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Predator-prey interactions in anthropogenic landscapes

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Abstract

Predator-prey interactions are shaped by several factors, including landscape features and hunting modes of predators. Within anthropogenic landscapes, humans can reshape predator-prey interactions by influencing the density, behaviour and survival of both predators and prey through activities such as hunting, forestry practices and land use. Understanding the role that humans play within ecological communities is becoming increasingly important as large carnivores are recolonizing parts of their historical ranges. In anthropogenic systems, harvest is the main mortality source for many ungulate prey populations, and with the return of large carnivores, ungulates now face mortality risk from multiple sources.

The objectives of this thesis were to: 1) assess the spatial attributes of hunter-killed and wolf (*Canis lupus*)-killed moose (*Alces alces*) during and after the hunting season and determine whether it resulted in contrasting or overlapping spatiotemporal patterns of risk for moose; 2) investigate habitat selection of moose in relation to the spatiotemporal distribution of hunting and wolf predation risk; 3) evaluate moose calf mortality during summer and winter in relation to risk from both humans and large carnivores (wolves and brown bears, [*Ursus arctos]*) and climatic and environmental variables (productivity and snow depth); and 4) assess whether the return of wolves had elicited either density- or behaviourally-mediated trophic cascades involving moose and their main browsing species, Scots pine. In order to do so, the Scandinavian Wolf Research Project (SKANDULV) and GRENSEVILT project obtained the locations of moose killed by hunters and fitted both moose and wolves with Global Positioning System (GPS) collars to search for kill sites and obtain data on moose habitat selection during summer, fall (i.e., the hunting season) and winter (i.e., after the hunting season). Additionally, female moose were approached three times during the year (at birth, at the onset of the hunting season and just before calf dispersal) from the ground to count the number of accompanying calves.

Spatiotemporal patterns of hunting and predation risk correlated to both environmental and anthropogenic features. Hunting risk was highest close to open spaces (e.g., clearcuts and bogs) and roads and in areas with low building density and low terrain ruggedness. Wolf predation risk varied temporally and was highest close to clearcuts/young forests, further away from bogs and in areas of low building density during the hunting season. After the hunting season, wolf predation risk was still highest closer to clearcuts/young forests and in areas of low building

density, but also close to main roads and in more rugged terrain. When comparing the spatial characteristics of hunter-killed and wolf-killed moose, I found contrasting risk patterns from hunters and wolves.

During the hunting season, moose avoided areas of high hunting risk during the day, while their habitat selection was not affected by hunting risk at night. After the hunting season, moose habitat selection was not influenced by hunting risk during the day or at night. Moose selected areas of high wolf predation risk during both day and night during and after the hunting season.

Moose calf mortality in summer varied significantly between years but was not related to predation, climatic or environmental variables. In winter, calf mortality correlated positively to snow depth and clearcuts/young forests in the presence of wolves and increased hunting risk.

Moose presence and abundance and browsing damage were positively correlated to the presence of wolves. Overall, environmental and anthropogenic features were more important in explaining moose presence and browsing damage than wolf presence. Although wolves did not kill moose randomly in the landscape and their presence resulted in a positive correlation between calf mortality and certain landscape features, I did not detect a behavioural response in moose consistent with the avoidance of places and times of higher risk. Consequently, wolves seem to not have elicited either density- or behaviourally-mediated trophic cascades in south-central Scandinavia.

My results indicate that while both hunting and wolf predation risk varied spatiotemporally, moose responded only to the stronger, more predictable mortality source: hunting. During the last century in Scandinavia, hunting has functionally replaced predation by wolves and bears on moose. With the return of wolves, hunters adjusted their harvest quotas on moose to compensate for the additive mortality of wolves. Because moose adjusted their behavioural response to hunting risk, this may indicate that humans might have the potential to trigger both density- and behaviourally-mediated trophic cascades within anthropogenic landscapes. On the other hand, wolves did not elicit behavioural responses in moose consistent with the avoidance of risky places during risky times, nor triggered cascading effects on lower trophic levels. The decreased availability of food resources during winter may force moose to select habitats with greater forage opportunities that are simultaneously coupled with a greater risk of wolf predation (e.g., clearcuts/young forests). Hence, the potential for wolves to initiate trophic cascades might be dampened, or even cancelled, by the need for moose to find optimal foraging places during winter.

Sammendrag

Interaksjoner mellom rovdyr og byttedyr er basert på flere faktorer, inkludert habitat og rovdyrets jaktmodus. Innenfor menneskepåvirkede landskap kan mennesker omforme interaksjoner mellom rovdyr og byttedyr ved å påvirke deres tetthet, atferd og overlevelse gjennom aktiviteter som jakt, skogsbruk og arealbruk. I menneskepåvirkede systemer er jakt den viktigste dødsårsaken for mange byttedyr, men med tilbakekomsten av store rovdyr står nå byttedyr overfor ytterligere dødlighetsrisiko.

Målene med denne oppgaven var å 1) undersøke plasseringen av jegerdrepte og ulvedrepte elg i landskapet under og etter jaktsesongen og vurdere om det resulterte i kontrasterende eller overlappende spatio-temporære risikomønstre for elg; 2) undersøke elgers habitatvalg i forhold til fordelingen av jakt- og ulvpredasjonsrisiko i tid og rom; 3) undersøke dødeligheten til elgkalv sommer og vinter i forhold til risiko fra både mennesker og store rovdyr (ulver og brunbjørn), og klimatiske og miljømessige faktorer (produktivitet og snødybde); og 4) vurdere om ulvens tilbakekomst hadde forårsaket enten tetthets- eller atferdsutløste trofiske kaskader som involverte elg og deres viktigste fødeart, furu. For å gjøre dette har det Skandinaviske ulveforskningsprosjektet (SKANDULV) og GRENSEVILT-prosjektet innhentet lokaliseringer av elg drept av jegere og utstyrt både elg og ulv med Global Positioning System (GPS) halsbånd for å søke etter bytterester og innhente data om elgens habitatvalg om sommeren, høsten (dvs. jaktsesongen) og vinteren (dvs. etter jaktsesongen). I tillegg ble merkede elgkuer oppsøkt til fots i felt tre ganger i løpet av året (ved fødsel, ved starten av jaktsesongen og like før kalvenes spredning om vårenkalvespredning) for å telle antall kalver.

Spatiotemporale Den romlige og tidsmessige variasjonen for jakt og predasjonsrisiko var korrelert med ulike naturlige og menneskeskapte faktorer. Jaktrisikoen var høyest nær åpne områder (f.eks. hogstflater og myrer) og veier, samt områder med lav bygningstetthet og liten grad av ulendt terreng. Ulvpredasjonsrisiko varierte tidsmessig og var høyest nær hogstflater/ungskog, lenger unna myr og i områder med lav bygningstetthet i jaktsesongen. Etter jaktsesongen var ulvepredasjonsrisikoen fortsatt høyest nærmere hogstflater/ungskog og i områder med lav bygningstetthet, men også nær hovedveier og i mer ulendt terreng. Når jeg sammenlignet de romlige egenskapene til jeger- og ulvedrept elg, fant jeg motsatte risikomønstre fra jegere og ulv.

I løpet av jaktsesongen unngikk elgen områder med høy jaktrisiko på dagtid, mens habitatvalget deres ble ikke påvirket av jaktrisiko om natten. Etter jaktsesongen ble ikke elgens habitatvalg

påvirket av jaktrisiko verken på dag eller nattestid. Elg valgte områder med høy ulvepredasjonsrisiko både dag og natt under og etter jaktsesongen.

Elgkalvdødeligheten om sommeren varierte betydelig mellom år, men var ikke relatert til verken predasjon fra ulv eller bjørn, klimatiske eller miljømessige variabler. Om vinteren var kalvedødeligheten positivt korrelert til snødybde og flatehogst/ungskog med nærvær av ulv, men også til økt jaktrisiko.

Forekomst og tetthet av elg, samt beiteskader, var positivt korrelert til forekomst av ulv. Samlet sett var miljømessige og menneskeskapte faktorer viktigere for å forklare elgforekomst og beiteskader enn ulveforekomst. Selv om ulv ikke drepte elg tilfeldig i landskapet og at deres tilstedeværelse resulterte i en positiv korrelasjon mellom kalvedødelighet og visse landskapstrekk, oppdaget jeg ingen tegn til at elg unngikk områder eller perioder med høyere risiko. Følgelig ser det ut til at ulver ikke har fremkalt verken tetthets- eller atferdsutløste trofiske kaskader i det sør-sentrale Skandinavia.

Resultatene mine tilsier at mens både jakt- og predasjonsrisiko varierte i tid og rom, responderte elg bare på jakt, som utgjør en større, men også mer forutsigbar risiko enn ulv. I løpet av det siste århundret har menneskers jakttradisjon på den Skandinaviske halvøy funksjonelt erstattet predasjon av ulv og bjørn på elg. Med tilbakekomsten av ulv justerte jegerne sine jaktkvoter på elg for å kompensere for den additive dødeligheten fra ulv. Elgens atferdsjustering på jaktrisiko kan tilsi at mennesker kan forårsake både tetthets- og atferdsutløste trofiske kaskader i menneskeskapte landskap. Ulver fremkalte derimot ikke atferdsresponser hos elg, som tilsier at elgen unngår risikofylte steder i risikofylte tider, og utløste heller ikke kaskadeeffekter på lavere trofiske nivåer. Den reduserte tilgjengeligheten av matressurser om vinteren kan tvinge elgen til å velge habitater med bedre næringstilgang som samtidig er kombinert med en større risiko for ulvepredasjon (f.eks. flatehogst/ungskog). Derfor kan ulvens potensiale til å sette i gang trofiske kaskader bli dempet, eller til og med kansellert, av elgens behov for næringstilgang om vinteren.

Preface

I am deeply indebted to Barbara Zimmermann, my main supervisor, for giving me the chance to work with a topic that is not only incredibly engaging, but also challenging and where, most likely, we will never truly understand all the mechanisms and processes at play. But that is exactly what makes it so fun! Thank you, Babs, for all the hours spent mumbling ideas, working in the field, explaining me statistics, making me laugh, trying to get me to speak Swiss German and all your amazing Norwegian-words-that-in-Swedish-mean-something-completely-different (Quidditch is really not child-friendly in Norway, Babs!). Thank you for always being happy, warm and welcoming - it is not random that Kristoffer and I call you our "wolf mum".

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Table of content

List of papers

This thesis is based on the following publications and manuscripts:

Paper I

Ausilio, G., Wikenros, C., Sand, H., Wabakken, P., Eriksen, A. and Zimmermann, B. (2022) Environmental and anthropogenic features mediate risk from human hunters and wolves for moose. *Ecosphere (in print).*

Paper II

Ausilio, G., Wikenros, C., Sand, H., Devineau, O., Wabakken, P., Eriksen, A., Aronsson, M., Persson, J., Mathisen, K.M., Zimmermann, B. Contrasting risk patterns from humans and wolves influence habitat selection of moose. *Manuscript.*

Paper III

Ausilio, G., Sand, H., Aronsson, M., Wikenros, C., Milleret, C., Nordli, K., Wabakken, P., Eriksen, A., Maartmann, E., Persson, J., Zimmermann, B. Effects of large carnivores, hunter harvest, and climate on the mortality of moose calves in a partially migratory population. *Manuscript.*

Paper IV

Ausilio, G., Sand, H., Månsson, J., Mathisen, KM. and Wikenros, C. (2021) Ecological effects of wolves in anthropogenic landscapes: the potential for trophic cascades is context-dependent. *Frontiers in Ecology and Evolution* 8, 577963.

1. Introduction: Predator-prey interactions

Predators are broadly defined as individuals of one species that consume a significant portion of the biomass of individuals belonging to another species (Krebs, 2000). Consequently, a prey is an individual of one species that an individual of another species consumes. While predation in the broad sense includes both herbivory and carnivory, I will in the following text use the term to define the real type of predation where animals kill other animals to consume them (Abrams, 2000). How predators and prey interact with each other is a focal subject in animal population ecology, since predator-prey interactions can shape the distribution, space use and habitat selection of animals, making them crucial drivers of ecosystem dynamics (Bonsall and Hassell, 2007). Investigating how predator and prey influence and respond to each other is a key pre-requisite to understand predator-prey interactions in ecological communities and whether these interactions extend and propagate to other trophic levels within an ecosystem.

Predators need the ability to effectively search and kill prey, whereas prey need the ability to avoid being killed by predators (Abrams, 2000). In order to do so, predators and prey have developed a vast array of specific traits to increase the chances of a successful attack and survive these attacks, respectively (Abrams, 2000). However, since prey have more to lose in the event of an attack from a predator (i.e., losing their lives) than a predator doing an unsuccessful attack (i.e., losing a meal), the behavioural traits of prey species are often subjected to a stronger selective pressure (Dawkins and Krebs 1979). Predator-prey interactions are also shaped by the costs and benefits associated with how predator and prey respond to each other (Sih, 2005). Frequency of encounter and population density are two key factors in determining costs and benefits associated with behavioural responses (Gehr, 2016). For instance, if a prey only encounters predators on rare occasions, the costs associated with displaying anti-predator responses continuously will likely outweigh the benefits of doing so, since the energy allocated to these behaviours often come at the cost of growth and reproduction (Boonstra et al., 1998; Cherry et al., 2016). As a result, prey species are often faced with the trade-off between foraging opportunities and anti-predator behaviours (Creel et al., 2005; Hebblewhite and Merrill, 2009).

1.2 Predation risk

Predators can have significant effects on the ecological communities they inhabit (Estes et al., 2011; Ripple et al., 2014). Because of this, it is important to define what predation risk represents in the context of predator-prey interactions. Broadly, the risk of predation is described as the probability for an individual of being killed by a predator per unit time (Lima and Dill, 1990; sensu Holling, 1959):

$$P(death) = 1 - e^{(-\alpha d T)}$$

Where α is the rate of encounter between predator and prey, d is the probability of death given an encounter, and T is the proportion of time spent being vulnerable to an encounter. Each of these risk components is influenced by other factors, for instance encounter rate is moderated by habitat structure, predator density and movement behaviour, whereas time spent vulnerable is dependent on the activity patterns of both predator and prey (Lima and Dill, 1990). Measuring all the above-mentioned risk components is difficult, which is why many studies use only one of these components (instead of all three) as a proxy for predation risk (however, see Hebblewhite et al., 2005). For example, some quantify predation risk using predator density (Mao et al., 2005; Fortin et al., 2005), or habitat characteristics, (Acebes et al., 2013; Pinard et al., 2012) or the distribution of kills (Kauffmann et al., 2007; Samelius et al., 2013; Lone et al., 2014).

1.3 Anti-predator behaviours

Predators can have direct effects on prey species by killing them (lethal, consumptive effect; (Werner and Peacor 2003; Preisser et al., 2005) but also by inducing behavioral, physiological or morphological changes in prey seeking to avoid predation (non-lethal, non-consumptive effect; (Lima 1998; Werner and Peacor 2003; Fortin et al. 2005; Creel and Christianson 2008), including the development of anti-predator responses, such as changes in habitat selection (Fortin et al., 2005) and activity patterns (Hudgens and Garcelon, 2011; Tambling et al., 2015)

However, anti-predator behaviours often carry costs that can result in additional physiological stress or foraging deficit for prey (Morgantini and Hudson, 1985), hence affecting growth (Pangle et al., 2007) and reproduction (Boonstra et al., 1998; Cherry et al., 2016). Therefore, costly anti-predator behaviours need to be traded off with the current level of predation risk experienced by prey (Lima and Dill, 1990).

Predation risk varies in space and time and prey may choose to adopt more pronounced anti-predator adaptations in more risky areas or during periods of higher predation risk (Ripple and

Beschta, 2004). For instance, elk (*Cervus elaphus canadensis*) in Yellowstone National Park have been found to adjust habitat selection temporally by using risky habitats during wolf (*Canis lupus*) activity downtimes (Kohl et al., 2019). The level of perceived risk is also dependent on extrinsic (e.g., group size) and intrinsic (e.g., reproductive status, age) factors that influence anti-predator strategies (Elgar, 1989; Lima and Dill, 1990; Treves, 2000; Frid and Dill, 2002). Reproductive status can shape risk-avoidance strategies, since neonates are often the most vulnerable age class to predation (Adams et al., 1995; Sand et al., 2005), and females with young may face a stronger selection pressure to exhibit anti-predator strategies to reduce predation risk than males or females without young. For instance, female caribous (*Rangifer tarandus*) in mountainous areas were found to give birth at higher elevations to reduce wolf predation, even though these areas entailed reduced access to high-quality forage (Bergerud et al., 1984; Bergerud and Page, 1987).

