Patterns and processes of recovering large mammal communities



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Declaration of authorship

The work presented in this thesis is my own. In each of the chapters presented here, I have developed the aims, concepts, and methodology, I performed the analyses, interpreted results, and written the manuscripts. During my thesis chapters, I have been lucky to collaborate with several excellent scientists. Below, I provide a full list of co-authors and a statement of their contributions for each chapter.

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Contributions – GP, FC and TC conceived and designed the study. GP, FC and FO coordinated the data gathering process. SO, NL, MC, CT, NB, GR and MC provided the data. GP performed the analysis. GP, FC and TC interpreted the results. GP wrote the manuscript with the help of TC and FC. authors reviewed and approved the final manuscript.

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Chapter 6

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Abstract

Despite the global biodiversity crisis, some ecosystems are showing encouraging signs of recovery, especially in Europe and North America. We do not have a clear understanding of how ecosystems recover from degraded states, of the causes and consequences of such recovery, or of how emerging species interactions affect and are affected by ecological processes. In this thesis, I investigate the patterns and processes emerging from recovering ecosystems by analysing population dynamics, species interactions and animal movement.

I explore the spatiotemporal trends of an expanding large mammal community in the Alps and investigate predator-prey interactions between wolves and their main prey. I assess the permeability of the Alpine landscape for recovering populations, by analysing the impact of natural and anthropogenic factors on the movement of a partially migratory ungulate. Studying species interactions in a dynamic and recovering system such as the Alps is challenging. I therefore focus on the Yellowstone ecosystem to analyse the impact of wolf predation on their prey and on other ecological processes. I develop a mechanistic, bio-energetic model of the vegetation-elk-wolf system, to study how energy acquired through resources flows across trophic levels influencing population dynamics and interactions. I then use this model to study how ecological and evolutionary change can affect complex tri-trophic systems.

I show that large mammal communities can recover relatively quickly in the right environment, and with the support of conservation and favourable environmental legislation. Nonetheless, humans can still have a significant impact on animal populations by affecting their movement patterns and habitat use. In the Alps, I could not detect an impact of wolf predation on prey populations because the recovery process is still ongoing and the system is highly dynamic. In Yellowstone, on the other hand, I show that wolf predation can have significant effects on the ecosystem, and that complex trophic interactions can respond in unexpected ways to ecological and evolutionary change.

My thesis offers advances for investigating complex terrestrial systems, for predicting the potential impacts of environmental change on ecosystems, and for informing future policy and landscape management decisions.

Contents

1 General Introduction 1

2 The recovery of a large mammal community in the Alps 23

3 Roads constrain movement across behavioural processes in a partially migratory ungulate 51

4 Investigating tri-trophic interactions using bio-energetic demographic models 104

5 Ecological and evolutionary perturbations of a trophic cascade 143

6 General discussion 176

Appendix 1 Effects of cumulated outdoor activity on wildlife habitat use 188

1

General Introduction

1.1 Introduction

The number of African elephants (*Loxodonta africana*, *Loxodonta cyclotis*) decreased by approximately 23% in the decade between 2007 and 2016, with population declines greater than 60% in certain regions (Thouless et al., 2016, Maisels et al., 2013). In contrast, wolves (*Canis lupus*) in Europe more than doubled their spatial range from the 1970s to the 2010s (Chapron et al., 2014). In Germany, the first wolf breeding pair returned in 2000 and the current wolf population counts more than 157 packs (DDBW, 2021). In 2015, 200,000 individuals (62% of global population) of saiga antelope (*Saiga tatarica*) died in three weeks due to a mass bacterial infection (Kock et al., 2018). Two years later, in 2017, the population rebounded recording a 41% increase in numbers (IUCN/SSC, 2018).

These examples provide evidence that we live in a rapidly changing world where ecosystems are no longer at equilibrium (Coulson, 2021). Global environmental change, directly or indirectly driven by humans, is causing a global biodiversity crisis (Western, 1992) and countless populations to decline or become extinct (Ceballos et al., 2015). In turn, changes in species abundance and distribution are having further effects on ecosystems, influencing ecological processes like trophic interactions, disease dynamics, nutrient cycling, stream morphology, and crop production (Ripple et al., 2014, Ripple et al., 2015).

Despite the global biodiversity crisis (Western, 1992), some ecosystems are showing encouraging signs of recovery. Most large carnivore and ungulate species in Europe have increased in both numbers and distribution in the last decades (Chapron et al., 2014, Linnell et al., 2020). In North America, reintroductions have reinforced the already expanding wolf populations in the Rocky Mountains (Ripple et al., 2001, Ditmer et al., 2022, Oakleaf et al., 2006). In Asia, some tiger (*Panthera tigris*) populations have shown a 40% increase between 2015 and 2021 after long term considerable declines (IUCN, 2021). Many species, including some of those cited here, potentially remain under threat,

however the recent recovery observed in some populations represents positive news for conservation, and will likely lead to changes in their ecosystems.

The recent expansions and changes locally observed in species composition offer an unprecedented opportunity to study the population dynamics and interactions emerging from recovering ecosystems. In this thesis, I do that by analysing population dynamics, trophic interactions and movement patterns in two study systems – The Alps and Yellowstone National Park (USA) (hereafter, "Yellowstone"). In the following section, I review the observed population trends in these study systems, I present the core concepts that motivate my research, and I briefly summarise the questions and findings of each chapter.

1.2 Trends in the Alpine and Yellowstone ecosystems

The Alps and Yellowstone have recently shown some degree of ecosystem recovery (Fuchs et al., 2013, Smith et al., 2020), however the ecological context and conditions of such recovery differ substantially.

1.2.1 The bottom-up recovery of the Alpine ecosystem

The return and expansion of large mammals in the Alps has followed a more general European trend (Linnell et al., 2020, Chapron et al., 2014). Until the mid-twentieth century, Europe hosted some of the most degraded ecosystems in the world (Navarro and Pereira, 2012) as a result of the industrial revolution, social conflicts and the rise in human population. Conversely, from 1950 to 2010, cropland decreased by nearly 19%, while forest cover increased by over 25% across Europe (Fuchs et al., 2013). This provided habitat for several wildlife species, including ungulates (Linnell et al., 2020) and carnivores (Chapron et al., 2014). Six ungulate and three large carnivore species are currently present in the Alps (roe deer – *Capreolus capreolus*, red deer – *Cervus elaphus*, chamois – *Rupicapra rupicapra*, Alpine ibex – *Capra ibex*, wild boar – *Sus scrofa*, and

mouflon – *Ovis Aries,* wolf – *Canis lupus*, bear – *Ursus Arctos*, and lynx – *Lynx lynx*) (Linnell et al., 2020, Chapron et al., 2014).

Reliable data on population size for the Alps are not available for ungulate species, although an attempt at quantifying their abundance and distribution at the European scale was made by Linnell et al. (2020). Ungulate populations have broadly increased across Europe and in the Alps in the last decades (Linnell et al., 2010, Sieff, 2020).

Carnivores have also expanded across Europe both in numbers and distribution, also thanks to local reintroductions of bears and lynx (Chapron et al., 2014). The latest estimates for these species in the Alpine population range between 420-550 wolves, 49-69 bears and 163 lynx (LCIE, 2022), although these numbers were reported for the period 2012-2016, and have likely increased since (Groff et al., 2021, LCIE, 2022). The reason for carnivore expansion across Europe is likely to be a combination of protective legislation, reduced human density, land cover change, and increasing prey abundance (Linnell et al., 2020, Chapron et al., 2014, Cimatti et al., 2021).

Despite this general ecosystem recovery, human impact in the Alps remains high and is likely to affect wildlife populations in several ways (see below – Tucker et al., 2018, Corradini et al., 2021, Passoni et al., 2021).

1.2.2 Elk decline and wolf reintroduction in the Yellowstone ecosystem

The Yellowstone ecosystem has likely never been as degraded as that of the Alps, since resident human presence has always been much lower (Sanderson et al., 2002, Venter et al., 2016). Nonetheless, human impact, mainly under the form of hunting outside of the national park, has been a significant determinant of species composition (Weaver, 1978, MacNulty et al., 2016).

The population trends observed in Yellowstone were mainly due to the establishment of a national park in 1872, several elk management policies, and the wolf reintroduction of 1995 (Ripple et al., 2001, Ripple and Beschta, 2012). The area hosts several species of

ungulates and carnivores, however in this section I will focus on a selection of species which have dominated the last decades of ecosystem research (i.e. elk – *Cervus canadensis*, bison – *Bison bison*, wolves – *Canis lupus*, grizzly bears – *Ursus arctos horribilis*, and cougars – *Puma concolor*) (Ripple and Beschta, 2012, Peterson et al., 2014).

Wolves were extirpated from the national park between the 1920s and the 1940s, as they competed with hunters for elk (Weaver, 1978). After wolf removal, elk numbers decreased as a result of human hunting until 1969, when the national park implemented an elk management policy based on natural regulation whereby the elk population was allowed to fluctuate depending on environmental conditions (MacNulty et al., 2016). Despite a few fluctuations, elk numbers began to rise until 1995 when wolves were reintroduced (Ripple and Beschta, 2012, MacNulty et al., 2016).

Since the return of wolves, the elk population in the Yellowstone Northern Range decreased from approximately 20.000 to 5.000 individuals by 2015 (MacNulty et al., 2016). Bison numbers increased from less than 1.000 to around 4.000 (Beschta et al., 2020), while the grizzly and cougar population also grew in the last three decades (Hamlin et al., 2009, Ruth et al., 2019, Peterson et al., 2014). These trends, together with changes in several forestry metrics, triggered a long debate about the causes of the elk decline and the impact of top predators on ecosystems (see below) (Ford and Goheen, 2015, Peterson et al., 2014).

1.3 Ecosystem recovery in human dominated landscapes

Humans have shaped ecosystems and species distribution for millennia (Andermann et al., 2020). Indeed, the recent recovery of ecosystems observed in Europe was mainly driven by the abandonment of farmland by people (Navarro and Pereira, 2012, Chapron et al., 2014, Cimatti et al., 2021, Linnell et al., 2020), as well as by several protective regulations (CoE, 1979, CoE, 1992). Understanding how ecosystems recover from a

previously degraded state, and how species interactions originate, is of paramount importance for contrasting the current biodiversity crisis. Studying this can support the appropriate implementation of ecological restoration and rewilding initiatives across the globe (Donadio et al., 2022).

Several studies on the European wildlife comeback have focused on large carnivores at a continental level, but failed to consider key components of the ecosystem (Chapron et al., 2014, Cimatti et al., 2021). For example, Cimatti et al. (2021) considered human population density and land cover changes as drivers for large carnivore expansion, however they did not consider ungulate prey. This was most likely due to the lack of reliable data on ungulate abundance and distribution at the European scale (Linnell et al., 2020). Nevertheless, research focusing on all key components of the ecosystem, from triggering drivers (e.g. human population, land cover) to ungulate and, ultimately, carnivore species, is currently needed.

While the European ecosystem recovery is a positive story in the face of the global biodiversity crisis, it does not come without costs. Species recolonisation in human-dominated landscapes can increase the chance of zoonotic disease spread (Sauter-Louis et al., 2021), damage to farmland (Gren et al., 2020), road accidents (Rolandsen et al., 2011), and, for carnivores, livestock depredation (Bautista et al., 2019). Hence, species recovery needs to be accompanied by a shift in human attitudes and by informed policies and management. Studying these issues is therefore important to minimise conflict and ensure coexistence between wildlife and people. In the second chapter, I analyse the spatio-temporal trends in abundance and distribution of human population, forest, ungulates, and carnivores in Trentino, a large province in the south-eastern Alps.

Despite their recent recovery in Europe, human dominated landscapes can still have a significant negative impact on wildlife through, for example, hunting, farming, infrastructure development, recreational activities and tourism (Tucker et al., 2018, Corradini et al., 2021, Passoni et al., 2021, Passoni et al., 2017, Bonnot et al., 2013).

These activities can alter animal behaviour, movement, and space use, ultimately affecting their distribution (Tucker et al., 2018). In particular, roads represent a substantial barrier to wide-ranging wildlife, potentially limiting their expansion and connectivity between viable populations (Kuehn et al., 2007, Kramer-Schadt et al., 2004). Previous research on ungulates showed that roads can alter movement within the home range, but also during key ecological processes such as dispersal and migration (Sawyer et al., 2016, Sawyer et al., 2013, Beyer et al., 2016).

To predict the spatial distribution of expanding wildlife populations such as those in the Alps, it is important to understand how natural and anthropogenic landscape features affect animal movement. In the third chapter, I investigate how roads and other landscape features affect the movement of a partially migratory ungulate in the Alps and central Europe.

1.4 Trophic interactions and ecosystems: bottom-up vs top-down regulation

The observed fluctuations in abundance and distribution described above enable the investigation of the relationships between populations and their biotic and abiotic environments. Understanding the effects of trophic interactions on population dynamics and ecosystem processes has been a major focus of ecology for decades (Lotka, 1927, Volterra, 1927), however these effects remain poorly understood (Ford and Goheen, 2015).

A major debate revolves around the relative importance of bottom-up and top-down processes in regulating ecosystems (Peterson et al., 2014). An ecosystem is regulated from the bottom-up when it is controlled by primary producers, such as vegetation, or by nutrient limitation (Pace et al., 1999). On the other hand, an ecosystem that is regulated from the top-down is controlled by a top-predator that affects lower trophic levels (Pace et al., 1999). Top-down regulation is also associated with the concept of trophic cascades, whereby a top predator reduces the abundance of its prey, which in turn releases its own

resource from consumption, resulting in an opposite response at each trophic level (Carpenter et al., 1985). Because multi-trophic interactions are often complex with several feedbacks acting at multiple levels (Sinclair and Krebs, 2002), the consequences of environmental change on these interactions can be unexpected and counterintuitive. As such, addressing these issues is important to understand the impact of climate change, diseases, human activities, and management decisions on our rapidly changing ecosystems.

Most of the work on trophic cascades has historically been carried out in aquatic environments or in mesocosms (Carpenter et al., 1985, Power, 1992, Wootton, 1992). In complex terrestrial systems, disentangling the effects of predation can be more difficult due to confounding factors, lack of controls and replications, and larger spatial and temporal scales (Kauffman et al., 2013). For this reason, most of the work has relied on correlative methods (Ford and Goheen, 2015), with few experimental studies (e.g. Ford et al. (2015), Krebs et al. (1995)).

One of the most famous and recognised examples of a trophic cascade was observed in kelp forests in Alaska, where sea otters (*Enhydra lutris*) controlled the population of kelp-feeding sea urchins, thus having a positive indirect effect on kelp abundance (Estes and Palmisano, 1974, Estes and Duggins, 1995). The effects of predators can also be mediated by behavioural processes in behaviourally-mediated trophic cascades. For example, Suraci et al. (2016) showed that fear of a large carnivore reduced racoons' predation, indirectly benefitting their prey. The cascading effects of top predators are not ubiquitous. The recovery of African wild dogs in central Kenya suppressed the abundance of their prey (i.e. dik-dik), but did not trigger a trophic cascade to lower trophic levels (Ford et al., 2015). In other systems, top-down and bottom-up regulations have been shown to coexist, either shifted in time (Meserve et al., 2003) or simultaneously (Lynam et al., 2017).

1.4.1 The Yellowstone debate

In Yellowstone, the occurrence of a trophic cascade triggered by the wolf reintroduction has been debated. According to some studies, wolves predate elk and alter their movement and habitat selection patterns, indirectly benefitting the recruitment of woody deciduous plants (Ripple et al., 2001, Fortin et al., 2005), however other studies found little or no recruitment in aspen (Kauffman et al., 2013, Kauffman et al., 2010, Brice et al., 2021). The extent to which the wolwes were responsible for the elk decline is also debated, as important confounding factors were often not considered (Peterson et al., 2014, Vucetich et al., 2005). Since the wolf reintroduction, Yellowstone experienced droughts, fires, human harvest of elk outside the park, and saw the increase in abundance of other species such as bears, cougars and bison (Peterson et al., 2014, Vucetich et al., 2005). Bears and cougars can contribute to the elk decline via direct predation, whereas bison compete for the same resource, but is less vulnerable to wolf predation (Tallian et al., 2017). The increase in bison population could therefore be one of the reasons for the limited aspen recruitment (Ripple et al., 2011, Beschta et al., 2020).

The cause of the elk decline in Yellowstone is likely a combination of all the factors listed above (Peterson et al., 2014). Notwithstanding, elk represent ~88% of all ungulates killed by wolves (Stahler et al., 2006, Smith et al., 2004, Tallian et al., 2017). Therefore, investigating the relationship between wolf, elk and the vegetation remains a key step towards understanding the Yellowstone ecosystem and its ecological processes. As mentioned above, appropriate experiments are impossible to implement in certain circumstances, but models offer a valuable alternative. In the fourth and fifth chapter of this thesis, I develop a mechanistic model that simulates the wolf-elk-vegetation interactions in Yellowstone, and investigate the potential effects of ecological and evolutionary perturbations on these interactions.

1.5 Thesis outline

1.5.1 Overview

In this thesis, I investigate the patterns and ecological processes emerging from recovering ecosystems. In the second chapter, I explore the spatiotemporal dynamics of an expanding community of large mammals in Trentino, a large province in the south-eastern Alps, and I investigate emerging trophic interactions. To assess the permeability of the Alpine landscape for expanding wildlife populations, in the third chapter, I test the impact of natural and anthropogenic landscape features on the different movement types of a partially migratory alpine ungulate.

As I discuss in chapter 2, the mammal community in the Alpine ecosystem is experiencing rapid changes in abundance and distribution. It is therefore difficult to study the interactions between species in this system. In order to investigate these dynamics, for the fourth and fifth chapters, I move to the Yellowstone ecosystem. In the fourth chapter, I present a mechanistic, bio-energetic model of the vegetation-elk-wolf system to study their complex trophic interactions. In the fifth chapter, I use this model to analyse the potential effects of ecological and evolutionary change on this tri-trophic system. Finally, in the sixth chapter, I summarise the main findings of the thesis, discuss the challenges and limitations, and propose future research needs.

In this section, I present the specific questions and main findings of each chapter.

1.5.2 Chapter 2: The recovery of a large mammal community in the Alps

In this chapter, I describe the recovery of a large mammal community in an Alpine province (Trentino, Italy), using an ecosystem-wide approach. I gather long term data on the spatiotemporal trends in human population, forest cover, ungulate populations (i.e. roe deer, red deer, alpine chamois, wild boar, and mouflon) and carnivore populations

(i.e. wolf and bear). I then quantify trophic interactions between wolves and their main prey, and test whether wolves are having an impact on their numbers.

I show that since the early 1900s, human population largely decreased in mountainous areas, while forest cover doubled across the province. Since the 1970s, all mammal species significantly increased in abundance. The wolf main prey were red deer and roe deer, however wolves killed a significant amount of livestock particularly in the summer. To date, wolf predation has not had a significant effect on the prey populations, despite a weak impact on the red deer population growth rate.

These results show that in the certain environmental conditions, large mammal communities can recover relatively quickly. Species interactions are likely to take longer to manifest themselves. In addition, detecting the impact of predation on a highly dynamic system and using count data alone is difficult (Peterson et al., 2003). Nonetheless, we expect that the increasing frequency of wolf predation will eventually affect wild ungulate populations as observed elsewhere (chapter 4, Passoni et al. (2022)). The patterns observed in Trentino represent a positive story for conservation, however future policy and management decisions must also take into considerations the challenges of living with wild animals.

1.5.3 Chapter 3: Roads constrain movement across behavioural processes in a partially migratory ungulate

Expanding animal populations can be significantly affected by human infrastructure. In ungulates, roads can limit movement both within their home range and during migration and dispersal, potentially reducing their ability to access resources and access novel ranges (Vistnes et al., 2004). Potential differences in response to roads across these movement modes have never been evaluated, but investigating this is important to assess the resistance of Alpine landscapes to wildlife expansions.

In this chapter, I focus on roe deer (*Capreolus capreolus*), a behaviourally-flexible species (Linnell, 1998) performing a high variety of movements, from home range movements to migration, as well as natal dispersal (Cagnacci et al., 2011, Ducros et al., 2020). I analyse the GPS trajectories of 95 individuals from 6 populations in the Alps and central Europe to investigate the impact of natural landscape features and roads on their movement and to test potential differences in road avoidance among resident, migratory and dispersing animals.

I show that roe deer move through more forested areas during the day and visited areas of open habitat mainly at night. During their movements, roe deer minimised elevation gains and losses, potentially to minimise energy expenditure (Gaudry et al., 2015). Roads crossings were strongly avoided at all times of day and night, and consistently across movement types, confirming that roads can represent a major constraint to wildlife movement in highly human dominated landscapes.

1.5.4 Chapter 4: Investigating tri-trophic interactions using bio-energetic demographic models

Studying species interactions in highly unstable and dynamic ecosystems such as the Alps is challenging (chapter 2). In addition, research on large terrestrial systems has typically lacked a mechanistic understanding of how predation and resources affect complex multi-trophic systems (Ford and Goheen, 2015).

In this chapter, I develop a mechanistic model of a tri-trophic system where the primary resource follows a seasonal growth function and an herbivore and a carnivore species are modelled using two integral projection models (IPM) as a function of body mass. Within each IPM, I structure the demographic functions with a bio-energetic approach, whereby each species is able to use the energy acquired through feeding to increase its body mass, energy reserves and breeding potential. Although general in nature, the model is parameterised to simulate the vegetation-elk-wolf system in Yellowstone.

By producing realistic predictions, the model shows that, after the wolf reintroduction the elk shifted from being bottom-up regulated to being controlled from the top-down. In particular, when wolves were added to the system, the elk population decreased by 61%, and caused an indirect increase in vegetation by 25% in the growing season (i.e. April to September) and by over 300% in the non-growing season (i.e. October to March). Wolves also caused an increase in the elk average body mass, by predating calves and weaker individuals with less energy reserves. Finally, in mechanistic tri-trophic systems, changes in certain components can have counter-intuitive consequences. For example, an improvement in wolf hunting efficiency on elk can lead to elk overconsumption and ultimately result in a decline in wolf numbers.

By investigating how energy flows through the system, I show that apex predators can have large and sometimes unexpected effects on their prey and on broader ecosystem processes.

1.5.5 Chapter 5: Ecological and evolutionary perturbations of a trophic cascade

Multi-trophic interactions can be complex, and changes in any of their component may result in unexpected and often-counterintuitive dynamics (chapter 4, Sinclair and Krebs (2002), Passoni et al. (2022)). Studying the effects that these changes have on complex ecosystems is of paramount importance to predict and tackle the impact of global environmental change.

In this chapter, I use the model developed in chapter 4 to investigate the consequences of ecological and evolutionary change on the Yellowstone system. By varying several model parameters, I test the effects of changing snow regimes, elk behavioural responses to wolf predation, diseases, scavenging of elk by other carnivores, and evolutionary improvements in wolf predation efficiency.

I show that, by regulating the ecosystem, wolves can act as buffers against fluctuations in the primary resource. The severity of the trophic cascade and the strength of feedbacks vary depending on context. Altering the snow regime led to non-linear dynamics, whereby the effects of bigger changes in snow regime would have the opposite direction of smaller changes in the same direction. I also show that 1) direct wolf predation is likely to have a bigger impact on elk compared to behaviourally-mediated processes; 2) energetic parameters are more important for both wolf and elk than predation and predation avoidance, respectively; 3) an increase in the abundance of scavengers causes a reduction in both the elk and the wolf populations; and 4) increasing the wolf hunting efficiency leads to a reduction in wolf numbers.

By using a mechanistic bioenergetic model of a trophic cascade, I show that, when perturbed, trophic cascades may behave in unexpected ways. The model adopted here can be adapted to and parameterised for any ecosystem, and can be used to formulate hypotheses in ecology and evolution. However, it is important that these hypotheses are tested with experimental approaches whenever possible.

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2

The recovery of a large mammal community in the Alps

Abstract

Despite the global biodiversity crisis, some ecosystems have shown encouraging signs of recovery, particularly in Europe. Researchers do not have a clear understanding of how ecosystems recover from degraded landscapes, of the causes and consequences of such recovery, or of how species interactions form and develop through time. Studying the recovery of large mammal communities is important to assess their impact on the landscape and ecosystems, to minimise human-wildlife conflicts, and to inform landscape restoration and rewilding initiatives globally. Research to date has mainly focused on large spatial scales or on single taxa.

In this chapter, we describe the recovery of a large mammal community in an Alpine province (Trentino, Italy), using an ecosystem-wide approach. We collated long term data on the spatiotemporal trends in human population, forest cover, ungulate populations (i.e. roe deer, red deer, alpine chamois, wild boar, and mouflon) and carnivore populations (i.e. wolf and bear). We then quantify trophic interactions between wolves and their main prey, and test whether wolves are having an impact on their numbers.

We showed that since the early 1900s, human population largely decreased in mountainous areas, while forest cover doubled across the province. Since the 1970s, all mammal species significantly increased in abundance. After their recent recolonisation, wolves mainly predated on red deer and roe deer, however they also killed a significant amount of livestock particularly in the summer. To date, wolf predation has not had a significant effect on the prey populations, despite a weak impact on the red deer population growth rate.

Our results show that in certain environmental conditions, large mammal communities can recover relatively quickly (i.e. a few decades) after local extirpation or population density declines. Species interactions are likely to take longer to manifest their effects at the population level, and detecting the impact of predation on a highly dynamic system and using count data alone is difficult. Nonetheless, we expect that the increasing frequency of wolf predation will eventually affect wild ungulate populations as observed elsewhere. The patterns observed in Trentino represent a positive story for conservation, however future policy and management decisions must also take into considerations the challenges of living with wild animals.

2.1 Introduction

We live in a period of rapid change where ecological systems are no longer at equilibrium (Coulson, 2021). Despite the global biodiversity crisis and population declines in ecosystems worldwide (Ceballos and Ehrlich, 2002, Ripple et al., 2015), some large mammal communities, particularly in Europe, have been recovering in the last decades (Chapron et al., 2014, Linnell et al., 2020). Until the mid-twentieth century, Europe had some of the most degraded ecosystems in the world (Navarro and Pereira, 2012) as a result of the industrial revolution, social conflicts and the rise in human population. However, since the world wars, rural populations in Europe have decreased in many regions, leading to land abandonment (Navarro and Pereira, 2012) and to a 25% increase in forested areas between 1950 and 2010 (Fuchs et al., 2013). This, together with protective environmental legislation, has been causing the return and expansion of several mammal species such as ungulates (Linnell et al., 2020) and carnivores (Chapron et al., 2014).

We do not have a clear understanding of how ecosystems recover from degraded states where ecological processes are significantly altered by humans. We also do not understand the exact causes and consequences of wildlife population expansions, or how species interactions form and develop through time. Large mammals can both affect and be affected by their environment. On the one hand, they need suitable habitat and resources to thrive. On the other, they are considered key components of healthy ecosystems and have been shown to affect ecological processes such as nutrient cycling, carbon storage, hydrology, species interactions, and disease dynamics (Ripple et al., 2014, Ripple et al., 2015, Apollonio et al., 2017). Studying their recovery is therefore important to assess their impact on the landscape and on existing ecological communities.

In some contexts, large mammal reintroductions have been proposed as solutions to help restore ecological processes in degraded landscapes, particularly since the start of the rewilding movement (Perino et al., 2019). While such reintroductions also require socio-

economic considerations, a thorough understanding of ecological implications is paramount. Studying the recent recovery of large mammal communities in Europe can therefore provide essential knowledge to inform landscape restoration and rewilding initiatives globally. Finally, large mammal expansions in densely populated areas can also lead to conflict with humans and have strong socio-economic effects (Linnell et al., 2020, Bautista et al., 2019). Understanding the causes and consequences of ecosystem recovery can therefore contribute to minimising these negative effects and achieve coexistence between humans and wildlife.

To date, research on the causes of the recent wildlife recovery in Europe has mainly focused on large spatial scales (i.e. continental) and on single taxa, particularly large carnivores. The main reasons identified for this expansion span from environmental legislation and declining human population, to land abandonment and improved habitat quality (Chapron et al., 2014, Cimatti et al., 2021). While these are indeed relevant drivers, current research on large carnivore recovery has overlooked the role of ungulate prey, which are a fundamental component of ecosystems, and directly interact with both primary resources and predators (Passoni et al., 2022). This shortfall is mainly due to the lack of reliable long-term data on ungulates at European level, despite current efforts to provide population estimates and information about spatial distribution (Linnell et al., 2010, Linnell et al., 2020). This has prevented researchers from addressing the issue with a holistic and systemic approach.

The recent recovery of top predators, such as the grey wolf, also offers the opportunity to study their impacts on prey populations. The role of top predators in affecting the dynamics of prey and wider ecosystem processes has been a long-standing topic in ecology (Lotka, 1927, Volterra, 1927, Hairston et al., 1960). However, studying this in large mammal communities is difficult due to several confounding factors, lack of controls, and scarce data on systems before predator recovery (Ford and Goheen, 2015).

In this chapter, we describe the recovery of a large mammal community in an Alpine province using an ecosystem-wide approach. We gather long-term data on the spatiotemporal trends in human population, forest cover, ungulate populations (i.e. roe deer – *Capreolus capreolus*, red deer – *Cervus elaphus*, alpine chamois – *Rupicapra rupicapra*, wild boar – *Sus scrofa*, and mouflon – *Ovies aries*) and carnivore populations (i.e. wolf – *Canis lupus*, and bear – *Ursus arctos*). We then use these data to quantify trophic interactions between wolves and their preferred prey, and test whether wolves are having an impact on their numbers. We focus on the Provincia Autonoma di Trento (hereafter "Trentino"), covering over 6,000km^2 in the South-eastern Alps (Italy). The area has seen the expansion and recovery of both the ungulate and carnivore populations cited above, with the bear being reintroduced in 2002, and the first wolf pack naturally returning in 2013 after several decades of local extinction (Groff et al., 2021). The availability of data on ecosystem components since the early '70s – and before the return of apex predators such as wolves – makes it an ideal study area to address our questions. We will focus on the initial recovery process which is still largely ongoing, both in Trentino and in many regions of Europe, and will provide a fundamental base for future research, landscape management and conservation efforts.

2.2 Methods

2.2.1 Study area

The Provincia Autonomia di Trento (Trentino) is an Italian province located in the South-eastern Alps, with a total population of more than 500,000 people and an area of 6,207 km^2 (Gobbi et al., 2019). The topography of Trentino is predominantly mountainous with a minimum elevation of 64 metres above sea level and a maximum altitude of 3,769 metres above sea level. Forests cover more than 60% of the entire territory and are made up of Norwegian spruce – *Picea abies* (70%), silver fir – *Abies*

alba (12%), beech – *Fagus sylvatica* (7%) and larch – *Larix decidua* (3%) (Gobbi et al., 2019).

The ungulate community currently includes roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), chamois (*Rupicapra rupicapra*), Alpine ibex (*Capra ibex*), wild boar (*Sus scrofa*), and European mouflon (*Ovis aries*). Of these, roe deer and chamois have always been present in the last centuries (Apollonio et al., 2019). Red deer was extinct on most of the Italian Alps until the beginning of the 1900s, when some individuals recolonised Trentino from neighbouring countries (Apollonio et al., 2019). This natural expansion was also reinforced by five localised reintroductions that occurred between 1938 and 1997 (Apollonio et al., 2019). Nevertheless, the red deer population in Trentino remained small until the beginning of the 1970s (Apollonio et al., 2019). Wild boar and mouflon were mainly reintroduced for hunting purposes and are not considered native species in Trentino. All ungulate species are hunted, except for ibex which are protected from hunting in Italy (Apollonio et al., 2019).

Large carnivore species mainly include brown bears (*Ursus arctos*) and wolves (*Canis lupus*). Bears were reintroduced between 1999 and 2002 (Mustoni et al., 2003), while wolves naturally recolonised the province with the first pack establishing in 2013 (Groff et al., 2021).

2.2.2 Data sources

We gathered data on human population, forest density, ungulate and carnivore abundance, and wolf predations on wild and domestic species.

Human population data were obtained from national and regional censuses performed in each of the 166 municipalities every 10 years between 1921 and 2021 (ISTAT/ISPAT, 2022). Data on forest cover were obtained for the years 1859, 1936, 1954, 1994, 2006, and 2015 from regional maps created by Gobbi (2021).

Ungulates

Ungulate data were available since the early 1970s (Sieff, 2020). Ungulate monitoring was historically performed by hunting associations for hunting purposes. Since 1991, the annual counts have been performed under the control of the province's wildlife service, and have become more systematic with the aim of underpinning the compulsory management and hunting plan for each of the 20 hunting districts in which the province is divided (Apollonio et al., 2019, Raganella Pelliccioni et al., 2013).

We gathered data on counts, hunting quotas and kills at the province level from 1971 to 2020 for roe deer, red deer, chamois, and mouflon. For wild boar, only data about hunting kills and culling by the province were available. For roe deer and red deer, we also gathered data on hunting quotas and kills for each hunting district from 1987 to 2020. Data were obtained from the province's wildlife service (Servizio Faunistico della Provincia Autonoma di Trento). See Apollonio et al. (2019) for more information about how hunting quotas are established.

Carnivores

Wolf and bear counts are carried out annually since the onset of populations in Trentino – i.e. 2002 for bears and 2011 for wolves – by the province's wildlife service (Groff et al., 2021). Since 2011, the province also records geo-located data on all signs of wolf presence (e.g. camera trap photos, footprints, scats, carcasses), including predation on wild and domestic species. Data on wolf predation on wild species were collected opportunistically based on carcasses encountered on the landscape and reported to the province. The cause of mortality (including wolf predation) is then confirmed in the field by a technician from the province. Data on livestock depredations are based on depredation reports by farmers. In the case of livestock, the cause of death is established in the field by a veterinarian. All data on carnivores were obtained from the province's wildlife service (Servizio Faunistico della Provincia Autonoma di Trento).

2.2.3 Analysis

Spatio-temporal trends at the province level

We present and describe trends in human population, forest density, and species abundance at the province level. For red deer and wolf, we also show their spatiotemporal expansion within Trentino.

Predator-prey relationship

We calculated descriptive statistics of the trends in wolf predation on wild ungulates and livestock from 2012 to 2020. We then tested whether wolf predation had an impact on wild prey at the population level, focusing on the wolf's main prey – roe deer and red deer. To do this, we first calculated the annual growth rate in hunting quotas for each prey in each district. We used hunting quotas – and not animal counts – because count data were not available at the district level. To ensure that hunting quotas reflected animal counts, we calculated their correlation coefficient at the province level, where both data types were available (Supplementary Information). The annual growth rate was calculated as:

$$w_t = \frac{N_{t+1}}{N_t} \quad [1]$$

Where N is the number of individuals. We then obtained the year in which the first predation occurred on roe deer and red deer in each district, and set that year to 0. Each year before that was progressively assigned a negative number, whereas each year after that was progressively assigned a positive number. This allowed us to align all districts around the time of the first wolf predation. In order to use only the most reliable data, for red deer we only used data from 9 years before to 9 years after wolf occurrence. For roe deer, we selected only the data from 2009 onwards, from 8 years before to 8 years after wolf occurrence. We considered these intervals to exclude the initial trends in red deer abundance until the early 2000s, to have a similar sample size for the periods before

and after wolf recovery, and to exclude the fluctuations in roe deer numbers observed in the early 2000s, due to a reported but inaccurately quantified decline of the population (Bragalanti pers. comm., see discussion).

