

RESEARCH ARTICLE

Forest disturbances increase the body mass of two contrasting ungulates

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Abstract

1. As climate change intensifies and demand for timber rises, forest disturbances are increasing. Disturbances in forests cause an abrupt loss in canopy cover and increase resource availability on the ground, which can have manifold effects on the habitat quality of forest-dwelling species. One pathway through which disturbances influence habitat quality is by creating edges within forests. Disturbance-created edges differ from edges to other land cover types in that they are transient, that is, they persist only for a limited period of time until canopy closes again. While the effects of permanent edges are well-studied in ecology, the role of transient edges remains largely unclear.
2. Here, we investigated whether edges caused by forest disturbances affect the individual fitness of two contrasting ungulates by examining the body mass of 378,602 roe deer (*Capreolus capreolus*) and Alpine chamois (*Rupicapra rupicapra*) yearlings collected between 1992 and 2019 in the Eastern Alps.
3. Transient edges had a significant positive effect on the body mass of both species. The effect size was larger for chamois than for roe deer, with yearling body mass increasing by up to 0.18 kg in female chamois for each 10 m ha⁻¹ increase in edge density. Elevation modulated the effect of edges on chamois body mass, with a weaker effect of transient edges in high-elevation forests that are naturally more open. The effect duration of transient edges was longer for roe deer than for chamois, lasting for up to 9 years post-disturbance.
4. The body mass effect of transient edges created by forest disturbances was an order of magnitude stronger than the effect of permanent edges between forests and other land cover types.
5. *Synthesis and applications:* Increasing forest disturbances under climate change could improve the fitness of ungulates, potentially affecting forest recovery through browsing. Managers and hunting authorities should consider the effect of disturbances and dynamically changing carrying capacity of forest landscapes more explicitly when making decisions regarding habitat management and hunting policies. Such a dynamic perspective is an important element in balancing vital ungulate populations and healthy forest ecosystems.

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KEYWORDS

chamois, edge effect, forest disturbances, roe deer, transient edges, ungulate

1 | INTRODUCTION

Forest disturbances have increased globally over the past decades (McDowell et al., 2020). In Europe, for instance, canopy disturbance rates have nearly doubled since 1986 (Senf et al., 2018, 2021), with accelerating dynamics in the past years (Senf & Seidl, 2021b). The main drivers of increasing canopy disturbance in Europe are growing utilization of timber (Palahí et al., 2021), but also increasing natural disturbances caused by large-scale storm events, bark beetle outbreaks and drought (Senf & Seidl, 2021b, 2021c). Ongoing climate change and increasing demand for timber are expected to further increase forest disturbances in the future (Anderegg et al., 2020; Seidl et al., 2017), with substantial consequences for future forest composition and structure (McDowell et al., 2020; Senf et al., 2021). Changing forest disturbance regimes can alter landscape structure, for example, changing forest configuration through increasing edge densities (i.e. the total length of forest edges per forest area) and changing the prevalence of early seral forests on the landscape.

Changing forest disturbances have important impacts on forest-dwelling species, which amount to more than 75% of the world's known terrestrial species and 68% of all mammals (FAO, 2020). Disturbances result in an abrupt change in habitat conditions by opening the canopy, increasing incoming solar radiation, changing the microclimate, releasing nutrients and promoting understory plants and tree regeneration (Oeser et al., 2021; Thom et al., 2020). As a consequence, various species benefit from disturbance-induced changes in forest habitats (Beudert et al., 2015; Hilmers et al., 2018), including focal species of conservation, such as hazel grouse (*Tetrastes bonasia*) and capercaillie (*Tetrao urogallus*) (Kortmann et al., 2018); and species of relevance for wildlife management, such as red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) (Oeser et al., 2021). While positive responses of insect taxa to disturbances are frequently reported in the literature and are explained by increased amounts of deadwood and higher temperatures (Seibold et al., 2016), the mechanistic understanding of disturbance effects on other taxa remains incomplete. This is particularly the case for large and mobile taxa, such as ungulates, that can dynamically modify their habitat use in response to disturbances and thus adapt to increasing disturbances at the landscape scale (Reimoser & Gossow, 1996).

One pathway through which disturbances influence habitat is by creating edges within forests. Edge effects—first defined by Odum (1958)—describe the consequence of edges between adjacent ecological systems on communities and populations (Fonseca & Joner, 2007). Edge effects have been studied extensively in ecology (Harris, 1988; Patton, 1975; Porensky & Young, 2013), highlighting that edges provide high-quality habitat for a number of ungulate species in temperate forests (Miyashita et al., 2008).