1.4 Spatiotemporal variation in predation risk

Patterns of predation risk vary in space and over time. Spatial variation in risk is usually the result of the interaction between the hunting mode of a predator (e.g., ambush; Lone et al., (2014) and cursorial; Kaufmann et al., (2007)), the predator's space use and specific habitat features associated with a higher risk of death given an encounter (Gaynor et al., 2021). Different predators use specific hunting modes to optimize predation efficiency (Schmitz, 2005; Preisser et al., 2007), which interact with different habitat domains and anthropogenic features within the landscape (Atwood et al., 2007; Miller et al., 2014; Preisser et al., 2007) For example, ambush predators like lynx (Lynx spp.) are favoured by cover to surprise-attack its prey, whereas cursorial predators like wolves often chase their prey over long distances (Schmidt and Kuijper, 2015). Therefore, prey may perceive a higher risk from lynx and wolf in dense forest cover and in open spaces, respectively.

Temporal variation in risk is also a function of predator space use and hunting mode interacting with photoperiods (e.g., daylight) (Smith et al., 2019), temperature (Rabaiotti and Woodroffe 2019) and changing environmental variables (e.g., snow cover) that can affect the capture efficiency of the predator (Lima and Dill 1990; Palmer et al. 2022). The concept of temporal variability of predation risk was formalized in the risk allocation hypothesis, which postulates that anti-predator behaviour in prey is a function of both the immediate and background level of predation risk (Lima and Bednekoff, 1999). Following this hypothesis, prey should exhibit the strongest anti-predator response during peaks of risks that occur in an otherwise low-background risk landscape (e.g., the case of rare but dangerous predators) and the weakest behaviour when the risk is not immediate in an otherwise high background risk situation (e.g., predator is locally absent in areas with otherwise high predator densities) (Lima and Bednekoff, 1999; Moll et al., 2016). The risk allocation hypothesis was further developed by Creel et al. (2008), who outlined two alternatives: the risky places hypothesis and the risky times hypothesis. The former stipulates that anti-predator responses vary as a function of the long-term background risk associated with specific habitat features, irrespective of pulses of risk or safety, whereas the latter states that they vary in relation to the presence or absence of the predator (i.e., pulses of risk), irrespective of background risk (Creel et al., 2008; Moll et al., 2016). Ultimately, these two hypotheses are not mutually exclusive since, as the risk allocation hypothesis postulates, prey responses to predators during peaks of high risk should be a function of the perceived long-term background level of risk (Lima and Bednekoff, 1998).

Although both predation risk and anti-predator responses can be predictable in time (Sih et al., 2000; Lima and Bednekoff, 1999; Ferrari et al., 2008; Palmer et al., 2022), few studies have explicitly explored how temporal changes in patterns of spatial risk influence prey responses (Palmer et al., 2022). Palmer et al. (2022) suggest that shifting temporal dynamics may create schedules of fear that generate from species-specific and environmental constraining factors limiting predator activity and prey vulnerability. Because prey might be able to identify spatially and temporally predictable risk co-occurring, they may also respond accordingly to minimize risk and reduce costs associated with anti-predator behaviours (Palmer et al., 2022). For example, a study from Germany found that common voles (*Microtus arvalis*) avoided foraging in un-mowed and mowed grass during the day and night, respectively, most likely as a result of weasels and owls being either more effective at hunting voles in un-mowed grass during the day or in mowed grass at night (Jacob and Brown, 2000). In California, Columbian black-tailed deer (*Odocoileus hemionus columbianus)* adjusted their temporal activity to decrease the risk of encountering human hunters and mountain lions in areas of high risk (Gaynor et al., 2021). These results highlight the importance of including both spatial patterns of risk and temporal variability in theoretical and empirical studies on predation risk and prey behavioural responses (Palmer et al, 2022).

1.5 Multipredator systems

When analysing spatiotemporal variation in predation risk and anti-predator behaviours in prey, the simplest model would include a single predator and prey. However, this is rarely the case as ecosystems are complex and prey are exposed to several predators with differing hunting modes simultaneously, which combined generate a mosaic of risk through which prey needs to move, reproduce, and forage. This may require prey to compromise and adjust antipredator strategies along a shifting gradient of risk depending on the predators present (Kotler et al., 1992; Stapley, 2004) and the strength of the perceived risk from each predator (Clermont et al., 2017).

Prey living in multi-predator systems might need to respond to multiple sources of risk, which are mediated by the physical landscape and combined may result in either overlapping or contrasting risk in both space and time (Lone et al. 2014; Norum et al. 2015; Gaynor et al., 2021). Overlapping risks have similar spatiotemporal patterns and may therefore allow prey to adopt a universal anti-predator strategy to reduce predation risk from multiple predators. Such overlap would likely also increase the frequency of refuge areas within the landscape, where the risk of predation from multiple predators is low. Far more common is when the accumulated effects of multiple predators result in spatially contrasting risk, i.e., multiple predators have different efficiency for killing prey in contrasting habitats (Gaynor et al., 2021; Lone et al. 2014; Norum et al. 2015), which might make refuge areas rare. However, if the risk of predation from multiple predators also contrast in time, for example one predator is diurnal and the other nocturnal, prey species can take advantage of temporally vacant hunting domains (Gaynor, et al., 2021; Kohl et al. 2019). This temporal segregation might therefore provide prey with the opportunity to adjust their anti-predator behaviours to times and to places where predators are less active (Sönnichsen et al., 2013; Lone et al., 2015; Kuijper et al., 2016).

1.6 Trophic cascades

Examples of predators acting as important top-down ecological drivers exist in marine, freshwater and terrestrial ecosystems (see Estes et al., 2011) and the consequences of these predator-prey interactions can ripple throughout food webs and impact entire ecosystems. Because prey invest more time into anti-predator behaviours, that would otherwise be spent foraging or reproducing, non-consumptive effects of predation have the potential to influence prey demography by affecting long-term survival and reproduction. Non-consumptive effects can be as important, or even more important, than consumptive ones, and these effects may become stronger as they cascade through other trophic levels (Preisser et al., 2005).

Predator-induced changes in prey density and behaviour can affect prey populations and may also be reflected in lower trophic levels (Ripple and Beschta, 2004; Schmitz, 2010; Ripple et al., 2014). The first pathway can lead to so-called density-mediated trophic cascades (Paine, 1966; Polis and Strong, 1996) whereas the second one can result in behaviourally-mediated trophic cascades (Abrams, 1984; Beckerman et al., 1997; Schmitz et al., 2004), since engaging in anti-predator behaviours comes at the cost of feeding opportunities for prey, which may positively influence lower trophic levels (Lima and Dill, 1990; Werner and Peacor, 2003; Schmitz et al., 1997;2004). A central subject of behaviourally-mediated trophic cascades is the prey's fear of predation, defined as an animal's conscious or unconscious perception of risk (Brown et al., 1999). Because of fear, behaviourally-mediated effects are often suggested to lead to stronger trophic cascades than density-mediated effects, since the former may influence the behaviour of multiple individuals, if not an entire population, whereas the latter only apply to the individuals that get killed (Schmitz et al., 2004; Schmitz 2005; Preisser et al., 2005). Behaviourally mediated interactions between predator and prey are also central to the landscape of fear model, which builds on the assumption that prey can perceive the level of risk they are exposed to (Lima and Steury, 2005). If this is the case, then the landscape of fear can be represented as peaks and valleys reflecting the spatiotemporal distribution of risk that a prey is exposed to in different parts of its home range (Brown et al., 1999; Laundré et al., 2001; 2010). Consequently, prey should exhibit detectable anti-predator strategies in and/or during peaks of risk (Moll et al., 2016; 2017).

Cascading effects of both consumptive and non-consumptive origin are documented in several systems (Werner and Peacor, 2003), especially in small-scale experimental studies involving invertebrates, amphibians, fish and birds (Schmitz, 1998; Peacor and Werner, 2001; Preisser et al., 2005; Cresswell, 2008). More ambiguous is the evidence surrounding these effects in terrestrial mammal communities. In Yellowstone National Park, studies suggested that wolves reduced elk density as well as indirectly decreased the intensity of browsing on riparian plants, leading to the recovery of plant species such as quaking aspen (*Populus tremuloides*) (Beschta et al., 2018) and willow (*Salix geyeriana*) (Beschta and Ripple, 2019). However, an increasing number of studies has provided alternative hypotheses for the changes in elk density and plant communities in Yellowstone National Park, such as human harvest, climate (Vucetich et al., 2005; Creel and Christianson, 2008; Kauffman et al., 2010) and as sampling bias (Brice et al., 2020). In other parts of the world, for example in Scandinavia, where wolves have recolonized parts of their historical ranges (Wabakken et al., 2001), studies have not confirmed density effects (Wikenros et al., 2015) or behavioral effects of wolves on moose (*Alces alces*) (see e.g., Nicholson et al., 2014; Wikenros et al., 2016, Sand et al., 2021). These results contrast with several studies of wolf-moose-plant systems in North America showing that wolf predation risk resulted in density or behavioural changes in elk, possibly releasing plants from browsing pressure (Ripple and Beschta, 2012; Ripple et al., 2015). The contrasting pattern between studies in North America (e.g., Yellowstone) and in Scandinavia may be driven by different degrees of human impact on these systems (Kuijper et al., 2016), which may change or reduce the ecological effects of predators on other trophic levels. Understanding the strength and the relative role of predation within anthropogenic landscapes can have considerable implications for wildlife management and conservation.

1.7 Predator-prey interactions in anthropogenic landscapes

The possible context dependence of top-down processes in ecosystems is becoming an increasingly important topic, as large carnivore populations are recovering in areas of Europe (Chapron et al., 2014) and North America (Ripple et al., 2014) with high degrees of anthropogenic impact. Humans can affect landscapes through multiple processes that in turn affect predator-prey dynamics (Ryall & Fahrig 2006), leading to the key question of “how and to what extent do humans play a role in shaping trophic networks in anthropogenic landscapes?”.

1.7.1 Human effects on predator and prey

Humans can affect predator-prey interactions by influencing their densities and behaviour (e.g., through legal and illegal hunting activity), available food resources (e.g., through agriculture, land use) and habitat (e.g., through forestry) (Kujiper et al., 2016). For instance, predators have been shown to avoid human activity and to change their own foraging patterns in response to it (Rogala et al., 2011; Theuerkauf et al., 2003; Ordiz et al., 2011). Prey, on the other hand, may be able to reduce predation risk by spending more time in proximity to human activities (so-called *human-shield effect* (Berger, 2007; Muhly et al., 2011; Kuijper et al., 2015), or are exposed to increased predation pressure from predators that spend less time at their kills due to human disturbance and therefore kill more prey (Smith et al., 2015).

Additionally, in many animal communities, humans have assumed the role of "super predators" (Darimont et al., 2015; Smith et al., 2017), with game harvesting being the leading cause of mortality among many ungulate species (Allendorf et al., 2008). Human hunting may strongly influence the behaviour and spatial distribution of prey (Proffitt et al., 2009), which can lead to reduced fitness (Grignolio et al., 2007; Neumann et al., 2009) and hence the development of anti-predator strategies aimed at reducing the risk of being killed by hunters (Lima and Dill, 1990; Lima, 1998; Caro, 2005; Creel and Christianson, 2008). When large carnivores return to anthropogenic systems, prey species become exposed to different sources of predation (Thaker et al., 2011; Chapron et al., 2014) and will be subjected to selection pressure to develop anti-predator responses to both wild and human predators (Kuijper et al., 2016). Spatial patterns of both human hunters and large carnivores are often shaped by the physical environment and anthropogenic features (e.g., buildings and human settlements, human-shield effect), since these can influence the detection and movement of both prey and predators (Lima and Dill 1990; Forrester and Steele 2004; Hebblewhite et al., 2005; Wirsing et al., 2010; Gaynor et al. 2019). Additionally, hunting and predation risk also vary temporally, at both finer (e.g., diel) and coarser (e.g. seasonal) timescales, following shifts in the foraging needs of both predator and prey (Druce et al., 2009; Hopcraft et al., 2014), the density of predators, but also the enforcement of restricted hunting times, seasons and areas (Proffitt et al., 2009). Hunters can deploy various hunting methods but often require open spaces and proximity to roads for safe shooting and accessibility. Therefore, the physical landscape also interacts with the hunting modes of hunters to shape spatiotemporal patterns of predation risk.

1.7.2 Combined effects of hunters and predators

The combined effects of hunters and large carnivores can generate spatiotemporal risk patterns that are overlapping or contrasting (Lone et al. 2014; Norum et al. 2015; Gaynor et al., 2021). In the literature, human hunting is often associated with habitat features different from those related to large carnivores (Cromsigt et al., 2013; Lone et al., 2014; Kuijper et al., 2016; Gaynor et al., 2021). These contrasting risk patterns also vary temporally, leading to a trade-off between the risks imposed by human hunters and large carnivores (Lone et al., 2014) and making it difficult for prey species to develop a behavioural strategy to avoid all predators simultaneously. Hence, prey should be expected to exhibit the strongest response towards the most predictable risk, which is most often hunting in anthropogenic landscapes (Kuijper et al., 2016). Hunting is typically restricted to daytime during specific hunting periods and to specific areas (Proffitt et al., 2009), which may provide prey with the opportunity to adjust their anti-predator behaviours only during risky times or in risky places (Sönnichsen et al., 2013; Lone et al., 2015; Kuijper et al., 2016). The risk effects imposed by human hunters can be expected to result in the strongest prey responses during the hunting season, while decreasing in importance in areas and at times when hunting is not permitted (Kuijper et al., 2016).

1.7.3 Trophic cascades in human-modified landscapes

So far, most studies on trophic cascades have been conducted in protected areas with little or no anthropogenic influence, like national parks (Kuijper et al., 2013). There is increasing evidence that within anthropogenic landscapes, human impacts may be more prominent than carnivores in influencing species at different trophic levels compared to more pristine ecosystems (Ciuti et al., 2012; Dorresteijn et al., 2015; Mehlhoop et al. (2022). This suggests that the potential for large predators to trigger trophic cascades is context-dependent, but also that previous studies carried out in protected areas may not be representative of the ecological effects of large predators on prey in other areas of the world (Kuijper et al., 2016).

1.8 The Scandinavian system

During the last centuries, the Scandinavian moose population has fluctuated in size and distribution (Lavsund et al., 2003). At the beginning of the 20th century, moose were present at very low densities mainly due to over-harvesting but began to recover and increased rapidly during the 1960s, becoming one of the most productive and heavily harvested moose populations in the world (Lavsund et al., 2003). Several factors caused this rapid increase in the moose population, but the two most important ones were likely changes in forestry practices, such as switching from closed to open logging (increasing the frequency of clearcuts and thereafter food availability for moose), and in harvest strategies by initiating harvest of juveniles instead of adults only (Lavsund et al., 2003). The absence or the low number of large carnivores, such as bears and wolves during the mid-20th century, when the moose population started to recover, is also likely to have contributed to its increase (Cederlund and Markgren 1987; Østgård 1987; Lavsund et al., 2003).

The Scandinavian wolf population declined strongly during the 19th century, but around the same time that the moose population showed a strong recovery, wolves were declared “functionally extinct” in Scandinavia (Wabakken et al., 2001). In early 1980s, two wolves belonging to the Finnish-Russian wolf population started to recolonize south-central Scandinavia (Wabakken et al., 2001). Since then, the wolf population has increased in numbers and geographical distribution, reaching 540 (95% CI = 427-702) individuals during the winter 2021/2022 (Wabakken et al., 2022).

Nowadays, moose in Scandinavia are exposed to three major sources of predation: they are the most important game species for hunters (Wikenros et al. 2020), the main prey of wolves (Sand et al., 2005, 2008) and in high density bear-areas can experience up to 26% calf mortality during summer (Swenson et al., 2007). Moose hunting is an important leisure activity with historical and cultural traditions, having a great economic and recreational value (Storaas et al. 2001; Boman et al. 2011). The most common hunting mode in Scandinavia is the use of unleashed dogs to find and push moose toward sit-and-wait hunters situated at pre-determined spots in the landscape. Along with the strong reduction in the wolf population during the 19th century, human harvest gradually functionally replaced predation and became the primary mortality source for moose (Lavsund and Sandegren, 1989; Stubsjøen et al., 2000; Lavsund et al., 2003).

In Scandinavia, forestry has a major societal and economic importance (Schlyter et al., 2006) and forested land covers approximately 55% and 39% of the total land area of Sweden and Norway (UN-ECE/FAO, 2000; Statistical Yearbook of Forestry, 2004). Forestry is based on mainly coniferous trees, especially Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). During winter, moose mainly browse on Scots pine (Cederlund, 1980; Hörnberg, 2001) and can cause significant browsing damage, which reduces the production and quality of timber and results in economic losses (Lavsund, 1987; Bergqvist et al., 2001).