To test for a potential impact of wolves, we ran a separate linear model for each prey species. In particular, we used the prey annual growth rate as response variable, and time – centred around 0 as explained above – as a predictor. In this way, we assessed the relationship between the prey growth rate and time. To specifically test whether wolves had an impact on their prey's growth rate, we split the data into pre-wolf and post-wolf presence and added this categorical variable alone and as an interaction with time, thus quantifying the difference in intercept and slope between the pre-wolf and post-wolf periods. The model formula was thus:

$$w_{prey} = \beta_0 + (\beta_1 \cdot time) + (\beta_2 \cdot wolf\ presence) + (\beta_3 \cdot time \cdot wolf\ presence) + \varepsilon \quad [2]$$

We hypothesise that wolves should reduce their prey's growth rate. We thus expect growth rate to decrease over time more strongly in the post-wolf occurrence period compared to before wolf recolonisation.

2.3 Results

2.3.1 Trends at the province level

Since 1921, the human population in Trentino consistently increased by 34% from 404,237 to 542,166 people. However, this rise in numbers was mainly observed in areas at low altitudes ($<$ 600 m), where the population increased by 66%. On the other hand, in areas above 600 metres, the population showed an overall decrease of 9%. This decrease is mainly due to an 18% reduction between 1921 and 1991. Since 1991, the population has grown by 12% even in areas above 600 metres (Figure 1).

Forest cover reached its minimum extension in 1936, with an area of 179,675 hectares across Trentino. In 2015, forest cover had increased by 100% to 359,294 hectares. This pattern was consistent across all altitudinal ranges (Figure 1).

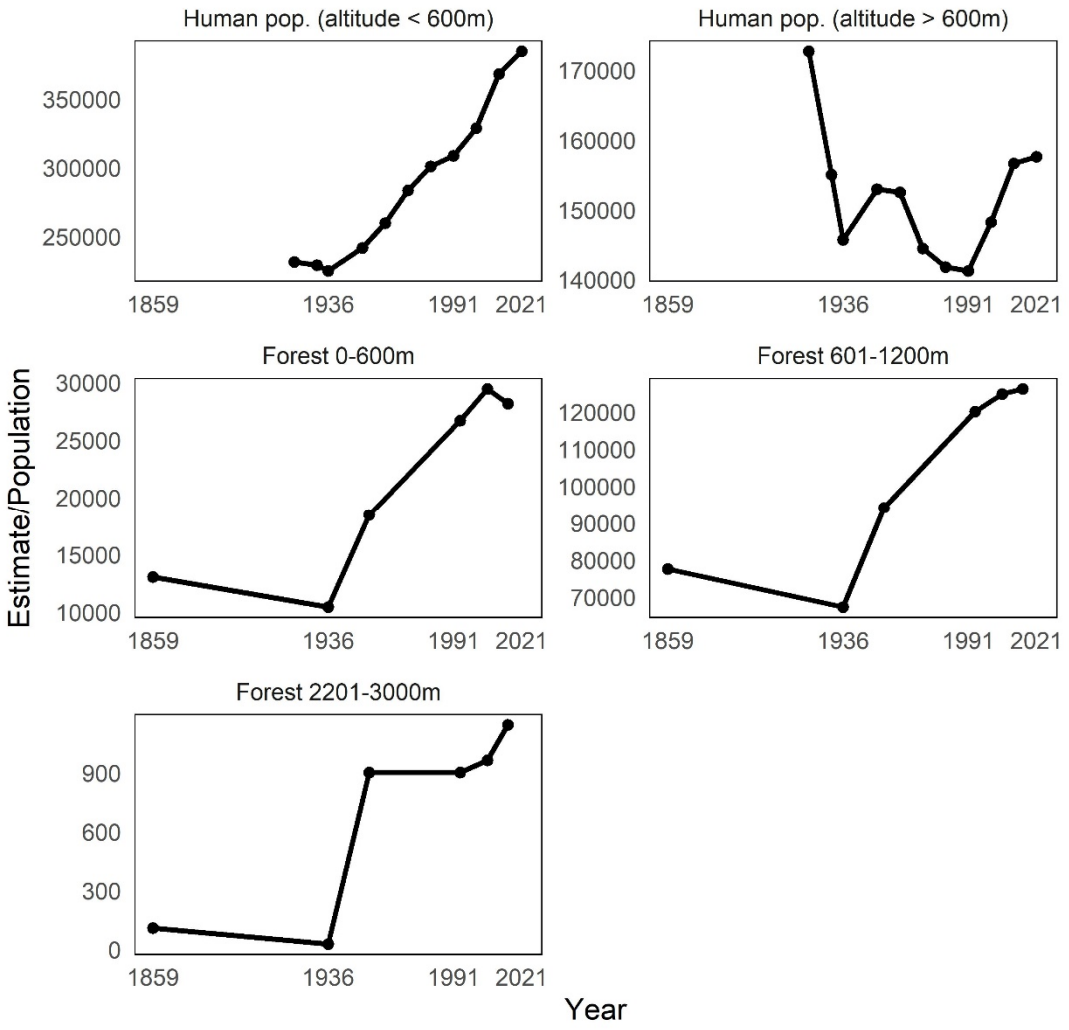


Figure 1 Long term trends in human population and forest cover density in Trentino.

With regards to wildlife, all species increased in numbers between 1970 and 2021 (Figure 2). Here, we report the trends in animal counts, hunting quotas and number of hunted animals, which were correlated (Supplementary Information). Roe deer counts increased by 143% from 14,500 to 35,185 across the whole study period, however they did not follow a regular pattern. In particular, from 2003 to 2006, roe deer numbers decreased from 31,519 to 21,220 (-33%), to then bounce back to 33,670 (+59%) by 2010. From 2010

to 2020 the numbers have been stable between 33,670 and 36,120 individuals. Quotas and kills have broadly followed these trends. Quotas increased by 249% between 1971 and 2020. However, after a local minimum of 3,472 individuals in 2006, quotas stabilised around 6,500 between 2010 and 2020. Kills increased by 128% since 1971, and from 2010 they have oscillated around 4,000 individuals (Figure 2).

The red deer population in Trentino increased nearly monotonically from 250 individuals in 1971 to 12,453 in 2020 (+639%). In the same period, quotas increased from 2 to 3,079 individuals, and kills grew from 2 to 2,557 animals (Figure 2). This increase in numbers was accompanied by a spatial expansion shown in Figure 3.

The number of chamois showed a constant increased from 5,500 in 1971 to 29,810 in 2020 (+442%). Hunting quotas followed this trend and increased from 509 in 1971 to 3,585 in 2020. Kills increased from 463 to 2,834, and remained stable around 2,800 until 2020 (Figure 2).

Similarly to all other species, mouflon also increased constantly from 30 individuals in 1973 to 1,372 individuals in 2020. Quotas and kills increased from 2 in 1975, to 414 and 208, respectively, in 2020 (Figure 2). Despite the general increase in hunting quotas and in the number of hunted animals. The request and realease of hunting permits has decreased significantly between 1993 and 2020 (Figure 2).

Unlike for other species, the management of wild boar in Trentino aims at the culling of the entire population. As such, only data about kills are available. These increased from 28 in 2000 to 493 in 2020 (Figure 2).

The first wolf pack formed in Trentino in 2013. Since then, packs expanded across most of the province (Figure 3) and constantly increased up to 26 packs in 2021. In 2021 the number of estimated wolf individuals was 178 (Figure 2). Bears were reintroduced in Trentino in 2002. Since then, the population increased from 8 to 66 individuals (minimum known number of individuals excluding cubs of the year) in 2020 (Figure 2).

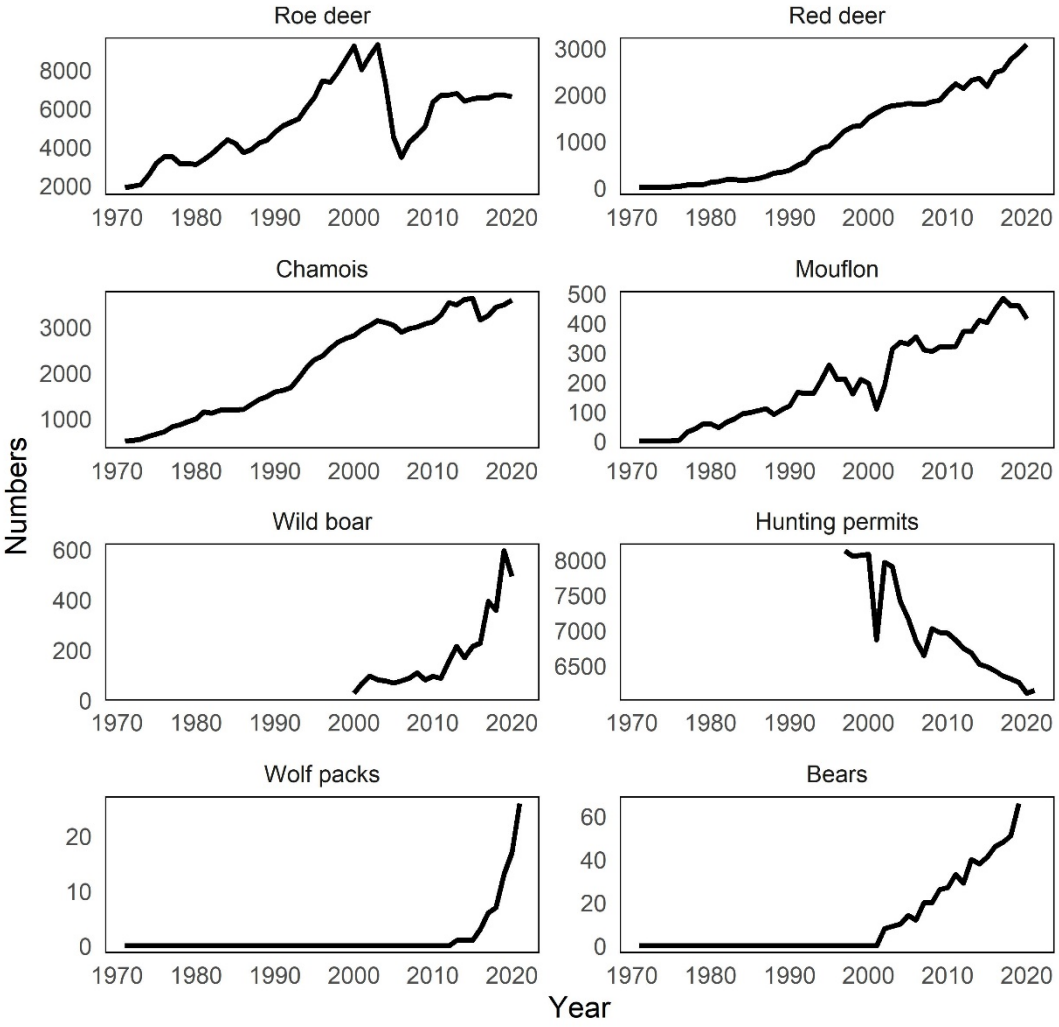


Figure 2 Long term trends in species abundance and hunting permits released. For ungulates, numbers indicate the number of animal killed by hunters each year. For bears and wolves we report the number of individuals and packs, respectively.

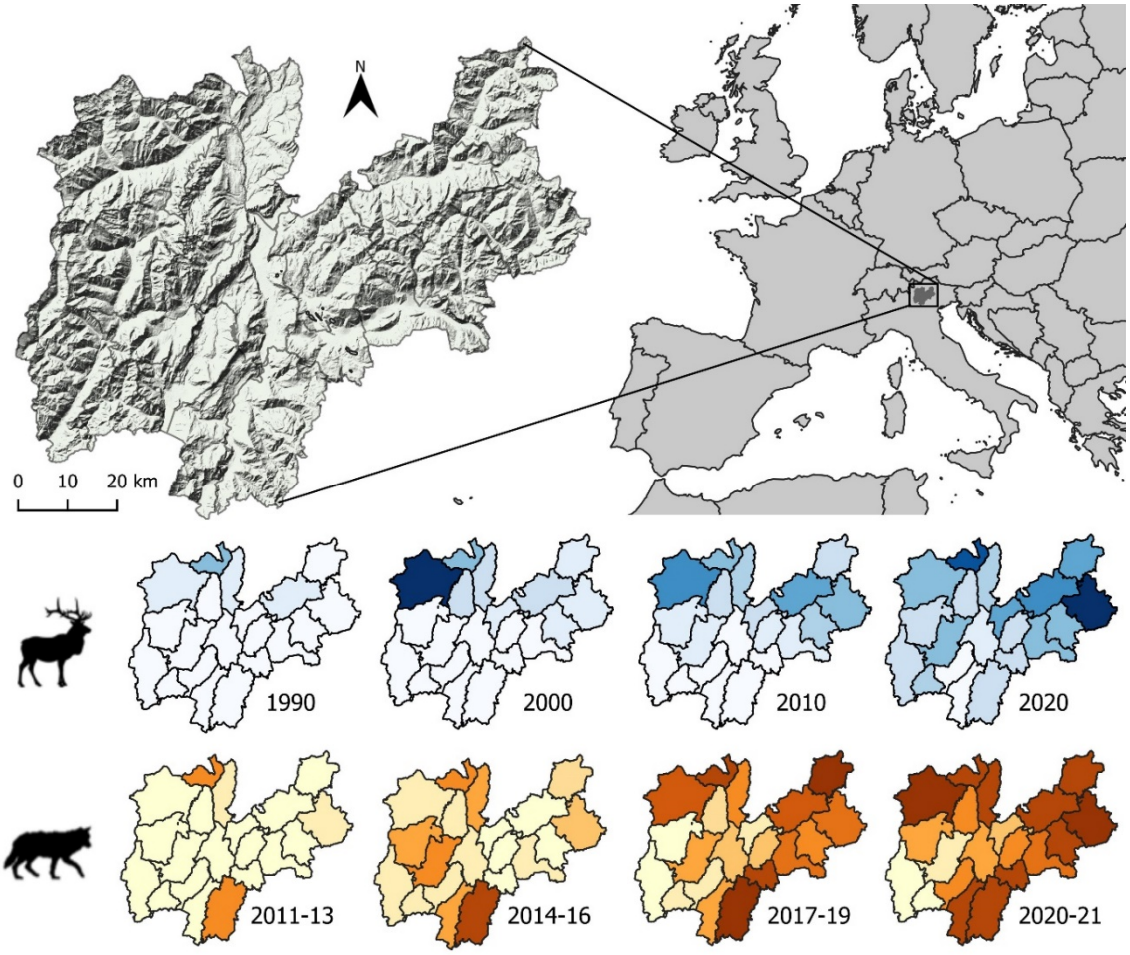


Figure 3 Spatiotemporal trends in red deer quotas and wolf presence signs in Trentino.

2.3.2 Predator-prey relationship

From 2011 to 2020, wolf predation events increased both for wild and domestic species (Figure 4). For wild ungulates, in 2019 there were 208 predation events (Figure 4). The lower number of predation events (161) recorded on wild species in 2020 was likely due to a lower monitoring effort due to the coronavirus pandemic. Since 2011, a total of 611 predation events were recorded on wild species. Among these, roe deer was the most frequent prey (42%), followed by red deer (32%) and mouflon (17%). Chamois and wild boar represented 8% and less than 1% of total predations, respectively. Depredation events on livestock increased from 4 in 2013 to 94 in 2020 (Figure 4).

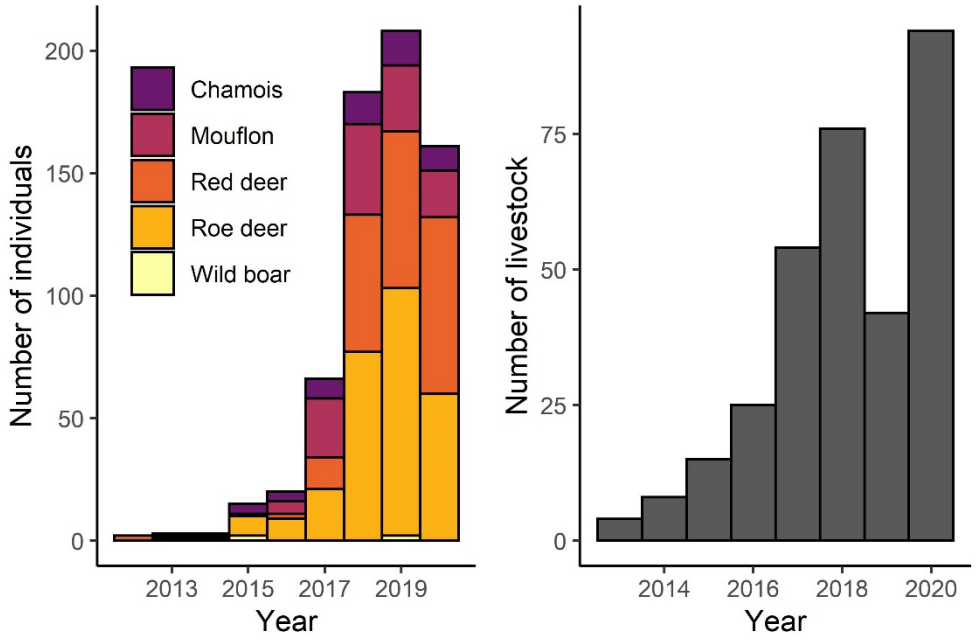


Figure 4 Wolf predation on wild and domestic ungulates by year.

The temporal distribution of predation events on wild and domestic species within the year was not homogeneous (Figure 5). In particular, predation on livestock concentrated in the summer months, when we recorded a reduction in predations on wild species.

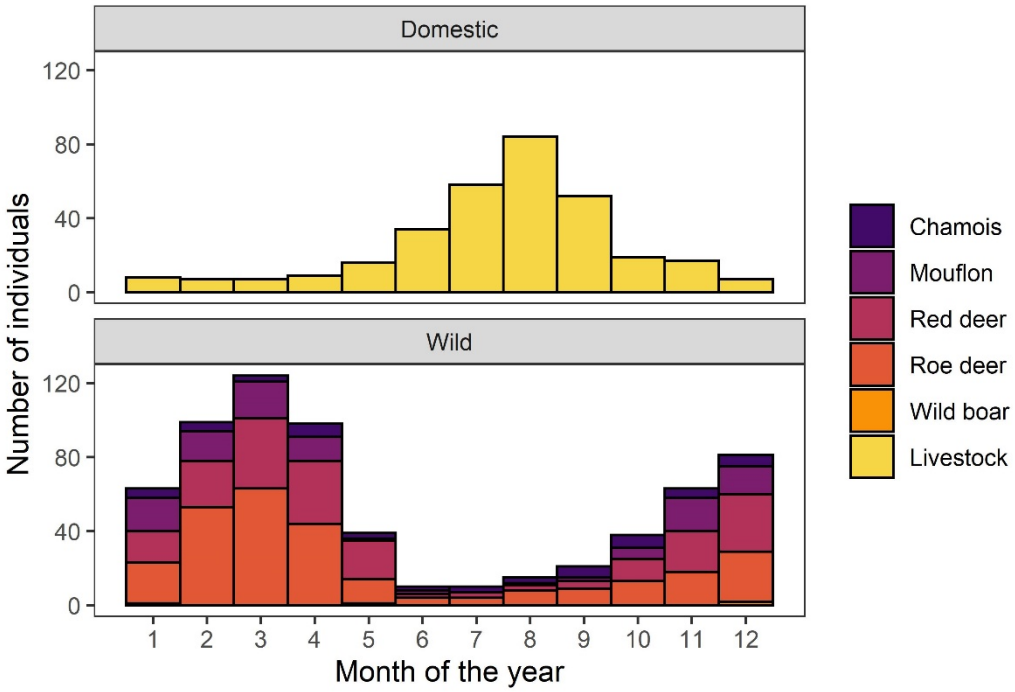


Figure 5 Wolf predation on wild and domestic ungulates by month of the year.

We found weak evidence for a negative impact of wolf predation on red deer growth rates, and no evidence for roe deer (Figure 6, Table 1). In particular, before wolf recolonisation, the average of red deer growth rates across years was larger than 1 and slightly increasing through time (β = 0.002, 95% CI [− 0.009, 0.012]). Following wolf recovery, red deer growth rates decreased through time, approaching an average growth rate below 1 (β = -0.012, 95% CI [-0.039, 0.015]) (Figure 6, Table 1). However, these patterns were not statistically significant (Table 1).

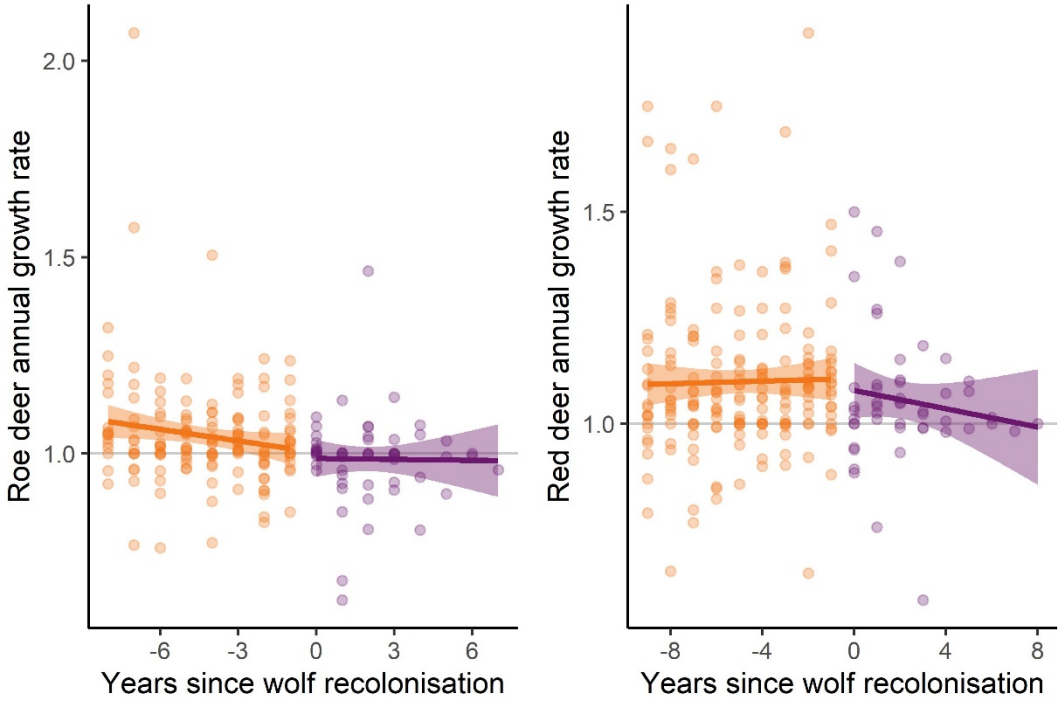


Figure 6 Roe deer and red deer growth rate before and after the wolf recovery. Growth rates before and after wolf recolonisation are represented in orange and purple, respectively.

Table 1 Impact of wolf predation on prey growth rate for roe deer and red deer. Statistically significant coefficients (i.e. those that are not overlapping zero) are highlighted in bold. For the categorical variable "Wolf occurrence", the coefficient for the category "After" should be interpreted as difference compared to the reference category "Before".

Species	Variable	Wolf occurrence	Coefficient	Confidence interval
Roe deer	Intercept	Before	**1.003**	**[0.957, 1.049]**
		After	-0.015	[-0.085, 0.055]
	Slope	Before	**-0.010**	**[-0.019, -0.0004]**
		After	0.009	[-0.013, 0.031]
Red deer	Intercept	Before	**1.107**	**[1.050, 1.164]**
		After	-0.028	[-0.122, 0.066]
	Slope	Before	0.002	[-0.009, 0.012]
		After	-0.012	[-0.039, 0.015]

2.4 Discussion

We described the recovery of a large mammal community in an Alpine province using an ecosystem-wide approach. We showed that since the early 1900s, human population largely decreased in mountainous areas, while forest cover doubled across the province. The long term trends in wildlife populations showed that all species considered here increased in overall abundance since the 1970s, although some species have remained stable or slightly decreased since the early 2000s. We also tested for a potential effect of wolf predation on the roe deer and red deer populations. Wolf predation to date has had only a weak effect on the red deer population, and this effect was not statistically significant.

The human population in the study area increased by over 30% since 1921. This trend was driven by areas at lower altitudes (below 600 metres above sea level), while higher areas broadly showed a reduction in human population. This trend is consistent to what has been observed in other areas across Europe, where people have largely abandoned remote and mountainous areas (Navarro and Pereira, 2012). Interestingly however, since the 1990s the human population has been increasing even at higher elevations, due to a phenomenon of repopulation of mountainous areas in the Alps termed "new migration", supported in Trentino by local policy efforts (Bender and Kanitscheider, 2012, Corrado, 2014, Löffler et al., 2014). Forest cover in Trentino doubled between 1936 and 2015, with a substantial increase across all altitudinal ranges. This expansion is due to farmland abandonment and has been observed elsewhere in Europe, where forest cover has increased by a quarter since the 1950s (Fuchs et al., 2013, Navarro and Pereira, 2012, Gobbi, 2021).

These socio-economic and landscape changes favoured the recovery of large mammal species (Linnell et al., 2020, Linnell et al., 2010, Chapron et al., 2014, Cimatti et al., 2021). The overall significant increase in ungulate numbers that we observed in Trentino since the 1970s is consistent with trends at the European and national level (Linnell et

al., 2020, Carnevali et al., 2009). All populations considered in our study except roe deer grew monotonically. Despite roe deer numbers also increased across the whole study period, they showed a strong decrease between 2004 and 2006, after peaking in the early 2000s. This decline in roe deer numbers is striking in the data on hunting quotas and on the number of hunted animals, and has been related to a population crash due to reported, but unquantified events such as winter and disease mortality (Bragalanti pers.comm.). As a result, estimates and quotas were drastically reduced with a cautionary approach (Apollonio et al., 2019, Carnevali et al., 2009) also due to harsh winter conditions (Bragalanti pers.comm.). Since 2007, the management and monitoring approach has been more consistent and roe deer numbers seem to have recovered and stabilised (Apollonio et al., 2019). These trends in roe deer numbers also correspond to the trends in the numbers of individuals found dead and reported to the province (Supplementary Information).

In addition to the ungulates considered in this study, the Alpine ibex (*Capra ibex*) is also present in Trentino. We did not consider this species because it occurs mostly along the administrative borders of the province, making the monitoring data within the province highly variable across years and therefore unreliable. The ibex was extinct in Trentino until the early 1970s, when it was reintroduced through several reintroduction programmes. The population reached a peak in abundance around 2002, after which it was decimated by sarcoptic mange (PAT, 2010). Currently, the ibex population in Trentino is estimated to be around 350-370 individuals (PAT, 2010).

With regards to carnivores, bears and wolves constantly increased in numbers since their first appearance. For bears, this was due to their reintroduction in 2002, whereas wolves naturally recolonised the province with their first pack recorded in 2013. The wolf recovery in both abundance and spatial distribution matches observed trends in other parts of Europe (Chapron et al., 2014, Reinhardt et al., 2019).

With the recovery of the wolf, ungulates and livestock started suffering from predation, with over 200 events reported for wild ungulates in 2019 and almost 100 domestic animals killed in 2020. The preferred prey species were roe deer and red deer, together representing 74% of all wild predation. Livestock were mainly killed in the summer months (June to September) when they are brought to graze at higher altitudes and are more exposed to wolf predation. Interestingly, the number of wild predation events peaked in March and significantly decreased in summer months. This may suggest the occurrence of prey switching behaviour by wolves as a result of changes in prey relative abundance or accessibility (Morehouse and Boyce, 2011). However, the decrease in wild ungulate predation in the summer might also be due to a lower monitoring effort and probability of detection of wild carcasses at higher altitudes. In addition, it has to be noted that the number of wild prey is underestimated relatively to the number of domestic prey, because livestock predation events are directly reported by farmers to receive financial compensations (Groff et al., 2021), whereas wildlife carcasses are reported opportunistically.

The increasing frequency of wolf predation is likely to eventually affect the wild ungulate populations (Smith et al., 2020, Ripple et al., 2014, Passoni et al., 2022). We found only weak evidence for such an impact on red deer and no evidence for roe deer at the population level. Detecting these impacts will be difficult due to the system being in a highly dynamic and unstable state whereby both the prey and predators are recovering in abundance and distribution (Peterson et al., 2003). When all species show a positive trend, it is hard to infer species interactions from count data alone (Peterson et al., 2003). Nonetheless, we expect the effects of wolf predation to be increasingly evident as the system stabilises and populations approach carrying capacity.

In addition to predation, the general recovery of the large mammal community might also lead to interspecific competition among ungulates. Such competition has already been suggested between chamois and red deer (Corlatti et al., 2019), and between roe

deer and red deer (Richard et al., 2010). We did not test for competition between herbivores because of the highly correlated nature of increasing population trends, and the scarcity of reliable data in the period before the red deer recovery.

In this study, we mainly used hunting data as an index of population abundance and distribution of ungulates species. These data alone have been shown to produce biased estimates of population density in certain contexts, especially when not adjusted for hunting effort (Pettorelli et al., 2007, Imperio et al., 2010). Nonetheless, hunting data have been extensively used as proxies for population estimates to analyse population dynamics and ecological processes (Moleón et al., 2013, Massei et al., 2015, Hagen et al., 2014, Grøtan et al., 2005, Cretois et al., 2020, Linnell et al., 2020). We agree that caution should be taken when analysing these type of data. However, we believe that hunting data represent a good proxy for the long term trends in ungulate abundance in Trentino for several reasons. Hunting quotas in Trentino are established based on population counts and other ecological factors (Apollonio et al., 2019). At the province level, where all data types are available, the population estimates from animal counts, hunting quotas, and the number of animals killed by hunters are correlated (Supplementary Information). Furthermore, most species (i.e. red deer, chamois, wild boar and mouflon) were not present, or were present at extremely low numbers at the beginning of the study period. Finally, despite the increase in hunting quotas and kills, the number of requests and releases of hunting permits significantly decreased, making it extremely unlikely that increasing population trends are due to growing hunting pressure.

We showed an example of a rapid and large-scale ecosystem recovery. This is a positive story that should inspire the future conservation of large mammal communities globally (McAfee et al., 2019). However, this recovery also has socio-economic implications that, if unaddressed, can negatively affect both humans and wildlife. It is therefore important that we continue to strengthen monitoring programmes, and that future policy and

management decisions take into considerations the challenges of living with wild animals (Linnell et al., 2020).

2.5 Supplementary information

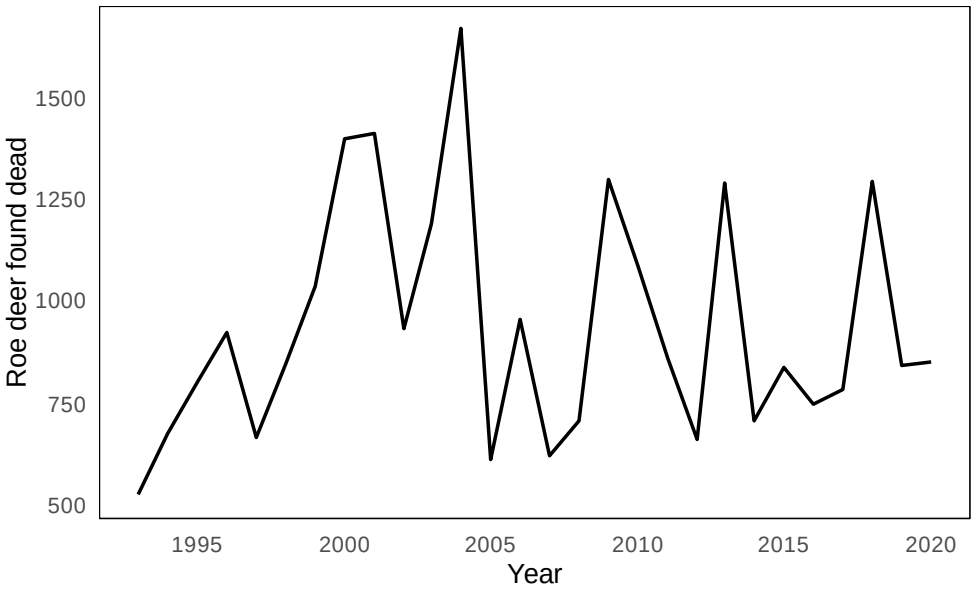


Figure 7 Number of roe deer found dead and reported to the province between 1993 and 2020.

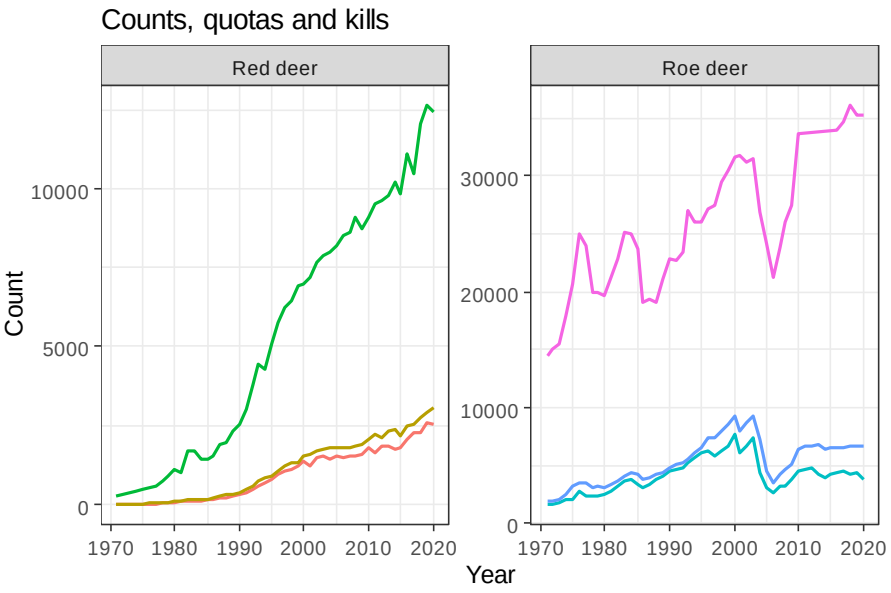


Figure 8 Individual counts, hunting quotas and number of hunted individuals for red deer and roe deer in Trentino between 1971 and 2020.