The preferred use of edges by ungulates may result from abundant and high-quality forage at the edge (DeCalesta, 1997), but could also be the effect of the close proximity of feeding areas (i.e. open land) and shelter (i.e. closed canopy forests), as observed, for example, for forest gaps (Kuijper et al., 2009; Tahtinen et al., 2014). Forest edges and the canopy gaps that create them may thus play a crucial role in ungulate browsing by offering favourable habitat conditions and increased forage availability through enhanced light and nutrient availability, promoting the growth of understory vegetation (Kuijper et al., 2009). For roe deer, Lovari et al. (2017), for instance, showed that home-range size decreases with increasing edge density, possibly because animals can optimize the cost-benefit trade-off between food and cover around edges. Besides movement patterns, edges also affect vital rates and key life-history traits, such as fecundity (e.g. in sika deer *Cervus nippon*: Miyashita et al., 2008 and roe deer: Zini et al., 2019) and body mass of ungulates (Ofstad et al., 2016). Body mass serves as a reliable indicator of individual fitness in ungulate species, such as roe deer and chamois (Kjellander et al., 2004; Pettorelli et al., 2002; Reiner et al., 2022). It is a robust proxy for energy reserves and the overall physiological condition of an individual, making it an essential metric in assessing the adaptive capacity, reproductive success, and survival of ungulates (Douhard et al., 2017; Plard et al., 2015; Wilder et al., 2016). Changes in body mass are thus an important indicator of the dynamics and vitality of ungulate populations, informing conservation strategies and management practices.

Previous research on the effect of forest edges on habitat quality has largely focused on edges which persist over long time spans (relative to the life span of the animals). These permanent edges occur between different land cover types, such as between forest and grassland. In contrast to such permanent edges, edges caused by forest disturbances (e.g. windthrow, wildfire, bark beetle outbreaks, tree harvesting) are transient. They exist only for a few years to decades as disturbed sites recover and canopy gaps close again. Consequently, we hereafter referred to them as *transient edges*, in contrast to *permanent edges* (cf. Pöppel & Seidl, 2021). In Europe, forests recover to closed canopy conditions within 30 years on average (Senf & Seidl, 2022), but the rate of canopy closure and, thus, the disappearance of a transient edge varies widely across environmental and management conditions (Senf et al., 2019). With increasing forest disturbances, transient edges will become more prevalent in the forests of the future. In addition, disturbance-created edges could become more persistent in the future if the potential of forests to recover from disturbance decreases as a result of climate change (Albrich et al., 2020; Turner et al., 2019, 2022). A better understanding of the habitat effects of transient edges, such as how they affect ungulate species, is thus needed.

Roe deer is the most widespread ungulate species in Europe and is frequently the subject of wildlife management to reduce browsing damage (Hothorn & Müller, 2010; Kupferschmid et al., 2020). Roe deer is a territorial, forest-dwelling ungulate (Lovari & San José, 1997; Putman, 1988) with a small home-range size (<50 ha; Lovari et al., 2017; Saïd et al., 2009; Tufto et al., 1996) and similar habitat selection in both sexes (Morellet et al., 2011). It colonizes a variety of forested habitats, from coniferous forests to Mediterranean “macchia” shrublands as well as agricultural areas with only scattered forest patches (Cibien et al., 1989; Lovari et al., 2017; Morellet et al., 2011). Roe deer are browsers and prefer to feed on woody, herbaceous and arboreal plants up to a height of 120 cm above-ground (Duncan et al., 1998; Lovari et al., 2017). Its physical characteristics, including its small body size (18–28 kg; Putman, 1988) and body shape, make it well-suited for moving through densely vegetated areas, such as recently disturbed sites with thick underbrush (Hansson, 1994).

Alpine chamois (*Rupicapra rupicapra rupicapra*) is the most abundant mountain ungulate of the European Alps (Corlatti et al., 2011). It is managed to reduce browsing in some regions (Kupferschmid et al., 2020), but there are also concerns regarding negative impacts of climate change on its populations (Mason et al., 2014; Reiner et al., 2021; Rughetti & Festa-Bianchet, 2012). The Alpine chamois is a relatively plastic species in its habitat choice; it can be found in Alpine areas above the tree line as well as in subalpine and montane forests (Reiner et al., 2021). Home-range sizes of Alpine chamois are larger than those of roe deer and show large variability (ranging from less than 100 ha to more than 650 ha; Boschi & Nievergelt, 2003; Lovari et al., 2006; von Hardenberg et al., 2000). The diet of Alpine chamois mainly consists of graminoids (Poaceae and Cyperaceae), herbs, sedges, and woody plants (Anderwald et al., 2016). In contrast to roe deer, female chamois are not territorial, and territoriality in males is less pronounced than in roe deer (Corlatti et al., 2015; Ferrari et al., 1988; Reiner et al., 2022).

Here our objective was to understand how transient edges originating from forest disturbances affect roe deer and Alpine chamois, with a specific focus on individual fitness as expressed by body mass. We first hypothesized that body mass increases with increasing transient edge density, as edges provide high-quality habitat for ungulate species. Second, we expected the effect of transient edges to differ between sexes because of the different competitive behaviour of female and male individuals for high-quality habitats (Coulon et al., 2006; Greenwood, 1980). Third, we hypothesized the effect of transient edges to vary unimodally with time since disturbance, with a peak a few years after disturbance (i.e. when forest floor vegetation has adapted to the newly available resources) and a subsequent decrease as regenerating trees increasingly outcompete other plants and the canopy closes again. Fourth, we expected the effect of transient edges to decrease with elevation because high-elevation forests (i.e. subalpine forests close to the tree line) generally have more open structures (i.e. more permanent edges) than lowland forests (i.e. montane and sub-montane forests), reducing the importance of transient openings in the canopy for the fitness of

ungulates. We tested our hypotheses on a dataset of 378,602 individuals of roe deer and Alpine chamois. All individuals were 1 year of age, which represents the life stage in which both species are most affected by environmental conditions (Reiner et al., 2021; Rughetti & Festa-Bianchet, 2012; Willisich et al., 2013), and hence where the strongest effects of transient edges on body mass can be expected.