Because of its history, Scandinavia is an interesting system to understand in terms of the interactions between humans, wolves, moose and important forage species to moose (Fig. 1). Firstly, humans can affect moose by direct lethal effects and/or by indirect, nonlethal effects. Humans also impact wolves directly through legal and illegal hunting and indirectly through displacement and avoidance behaviours. Wolves can also indirectly influence human behaviours, since hunters may actively avoid hunting in areas where wolves have been spotted to avoid potential encounters between hunting dogs and wolves (Fig. 1). Secondly, wolves can interact with moose by direct killing but also by inducing behavioural changes as a result of predation risk (Fig. 1). Thirdly, moose have a direct effect on Scots pine as a result of winter browsing behaviour (Fig. 1). Fourthly, humans may have additional indirect effects on moose through forestry activity, by actively shaping the structure, composition and richness of forage available to moose (Fig. 1). Finally, both wolves and humans may elicit indirect effects on the lower trophic level, Scots pine, by influencing moose density and behaviours (Fig. 1).

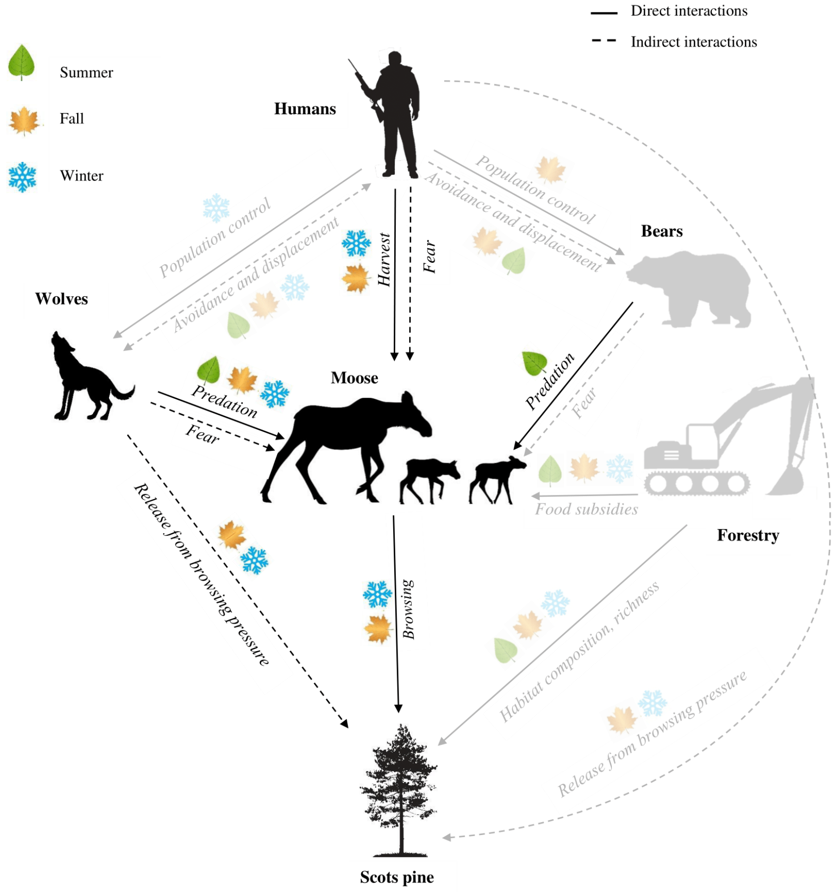

Figure 1: Theoretical network of the trophic interactions and their timeframe within the anthropogenic landscapes of Scandinavia. The black lines indicate the interactions and processes that is the focus of this thesis, whereas the shaded lines represent the interactions that were not included in this thesis and the shade figures show trophic levels that were only partially or indirectly involved (brown bear predation and forestry). When there is only information about the timeframe of one interaction between one trophic level and another, this means that the same timeframe applies also for the other. In this system, wolves and humans can influence moose by direct killing or by indirectly inducing behavioural changes, which can then ripple through the ecosystem to lower trophic levels (e.g., Scots pine). For instance, increased predation risk may lead to increased vigilance behaviour and reduced browsing activity, possibly releasing Scots pine from browsing pressure in areas of wolf presence compared to areas without wolves (modified from Kuijper et al., 2016).

2. Objectives

The main objective of the thesis was to investigate predator-prey interactions in a human-wolf-moose-pine system using a combination of data collected from GPS-collared wolves and moose (paper I, II and III), surveys with hunters (paper I and II) and a long-term browsing damage inventory (paper IV).

Paper I investigates the following question: **How do spatial attributes influence the risk of wolf predation and human hunting for moose during fall and winter, and are these risks associated with contrasting habitat features?**

Once I knew which environmental and anthropogenic features were important for wolf predation and human hunting, I then addressed the following question in paper II: **do moose follow the temporal variation in wolf predation and human hunting risk and adjust their diel and seasonal habitat selection relative to the spatial variation in each risk?**

To disentangle the effects of wolf predation and human hunting even further, I investigated how these affected moose calf mortality throughout the year and whether calf mortality differed between migratory females and resident ones. Paper IV had the following question: **How do wolf predation risk and hunting risk affect moose calf mortality during summer and winter, and are these effects related to the migratory strategy of female moose?**

In my last paper I tested whether the recolonization of wolves had resulted in density and/or behavioural changes in the moose population, and whether these effects had rippled through the system to lower trophic levels. Paper IV sets out to address the following question: **Has the recolonization of south-central Sweden by wolves led to changes in moose abundance and habitat selection, and have these changes resulted in decreased browsing damage on Scots pine during winter?**

3. Materials and methods

3.1 Study area

The study area spans across three distinct geographic regions and two timeframes: paper I and II were carried out between 2018 and 2020 along the Swedish-Norwegian border (60°33’-61°15’N, 11°45’ – 12°55’E), covering an area of 1699 km^2 in south-eastern Norway and 969 km^2 in south-western Sweden (Fig. 2B); paper III was conducted between 2018 and 2022 in the same area as paper II and III but included also the area around the Fulufjället National Park (Fig. 2B); and paper IV was conducted between 2003 and 2016 across the breeding range of wolves in south-central Sweden (56°50´ - 63°N, 11°50´ - 17°E, approximately 102,916 km^2, Fig. 2A). In general, snow covers the ground mainly between December and March. Intensive forestry has led to an extensive network of gravel roads which, together with national and regional roads, resulted in a mean road density of 0.84 km/km^2 within the study area. Moose winter density within the study area averaged approximately 1.3 per km^2 (Zimmermann et al., 2014). Each year, moose hunting is managed by management units composed of several hunting teams within the same area (see Wikenros et al. 2020 for detailed information on how the Norwegian and Swedish hunting management system works). The official hunting season started each year on the 25th of September and ended on the 23rd of December in Norway, whereas in Sweden, it began in the first week of September and ended on the last day of February. Between 2002 and 2022, the wolf population increased from 22 to 83 family groups and territorial pairs (Wabakken et al., 2004; 2022). Moose is the primary prey species of Scandinavian wolves and makes up more than 95% of their diet (Sand et al. 2005; 2008). During winter, approximately 70% of moose killed by wolves are calves (Sand et al. 2005).

Within our study area, the landscape is predominantly boreal forest, composed of Scots pine, Norway spruce and a few deciduous species such as birch (Betula spp.) (Antonson 2011; Christiansen 2014; sentralbyrå 2021). Scots pine represents quantitatively the most important food source for moose in winter in Sweden, despite being less selected than other less common deciduous tree species (Månsson et al., 2007). Moose select for rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and willows (*Salix* spp.) but also browse on silver birch (*Betula pendula*), downy birch (*Betula pubescens*) and Scots pine (Månsson et al., 2007).

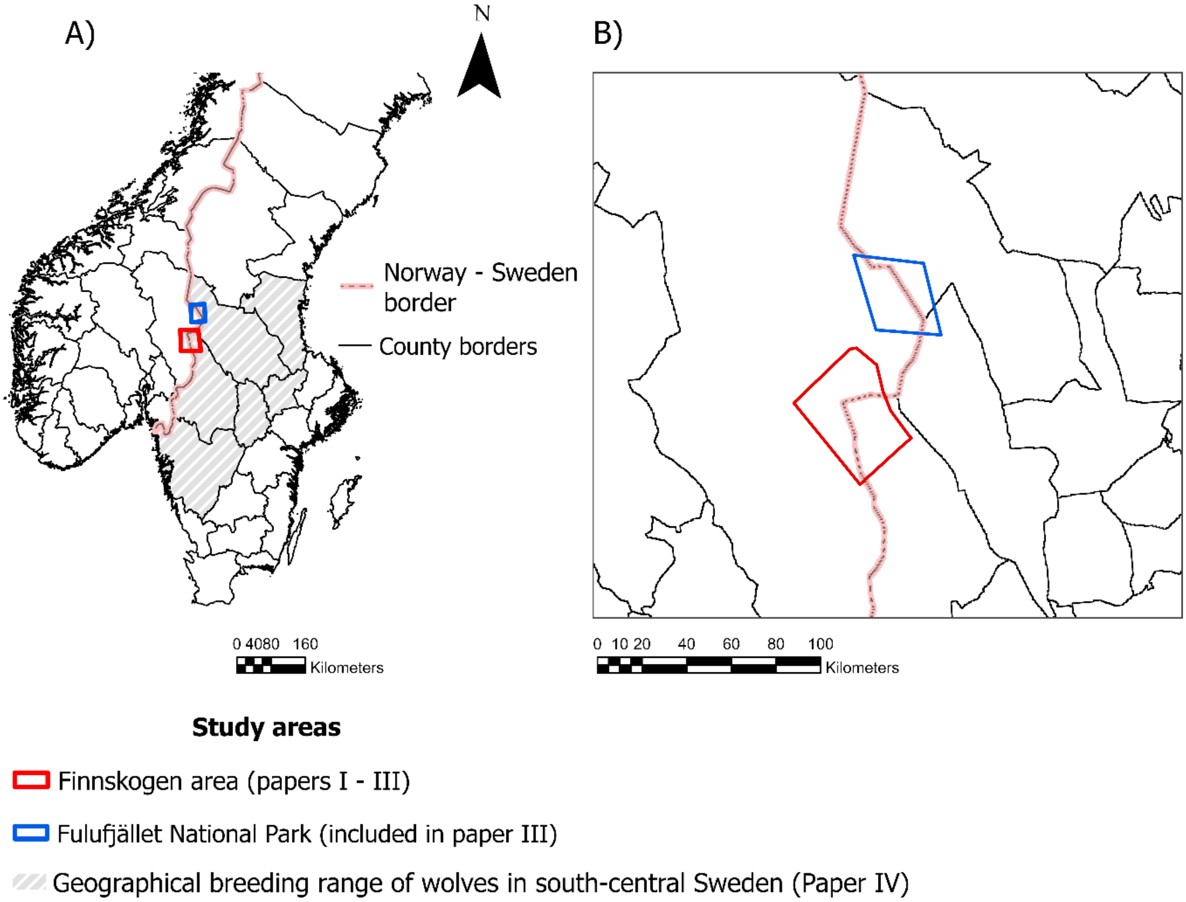

Figure 2: Geographical distribution of the study areas used in the thesis. Papers I and II were carried out between 2018 and 2020 along the Swedish-Norwegian border covering an area of 1699 km^2 in south-eastern Norway and 969 km^2 in south-western Sweden (Fig. 2B). Paper III was conducted between 2018 and 2022 in the same area as paper II and III but also included the area around the Fulufjället National Park (Fig. 2B); Paper IV was conducted between 2003 and 2016 across the breeding range of wolves in south-central Sweden (approximately 103 km^2) (Fig. 2A).

3.2. Data collection

3.2.1 Animal tagging

Between February to Mid-March in the years 2018-2021, 39 adult moose were immobilized by darts from helicopters (Arnemo and Evans, 2017) and equipped with GPS collars (Vectronics Survey collars with Iridium link and VertexPlus with GSM link). The baseline programming of the moose collars was to acquire one position every two hours. Between January and March in the years 2018-2021, wolves belonging to five packs along the Swedish-Norwegian border were located on snow and immobilized by darts from helicopters (Arnemo and Evans, 2017). The collars were programmed to acquire one position every four hours, except during predation studies when the programming was changed to one position per hour. Handling protocols fulfilled the ethical requirements for research on wild animals in Sweden (decision C281/6 and C315/6) and Norway (The Norwegian Food Safety Authority, decision id 15370).

3.2.2 Wolf kill site detection

During wolf predation studies, hourly GPS-positions of the studied wolves were categorized into cluster- and single positions using ArcGIS (ESRI Inc, Version 2.9). A cluster was defined as two or more positions no more than 200 m apart from each other (Sand et al. 2005). All clusters were searched for prey remains in the field shortly after wolves had left the area. Prey remains were categorized into species, sex, age and cause of death based on carcass characteristics and wolf tracks (Sand et al. 2005). I defined all clusters where moose were found killed or probably killed by wolves as kill sites, and from the first wolf position at the site, I was able to extract the time of death.

3.2.3 Counts of faecal pellet groups to assess moose density

For paper I, I conducted counts of faecal pellet groups shortly after snow melt, to map the distribution and density of moose during winter. Five sample plots of 100 m^2 were clustered in a square of 50 * 50 m, and the squares were evenly distributed throughout the Finnskogen study area (Fig. 2) at a distance of 3.5 km. Each plot was searched for pellet groups deposited after leaf fall. For paper IV, I obtained data on moose pellet counts from the Swedish National Forestry Inventory, where the surveys were conducted between May and September in forest habitats (Fridman et al., 2014).

3.2.4 Hunter survey to find moose harvest sites

Within the Finnskogen study area (Fig. 2), I contacted and surveyed 106 hunting teams for the coordinates, date and time of all the moose harvested during the hunting seasons of 2018/19 and 2019/20. Obtaining the exact time of the day when moose were shot proved to be very difficult, but all hunters confirmed to have shot moose during daylight hours between 8:30 and 18:00.

3.2.5 Calf survival checks

During the calving season (May-July), I used rolling minimum convex polygon (rMCP; Nicholson et al., 2019) to estimate potential calving events for each GPS-collared female. Once I detected a calving event, each female was approached from the ground to determine the number of calves born. I waited a minimum of 2 days from parturition before each calf check, to allow each female enough time to bond with her neonate calf/calves. Each calf check was carried out on foot and using a handheld receiver (RX98, Followit, Lindesberg, Sweden). Within one month before the onset of the hunting season, each cow was re-approached and the number of calves determined again using the same procedure. Finally, each cow was checked one last time before the dispersal of her calf/calves (April of the following year). I conducted the calf checks during three consecutive years (2018-2021).

3.3. Environmental variables

3.3.1 Topographic variables and vegetation

For my thesis, I included several topographic and vegetation variables. These were: tree cover, productivity, terrain ruggedness, clearcuts/young forests and bogs. Tree cover was measured as the proportion of a sample plot covered by different tree species (Fridman et al., 2014). I used the Normalized Difference Vegetation Index (NDVI; raster 300*300) as a proxy for habitat productivity and calculated the mean cumulative summer NDVI for each female moose’s home range. Terrain ruggedness was derived from a Digital Elevation Map with pixel size of 25 m (Copernicus Land Monitoring 2018). I used data on clearcuts/young forests and bogs from the Corine Land Cover (CLC) inventory (Copernicus Land Monitoring 2018) to generate a Euclidean distance raster to clearcuts/young forests and bogs. I used cumulative average winter snow depth from October to March of each study year as a proxy for winter severity. The data was obtained from the Norwegian Water Resources and Energy Directorate (NVE) (for more information on the interpolation method used see Saloranta, 2012).

3.3.2 Anthropogenic features

I also included variables to represent anthropogenic features in the landscape. These were: main and secondary roads and building density. Main and secondary roads were then used to calculate the distance to each type of road. Building density was calculated as the number of buildings (houses, cabins, farms and other buildings) per square kilometre.

3.3.3 Brown bear density

A relative index of bear density was calculated for each year with data from the annual bear harvest (both regulated and protective harvest, see www.rovbase.no), using a search radius of 100 km, and expressed as the number of shot bears per 1000 km^2. Earlier studies have found that harvest density is a good proxy of absolute densities of brown bears (Swenson et al. 1998, Kindberg et al. 2009).