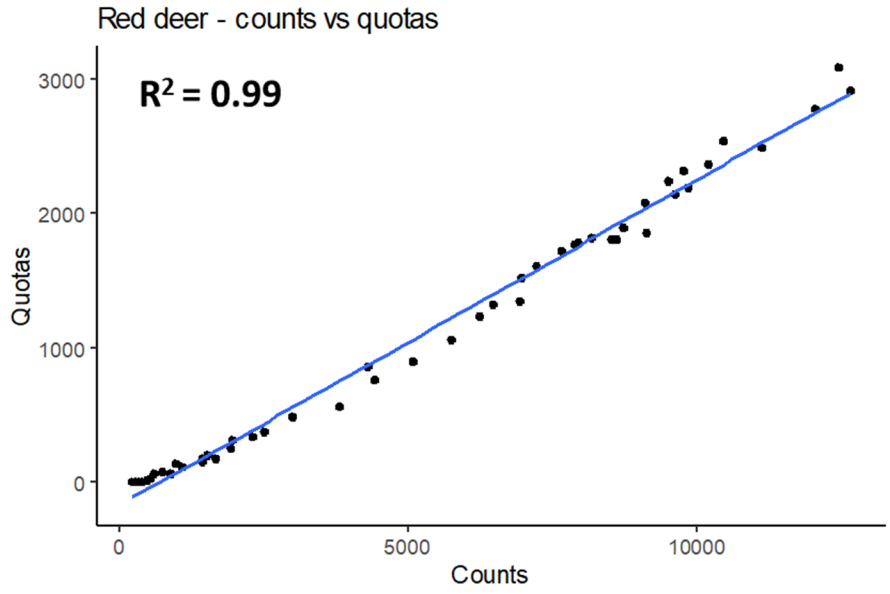


Figure 9 Correlation between red deer counts and red deer hunting quotas

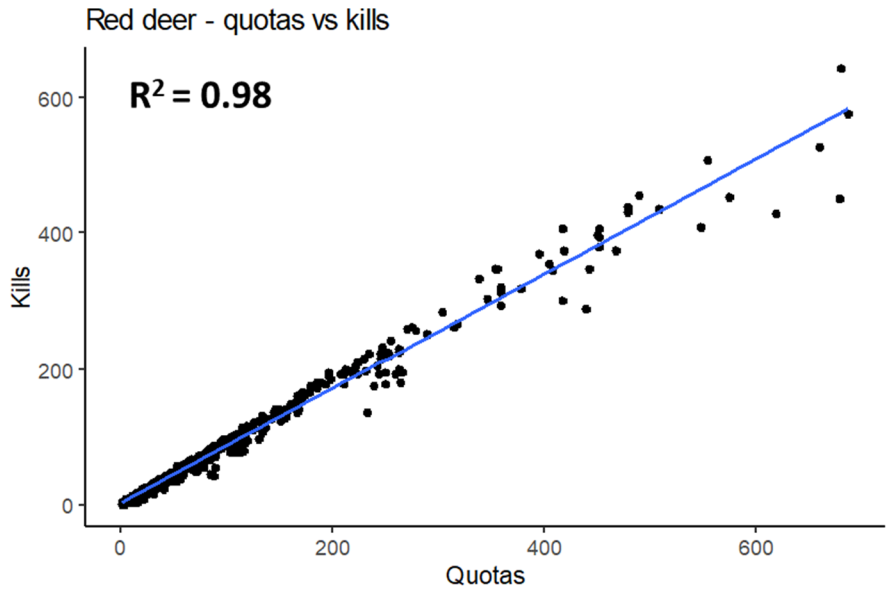


Figure 101 Correlation between red deer hunting quotas and number hunted red deer individuals

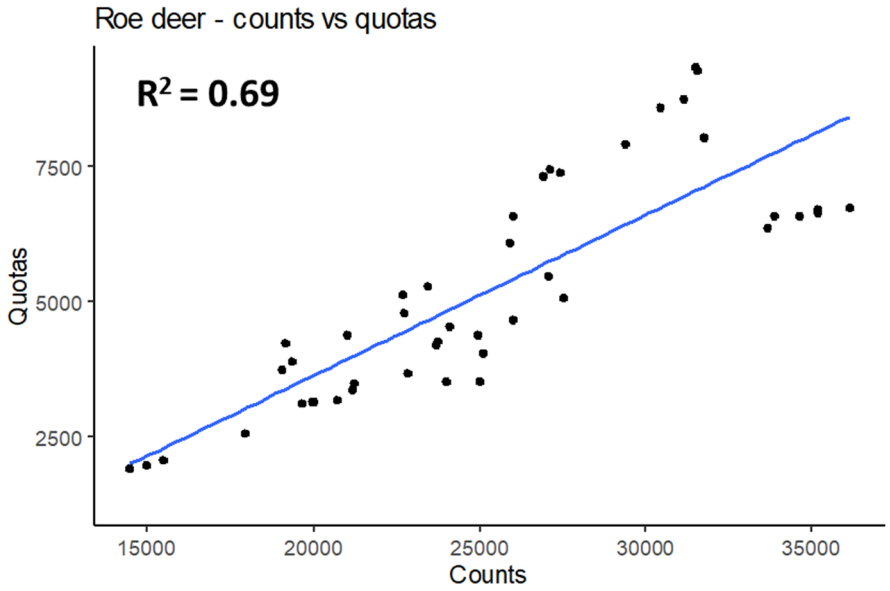


Figure 11 Correlation between roe deer counts and roe deer hunting quotas

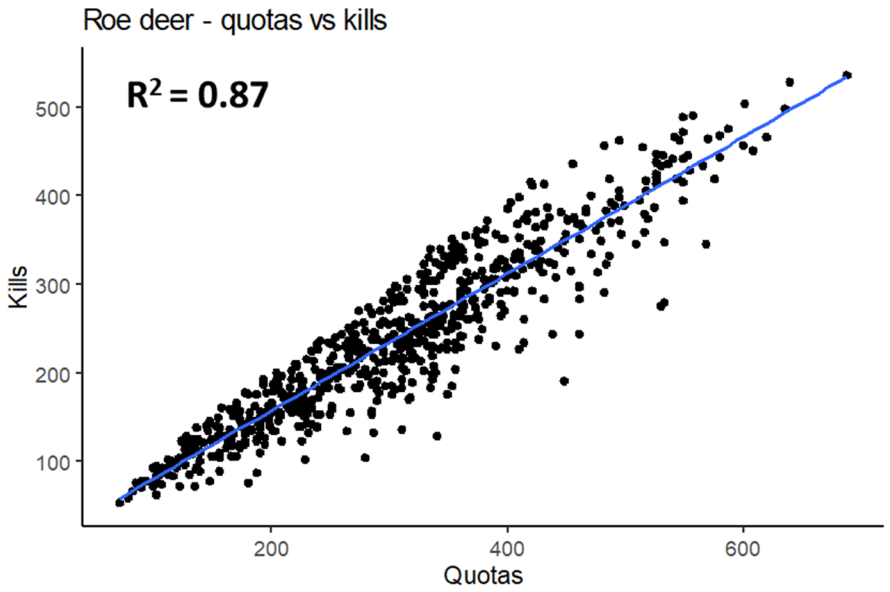


Figure 12 Correlation between roe deer hunting quotas and number hunted roe deer individuals

2.6 References

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3

Roads constrain movement across behavioural processes in a partially migratory ungulate

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Abstract

Human disturbance alters animal movement globally. Infrastructure, such as roads, can act as physical barriers that impact behaviour across multiple spatial scales. In ungulates, roads can particularly hamper key ecological processes such as dispersal and migration, which ensure functional connectivity among populations, and may be particularly important for population performance in highly human-dominated landscapes. The impact of roads on some aspects of ungulate behaviour has already been studied. However, potential differences in response to roads during migration, dispersal and home range movements have never been evaluated. Addressing these issues is particularly important to assess the resistance of European landscapes to the range of wildlife movement processes, and to evaluate how animals adjust to anthropogenic constraints.

We analysed 95 GPS trajectories from 6 populations of European roe deer (*Capreolus capreolus*) across the Alps and central Europe. We investigated how roe deer movements were affected by landscape characteristics, including roads, and we evaluated potential differences in road avoidance among resident, migratory and dispersing animals (hereafter, movement modes). First, using Net Squared Displacement and a spatio-temporal clustering algorithm, we classified individuals as residents, migrants or dispersers. We then identified the start and end dates of the migration and dispersal trajectories, and retained only the GPS locations that fell between those dates (i.e., during transience). Finally, we used the resulting trajectories to perform an integrated step selection analysis.

We found that roe deer moved through more forested areas during the day and visited less forested areas at night. They also minimised elevation gains and losses along their movement trajectories. Road crossings were strongly avoided at all times of day, but when they occurred, they were more likely to occur during longer steps and in more forested areas. Road avoidance did not vary among movement modes and, during dispersal and migration, it remained high and consistent with that expressed during home range movements.

Roads can represent a major constraint to movement across modes and populations, potentially limiting functional connectivity at multiple ecological scales. In particular, they can affect migrating individuals that track seasonal resources, and dispersing animals searching for novel ranges.

3.1 Introduction

Human disturbance negatively impacts wildlife and limits animal movement globally (Tucker et al., 2018). Infrastructure, such as roads, can reduce and fragment available habitat, increase wildlife mortality due to collisions with vehicles, and act as physical barriers that can impact behaviour across a range of spatial scales (Forman et al., 2003, Fahrig and Rytwinski, 2009). In recent decades, the discipline of road ecology has developed to address these issues, focusing on various animal taxa and regions (Laurance et al., 2009, Trombulak and Frissell, 2000). In ungulates, roads can particularly hamper movement processes such as dispersal and migration (hereafter called "long range movements"), which are typically associated with long distance movements and key ecological processes (Benoit et al., 2020).

Seasonal migration allows individuals to exploit spatial variation in resource availability, potentially reducing intra-specific competition and, in some cases, predation risk (Peters et al., 2017, Hebblewhite and Merrill, 2007). Dispersal occurs when individuals leave their natal (or breeding) area to settle in their first (or a new) breeding range, impacting population genetic structure and metapopulation dynamics (Bowler and Benton, 2005, Thompson and Gonzalez, 2017, Clobert et al., 2012). Long range movements ensure functional connectivity among populations, and may be particularly important for population performance in highly human dominated and mountainous areas where anthropogenic or topographic barriers may separate suitable habitat (e.g., roads, mountain ridges) (Bowler and Benton, 2005).

In ungulates, movement and habitat selection are mainly shaped by landscape features such as topography and forest cover (Coulon et al., 2008), seasonal dynamics like vegetation phenology (Aikens et al., 2020), and human disturbance (Sawyer et al., 2013). Some of these aspects, in particular the impact of roads on resident, migratory or dispersing animals, have already been investigated in a number of systems. For example, roads significantly reduced long-distance movements in reindeer (*Rangifer tarandus*) in

Norway (Beyer et al., 2016), and limited gene flow among different populations of roe deer in Switzerland (Kuehn et al., 2007). Mule deer (*Odocoileus hemionus*) were also shown to avoid roads and move faster when migrating across roads (Sawyer et al., 2013).

Despite this body of knowledge, potential differences in response to roads during different movement modes, in particular residency, dispersal and migration as observed in partially migratory populations, have never been evaluated. Since habitat selection along these movement modes can differ (Killeen et al., 2014), animals may show different responses to semi-permeable barriers such as roads. In resident individuals, roads can alter space use within the home range (Coulon et al., 2008, Bonnot et al., 2013) and increase home range size and mortality risk (Jerina, 2012, Niemi et al., 2015). Indeed, mortality risk was shown to be higher for roe deer (*Capreolus capreolus*) moving in unfamiliar areas on the outskirts of their home range (Gehr et al., 2020). By shaping space use (Ranc et al., 2020b, Ranc et al., 2020a), site familiarity could therefore lead to a relatively strong road avoidance in resident individuals.

Long distance movements can also be costly in human-dominated environments, as the likelihood of crossing roads increases (Sawyer et al., 2016). Moving into new areas carries costs, and venturing out of an established home range can force individuals through areas with higher road densities. For example, Benoit et al. (2020) showed that dispersing roe deer spent more energy than resident individuals, especially when moving through fragmented areas with high road densities. Additionally, site familiarity during long range movements can vary. Migration is a recurrent behaviour that generally occurs annually and can be culturally transmitted (Jesmer et al., 2018). While migrating, animals may therefore have some familiarity with the surrounding landscape (Sawyer et al., 2018), and may be able to avoid roads more effectively. On the other hand, dispersal mostly occurs through unfamiliar landscapes (Debeffe et al., 2013). As such, knowledge of the spatial distribution of roads and associated sources of risk is likely lower or absent. Addressing these issues is particularly important to assess the resistance of human-

dominated landscapes to the range of different wildlife movements, and to evaluate how animals adjust their behaviour to anthropogenic constraints.

In this study, we focused on six populations of European roe deer across the Alps and central Europe, with two main objectives: i) to investigate how roe deer movements are affected by roads and other landscape characteristics; and ii) to identify potential differences in road avoidance among resident, migratory and dispersing animals. The European roe deer is a widespread ungulate in Europe that lives in habitats as diverse as boreal forests and Mediterranean shrublands (Linnell, 1998). They are behaviourally flexible, showing a wide variety of movement modes, from sedentary behaviour to migration, as well as several tactics of natal dispersal (Ducros et al. 2020). In the populations considered in this study, the roe deer is a partial and facultative migrator, with only part of the population migrating each year, generally following the elevation gradient (Cagnacci et al., 2011, Peters et al., 2017). In turn, roe deer dispersal is a relatively conserved behaviour across populations (Gaillard et al., 2008).

To investigate movement-specific habitat selection and test for differences in road avoidance among different movement modes, we performed an integrated step selection analysis (iSSA, (Avgar et al., 2016)). We expected roe deer movements to be affected by resource availability, landscape topography and risk avoidance. With regards to resources, we predicted that roe deer should select areas with higher NDVI values (Normalised Difference Vegetation Index – i.e., a proxy for the availability of food). Roe deer should also minimise unnecessary energy expenditure, and thus the elevation gains and losses along their movement trajectories. We expected roe deer to avoid risks, especially those linked to human disturbance. In this context, roe deer should select forested areas further away from roads during the day, and more open areas closer to roads during the night time (Bonnot et al., 2013, Lagos et al., 2012). Moreover, when close to roads, roe deer should select areas with higher forest density (Coulon et al., 2008) in order to seek protection from human disturbance, as shown for other ungulates

(Prokopenko et al., 2017, Hebblewhite and Merrill, 2009). With regards to how road avoidance may vary among movement modes, we predicted that it should be strongest for resident individuals with relatively high site familiarity and weakest for dispersers that move longer distances across unknown landscapes, with intermediate levels for migratory individuals.

3.2 Methods

3.2.1 Animal relocation data and study areas

The data used for this study were obtained from the EURODEER database of the EUROMAMMALS initiative (www.euromammals.org), a collaborative science project that stores and manages spatial data of European mammals from across Europe. We initially considered data from 344 individuals fitted with GPS collars between 2004 and 2015, for a total of 2,264,497 locations. Intervals between consecutive locations spanned between 15 minutes and 12 hours.

The collared individuals were from six different populations in mountainous or sub-mountainous areas in the Alps and central Europe (Figure 1 – Switzerland: Bernese Oberland (n=74); Italy: Val Rendena (n=27 individuals), Monte Bondone (n=26 individuals); Germany: Bavarian Forest (n=179 individuals), Hegau (n=12 individuals); Austria: Leoben (n=26 individuals)).

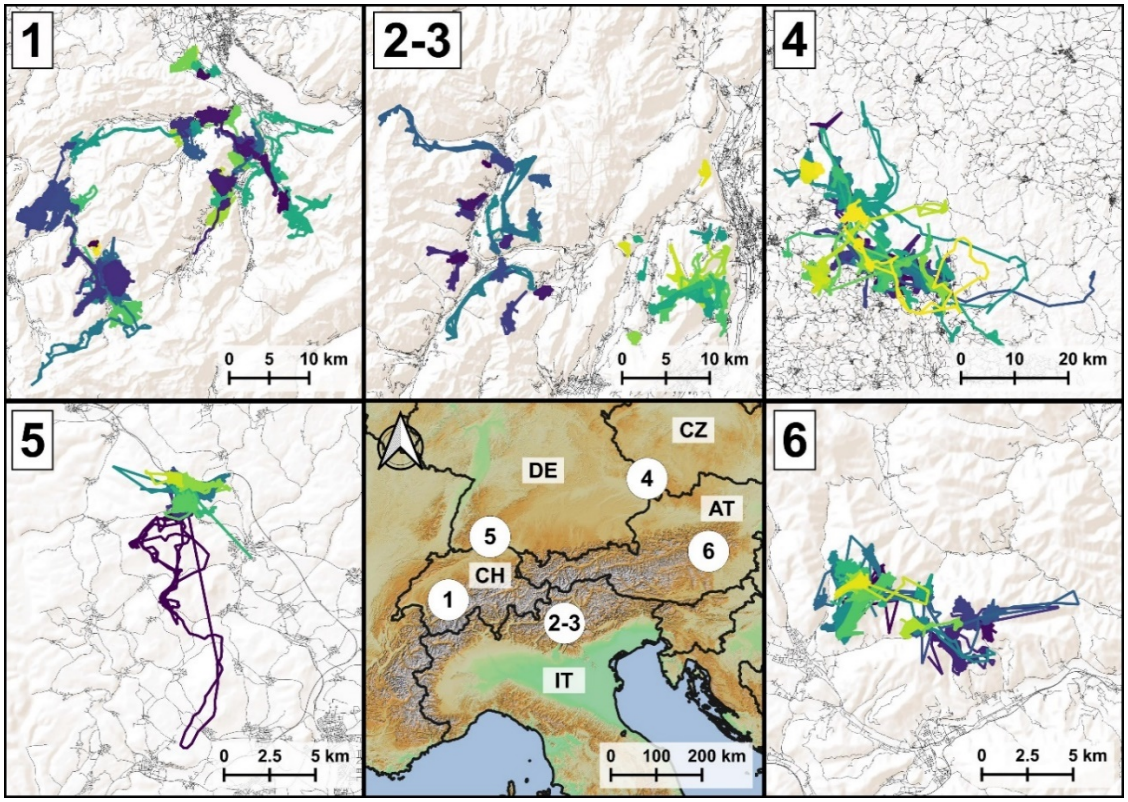


Figure 1 Map showing the location and key information of the 6 study areas (1 = Bernese, 2 = Rendena, 3 = Bondone, 4 = Bavaria, 5 = Hegau, 6 = Leoben). For each area, we show the trajectories of the GPS tracked roe deer, the road network and the digital elevation model.

Despite being different in many aspects, the selected areas are characterised by a mountainous topography, the presence of natural or semi-natural areas, and a limited proportion of agricultural areas. Roads, human settlements and urban areas are mostly concentrated at the bottom of the valleys (see Supplementary Information for more information about study areas). Furthermore, individuals in these populations are known to perform all the movement modes considered in this study (i.e., home range movements, migration, dispersal).

3.2.2 Movement data management and classification of movement patterns

From the initial dataset, we retained only the individuals with a fix interval of up to 5 hours. Between January and March, movements are generally limited within the winter ranges. As such, we selected the GPS trajectories with at least 10 months of data from

a start date between 1st and 31st March to an end date between the 1st and 31st January of the following year. These dates were chosen based on Peters et al. (2017) and Peters et al. (2019) to ensure that we captured migration and dispersal events, and to maximise sample size. Each GPS trajectory was then truncated by discarding locations falling outside of our specified date window.

In order to classify movement patterns, we used the Net Squared Displacement method (NSD – (Bunnefeld et al., 2011). The NSD is calculated as the squared geographical distance of each GPS location from a first, reference location. In this case, we ensured that the first location fell in an animal's winter range. The NSD method fits several non-linear models to the observed NSD values, each representing a movement mode (i.e. resident, migrant, disperser). The best model, which classifies the movement pattern of each individual, is then selected based on the Akaike Information Criteria (AIC) (Bunnefeld et al., 2011). The NSD analyses were conducted using the 'migrateR' package (Spitz et al. (2017) – parameters available in Supplementary Information) in R 3.5.1 (R Development Core Team 2013). Animal trajectories were also spatially investigated using SeqScan, a spatio-temporal clustering algorithm available in the QGIS plugin 'MigrO' which has previously proved effective for the analysis of movement patterns from GPS trajectories (Damiani et al., 2015b, Damiani et al., 2015a). The use and comparison of multiple methods is recommended for a more accurate classification of movement patterns, especially in species like roe deer with a wide range of movement behaviours (Cagnacci et al., 2016). If the classification was ambiguous using the NSD method and SeqScan, the trajectory was discarded.

Because we were interested in comparing step selection among different movement modes, for migration and dispersal, we only retained the trajectory of the transience phase (i.e. the segment of trajectory during the period of migration and dispersal). To do this, we identified the start and end dates of these events from the NSD plot using the '*locator()'* function in the 'graphics' R package and we used these dates to truncate

the trajectories. As such, spring migration trajectories start from the time when an animal leaves its winter range to the time it settles in the summer range. Similarly, for dispersal trajectories, we considered only the movement between the two ranges, ignoring locations within the two ranges. Stopovers and multi-trip migrations (i.e. including multiple trips between seasonal ranges before settling – (Cagnacci et al., 2011)) were included, as long as they occurred in the isolated segments. The trajectories of resident individuals were truncated using the median start and end times of migratory animals in order to evaluate behaviour during comparable periods. We report these values in the results section.

Once we classified each movement category and obtained the trajectories, we excluded all the individuals with a gap of more than 7 days of consecutive missing data. All trajectories were then re-sampled by retaining points at a fix interval of 3 to 5 hours. We did not re-sample to a single fix interval because trajectories can only be re-sampled to a multiple of the original fix intervals, which in our case were 3, 4 and 5 hours (i.e. the least common multiple would be 60 hours, which is much larger than the scale we wanted to focus on). Following this process, we retained a total of 95 trajectories from 79 individuals, which represent the final dataset used in the model (Italy: Val Rendena (n=10 individuals), Monte Bondone (n=9); Germany: Bavarian Forest (n=26), Hegau (n=2); Switzerland: Bernese Oberland (n=31); Austria: Leoben (n=1)). The re-sampling of the trajectories was carried out using the R package 'adehabitatLT' (Calenge, 2016).

3.2.3 Integrated step selection analysis

In order to assess the impact of spatial variation in resources, topography, and roads on roe deer movement, we conducted an integrated step selection analysis (iSSA – (Avgar et al., 2016). iSSA jointly estimates resource selection and animal movement parameters (e.g. step length), by relaxing the implicit assumption that these are independent (Avgar et al., 2016).

In iSSA, each observed animal step (i.e., movement between two consecutive GPS fixes) is compared to a set of random steps (i.e., that animal could have taken) using conditional logistic regression. In this study, we matched each observed step with 10 random steps, computed using distances sampled from a gamma distribution fitted to the empirical step length distribution and random turning angles, using the R package 'amt' (Signer, 2018) (see Supplementary information for the step length and turning angle distributions used to generate random steps). Because our trajectories had different fix intervals ranging between 3 and 5 hours, for each fix interval we generated random steps using the distribution of steps at the corresponding interval (e.g., random steps for an individual with a fix interval of 3 hours were generated using the step distribution of individuals with a fix interval of 3 hours) (Supplementary Information). The number of random steps was chosen based on the recommendations of Thurfjell et al. (2014), to create a sufficiently large sample size while preventing excessively long computational processing times. To ensure that 10 random steps were enough, we performed a sensitivity analysis by running separate models using 1 to 10 random steps, and recorded model coefficients for each model (Supplementary Information).

We extracted environmental covariates at the end of each step, together with the number of road crossings along each step, the time of day (categorical: day, twilight, night – see Supplementary Information for details on how this was calculated) and step length (see Table 1 for the complete list of variables). All variables were scaled and centred, and screened for collinearity using the Pearson's correlation coefficient with a threshold of $|r| > 0.7$ (Dormann et al., 2013). We performed an iSSA using mixed-effect conditional logistic regression to identify the main predictors of movement using the full set of covariates (see Table 2 for model terms), since we did not find any substantial collinearity between variables (Supplementary Information). To account for differences in habitat selection during different times of the day and when crossing roads (Prokopenko et al., 2017), we added interactions between forest density and time of day, number of road crossings and time of day, and forest density and number of road crossings. To specifically

test for differences in road avoidance among the three movement modes, we added the interaction between number of road crossings and the movement mode of each individual. To control for the fact that longer steps are statistically more likely to cross roads, we included an interaction between number of road crossings and the natural logarithm of step length (Avgar et al., 2016). To account for the fact that our trajectories had different fix intervals and to avoid biased model coefficients, we used the hourly step length, obtained by dividing each step length by the relative fix interval (Table 1, Supplementary Information). Finally, we controlled for potential differences in step length and number of road crossings for the two sexes. Nested random effects were included for individuals and populations to control for repeated measures. This decision was made to account for unequal number of steps for each individual and unequal numbers of individuals in each population. Models were fitted using the R package 'coxme' (Zeller et al., 2014, Therneau, 2015). We also attempted to account for variation among individuals by fitting random slopes using multiple approaches described by Muff et al. (2020), Craiu et al. (2011), and (Therneau, 2015) unfortunately failing due to convergence issues (see Supplementary Information for the R code with the attempts to run these models and the section "Caveats and Potential Biases" in the Discussion).

The importance of each explanatory variable in predicting habitat selection was assessed by removing one variable at a time from the full model, which included all predictors, and recording the change in AIC value for each sub-model (here called $\Delta AIC_{REMOVED}$). The most important variables were identified as those that, when removed, caused the highest increase in AIC (i.e. the variables with the highest $\Delta AIC_{REMOVED}$).

Table 1 Variables used in the model. For each variable we report the resolution, a general description of the variable and the source from which the variable was obtained.

Variable	Resolution	Description	Source
Elevation difference	25 m	Difference in altitude between start and end of a step	European Environment Agency (EEA) – EU Copernicus. European Digital Elevation Model (EU-DEM), version 1.1
Slope	25 m	Slope in degrees (0 to 90)	
Forest density	20 m	Percentage of area covered by trees (0-100%)	European Environment Agency, 2012
NDVI	250 m	Mean NDVI value (time series of 8 days composite)	Modis - Institute of Surveying, Remote Sensing and Land Information of the University of Natural Resources and Applied Life Sciences, Vienna (2004-2015)
Road crossings	-	Number of road crossings per step	Open street map. Only paved roads were considered.
Time of day	-	Categorical (day, twilight, night) (See Supplementary Information for details on how it was calculated)	GPS collar data
Log(Step length)	-	Natural logarithm of hourly step length in meters (See Supplementary Information)	GPS collar data
Movement mode		Resident, migrant or disperser	Analysis (see main text)
Sex	-	Sex of the individual	Collected at capture

Table 2 Terms used in the step selection function with the associated predictions.

Model terms	**Predictions**
Forest Density + Forest density : Time of day	Selection of more forested areas during the day and more open areas during night time (Bonnot et al., 2013).
Slope + Slope^2	Selection of flatter areas (Gaudry et al., 2015). A quadratic term was added to evaluate selection of slopes with intermediate steepness.
Elevation difference + Elevation difference^2	Selection of steps with low elevation difference – i.e. low elevation gain/loss (i.e. around zero).
NDVI + NDVI^2	Selection of areas with higher NDVI values. A quadratic term was added to evaluate selection of intermediate values, especially during migration (Sawyer and Kauffman, 2011).
Road crossings	General avoidance of road crossings (Prokopenko et al., 2017).
Road crossings : Time of day	Road crossings should be avoided at all times of day, but particularly during the day and twilight, when traffic is more intense (Lagos et al., 2012, Paton et al., 2017).
Road crossings : Forest density	Road crossings should occur preferentially in more forested areas (Prokopenko et al., 2017, Coulon et al., 2008)
Road crossings : Movement mode	Road avoidance should be strongest for resident individuals, intermediate for migrants and weakest for dispersers.
log(Step length)	Statistical estimator of the parameters of the assumed step-length distribution (Avgar et al., 2016).
log(Step length) : Sex	Control to account for potentially different step lengths between sexes.
Road crossings : log(Step length)	Control to account for the fact that longer steps are more likely to cross roads.
Road crossings : Sex	Control to account for potentially different road avoidance between sexes.

3.3 Results

3.3.1 Trajectories and movement patterns

Of the 95 retained trajectories, 25 were migratory events, 8 were dispersal events and 62 were extracted from resident individuals.

The median start date for migration was 6 April (min. 29 February; max. 3 May), while the median end date was 23 May (min. 25 March; max. 10 September). For dispersal, the median start date was 4 May (min. 28 February; max. 2 August) and the median end date was 7 June (min. 17 March; max. 20 August). For all resident animals, the start and end dates were set to 10 April and 27 May (i.e. the median start and end date for migration and dispersal), respectively. The median durations for migration, dispersal and resident movements were 61 days (min. 20; max. 192), 27 days (min. 16; max. 65) and 47 days (min. 47; max. 47; by definition), respectively.

3.3.2 Integrated step selection analysis

In Table 3, we report the coefficients and confidence intervals of the full model, as well as the $\Delta AIC_{REMOVED}$ for each variable. The most important variables were forest density ($\Delta AIC_{REMOVED} = 1784$), its interaction with time of day ($\Delta AIC_{REMOVED} = 1738$), and number of road crossings ($\Delta AIC_{REMOVED} = 1076$). Despite most of the other variables being significant, they were relatively less important for explaining step selection (Table 3).

Table 3 Summary of the full model showing model coefficients (β) with 95% confidence intervals, the standard deviation of the random effects, and the number of observations. These were obtained from the full model. Additionally, for each variable, we also report the $\Delta AIC_{REMOVED}$, i.e., the difference in AIC between the full model and the full model without that variable. Hence, the variables with the highest $\Delta AIC_{REMOVED}$ are the most important because, when removed, they caused the highest increase in AIC. Variables are listed in order of importance. The AIC of the full model including all variables was 129748.

Variable	**β**	**95% C.I.**	**$\Delta AIC_{REMOVED}$**
log(Step length)	-0.407	[-0.425, -0.389]	4697
Forest density	0.347	[0.324, 0.371]	1784
Forest density : Time of day			1738
Forest density (day)	0.347	[0.324, 0.371]	
Forest density (night vs day)	-0.787	[-0.825, -0.749]	
Forest density (twilight vs day)	-0.423	[-0.486, -0.36]	
Road crossings	-1.379	[-1.505, -1.252]	1076
Road crossings : log(Step length)	0.231	[0.205, 0.257]	284
log(Step length) : Sex			142
log(Step length) (female)	-0.407	[-0.425, -0.389]	
log(Step length) (male vs female)	0.143	[0.119, 0.168]	
Slope	0.107	[0.081, 0.133]	129
Slope^2	-0.076	[-0.092, -0.06]	98
Road crossings : Forest density	0.068	[0.046, 0.09]	44
Road crossings : Time of day			29
Road crossings (day)	-1.379	[-1.505, -1.252]	
Road crossings (night vs day)	0.110	[0.065, 0.156]	
Road crossings (twilight vs day)	0.047	[-0.034, 0.129]	
Elevation difference^2	-0.014	[-0.02, -0.007]	28
Elevation difference	0.003	[-0.015, 0.021]	26
NDVI	0.056	[0.005, 0.107]	24
Road crossings : Sex			16
Road crossings (female)	-1.379	[-1.505, -1.252]	
Road crossings (male vs female)	-0.066	[-0.111, -0.02]	
NDVI^2	-0.023	[-0.047, 0.002]	11
Road crossings : Movement mode			7
Road crossings (resident)	-1.379	[-1.505, -1.252]	
Road crossings (disperser vs resident)	0.010	[-0.061, 0.081]	
Road crossings (migrant vs resident)	0.030	[-0.023, 0.084]	
Random effects	**Standard deviation**		
Individual animals (N=79)	0.041		
Populations (N=6)	0.020		
Number of events: 26892 observed + 268920 random steps			

In general, roe deer tended to select steps with higher forest density during the day, but with more open habitat during night time (day: β = 0.35; 95% CI [0.32, 0.37], night compared to day: β = -0.79; 95% CI [-0.83, -0.75] – Table 3, Figure 2). Roads were strongly avoided at all times of the day (β = -1.38; 95% CI [-1.51, -1.25]), but were crossed more frequently in areas with higher forest density (β = 0.07; 95% CI [0.05, 0.09]). The number of road crossings increased with step length (β = 0.23; 95% CI [0.21, 0.26]). Furthermore, males tended to have longer steps than females (females: β = -0.407; 95% CI [-0.43, -0.39]; males vs females: β = 0.143; 95% CI [0.119, 0.168]).

On average, roe deer tended to select areas with slopes of intermediate steepness, at around 10 degrees (β = -0.08; 95% CI [-0.09, -0.06]), and minimised elevation gains or losses along their steps, as shown by the negative coefficient for the squared elevation difference term (β = -0.01; 95% CI [-0.02, -0.01]). NDVI was the penultimate variable in the model in terms of importance ($\Delta AIC_{REMOVED}$=24), despite having a positive and significant coefficient (β = 0.06; 95% CI [0.01, 0.11]). The interaction between movement mode and number of road crossings was not significant (dispersers compared to residents: β = 0.01; 95% CI [-0.06, 0.08], migrants compared to residents: β = 0.03; 95% CI [-0.02, 0.08]) and was the least important variable in our model ($\Delta AIC_{REMOVED}$=7).