2 | MATERIALS AND METHODS

2.1 | Study area

This study did not require ethical approval, and permits to carry out fieldwork were not needed. Our work was conducted in the Eastern Alps, with the study area (20,700 km²) covering about 90% of the Austrian federal provinces of Salzburg and Styria (Figure 1a; approximately 46°38' N–47°50' N, 12°04' E–16°00' E). The study area is characterized by mountainous terrain, with an elevation range from 200 to approx. 3700 m a.s.l. Given our focus on forest edges we excluded all areas above the tree line (approx. 2000 m a.s.l.) from the analysis (Pecher et al., 2011). The study area was subdivided into 3199 hunting areas, that is game management units of at least 1.15 km² in size reflecting ownership structure. The mean size of roe deer hunting areas ($n=3150$) was 5.45 km², and the mean size of chamois hunting areas ($n=1502$) was 6.40 km². In 1453 hunting areas, both chamois and roe deer were hunted. The wide elevation range in our study area results in a large variation of forest communities, with broadleaved-dominated forest types in the submontane elevation belt (i.e. roughly below 750 m a.s.l.), mixed broadleaved-coniferous forest types in the montane elevation belt (between 750 and 1400 m a.s.l.) and conifer forests in the subalpine zone (above 1400 m a.s.l.). The share of forest cover on the total land area in roe deer hunting areas ranged between 2.6% and 100% (median 69%), with values between 3.5% and 100% (median 84%) in chamois hunting areas. While in lower elevations, forest cover is low and open habitats dominate (i.e. a high share of arable land and grassland), forest cover increases in the montane zone and decreases again in the subalpine zone, where high mountain pastures and natural grasslands are more common.

2.2 | Ungulate body mass

To investigate the potential effect of transient edge density on body mass of roe deer and chamois we analysed long-term harvest data of 361,732 yearling roe deer (173,845 female and 187,887 male) and 16,870 yearling chamois (8789 female and 8081 male). The data were collected routinely by local hunting authorities between 1998 and 2019 for roe deer and 1992 and 2019 for chamois. For roe deer yearlings, the hunting season was from May 1 to October 31 for males and until December 31 for females, whereas for chamois the hunting season was from July 16 to December 15 in Salzburg, and from August 1 to December 31 in Styria. In both species, yearlings