3.3.4 Browsing damage inventory

I used data on moose browsing damage recorded by the Swedish National Forestry Inventory during spring using a nationwide moose browsing damage monitoring scheme, called Äbin (Kjellander, 2007; Kalén et al., 2018). The same sample plots surveyed for pellet count inventory are also used for Äbin. In the survey, browsing intensity is estimated as the proportion of damaged trees (i.e., stem breakage, bark stripping and top shoot browsing, Bergman and Åkeberg, 2006). Äbin also documents the presence or absence of four deciduous tree species: rowan, aspen, willows and oak (*Quercus robur*), which are often referred to by the acronym RAWO.

3.4 Data analysis

3.4.1 Wolf kill sites (paper I)

I extracted wolf movement characteristics for each cluster of GPS positions visited during the predation studies in the fall and winter of 2019. These movement characteristics, e.g., number of positions and revisits, were used in machine learning models (gradient boosting) to differentiate between clusters containing a kill site and other non-kill clusters, e.g. bed sites. My machine learning models had an overall accuracy of 94% and 98% for fall and winter, respectively. The final models were used to predict kill sites throughout the entire fall and winter seasons, and I was able to identify 100 potential kill sites during the moose hunting season (1st September – 15th January) and 62 kill sites after the moose hunting season. Each identified kill site was also timestamped using the time of the first recorded GPS position at the kill site.

3.4.2 Wolf variables (papers I, III and IV)

In my thesis, I used three variables related to wolves: wolf presence, space use and time since territory establishment. The first was generated using data from the annual wolf-monitoring system of the County Administrative boards (Liberg et al., 2012) and GPS positions from the collared individuals to create 100% minimum convex polygons for each wolf pack. Wolf space use (paper I) was estimated for each wolf pack during and after the hunting season using kernel density estimators to generate population-level utilization distributions (UDs). Time since wolf territory establishment (paper IV) was calculated as the sum of years since a wolf territory was first documented to the time of the moose and browsing damage survey.

3.4.3 Moose density (paper I)

I turned the number of moose pellet groups found per square into winter moose densities by applying a defecation rate of 14 pellet group per moose and day (Persson et al., 2000; Rönnegård et al., 2008). I then used co-kriging to interpolate moose densities across the study area and added snow depth, distance to bogs and solar radiation as covariates in the interpolation model in ArcGIS Pro (Esri Inc, 2020).

3.4.4 Risk maps (paper I)

I used the kill sites identified by the wolf kill model and the hunter survey to model the probability of a site being a kill site relative to a random location (Fithian and Hastie, 2013). I included moose density (3.4.3) in these models to account for variation in the spatial distribution and abundance of moose. In the wolf model, I also included the wolf utilization distribution (3.4.2). Based on the best kill site models, I predicted for any given location (raster of 25*25 m cell size), and separately for the seasons fall and winter, and day and night hours, the risk for moose to be killed by wolves and hunters. I also used the characteristics of the kill sites to differentiate between the two causes of death (hunting and wolf predation). For this, I applied logistic regression, resulting in an odds ratio that described the relative probability of a hunter- versus a wolf-killed moose for a given combination of landscape variables.

3.4.5 Resource selection functions to study moose space use in relation to risk (paper II)

I investigated third order (Johnson, 1980) moose habitat selection with logistic regression using generalized linear mixed models. For each moose, I created a home range for the hunting season and one for after the hunting season using 95% MCPs. I generated random points within each moose home range to define available habitat and matched them to actual GPS locations. I then extracted the odds ratio of being killed by hunters or wolves for each GPS position and random point, using the risk maps I had created in paper 1. Additionally, I also annotated both GPS and random points with the environmental and anthropogenic variables included in the top model predicting the probability of being killed by a hunter or a wolf during and after the hunting season (paper 1). This model procedure was done separately for the four combinations of time of day (day and night) and season (hunting season, after hunting season).

3.4.6 Moose home ranges and migratory strategy (papers III and IV)

I used moose GPS positions to estimate moose home ranges as 100% MCPs for each individual. The MCPs were calculated for the summer (May – August), hunting season (September – January), after the hunting season (January – April) and for the whole winter (September - April). I used Net Squared Displacement (NSD) (Bunnefeld et al., 2011; Singh et al., 2016) to distinguish between two different movement strategies: migration and residency (Bunnefeld et al., 2011; Singh et al., 2012; Börger et al., 2012) and additional visual inspection of the annual movement of the moose.

3.4.7 Mortality analysis (paper III)

I first classified each summer moose home range according to wolf presence and extracted the mean of the following variables: bear density, productivity, proportion of clearcuts/young forests, and secondary road density. Winter home ranges were annotated with the following features: wolf presence/absence, hunting risk, proportion of clearcuts/young forests, secondary road density and snow depth. Winter home ranges that overlapped with my risk maps from paper I were also annotated with the average hunting risk and wolf predation risk.

To investigate moose calf mortality, I used generalized linear models. In addition to the environmental variables mentioned above, I included the interaction term wolf*road density in the summer model, and wolf*snow and wolf*clearcuts/young forests in the winter model.

3.4.8 Trophic cascade analysis (paper IV)

I used logistic regression to model the probability of moose presence and browsing damage and zero-inflated negative binomial models for moose abundance and browsing intensity. My main explanatory variables in these models were wolf presence and time since wolf territory establishment, and I also added the proportion of pine, presence of RAWO, and the distance to nearest forest road and main road into all models. In the moose presence and abundance models, I additionally included forest age class, and in the browsing damage and intensity models, I also included moose abundance and the number of trees with previous browsing damage.

4. Results

4.1 Spatiotemporal patterns of mortality risks for moose (paper I)

The risk of moose being killed by hunters and wolves varied across the landscape both temporally and spatially (Fig. 3). Hunters killed moose during daytime, whereas wolves killed moose mostly during night hours both during and after the hunting season, respectively. Relative hunting risk increased with increasing moose density, but decreased with increasing building density, distance to clearcuts/young forests, terrain ruggedness, distance to bogs and distance to main and secondary roads. During the hunting season, relative wolf predation risk decreased with increasing building density and distance to clearcuts/young forests but increased with increasing wolf space use and distance to bogs. After the hunting season, relative wolf predation risk increased with increasing moose density, wolf space use and terrain ruggedness but decreased with increasing building density, distance to main roads and distance to clearcuts/young forests. The probability of a hunter-killed moose in relation to a wolf-killed moose increased with increasing building density, but decreased with increasing distance to bog, terrain ruggedness, and distance to main roads.

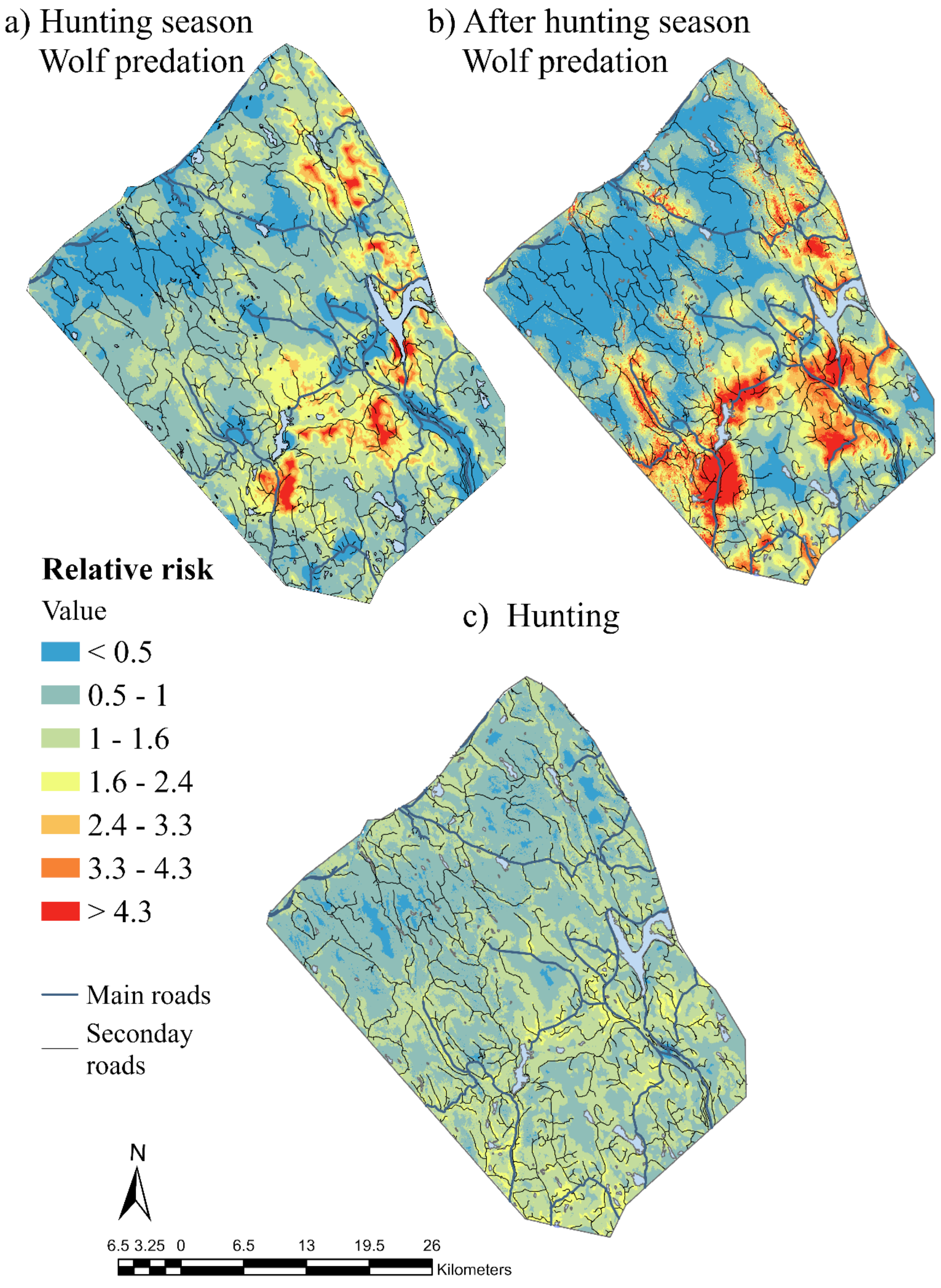

Figure 3: Predicted risk for relative wolf predation (a) during and (b) after the hunting season, and for relative hunting risk. A value of 5 indicates that there is a 5 times higher predation risk than average in that location, whereas a value of 0.5 denotes 50% of the average risk.

4.2 Moose habitat selection in relation to risk factors (paper II)

During the hunting season, moose habitat selection was negatively correlated with hunting risk during the day but was not affected by hunting risk at night (Fig. 4a). After the hunting season, moose habitat selection was not affected by hunting risk (Fig. 4b) during the day, while at night, moose selected for high hunting risk areas (Fig. 4b). Both during and after the hunting season, moose selected for areas of high wolf predation risk during both day and night (Fig. 4a, b).

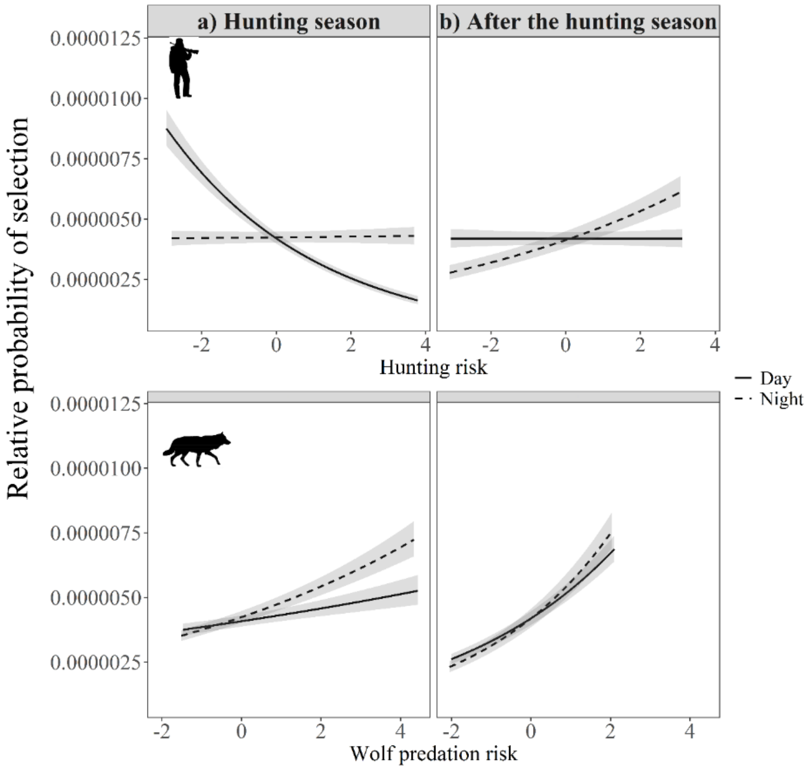

Figure 4: Relative probability of selection by moose in relation to hunting risk and wolf predation risk for day and night (expressed as *scaled* odds ratio values) during the hunting season (September 01 – January 15; panel a); and after the hunting season (January 16 – April 01; panel b). The data were collected in south-central Scandinavia during two consecutive winters (2018/19 and 2019/20). The relative probability was estimated using logistic regression where moose GPS positions were compared to random locations within each moose home range. Hunting risk and wolf predation risk were estimated using wolf- (N = 161) and hunter-killed (N = 887) moose compared to random locations (ratio 1:50).

4.2.1 Moose habitat selection in relation to risky landscape features (paper II)

During the hunting season at daytime, moose avoided areas close to clearcuts/young forests, bogs and secondary roads and areas with high building density but selected for areas closer to main roads. At night, moose selected for areas closer to main and secondary roads, while they still avoided bogs, clearcuts/young forests and areas with high building density. After the hunting season, during both day and night, moose selected for areas closer to clearcuts/young forests, main roads, high building density and low terrain ruggedness.

4.3 Moose calf mortality in a landscape of risks (paper III)

Across our three-year study period, I had data from 39 female moose and a total of 77 calves. I found that summer mortality for moose calves varied significantly between years, being lowest in 2019 (8%) and highest in 2020 (42%). Summer calf mortality was unrelated to large carnivores (wolf presence and bear density), habitat productivity, clearcuts/young forests proportion, secondary road density, and migratory strategy. During winter, calf mortality was positively related to snow depth in the presence of wolves and vice versa in the absence of wolves (Fig. 5A). The positive relationship between proportion of clearcuts/young forest and calf mortality was more pronounced inside than outside wolf territories (Fig. 5B). Winter calf mortality was higher for migratory females compared to stationary ones (Fig. 5C). Hunting pressure and density of secondary roads were unrelated to calf mortality during winter. However, for a subset of moose cows within the area where I had assessed mortality risk from wolf and hunt (paper I), winter calf mortality was positively related to hunting risk.

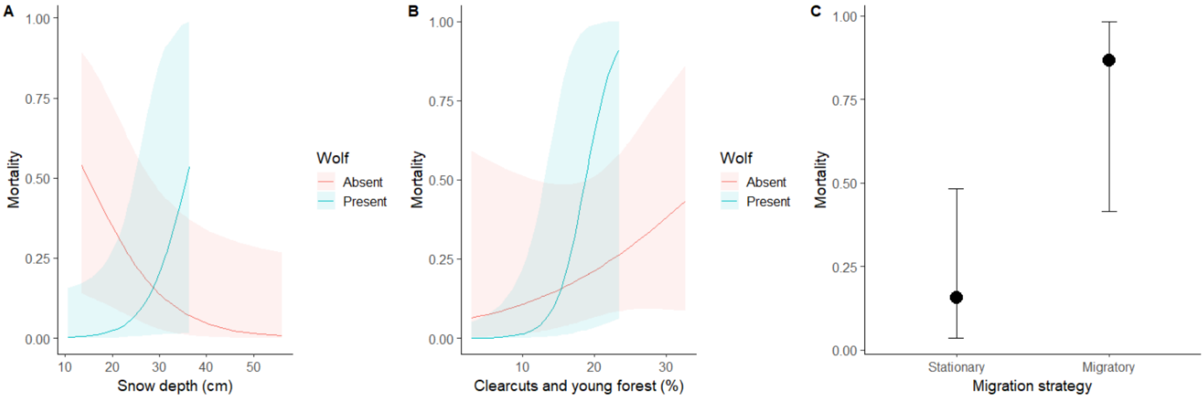

Figure 5: Probability of calf mortality in south-central Scandinavia between 2019 and 2021 in relation to **(A)** wolf presence and snow depth; **(B)** wolf presence and proportion of clearcuts/young forests in the mother's home range; and **(C)** migratory strategy of the mother.