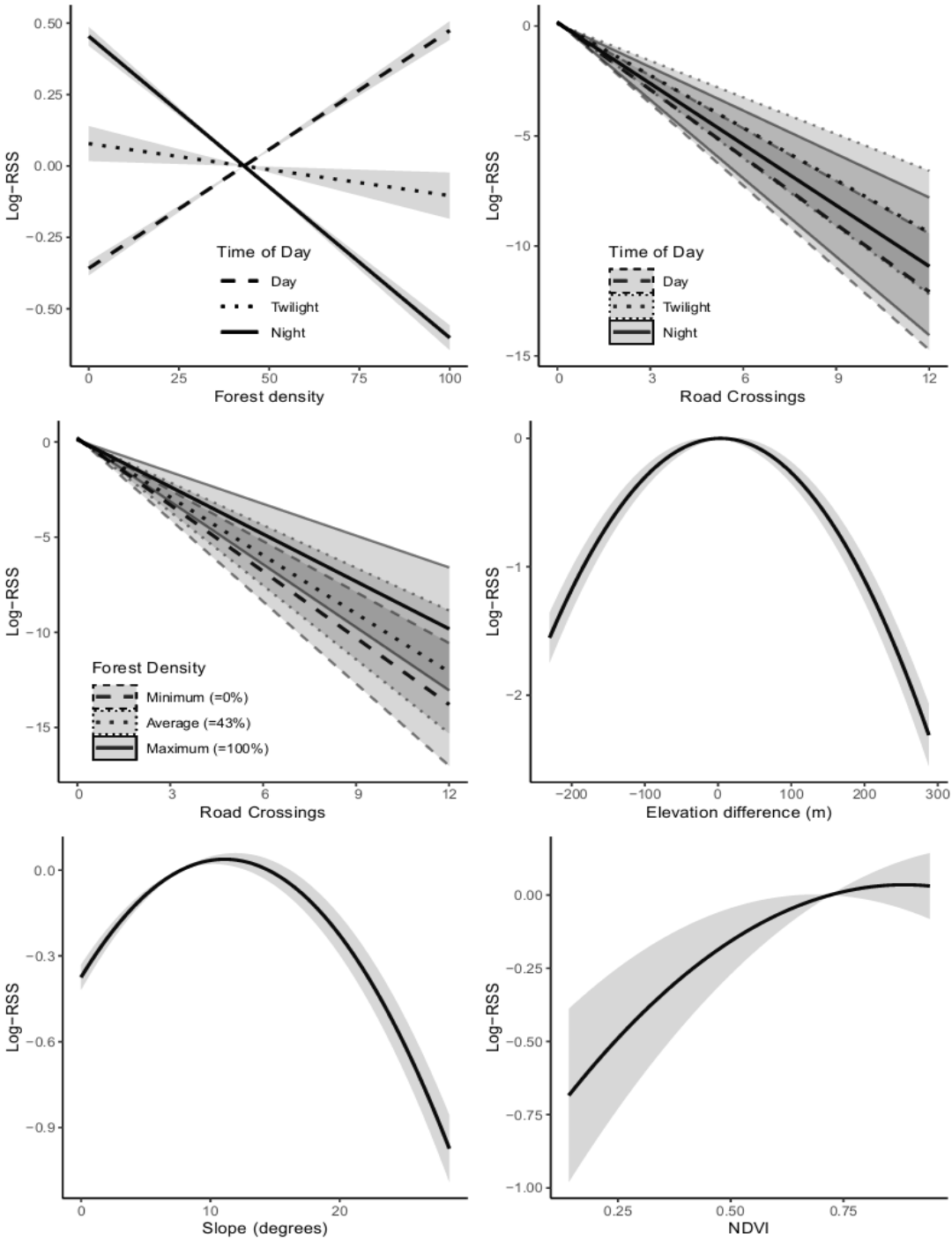


Figure 2 Response curves calculated using the fixed effect coefficients of the step selection function and showing the Relative Selection Strength (Log-RSS) for the most important model predictors with 95% confidence intervals (shaded areas) (Avgar et al., 2017). The range of values of the predictors on the x-axis corresponds to observed ranges, thus meaning that we did not project the predictions to unobserved or unrealistic values.

3.4 Discussion

Using an integrated step selection approach, we investigated habitat selection of roe deer during various movement modes across six populations in mountainous regions with a considerable human footprint. We showed that roe deer mainly selected forested areas, minimised elevation differences along their movement trajectories, and consistently minimised the number of roads crossed during migration, dispersal, and home range movements.

As expected, we found that higher forest densities were selected during the day, while less forested areas were visited more frequently at night, in accordance with other studies investigating roe deer habitat selection (De Groeve et al., 2016, Bonnot et al., 2013). Roads were strongly avoided at all times of the day, and crossings tended to be more common during longer movements. Roads have been shown to limit movement and space use in many animal taxa, including large carnivores (Corradini et al., 2021), small mammals (Grilo et al., 2018), reptiles (Shepard et al., 2008), amphibians (Cayuela et al., 2019), and even fish (Pépino et al., 2012). In ungulates, road crossings were avoided also by elk (*Cervus canadensis*), pronghorn (*Antilocapra americana*) and moose in North America (Prokopenko et al., 2017, Seidler et al., 2015, Beyer et al., 2013), and reindeer in Norway (Beyer et al., 2016). Studies on roe deer had previously suggested that they avoid roads at the home range scale, although focusing on the distance to the nearest road (Coulon et al., 2008), rather than actual crossings. We found that when animals did cross roads, they also tended to end their steps in more forested areas, potentially to seek protection and reduce risk of exposure to predators and disturbance, as shown for elk in North America (Prokopenko et al., 2017). Coulon et al. (2008) and Bonnot et al. (2013) also showed that roe deer selected forested areas more strongly when in proximity of roads.

In general, roe deer selected slopes of intermediate steepness (~10 degrees) as also found by (Ranc et al., 2020a). However, this differed from other studies arguing that roe deer

should select flatter areas to minimise energy expenditure (Gaudry et al., 2015). Our result may be due to the fact that, in human-dominated mountainous areas like those considered here, urbanisation and human activities are usually concentrated in the lower and flatter parts of the valley. Nonetheless, minimisation of energy expenditure is likely the reason why we found that roe deer also tended to minimise elevation gained or lost along their movements. Moreover, in summer, mountain ungulates tend to follow the elevation green up of the vegetation ('surfing the green wave', e.g. Aikens et al. (2017)). Hence, excessively large altitudinal displacements may result in a spatial mismatch between the location of the animal and the distribution of optimal resources (Aikens et al., 2017). In the French Alps, larger displacements towards high elevations were observed in correspondence of higher primary productivity, where more abundant resources could compensate for higher movement costs (Gaudry et al., 2015). In our case, NDVI had only a weak positive effect on roe deer step selection. This may be due to the fact that, in human-dominated landscapes, the effects of anthropogenic disturbance on ungulate behaviour can exceed those of natural processes (Ciuti et al., 2012). It is therefore possible that roe deer are forced to select sub-optimal resources in order to avoid roads and other sources of human disturbance (Ciuti et al., 2012). Nonetheless, it is also possible that the resolution of the NDVI variable considered in this study (8-day average at 250 metres) may be too coarse to capture its effect on roe deer step selection (average step length = 159 metres in 3 hours). In accordance with this, Aikens et al. (2020) showed that roe deer do not follow the plant green up as closely as other species, but select the most productive habitats at a finer scale (Mancinelli et al., 2015).

We did not find any evidence that road avoidance varied across migration, dispersal or home range movements. In other words, although roe deer may be less familiar with the landscape, and may be forced to frequently cross roads during migration and dispersal (Benoit et al., 2020), their level of road avoidance remained high and consistent with that expressed during home range movements. Roads can therefore pose a significant barrier for migrating roe deer to reach seasonal ranges and potentially access better

resources (Peters et al., 2017, Singh et al., 2012), and for dispersing roe deer to establish in a novel range, thus connecting spatially distinct populations (Ducros et al., 2020). In a partially migratory species, this may thus constrain migratory movements and reduce the relative proportion of migrants in high-road density areas. However, road crossings inevitably still occur, and resulting collisions with vehicles represent an important cause of mortality for roe deer in Europe, especially in relation to migration and dispersal events (Rodriguez-Morales et al., 2013). Additionally, even with regards to resident movements, the high level of road avoidance suggests a general constraint of human infrastructure on roe deer mobility. Future studies should focus on investigating fine scale behavioural adjustments to such constraints. For example, roads, as a source of risk, might be kept at the periphery of the home range (Seigle-Ferrand et al. unpubl.). This hypothesis is supported by recent work on the role of familiarity in shaping resource use (Ranc et al., 2020a, Ranc et al., 2021) and risk avoidance, whereby roe deer are more likely to constrain their movements to familiar areas, even within an established home range, where they experience lower mortality (Gehr et al., 2020).

Further research is also needed to evaluate the impact and consequences of human disturbance for dispersal and metapopulation functioning. We showed that road avoidance behaviour did not vary between resident (n=62) and migratory (n=25) individuals. However, due to low data availability, we could not draw strong conclusions for dispersing individuals (n=8). Another priority for research is to integrate other behavioural processes among the drivers of movement. For example, it has been shown that memory plays an important role in ungulate movement and space use (Bracis and Mueller, 2017). However, most studies integrating memory in habitat selection analysis have focused on space use within the home range, with a few exceptions (Bracis and Mueller, 2017, Merkle et al., 2019, Ranc et al., 2020a). Finally, future research should focus on relating movement and habitat selection to energetics and demography to quantify their costs and benefits for individual performance and ultimately population dynamics.

3.4.1 Caveats and Potential Biases

In our model, we included random intercepts for individuals and populations to account for repeated measures. In order to obtain more accurate estimates and account for variation among individuals (Muff et al., 2020), we also attempted to include random slopes using multiple recently-developed methods, unfortunately without success. First, we tried using 'coxme()' (Therneau, 2015) and the approaches proposed by Muff et al. (2020). These approaches worked well for simpler formulations of our model, providing very similar outputs as obtained without random slopes, however they failed to provide outputs as soon as the model became more complex (e.g., inclusion of interactions and nested random slopes) due to convergence issues. Indeed, these models can be challenging to fit (Fieberg et al., 2021, Muff et al., 2020). We also tried to use the two-step approach described in Craiu et al. (2011), but this was not applicable as the values of several variables in our model remained constant within all strata of at least one cluster. This is the main limitation of the two-step approach (Craiu et al., 2011, Muff et al., 2020, Fieberg et al., 2021). The R code used to run all the above-mentioned models is provided in the Supplementary Information.

Including mixed effects in conditional logistic regressions remains challenging and is a developing topic in iSSA (Fieberg et al., 2021). The use of random slopes has been recommended to fully account for inter-individual heterogeneity (Muff et al., 2020). Indeed, random-intercept-only models like the one presented here cannot account for among-individual variation in the regression slopes. Nonetheless, while we think that individual variation is important, the main aim of this study was to investigate how roads and other environmental factors can affect roe deer movement at the population level. According to recent findings, adding random slopes to our model could have produced more accurate estimates and allowed for more variance around random intercepts (Muff et al., 2020). However, iSSAs including random slopes have also been

shown to produce biased parameters when movement characteristics were included in the model (e.g. step length) (Muff et al., 2020, Fieberg et al., 2021).

In conclusion, we are aware that including random slopes would have better accounted for uncertainty around our coefficients and possibly resulted in slightly different estimates of effect sizes (Fieberg et al., 2021). However, given the computational challenges and the scarcity of research on mixed-effect iSSAs, we could not implement any of the currently available approaches in practice. Finally, considering the coherence of our results with the vast literature on roe deer ecology, and the consistency of outputs between the different approaches when using simpler model formulations with and without random slopes, it is unlikely that adding random slopes to the full model would have significantly changed our key findings.

3.5 Conclusions

This study showed that roads can represent a major constraint to movement across populations and movement modes, even for a species with relatively low movement propensity, and can therefore limit ecological connectivity at different scales (Kuehn et al., 2007). This is particularly relevant in mountainous areas, where roads are generally concentrated along valley bottoms, and high mountains can also represent barriers to individual movement and population spatial distribution. In the future, a spatially explicit model integrating other wide-ranging Alpine species (e.g. red deer, chamois, lynx, bear and wolf), could help predict the areas where roads have the strongest impact on functional connectivity, thus providing important guidance for targeted policy decisions and management interventions at the landscape scale.

3.6 Supplementary information

Study area summary statistics

Table 4 Summary statistics for the six study areas including environmental variables (mean [min-max]) and final number of individuals, trajectories and steps used in the model. *The fix interval in Leoben is actually 3 hours 15 minutes.

Study Area	Area (km^2)	Elevation (m)	Forest density (%)	Slope (degrees)	Road density (km/km^2)	No. of trajectories	No. of individuals	No. of steps per fix interval		
								3h	4h	5h
Bondone	194	872 [183-2125]	63 [0-100]	11 [0-34]	2.36	9	9	0	1930	0
Bavaria	1629	888 [417-1441]	62 [0-100]	4 [0-24]	1.12	31	26	515	546	5788
Leoben	86	1025 [568-1639]	72 [0-100]	10 [0-20]	0.64	1	1	139*	0	0
Rendena	357	1465 [461-3135]	59 [0-100]	13 [0-34]	1.26	10	10	3376	0	0
Bernese	1047	1474 [558-3002]	33 [0-98]	11 [0-34]	1.30	42	31	14465	0	0
Hegau	71	644 [455-874]	21 [0-94]	4 [0-17]	2.08	2	2	133	0	0
Total						**95**	**79**	**18489**	**2476**	**5788**

MigrateR parameters

Table 5 List of migrateR parameters used for the NSD analysis .

Parameter	Description	Value	Unit
l.d	NSD separating the first and second range (lower constraint)	5	Km^2
s.d	NSD separating the first and second range (starting value)	100	Km^2
l.r	Duration of occupancy on second range (lower constraint)	60	Days
u.r	Duration of occupancy on second range (starting value)	270	Days
l.g	Mean NSD of resident range (lower constraint)	0.07	Km^2
s.g	Mean NSD of resident range (starting value)	3	Km^2
u.g	Mean NSD of resident range (upper constraint)	5	Km^2
l.p	Time to complete 1/2 to 3/4 of departing movement (lower constraint)	1	Days
s.p	Time to complete 1/2 to 3/4 of departing movement (starting value)	1	Days
s.p2	Time to complete 1/2 to 3/4 of returning movement (starting value)	1	Days
u.p2	Time to complete 1/2 to 3/4 of returning movement (upper constraint)	1	Days
l.z	Difference in distance separating second and third range (lower constraint)	0.03	%

Generation of random steps and use of step length as a variable in the model.

Random steps were generated using the R package "amt" (Signer, 2018). Because our GPS data for two of the six populations had different fix intervals between 3 and 5 hours, for each fix interval we sampled random steps from its respective distribution (e.g. for individuals with 3 hours fix interval, we sampled the random steps from a distribution drawn using observed steps at 3 hours fix interval). This can be seen in figure 3A, which shows that individuals with larger fix intervals have longer generated steps on average (slope = 79.6; 95% C.I. = [59.3; 99.9]).

To account for these differences in our model, we normalised the step length in figure 3A by dividing it by the fix interval, thereby obtaining the hourly step length (m/h). As can be seen in figure 3B, the newly created variable (i.e. step length per hour) does not significantly change with fix interval (slope = 2.1; 95% C.I. = [-2.8; 7.0]). In our model, we therefore used the normalised variable 'step length per hour' to avoid a biased estimation of the model coefficients.

In table 6, we also report raw summary statistics. In figure 4, we show the distributions of used and available steps as a function of all habitat covariates at 3- and 5-hour fix intervals. Finally, in table 7, we report the parameters of the step length and turn angle distributions used to generate random steps.

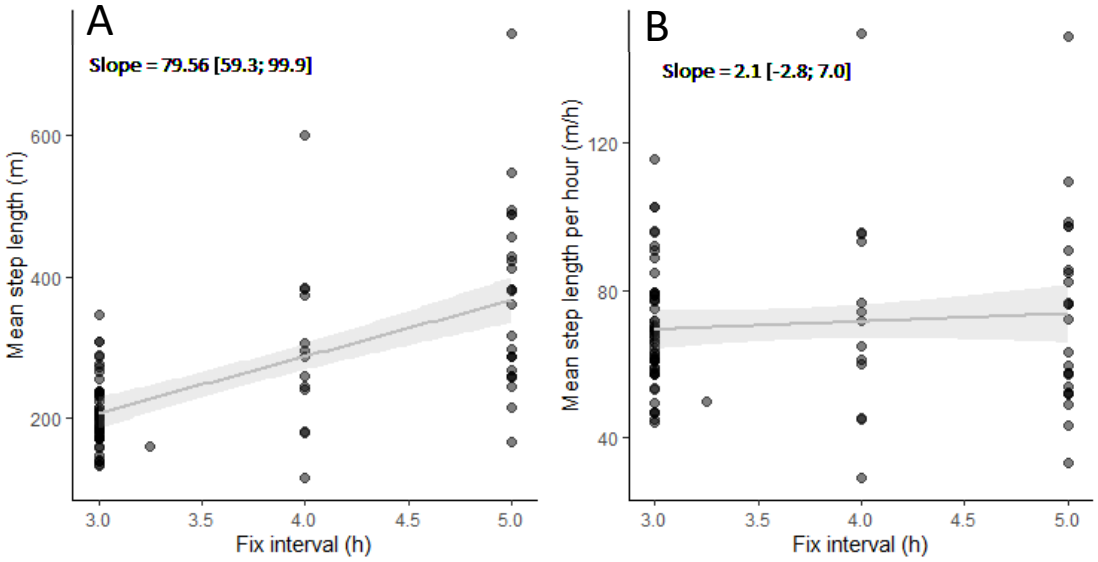


Figure 3 Plots showing the mean step length in metres (A) and the mean hourly step length in metres per hour (B) of generated steps as a function of fix interval. Each point represents the mean value of each individual animal. In each graph, we report the slope coefficient and 95% confidence intervals of a linear model fitted through the data (grey line and shadow).

Table 6 Table showing summary statistics for step length (m) and hourly step length (m/h) of the generated steps for each fix interval.

Fix interval (hh:mm)	No. of individuals	Step length (m)				Hourly step length (m/h)			
		Min	Mean	Median	Max	Min	Mean	Median	Max
03:00	56	0	208	164	2883	0	60	44	1306
03:15	1	1	162	136	838	0	50	42	258
04:00	13	0	296	211	3301	0	74	53	825
05:00	25	0	365	262	5761	0	73	52	1152

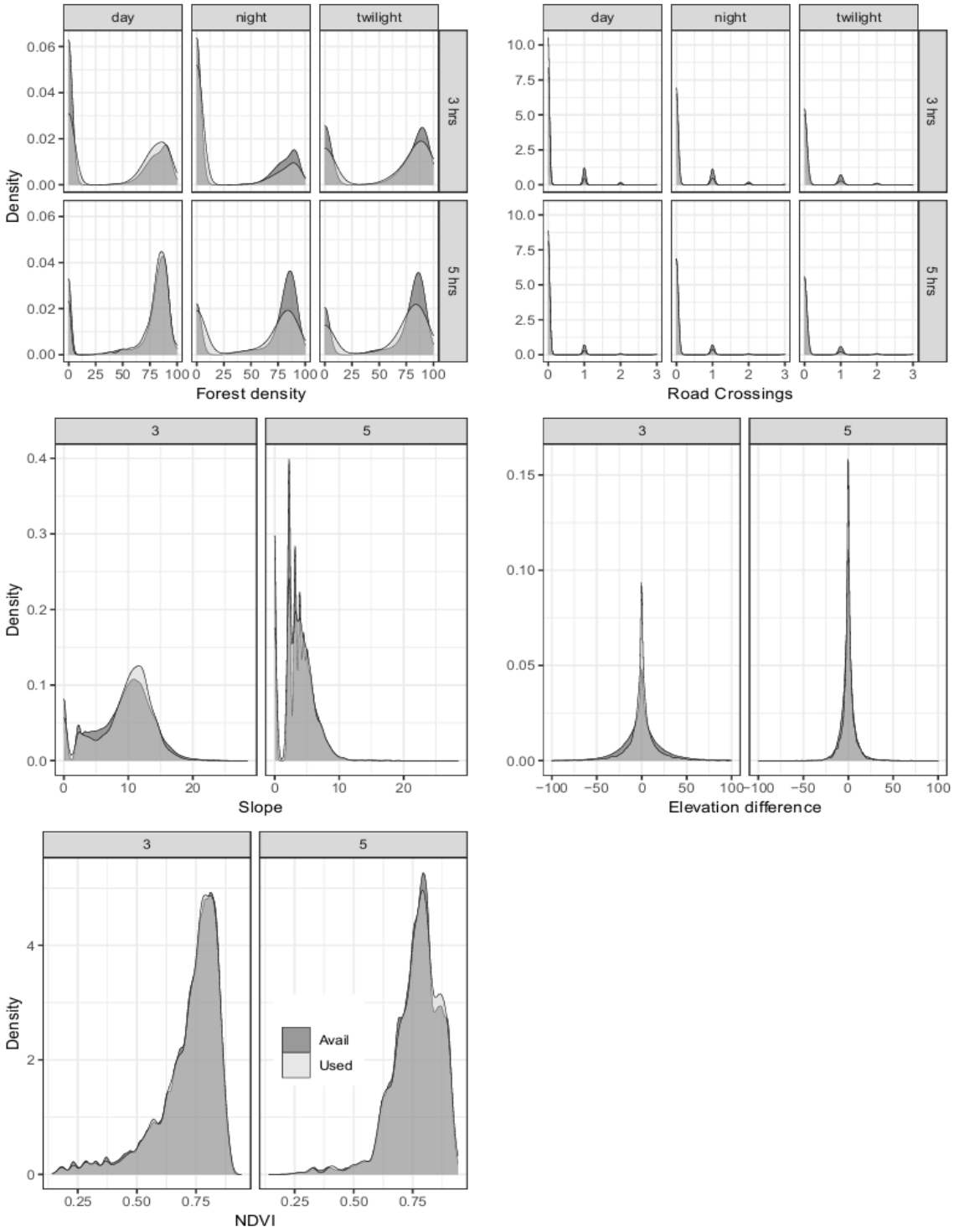


Figure 4 Distributions of used and available steps as a function of all habitat covariates at 3- and 5-hour fix intervals

Table 7 Parameters of the step length and turn angle distributions used to generate random steps.

			Fix interval (hours)			
Metric	**Distribution**	**Parameter**	**3**	**3.25**	**4**	**5**
Step length	Gamma	Scale	0.022	0.038	0.018	0.019
Step length	Gamma	Shape	1.547	1.901	1.384	1.341
Turning angle	Von Mises	Kappa	0.006	0.038	0.022	0.011

Sensitivity analysis for number of available steps

To ensure that 10 random steps were enough for the estimation of the iSSF, we performed a sensitivity analysis by running separate models using 1 to 10 random steps, recording model coefficients for each model.

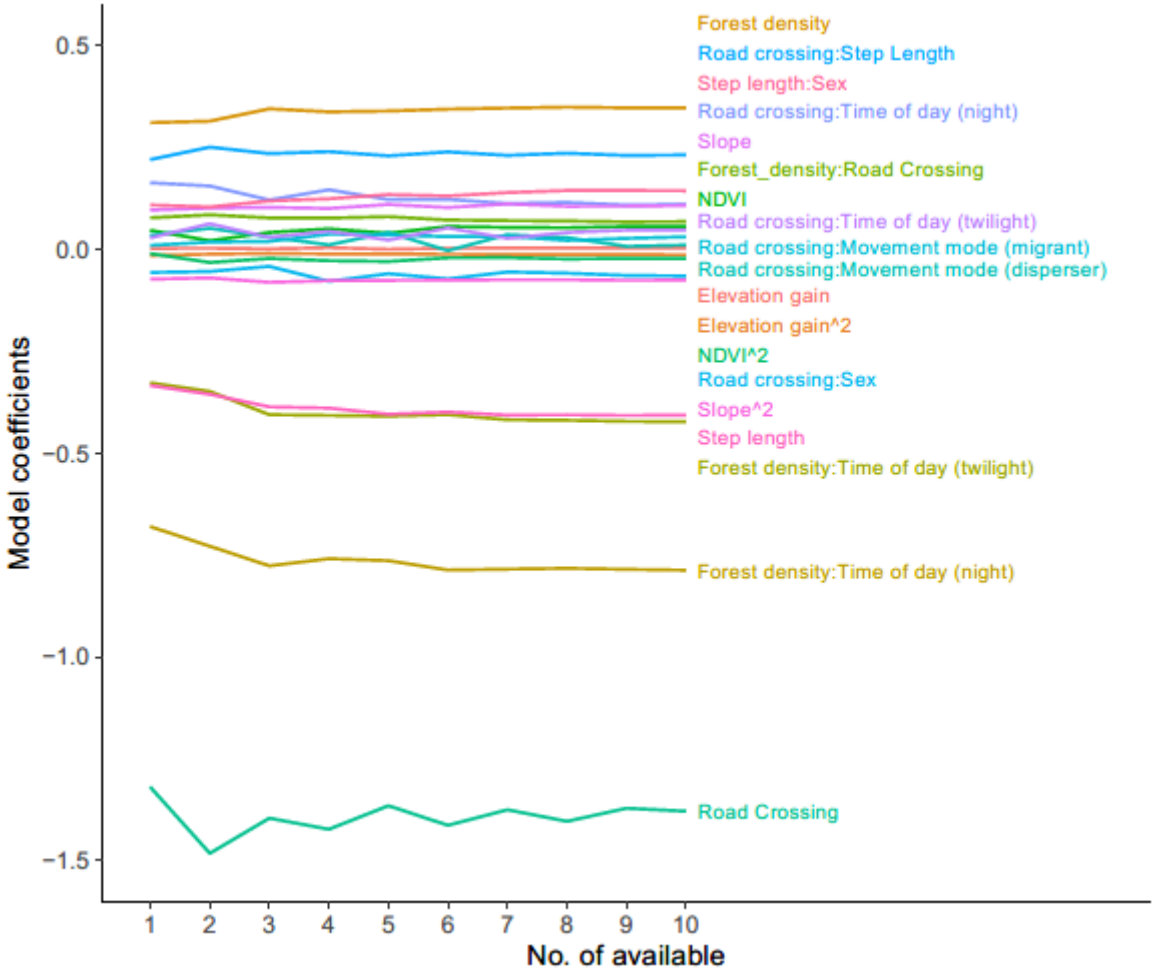


Figure 5 Sensitivity analysis to determine the number of available steps in the iSSF. The figure shows the change in model coefficient for each variable as a function of the number of available steps used in each model.

Definition of the variable "Time of day"

In our model, Time of day is a categorical variable with three levels: day, night and twilight. This categorisation was performed taking into account the position of the sun using the 'getSunlightTimes()' function in the 'suncalc' package in R.

The three levels are defined as follows:

Day: starts at the end of sunrise (i.e. when the bottom edge of the sun touches the horizon) and ends at the beginning of sunset (i.e. when the bottom edge of the sun touches the horizon);

Night: starts at dusk (i.e. start of evening nautical twilight and end of civil twilight with sun at 6 $^{\circ}$) and ends at dawn (i.e. end of morning nautical twilight and start of morning civil twilight with sun at 6 $^{\circ}$);

Twilight:

starts at dawn (i.e. end of morning nautical twilight and start of morning civil twilight with sun at 6 $^{\circ}$) and ends at the end of sunrise (i.e. when the bottom edge of the sun touches the horizon), and;

starts at beginning of sunset (i.e. when the bottom edge of the sun touches the horizon) and ends at dusk (i.e. start of evening nautical twilight and end of civil twilight with sun at 6 $^{\circ}$).

The categorisation is summarised in the table below, together with the number of steps included in each time of day category.

	Sunlight times	Definition	Time of day category in this paper	Number of steps per fix interval		
				3h	4h	5h
	Sunrise end	Bottom edge of the sun touches the horizon				
			Day	11173*	1282	3262
	Sunset start	Bottom edge of the sun touches the horizon				
			Twilight	958*	418	823
Time ↓	Dusk	Start of evening nautical twilight and end of civil twilight				
			Night	6497*	776	1703
	Dawn	End of morning nautical twilight and start of morning civil twilight				
			Twilight	as above		
	Sunrise end	Bottom edge of the sun touches the horizon				

*of these 79, 21 and 39 steps (for day, twilight and night respectively) had a fix interval of 3 hours 15 minutes.

Collinearity of model predictors

We screened for potential collinearity among model predictors using the Pearson's correlation coefficient (threshold of $|r| > 0.7$ - Dormann et al. (2013)) (Figure below)

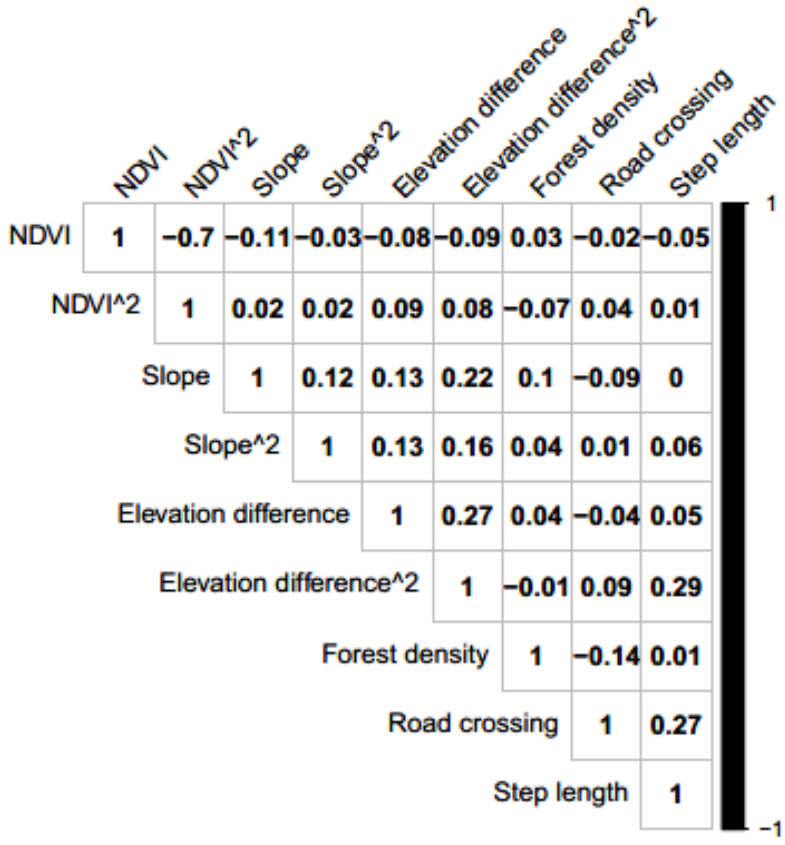


Figure 6 Pearson's correlation coefficients (R) for model predictors.

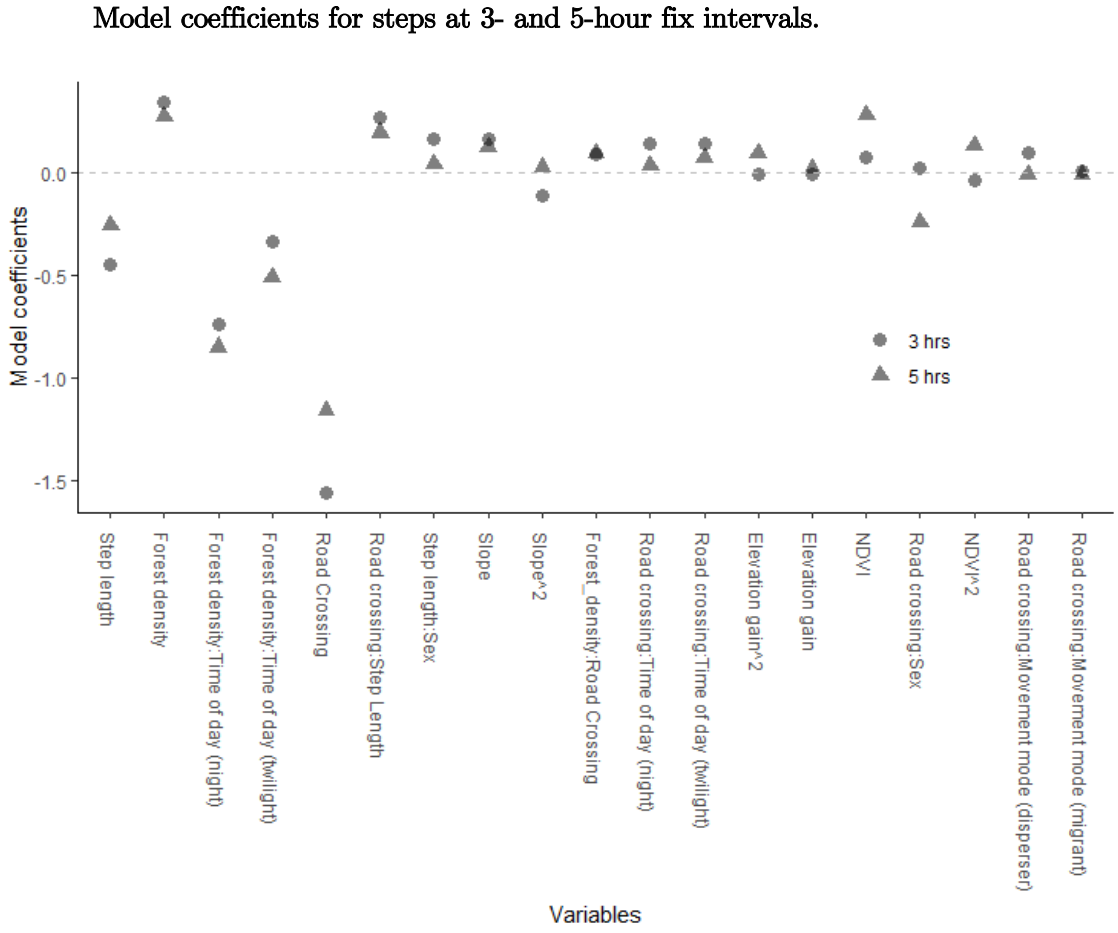


Figure 7 Model coefficients for steps at 3- and 5-hour fix intervals.

R code used to fit random slopes models

We report the R code that we created to attempt to fit the random slopes models using four different approaches, together with the reason why they did not work. For some approaches, we did not include interactions between predictors as random slopes as the model did not converge even with simpler formulations.

Coxme (Therneau, 2015)

```
coxme_rdm <- coxme(formula = Surv(time = ones, event = use_avail) ~
                   ndvi + I(ndvi^2) + slope + I(slope^2) + forest_density +
elevation_diff +
                   I(elevation_diff^2) + forest_density:timeofday + road_cross +
road_cross:sex +
                   step_length + step_length:sex + road_cross:step_length +
road_cross:forest_density +
                   road_cross:timeofday +  road_cross:move_mode + strata(step_id) +
                   (ndvi | study_area) + (ndvi | animal_id) +
                   (I(ndvi^2) | study_area) + (I(ndvi^2) | animal_id) +
                   (slope | study_area) + (slope | animal_id) +
                   (I(slope^2) | study_area) + (I(slope^2) | animal_id) +
                   (forest_density | study_area) + (forest_density | animal_id) +
                   (elevation_diff | study_area) + (elevation_diff | animal_id) +
                   (I(elevation_diff^2) | study_area) + (I(elevation_diff^2) | animal_id)
+
                   (road_cross | study_area) + (road_cross | animal_id) +
                   (step_length | study_area) + (step_length | animal_id),
                 data = dat, na.action = "na.fail")
```

We interrupted the model after 24 hours of non-convergence.

Two-step clogit (Craiu et al., 2011)

```
twostep_rdm <-  Ts.estim(formula = use_avail ~
                    ndvi +  I(ndvi^2) + slope + I(slope^2) + forest_density +
                      elevation_diff +  I(elevation_diff^2) +  forest_density:timeofday
+
```

```
                    road_cross + road_cross:sex + step_length + step_length:sex +
                    road_cross:step_length +  road_cross:forest_density +
road_cross:timeofday +
                    road_cross:move_mode + strata(step_id) + cluster(animal_id),
                  data = dat,
                  random = ~ ndvi +  I(ndvi^2) + slope + I(slope^2) + forest_density
+
                    elevation_diff +  I(elevation_diff^2) +  forest_density:timeofday +
                    road_cross + road_cross:sex + step_length + step_length:sex +
                    road_cross:step_length +  road_cross:forest_density +
                    road_cross:timeofday + road_cross:move_mode,
                  all.m.1=F, D="UN(1)")
```

The model could not be fitted because the value of several variables remains constant within all strata of at least one cluster.

