, C. R. (2022). Rewriting results sections in the language of evidence. *Trends in Ecology & Evolution*, *37*(3), 203–210.

Naughton-Treves, L. (1998). Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. *Conservation Biology*, *12*(1), 156–168.

Nkurunziza, L., Watson, C. A., Oborn, I., Smith, H. G., Bergkvist, G., & Bengtsson, J. (2020). Socio-ecological factors determine crop performance in agricultural systems. *Scientific Reports*, *10*(1), 4232.

Pęksa, Ł., & Ciach, M. (2018). Daytime activity budget of an alpine ungulate (Tatra chamois *Rupicapra rupicapra tatrica*): Influence of herd size, sex, weather and human disturbance. *Mammal Research*, *63*(4), 443–453.

Pfeffer, S. E., Singh, N. J., Cromsigt, J. P. G. M., Kalén, C., & Widemo, F. (2021). Predictors of browsing damage on commercial forests—A study linking nationwide management data. *Forest Ecology and Management*, *479*, 118597.

Presley, S. J., Cisneros, L. M., Klingbeil, B. T., & Willig, M. R. (2019). Landscape ecology of mammals. *Journal of Mammalogy*, *100*(3), 1044–1068.

QGIS Development Team. (2021). *QGIS Geographic Information System*. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

Ravenelle, J., & Nyhus, P. J. (2017). Global patterns and trends in human-wildlife conflict compensation. *Conservation Biology*, *31*(6), 1247–1256. https://doi.org/10.1111/cobi.12948

Reimoser, F., & Putman, R. (2011). Impacts of wild ungulates on vegetation: Costs and benefits. In R. Putman, M. Apollonio, & R. Andersen (Eds.), *Ungulate Management in Europe—Problems and practices* (pp. 144–191). Cambridge University Press.

Retamosa, M. I., Humberg, L. A., Beasley, J. C., & Rhodes, O. E., Jr. (2008). Modeling wildlife damage to crops in northern Indiana. *Human-Wildlife Conflicts*, *2*(2), 225–239.

Ringle, C. M., Wende, S., & Becker, J. M. (2015). *SmartPLS 3*. SmartPLS GmbH. http://www.smartpls.com

Searle, K. R., Hobbs, N. T., & Gordon, I. J. (2007). It's the 'foodscape', not the landscape: Using foraging behavior to make functional assessments of landscape condition. *Israel Journal of Ecology and Evolution*, *53*(3–4), 297–316.

Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E., & Swift, D. M. (1987). Large herbivore foraging and ecological hierarchies. *BioScience*, *37*(11), 789–799.

Setsaas, T., Hunninck, L., Jackson, C. R., May, R., & Røskaft, E. (2018). The impacts of human disturbances on the behaviour and population structure of impala (*Aepyceros melampus*) in the Serengeti ecosystem, Tanzania. *Global Ecology and Conservation*, *16*, e00467.

Smith, B. L. (2001). Winter feeding of elk in western North America. *Journal of Wildlife Management*, *65*(2), 173–190.

Spitzer, R., Churski, M., Felton, A., Heurich, M., Kuijper, D. P., Landman, M., Rodriguez, E., Singh, N. J., Taberlet, P., & van Beeck Calkoen, S. T. (2019). Doubting dung: eDNA reveals high rates of misidentification in diverse European ungulate communities. *European Journal of Wildlife Research*, *65*, 1–14. https://doi.org/10.1007/s10344-019-1264-8

Spitzer, R., Coissac, E., Felton, A., Fohringer, C., Juvany, L., Landman, M., Singh, N. J., Taberlet, P., Widemo, F., & Cromsigt, J. P. G. M. (2021). Small shrubs with large importance? Smaller deer may increase the moose-forestry conflict through feeding competition over *Vaccinium* shrubs in the field layer. *Forest Ecology and Management*, *480*, 118768.

Spitzer, R., Felton, A., Landman, M., Singh, N. J., Widemo, F., & Cromsigt, J. P. G. M. (2020). Fifty years of European ungulate dietary studies: A synthesis. *Oikos*, *129*(11), 1668–1680.

Statens Offentliga Utredningar. (2014). Vildsvin och viltskador—om utfodring, kameraövervakning och arrendatorers jakträtt. *SOU*, *2014*, 54.

Svenska Jägareförbundet. (2021). Viltdata. https://rapport.viltdata.se/statistik/

Swedish Meteorological and Hydrological Institute (SMHI). (2021). Månads-, årstids- och årskartor. https://www.smhi.se/data/meteorologi/kartor

Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., Niemann, S. M., & Slotow, R. (2011). Minimizing predation risk in a landscape of multiple predators: Effects on the spatial distribution of African ungulates. *Ecology*, *92*(2), 398–407.

Thulin, C.-G., Malmsten, J., & Ericsson, G. (2015). Opportunities and challenges with growing wildlife populations and zoonotic diseases in Sweden. *European Journal of Wildlife Research*, *61*(5), 649–656.

van Beest, F. M., Gundersen, H., Mathisen, K. M., Milner, J. M., & Skarpe, C. (2010). Long-term browsing impact around diversionary feeding stations for moose in Southern Norway. *Forest Ecology and Management*, *259*(10), 1900–1911. https://doi.org/10.1016/j.foreco.2010.02.002

Vinzi, V. E., Chin, W. W., Henseler, J., & Wang, H. (2010). *Handbook on partial least squares: Concepts, methods and applications*. Springer.

Vistnes, I., & Nellemann, C. (2007). The matter of spatial and temporal scales: A review of reindeer and caribou response to human activity. *Polar Biology*, *31*(4), 399–407.

Widemo, F., Elmhagen, B., & Liljebäck, N. (2019). *Viltets ekosystemtjänster—en kunskapssammanställning*. Rapport 6889. Naturvårdsverket.

Widén, A., Cromsigt, J. P. G. M., Dressel, S., Felton, A., Singh, N. J., & Widemo, F. (2023). Data from: Direct and indirect effects of food, fear and management on crop damage by ungulates. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.nk98sf7xw

Zanette, L. Y., & Clinchy, M. (2020). Ecology and neurobiology of fear in free-living wildlife. *Annual Review of Ecology, Evolution, and Systematics*, *51*(1), 297–318.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Parameter estimates (est), standard deviations (STDEV), *T*, *p* values and F2 values, and 97.5% confidence interval of path analysis model, showing direct effects, specific indirect effects, total indirect effects and total effects. *p*-values showing strong evidence of effect ($p = 0.01–0.001$) are marked in orange and *p*-values showing moderate evidence of effect ($p = 0.05–0.01$) according to Muff et al. (2022), are marked in blue.

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