4.4 Trophic cascades within anthropogenic landscapes (paper IV)

I did not find evidence for neither a density- nor behaviourally-mediated trophic cascade in south-central Scandinavia following the reintroduction of wolves. In fact, moose presence and abundance were higher inside wolf territories than outside and increased with time since wolf territory establishment. Browsing damage was higher inside wolf territories, further away from main roads, in the presence of previous browsing damage and increased with increasing moose abundance (Fig. 6). Browsing intensity increased with distance to main and forest roads, moose abundance, previous browsing damage and the presence of RAWO species. Environmental and anthropogenic features were more important than wolf variables in explaining variation in moose presence and abundance.

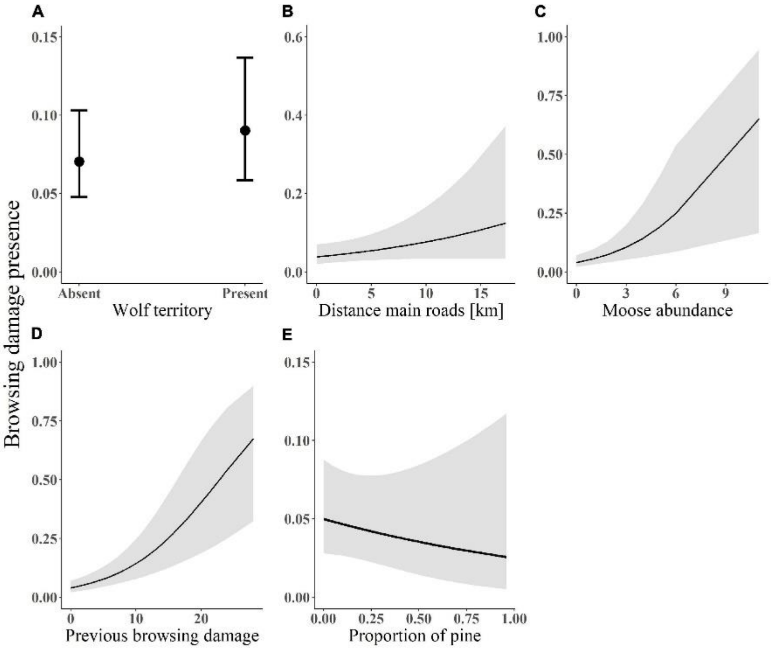

Figure 6: Predicted probability of browsing damage presence on Scots pine in relation to **(A)** wolf presence; **(B)** distance from main roads; **(C)** moose abundance; **(D)** previous browsing damage; and **(E)** pine proportion. Data on browsing was collected within south-central Sweden between 2003 and 2016. The lines (in plot **B–D**) indicates the fitted values with associated standard errors from the model-averaged estimates. Plot A shows the coefficients and confidence intervals of the predicted probability of browsing damage presence in relation to presence/absence of a wolf territory.

5. Discussion

Because humans can affect natural landscapes and predator-prey interactions through different pathways (Ryall and Fahrig, 2006), I ended my introduction by asking the question "*how and to what extent do humans play a role in shaping trophic networks in anthropogenic landscapes?*". My thesis provides some novel and useful insight into some key aspects needed to answer this question (Fig. 7), although much more research on the topic is needed to fully disentangle and understand the effects of humans on predator-prey interactions.

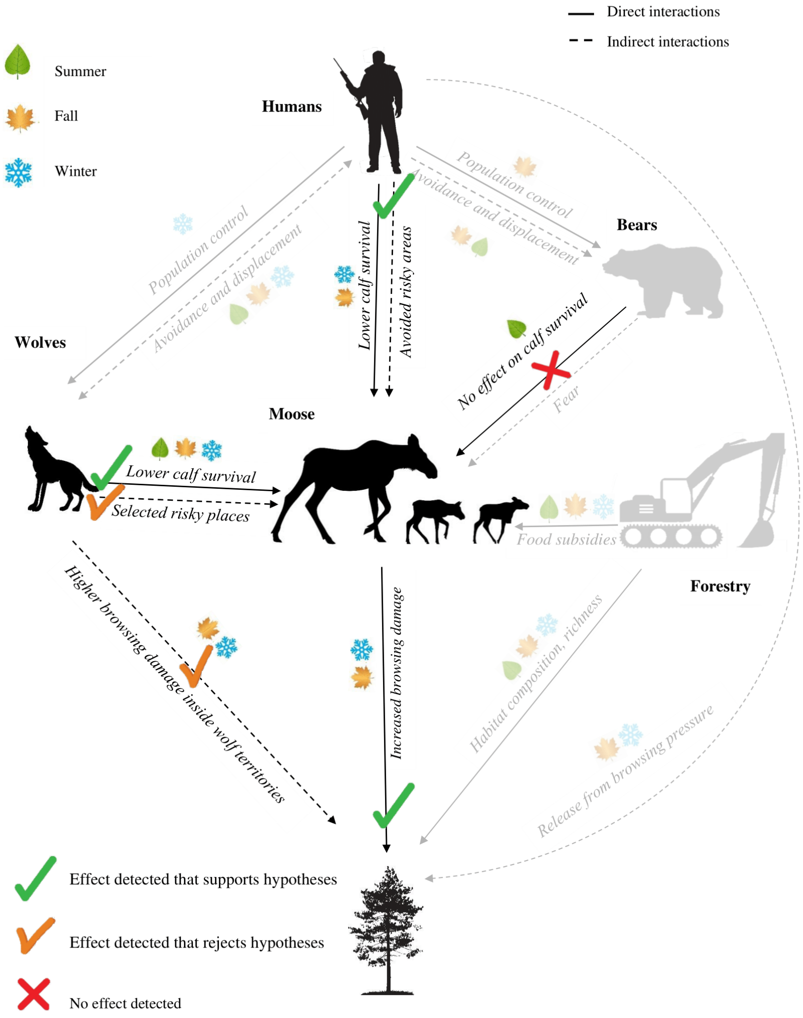

Figure 7: Theoretical network of the main trophic interactions and their timeframe within the anthropogenic landscapes of Scandinavia with adjustments based on the results of my thesis. The black lines indicate the interactions and processes that this thesis has focused on, the shaded lines represent interactions that were not included in this thesis and the shaded figures are trophic levels that were only partially included (brown bear predation and forestry). When there is only information about the timeframe of one interaction between one trophic level and another, the same timeframe also applies to the other. I added the effects found for each of the interactions

studied and whether they supported or rejected the initial hypotheses, or if no effect was detected. In this network, wolves and humans were positively correlated to moose calf mortality. Hunting risk was negatively associated with moose habitat selection, whereas wolf predation risk was positively related to it. Moose presence and abundance increased the probability of browsing damage, but I found no indirect effect of wolves on browsing damage.

5.1 On the importance of habitat

Humans can affect predator and prey populations in anthropogenic landscapes by altering their densities, behaviours, food resources and habitat (Kujiper et al., 2016). Humans have become super-predators for many animal species, and game harvesting has become the leading cause of mortality among many prey populations (Allendorf et al. 2008; Darimont et al. 2015). I found that hunting risk was not evenly distributed in the landscape but higher close to open areas and roads. Moose avoided these high-risk areas during daytime in the hunting season, and calf mortality was higher in high-risk areas. My results are in line with the risky times hypothesis (Creel et al., 2008) and the schedules of fear concept (Palmer et al., 2022), as it seems that in the case of hunting, moose were able to identify the most predictable risk during both day and night and adjusted their diel habitat selection in accordance with pulses of hunting risk to minimize exposure. Hence, habitat is an important driver of spatiotemporal patterns of risk and prey responses (Kauffmann et al., 2007) that affects almost all factors and interactions I presented in Figures 1 and 6. Habitat mediates risk of hunting and predation because the respective hunting modes of hunters and large carnivores are somewhat dependent on landscape features that affect the detection and killing of prey (Lima and Dill 1990; Mech et al. 1998; Forrester and Steele 2004; Hebblewhite et al., 2005; Wirsing et al., 2010; Gaynor et al. 2019). While large carnivores cannot alter habitats to facilitate their hunting efficiency and success, human activities can indirectly affect how the landscape interacts with both hunters and large carnivores. This could happen through different pathways that each can lead to differing outcomes. Here I present some examples of how human activities that alter landscape features can influence the interactions between humans, large carnivores, and ungulates.

5.1.1 Human settlements

Human settlements may allow ungulate prey to use human presence as a shield to reduce predation risk, since large carnivores are known to avoid such areas (Berger 2007; Rogala et al. 2011; Lesmerises et al., 2012). This could result in decreased kill rates for large carnivores and eventually greater conflicts between humans and wild animals (Bacon and Boyce, 2016). However, large carnivores might take advantage of these higher prey densities (Basille et al. 2009) by hunting near human settlements during times of low human activity (e.g., at night).

Additionally, higher disturbance at carnivore kills located in areas with high housing density might reduce the utilization of carcasses by large carnivores, leading to increased kill rates (Smith et al., 2015). On the other hand, one could also expect ungulate species to avoid densely populated areas because of a higher perceived mortality risk, which could result in greater predation risk by large carnivores. However, some studies have shown that ungulates seem less sensible to high human disturbances than large carnivores (Muhly et al., 2011; Rogala et al., 2011). In my study area, moose avoided areas of high building densities during hunting time, independent of time of day, but selected for such areas after hunting season was over. To what extent this can be explained by a human shield strategy and/or by access to moose winter forage in more productive, less snow-rich areas in the valley bottoms, where also people settle (Carricondo-Sanchez et al., 2020), is difficult to disentangle.

5.1.2 Forestry and roads

Humans can also greatly modify the landscape through forestry practices and road development, which can alter the spatial distribution of predation risk (Kuijper et al. 2016; Kunkel and Pletscher 2000). For example, intensive forestry practices that involve disturbances related to logging and road development have been negatively associated with the presence of grizzly bears (*Ursus arctos horribilis*) in Canada (Nielsen et al. 2008). Conversely, forestry practices may facilitate the hunting and killing of prey by large carnivores, for instance by creating edge habitats (e.g., wolves in Poland, Bojarska et al. 2017). Clearcutting and forest subdivisions replaces more homogeneous forests with open spaces and habitat edges, respectively, which may increase predation rates from large predators (Kunkel and Pletscher, 2000; Bergman et al., 2006). Linear features, such as roads, are well-known to facilitate movement for large carnivores (e.g., wolves, Zimmermann et al., 2014; Dickie et al., 2016), possibly also leading to higher encounter rates with their prey (Latham et al. 2011; Whittington et al. 2011; McKenzie et al. 2012). This could result in lower survival rates in areas with higher road density. However, roadsides may also provide ungulates with increased foraging opportunities due to activities such as ditching that increase plant species diversity (Zielinska et al., 2013; Jakobsson et al., 2018). The results of my study indicate such a trade-off: moose during hunting season avoided forest roads at daytime, likely as a response to increased hunting risk, and selected for them at night, likely to browse along roadsides and use roads as easy access to forage patches, such as young forest stands.

5.2 Predator-prey interactions in human-altered habitat

All the above-mentioned human practices have the potential to reshape the distribution of risk in the landscape for prey species, regardless of whether they positively or negatively affect large carnivores. Moreover, human activities may also influence the effects of humans on prey, e.g., increased clearcutting may expose ungulates to a higher risk of being killed by hunters, and hence force them to trade-off foraging opportunities with anti-predator behaviours. Because human hunters and large carnivores are often associated with contrasting landscape features (Proffitt et al., 2009; Lone et al., 2014; Gaynor et al., 2021), habitat alterations favour hunting efficiency of the former are likely to decrease it for the latter. Hence, there is an increasing need to understand how prey species are affected by human activities, such as hunting and habitat alterations, to what extent large carnivores can successfully incorporate them into their hunting strategy, and whether large carnivores are able to elicit cascading trophic effects similar to those in more pristine ecosystems.

5.3 Trophic cascades within anthropogenic landscapes

Kujiper et al. (2016) suggested that within anthropogenic landscapes, the potential for density-mediated trophic cascades might be limited to less productive areas, where humans do not influence the food resources available to prey, or to areas where carnivores are allowed to reach ecologically meaningful densities to significantly regulate prey populations. Behaviourally-mediated cascades might have a greater potential to be generated within anthropogenic landscapes, because even low carnivore densities are sufficient to affect prey behaviour (Laundré et al., 2001). However, some studies reported stronger effects of human activity than by large carnivores on the behaviour of ungulates (Ciuti et al., 2012) with cascading effects on lower trophic levels (Dorrejstein et al., 2015). Others noted that human influence on vegetation may strengthen bottom-up effects and weaken top-down effects in ecosystems (Muhly et al., 2013). Human activities, such as hunting, are likely to be the most predictable and strongest risk perceived by ungulates, which are then expected to show a strong response towards that risk (Kujiper et al., 2016). For example, harvest rates inside wolf territories in south-central Scandinavia were estimated to be 2.4-3.5 times higher than wolf predation rate (Zimmermann et al., 2019). However, because hunting is usually restricted in time and space (Proffitt et al., 2009), ungulates may be able to adjust their anti-predator behaviours only in risky places or during risky times (Sönnichsen et al., 2013; Lone et al., 2015). Consequently, the potential for large carnivores to initiate trophic cascades, and how anthropogenic landscapes influence predator-prey interactions, is highly species-, context-, and season-dependent.

My thesis provides useful insight into the mechanisms behind the context- and seasonal-dependency of the effects of large carnivores within anthropogenic landscapes (Fig. 7). The combined effects of hunters and wolves during the hunting season resulted in contrasting spatiotemporal risk patterns for moose, presumably because of the differing hunting modes of wolves (i.e., cursorial predators that chase prey) and hunters (i.e., sit-and-wait, baying dogs) and their opposite activity patterns interacting with environmental and anthropogenic features. Moose altered their habitat selection to minimize exposure to hunting risk during the day while not responding to wolf predation risk. With the disappearance of hunting risk from the landscape in early winter, moose ceased to adjust their habitat selection in relation to hunting risk. However, moose failed to respond to wolf predation risk (the main mortality source after the hunting season) and selected for areas of high wolf predation risk, most likely due to higher food availability in those areas (i.e., clearcuts/young forests). Hence, moose habitat selection after the hunting season seemed to be driven more by bottom-up processes (i.e., forage restriction) than top-down effects. During the hunting season, however, habitat selection was consistent with the avoidance of the stronger and more predictable mortality source (hunting), suggesting that either top-down forces were more important, and/or forage availability was not as limited.

The fact that both hunting and wolf predation reduced the survival of moose calves, and yet moose adjusted habitat selection in response only to the former, is an interesting finding. This indicates either that a) moose in Scandinavia are currently naïve to wolves (Sand et al., 2006), likely due to the temporary absence of wolves before their recolonization and the intense harvest pressure; and/or b) forage availability during winter might lead to a trade-off between predation risk and feeding for moose, where the latter is more important as food resources become scarcer and more patchily distributed in the landscape (e.g., clearcuts/young forests). This may suggest that in systems where hunters are the strongest perceived risk, top-down effects of hunting might drive responses of moose during risky times, whereas bottom-up effects might become more important in shaping moose responses as winter progresses and food becomes limited. Hence, the potential for wolves to initiate trophic cascades might be dampened, or even cancelled, by the need to find optimal foraging places during winter.

Wolf-induced trophic cascades in south-central Sweden might be further attenuated by the responses of hunters to the establishment of wolves, adjusting the number of harvested moose to compensate for the additive mortality of wolf predation (Wikenros et al., 2015). Indeed, I found that the establishment and presence of wolves in south-central Sweden had not resulted in cascading effects onto lower trophic levels (i.e., Scots pine) (Fig. 7) which is in contrast with studies from pristine ecosystems from North America where wolves indirectly released certain plant species from browsing through alterations in ungulate density and behaviour (Fortin et al., 2005; Ripple and Beschta, 2003, 2012). In protected areas such as Yellowstone National Park, there is often little to no anthropogenic activity and the relative importance of wolves to shape the dynamics of an ecosystem is potentially much higher (Mech, 1966, 2012; McLaren and Peterson, 1994; Berger et al., 2001; Terborgh and Estes, 2010; Kuijper et al., 2016).

Human-induced trophic cascades

Humans might be able to initiate both density- and behaviourally-mediated trophic cascades, because not only can human disturbances, like hunting, elicit numerical and anti-predator responses in ungulates (Ciuti et al., 2012; Ripple and Beschta, 2004; Spitz et al., 2019, paper II), but these effects seem to be able to exceed those of large carnivores (Ciuti et al., 2012; Dorresjtein et al., 2015). For instance, while I did not detect cascading effects of wolf presence on browsing damage on Scots pine in south-central Sweden (paper IV), Mehlhoop et al. (2022) documented potential cascading effects of hunting risk on the recruitment of tree species browsed by moose in Norway (Fig. 7). Because I found that hunting risk did alter habitat selection of moose during the hunting season, which resulted in the avoidance of clearcuts/young forests (paper II), it is plausible that tree species found in clearcuts and young forests might experience some degree of release from browsing pressure during the hunting season, and unrelated to wolf presence, in my study area too.