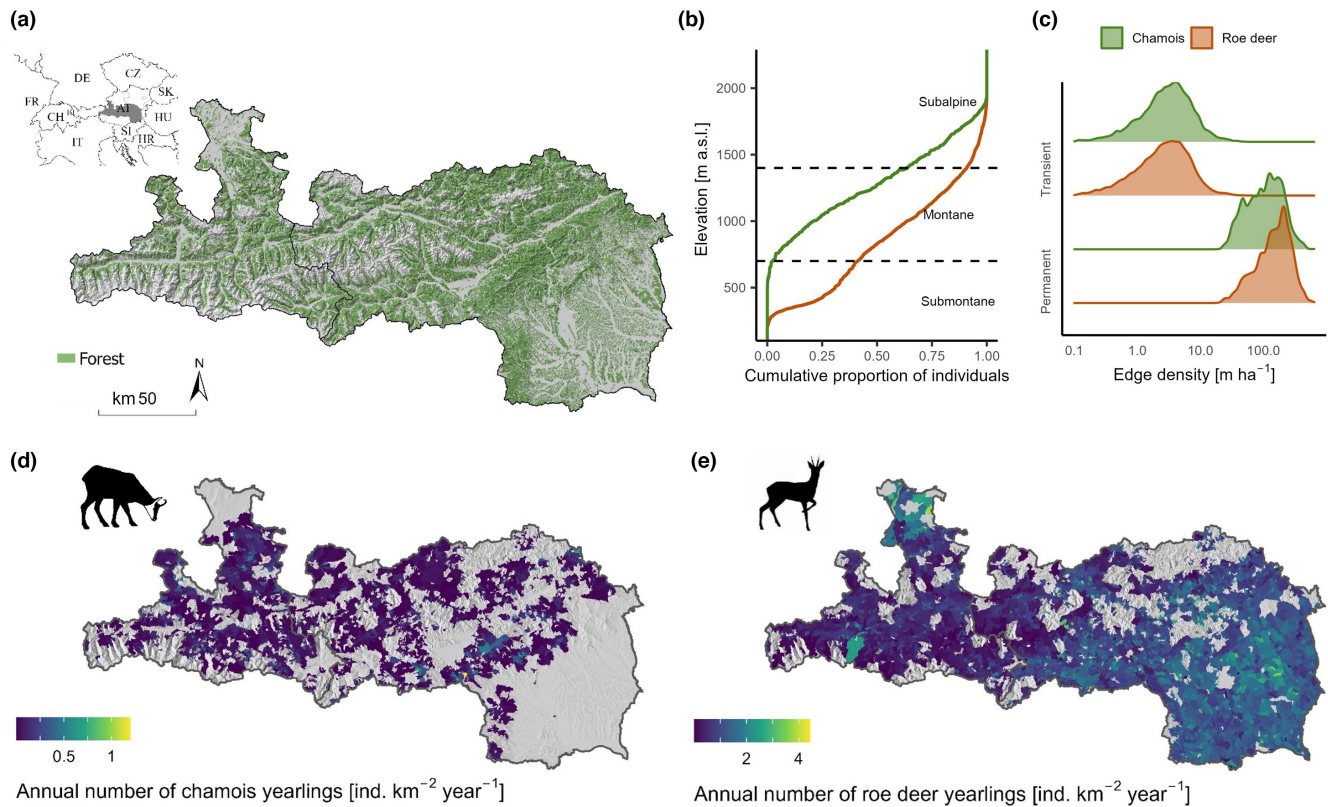


FIGURE 1 Data used to analyse the effect of transient forest edges on the body mass of roe deer and chamois. (a) The study area is in the Austrian federal provinces of Salzburg and Styria, located in the Eastern Alps (small insert). Green areas indicate forest cover. (b) Cumulative elevation distribution of 361,732 roe deer (red line) and 16,870 chamois hunting locations (green line). (c) Distribution of transient and permanent edge densities (note that the x-axis is log-transformed and scaled to the 99th percentile of observed values). Spatial distribution of chamois (d) and roe deer (e) hunting areas, with colours indicating mean annual hunting density (individuals km⁻² year⁻¹). Grey areas indicate hunting areas for which no data were available, or which were excluded due to being situated above the timberline (mean elevation >2000 m a.s.l.).

are hunted based solely on numerical quotas set by hunting authorities and not by physical characteristics. Biometric measurements were taken for all hunted individuals according to provincial hunting regulations (Reiner et al., 2020; Trouwborst & Hackländer, 2018). For each animal shot, body mass (eviscerated, without head, with skin) was recorded with an accuracy of 0.5 kg. Roe deer were classified as yearlings based on dentition, for chamois horn growth annuli were counted to determine age (Schröder & von Elsner-Schack, 1985). The harvest date was converted to Julian day and ranged from days 121 (May 1) to 365 (December 31; days 122–366 in leap years) for roe deer and from days 197 (July 16) to 365 (December 31; days 198–366 in leap years) for chamois.

2.3 | Transient forest edges

Transient edges are here defined as edges from both human and natural forest disturbances that only persist for a limited amount of time until trees have regenerated on the disturbed patch (i.e. there is no change in land use). We here calculated transient forest edges from a spatially explicit forest disturbance map created from satellite data (Senf & Seidl, 2021a). While the full details of the processing

are given in the original publication, we repeat the salient details needed to follow the analyses presented here. The disturbance map is based on annual imagery from the Landsat archive, spanning the period 1986–2020. Pixel-wise spectral trajectories were classified into disturbed/non-disturbed using an extensive reference dataset of manually interpreted spectral trajectories (Senf et al., 2021). The map depicts a loss of the top canopy >50% identifiable by a spectral change at 30 m spatial grain, with the single biggest canopy loss event between 1986 and 2020 being mapped per pixel regardless of its cause (Senf & Seidl, 2022). Any loss of understory trees (i.e. trees not visible by satellite data) or individual tree mortality below a spatial grain of 30 m (i.e. single trees dying from competition) are not considered. The disturbance map used in this study has been validated both at the continental level (Senf & Seidl, 2021a) and locally with a focus on Austria (Sebold et al., 2021), and agreement with both national statistics and observations of forest managers was high. The disturbance map is thus well able to capture the disturbance regimes of our study region.

From the annual disturbance map we identified all edge pixels of a disturbance patch, with disturbance patches defined as groups of neighbouring pixels disturbed in the same year. We used a queen neighbourhood definition to identify neighbouring pixels and

measured the edge length as the outer perimeter of the patch. We summed the number of disturbance-induced edges created per year and hunting area, from which an annual transient edge density was calculated by dividing the length of the edge perimeter per year by the total forest area within each hunting area. In addition to transient edges created by disturbances, we also calculated edge densities for permanent edges, that is, edges between forest and other land cover types that persist over the entire study period (1986–2020). Permanent edge densities were calculated similarly to transient edges.

2.4 | Statistical analysis

The response variable in our analysis was individual body mass, which was adjusted for variation in shooting date by fitting generalized additive models between body mass and Julian date for each species and sex. From these models, body mass was predicted for the mean species-specific shooting date, which was day 301 for chamois (October 28; October 27 in leap years) and day 225 for roe deer (August 13; August 14 in leap years). To account for density-dependent variation in body mass across hunting areas, we used the annual number of individuals harvested relative to the suitable habitat (in km²) in each hunting area as a density index in further analysis (Reiner et al., 2021, 2022). For roe deer, all terrestrial land cover types except artificial areas were defined as suitable habitats, while for chamois, agricultural areas except pastures were also classified as unsuitable.