INLA (Muff et al., 2020)

```
Zlt <- as(model.matrix(~ 0 + study_area:animal_id, data = dat), "Matrix")
inla_rdm_formula <- use_avail ~  -1 +  forest_density +  road_cross +  ndvi +
I(ndvi^2) +
  slope +  I(slope^2) +  step_length + forest_density:timeofday + elevation_diff +
  I(elevation_diff^2) + road_cross:timeofday + road_cross:forest_density +
road_cross:move_mode +
  f(step_id, model="iid",hyper=list(theta = list(initial=log(1e-6),fixed=T))) +
  f(IDi1,road_cross, model="z", Z=Zlt,
hyper=list(theta=list(initial=log(1),fixed=F,prior="pc.prec",param=c(3,0.05)))) +
  f(IDi2, forest_density, model="z", Z=Zlt,
hyper=list(theta=list(initial=log(1),fixed=F,prior="pc.prec",param=c(3,0.05)))) +
  f(IDi3, ndvi, model="z", Z=Zlt,
hyper=list(theta=list(initial=log(1),fixed=F,prior="pc.prec",param=c(3,0.05)))) +
  f(IDi4, I(ndvi^2), model="z", Z=Zlt,
hyper=list(theta=list(initial=log(1),fixed=F,prior="pc.prec",param=c(3,0.05)))) +
  f(IDi5, slope, model="z", Z=Zlt,
hyper=list(theta=list(initial=log(1),fixed=F,prior="pc.prec",param=c(3,0.05)))) +
```

```
  f(IDi6, I(slope^2), model="z", Z=Zlt,
hyper=list(theta=list(initial=log(1),fixed=F,prior="pc.prec",param=c(3,0.05)))) +
  f(IDi7, elevation_diff, model="z", Z=Zlt,
hyper=list(theta=list(initial=log(1),fixed=F,prior="pc.prec",param=c(3,0.05)))) +
  f(IDi8, I(elevation_diff^2), model="z", Z=Zlt,
hyper=list(theta=list(initial=log(1),fixed=F,prior="pc.prec",param=c(3,0.05))))


inla_rdm <- inla(inla_rdm_formula, family ="Poisson", data=dat,
                 control.fixed = list(mean = mean.beta, prec = list(default =
prec.beta)), verbose=TRUE)
```

The model did not converge and stopped running after more than 5 hours.

GlmmTMB (Muff et al., 2020)

```
tmb_struc_rdm =  glmmTMB(use_avail ~
      ndvi +  I(ndvi^2) + slope + I(slope^2) + forest_density + elevation_diff +
      I(elevation_diff^2) +  forest_density:timeofday +  road_cross +
      road_cross:sex +
      step_length + step_length:sex + road_cross:step_length +
      road_cross:forest_density + road_cross:timeofday + road_cross:move_mode
      +                    (1 | step_id) + (0 + ndvi | study_area/animal_id) +
      (0 + I(ndvi^2) | study_area/animal_id) + (0 + slope | study_area/animal_id)
      +                    (0 + I(slope^2) | study_area/animal_id) + (0 +
      forest_density | study_area/animal_id) + (0 + elevation_diff |
      study_area/animal_id) +
      (0 + I(elevation_diff^2) | study_area/animal_id) +
      (0 + forest_density:timeofday | study_area/animal_id) +
      (0 + road_cross | study_area/animal_id) +
      (0 + road_cross:sex | study_area/animal_id) +
      (0 + step_length | study_area/animal_id) +
      (0 + step_length:sex | study_area/animal_id) +
      (0 + road_cross:step_length | study_area/animal_id) +
      (0 + road_cross:forest_density | study_area/animal_id) +
      (0 + road_cross:timeofday | study_area/animal_id) +
      (0 + road_cross:move_mode | study_area/animal_id),
```

family=poisson, data=dat, doFit = FALSE)

tmb_struc_rdm$parameters$theta[1] = log(1e3)

tmb_struc_rdm$mapArg =
list(theta=factor(c(NA,1:(length(tmb_struc_rdm$parameters$theta)-1))))

glmmTMB_rdm <- glmmTMB:::fitTMB(tmb_struc_rdm)

The model did not converge and stopped running after 10'.

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4

Investigating tri-trophic interactions using bio-energetic demographic models

Abstract

A central debate in ecology has been the long-running discussion on the role of apex predators in affecting the abundance and dynamics of their prey. In terrestrial systems, research has primarily relied on correlational approaches, due to the challenge of implementing robust experiments with replication and appropriate controls. A consequence of this is that we largely suffer from a lack of mechanistic understanding of the population dynamics of interacting species that can be surprisingly complex.

Mechanistic models offer an opportunity to examine the causes and consequences of some of this complexity. We present a bioenergetic mechanistic model of a tri-trophic system where the primary vegetation resource follows a seasonal growth function, and the herbivore and carnivore species are modelled using two integral projection models (IPMs) with body mass as the phenotypic trait. Within each IPM, the demographic functions are structured according to bioenergetic principles, describing how animals acquire and transform resources into body mass, energy reserves and breeding potential. We parameterise this model to reproduce the population dynamics of grass, elk and wolves in northern Yellowstone (USA), and investigate the impact of wolf reintroduction on the system.

Our model generated predictions that closely matched the observed population sizes of elk and wolf in Yellowstone prior to and post wolf reintroduction. The introduction of wolves into our basal grass-elk bioenergetic model resulted in a population of 99 wolves, and a reduction in elk numbers by 61% (from 14,948 to 5,823) at equilibrium. In turn, vegetation biomass increased by approximately 25% in the growing season and more than 3-fold in the non-growing season. The addition of wolves to the model caused the elk population to shift from being food-limited to being predator-limited, and had a stabilising effect on elk numbers across different years. Wolf predation also led to a shift in the phenotypic composition of the elk population, via a small increase in elk average body mass.

Our model represents a novel approach to the study of predator-prey interactions. Explicitly considering and linking bioenergetics, population demography and body mass phenotypes can provide novel insights into the mechanisms behind complex ecosystem processes.

4.1 Introduction

A central debate in ecology has been the long running discussion on the role of apex predators in affecting the abundance and dynamics of their prey. Wildlife management approaches have predominantly been based on the assumption that predators simply reduce prey abundance (Murie 1944) although apex predators are often highly selective, removing sick and weak individuals (Packer et al. 2003, Hudson, Dobson, and Newborn 1992). Early models by Lotka & Volterra predicted simple unstable dynamics of predator-prey relationships (Lotka 1927, Volterra 1927). Field experiments on the snowshoe hare in the Kluane project (Krebs, Boutin, and Boonstra 2001) revealed that both predation and food influence the dynamics of the hare population, demonstrating the complexity of tri-trophic interactions (Sinclair and Krebs 2002). Moreover, studies have shown that in some contexts food may be limiting while in others predation may be limiting (Meserve et al. 2003, Lynam et al. 2017). As such, the challenge is to understand both the effects of vegetation on the herbivore and how these interact with the effects of predation.

Understanding these processes will improve our ability to assess the ecosystem effects of global changes in predator abundance (Chapron et al. 2014, Ripple et al. 2014) and to predict population performance under environmental change (Lachish et al. 2020). It will also help inform landscape management decisions such as species reintroductions (Nilsen et al. 2007), and enhance our knowledge of complex natural systems.

Empirical evidence to address these issues has come primarily from freshwater systems where community structure can be manipulated through mesocosms, evaluating the effects of predation and competition for food (Carpenter et al., 1985, Power, 1992, Wootton, 1992). However, such studies do not necessarily extrapolate to natural terrestrial systems where the food web can be dominated by apex carnivores such as lions or wolves (Polis et al., 2000, Ripple et al., 2016). In part, this is because in complex terrestrial systems it is difficult to implement robust experimental approaches that involve adequate replication and appropriate controls at a landscape scale (Ford and

Goheen, 2015). Most observational studies in terrestrial systems thus have weak inferential strength (Ford and Goheen (2015), Peterson et al. (2014), but see Ford et al. (2015)). Mathematical modelling of ecosystem dynamics offers an alternative approach to understanding species interactions at landscape scales and capturing the key elements of the ecosystems. These models can be fitted to long term data to assess the effects of vegetation dynamics and predator addition and removal on herbivore populations. However, to date, most models have lacked a mechanistic underpinning of the biological interactions limiting the accuracy of inferences (Ford and Goheen 2015, Ford 2015). These dynamics can both affect and be affected by the phenotypic traits of individuals within populations (e.g. body mass) and can potentially generate unexpected feedbacks among different trophic levels (DeLong et al. 2015, Ozgul et al. 2010, Lachish et al. 2020). These issues can be addressed through the mechanistic modelling of the bioenergetics, which can capture the intake of food by the herbivore, their growth and reproduction, and the flow of this energy into the predator population.

Structured Populations Models, such as Integral Projections Models (IPM), can be used to describe population dynamics by linking demographic rates with phenotypic traits (Coulson 2012). IPMs have already been used to model consumer-resource dynamics between two trophic levels (Lachish et al. 2021, Smallegange et al. 2016). These models obtained the demographic functions (i.e. survival, growth, reproduction and inheritance) within a modelling framework based on bioenergetic principles, which defined how animals acquire and transform resources into body mass, energy reserves and breeding potential (Lachish et al. 2020). This approach can be extended to a third trophic level to provide a deeper understanding of how tri-trophic interactions are affected by resources and predation.

We develop a bioenergetic mechanistic model of a tri-trophic system where the primary vegetation resource follows a simple seasonal growth function, and the herbivore and carnivore species are modelled using two IPMs with body mass as the phenotypic trait.

Within each IPM, the demographic functions are bioenergetic in form (Lachish et al. (2020), describing how animals acquire and transform resources into body mass, energy reserves and breeding potential. Adapting and extending the model developed in Lachish et al. (2020), we parameterize this model to reproduce the population dynamics of grass, elk and wolves in the northern part of Yellowstone National Park and the adjoining areas of Montana (hereafter, "Northern Yellowstone"; MacNulty et al. (2016)).

We chose this study system for several reasons. First, we have sufficient data available on the demography, vital rates and energetics of each species to allow model parameterisation (Lachish et al. 2020). Second, since the wolf reintroduction, ecosystem changes including a rapid decline in the population of elk, an heterogeneous resurgence in aspen and willow, and increases in biodiversity have been observed (MacNulty et al. 2016, Smith, Stahler, and MacNulty 2020, MacNulty et al. 2020, Peterson et al. 2020). These changes have been attributed to the return of the wolf (Ripple et al. 2001), although other ecological factors have been documented including the role of other predators (i.e. cougars, bears), droughts, severe winters, and hunting (MacNulty et al. 2016). For this reason, the role of the wolf has been debated (Ford and Goheen 2015, Vucetich, Smith, and Stahler 2005, Peterson et al. 2014, MacNulty et al. 2020). A more mechanistic understanding of the system dynamics can contribute to explain the causality between wolf presence, elk decline and vegetation recovery. In this paper, we use our model to identify the key biological features shaping tri-trophic dynamics and to assess the impact of wolves on the elk-grass system in Yellowstone.

4.2 Methods

4.2.1 Methodological overview

To investigate population dynamics and body mass in a tri-trophic system, we developed a mechanistic, bioenergetic model extending and advancing the approach described by Lachish et al. (2020). The model is built to simulate the ecology and the population

dynamics of a herbivore and a carnivore population and comprises three trophic levels: the vegetation base, a herbivore feeding on the vegetation, and a predator feeding on the herbivore. While the model is iterated monthly, the three components have an annual life history that can be determined by seasonal variation in the weather. The base of the model is the vegetation. Vegetation growth follows a simple growth function based on environmental conditions and herbivore consumption. Each month, the herbivores feed on the vegetation and, if they survive, they transform the acquired energy into body mass. Here, we define total body mass (Z) as the sum of a structural body mass (Z_S), which is made of bones and essential organs and cannot decrease over time, and a reserve mass (Z_R) which is made of muscle and fat and can fluctuate over time. Herbivores in our model partition the energy acquired through food between structural and reserve mass according to some parameters. Then, depending on these masses, they have different probabilities to survive, grow and, in one month per year, reproduce, by allocating a proportion of their stored reserves to their offspring. Herbivores' survival in our model is also dependant on predation, which is a function of the number of predators. The predator component works in a very similar way, by feeding on the herbivores, and growing and reproducing analogously. The herbivore and the carnivore populations are modelled using two distinct IPMs that model the demographic outcomes as functions of the distribution of individual body masses (Z). Although the model is generalizable, we parameterised it using existing knowledge about vegetation, elk and wolves in Northern Yellowstone.

Here, we start by describing the dynamics of the vegetation. We then outline the generic structure of the two IPMs; we illustrate the survival, growth, reproduction and investment in offspring functions; and explain how they were parameterised. Finally, we describe how we performed a sensitivity analysis to assess the sensitivity of our model to the input parameters.

4.2.2 Dynamic of the vegetation and herbivore consumption

The model describing vegetation dynamics is formulated to capture the dynamics of grassy vegetation in a seasonal environment (grasses constitute more than 75% of elk winter diet in Northern Yellowstone (Christianson and Creel 2007). The model structure follows that described in Lachish et al. (2020).

Over a six-month growing season, and in the absence of herbivores, vegetation (V) grows according to the following equation

$$V_{t+1} = (1 - a_t)V_{max} + a_t V_t \quad [1]$$

where $0 < a < 1$. Thus, in each month of the growing season the biomass of vegetation increases asymptotically towards V_{max}. During the remaining six months of the year vegetation does not grow ($a = 1$) and can be covered by snowfall. The biomass of vegetation is reduced via herbivore consumption, which is modelled according to bioenergetics principles, as described in Lachish et al. (2020). Consumption follows a type II functional response with vegetation biomass (Owen-Smith 2002) and maximum ingestion rate is proportional to structural mass$^{2/3}$ ($Z_S^{2/3}$, (Illius and O'Connor 2000, van der Meer 2006, Lachish et al. 2020)). Overconsumption is limited by modelling consumption as a sigmoid function that grows asymptotically towards a target ratio of reserve mass to total mass (Z_R/Z, (De Roos, Galic, and Heesterbeek 2009). Thus, the maximum vegetation consumed by a herbivore each month is defined by:

$$C_{max_e}(Z_{S_e}) = (c_e Z_{S_e}^{2/3})(\frac{V_t}{\theta_e + V_t})(\frac{1}{1 + e^{-\eta_e(f_e Z_e - Z_{R_e})}}) \quad [2]$$

where c_e is the slope of the power function, θ_e represents the value at which half of the maximum consumption rate is reached (i.e. the half saturation constant), η_e determines the steepness in satiation scaling of consumption rate, and f_e is the target energy reserve mass as a fraction of total body mass (Z_e).

The total maximum consumption for all herbivores is described as $\int H_e(Z_{S_e}, t) C_{max_e}(Z_{S_e}) dZ_{S_e}$, where $H_e(Z_{S_e}, t)$ represents the distribution of structural mass, Z_{S_e}, in the herbivore population (details below).

The vegetation cannot be consumed to full depletion. The value V_{min} represent the minimum quantity to which the resource can be consumed and reflects the minimum height of the vegetation that herbivores can graze. To ensure that the vegetation never goes below V_{min}, we scaled resource consumption by a constant, p, defined as follows:

$$p = \begin{cases} 0 \; if \; (V_t \leq V_{min}) \\ 1 \; if \; (V_t - \int H_e(Z_{S_e}, t) C_{max_e}(Z_{S_e}) dZ_{S_e} > V_{\min}) \\ \dfrac{V_t - V_{min}}{\int H_e(Z_{S_e}, t) C_{max_e}(Z_{S_e}) dZ_{S_e}} \; if \; V_t - \int H_e(Z_{S_e}, t) C_{max_e}(Z_{S_e}) dZ_{S_e} < V_{min} \end{cases} \quad [3]$$

Finally, in winter months, snow can cover the resource, which reduces the vegetation available to herbivores by a constant proportion, ς. The whole dynamic of the resource is therefore defined by:

$$V_{t+1} = (1 - a) V_{max} + a V_t - \varsigma p \int H_e(Z_{S_e}, t) C_{max_e}(Z_{S_e}) dZ_{S_e} \quad [4]$$

Where $\varsigma = 0.5$ when snow falls, and $\varsigma = 1$ otherwise.

4.2.3 Generic IPM structure

The overall model is composed of two distinct but interacting single-sex bioenergetic IPMs for two populations of female herbivores and carnivores, respectively. Although they are two distinct models, their structure is analogous and is based on a single-species model published by Lachish et al. (2020). The dynamics of each population are defined by an IPM that models the demographic outcomes as functions of the distribution of individual body masses. For both herbivores and predators, we assume an annual life history, iterated forward on a monthly time step. For each month, the IPM calculates the distribution of body masses (Z) from time t, H(Z, t), to time t+1, H(Z', t+1), using the following equation:

$$H(Z', t+1) = \int_{\Omega} [D(Z'|Z,t)R(Z,t) + G(Z'|Z,t)S(Z,t)]H(Z,t)dZ \quad [5]$$

where the survival function S(Z, t) is the probability that individuals of mass Z survive and the growth function G(Z'|Z, t) is the probability that individuals of mass Z at time t, if they survive, grow to mass Z' at time t+1. The reproduction function R(Z, t) calculates the number of offspring produced by an individual of mass Z between time t and t+1. Finally, the investment in offspring function D(Z'|Z, t) gives the probability that the offspring of an individual of mass Z have mass Z' at time t+1. While the survival functions of herbivores and predators differ, the reproduction, growth and investment in offspring functions are analogous – i.e. they have the same structure but different parameters. To simplify readability, when equations are analogous, we report one single equation in its generic form for both herbivores and predators. The subscripts "e", for elk, and "w", for wolf, will be added only when needed for clarity. For example, Z represents the total mass in its generic form (and valid for either elk or wolf), Z_e is the total mass of elk only, and Z_w is the total mass of wolf only.

4.2.4 Survival

Herbivore survival function

Bigger, older elk have higher survival rates than smaller, younger elk in the Northern Yellowstone, while individuals in poorer conditions (those with less body fat) experience higher mortality rates (Wright et al. 2004). We thus modelled mortality as a function of total body mass using a logit function, with a survival threshold determined by the ratio of reserve mass to body mass. We also made survival a function of predation. Survival is thus described as:

$$S_e(Z_e, t) = \begin{cases} 0 \; if \; \left(\frac{Z_{R_e}}{Z_e} < b_e\right) \\ \frac{1}{1 + e^{-(\beta_{0_e} + \beta_{1_e} Z_{R_e} - \xi W_t)}} \; otherwise \end{cases} \quad [6]$$

where b_e is the starvation ratio, W_t is the total wolf biomass, and ξ regulates the extent to which the total wolf biomass impacts elk survival.

Predator survival function

Similarly to the elk, we modelled wolf survival as a function of body mass and condition, such that bigger individuals survive at higher rates than smaller individuals, while those with insufficient reserve mass die. We also included a density-dependent term to account for the negative effect of intra-specific aggression on wolf survival (Cubaynes et al. 2014). Survival is thus described as:

$$S_w(Z_w, t) = \begin{cases} 0 \; if \; \left(\frac{Z_{R_w}}{Z_w} < b_w\right) \\ \frac{1}{1 + e^{-(\beta_{0_w} + \beta_{1_w} Z_{R_w} - \varrho W_t)}} \; otherwise \end{cases} \quad [7]$$

Where b_W is the starvation ration, W_t is the total wolf biomass at time t, and ϱ represents the strength of intraspecific aggression.

4.2.5 Herbivores as a resource and predator consumption

To survive, grow and reproduce, predators are able to hunt and feed on herbivores. The total elk biomass (P_t) that predators can eat at time t is:

$$P_t = \int \left(1 - S_e(Z_e, t)\right) H_e(Z_e, \mathrm{t})\, dZ_e \quad [8]$$

Maximum ingestion rate of wolves is modelled proportional to structural mass$^{2/3}$, with consumption of elk described by a type II functional response (Hebblewhite 2013, Becker et al. 2008, Zimmermann et al. 2015) and a check on overconsumption (as described above for vegetation consumption by elk):

$$C_{max_w}(Z_{S_w}) = (c_w Z_{S_w}^{2/3})(\frac{P_t}{\theta_w + P_t})(\frac{1}{1 + e^{-\eta_w(f_w Z_w - Z_{R_w})}}) \quad [9]$$

where c_w is the slope of the power function, θ_w represents the half-saturation constant, η_w determines the steepness of the curve towards satiation, and f_w is the target proportion of energy reserve mass and total mass.

4.2.6 Growth

The growth functions describe the way in which consumed resources are converted into energy and allocated to the individual structural and reserve mass. For herbivores, as described in the equations above, the maximum quantity of resources consumed by each individual corresponds to $pC_{max_e}(Z_{S_e})$. The energy assimilated by a herbivore from these resources is thus $j_e pC_{max_e}(Z_{S_e})$, where j_e is the energy content of the resource.

Predators assimilate energy in a similar way, however wolves do not consume elk carcasses in their entirety (as parts of the carcass are inedible) and moreover often lose a portion of their kills to other carnivores and scavengers in the ecosystem (Wilmers et al. 2003, Metz et al. 2012). Hence, the expected total resource consumed by any individual predator is given by, $\mathrm{d}(1-\mathrm{l})\mathrm{C}_{max_w}(Y_{\mathrm{S}})$ where d is the edible proportion of elk biomass and l is the proportion of dead elk biomass scavenged by other species. The expected amount of assimilated energy is then $j_w \mathrm{d}(1-\mathrm{l})\mathrm{C}_{max_w}(Z_{S_w})$ where j_w is the energy content of prey meat.

For both herbivores and predators, part of the assimilated energy is spent on maintenance costs, while the rest is allocated to growth and reproduction. According to the Kleiber's law, we assume that daily metabolic costs scale to a three-quarters power law with body mass (Savage et al. 2004). Monthly maintenance costs for both herbivores and predators are calculated by multiplying daily metabolic costs by the number of days in a month:

$$M(Z) = 30 * \delta Z^{\frac{3}{4}} \qquad [10]$$

The amount of energy available for growth and reproduction in herbivores and predators is thus calculated by subtracting maintenance costs from the total energy consumed:

$$\Delta E_e(Z_e) = j_e p C_{max_e}(Z_{S_e}) - M_e(Z_e) \quad [11]$$

$$\Delta E_w(Z_w) = j_w d(1-l) C_{max_w}(Z_{S_w}) - M_w(Z_w) \quad [12]$$

This energy is added to an individual's stored resources

$$Z_R^o = Z_R + m^{-1}\Delta E(Z) \quad [13]$$

Where the metabolic coefficient m defines the conversion between assimilated energy and energy reserves. This coefficient varies between anabolic conditions, when $\Delta E(Z)$ is positive, and catabolic conditions when $\Delta E(Z)$ is negative.

Smaller (younger) individuals can grow their structural mass (Z_S) until a certain threshold k. Individuals below this threshold turn a proportion ψ of their stored resources into structural mass with a constant efficiency ε_1, while the remaining stored resources are added to their reserve mass. Once k is reached, the individual's structural mass stops growing and, in non-breeding months, all stored resources are allocated to the reserve mass. Structural and reserve mass at time t+1 are thus calculated as follows:

$$Z_S' = \begin{cases} Z_S + \psi\varepsilon_1 Z_R^o \; if \; (Z_S \leq k) \\ Z_S \; if \; (Z_S > k) \end{cases} \quad [14]$$

$$Z_R' = \begin{cases} (1-\psi) Z_R^o \; if \; (Z_S \leq k) \\ Z_R^o \; if \; (Z_S > k) \end{cases} \quad [15]$$

During one month per year, those individuals that are fully grown ($Z_S > K$) can reproduce, providing that the proportion of stored energy to total mass (Z_R^o/Z) is above a certain threshold g. We call the individuals who satisfy these two conditions 'potential breeders'. In the breeding month, potential breeders allocate a proportion τ of their stored resources to reproduction (see dedicated section below). The change in reserve mass after the breeding period is thus defined by:

$$Z_R' = \begin{cases} (1-\psi) Z_R^o \; if \; (Z_S \leq k) \\ Z_R^o \; if \; (Z_S > k \; and \; Z_R^o : Z \leq g) \\ (1-\tau) Z_R^o \; if \; (Z_S > k \; and \; Z_R^o : Z > g) \end{cases} \quad [16]$$

In our model, we then assume that the distribution of phenotypic values at time t+1 for any given value at time t is Gaussian. Growth for Z_S or Z_R is then described as:

$$G(X'|X,t) = N(\mu_X, \sigma_X^2) = \frac{1}{\sqrt{2\pi\sigma_X^2}} e^{\frac{-(X'-\sigma_X^2)^2}{2\sigma_X^2}} \quad [17]$$

Where X is either Z_S or Z_R, N is a normal distribution, and μ and σ^2 are its mean and variance, respectively. The mean is obtained from equations 14, 15 or 16, while the variance is assumed to be phenotype-dependent and is defined as

$$\sigma_{X'}^2 = \vartheta - e^{-\gamma X} \quad [18]$$

Where X is either Z_S or Z_R, and ϑ and γ represent the intercept and slope of the function.

4.2.7 Reproduction

Reproduction occurs once every year. As described above, to reproduce, an individual has to reach a threshold structural mass k and have a sufficient ratio g between reserve mass and total body mass. In our model, we assumed litter size to be 1 and we account for a fixed proportion of neonates (ω) experiencing immediate mortality. Reproduction is described by:

$$R(Z,t) = \begin{cases} 0 \; if \; (Z_S \leq k) \; or \; (Z_S > k \; and \; Z_R^o : Z \leq g) \\ 1 - \omega \; if \; (Z_S > k \; and \; Z_R^o : Z > g) \end{cases} \quad [19]$$

4.2.8 Investment in offspring

The investment in offspring function describes how the phenotypes are inherited from the parents to the offspring. From the growth equations above, we see that potential breeders allocate a proportion of their stored resources (τ) to reproduction. Of these, a proportion υ is allocated to the offspring structural mass, while the remainder forms the offspring reserve mass. The parent stored resources are converted into the offspring structural and reserve mass with efficiency ε_2 and ε_3, respectively.

$$Z'_{S_{offspring}} = \begin{cases} 0 \; if \; (Z_S \leq k) \; or \; (Z_S > k \; and \; Z_R^o : Z \leq g) \\ \upsilon * \varepsilon_2 * \tau * Z_R^o \; otherwise \end{cases} \quad [20]$$

$$Z'_{R_{offspring}} = \begin{cases} 0 \; if \; (Z_S \leq k) \; or \; (Z_S > k \; and \; Z_R^o : Z \leq g) \\ (1 - \upsilon) * \varepsilon_3 * \tau * Z_R^o \; otherwise \end{cases} \quad [21]$$

The distribution of Z_S and Z_R in the offspring for any given value in the parents is then described by an equation which is analogous to equation 13 for growth. Hence,

$$D(X'|X,t) = N(\mu_X, \sigma_X^2) = \frac{1}{\sqrt{2\pi\sigma_X^2}} e^{\frac{-(X'-\mu_X)^2}{2\sigma_X^2}} \quad [22]$$

Where X is either Z_S or Z_R. As for the growth functions, the variance σ^2 of the normal distribution N is phenotype-dependent and calculated with the equation

$$\sigma_{X'}^2 = \lambda - e^{-\varsigma X} \quad [23]$$

Where λ and ς are the intercept and slope of the function, respectively.

4.2.9 Model parameterisation

Although the model above is generalizable, we parameterised it for vegetation, elk and wolves in the Northern Yellowstone. Grasslands and shrublands mainly composed of sagebrush represent the main habitat for grazing ungulates such as elk, bison, mule deer, pronghorn and bighorn sheep (Garroutte, Hansen, and Lawrence 2016). Among these species, the elk is one of the most abundant, despite a recent population decline and increasing bison numbers (Ripple and Beschta 2012, Metz et al. 2020). Elk is also the wolf's main prey, representing ~88% of all ungulates killed by wolf (Tallian et al. 2017, Metz et al. 2020, Metz et al. 2012). For these reasons, we only consider grassy vegetation, wolves and elk, without explicitly modelling other species. Given the complexity of elk migration dynamics and the non-spatial nature of our model, we do not model elk movement outside of the northern range, although this movement can be significant in the winter. Moreover, we do not model wolf pack dynamics. In a typical pack, only the alpha female is able to breed (Mech and Boitani 2003) and, in Yellowstone, females give

birth to a litter of around five pups on average (Stahler et al. 2013). We do not model this social complexity and instead make the simplifying assumption that each individual wolf could give birth to one pup. This generated mean reproductive rates that were similar to those observed across the whole population (Smith et al. 2020). Incorporating pack structures and more realistic social group interactions among predators is the focus of ongoing work.

All parameters were obtained from the available literature and are shown in the Supplementary Information together with their values and references. Parameters for the vegetation and elk closely follow those detailed in Lachish et al. (2020), while wolf parameters are described below. While our model is based on the elk-only model published by Lachish et al. (2020), it is important to note that unlike Lachish et al (2020) we do not incorporate stochasticity in the dynamics of vegetation growth, instead modelling the abiotic environment as seasonal within years but constant across different years. For this reason, the results presented in this study can slightly differ from those of Lachish et al. (2020). The model was run for 1500 months (125 years), to make sure it would reach population values at equilibrium.

Wolf parameters

Adult female wolves in Yellowstone weigh around 41 kg on average ((MacNulty et al. 2009). Of these, 21-30% can be catabolised before all internal energy reserves are exhausted (Mech and Boitani 2003). We created a vector of 25 values between 0.1 and 43 kg for structural mass (Z_S) and a vector of 25 values from 0.1 to 27 for reserve mass (Z_R). We combined these two vectors as we did in the elk, obtaining a vector of 625 possible total body masses (Z) ranging from 0.2 to 70 kg. Our starting values were limited to the observed weight range (0.1 to 37 for Z_S, and 0.1 to 21 for Z_R).

4.2.10 Sensitivity analysis

We performed a sensitivity analysis to assess how model predictions varied by altering parameters values, and quantify the effect of each parameter on the final model outcome. We varied the value of each individual parameter by -5%, -2.5%, +2.5% and +5%, running a separate model each time, and recording the amount of vegetation, elk and wolves after the model reached equilibrium (after 1500 months).

4.3 Results

4.3.1 Population estimates

We ran our model with and without wolves until equilibrium (Figure 1). In the model without wolves, the elk population at equilibrium oscillated between 14,938 and 25,289 (mean=19,944) individuals throughout the year. These estimates reflected the Northern Yellowstone elk counts before the reintroduction of wolves (19,045 individuals in January 1994, just before wolf reintroduction - MacNulty et al. (2016)), and were similar to those obtained by Lachish et al. (2020). Our results did not match exactly those in Lachish et al. (2020) since we did not consider environmental stochasticity across different years (see Methods section). Other than the expected monthly fluctuation in elk numbers due to breeding and seasonality, the elk population showed a biennial cycle. This cyclical fluctuation occurred because, due to the increase in elk numbers in the absence of predation, vegetation periodically reached its minimum biomass (V_{min}), causing the elk to starve and temporarily decline in numbers (Lachish et al. 2020).

When we added wolves to the model, the elk population fluctuated between 5,805 and 10,280 (mean = 7,911) individuals, and wolf numbers varied between 56 and 100 (mean = 67). In this case, no cycles were observed beyond those typical of breeding and seasonality, and across the 1500 months, the vegetation never reached its minimum value. The values from the model for the elk and wolf populations were consistent with estimates obtained in Northern Yellowstone after wolf reintroduction (5,800 elk in March 2018 -

Loveless, Smith, and Hemenway (2019), MacNulty et al. (2016); 55 wolves in December 2019 Smith et al. (2020)).

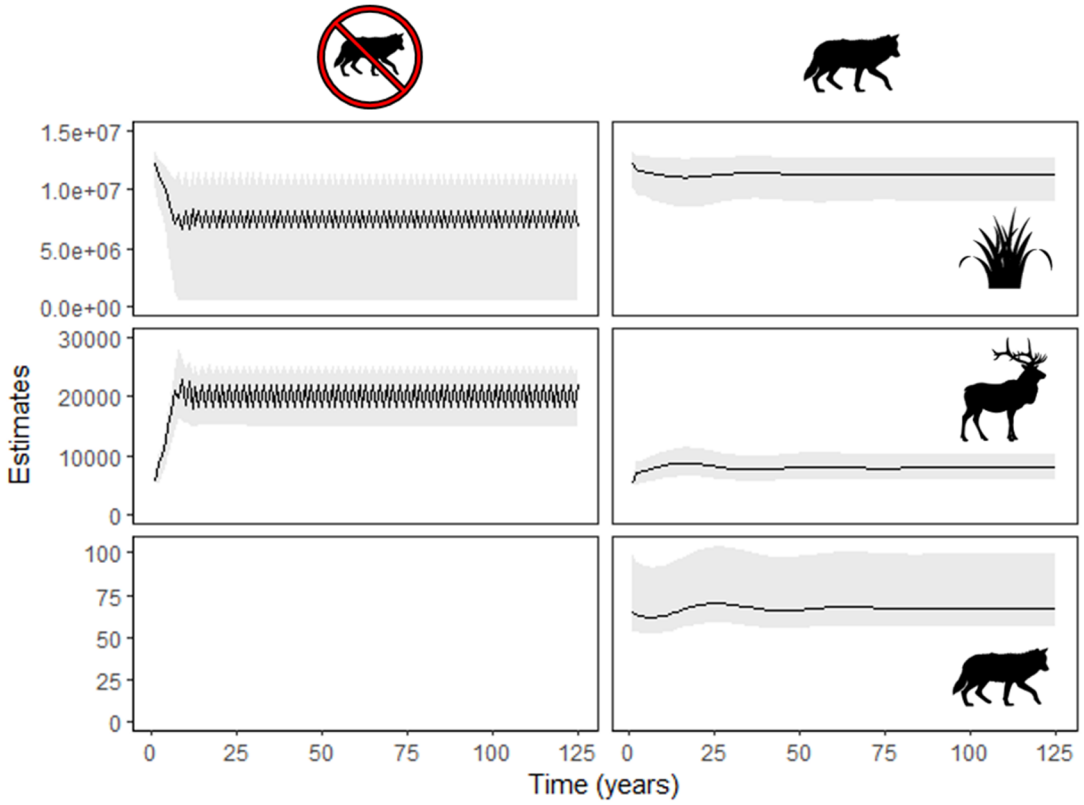


Figure 1 Population trends for vegetation, elk and wolf (top to bottom) modelled in absence (left) and presence (right) of wolves. The black line shows the mean estimates per year, whereas the grey shadings show the minimum and the maximum in every year (oscillations within the years are due to reproduction and mortality).

4.3.2 Elk and wolf body mass distributions

In our model, the elk average body mass in March was 210 kg in the absence of wolves and 214 kg with wolves. These weights broadly are consistent with those observed in the field in the same season (189–275 kg, Cook, Cook, and Mech (2004)) (Figure 2). Wolf predation changed the elk body mass distributions, because wolves selected prey with smaller structural and reserve mass (Figure 2). In wolves, the average body mass in

March was 44 kg (Figure 3), which also matches the observed range for female adults in Yellowstone (ca. 30-52 kg, MacNulty et al. (2009)).