Future research

There is increasing evidence that humans have a more prominent effect than carnivores on species at different trophic levels within anthropogenic landscapes, as compared to more pristine ecosystems (Ciuti et al., 2012; Dorresteijn et al., 2015; Mehlhoop et al., 2022), although these effects might be restricted to time periods when human activities are dominant. Seasonal variation in trophic cascades arises when measurement of the same "effects" at different time periods yields different ecologically relevant results, most likely because of shifting abiotic conditions (Piovia-Scott and Wright, 2017), like foraging availability and climate. A key question for future research is whether trophic cascades are not only context and species-dependent, but also season-dependent. There is an increasing need to understand whether humans elicit both density- and behaviourally-mediated trophic cascades that are temporally restricted to periods of high human activity, therefore making it possible for large carnivores to initiate top-down effects in periods of low human activity. In conclusion, the effects of large carnivores in anthropogenic landscapes are likely to be influenced by multiple factors, but ultimately, they depend on how much and for how long humans have perturbed the ecosystems in relation to long-term density of carnivores, and how these alterations affect both carnivores and the prey they share. Consequently, the behaviour of humans in response to the recolonization of large carnivores, such as wolves, will govern the impact of each predator in these types of ecosystems.

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Dissertation articles

Paper I

Accepted Ecosphere

Environmental and anthropogenic features mediate risk from human hunters and wolves for moose

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2

Paper II

Manuscript

Contrasting risk patterns from humans and wolves influence habitat selection of moose

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Keywords: *Alces alces*, anthropogenic landscape, anti-predator behaviour, *Canis lupus*, harvest, predation

Paper III
Manuscript

Effects of large carnivores, hunter harvest, and climate on the mortality of moose calves in a partially migratory population

Ausilio, G.[1], Sand, H.[2], Aronsson, M.[2], Wikenros, C.[2], Milleret, C.[3], Nordli, K.[1], Wabakken, P.[1], Eriksen, A.[1], Persson, J.[2], Maartmann, E.[1], Zimmermann, B.[1]

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Keywords: *Alces alces*, predation risk, *Canis lupus*, survival, ungulate, *Ursus arctos*, snow

4

Paper IV

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Ecological Effects of Wolves in Anthropogenic Landscapes: The Potential for Trophic Cascades Is Context-Dependent

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In recent years, large predators have made a comeback across large parts of Europe. However, little is known about the impact that recolonizing predators may have on ecosystems with high degrees of anthropogenic influence. In Scandinavia, wolves (*Canis lupus*) now inhabit areas affected by intense forestry practices and their main prey, moose (*Alces alces*), are exposed to significant human hunting pressure. We used long-term datasets to investigate whether the return of wolves has affected moose distribution (i.e., presence and abundance) as well as browsing damage (i.e., presence and intensity) by moose on Scots pine (*Pinus sylvestris*). We found that the probability of moose presence and abundance increased with time since wolf territory establishment and was higher inside wolf territories than outside. Additionally, the probability of browsing damage was also higher inside wolf territories compared to outside, but wolf occurrence had no effect on browsing damage intensity. We suggest two possible underlying mechanisms behind these results: (1) wolves might select to establish territories in areas with higher moose abundance, increasing their probability of encounters, and/or (2) hunters within wolf territories reduce the number of harvested moose to compensate for wolf predation. This study highlights that the return of large predators to landscapes with strong anthropogenic influence may result in alternative effects than those described in studies on trophic cascades located in protected areas.

Keywords: ***Canis lupus***, ***Alces alces***, ***Pinus sylvestris***, **pellet counts, browsing, predation, anthropogenic landscape, trophic cascade**

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INTRODUCTION

Predators often play a large role in shaping the ecological communities they inhabit (Estes et al., 2011; Ripple et al., 2014). They moderate prey populations by killing (lethal effects) or inducing behavioral and/or physiological changes in prey (non-lethal effects) (Fortin et al., 2005; Stoks et al., 2005; Trussell et al., 2006; Creel and Christianson, 2008). Predator-induced changes in the density and behavior of herbivore prey can results in altered plant community structure (McLaren and Peterson, 1994; Schmitz et al., 1997; Smith et al., 2003; Ripple and Beschta, 2004; Beyer et al., 2007), through density or behaviorally mediated trophic cascade, respectively (Estes and Duggins, 1995;

Halofsky and Ripple, 2008; Ripple and Beschta, 2012). For example, the reintroduction of wolves to Yellowstone National Park is believed to have reduced both the density of elk (*Cervus elaphus canadensis*) as well as the browsing intensity on riparian plant communities, which resulted in the recovery of plant species such as quaking aspen (*Populus tremuloides*) (Beschta et al., 2018) and willow (*Salix geyeriana*) (Beschta and Ripple, 2018). Importantly, an increasing number of studies has refuted this idea and provided alternative hypotheses for the observed changes in elk density and plant communities in Yellowstone National Park, such as human harvest and climate, respectively (Vucetich et al., 2005; Creel and Christianson, 2008; Kauffman et al., 2010), as well as sampling bias (Brice et al., 2020). So far, the majority of studies focusing on trophic cascades have been conducted in protected areas with no or little anthropogenic influence, like national parks (Kuijper et al., 2013), however, such dynamics remain to be explored outside of protected areas. Where predators and humans share landscapes, the predators' effect on the prey and other trophic levels may be modified by human activities such as land use and hunting (Kuijper et al., 2016). Because land-use practices such as agriculture and forestry are among the main drivers influencing landscape features, the distribution of predation risk within a landscape will vary and could result in behavioral changes in ungulate prey (Kuijper et al., 2016). Land-use can also alter the productivity and plant species composition, thus influencing the distribution and availability of resources used by prey and predators in a landscape (Bjørneraas et al., 2011; Kuijper et al., 2016). Human hunting of the same prey populations as large predators is also likely to modify the dynamics and extent of predator-prey interactions in anthropogenic landscapes (Kuijper et al., 2016). For instance, human harvest may outweigh the impact of large predators on prey demography (see Gervasi et al., 2012), which could reduce or hinder the potential for large predators to affect prey abundance as they would in the absence of human hunting (e.g., in national parks). It is therefore, likely that returning large predators will have a less pronounced role in anthropogenic ecosystems compared to protected ones (Sergio et al., 2008; Kuijper et al., 2016).

In Scandinavia, recolonizing wolves (*Canis lupus*) (Wabakken et al., 2001) now inhabit landscapes that are affected through intense forestry practices and where their main prey, moose (*Alces alces*) (Sand et al., 2005, 2008), are exposed to some of the highest harvest levels in the world due to a high moose density and productivity (Lavsund et al., 2003). In winter, moose mainly browse on Scots pine (*Pinus sylvestris*) (Cederlund, 1980; Hörnberg, 2001)—a commercially important tree species—and consequently cause browsing damage, which reduces the quality of timber and results in economic losses (Lavsund, 1987; Bergqvist et al., 2001). Wolves have therefore, not only the potential to affect both population density and behavior of moose, but may also have an indirect impact on the presence and intensity of browsing damage. However, most of the previous findings in Scandinavia have not confirmed either a density (Wikenros et al., 2015) or behavioral effect of wolves on moose (see e.g., Nicholson et al., 2014; Wikenros et al., 2016; Månsson et al., 2017). A recent study found that moose browsing damage on Scots pine in south-central Sweden was higher inside wolf territories than outside (Gicquel et al., 2020). These results contrast with several studies of wolf-moose-plants systems in North America (Fortin et al., 2005; Ripple and Beschta, 2012; Painter et al., 2015; Ditmer et al., 2018). Such a difference may be explained by different degrees of anthropogenic impact in these systems (Kuijper et al., 2016), which may change or reduce the ecological effects of wolves on other trophic levels. Understanding the strength and the relative role of predation within human-influenced landscapes can have considerable implications for wildlife management and conservation. For instance, ungulate populations under the pressure of both predation and human harvest may decline (Vucetich et al., 2005). The possible context-dependence of top-down processes in ecosystems is becoming an increasingly important topic, as apex predator populations are recovering in large areas of Europe (Chapron et al., 2014) and North America (Ripple et al., 2014) with high degrees of anthropogenic landscapes.

In this study, we tested the hypotheses that wolf presence and time since wolf territory establishment result in: (1) a negative effect on moose presence and abundance, and (2) a change in habitat use of moose to avoid wolf encounters. We further hypothesized that if wolf presence and time since wolf territory establishment are negatively correlated to moose presence and abundance, this could potentially reduce browsing damage on Scots pine trees. Hence, we also tested the hypothesis that (3) wolf presence and time since wolf territory establishment are negatively associated with presence and intensity of browsing damage on Scots pine trees. Finally, we investigated the influence of human activities on moose and browsing damage by including variables mirroring either anthropogenic attributes or human-controlled features in the landscape, such as roads and silviculture (i.e., forest age stages).

MATERIALS AND METHODS

Study Area

The study was conducted between 2003 and 2016 across the breeding range of wolves in south-central Sweden (56°50′–63°N, 11°50′–17°E, approximately 102,916 km^2). The landscape is dominated by intensively managed boreal forest (Jansson and Antonson, 2011) and the predominant tree species are Scots pine, Norway spruce (*Picea abies*) and birch (*Betula* spp.) (Christiansen, 2014). During the study period, the wolf population increased from 22 to 54 family groups and territorial pairs (Wabakken et al., 2004, 2016). The dominant prey species of wolves within the study area is moose followed by roe deer (*Capreolus capreolus*) (Sand et al., 2005, 2008). Moose winter density within the study area averages approximately 1.3 per km^2 (Zimmermann et al., 2014). Scots pine represents quantitatively the most important food source for moose during winter in Sweden, despite being less selected than several less common deciduous species (Cederlund, 1980). Moose select for rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and willows (*Salix* spp.), but also browse on other species such as silver birch

(*Betula pendula*), downy birch (*Betula pubescens*), and Scots pine (Månsson et al., 2007).

Moose Pellet Counts

Pellet group counting can serve as an indirect method to index ungulate abundance in order to estimate densities and manage populations (Bennett et al., 1940; Neff, 1968; Mayle et al., 1999; Marques et al., 2001; Smart et al., 2004). We used pellet group counts to gather presence and absence data on moose and to calculate a relative index for moose abundance. The Swedish National Forestry Inventory carries out yearly surveys of moose pellet counts throughout south-central Sweden (Tokola, 2006; Fridman et al., 2014). Moose pellet counts surveys are conducted between May and September in forest habitats belonging to either one of four different forest age stages in accordance with silvicultural practices: (1) clear-cut, when there are no or very few, sparse trees; (2) young, when the average height in the stand is between 1 and 4 m; (3) thinned, when the majority of trees in a stand are larger than 10 cm in diameter at chest height; and (4) mature, when the forest stand has reached the lowest recommendable final felling age (between 65 and 100 years for Scots pine; Fries et al., 2015). We considered forest of different age stages as proxies for human-controlled features in the landscape, since they are strictly regulated through specific silvicultural practices aimed at maximizing production of commercially important tree species. During our study period, a total of 10,358 circular sample plots (area = 38 m^2) were surveyed (range of plots sampled per year: 578–802).

Moose Browsing Damage

Moose browsing damage is recorded by the Swedish National Forestry Inventory during spring, within the same sample plots used for the pellet count survey, using a nationwide moose browsing damage monitoring scheme (Äbin; Kjellander, 2007; Kalén et al., 2018). The method generates an index of browsing intensity by estimating the proportion of damaged trees, i.e., bark stripping, stem breakage and browsing on top shoots (Bergman and Åkerberg, 2006). The survey is restricted to young Scots pine stands with more than 10% pine trees within a plot and a height between 1 and 4 m (725 sample plots between 2003 and 2016). Browsing damage caused during the preceding winter is categorized as fresh, whereas older damage is classified as non-fresh damage, including dead trees and other malformations known to be caused by moose browsing damage (e.g., multiple stems). Browsing damage was aged by the color of the bite surface and resins, as well as by the amount of dead bark tissue beneath the bites. We classified the presence or absence of fresh browsing damage within a plot as the presence or absence of freshly damaged trees (hereafter browsing damage). The number of trees with fresh damage was used as a proxy for browsing damage intensity.

Tree Cover

The cover of aspen, rowan, willow, pedunculate oak (*Quercus robur*), Scots pine, and lodgepole pine (*Pinus contorta*) was recorded in larger sample plots of 7 m radius (153 m^2), with the same plot-centroid as for moose pellet counts and browsing damage surveys. These plots are surveyed to record the cover of living parts of tree species within the browsing height of moose (0.3–2.5 m). We summed the cover (m^2) of lodgepole pine and Scots pine (hereafter pine) and converted it to a proportion to generate an index of food availability for tree species that are quantitatively important for moose during winter. We also generated an index of food availability for tree species that are highly selected by moose by summing the cover (m^2) of aspen, rowan, willow and oak (hereafter RAWO). However, due to a high amount of sample plots without the occurrence of RAWO species, we converted the food availability index for RAWO to a two-categorical variable (presence or absence of RAWO species).

Roads

The Swedish national road database was obtained from the Swedish Transport Administration. In this database, roads are divided into functional classes (0–9) according to their importance to the connectivity of the total Swedish road network (Trafikverket, 2017). Roads belonging to classes 0–6 include national, regional and local roads, whereas forest roads belong to classes 7–9. Road data were divided into two groups according to the same classification as the Swedish national road database: (I) forest roads (7–9), and (II) main roads (0–6). Distance (km) between each plot and the nearest main and forest road was calculated in ArcGIS (Version 10.7.1; Environmental Systems Research Institute). Distance to forest and main roads were considered as proxies representing anthropogenic features of the landscapes.

Wolf Presence and Time Since Wolf Territory Establishment

We used two variables to test the effect of wolves on moose presence and browsing damage: (a) wolf presence (2-level categorical: presence or absence of a wolf territory), and (b) time since wolf territory establishment (continuous, range 1–27 years, where 1 equals the year of wolf territory establishment), both obtained from the national wolf-monitoring system conducted annually by the County Administrative Boards (Liberg et al., 2012). The range of wolf territories was calculated using the 100% minimum convex polygon method (MCP; Mohr, 1947) based on available locations during the monitoring season (October to February/March; Wabakken et al., 2004, 2016). Locations were obtained by snow tracking, DNA-samples and GPS locations of collared individuals. Since we do not have full knowledge about the true borders of the wolf territories, we created a buffer around each polygon centroid based on the average wolf territory size in Scandinavia (radius 18.0 km, average size = 1,017 km^2; Mattisson et al., 2013). Each sample plot was then classified as: (a) **inside** an average wolf territory, when the plot was located either within the observed borders of a wolf territory (monitoring scheme) or within a distance corresponding to the average wolf territory radius from the nearest polygon centroid; or (b) **outside** a wolf territory if the distance from the nearest polygon centroid was longer than the radius used to classify an average territory (**Supplementary Appendix S1**: **Supplementary Figure S1**; Wikenros et al., 2017).

We noticed that many of the plots classified as outside during the year of the inventory had been inside a wolf territory for several years just before the inventory year. This meant that potential spatial and temporal effects of wolf presence could be missed if sample plots were categorized as outside just based on their location during the year of the inventory. Therefore, we extended the definition of a plot classified as inside to include a plot that was outside a wolf territory the year of the inventory, but had been inside for ≥ 3 consecutive years without gaps of ≥ 3 years since the first year of wolf territory establishment for that sample plot. We set our year gap threshold to ≥ 3 years because prey species can re-adapt to the presence of predators in an as short time as one generation, which for moose may correspond to 4 or 5 years (Berger et al., 2001b; Laundré et al., 2001; Sand et al., 2006). Time since territory establishment was calculated as the total sum of years a plot had been inside, or was classified as inside, a wolf territory. Time of territory establishment for plots classified as inside the year of the inventory but with gaps of ≥ 3 years since the first year of wolf establishment was calculated as the sum of years inside a territory after the gap.