To analyse the effect of transient edges on ungulate body mass, we fit Gaussian linear mixed models for each species, with body mass as the response variable and population density index, elevation and transient edge density as fixed effect variables. We further added relative forest cover and absolute forest area as covariates, controlling for overall habitat availability and characteristics within each hunting area. To explore whether the effect of transient edges decreases with elevation, we tested for a potential interaction between transient edge density and mean elevation of hunting area for each year after disturbance. Random variation in the intercept and in the effects of population density and transient edge density (i.e. random slopes) were allowed among hunting areas, accounting for random spatial variation in both the intercept and edge density effect. We also added a crossed random intercept among years, allowing for inter-annual variation in average body mass not explained by our data (such as caused by variation in weather conditions). To compare the effect of transient edges on body mass to the effect of permanent edges, we fitted the same model but replaced transient edge density with permanent edge density. The other covariates remained the same, but we removed forest cover because of collinearity with permanent edge density and the random slopes for edge density, as there was no variability in permanent edges over time per hunting area.

To test our specific hypotheses, we fitted the above-described model separately for each year after disturbance (0–10 years) and

derived the strength of the effect of transient edges over time since disturbance. While our harvest data included the exact shooting date of each individual, the occurrence of forest disturbances was only available on a yearly basis (with an error of ± 1 year). Due to this mismatch in temporal resolutions, we did not know if animals were shot before or after a transient edge was created in a certain year. We, therefore, applied a 3-year moving window to each hunting area time series of transient forest edges, considering all transient edges from the year before, during and after the reported age of the edge. For example, the edge density of 1-year-old edges was calculated as the mean edge density of 0-, 1- and 2-year-old edges. This approach was also supported by preliminary analyses showing lower AICc weights of models with 3-year moving windows compared to models considering only edges from a single year. All continuous explanatory variables were centred and scaled prior to analysis, improving model convergence and fostering interpretability of effect sizes and interactions. All models were fit using R 4.1.2 (R Core Team, 2021) and the “lme4” package (Bates et al., 2015). Marginal effects were visualized using the package “ggplot2” (Wickham, 2016). For the linear predictors, we did not include variables with a Pearson correlation coefficient ≥ 0.7 (Dormann et al., 2013) and kept variables with variance inflation factors < 3 to avoid multicollinearity. Normality and homoscedasticity assumptions were checked by inspecting standardized residuals against fitted values (Zuur et al., 2009).

3 | RESULTS

Mean body mass of roe deer was 11.7 ± 1.7 kg (SD) for female and 12.4 ± 1.9 kg for male yearlings. In chamois, mean body mass was 14.6 ± 2.4 kg and 15.3 ± 2.5 kg for female and male yearlings, respectively (Figure S1). For roe deer, the average annual number of yearlings shot was 1.01 ± 0.66 individuals km⁻² and ranged from 0.004 to 4.44 individuals km⁻² (Figure 1e). Mean annual chamois hunting density was 0.10 ± 0.11 yearlings km⁻², ranging between 0.0009 and 1.11 individuals km⁻² (Figure 1d). Due to different habitat preferences of the two species, the mean elevation of hunting locations differed considerably, with 834 ± 405 m a.s.l. for roe deer and 1281 ± 318 m a.s.l. for chamois (Figure 1b). Mean annual transient edge density (considering edges 1–3 years post-disturbance; in the following, referred to as *transient edge density* for simplicity) was 3.44 ± 3.85 m ha⁻¹ and 3.88 ± 4.23 m ha⁻¹ for roe deer (ranging between 0 and 68.4 m ha⁻¹) and chamois hunting areas (ranging between 0 and 51.9 m ha⁻¹), respectively (Figure 1c).

Transient edge density had a significant positive effect on female yearling body mass in both species, while no significant effect was detected for males (Table S1). We hence focus on females only in the following analyses. For roe deer, the positive effect of transient edges lasted up to 9 years post-disturbance (Figure 2a), whereas for chamois transient edges only had an impact in the second and third year after disturbance (Figure 2b). The edge effect on roe deer increased in the initial years after disturbance, with the strongest effect between years four and seven after disturbance, and decreased after that (Figure 2a).