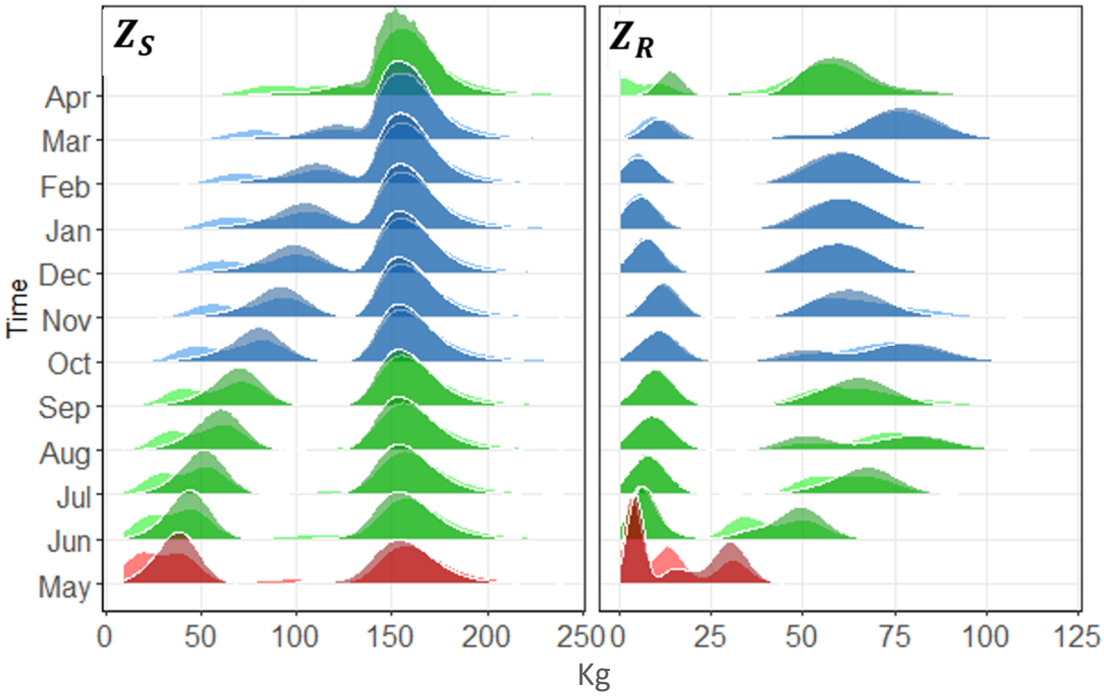


Figure 2 Elk body mass distributions for structural (Zs) and reserve mass (Zr). Lighter distributions refer to the elk population in the model without wolves, while darker distributions refer to the elk population in the presence of wolves. The months when the vegetation grows are represented in green, non-growing months in blue and the breeding month in red.

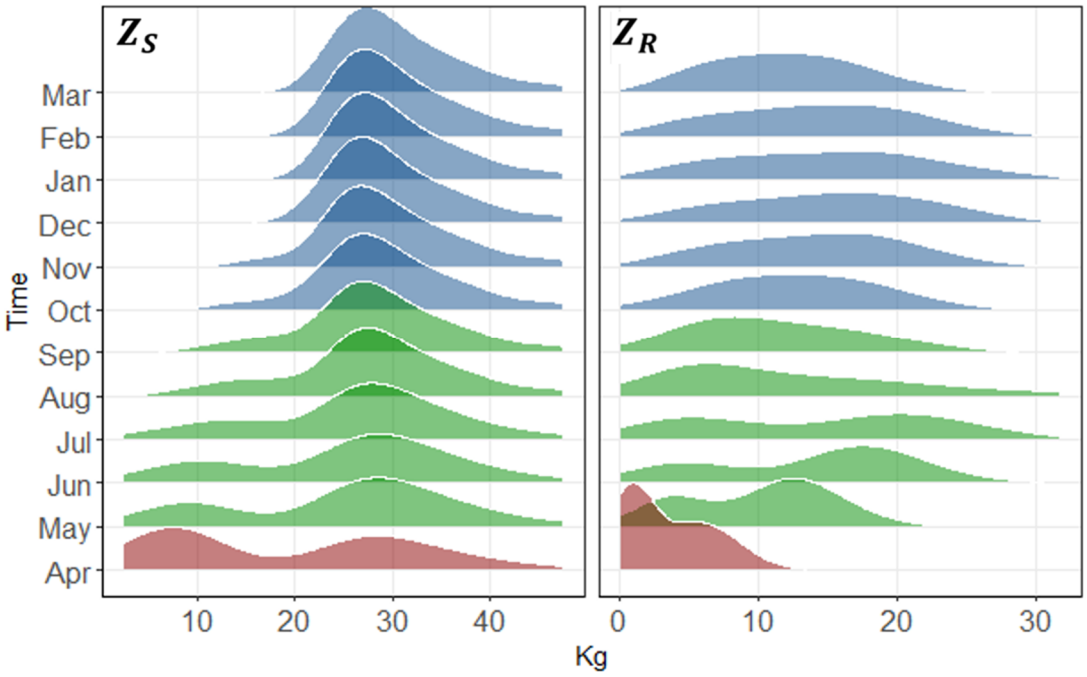


Figure 3 Wolf body mass distributions for structural (Zs) and reserve mass (Zr). The months when the vegetation grows are represented in green, non-growing months in blue and the breeding month in red.

4.3.3 Sensitivity analysis

Perturbing each model parameter from -5% to +5% showed that different parameters can have different effects on the final model estimates, and that these effects can vary for the three trophic levels (figure 4).

Overall, the elk was the most affected trophic level in the sensitivity analysis (Figure 4). The parameters causing the largest changes in elk population estimates were: the wolf satiation threshold (f_w - i.e. the ratio of energy reserve mass above which wolf food consumption decreases); the reserve allocation to offspring in wolves (υ_w – i.e. the proportion of parent's reserve mass converted into offspring structural mass in wolves); the wolf survival intercept (β_{0_w} – i.e. the intercept of the logit function describing wolf survival); the wolf metabolic costs (δ_w – i.e. a scalar constant of wolf daily metabolic costs); the wolf metabolic conversion rate (m_w – i.e. the coefficient for catabolic conversion between assimilated energy and energy reserves in wolves); the elk survival

intercept (β_{0_e} – i.e. the intercept of the logit function describing elk survival); the vegetation energy content (j – i.e. the energy content of the vegetation); and elk ingestion rate (c_e – i.e. a scalar content for ingestion rate for elk).

These parameters were the same for the vegetation, although in a slightly different order. Perturbing the wolf satiation threshold (f_w) from -5% to +5% caused the largest change in the overall model, having a positive effect on vegetation biomass (+381%) and wolf numbers (+842%), and a negative effect on elk numbers (-72%). Varying parameter values always had opposing effects on vegetation and elk. As such, varying parameters in favour of the elk population would increase herbivory leading to a reduction in vegetation biomass and *vice versa*. For example, perturbing the wolf survival intercept (β_{0_w}) from -5% to +5% caused a change of +308% in vegetation biomass and -71% in elk estimates. In comparison, perturbing the elk survival intercept (β_{0_e}) generated a change of -52% in vegetation biomass and +140% in elk numbers (figure 4).

For wolves, the parameters that, when perturbed, had the highest impact on population size were: the wolf satiation threshold (f_w - i.e. the ratio of energy reserve mass above which wolf food consumption decreases; the reserve allocation to offspring in wolves (υ_w – i.e. the proportion of reserve mass converted to offspring structural mass in wolves); the vegetation energy content (j – i.e. the energy content of the vegetation); the elk ingestion rate (c_e – i.e. a scalar content for ingestion rate for elk); the elk survival intercept (β_{0_e} – i.e. the intercept of the logit function describing elk survival); the elk metabolic costs (δ_e – i.e. a scalar constant of elk daily metabolic costs), the elk satiation threshold (f_e - i.e. the ratio of energy reserve mass above which elk food consumption decreases); and the wolf metabolic conversion rate (m_w – i.e. the coefficient for catabolic conversion between assimilated energy and energy reserves in wolves). It is interesting to note that some vegetation-related and elk-related parameters are relatively more important for wolves than they are for the vegetation and elk population themselves. For example, the energy content of the vegetation (j) is the sixth and seventh most important

parameter for the vegetation and the elk respectively, however it is the third most important parameters for the wolf. On the other hand, the wolf survival intercept (β_{0_w}), is the second and third most important parameter for the vegetation and the elk, but only the tenth for the wolf.

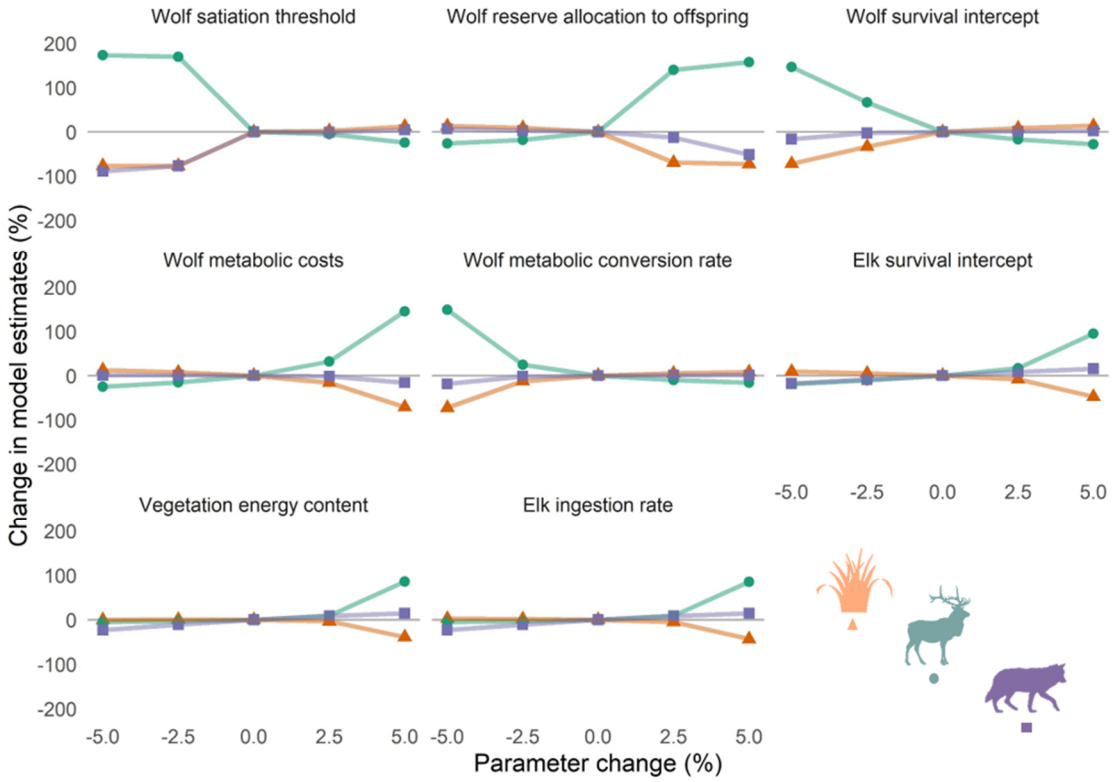


Figure 4 Sensitivity analysis showing the effects that changing parameters from -5% to +5% has on model estimates (in March) for the most important parameters. Change in model estimates is quantified as relative changes compared to the model with unchanged parameters. For parameter explanation, see the Supplementary Information.

An interesting parameter is the wolf hunting efficiency (ξ), which regulates the extent to which wolves kill elk. Increasing the value of this parameter caused the wolf to kill more elk and reduce future prey availability, eventually resulting in a reduced wolf population (Figure 5). Finally, some parameters showed some non-linear responses to the sensitivity analysis (e.g. the wolf satiation threshold – f_w, Figure 4). Varying all other parameters had small effects on model predictions.

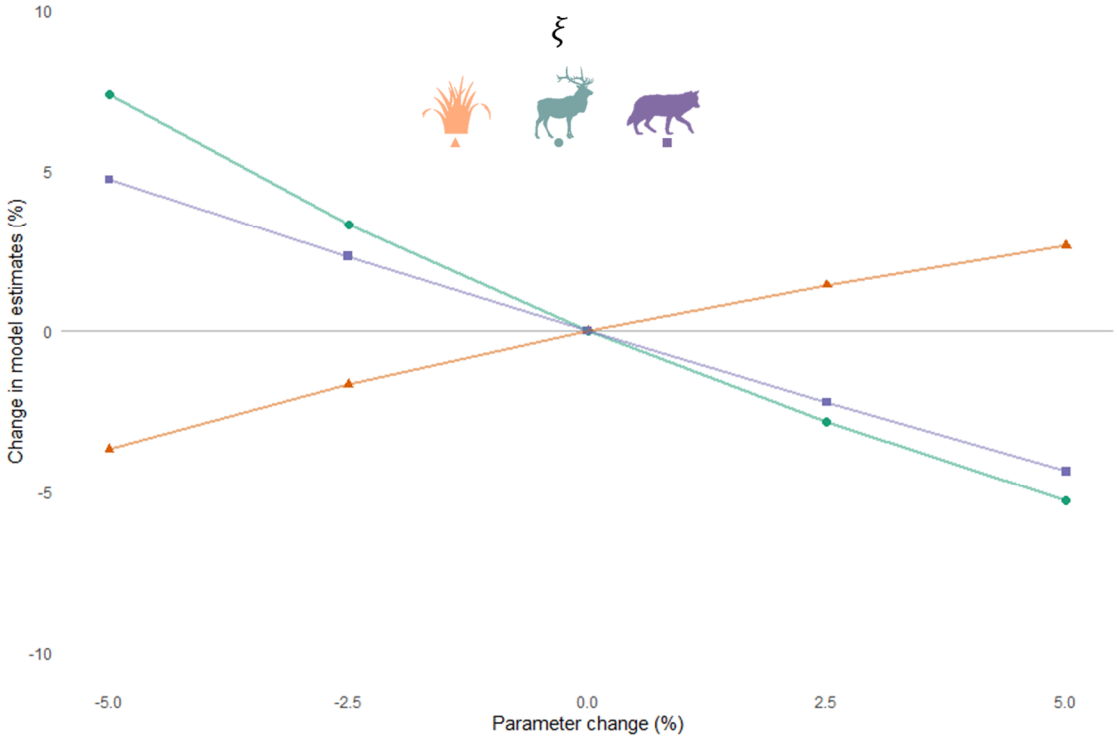


Figure 5 Effect that changing the wolf hunting efficiency (ξ – i.e. the coefficient regulating the effect of predation on elk) from -5% to +5% has on model estimates (in March). Change in model estimates is quantified as relative changes compared to the model with unchanged parameters.

4.4 Discussion

We developed a bioenergetic mechanistic model to describe population dynamics in tri-trophic systems, explicitly considering population sizes and body masses. We applied our model to wolves, elk and grassy vegetation in Northern Yellowstone, and showed that the reintroduction of the wolf is expected to cause a significant decline in elk numbers that translates into higher vegetation growth. Coupled with this, wolf predation led to a shift in the phenotypic composition of the elk population, via a small increase in elk average body mass. Our sensitivity analysis shows that our general results are robust over a wide range of parameter values, although the exact quantification of effects remains a challenge. Changing parameter values affected trophic levels in different ways, and the most important parameters were not the same for all levels. Moreover, the

sensitivity analysis highlighted interesting feedbacks in the system, which sometimes led to counterintuitive model outcomes.

Introducing the wolf into our model led to a population of 99 individuals (including pups in the breeding month) at equilibrium, and a 61% reduction in elk numbers (from 14,948 to 5,823), consistent with observed trends in elk population size post wolf reintroduction into Yellowstone (MacNulty et al. 2016). In turn, vegetation biomass, on average, increased by approximately 23% in the growing season and more than 3-fold (328%) in the non-growing season. In winter, when we excluded wolves from the model, vegetation biomass reached its minimum value (V_{min}), suggesting that, in the absence of wolves, the elk is largely food-limited and the entire system is controlled by primary production (bottom-up regulation). When wolves were added to the model, vegetation biomass at equilibrium increased across all seasons because of reduced herbivory, suggesting that the elk population became predator-limited, while the wolf population became food-limited (top-down regulation). The addition of the wolf also had a stabilising effect on elk numbers, which population at equilibrium became constant across years, rather than exhibiting biannual cyclic fluctuations (Figure 1). This stabilising effect of predation on prey fluctuations is consistent with what has been observed in other systems (Pople et al. 2000, Letnic and Crowther 2013, Wilmers et al. 2006).

Overall, our bioenergetic ecosystem model revealed subtle nuances in the mechanisms underlying tri-trophic interactions between vegetation, elk and wolves. Nevertheless, it did not produce precise predictions on broader ecosystem processes. Such processes may well arise with the contribution of other interacting factors that we did not consider in our analysis (Peterson et al. 2014). For example, increases in vegetation biomass following predator introductions that are predicted by our model may be less evident in the field (Brice, Larsen, and MacNulty 2021), because the vegetation may become available to other herbivores. This effect was experimentally demonstrated in Kenya, where wild dog recolonization reduced dik-dik numbers by 33%, but did not translate into reduced overall

herbivory and vegetation recovery (Ford et al. 2015). Our model did not include herbivory by bison within Northern Yellowstone because wolves do not heavily prey upon them (Tallian et al. 2017). However bison compete with elk for resources while being less vulnerable to wolf predation (Tallian et al. 2017). As such, the increase in vegetation predicted by our model could be one of the causes for the observed increase in bison numbers (from ~500 in 1995 to ~4,000 in 2018 - Beschta et al. (2020).

Some researchers have argued that the observed decline in the Yellowstone elk population is not directly, or solely, due to the reintroduction of wolves, but rather a consequence of broader ecosystem changes including more frequent droughts and fires, increases in human harvesting, and increased predation by other carnivores (MacNulty et al. 2016, Peterson et al. 2014). While models show that reductions in resource availability due to greater environmental variation can have substantial impacts on elk population size (Lachish et al. 2020), this impact should decrease when predators are added to the system and the elk becomes predator-limited (Letnic and Crowther 2013, Wallach, Ripple, and Carroll 2015, Wilmers et al. 2006). Other carnivores, such as grizzly bears and cougars, have also increased in numbers over the same period as the wolf reintroduction and recovery (Hamlin, Cunningham, and Alt 2009, Ruth, Buotte, and Hornocker 2019). Despite the paucity of detailed information about the interaction between elk and these other two carnivores, it has been argued that their effect on elk can match or even exceed that of wolves (Peterson et al. 2014).

Including the wolf in the model also altered the elk body mass distribution. While wolf predation caused only a 2% reduction in elk average body mass (from 214 kg to 210 kg), the distribution of body masses (Figure 2) shows that wolves selectively removed individuals with a low structural mass (i.e. younger individuals) consistently across all months of the year, and those with a lower reserve mass in the breeding month and during the growing season (i.e. females with lower reproductive values). This finding supports the healthy herd hypothesis, whereby predators remove weaker (sick, starving,

or injured) individuals from a population and giving a selective advantage to bigger individuals with better body condition (Packer et al. 2003, Hudson, Dobson, and Newborn 1992). The body mass distributions predicted by our model were broadly similar to those observed in Yellowstone (189–275 kg, Cook, Cook, and Mech (2004)). In wolves, the average body mass predicted by our model in March was 44 kg (figure 3), which also falls within the observed range for female adults in Yellowstone (ca. 30-52 kg, MacNulty et al. (2009)).

The sensitivity analysis showed that our results are relatively stable across a wide range of parameter values and highlighted some interesting patterns in wolf-elk dynamics. For example, increasing the wolf hunting efficient (ξ) leads to a reduction in wolf numbers, a seemingly counterintuitive finding. However, increased predation causes a decline in prey numbers, ultimately resulting in lower available resource for predators. Other parameters show some non-linear responses in the sensitivity analysis. An example of this is the wolf satiation threshold (f_w). Reducing this threshold from 0 to -2.5 led to a reduction in wolf numbers, because wolves do not eat enough. However, increasing the same parameter from 0 to +2.5% also caused a very small decline in the wolf population, perhaps because wolves then can overeat elk, causing their own resources to decrease as explained above. While the patterns observed in these two examples could derive from the way in which we constructed our model, they also demonstrate the complexity of trophic interactions and wider ecosystem processes.

Our model is based on two major assumptions. First, because our model is not spatially explicit and the migration patterns of the Northern Yellowstone elk are complex with significant heterogeneity in migration distance and direction (White et al. 2010), we treated our study area as a closed system with no animal movement from and to adjacent areas (Lachish et al. 2020). Secondly, we did not consider wolf sociality and pack dynamics (Brandell et al. 2021). Given the complexity of our model, we made the simplifying assumption that all adult female wolves that reached a threshold of structural

mass (K_w = 24 kg) could reproduce, giving birth to one offspring annually. We checked that this assumption was appropriate by ensuring that the reproductive rates in the model (45 wolf pups with a population size of 56 wolves at equilibrium) were similar to those expected in a real population (42 pups for 52 wolves in Yellowstone National Park in 2019 - Smith et al. (2020)). Nonetheless, we acknowledge that this is an important aspect of wolf biology (Mech and Boitani 2003) and inclusion of these components in the model is the focus of ongoing work.

Our model represents a novel approach to the study of predator-prey interactions and trophic cascades. Explicitly considering and linking bioenergetics, population sizes and body masses can provide novel insights into the mechanisms behind complex ecosystem processes. The proposed approach can be useful to test theoretical hypotheses, to construct and assess large scale scenarios for landscape management and planning, or to provide more accurate predictions about ecosystem dynamics. Further developments can therefore include the addition of other species, consideration of the impacts of environmental variation, or evaluation of the effects of infectious diseases or management actions.

4.5 Supplementary information

Parameters used in the model, together with parameter names and notations, units, descriptions, values and references.

Parameter	Name in R code	Name in Article	Unit	Description	Value - elk	Value - wolf	Source - elk/vegetation	Source - wolf
State Variables								
Z_S	...		Kg	Mass of structural components	0.1-240	0.1-43	(Field et al., 2003)	(Coulson et al., 2011)
Z_R	...		Kg	Mass of energy reserve components	0.1-120	0.1-27	(Field et al., 2003)	(Mech and Boitani, 2003)
Z	...		Kg	Total body mass	0.2-360	0.2-70	(Cook et al., 2004, Griffin et al., 2011)	(Coulson et al., 2011)
V_{max}	veg_max	Maximum vegetation biomass	Kg	Maximum vegetation biomass	1.4×10^7	...	(Garroutte et al., 2016)	...
V_{min}	veg_min	Minimum vegetation biomass	Kg	Minimum vegetation biomass	4.2×10^5	...	(Lachish et al., 2020)	...
Vegetation parameters								
a	veg_growth_rate	Vegetation growth rate		Growth rate of vegetation	0.35	...		
θ	half_sat_value	Half saturation constant	Kg	Half-saturation constant in feeding rate	10000	10000	(Owen-Smith, 2002)	(Owen-Smith, 2002)
η	steepness	Satiation scaling of intake rate	Kg^{-1}	Steepness in satiation scaling of intake rate	15	15	(De Roos et al., 2009)	(De Roos et al., 2009)

j	veg_energy	Vegetation energy content	MJ Kg^{-1}	Energy content of the vegetation	10	...	(Cook et al., 2004)	...
ς	snow_effect	Snow effect	%	Reduction in maximum consumption due to snow cover	0.5	...	(Visscher et al., 2006)	...
Demographic parameters								
K	ZS_threshold_k	Structural breeding mass	Kg	Threshold structural mass for breeding	140	24	(Cook et al., 2013)	(MacNulty et al., 2009)
g	breeding_ZR_threshold	Reserve breeding mass	%	Ratio of energy reserve mass to total mass needed to breed	0.1	0.1	(Cook et al., 2013)	(Cook et al., 2013)
f	fat_threshold	Satiation threshold	%	Ratio of energy reserve mass to total mass above which consumption decreases	0.3	0.4	(Lachish et al., 2020)	(Mech and Boitani, 2003)
b	starvation_ratio	Starvation ratio	%	Ratio of energy reserve mass to total mass below which animals die for starvation	0.03	0.03	(Cook et al., 2004)	(Mech and Boitani, 2003)
β_0	surv_int	Survival intercept	$Month^{-1}$	Intercept of the logit function describing survival	3.2	4.2	(Eberhardt et al., 2007)	(Cubaynes et al., 2014)
β_1	surv_slope	Survival slope	$Month^{-1}$	Slope of the logit function describing survival	0.03	0.025	(Eberhardt et al., 2007)	(Cubaynes et al., 2014)
ω	neonate_mortality	Neonate mortality	$month^{-1}$	Constant mortality of neonates	0.1	0.1	(Delgiudice et al., 1991)	(Pletscher et al., 1997)
Bioenergetic parameters								
c	cmax_slope	Ingestion rate	Kg $kg^{-2/3}$ $month^{-1}$	Scalar constant of ingestion rate	6	28	(Jiang and Hudson, 1992)	(Stahler et al., 2006, Mech et al., 2001)

δ	burn_slope	Metabolic costs	MJ $kg^{-3/4}$ $Month^{-1}$	Scalar constant of daily metabolic costs	0.45	1.18	(Jiang and Hudson, 1992, Vetharaniam et al., 2009)	(Mech and Boitani, 2003)
m	m_anabolic/m_catabolic	Metabolic conversion rate	MJ Kg^{-1}	Coefficient for anabolic/catabolic conversion between assimilated energy and energy reserves	54.6 / 39.3	54.6 / 39.3	(Illius and O'Connor, 2000)	(Illius and O'Connor, 2000)
ψ	ZR_to_ZS	Energy reserve conversion	%	Proportion of energy reserve mass converted to structural mass in individuals that grow (ZS < k)	0.5	0.25	(Lachish et al., 2020)	...
ε_1	convert_coef_1	Energy conversion efficiency 1	%	Efficiency with which energy reserve mass is converted to structural mass	0.95	0.95	(Lachish et al., 2020)	(Lachish et al., 2020)
τ	ZR_to_reproZ	Energy allocated to reproduction	%	Proportion of energy reserve mass allocated to reproduction (offspring production and provisioning) by breeders	0.6	0.6	(Lachish et al., 2020)	(Lachish et al., 2020)
ϑ/γ	...		...	Intercept and exponent of function describing variance in growth of structural and energy reserve mass	5 / 0.05	5 / 0.05	(Lachish et al., 2020)	(Lachish et al., 2020)
υ	reproZ_to_offspringZS	Reserve allocation to offspring	%	Proportion of the allocated reproductive reserve that is converted to offspring structural mass	0.9	0.9	(Lachish et al., 2020)	(Lachish et al., 2020)
$\varepsilon_2/\varepsilon_3$	convert_coef_2/3	Energy conversion efficiency 2/3	%	Efficiency with which mother's energy reserves are converted to offspring structural/energy reserve mass	0.95 / 0.95	0.95 / 0.95	(Lachish et al., 2020)	(Lachish et al., 2020)

λ/ς	...		...	Intercept and exponent of function describing variance in development of structural and energy reserve mass in offspring	1.5 / 0.03	1.5 / 0.03	(Lachish et al., 2020)	(Lachish et al., 2020)
d	edible_parts	Edible meat ratio	%	Proportion of herbivore meat which is edible	0.68	...	(Wilmers et al., 2003, Metz et al., 2012)	...
h	elk_energy	Elk energy content	MJ Kg^{-1}	Energy content of elk meat	7.7	...	(Głowaciński and Profus, 1997)	...
Behavioural parameters								
ξ	coef_pred_mort	Hunting efficienty	$Month^{-1}$	Coefficient regulating the effect of predation on herbivore survival	0.00031	...	(Evans et al., 2006, Barber-Meyer et al., 2008)	...
l	scavenging	Scavenging rate	%	Proportion of herbivore meat which is scavenged by other predators	0.25	...	(Wilmers et al., 2003)	...
ϱ	wolf_aggr	Intraspecific aggression	$Month^{-1}$	Coefficient regulating the effect of predator intraspecific aggression	...	0.00022	...	(Cubaynes et al., 2014)

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5

Ecological and evolutionary perturbations of a trophic cascade

Abstract

Understanding the effects of predators on ecosystem processes has been a major focus of ecology for decades, however these effects remain poorly understood in complex terrestrial systems. Theory predicts that predators control herbivory by reducing herbivore populations, thus causing a trophic cascade that propagates and benefits lower trophic levels. One of the most famous examples of a trophic cascade is that of Yellowstone National Park, where wolves were reintroduced in 1995. Since then, the elk population has significantly declined and woody vegetation has recovered in some areas. Nonetheless, the occurrence of a trophic cascade is still debated.

We use a bioenergetic, tri-trophic, mechanistic model developed by Passoni et al. (2022) to investigate the potential effects of ecological and evolutionary change on the trophic interactions between wolves, elk, and vegetation in the Northern Yellowstone ecosystem. First, we test the trophic cascade hypothesis by applying a numerical perturbation to each trophic level and recording its effects on the system. Secondly, we investigate how ecological and evolutionary change may affect trophic cascades by altering specific sets of model parameters. In particular, we assess the potential impact of changing snow regimes, elk behavioural responses to wolf predation, diseases, scavenging of elk by other carnivores, and evolutionary improvements in wolf predation efficiency.

The emerging dynamics are complex. The single trophic level population perturbations showed that the overall system is food-limited when the wolf is absent and predator-limited when the wolf is present. When the overall system is predator-limited, the severity of a trophic cascade and the strength of feedbacks vary depending on context. For example, increasing the number of months with snow in each year initially led to a small reduction in the population of all trophic levels. However, an additional increase in snow months led the wolf population to decrease further, ultimately causing an actual increase in elk numbers. We show similar results in other contexts, with different emerging dynamics depending on the altered parameters and their values.

Our novel bioenergetic approach enabled us to explore the underlying mechanisms of trophic interactions, and provided insights into how these interactions may evolve in a rapidly changing world.

5.1 Introduction

Understanding the effects of predators on ecosystem processes has been a major focus of ecology for decades, however these effects remain poorly understood in complex terrestrial systems (Ford, 2015). Theory predicts that predators control herbivory by reducing herbivore populations, thus causing a trophic cascade that propagates and benefits lower trophic levels (Hairston et al., 1960, Estes and Palmisano, 1974). The occurrence of trophic cascades has been demonstrated in a variety of systems, such as lakes and rivers, kelp beds, tropical rainforests, salt marshes, and mountain forests.

Despite the large number of examples, empirical support for trophic cascades in complex terrestrial systems remains scant. Moreover, the majority of studies have relied on correlative methods with few controls and inadequate replication and have contributed little to a mechanistic understanding of underlying processes (Ford et al 2015). For this reason, it can prove difficult to predict when trophic cascades will occur and how the ecosystem will respond to predator recovery. Studying this is crucial because it can help us understand and predict the effects of environmental change, species recovery, species invasion, animal diseases, and anthropogenic activities (Gilman et al., 2010).

One of the most famous, yet contested, examples of a trophic cascade is that of Yellowstone national park, where wolves were reintroduced in 1995 (Peterson et al., 2020, Peterson et al., 2014). Since then, the elk population has significantly declined, and woody vegetation has recovered in some areas (Peterson et al., 2020). The cause of these trends was largely attributed to the wolf recovery. Nonetheless, at the same time, the area experienced severe droughts and wild fires which could have also been responsible for a decline in vegetation growth and, thus, in the elk population (Peterson et al., 2014, MacNulty et al., 2020). In addition, other carnivore populations, such as bears and cougars, also recovered in numbers since the wolf reintroduction (Stahler et al., 2020). This, and the lack of strong experimental support, resulted in a debate about the underlying cause of elk population declines. Indeed, one of the biggest debates around

Yellowstone concerns whether the system is mainly regulated by resource availability (bottom-up control) or predation by carnivores (top-down control).

Here, we review several aspects that may impact the Yellowstone trophic cascade. Trophic interactions in Yellowstone can be affected by environmental, ecological and evolutionary factors. One of these factors is climate change. In particular, snow can reduce the availability of vegetation for herbivores and affect several aspects of wolf-elk dynamics by increasing predation success (Mech et al., 2001), altering the composition of wolf-killed elk (Wilmers et al., 2020), and increasing the amount of carrion available for scavengers (Wilmers and Post, 2006). In turn, wolves can serve as buffers against climate variability by reducing climate-driven fluctuations in prey numbers (Wilmers et al., 2006, Sala, 2006). In the last decades, winter in Yellowstone has been getting shorter, with less snowfall and more days with temperatures above freezing (Wilmers and Getz, 2005).

Trophic cascades are ecologically and evolutionarily dynamic. As such, any ecological and evolutionary change in the system has the potential to affect trophic interactions. For example, fear of predation can induce a behavioural response in herbivores that can enhance vegetation growth, causing a behaviourally mediated trophic cascade (BMTC) (Schmitz et al., 1997, Ripple and Beschta, 2004). In Yellowstone, it has been proposed that elk may reduce their chance of being predated by shifting habitat selection from aspen stands to conifer forests, thereby allowing aspen to regenerate (Fortin et al., 2005). In addition, elk and caribou elsewhere in North America have been shown to increase their movement rate, displacement and vigilance when in the proximity of wolves (Basille et al., 2015, Middleton et al., 2013). This can potentially affect energy acquisition and expenditure by elk (Christianson and Creel, 2010). Indeed, elk can experience substantial nutritional deprivation in the presence of wolves (Christianson and Creel, 2010). Notwithstanding, the occurrence of a BMTC in Yellowstone has been debated and seems

to be less important compared to the direct consumptive effects of wolf predation (Kauffman et al., 2010, Cusack et al., 2019, Brice, 2022).

Trophic cascades in Yellowstone can also be affected by diseases, such as sarcoptic mange and canine distemper virus (Cross et al., 2016, Wilmers et al., 2006, Almberg et al., 2010). In particular, sarcoptic mange is an infectious disease transmitted to wolves by the mite *Sarcoptes scabiei*, which causes severe skin lesions and hair loss (Bornstein et al., 2001). The prevalence of hair loss due to mange in Northern Yellowstone oscillates between 5% and 20% peaking in the winter months (Cross et al., 2016). The lack of hair increases heat loss in infected individuals, resulting in an increase in energy expenditure at the population level in Northern Yellowstone of approximately 4% (Cross et al., 2016). Assuming that mange-induced mortality is low and not additive, infected wolves can compensate heat loss by adjusting their behaviour and reducing other energy demands (e.g. by moving less), or by increasing consumption rates on their prey (Cross et al., 2016).

Finally, Northern Yellowstone is a highly complex ecosystem hosting other species that can all influence trophic cascades. For example, in recent years, grizzly bears (*Ursus arctos horribilis*), cougars (*Puma concolor*) and bison (*Bison bison*) have all increased in numbers in Northern Yellowstone (Hamlin et al., 2009, Ruth et al., 2019). In particular, bears and cougars can increase predation pressure on elk both through direct predation and through interference competition with wolves (Stahler et al., 2020). On the other hand, bison compete for the same resource as elk but are less vulnerable to wolf predation, although bison consumption by wolves has recently increased through scavenging (Tallian et al., 2017, Metz et al., 2020).