Statistical Analysis

To investigate the relative influence of wolf presence on moose and browsing damage, we divided the analyses in two parts based on the response variables and then used two approaches to analyze them: (i) binomial (i.e., presence and absence of moose or browsing damage) and (ii) continuous (i.e., moose abundance and browsing damage intensity). We modeled the probability of moose presence and browsing damage using logistic regressions (0 = absent, 1 = present). Because moose abundance and browsing damage intensity were both zero-inflated and over-dispersed (Harrison, 2014; Fox et al., 2015), we used zero-inflated negative binomial models. For moose presence and abundance, we added six explanatory variables in addition to wolf presence or time since wolf territory establishment: pine proportion, RAWO presence, distance to the nearest forest road (km), distance to the nearest main road (km), and forest age stage (4-level categories). We included an interaction term between forest age stage and wolf presence/time since territory establishment to test the hypothesis of a change in habitat use by moose in response to the return of wolves. For browsing damage (presence and intensity), we also included six explanatory variables in addition to wolf presence or time since wolf territory establishment: moose abundance, previous browsing damage (number of trees), pine proportion, RAWO presence, distance to forest roads (km) and main roads (km). We included year of inventory as a random factor in all analyses to account for year effects.

We standardized all continuous predictors by subtracting the mean from our predictor variables and then dividing it by its standard deviation, and used sum-to-zero contrasts on the categorical variables. Sum-to-zero contrasts code categorical variables as deviations from a grand mean, which is conceptually similar to centering continuous variables and then dividing them by two standard deviations. Standardizing continuous variables can eliminate collinearity between interactions and the individual covariates, as well as improve the interpretability of both interactive and individual coefficients in a regression, without affecting inference about the different covariates (Engqvist, 2005; Schielzeth, 2010). We tested for potential multicollinearity between our explanatory variables using Variance Inflation Factors (VIF) and tolerance values obtained using the *check_correlation* function in the "*performance*" package (Lüdecke et al., 2020). The analysis showed that there was low to no correlation in all of our models (see **Supplementary Appendix S1**: **Supplementary Figure S2** and **Supplementary Appendix S2**: **Supplementary Table S1**).

We compared models using the Akaike information criterion (AIC), ΔAIC and AIC weights (w_i) from the *dredge* function in the "*MuMIn*" package (Barton and Barton, 2019) to identify the most parsimonious models. Model averaging was then used to retain all models with ΔAIC <2 and to generate model-averaged parameter estimates (Burnham and Anderson, 2002) which were then back-transformed. For all the logistic regression models, we also assessed the contribution of random effects and predictors by using pseudo-R^2, which are equivalent of R^2 in ordinary logistic regression, but specifically for logistic regression analysis. For mixed-effects models, pseudo-R^2 was defined in two ways, called marginal and conditional. The former provides a measure of the variance explained by the fixed effects, whereas the latter shows the variance explained by the whole model (random and fixed effects) (Barton and Barton, 2019).

Supplementary analyses using an additional classification of wolf presence based on territory size according to Mattisson et al. (2013) are available in **Supplementary Appendix S3**. These were carried out as a way to account for potential bias in the classification of sample plots as inside or outside a wolf territory, since the true borders of a territory are unknown. Using this alternative classification of wolf presence did not alter the results obtained with the original 2-category classification. All statistical analyses were conducted in R [version 3.6.1. (R Core Team, 2018)] using standardization and multicollinearity analyses in the *performance* package (Lüdecke et al., 2020), general linear mixed models in the *lme4* package (GLMM; Bates et al., 2015), zero-inflated mixed models in the *glmmTMB* package (Brooks et al., 2017), R^2 analysis in the *MuMIn* package (Barton and Barton, 2019) and plot modeling in the *SjPlot* package (Lüdecke and Lüdecke, 2017).

RESULTS

Moose Presence and Abundance

The top-ranked model predicted the probability of moose presence to increase with wolf presence (β = 0.12, *SE* = 0.031, **Figure 1A**) and time since wolf territory establishment (β = 0.06, *SE* = 0.03, **Figure 1B**; see **Supplementary Appendix S1**: **Supplementary Figure S3A** for forest plots and **Supplementary Appendix S2**: **Supplementary Table S2** for models). None of the top-ranked models included the interaction between wolf presence and forest age stage. The top-ranked model for moose abundance also indicated that moose abundance was higher where wolves were present (β = 0.1, *SE* = 0.03, **Figure 2A**) and increased with time since wolf territory establishment (β = 0.1, *SE* = 0.04, **Figure 2B**; see **Supplementary Appendix S2**: **Supplementary Table S3** for models).

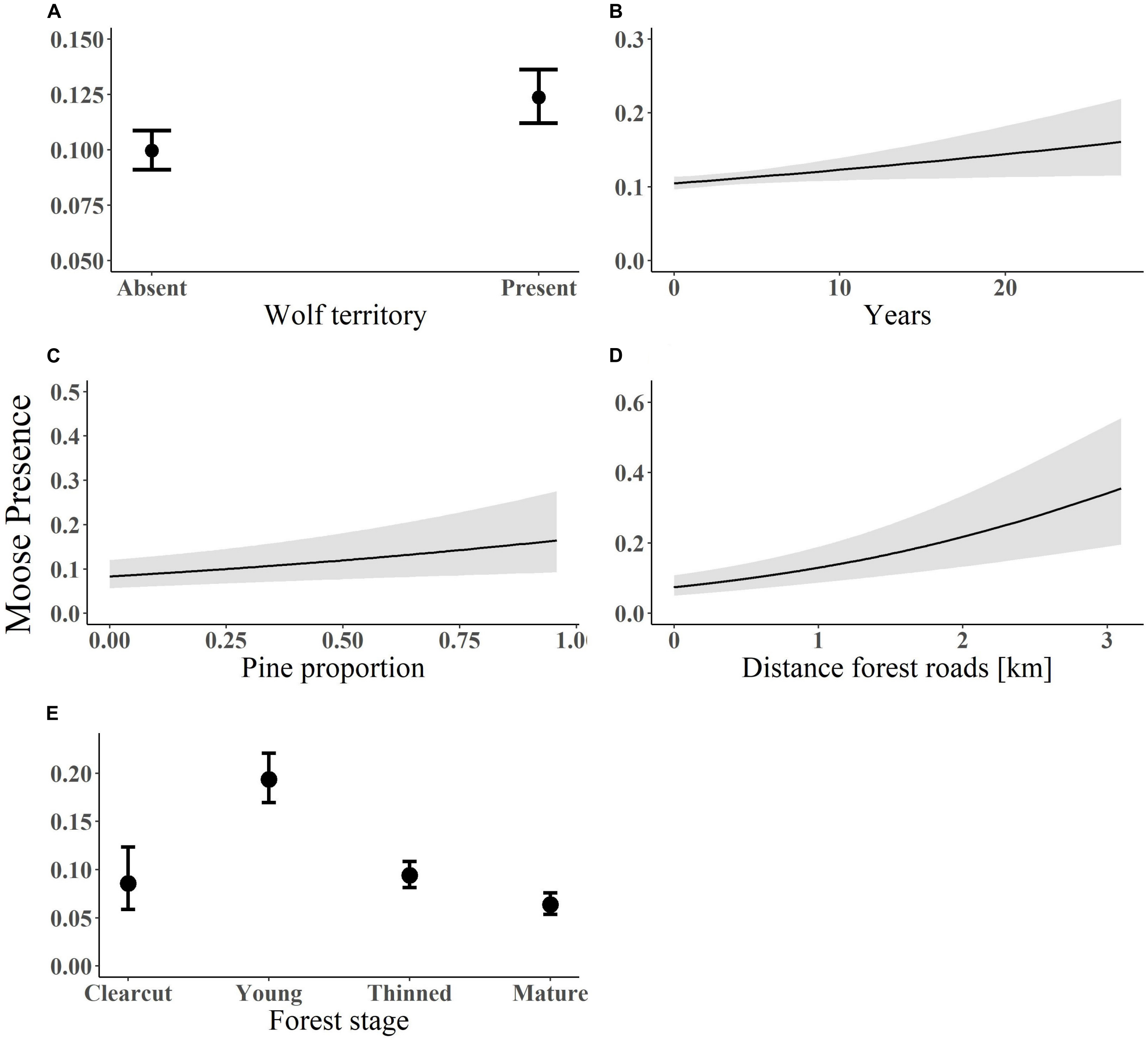

FIGURE 1 | Predicted probability of moose presence in relation to **(A)** wolf presence; **(B)** years since wolf territory establishment; **(C)** pine proportion; **(D)** distance from forest roads; and **(E)** forest age stage. Data on moose presence was recorded in south-central Sweden between 2003 and 2016. The lines (in plot **B–D**) represent the fitted values and associated standard errors from the model-averaged estimates. Plot a and e show the coefficients and confidence intervals of the predicted probability of moose presence in relation to the presence/absence of a wolf territory **(A)** and across four forest age stages **(E)**.

Probability of moose presence increased with pine proportion (β = 0.76, *SE* = 0.27, **Figure 1C**), distance from forest roads (β = 0.14, *SE* = 0.03, **Figure 1D**) and was higher in young forests (β = 0.9, *SE* = 0.2, **Figure 1E**; see **Supplementary Appendix S1**: **Supplementary Figure S3B** for forest plots and **Supplementary Appendix S2**: **Supplementary Table S2** for models). The fixed factors explained 8% of the variation in moose presence. Moose abundance increased with distance from forest roads (β = 0.11, *SE* = 0.04, **Figure 2C**), was higher in young forests (β = 0.9, *SE* = 0.17, **Figure 2D**), but decreased with distance from main roads (β = -0.08, *SE* = 0.04, **Figure 2E**; see **Supplementary Appendix S2**: **Supplementary Table S3** for models). In the zero-inflated part of the model for moose abundance, pine proportion, and distance from main roads had a negative effect on the probability of an extra zero, i.e., there was a lower probability of moose absence with increasing pine proportion and distance from main roads. The standardized regression coefficients showed that young forests and proportion of pine were the two most important variables explaining both moose presence and abundance, followed by distance to forest roads and wolf presence.

Browsing Damage

Wolf presence was included in the top-ranked models, which predicted the probability of browsing damage to be higher inside wolf territories than outside (β = 0.14, *SE* = 0.13; **Figure 3A**; see **Supplementary Appendix S1**: **Supplementary Figure S2** for forest plots and **Supplementary Appendix S2**:

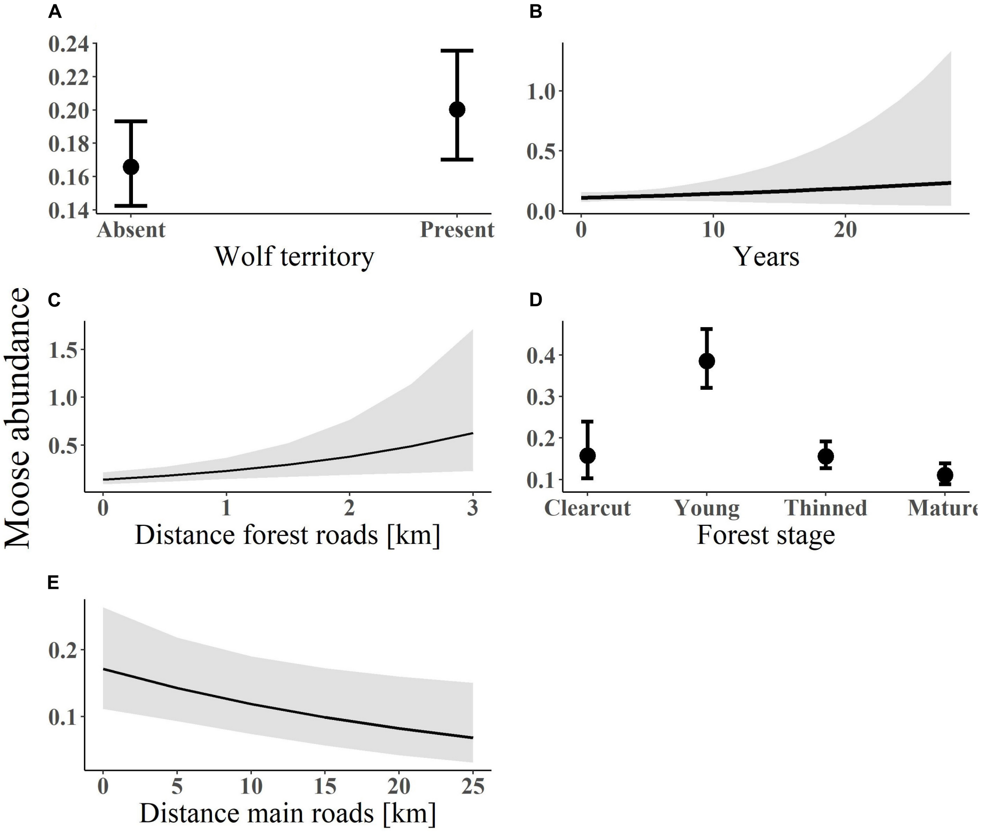

FIGURE 2 | Predicted values of moose abundance (measured as the number of pellet counts) in relation to **(A)** wolf presence; **(B)** years since wolf territory establishment; **(C)** distance from forest roads; **(D)** forest age stage; and **(E)** distance from main roads. Data on moose pellet counts were recorded within south-central Sweden between 2003 and 2016. The lines (in plot **B–E**) represent the fitted values with associated standard errors from the model-averaged estimates. Plot a and d show the coefficients and confidence intervals of the predicted values of moose abundance in relation to presence/absence of a wolf territory **(A)** and across four forest age stages **(D)**.

Supplementary Table S3 for models). The top-ranked models for browsing damage intensity did not include wolf presence or time since wolf territory establishment.

Additionally, the probability of browsing damage increased with distance from main roads (β = 0.21, *SE* = 0.11; **Figure 3B**), with moose abundance (β = 0.33, *SE* = 0.10, **Figure 3C**) and with previous browsing damage (β = 0.50, *SE* = 0.09; **Figure 3D**), but decreased with proportion of pine (β = −0.11, *SE* = 0.15, **Figure 3E**; see **Supplementary Appendix S1**: **Supplementary Figure S3B** for forest plots and **Supplementary Appendix S2**: **Supplementary Table S4** for models). The whole model explained 17% of the variation in browsing damage (15% by fixed factors). In the conditional part of the top-ranked browsing damage intensity model, intensity increased with moose abundance (β = 0.2, *SE* = 0.07, **Figure 4A**), distance from forest roads (β = 0.2, *SE* = 0.09, **Figure 4B**) and distance from main roads (β = 0.14, *SE* = 0.09, **Figure 4C**), previous browsing damage (β = 0.57, *SE* = 0.09, **Figure 4D**) and was higher in plots with presence of RAWO (β = 0.5, *SE* = 0.2, **Figure 4E**; see **Supplementary Appendix S2**: **Supplementary Table S5** for models). In the zero-inflated part of the model, moose abundance and previous browsing had a negative effect on the probability of an extra zero, i.e., there was a smaller probability of browsing absence with increasing moose abundance and previous browsing. Previous browsing damage and moose abundance were the two most important variables explaining the presence of fresh moose browsing damage, followed by distance from main roads and wolf presence. Variation in browsing damage intensity, however, was best explained by previous browsing damage and RAWO presence, followed by moose abundance and distance from forest roads (see standardized coefficients above).