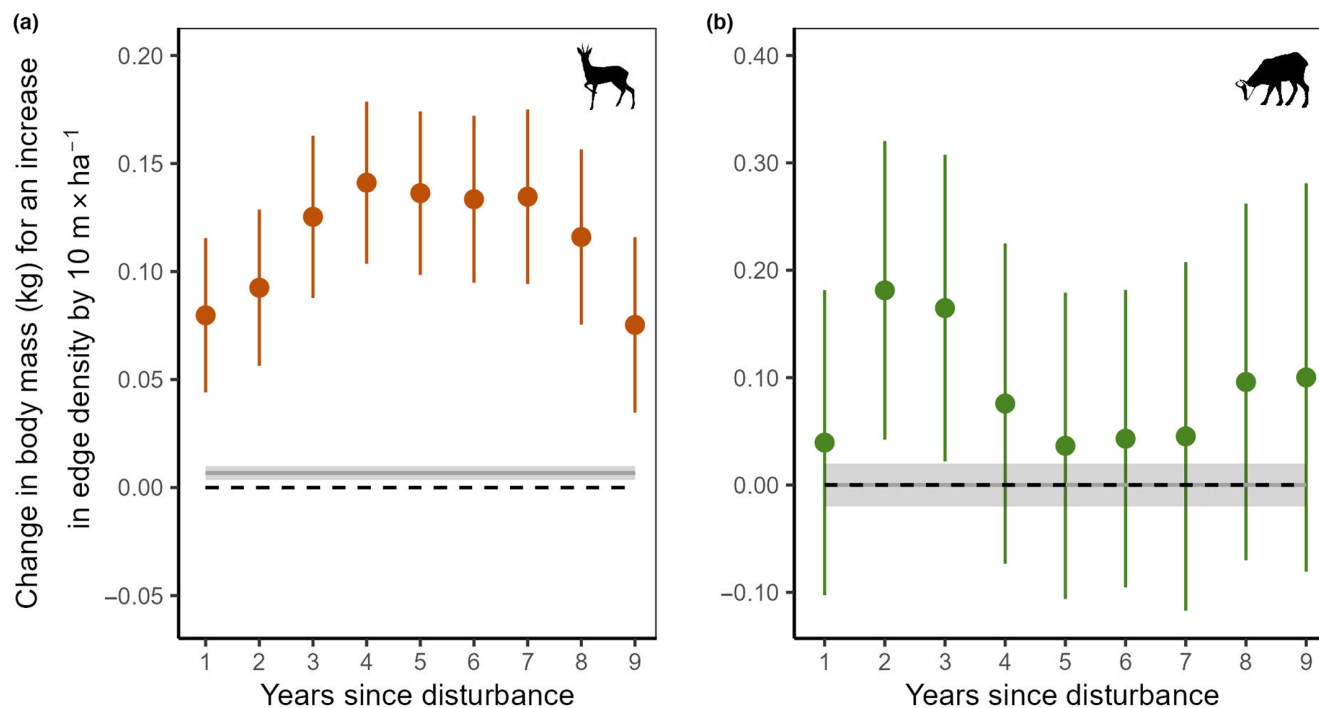


FIGURE 2 The effect of transient (points and whiskers) and permanent (solid grey line) forest edges on the body mass of 1-year-old female roe deer (a) and Alpine chamois (b) harvested between 1992 and 2019. Shown are modelled responses for an increase in edge density by 10 m ha^{-1} , with all other terms of the models kept at their mean values. Values on the x-axis are relevant for transient edges only, as permanent edge effects do not change over time. Dashed lines correspond to zero—no effect. Whiskers and shaded areas indicate 95% confidence intervals.

For chamois, the positive edge effect was strongest in the second year after disturbance and declined thereafter (Figure 2b).

Comparing the effects of transient and permanent edges for roe deer showed that permanent edges had a significant but weaker effect than transient edges for both females and males. In chamois, there was no effect of permanent edges on body mass (Table S1; Figure 2).

To analyse whether the effect of transient edges changes with elevation, we tested for a potential interaction between mean elevation of hunting area and transient edge density. We found no significant interaction between transient edge density and elevation for roe deer, and models considering this interaction showed higher AICc values ($\Delta \geq 5$) compared to models without interaction. We, therefore, present the results for models without interactions between transient edge density and elevation for roe deer in Table S1. In contrast, a significant interaction between transient edge density and elevation up to 4 years post-disturbance indicates that elevation modulates the effect of transient edges for chamois (Table S2; Figure 3b), with a decreasing edge effect with elevation.

4 | DISCUSSION

Based on harvest data from the Eastern Alps we here show that transient edges have a positive effect on the body mass of female

chamois and roe deer, supporting our first and second hypotheses. Edges can promote productivity and cover of understory plants, resulting in a greater diversity of plant species. This can enhance the habitat quality for ungulates, providing them with increased forage availability and quality (Takatsuki, 1989). Even small variation in forage quality can have significant effects on ungulate body mass, as differences in forage quality are multiplied throughout the foraging process (White, 1983). For example, better forage quality reduces the energy required for foraging and digestion, allowing a higher proportion of nutrients per unit of feed to pass through the gut. In combination, these effects can have a substantial effect on the body mass of ungulates (Herfindal et al., 2006; Van Soest, 1994).

While the positive effect of permanent edges on ungulates has been well described in the existing literature (McLoughlin et al., 2007; Miyashita et al., 2008), our results demonstrate that such a positive effect also exists for transient forest edges created by disturbances. In fact, the effect sizes found for transient edges are even higher than those of permanent edges in both species. A possible explanation for this finding is that edges caused by forest disturbances may provide more diverse and higher quality forage compared to edges between forests and other landcover types, which also include landcover types that are less suitable habitat for ungulates (e.g. arable lands and artificial surfaces) (Kuijper et al., 2009; Reimoser & Gossow, 1996). However, the effect of transient edges on ungulate body mass varied by species and sex. The difference in effect size between roe deer and chamois (greater effect for chamois than roe