Complex terrestrial systems are characterised by often indirect interactions and feedbacks occurring among the different trophic levels and the environment. The large number of confounding factors mentioned above, and the lack of replicates, makes studying trophic cascades in the wild very challenging. Mechanistic models can offer a solution to this

problem. By varying input data, parameters and equations, models allow us to systematically explore various processes that can influence trophic cascades and that cannot be reproduced in the wild.

In this study, we use a bioenergetic, tri-trophic, mechanistic model developed by Passoni et al. (2022) to investigate the potential effects of ecological and evolutionary change on the trophic interactions between wolves, elk, and vegetation in the Northern Yellowstone ecosystem. First, we test the trophic cascade hypothesis by applying a numerical perturbation to each trophic level and recording its effects on the system. Secondly, we investigate how ecological and evolutionary change may affect trophic cascades by altering specific sets of model parameters. In particular, we assess the potential impact of changing snow regimes, elk behavioural responses to wolf predation, diseases, scavenging of elk by other carnivores, and evolutionary improvements in wolf predation efficiency.

5.2 Methods

5.2.1 Model summary

To investigate the effect of ecological perturbations and eco-evolutionary scenarios on wolf-elk-vegetation interactions in Northern Yellowstone, we use a mechanistic bioenergetic model developed by Passoni et al. (2022). In this section, we provide a concise summary of the model. For the full description, see Passoni et al. (2022).

The model is iterated monthly and is formed of three components that recreate the key yearly events in the lives of the wolf and elk and that interact such as:

i) the grass grows seasonally following a simple growth function;

ii) the elk feed on the grass;

iii) the wolves feed on the elk.

5.2.2 Vegetation

The grass grows following a simple growth function during the growing season (from April to September), while in the remaining months (from October to March) the vegetation is dormant. The vegetation is depleted by elk herbivory throughout the year. However, during three winter months (December to February), snow covers the vegetation, reducing the elk access to vegetation. Vegetation growth is defined by:

$$V_{t+1} = (1 - a)V_{max} + aV_t - \varsigma p \int H_e(Z_{S_e}, t) C_{max_e}(Z_{S_e}) dZ_{S_e} \quad [1]$$

Where a describes the vegetation growth rate (with $0 < a < 1$ in the growing season and $a = 0$ in the non-growing season). V_{max} is the maximum vegetation biomass, $\varsigma p \int H_e(Z_{S_e}, t) C_{max_e}(Z_{S_e}) dZ_{S_e}$ is the total amount of grass eaten by the elk population and is proportional to the elk body mass distribution (Z_{S_e}). This amount is affected by p, which reduces the intensity of elk grazing when vegetation reaches a minimum threshold, and ς, which reduces the vegetation available to the elk when snow falls.

5.2.3 Generic structure of the IPM

Elk and wolf are modelled with two distinct but analogous IPMs which model the demographic outcomes as functions of the distribution of individual body masses (Z). Body mass is the sum of two components: a structural body mass (Z_S), formed of bones and essential organs that cannot decrease in time, and a reserve body mass (Z_R), formed of fat and muscle that can increase or decrease over time. Each month, the models iterates the body mass distribution at time t, $H(Z, t)$, to time $t + 1$, $H(Z, t + 1)$, with the following generic structure:

$$H(Z', t + 1) = \int_{\Omega} [D(Z'|Z, t)R(Z, t) + G(Z'|Z, t)S(Z, t)]H(Z, t)dZ \quad [2]$$

Where the survival function $S(Z, t)$ defines the survival probability of an individual with trait value Z at time t; the growth function $G(Z'|Z, t)$ gives the probability that animals

grow from mass Z to mass Z'; the reproduction function $R(Z,t)$ describes the number of offspring produced by individuals of mass Z between time t and $t+1$; and the investment in offspring function $D(Z'|Z,t)$ describes how body mass is inherited from parents of mass Z to offspring of mass Z'. In the following sections, we will provide an overview of these functions.

5.2.4 Survival

Survival for both elk and wolves is described by a logistic function where bigger individuals are more likely to survive than smaller ones. Additionally, both elk and wolves are more likely to die with increasing wolf numbers. This is due to predation in the case of elk, and intraspecific aggression in the case of wolves (Cubaynes et al., 2014). Finally, individuals with low reserve mass die of starvation. Survival in both components is described as:

$$S(Z,t) = \begin{cases} 0 \; if \; \left(\frac{Z_R}{Z} < b\right) \\ \frac{1}{1+e^{-(\beta_0+\beta_1 Z_R - XW_t)}} \; \text{otherwise} \end{cases} \quad [3]$$

Where Z is the total body mass, Z_R is the reserve mass, b is a threshold below which animals die of starvation, and W_t is the total wolf biomass at time t. X is either ξ for elk or ϱ for wolves, where ξ regulates the extent to which the total wolf biomass impacts elk survival, while ϱ represents the strength of wolf intraspecific aggression.

5.2.5 Elk as a resource for wolves

As shown above, the elk population is reduced by wolf predation. As wolves feed on elk the total elk biomass potentially available for the wolves is represented by the biomass of dead elk. However, the amount of biomass which is actually acquired by the wolf population depends on the wolf body mass distributions, on the proportion of edible biomass (d), and on scavenging by other species (l).

5.2.6 Growth and reproduction

To calculate the obtained energy, the acquired food resources are multiplied by a parameter j, representing the energy content of the vegetation for elk (j_e) and of elk meat for wolves (j_w). At the same time, monthly maintenance costs are calculated by multiplying daily metabolic costs by the number of days in a month:

$$M(Z) = 30 * \delta Z^{\frac{3}{4}} \quad [4]$$

Where δ is a constant of daily metabolic costs. Monthly maintenance costs are then subtracted from the acquired energy to obtain energy reserves, which are added to an animal's stored resources (Z_R^o) and allocated to growth and reproduction in different proportions depending on Z_R and Z_S.

In particular, when $Z_S \leq k$, where k is the minimum structural mass for sexual maturity, animals allocate their stored resources towards both Z_S and Z_R, and cannot reproduce. On the other hand, when $Z_S > k$ (i.e. when sexual maturity is reached) animals allocate their stored resources to Z_R and reproduction, by giving part of their stored resources to their offspring. Reproduction only occurs when animals have enough Z_R and each breeding individual can only produce a maximum of one offspring per year.

5.2.7 Model parameterisation

The model was parameterised as in Passoni et al. (2022), based on published information about the vegetation-elk-wolf system in Northern Yellowstone. A full table of parameters is available in the Supplementary Information.

5.2.8 Perturbations and scenarios

We used the model to investigate the effects of different ecological and evolutionary scenarios on tri-trophic interactions in Northern Yellowstone. In particular, we perturbed the model in two different ways. First, we perturbed each trophic level by reducing its

population size or biomass at a point in time, before studying the resulting dynamics of each species, to test the relative importance of top-down and bottom-up processes. Secondly, we varied several sets of model parameters to simulate and assess the effects of plausible ecological and evolutionary changes in the system.

Population perturbations

To test the relative importance of each trophic level in mediating the dynamics of the system, we numerically perturbed each trophic level in turn. In the case of the elk and wolf components, we reduced their population abundance by 25% in a given month while keeping the same population structure. For the vegetation, we reduced the maximum biomass (V_{max}) by 25% for twelve months. These perturbations were applied in March to both the systems with and without wolves. To quantify the effect of each perturbation, we measured the extent to which the abundance of each component varied before returning at equilibrium. We chose to perturb the system in March because it is the month before the wolf and the elk reproduce (in April and May respectively).

Ecological and evolutionary scenarios

To investigate how complex trophic interactions and feedback loops affect population dynamics, we simulated six ecological and evolutionary scenarios by simultaneously varying multiple model parameters.

Scenario 1: changing snow regimes

In the last decades, winter in Yellowstone has been getting shorter, with less snowfall and more days with temperatures above freezing (Wilmers and Getz, 2005). To investigate a potential effect of climate change on our model, we varied the number of snow months per year from 2 to 3 and 4. In the model, snow decreases the vegetation biomass available to the elk via the parameter ς in equation 1. In this case, we do not model other effects that snow may have on the system. However in scenario 6 below, we

test the effect of increasing hunting efficiency by wolf, which has been shown to change as a function of winter severity in Yellowstone (Mech et al., 2001).

Scenario 2: behaviourally-mediated trophic cascade

Fear of predation can induce a behavioural response in herbivores and cause a behaviourally mediated trophic cascade (Ripple and Beschta, 2004). In Yellowstone, it has been proposed that elk may reduce their chance of being predated by shifting habitat selection from aspen stands to less suitable conifer forests, thereby allowing aspen to regenerate (Fortin et al., 2005). Indeed, elk can experience substantial nutritional deprivation in presence of wolves (Christianson and Creel, 2010). Nonetheless, the occurrence of a BMTC in Yellowstone has been debated (Kauffman et al., 2010, Cusack et al., 2019, Brice, 2022). In this scenario, we test the plausibility and quantify the potential effects of this hypothesis by simulating a BMTC. We therefore decreased the effect of wolf predation on elk (ξ), while also decreasing the energy content of the vegetation (j).

Scenario 3: increased energy expenditure due to elk response to wolf presence

Predator-prey interactions might not always lead to strong spatiotemporal patterns in distribution or habitat selection (Cusack et al., 2019). Nonetheless, some ungulate species alter their movement patterns when near a potential predator, increasing their movement rate, displacement and vigilance (Basille et al., 2015, Middleton et al., 2013) with potential impacts on their energy budget. In this scenario, we simulated a stronger response of elk to wolf presence by increasing their energy expenditure (δ_e), while reducing the effect of wolf predation on elk (ξ).

Scenario 4: diseases

It has been proposed that wolves infected with sarcoptic mange can compensate for heat lost due to the disease by adjusting their behaviour and reducing other energy demands (e.g. by moving less), or by increasing consumption rates on their prey (Cross et al.,

2016). In this scenario, we simulate a potential effect of mange by increasing the wolf energy expenditure (δ_w) and their predation pressure on elk (ξ).

Scenario 5: multiple predator effects

Since wolf reintroduction, grizzly bears and cougars have also increased in numbers in Northern Yellowstone (Hamlin et al., 2009, Ruth et al., 2019). In this scenario, we simulate the effect of their presence by decreasing elk survival (β_{0_w}) and increasing the proportion of elk edible meat scavenged by carnivores other than wolves (l).

Scenario 6: wolf hunting efficiency

Wolves were shown to have a higher predation success in winter and in deep snow in Yellowstone (Mech et al., 2001) and other areas (Post et al., 1999, Huggard, 1993). In this scenario, we reproduce this by increasing wolf predation on elk during snow months (ξ).

We also provide a sensitivity analysis for all the individual parameters used in these scenarios (see Supplementary Information).

5.3 Results

As shown in Passoni et al. (2022), the model produced population estimates which were consistent with those observed in Northern Yellowstone both before and after wolf reintroduction (MacNulty et al., 2016, Smith et al., 2020). In particular, Passoni et al. (2022) showed that, without wolves, the elk population oscillated following biennial cycles. In contrast, when wolves were included on the landscape, the elk population declined by around 60% and stabilised around a constant value, while the vegetation never reached its minimum values (Passoni et al., 2022). Below, we report the results of the population perturbations, and of the ecological and evolutionary scenarios.

5.3.1 Population perturbations

Perturbation in the system without wolves

Perturbing the vegetation caused the vegetation itself to initially decrease from 8M Kg to 5.7M Kg (28.6%). This reduced the numbers of elk from 23807 to 4781 (-80%) in two years, leading to reduced grazing and, therefore, an increase in vegetation up to 12.9M Kg (+126%) (Figure 1).

Perturbing the elk had a much smaller impact, with elk numbers decreasing from 23806 to 18967 (-20%), and bouncing back up to 27195 (+43%) in two years, before starting to returning to equilibrium. The impact on grass was even more limited, with vegetation biomass varying from 8M Kg to 8.6M Kg (+8%), before returning to equilibrium.

It is also interesting to show that the system without wolves shows cyclical biennial fluctuations.

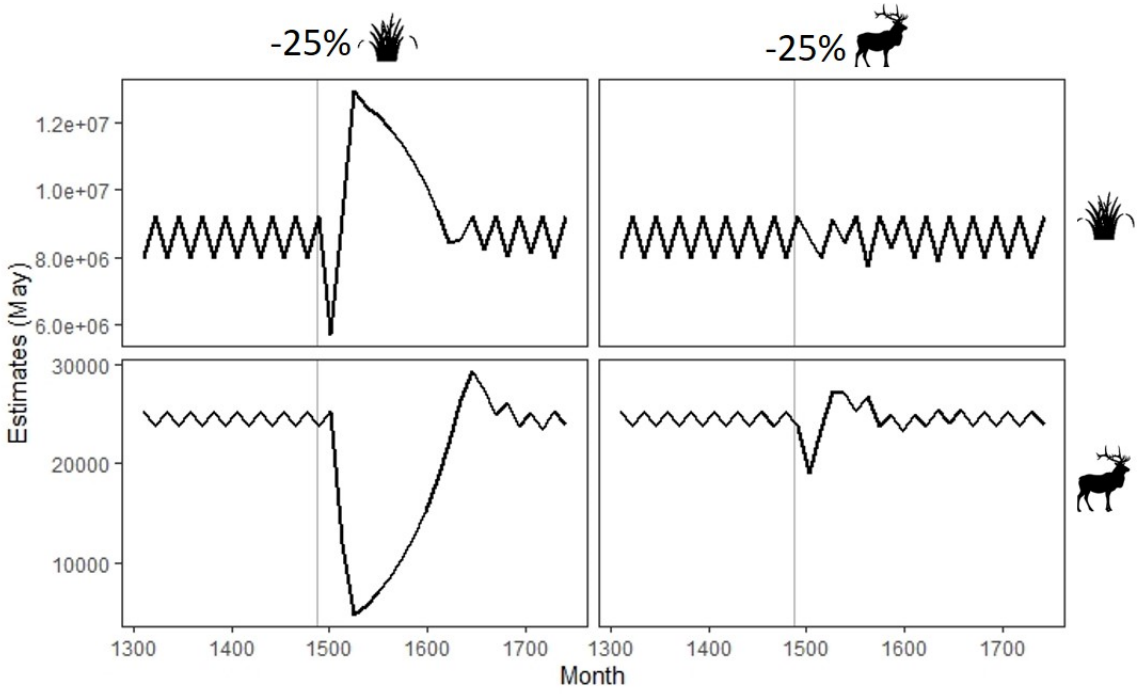


Figure 1 Populations perturbations in the system without wolves. The left and right columns respectively show the effects of the perturbations applied to the vegetation and the elk. The top and bottom rows, on the other hand, show the effects of those perturbations on the vegetation and the elk, respectively. The grey lines represent the time when the perturbations were applied.

Perturbations in the system with wolves

The addition of the wolf to the model stabilised the overall system, as shown by the lack of cyclical fluctuation in figure 2 compared to figure 1. Reducing the maximum vegetation biomass in the system (Figure 2) caused the vegetation to oscillate between 11.4M Kg and 9.1M Kg (-20%) before settling close to equilibrium in 3 years. The elk and wolf were only marginally affected, with variations being smaller then 0.1%.

Perturbing the elk population by 25% (from 10228 to 7675) caused an increase in vegetation from 11.4M Kg to 12M Kg (+6%) in two years, and a reduction in wolf numbers from 75 to 62 (-17%) over a 9-year period. This fall in predator numbers created a feedback in the elk population, which increased from 7675 to 12452 (+62%) individuals over 19 years before tending back towards equilibrium. The wolf and the vegetation followed this rise in prey numbers. In particular, the wolf population peaked at 80 individuals over a 21-year period from their minimum of 62 (+29%) (Figure 2).

Perturbing the wolf had the biggest impact on the system. Reducing the wolf population by 25% (75 to 56 individuals) caused a sudden increase in elk numbers by 43% (from 10228 to 14579) over an 11-year period. This led to a reduction in vegetation biomass (-10% in 12 years) and a subsequent increase in wolf numbers by 46% (from 56 to 82) over 22 years. The elk then decreased from 14579 to 9299 (-36% in 24 years), before the system started moving towards equilibrium again (Figure 2).

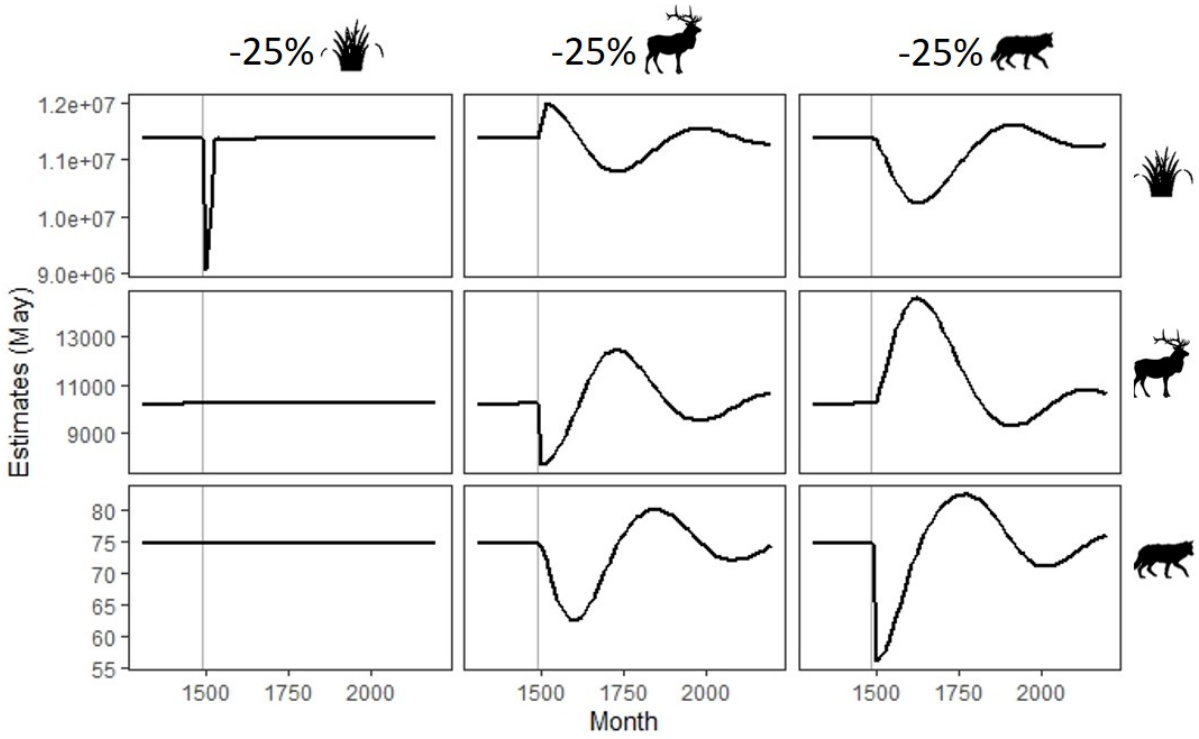


Figure 2 Population perturbations in the system with wolves. The left, middle and right columns respectively show the effects of the perturbations applied to the vegetation, elk and wolf. The top, central and bottom rows, on the other hand, show the effects of those perturbations on the vegetation, elk and wolf, respectively. The grey line shows the time of the perturbation.

5.3.2 Ecological and evolutionary scenarios

Scenario 1: changing snow regimes

Varying the number of snow months per year resulted in relatively big changes in model estimates (figure 3). Changing the number of snow months per year from two to three and four months caused a decline in the 80-year average of vegetation biomass from 9.6M Kg, to 9.3M kg and 8.6M kg, respectively. On the other hand, the elk population initially decreased slightly from 6289 to 5932 individuals, and then increased to 7919 individuals. Finally, wolf numbers declined from 62, to 56 and 37. It is interesting to note the non-linearity in the elk population response that initially decreases and later grows with increasing snow months. This suggests the presence of feedbacks in the system.

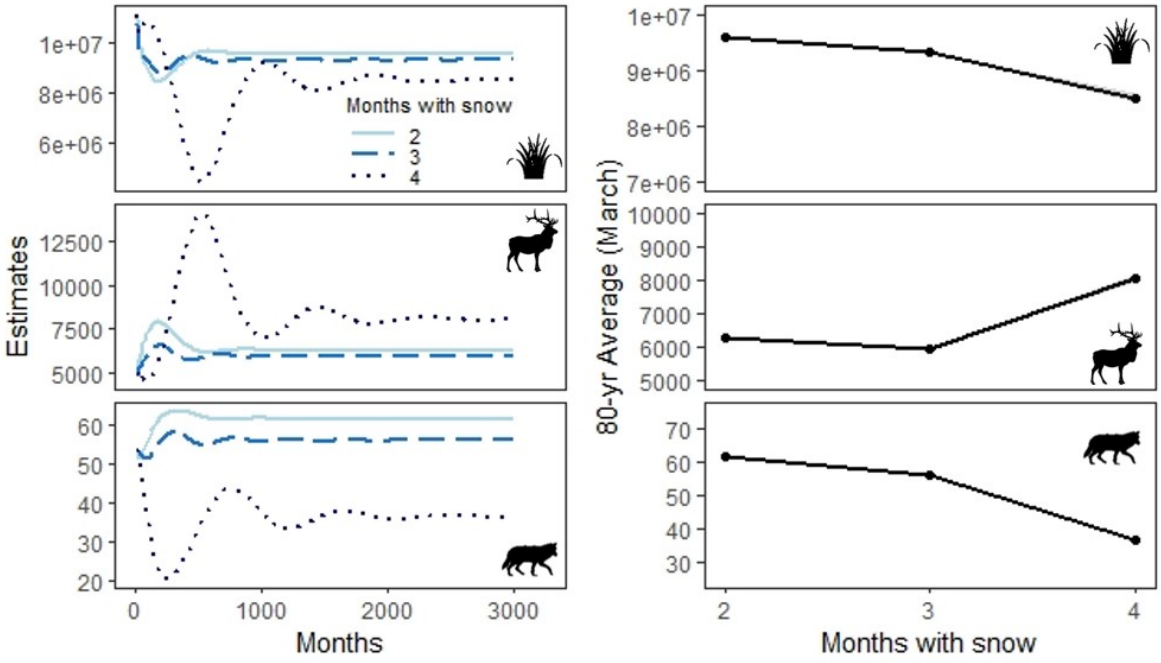


Figure 3 Population estimates for 3 separate models run with 2, 3 and 4 months of snow, respectively (scenario 1). The graph on the left shows population estimates in each model iteration in the month of March, whereas the graph on the right shows the population averages for the last 80 years in March. The grey shadings represent the extent (minimum and maximum) of the fluctuations in those 80 years.

Scenario 2: behaviourally-mediated trophic cascade

Simulating a behaviourally mediated trophic cascade (Figure 4) caused a 16% reduction in elk numbers (from 11900 to 10020) and a 28% decrease in wolves (from 83 to 60). The vegetation was not significantly affected (-2% change overall). Despite these small effect, it is interesting to note that vegetation biomass had a non-linear response to the change in parameter values, first increasing by 2.8%% and then decreasing by 0.3%.

Scenario 3: increased energy expenditure due to elk response to wolf presence

Increasing the energy expenditure of the elk (δ_e) and reducing the effect of wolf predation on elk (ξ) led to a significant reduction in wolf numbers (-22%; from 79 to 62). The elk and the vegetation were only marginally affected (elk: -3% from 10402 to 10092; vegetation: -1%) (Figure 4).

Scenario 4: diseases

In this scenario we increased the wolf energy expenditure (δ_w) and predation pressure on elk (ξ) to simulate a potential effect of sarcoptic mange on wolves. Varying these parameters caused a 20% reduction in wolf numbers (from 79 to 63) and a subsequent increase of 206% in elk (from 7943 to 24298). In turn, the rise in elk numbers led to a 32% reduction in vegetation biomass.

Scenario 5: multiple predator effects

Simulating the presence of other carnivores by reducing elk survival (β_{0_w}) and increasing scavenging of elk meat (l) significantly reduced the wolf and elk populations (wolf: from 87 to 61; -30% change – elk: from 17929 to 8672; -52% change), which led to a 25% increase in vegetation biomass (Figure 4).

Scenario 6: wolf hunting efficiency

Increasing wolf predation on elk during winter months (ξ) caused a 2% decline in elk numbers (from 10346 to 10156), and counterintuitively also reduced wolf numbers, although only marginally (from 75 to 74; -1% change). Vegetation remained stable with a 0.4% increase (Figure 4).

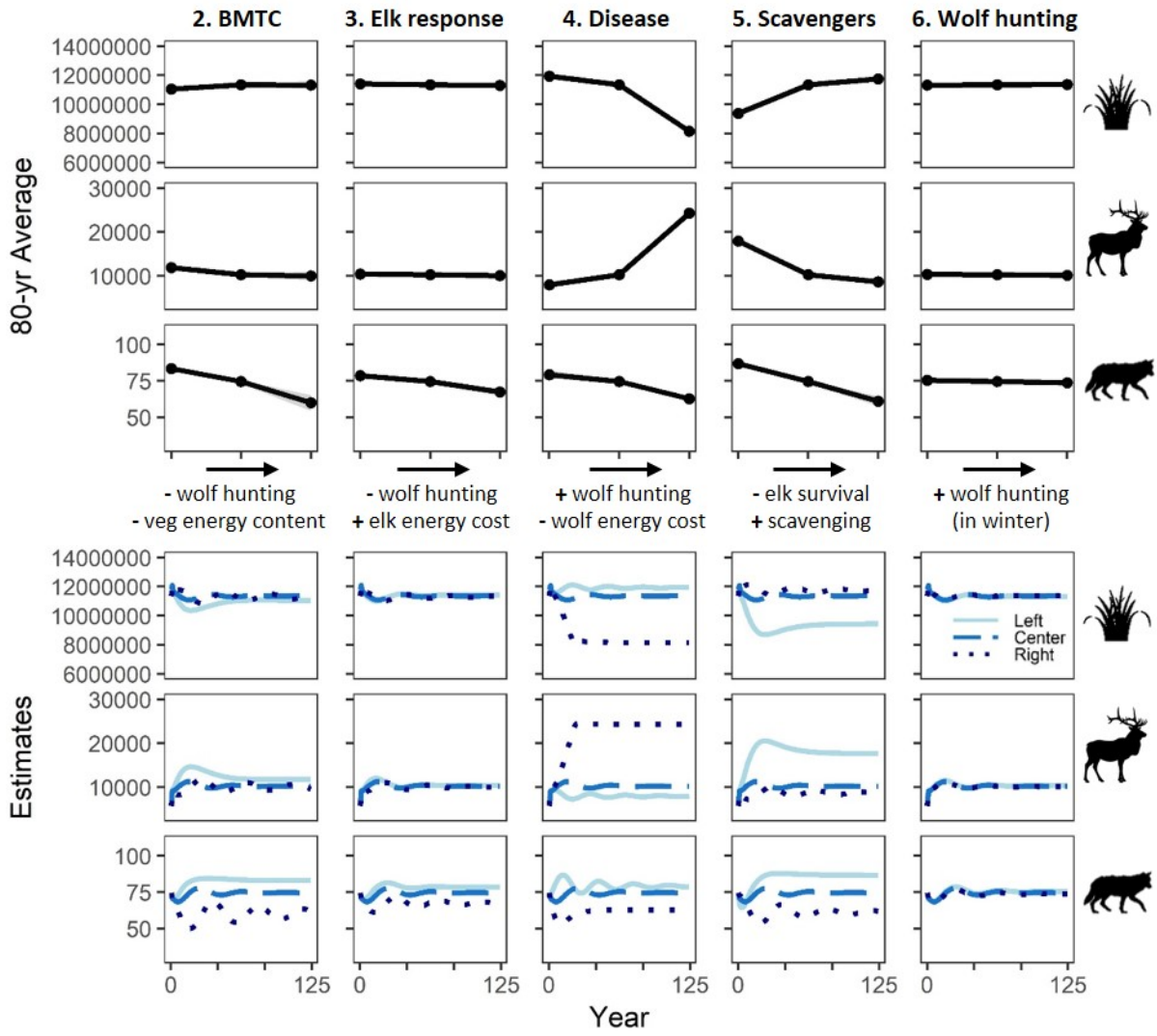


Figure 4 Results of the ecological and evolutionary scenarios (scenario 2 to 6, excluding scenario 1). Each column represent a scenario as summarised at the top. The top plots show how the population averages of the last 80 years in May change as the parameters vary. The grey shadings represent the extent (minimum and maximum) of the fluctuations observed in the last 80 years. The changes in parameters are summarised on the x axes. The bottom plots show population estimates through time in the month of May for each change in parameter values from the left (continuous light blue), through the center (blue dashed line), and to the right (dotted dark blue line) of the top plots..

5.4 Discussion

We investigated the potential effects of ecological and evolutionary change on the trophic interactions between wolves, elk and vegetation in the Northern Yellowstone ecosystem. The emerging dynamics among trophic levels are complex. The population perturbations

showed that the overall system is food-limited when the wolf are absent, and predator-limited when the wolves are present. When the overall system is predator-limited, the severity of a trophic cascade and the strength of feedbacks vary depending on context. For example, increasing the number of months with snow in each year initially led to a small reduction in all trophic levels. However, increasing snow months further led the wolf population to decrease further, causing an actual increase in elk numbers at equilibrium. We show similar results in other eco-evolutionary scenarios, with different emerging dynamics depending on the altered parameters and their values.

The population perturbations show that in the absence of wolves the elk is food limited, and the system is regulated by bottom-up processes. However, when we added the wolf to the model, perturbing vegetation biomass had no significant effects on the overall system, whereas changing wolf numbers had the biggest impact. This supports the hypothesis that the elk is predator-limited and that wolves exert significant top-down regulation (Ripple et al., 2001, Hairston et al., 1960). Nonetheless, other herbivores such as bison could potentially still limit the resources available to elk via direct competition (Tallian et al., 2017). Moreover, the fact that vegetation biomass did not have a significant effect also confirms that wolves can act as buffers against fluctuations in resource variability (Wilmers and Getz, 2005). Perturbing the elk population had a limited impact when wolves were absent, but became significantly more important when wolves were added to the system. As shown here, elk can have significant impacts on ecosystems and is often considered a keystone species (Frank et al., 2016, Starns et al., 2015, Ripple et al., 2015).

Winter and snow cover are key drivers of ecological interactions in terrestrial systems (Williams et al., 2015). We showed that varying the number of months with snow can lead to some unexpected outcomes. In particular, shifting from two to three months reduced the vegetation available to the elk, causing both elk and wolf numbers to decrease. Interestingly, increasing the number of months further to four led to stronger

reductions in wolf numbers, releasing elk from predation and ultimately causing an increase in elk numbers. Given that winter in Yellowstone has been getting shorter (Wilmers and Getz, 2005), it is likely that future changes will lead to an overall increase in both elk and wolf numbers. Additionally to these numerical effects, snow may affect trophic interactions also indirectly via processes that we did not explicitly consider in our snow regime scenario. For example, wolf kill rates on elk have been shown to increase with snow depth (Huggard, 1993, Mech et al., 2001) possibly due to increased encounter rates or reduced prey mobility (Fuller, 1991, Huggard, 1993). In our sixth scenario, we show that increasing wolf hunting efficiency only led to limited impacts on the system. As such, the direct effects of snow on vegetation are likely to be more important. Snow cover may affect the system also by causing the elk to switch from grazing to browsing (Creel and Christianson, 2009). We did not consider this aspect because our model does not distinguish between grassy and woody vegetation.

The ecological and evolutionary scenarios showed that varying multiple parameters simultaneously can have unexpected outcomes. In the second scenario, we tested the hypothesis of a behaviourally-mediated trophic cascade (BMTC). Our result shows that both the elk and wolf numbers would decrease in presence of a BMTC. As such, the direct consumptive effects of wolf predation are likely to be more important than behavioural ones in affecting the Yellowstone trophic cascade (Kauffman et al., 2010, Brice, 2022). In the third scenario, we tested the effects of a potentially increased proactive response of elk to wolf predation risk. Increasing the elk energy expenditure led to a marginal reduction in elk numbers, even though predation by wolves decreased. Ungulates have been shown to increase their movement rate, displacement and vigilance when near a potential predator (Basille et al., 2015, Middleton et al., 2013). Our results confirm the findings of Cusack et al. (2019), who did not find evidence for a strong proactive response. In our fourth scenario, we increased wolf energy expenditure and hunting efficiency to test the impact of sarcoptic mange. Analogously to the previous scenario, energy expenditure was the more important factor and had more impact than

wolf hunting efficiency. As such, the wolf population performed better when it minimised energetic costs. Our result thus seems to support the hypothesis that wolves may compensate for the heat loss due to mange by reducing energy demands (Cross et al., 2016). Finally, in the fifth scenario, we simulate an increased presence of other predators by reducing elk survival and increasing the proportion of meat lost from wolves to scavengers. Unsurprisingly, both the elk and the wolf population decreased, probably due to increased predation and competition, respectively (Tallian et al., 2022, Stahler et al., 2020).

One potential limitation of our scenarios is that, while we varied all parameters by 5%, it is possible that, in reality, factors related to each parameters change to different extents. For example, the benefit gained by avoiding predation may be higher than the energetic cost of escaping. Nonetheless, our scenarios give insights on how several factors may affect trophic cascades. For more details about the limitations of the model, refer to Passoni et al. (2022).

We investigated how different ecological and evolutionary factors may affect the Yellowstone trophic cascade. Our novel bioenergetic approach enabled us to explore the underlying mechanisms of trophic interactions, and provided insights into how these interactions may evolve in a rapidly changing world. Our model can be expanded to other systems, it can be adapted to test other hypotheses in ecology and evolution, and can be used to inform ecosystem management actions.

5.5 Supplementary information

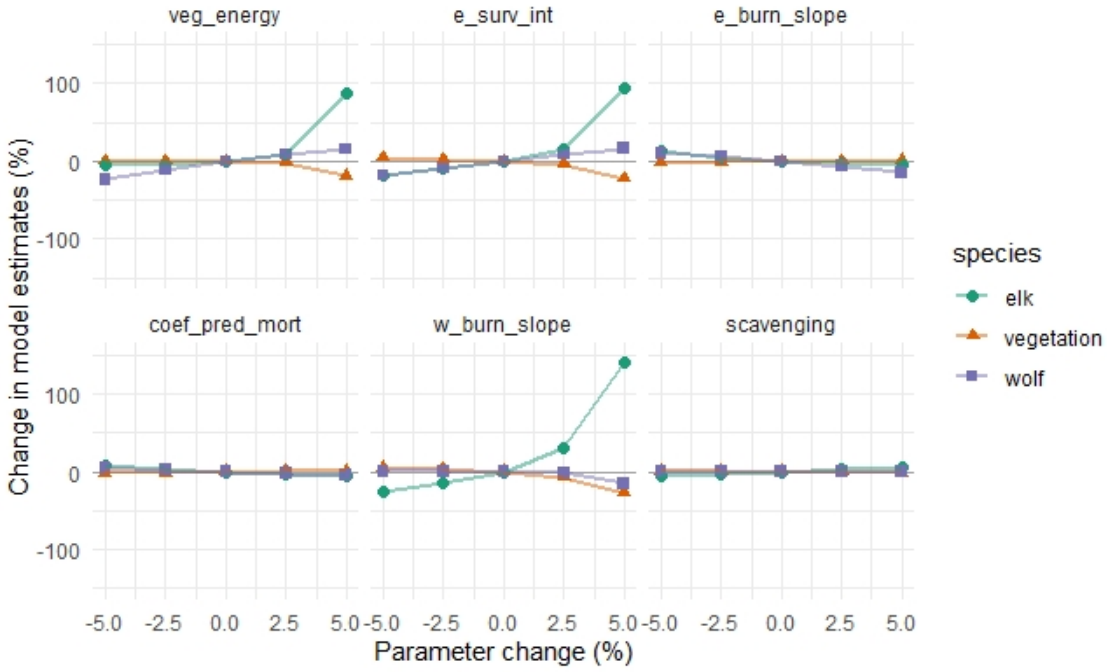


Figure 5 Sensitivity analysis for single parameters used in the eco-evolutionary scenarios

Table 1 Parameters used in the model, together with parameter names and notations, units, descriptions, values and references.