DISCUSSION

Moose Presence and Abundance

Contrary to our predictions, the probability of moose presence and moose abundance increased with time since wolf territory establishment and was higher inside wolf territories. Further, we found no support for our second hypothesis that moose have responded to the presence of wolves by changing habitat (in this case, forest age stages). A possible explanation may be that wolves establish their territories in areas with higher moose

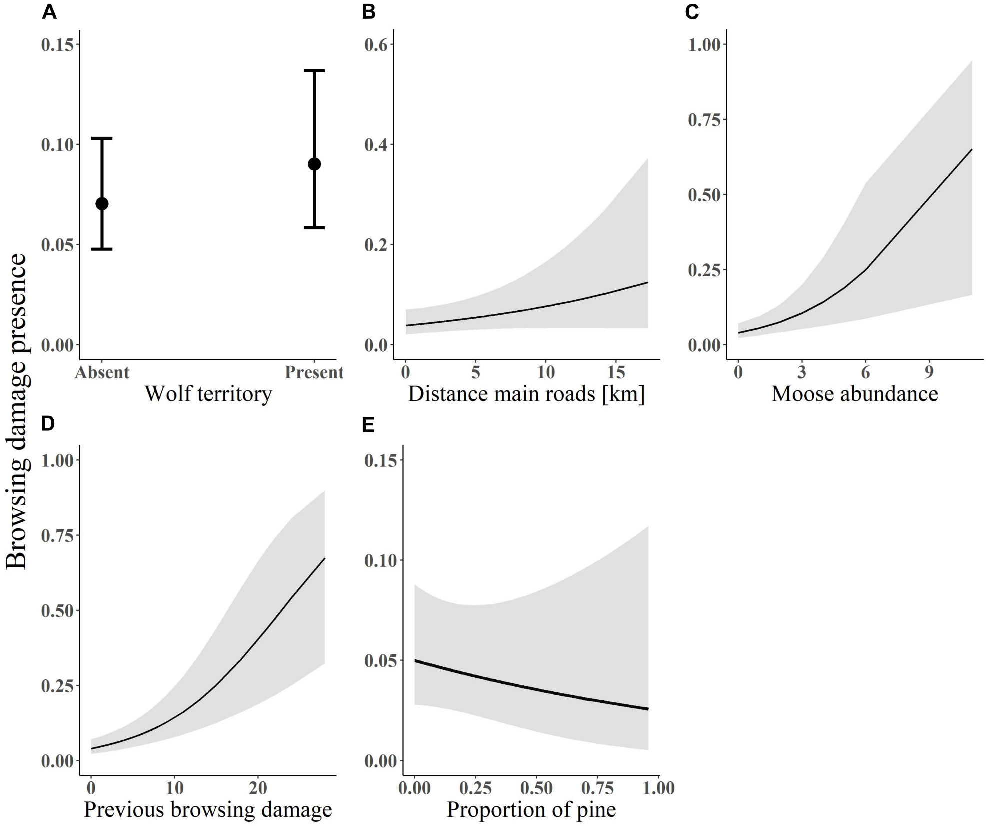

FIGURE 3 | Predicted probability of browsing damage presence on pine in relation to **(A)** wolf presence; **(B)** distance from main roads; **(C)** moose abundance; **(D)** previous browsing damage; and **(E)** pine proportion. Data on browsing was collected within south-central Sweden between 2003 and 2016. The lines (in plot **B–D**) indicates the fitted values with associated standard errors from the model-averaged estimates. Plot a shows the coefficients and confidence intervals of the predicted probability of browsing damage presence in relation to presence/absence of a wolf territory.

density to increase encounter rates. Selecting areas with high prey density allows predators to maximize prey encounter rate, which in turn increases the chances of successful predation (Bergman et al., 2006; Hopcraft et al., 2010). Previous research from North America shows that wolves disproportionately use areas of high moose abundance, and hunt in areas with a higher likelihood of encountering prey (Kittle et al., 2017; Woodruff et al., 2018). In Scandinavia, wolves maximize their hunting success by actively searching in areas of higher moose density, where the detection of prey, and hence an attack, are more likely to be successful (Gervasi et al., 2013). Additionally, during the early phases of recolonization in Scandinavia, wolves established in areas with high relative moose density (Wikenros et al., 2015). A decade after wolf establishment, moose densities in those areas were still high enough to sustain a larger moose harvest than in areas with no wolves (Wikenros et al., 2015), providing a potential explanation for the positive relationship found between moose presence/abundance and time since wolf territory establishment.

We suggest an additional, but not mutually exclusive, explanation for why moose presence and abundance was higher inside wolf territories compared to outside. When wolves re-established in Sweden, human hunters responded by reducing both the total number of individuals and the proportion of females harvested (Wikenros et al., 2015). The most severe reductions were observed the first year after wolf territory establishment (Wikenros et al., 2015). Thus, the higher abundance of moose in wolf territories could be from lowered human harvest (i.e., an indirect effect of wolf re-establishment) rather than a direct result of wolves. As well, moose hunters preferentially harvest calves and adult males (Nilsen et al., 2005; Nilsen and Solberg, 2006), whereas wolves favor calves and old females (Sand et al., 2008, 2012). This results in a stronger effect of hunter harvest on moose population growth per unit kill compared to wolves (Wikenros et al., 2015). Hence, the positive relationship between moose presence/abundance and wolf presence could also be explained by the fact that once wolves have established a territory, hunters within that area reduce and/or change the composition of the harvest of moose to compensate for moose mortality caused by wolves (Sand et al., 2012). This could lead to an overall higher probability of moose presence and abundance within wolf territories.

While we found a weak, positive effect of wolves, other variables were more important in affecting both moose presence and abundance, such as forest age stage and forage availability (in this case, the proportion of pine). Moose were likely to be present and more abundant in young forests, which is in accordance with previous research (Gundersen et al., 2004). Forage availability has repeatedly been shown to be an important

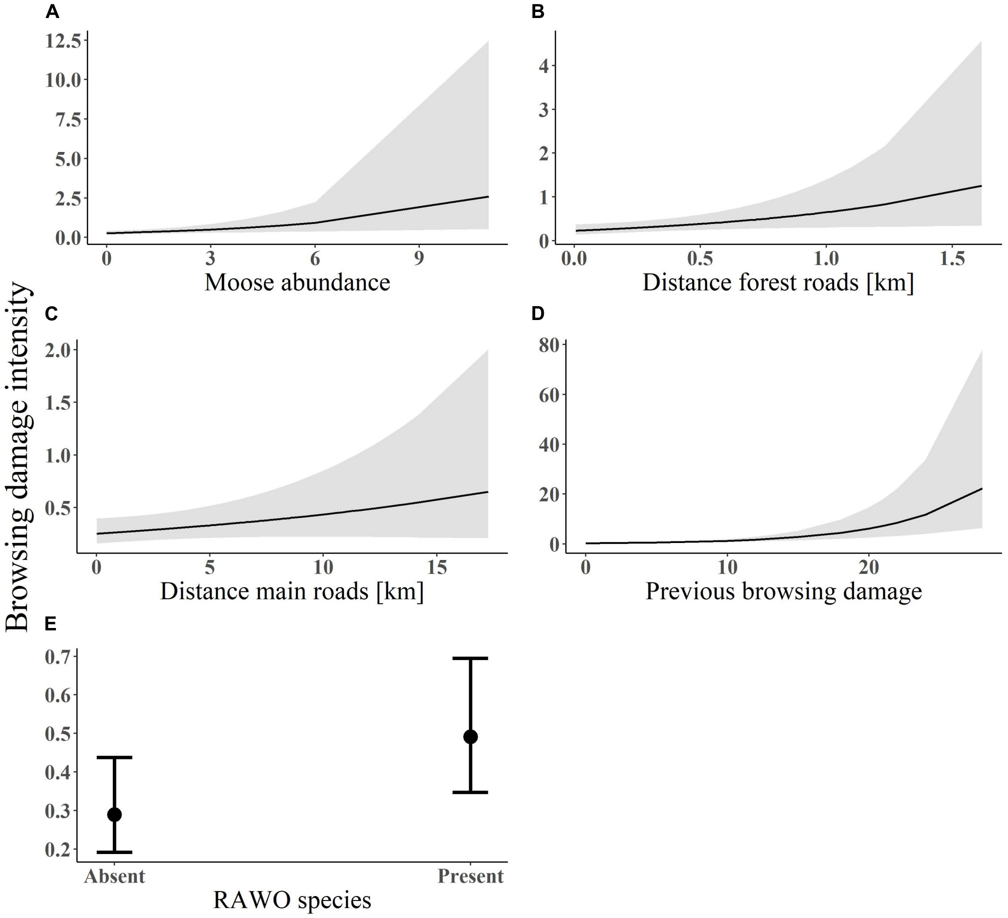

FIGURE 4 | Predicted values of browsing damage intensity (number of damaged stems per plot) in relation to **(A)** moose abundance; **(B)** distance from forest roads; **(C)** distance from main roads; **(D)** previous browsing damage; and **(E)** RAWO presence. Data on browsing damage was collected within south-central Sweden between 2003 and 2016. The lines in figure **A–D** indicate the fitted values with associated standard errors from the model-averaged estimates. Plot **(E)** shows the coefficients and confidence intervals of the predicted values of browsing damage intensity in relation to presence/absence of RAWO (rowan, aspen, willow and oak) species.

factor for explaining spatial distribution of moose and other ungulates (Senft et al., 1987; Edenius et al., 2002; Månsson et al., 2012), and in this study moose were more abundant where there was a higher proportion of pine trees. Moreover, moose presence and abundance increased with increasing distance from forest roads, supporting previous findings that moose avoided forest roads (Laurian et al., 2012). The avoidance of forest roads may be caused by the presence of heavy equipment and logging trucks that act as disturbance (Van Langevelde et al., 2009), but also because hunters and wolves use forest roads (James and Stuart-Smith, 2000; Whittington et al., 2005; Houle et al., 2010; Zimmermann et al., 2014). Our results indicate that environmental and human factors were more important than the presence of a predator in explaining moose presence and abundance. In our study, we included distance to forest and main roads and forest age stage as proxies for human influence in the landscape, but our models could only explain a small portion of the variation in moose presence and abundance. This indicates that other factors, such as human hunting, may be important players in shaping moose populations. Unfortunately, hunting statistics for our study area and period were unavailable and could therefore not be included.

Browsing Damage

We did not find support for our hypotheses that wolf presence and time since territory establishment would be negatively correlated with the presence and intensity of browsing damage. In fact, our results showed that the probability of browsing damage was higher inside wolf territories, which is in contrast with previous studies [see e.g., Ripple et al., 2001; Ripple and Beschta, 2006, 2007; Beyer et al., 2007 for effects of wolves on browsing by elk (*Cervus elaphus*)]. The higher probability of browsing damage inside wolf territories is likely a result of the higher probability of moose presence and abundance also found within wolf territories. Our findings on browsing damage are similar to those of Gicquel et al. (2020), who also found higher browsing damage inside wolf territories than outside. Compared to Gicquel et al. (2020) our study occurred over a longer time-period and included moose abundance derived from pellet counts instead of bag size, which are higher spatial resolution data. Nevertheless, although the time periods, spatial scale studied and some of the explanatory variables differed, both our studies showed that moose browsing damage is higher inside wolf territories compared to outside. However, we found that the most important factors affecting the presence and intensity of browsing damage were previous browsing damage, moose abundance and RAWO presence. The positive correlations between browsing damage and moose abundance are in accordance with other studies (Månsson et al., 2007). Previous browsing has also been identified as an important predictor of fresh browsing intensity by moose (Bergqvist et al., 2003; Mathisen et al., 2017), here supported by a positive correlation between previous and fresh browsing damage. In addition, we found significantly lower levels of fresh browsing near forest roads, which is likely a consequence of moose avoiding forest roads.

Our findings are supported by recent studies showing that human-modified attributes and environmental factors are more important for moose abundance and browsing damage than wolf presence and time since wolf territory establishment (Gicquel et al., 2020). These results contrast with studies from protected areas where wolves have both density and behaviorally mediated effects on lower trophic levels (Fortin et al., 2005; Ripple and Beschta, 2012; Ripple et al., 2015; Ditmer et al., 2018). In protected areas such as Yellowstone National Park, there is often little to no anthropogenic activity and therefore, the relative importance of wolves to shape the dynamics and functions of an ecosystem is potentially higher (Mech, 1966, 2013; McLaren and Peterson, 1994; Berger et al., 2001a; Terborgh and Estes, 2010; Kuijper et al., 2016). However, the existence and extent of such effects is still being investigated and questioned (Kauffman et al., 2010; Winnie, 2012; Brice et al., 2020). Outside of protected areas, however, the effects of predators on the density and behavior of the prey populations may be reduced and/or altered due to anthropogenic activities that have a much stronger impact on most trophic levels, from vegetation to herbivores and large predators (Eriksen et al., 2011; Mech, 2012; Kuijper et al., 2016; Gicquel et al., 2020). Dorresteijn et al. (2015) found that both direct and indirect effects of humans influenced the ecosystem, and all trophic levels within it, more strongly than other apex predators did. Because humans can influence both predators and their prey, they also strongly shape the potential for trophic cascades, either by directly affecting their densities or/and their behaviors or indirectly by modifying the resource landscapes exploited by both predators and prey (Kuijper et al., 2016).

In Scandinavia, human harvest has functionally replaced natural predation on moose by wolves throughout the last century (Sand et al., 2006). Hunter harvest accounts for most of the moose mortality both on a national scale (Laundré et al., 2001) and within most wolf territories (Wikenros et al., 2015). Where moose mortality from natural predators is absent or lower (wolf territories) compared to hunting-related mortality, anti-predator behaviors may take a longer time to be selected for, as the hunting pressure from humans may lead to selection against such traits (Sand et al., 2006; Kuijper et al., 2016). Standing ground and being aggressive toward wolves has been documented as the most successful anti-predator behavior for moose in e.g., Isle Royale (Mech, 1966, 1970; Peterson, 1977). However, moose in Scandinavia were less likely to make a stand when attacked by wolves and instead chose to flee (Wikenros et al., 2009). Such differences in behavior may be a result of the hunting mode and the constant hunting pressure Scandinavian moose have been exposed to for more than 100 years. Moose in Scandinavia are often hunted using baying dogs to keep the moose at bay while the hunter stalks the moose. Hence, taking a stand and being aggressive toward baying dogs and hunters would likely increase the chances of being shot compared to fleeing, and will therefore be selected against. Additionally, the response of hunters to the return of wolves may also influence moose densities (Wikenros et al., 2015). Hunters may decide not to change moose harvest to compensate for wolf mortality (Wikenros et al., 2015) and in that case the additive mortality of wolves and hunters may lead to reduced moose densities (Jędrzejewski et al., 2000). In anthropogenic landscapes, humans can also affect predators and prey by modifying the availability and quality of resources (Kuijper et al., 2016). For instance, forestry practices create clear-cuts, which results in the recruitment of attractive forage species for ungulates such as rowan, aspen, and willow (Kuijper et al., 2009). Consequently, the behavior of humans in response to the recolonization of large predators such as wolves will ultimately govern the impact of predators in these types of ecosystems. Future research about the ecological effects of large predators in anthropogenic landscapes should include humans because of the great impact humans have on ecosystems all across the globe (Steffen et al., 2007).

CONCLUSION

Our findings add to the growing body of literature investigating the ecological effects of large carnivores in human-dominated landscapes. In our study, the predator's presence was positively correlated with prey abundance and browsing damage. This is in contrast to research from North America. However, we found that other human and environmental variables were more important for moose abundance and browsing damage. There is increasing evidence that human influence may be more prominent than carnivores in affecting species at different trophic levels within anthropogenic landscapes compared to more pristine ecosystems (Dorresteijn et al., 2015). This suggests that the potential for large predators to initiate trophic cascades is context-dependent, but also that previous studies of predator-prey interactions carried out in protected areas may not be representative of the ecological effects of large predators on prey over vast areas of the world. A key question is therefore, to understand how natural and human predators interact with each other to influence ungulate populations across different gradients of anthropogenic pressure, and how bottom-up processes, which humans also modify, can influence such interactions. Studies increasing the understanding about how and to what extent human activities influence the functional role of large carnivores in anthropogenic landscapes have important conservation and management implications.

DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found in the online repositories. The names of the repository/repositories and accession number(s) can be found below: https://datadryad.org/stash/share/svRCeH_hvPZVH2UjmzWQOvErl-B6deccaKMXgGEeHtM, Dryad Repository.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because no invasive techniques were used in the study.

AUTHOR CONTRIBUTIONS

GA conceived and designed the study, compiled data, carried out the statistical analyses, and drafted the manuscript. HS secured funding, conceived and designed the study, and revised the manuscript. JM secured funding, conceived and designed the study, and revised the manuscript. KM revised the manuscript. CW secured funding, conceived and designed the study, and revised the manuscript. This work derives in part from a master thesis conducted by GA and supervised by CW, HS, and JM. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.577963/full#supplementary-material

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Predator-prey interactions are important drivers of ecosystems dynamics that are influenced by factors such as landscape features and hunting modes of predators. Within anthropogenic landscapes, predator-prey interactions can be altered by human activities such as hunting and forestry practices, which can lead to changes in the density, behaviour and survival of both predator and prey species. In many anthropogenic systems, human harvest has become the main mortality source for several ungulate prey populations. In this thesis, I wanted to 1) assess the spatial attributes of hunter-killed and wolf *(Canis lupus)*-killed moose *(Alces alces)* during and after the hunting season; 2) investigate habitat selection of moose in relation to hunting and wolf predation risk; 3) evaluate moose calf mortality in relation to risk from humans and large carnivores and 4) assess whether wolves had triggered either density- or behaviourally-mediated trophic cascades involving moose and Scots pine. I found that hunting and wolf predation risk varied spatiotemporally, but moose responded to the stronger, more predictable risk: hunting. Calf mortality was negatively associated with both hunting and wolf predation risk. However, wolves did not elicit behavioural responses in moose consistent with the avoidance of risky places during risky times, nor triggered cascading effects on lower trophic levels. The decreased availability of food resources during winter may force moose to select habitats with greater forage opportunities that are simultaneously coupled with a greater risk of wolf predation (e.g., clearcuts/young forests). Hence, the potential for wolves to initiate trophic cascades might be dampened, or even cancelled, by the need for moose to find optimal foraging places during winter.