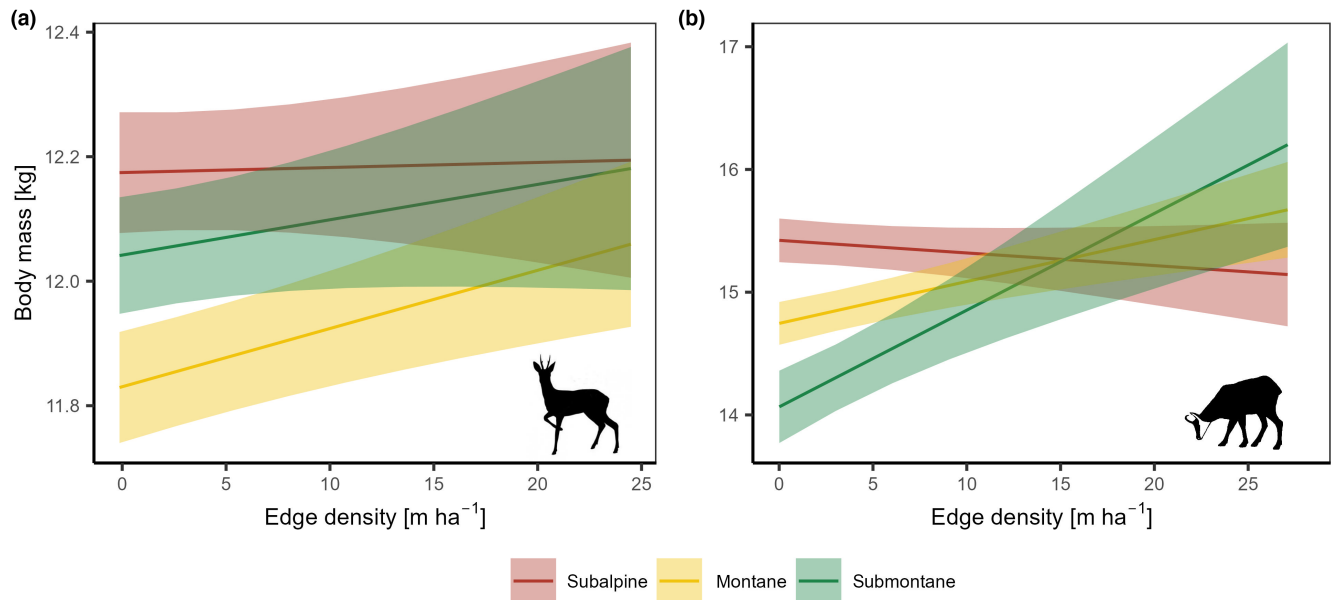


FIGURE 3 Marginal effects of the interaction between transient edge density (2 years after disturbance for roe deer and four for chamois) and elevation on the body mass of 1-year-old roe deer (a) and chamois (b). Three contrasting elevations were predicted to facilitate visualization of the interaction. Colours correspond to the submontane (400 m a.s.l.; green), montane (1000 m a.s.l.; yellow) and subalpine (1600 m a.s.l.; red) zone. Shaded areas indicate 95% confidence intervals (all other terms of the models are kept at their mean values). x-axes are scaled to the 99th percentile of observed edge density values.

deer) may be related to the less pronounced territoriality of chamois (Ferrari et al., 1988; Reiner et al., 2022), as individual transient edges may be utilized by numerous chamois but only by single or few roe deer. The more pronounced territorial behaviour of male roe deer compared to females (Andersen et al., 1998) may also explain the lower effect of transient edge density on male body mass: High-quality habitats (e.g. areas with high edge density) will frequently be occupied by adult males, and male yearlings may therefore not be able to take advantage of these favourable habitats.

While our results provide evidence that transient edges are important habitat features for ungulates, we also show that their effect on body mass changes dynamically over time, which is consistent with our third hypothesis. The most important feature of transient edges compared to permanent ones is that the disturbed areas forming the edge undergo post-disturbance recovery and develop back towards a closed-canopy forest within years to a few decades (Senf & Seidl, 2022). With post-disturbance forest development, the densities of herbaceous and shrubby plants change, thus altering food availability and quality for ungulates. Therefore, our finding of a dynamically changing effect of transient edges on body mass is in line with expectations and mirrors the different habitat preferences of both species. For instance, the strong positive response of chamois body mass to transient edges already 1 or 2 years post-disturbance can be explained by their preference for graminoids (*Poaceae* and *Cyperaceae*) (Anderwald et al., 2020), which emerge immediately after disturbance and disappear with increasing tree and shrub cover. Roe deer, in contrast, are browsers that prefer to feed on woody, herbaceous and arboreal plants up to a height of 120 cm (Duncan et al., 1998), which experience a peak in biomass 3–6 years after a

disturbance (Zehetgruber et al., 2017), but are more persistent as trees recover. Overall, however, the time span during which transient edges have a positive effect on the body mass of roe deer and chamois is much shorter than forest recovery intervals (Senf & Seidl, 2022). While we cannot make conclusive inferences on the reasons for this finding from our data, one factor curtailing the edge effect could be negative density-dependent feedback within the ungulate population: Increasing reproductive rates and population sizes due to improved habitat conditions could increase inter- and intraspecific competition, diminishing the positive effect of transient edges with time (Miyashita et al., 2008; Zini et al., 2019).

Finally, we found support for our fourth hypothesis that the positive effect of transient edges on body mass decreases with increasing elevation, even though this effect was only significant for chamois. The difference between species might be explained by the fact that chamois populations typically inhabit areas with a wide range of elevations and thus can take advantage of different plant phenological developmental stages, which vary strongly along elevational gradients (Geist, 1987; Myrsterud et al., 2001). This advantage in foraging as well as the forest structure in subalpine forests may explain the significant interaction effect between transient edge density and elevation for chamois. The generally lower canopy cover in subalpine forests allows for a higher density of the herb and shrub layer and may have a similar effect on forage quality for chamois like canopy openings after disturbances. In contrast, roe deer are more dependent on forest habitats and occur less frequently in the subalpine zone (Figure 1b). This might be the reason why the interaction between transient edge density and elevation was not significant for roe deer.

While we provide large-scale evidence of a positive effect of transient edges on ungulate body mass, some limitations of our data and study design need to be considered when interpreting our results. First, our data did not include individual-specific coordinates; consequently, our analysis grain is hunting areas. This can lead to a modifiable areal unit problem (Wong, 2004) because there can be a spatial mismatch between the space occupied by individuals and the areas affected by disturbance. We also cannot rule out that some individuals transit from one to another hunting area, increasing the uncertainty in our analyses. Second, the weighting of body mass was done with a precision of only 0.5 kg, which is in the range of our estimated effect sizes. While measurement errors are expected to be random and thus not to bias our results, limited measurement precision is a potential source of uncertainty in our analysis. Finally, the disturbance data used in our analysis is based on satellite images with a spatial grain of 30 m. While being the most detailed large-scale dataset available on forest disturbances in Europe to date, some disturbances might be missing due to omission errors (see Senf & Seidl, 2021a for details). Furthermore, disturbances below the grain of analysis (i.e. individual tree mortality events), disturbances affecting the subcanopy and events of low severity were omitted. Notwithstanding these limitations, the ecological plausibility of our results in combination with the size of our dataset, gives confidence to our findings.

5 | CONCLUSIONS

Edge effects are well-studied in ecology, but most previous studies focused on permanent edges. Here we show that also transient edges created by forest disturbances have a distinct effect on key life-history traits of ungulates. Consequently, managers and hunting authorities should consider the effect of disturbances on habitat quality explicitly, accounting for disturbance-induced changes in carrying capacity when setting hunting quotas. Specifically, our analyses suggest that forested landscapes can sustain higher populations of ungulates in periods that follow episodes of disturbance. Furthermore, our analyses indicate that increasing forest disturbances under climate change (McDowell et al., 2020; Seidl et al., 2017) could generally improve the fitness of roe deer and chamois. However, this increase in fitness could create negative feedback on vegetation development: Intensive herbivory and preferential browsing of individual tree species by ungulates can negatively impact post-disturbance forest development, with long-lasting implications on vegetation composition, structural integrity, and forest resilience (Didion et al., 2009; Kuijper et al., 2009; Reimoser & Gossow, 1996; Seidl & Turner, 2022; Senn et al., 2002). The dynamic interactions between ungulates and post-disturbance forest development should thus be an increasing focus of research and management. We conclude that transient edges, which change dynamically because of climate change and land use, are important habitat features for ungulates and should be considered in management accordingly.

AUTHOR CONTRIBUTIONS

Rudolf Reiner: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Methodology (equal); Validation (equal); Visualization (lead); Writing—original draft preparation (lead); Writing—review and editing (equal). **Rupert Seidl:** Conceptualization (supporting); Methodology (supporting); Validation (supporting); Writing—original draft preparation (supporting); Writing—review and editing (equal). **Sebastian Seibold:** Conceptualization (supporting); Methodology (supporting); Validation (supporting); Writing—original draft preparation (supporting); Writing—review and editing (equal). **Cornelius Senf:** Conceptualization (supporting); Data curation (equal); Formal analysis (equal); Methodology (equal); Validation (equal); Visualization (supporting); Writing—original draft preparation (supporting); Writing—review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Forest disturbance map available via Zenodo <https://doi.org/10.5281/zenodo.3924381> (Senf & Seidl, 2020). Ungulate data available via Figshare <https://doi.org/10.6084/m9.figshare.21981341.v1> (Reiner et al., 2023).

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SUPPORTING INFORMATION

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

Table S1. Set of models to explain the effects of transient and permanent forest edges on body mass of roe deer and chamois yearlings. The table reports the number of observations, the R^2

(Nakagawa pseudo- R^2), the explanatory variables with their beta estimates and 95% confidence intervals (brackets). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. $p > 0.05$.

Table S2. Set of models to explain the effects of transient and permanent forest edges on body mass chamois yearlings. The table reports the number of observations, the R^2 (Nakagawa pseudo- R^2), the explanatory variables with their beta estimates and 95% confidence intervals (brackets). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. $p > 0.05$.

Figure S1. Spatial distribution of roe deer (a, b) and chamois (c, d) hunting areas, with colors indicating mean body mass (kg).

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