Parameter	Name in R code	Name in Article	Unit	Description	Value - elk	Value - wolf	Source - elk/vegetation	Source - wolf
State Variables								
Z_S	...		Kg	Mass of structural components	0.1-240	0.1-43	(Field et al., 2003)	(Coulson et al., 2011)
Z_R	...		Kg	Mass of energy reserve components	0.1-120	0.1-27	(Field et al., 2003)	(Mech and Boitani, 2003)
Z	...		Kg	Total body mass	0.2-360	0.2-70	(Cook et al., 2004, Griffin et al., 2011)	(Coulson et al., 2011)
V_{max}	veg_max	Maximum vegetation biomass	Kg	Maximum vegetation biomass	1.4×10^7	...	(Garroutte et al., 2016)	...
V_{min}	veg_min	Minimum vegetation biomass	Kg	Minimum vegetation biomass	4.2×10^5	...	(Lachish et al., 2020)	...
Vegetation parameters								
a	veg_growth_rate	Vegetation growth rate		Growth rate of vegetation	0.35	...		
θ	half_sat_value	Half saturation constant	Kg	Half-saturation constant in feeding rate	10000	10000	(Owen-Smith, 2002)	(Owen-Smith, 2002)
η	steepness	Satiation scaling of intake rate	Kg^{-1}	Steepness in satiation scaling of intake rate	15	15	(De Roos et al., 2009)	(De Roos et al., 2009)
j	veg_energy	Vegetation energy content	MJ Kg^{-1}	Energy content of the vegetation	10	...	(Cook et al., 2004)	...
ς	snow_effect	Snow effect	%	Reduction in maximum consumption due to snow cover	0.5	...	(Visscher et al., 2006)	...
Demographic parameters								

K	ZS_threshold_k	Structural breeding mass	Kg	Threshold structural mass for breeding	140	24	(Cook et al., 2013)	(MacNulty et al., 2009)
g	breeding_ZR_threshold	Reserve breeding mass	%	Ratio of energy reserve mass to total mass needed to breed	0.1	0.1	(Cook et al., 2013)	(Cook et al., 2013)
f	fat_threshold	Satiation threshold	%	Ratio of energy reserve mass to total mass above which consumption decreases	0.3	0.4	(Lachish et al., 2020)	(Mech and Boitani, 2003)
b	starvation_ratio	Starvation ratio	%	Ratio of energy reserve mass to total mass below which animals die for starvation	0.03	0.03	(Cook et al., 2004)	(Mech and Boitani, 2003)
β_0	surv_int	Survival intercept	$Month^{-1}$	Intercept of the logit function describing survival	3.2	4.2	(Eberhardt et al., 2007)	(Cubaynes et al., 2014)
β_1	surv_slope	Survival slope	$Month^{-1}$	Slope of the logit function describing survival	0.03	0.025	(Eberhardt et al., 2007)	(Cubaynes et al., 2014)
ω	neonate_mortality	Neonate mortality	$month^{-1}$	Constant mortality of neonates	0.1	0.1	(Delgiudice et al., 1991)	(Pletscher et al., 1997)
Bioenergetic parameters								
c	cmax_slope	Ingestion rate	$Kg\ kg^{-2/3}\ month^{-1}$	Scalar constant of ingestion rate	6	28	(Jiang and Hudson, 1992)	(Stahler et al., 2006, Mech et al., 2001)
δ	burn_slope	Metabolic costs	$MJ\ kg^{-3/4}\ Month^{-1}$	Scalar constant of daily metabolic costs	0.45	1.18	(Jiang and Hudson, 1992, Vetharaniam et al., 2009)	(Mech and Boitani, 2003)
m	m_anabolic/m_catabolic	Metabolic conversion rate	$MJ\ Kg^{-1}$	Coefficient for anabolic/catabolic conversion between assimilated energy and energy reserves	54.6 / 39.3	54.6 / 39.3	(Illius and O'Connor, 2000)	(Illius and O'Connor, 2000)
ψ	ZR_to_ZS	Energy reserve conversion	%	Proportion of energy reserve mass converted to structural mass in individuals that grow (ZS < k)	0.5	0.25	(Lachish et al., 2020)	...

ε_1	convert_coef_1	Energy conversion efficiency 1	%	Efficiency with which energy reserve mass is converted to structural mass	0.95	0.95	(Lachish et al., 2020)	(Lachish et al., 2020)
τ	ZR_to_reproZ	Energy allocated to reproduction	%	Proportion of energy reserve mass allocated to reproduction (offspring production and provisioning) by breeders	0.6	0.6	(Lachish et al., 2020)	(Lachish et al., 2020)
ϑ/γ	...		...	Intercept and exponent of function describing variance in growth of structural and energy reserve mass	5 / 0.05	5 / 0.05	(Lachish et al., 2020)	(Lachish et al., 2020)
υ	reproZ_to_offspringZS	Reserve allocation to offspring	%	Proportion of the allocated reproductive reserve that is converted to offspring structural mass	0.9	0.9	(Lachish et al., 2020)	(Lachish et al., 2020)
$\varepsilon_2/\varepsilon_3$	convert_coef_2/3	Energy conversion efficiency 2/3	%	Efficiency with which mother's energy reserves are converted to offspring structural/energy reserve mass	0.95 / 0.95	0.95 / 0.95	(Lachish et al., 2020)	(Lachish et al., 2020)
λ/ς	...		...	Intercept and exponent of function describing variance in development of structural and energy reserve mass in offspring	1.5 / 0.03	1.5 / 0.03	(Lachish et al., 2020)	(Lachish et al., 2020)
d	edible_parts	Edible meat ratio	%	Proportion of herbivore meat which is edible	0.68	...	(Wilmers et al., 2003, Metz et al., 2012)	...
h	elk_energy	Elk energy content	MJ Kg^{-1}	Energy content of elk meat	7.7	...	(Głowaciński and Profus, 1997)	...
Behavioural parameters								

ξ	coef_pred_mort	Hunting efficienty	$Month^{-1}$	Coefficient regulating the effect of predation on herbivore survival	0.00031	...	(Evans et al., 2006, Barber-Meyer et al., 2008)	...
l	scavenging	Scavenging rate	%	Proportion of herbivore meat which is scavenged by other predators	0.25	...	(Wilmers et al., 2003)	...
ϱ	wolf_aggr	Intraspecific aggression	$Month^{-1}$	Coefficient regulating the effect of predator intraspecific aggression	...	0.00022	...	(Cubaynes et al., 2014)

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6 General discussion

6.1 Recovering ecosystems and the emergence of species interactions

In this thesis, I investigated the patterns and ecological processes emerging from recovering ecosystems. In chapter 2, I explored the spatiotemporal trends of a recovering large mammal community in the Alps, and investigated the predator-prey interactions between wolves and their main prey. I showed that, since the early 20th century, the human population at higher altitudes decreased, forest cover doubled and, since 1970, all large mammal species significantly increased in abundance and distribution. This example demonstrates that, with the right environmental conditions and the support of conservation and environmental legislation, large mammal communities can bounce back from degraded states relatively quickly. I also showed that, in their first period of occurrence, wolf consumed a wide variety of wild and domestic prey species, although roe deer and red deer alone made up around 74% of their wild prey. Despite this, I could not detect any effect of wolf predation on prey populations. This should not come as a surprise. Because the ecosystem recovery process is still ongoing and all species are increasing, population trends are highly correlated with one another, resulting in an increasing predator population following equally expanding prey populations. Identifying and quantifying the negative effect of predation on a growing prey population in a highly unstable system can be difficult using count data alone (Peterson et al., 2003). Nonetheless, I expect these effects to gradually become more evident as populations approach stability, as shown in other systems (Passoni et al., 2022, Ripple et al., 2014).

In chapter 3 and appendix 1, I showed that, in human dominated Alpine environments, human infrastructure and disturbance can impact wildlife movement and space use (i.e. roe deer and bears) (Passoni et al., 2021, Corradini et al., 2021). In particular, in the third chapter, I investigated how roe deer movements were affected by roads and other landscape features, and evaluated potential differences in road avoidance among resident, migratory and dispersing animals. I found that road crossings were strongly avoided at all times and did not vary among movement patterns. As such, during dispersal and

migration, road avoidance by roe deer remained high and consistent with that expressed during home range movements (Passoni et al., 2021). Therefore, major roads and other infrastructure have the potential to represent a major constraint to wildlife movement and ecological connectivity in human-dominated landscapes (Beyer et al., 2016, Kuehn et al., 2007, Kramer-Schadt et al., 2004). In these regards, some species may be affected more than others, and human infrastructure may hamper the return of other large mammals such as the Eurasian lynx (Kramer-Schadt et al., 2004).

In the Alps, I could not detect any significant impact of wolves on deer populations (chapter 2). To study the impacts of apex predators on their prey and the landscape, I therefore focused on the Yellowstone ecosystem, where the large mammal community has been more stable and the wolf has been present for over 20 years (Smith et al., 2020). The majority of studies in Yellowstone and other terrestrial systems used correlational approaches through the analysis of time series data, similarly to the approach I used in chapter 2 (Peterson et al., 2014). The problem with these approaches is that it is very difficult to infer causality (Ford and Goheen, 2015, Peterson et al., 2014). To gain a deeper mechanistic understanding of predator-prey relationships, in chapter 4 I developed a bio-energetic model that simulated how energy flows across trophic levels, from the vegetation to the top predator, influencing population dynamics. I showed that wolf predation significantly reduced prey abundance and caused an increase in the prey's body size distribution by removing smaller and weaker individuals. In turn, lower herbivore numbers caused vegetation biomass to increase (Passoni et al., 2022). After the wolf reintroduction, the elk population also shifted from being food-limited to being predator-limited (Passoni et al., 2022).

In chapter 5, I used the model developed in chapter 4 to investigate the effects of ecological and evolutionary change on the grass-elk-wolf system in Yellowstone. This exercise demonstrated once again the complexity of this system and led to some unexpected and counter-intuitive results. For example, an evolutionary improvement in

wolf hunting efficiency on elk led to elk overconsumption and ultimately resulted in a decline in wolf numbers. I also found that variation in the snow regime affected the elk population by acting on the quantity of vegetation available for grazing. In turn, these changes in elk abundance affected the wolf population, ultimately leading to a feedback that tumbled back down to lower trophic levels in a non-linear way. Finally, I showed that, by regulating the system from the top down, wolves can act as buffers against fluctuations in resource availability (Wilmers and Getz, 2005).

6.2 Challenges and limitations in the study of large mammal communities and species interactions

Studying the ecological causes and consequences of fluctuations in large mammal communities has proven difficult for decades (Peterson et al., 2014, Ford and Goheen, 2015, Krebs et al., 1995, Sinclair and Krebs, 2002, Sinclair et al., 2007). The main challenge lies in the inherent complexity of terrestrial ecosystems and in the presence of a multitude of confounding factors (Peterson et al., 2003, Peterson et al., 2014). Because of the interconnected nature of ecosystem components, inferring causality from observed patterns is often problematic in the absence of appropriate controls and replication (Ford and Goheen, 2015). In chapter 2, I could not detect significant effects of wolf predation on prey populations. The main reason for this is that the wolf has only been present in Trentino for less than ten years, the ecosystem is not stable as it is recovering as a whole, and I only had animal count data derived from hunting statistics. While hunting statistics offer an important contribution to wildlife monitoring in Europe (Cretois et al., 2020), count data in non-stationary system are not sufficient to infer species interactions (Ford and Goheen, 2015).

For this reason, to study the impact of apex predators on the dynamics of their prey and on the wider ecosystem, I focused on Yellowstone, where a large amount of information are available about demography, vital rates, species interactions and energetics (chapter 4 and 5). My bioenergetic model enabled me to examine the mechanistic processes

underlying trophic interactions, and to isolate the effects of wolf predation on elk, disentangling them from other effects (e.g. elk predation by other species, elk competition with bison). The flip side of the coin was that, for the same reasons, my approach ignored several confounding factors that likely play an important role in shaping the Yellowstone ecosystem. As a result, some of my model predictions may not exactly match what we see in the field. For example, the increase in vegetation biomass predicted by my model following wolf reintroduction may be overestimated because I did not consider grazing by the growing bison population (Tallian et al., 2017, Beschta et al., 2020). In addition, in order to ease the interpretability of the results, my model assumed the elk population to be resident within the study area year round. In reality, elk migration patterns are complex, and a proportion of the population can migrate outside of the study area during the winter months (White et al., 2010). Despite this, this proportion is relatively small (White et al., 2010) and I do not expect that considering elk migration or bison numbers would significantly affect my findings beyond relatively small changes in population estimates.

I also did not explicitly consider wolf pack dynamics. In a typical pack, only the alpha female is able to breed, giving birth to an average of 5 pups (Stahler et al., 2013, Mech and Boitani, 2003). In my model, I made the simplifying assumption that each female can produce one pup. To check that this assumption was appropriate, I ensured that the reproductive rates predicted by my model across the whole population matched those observed in the field. Moreover, model parameterisation represented a major challenge. The model includes over 50 parameters which values were obtained from the published literature. The challenge primarily lied in the fact that some parameters were not readily available in the needed format and had to be estimated from available information. For example, the parameter regulating wolf intraspecific aggression was obtained by eyeballing a plot displaying wolf adult survival as a function of wolf density, published by Cubaynes et al. (2014). To ensure that the model was not excessively sensitive to parameter values, I therefore performed the sensitivity analysis in chapter 4. Nonetheless,

future work should aim at estimating parameters with a more statistical and data-driven approach.

In chapter 3 and in appendix 1, I showed that humans can also impact large mammal populations by affecting species movement and space use (Corradini et al., 2021, Passoni et al., 2021). People are likely to also influence the composition of large mammal communities through, for example, direct disturbance, hunting, and infrastructure development (Dorresteijn et al., 2015). However, the lack of information on species demography and cause-specific mortality in the Alps prevented me from quantifying these impacts. Future studies should therefore investigate the role of humans in affecting population dynamics and species interactions through the alteration of animal movement patterns.

6.3 Relevance and prospects for ecosystem research and landscape management beyond the Alps and Yellowstone

This thesis offers useful advances for investigating species interactions in complex terrestrial systems, for predicting the potential impacts of environmental change on ecosystems, and for informing future policy and landscape management decisions.

A key messages of chapter 2 is that ecosystem recovery can be relatively fast. In the Alps and in other European areas, they have been possible thanks to the availability of suitable habitat brought by socio-economic changes, favourable environmental legislation and conservation efforts (Chapron et al., 2014, Cimatti et al., 2021, Linnell et al., 2020). This should be an inspiration for the conservation of large mammal communities and should encourage ecological restorations globally (McAfee et al., 2019, Donadio et al., 2022). However, population expansions in human dominated landscapes are also likely to have socio-economic consequences (Linnell et al., 2020, Martin et al., 2020). In addition, changes in community composition can alter the nature of human-wildlife conflicts. For example, the recovery of wolves in central Italy caused increasing livestock depredation,

but reduced wild boar damages to crops in areas with high wolf densities (Davoli et al., 2022). To ensure the long term coexistence between human and wildlife, it is of paramount importance that monitoring programs are strengthened across administrative borders, and that prevention and compensation measures are put in place to minimise conflicts (Linnell et al., 2020).

In chapter 3, I showed that humans can significantly interfere with animal populations ny affecting their movement and space use. However, the consequences of these impacts on demography and population dynamics are poorly understood. Future studies should aim at integrating different types of data about population estimates, animal movement, species interactions, demography, environmental factors, and human activities. These data should be shared and integrated across international institutions, and used in collaborative projects following the example of recent initiatives such as Euromammals (Urbano and Cagnacci, 2021) and Movebank (Kranstauber et al., 2011). This will also be relevant globally for those regions where ecosystems are deteriorating (Ceballos and Ehrlich, 2002, Ripple et al., 2015, Ripple et al., 2014).

Chapter 4 and 5 highlighted the complex dynamics underpinning species interactions, and showed the unexpected ways in which they can react to ecological and evolutionary change. Yellowstone was the perfect system to develop my model and address these issues. Nonetheless, complex population dynamics may vary in different systems due to differences in climate, biological productivity, environmental conditions, community composition, species biology, life histories, and human impact (Borer et al., 2005, Heath et al., 2014). As such, more research is needed in more diverse ecosystems and biomes beyond the handful of well-studied systems such as Yellowstone, Isle Royale (USA), or the Serengeti (Tanzania) (Ford, 2015). Future research questions could also focus on the role of community composition (Sinclair et al., 2003), behavioural processes such as migration (Bauer and Hoye, 2014), diseases (Monk et al., 2022), and human disturbance (Hebblewhite et al., 2005).

6.4 Conclusions

Ecosystems worldwide are changing rapidly. While some are deteriorating due to humans, others are showing encouraging signs of recovery. Fluctuations in population abundance and distribution lead to the emergence of complex dynamics between species and their environment which are challenging to study. In this thesis, I addressed some of this complexity by analysing population dynamics, species interactions and animal movement patterns using different approaches. In the right conditions, ecosystems can rapidly recover from degraded states, however humans still have a significant negative impact on biodiversity globally. If we are to reverse the current biodiversity crisis, we must continue to improve our understanding of ecosystem dynamics, and examine the diverse ways in which humans can influence them.

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Appendix 1
Effects of cumulated outdoor activity on wildlife habitat use

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Effects of cumulated outdoor activity on wildlife habitat use

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ABSTRACT

Humans profoundly affect animal distributions by directly competing for space, not only transforming, but actively using their habitat. Anthropogenic disturbance is usually measured via structural proxies such as infrastructure and land use that overlook the impact of human presence, or functional disturbance. In this study, we propose a methodology unifying two paradigms, human mobility and animal movement, to fill this gap. We developed a novel spatially-explicit index of anthropic disturbance, the Cumulative Outdoor activity Index (COI), and validated it with ground truth observations derived from camera trapping ($r = +0.63$, $p < 0.001$). Building on previous work from Peters et al. (2015, Biol. Cons. 186, 123–133) on a Critically Endangered brown bear population in the Alps, we used Resource Selection Analysis to assess the influence of different forms of anthropogenic disturbance on the relative probability of habitat selection. The intensity of COI provided an effective measure of functional anthropogenic disturbance, and it outperformed all alternative and commonly-used proxies of structural disturbance in predicting bear habitat use. Our predictions suggest that brown bear shrinks its ecological niche as a consequence of intense human use of otherwise suitable habitat. These constraints may limit the potential range expansion of bears to establish a viable Alpine-Dinaric metapopulation. Conclusive conservation and future land use planning towards human-wildlife coexistence should account for the functional presence of humans on the landscape. The proposed COI could help determine where mitigation measures should be enforced.

1. Introduction

Human impact has become the most relevant determinant of animal species distribution and persistence, with the extirpation of populations and extinction of species occurring at an unprecedented rate (Ceballos et al., 2015). Alongside indirect modification of abiotic conditions (i.e., pollution, climate change) (Pecl et al., 2017), harvesting (Ripple et al., 2016), and the introduction of invasive species (Gallardo et al., 2016), humans affect animal distribution by directly competing for space. Several methods have been applied to assess the effect of habitat fragmentation, urbanisation and connectivity loss on animal population distribution, occurrence, and space use behaviour (Compton et al., 2007; Crooks et al., 2011; Panzacchi et al., 2016; Prokopenko et al., 2017). Recently, by using the Global Human Footprint Index, Tucker et al.

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(2018) showed that mammal species moved shorter distances under high human exposure. These analyses mainly utilized structural (i.e. passive) proxies of human competition for space based on infrastructure, land use, human accessibility (e.g., linear features such as roads, land- and waterways), and encroachment (e.g., population density, night-lights). However, direct competition for space should emerge by functional (i.e. active) utilisation of the aforementioned infrastructures, specifically human mobility.

Human mobility has exponentially grown in the Western world after WWII (Freund and Martin, 1993), and globally in the last 3 decades (Susilo et al., 2007). An entire branch of human geography is dedicated to the measurement and analysis of human mobility (Barbosa et al., 2018) and has been spurred by the global spread of personal tracking devices (e.g., navigation systems, mobile phones, GPS watches). Human mobility big data are analysed for many applications, from marketing (Wedel and Kannan, 2016), to traffic control (Herrera et al., 2010), and rescue services (Amin et al., 2012), which target human behaviour and space use. Only a few studies can be found that assess the impact of human mobility on wildlife, with the exception of a wide literature on traffic and roadkills (Trombulak and Frissell, 2000; Coffin, 2007; Dean et al., 2019). Beyond motorized mobility, human presence in wild habitats at the fine scale has been assessed using camera traps (Oberosler et al., 2017) or handheld tracking devices (Moen et al., 2012; Squires et al., 2019).

Recently, a diversity of mobile device software applications to track recreational outdoor activities, such as hiking, running or cycling, have become increasingly popular. In particular, the tools provided by Strava (San Francisco, CA, USA) are used worldwide to track user movements and access a crowdsourced Global Heatmap (Strava, 2018a). The Global Heatmap is a visualisation of the cumulative outdoor activity tracks recorded and marked as public by users, with monthly updates. Since its establishment as a tracking app, trajectories have been uploaded at an exponential rate, reaching over two billion records (Strava Press, 2018a), making the Global Heatmap the world's largest freely-viewable collection of GPS-tracked human outdoor activities of its kind. Strava data (Strava, 2018b) have been used for urban planning purposes or public health studies (Table S1.1). Despite this great potential, Strava-derived data have never been integrated into ecological studies.

In this work we introduce the Cumulative Outdoor activity Index (COI), a novel spatially-explicit index of anthropic disturbance based on the Strava heatmap, and used to assess active competition for space as opposed to structural indicators of anthropic disturbance (i.e., human settlements and linear features such as trails or roads). Building on previous work from Peters et al. (2015), we modelled habitat selection by a brown bear population reintroduced in the Eastern Italian Alps (Fig. 1) as a critical case study. Brown bears were reintroduced in Western Trentino in the early 2000, after the local population had been functionally extirpated, with the goal to reestablish a Alpine-Dinaric metapopulation (Duprè et al., 2000; Kaczensky et al., 2012). Despite the steady population increase in the first period after reintroduction, it did not substantially expand its range, nor was the goal to reestablish an Alpine-Dinaric metapopulation met. As a result, the Alpine brown bear population remained isolated and was listed as Critically Endangered due to the low number of mature individuals (< 50, Criteria D1; IUCN, 2001) (Huber, 2018). Conversely, human-bear conflict emerged (Groff et al., 2019) and several bears died from anthropogenic causes (Tenan et al., 2016). We hypothesise that direct competition for space with humans has limited the selection of preferred sites within the home ranges of bears, more so than environmental restrictions and structural proxies identified in previous studies (Duprè et al., 2000; Peters et al., 2015). Given that biological processes can be observed and interpreted differently at various scales (Ciarniello et al., 2007; Mateo Sanchez et al., 2014), we considered the relative effect of anthropogenic disturbance at the home range scale (i.e., third-order selection; Johnson, 1980).

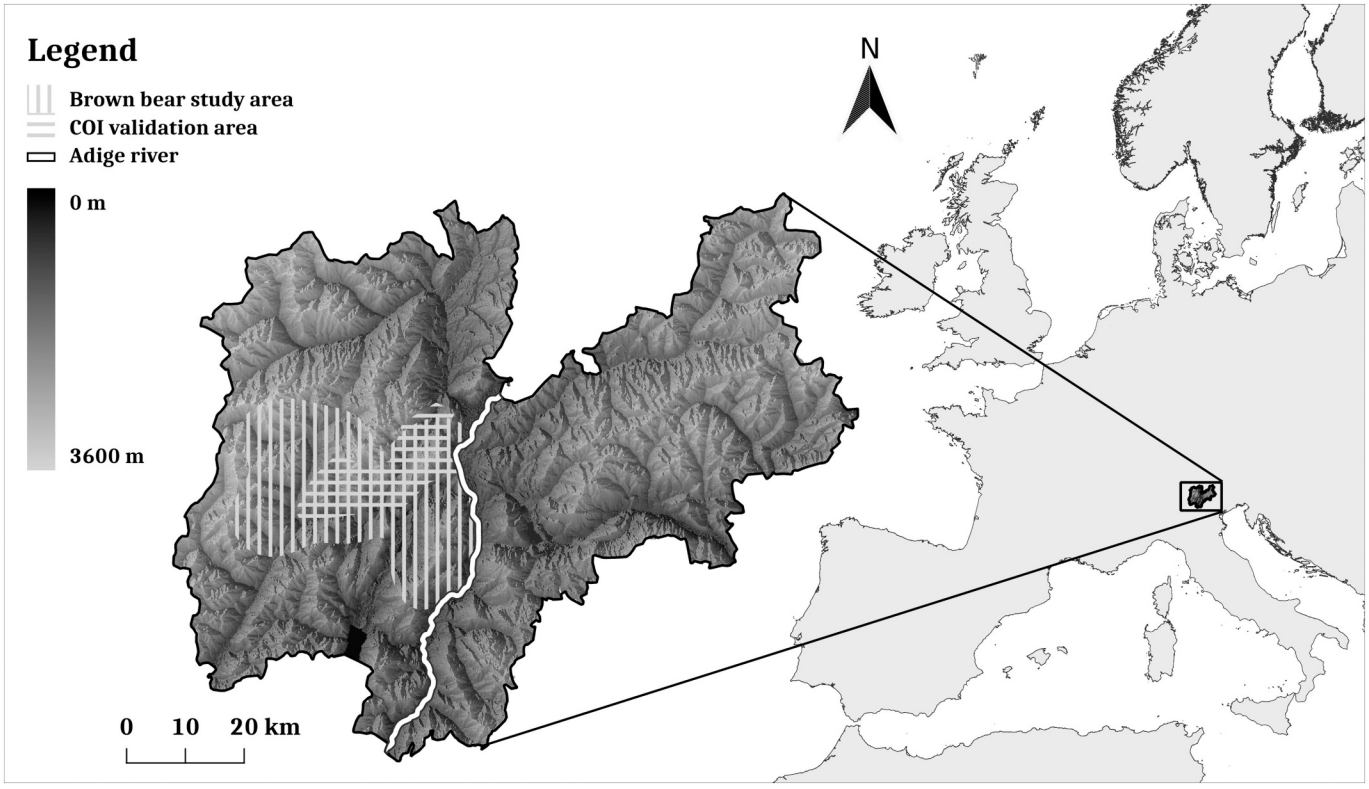


Fig. 1. Digital Terrain Model of the study area. The Adige river watershed divides the area in two sectors: Western and Eastern Trentino. The brown bear area (vertical hatching) is represented by a 95% Kernel Density Estimation of all GPS locations. The area of validation of the Cumulated Outdoor activity Index with ground truth from camera trap observations is indicated by horizontal hatching.

2. Materials and methods

2.1. Assessing functional anthropic disturbance: the Cumulative Outdoor activity Index

In order to assess the active competition for space between humans and wildlife, we developed an index measuring the effective use of structural linear features, or any portion of the habitat, through outdoor activities. For this purpose, we visualised and processed the Strava Global Heatmap (Strava, 2018a) at the highest resolution freely viewable online without registration (i.e. 20 m, or zoom level 13 OpenStreetMap Wiki contributors, 2019).

2.1.1. Strava Global Heatmap structure

The Strava Global Heatmap displays a colour gradient of outdoor activity tracks (rides, runs, water, and winter activities) recorded by users, where brighter tones (i.e., higher heat) represent an intense use, i.e. many overlapped activity tracks. Activity tracks are recorded as 'pixel paths' connecting consecutive GPS locations (Robb, 2017), so that the count of paths overlapping in each pixel corresponds to a raw 'heat' count. Such counts are then normalised to the bounded range (0,1) using a Cumulative Distribution Function (CDF), and weighted with respect to the neighbour context of intensity of use (i.e., the heat values are not comparable at a large distance, but are comparable in the proximity-about 50 km diameter at our zoom level, see below). For more technical details on how the Strava Global Heatmap is built, see Supporting information S2.

2.1.2. Deriving the Cumulative Outdoor activity Index

We derived the Cumulated Outdoor activity Index using the freely viewable Strava Global Heatmap. The approach requires few parameters and it is best achieved in a GIS environment. The extraction took place as follows: (i) an area of interest (Western portion of Trento Province, Fig. 1, and paragraph 'Study area') was displayed in the Strava Global Heatmap website (Strava, 2018a); (ii) we set the zoom level to 13 (OpenStreetMap Wiki contributors, 2019), the highest displayable without the need to register with a private account; (iii) we set the Heatmap Colour as "blue" (see below), the desired Activity Type to "All", the Heat Opacity to 100%, and we removed all background layers; (iv) we took a screenshot of the displayed area and saved it as a raster PNG image; (v) we georeferenced the raster image in a GIS environment using 6 control points. We used the WGS 84/Pseudo-Mercator Coordinate system (EPSG: 3857), as it was the projected coordinate system used to build the Global Heatmap (Robb, 2017); (vi) we repeated the procedure as many times as needed to cover the entire study area, and merged all the georeferenced raster layers; (vii) we manually removed the activities overlaying ski slopes and water bodies, which were not of interest for the purpose of this study, using subtracting masks obtained from local geographic layers (Autonomous Province of Trento, 2019); (viii) we displayed single pixels as a 256-element colour spectrum array (Robb, 2017), so that when the aggregated activities are shown as "blue", the array matches perfectly the Blue colour spectrum of an RGB colour model (0, 255); (ix) we rescaled the value so the index (COI) ranged from 0 to 1.

2.1.3. Validation of COI through ground truth observations

In order to validate the COI as an honest proxy of human use of wildlife habitats, we compared its values with human detections obtained via independent counts recorded on camera traps. In a subset of our study area (Fig. 1), an extensive, systematic camera trap survey ($n = 60$) was conducted (Oberosler et al., 2017; see Supporting information for details), recording both wildlife and human presence along forest roads and trails (30 sites in each category). Humans passages were recorded either as pedestrians/bikers or vehicles (cars, motorbikes, tractors, and trucks). We considered the former as ground truth observations, and excluded the latter as not matching the purpose of this study. We tested the validity of the COI by comparing it with ground truth observations, measured by the number of 'independent' human events per site, i.e., sequential detection events separated by an interval of 1 h. First, we extracted the value of COI associated with each camera trapping site. To account for spatial imprecision, we drew a 50 m radius buffer around each trapping location and extracted the 95th percentile COI value within that buffer. We finally tested the statistical dependence between COI values and number of human detection events using Spearman's rank correlation coefficient (Spearman's ρ).

2.2. A case study: assessing the effect of anthropogenic disturbance on a reintroduced brown bear population

We applied our proxy for functional human disturbance, measured as cumulated outdoor activity, to evaluate habitat selection and predict probability of space use in a reintroduced population in Trentino, Central-Eastern Italian Alps. We used the same third-order Resource Selection Analysis (RSA) as Peters et al. (2015).

2.2.1. Study area and brown bear population

The study was carried out in the Province of Trento, a 6.200 km^2 (Fig. 1) area characterized by rugged mountainous terrain (from 65 to 3769 m a.s.l.) and covered by forests and prairies according to the altitudinal succession. Valleys are largely human-dominated (87 inhabitants/km^2), with a developed network of roads and railways (density = 95 km/100 km^2). The vast infrastructural system of the Adige basin effectively constitutes a connectivity barrier for many animal species, dividing the study areas into two sectors (Fig. 1). Between 1999 and 2002, 10 adult bears from Slovenia were released in the Adamello Brenta Nature Park, Italy (PACOBACE, 2010). The newly established population colonized large parts of Western Trentino. In the study period, the brown bear population estimates (2012–2018) varied from 29 to 55, as a result of a positive, albeit variable, growth rate since 2002 (Groff et al., 2019). However, the population is still listed as Critically Endangered due to the small number of mature individuals (<50, Criteria D1; IUCN, 2001) (Huber, 2018). The brown bear is currently protected under European (Habitats Directive 92/43/EEC) and Italian Laws (L. 157/92), except for the removal of bears considered as dangerous (PACOBACE, 2010).

2.2.2. Movement data

We used the GPS trajectories of animals collared between 2011 and 2019 (8 females, 4 males; Vectronic GPS–GSM collars, Vectronic Aerospace GmbH, Berlin, Germany) for a total of 21 animal/year as part of monitoring activities undertaken by the Autonomous Province of Trento (PACOBACE, 2010; Supporting information for further information on trapping and handling). The number of surveyed individuals corresponded to about 25% of the estimated yearly average of bears in the study period (about 45 bears/year; Groff et al., 2019). The trajectories were limited to non-hibernating periods and regularized at a 6-hour fix rate using the functions in the R package adehabitatLT (Calenge, 2006), excluding a-priori data collected with less frequent schedules.

2.2.3. Environmental layers

First we extracted core environmental covariates based on Peters et al. (2015), using newer spatial layers with higher resolution and accuracy where possible, including topographic variables (altitude, slope), canopy cover, and land use (cultivated lands without orchards). We used the distribution of human settlements and linear infrastructure (trails, unpaved forest roads, and main paved roads) as proxies for structural human disturbance, as well as a combined composite layer (Table S5.1). Finally, we used the newly-derived COI as a proxy of *functional anthropogenic disturbance* (Table 1). All raster layers were resampled to a spatial resolution of 20 m pixel size (see Supporting information S5) and were rescaled by min-max normalization to a defined range of 0 and 1.

To create the structural disturbance layers, we generated a raster

Table 1
Set of a-priori hypothesis and corresponding models to assess anthropogenic disturbance on brown bear habitat selection at the third-order of selection (within home range). Each a-priori model contained a core set of environmental variables (topography, canopy cover, land use) as predictors and in addition one or more variable(s) for testing anthropogenic disturbance.

ID	Model	Expected disturbance	Covariates
MD1	Aggregate disturbance	Influence of human settlement proximity on selection	Core model + DHS
MD2	Generic linear disturbance	Influence of generic linear infrastructure proximity on selection	Core model + DRT
MD3	Specific linear disturbance	Influence of specific linear infrastructure proximity on selection	Core model + DMR + DFR + DHT
MD4	Density of structural disturbance	Influence of infrastructure network density on selection	Core model + dRTN
MD5	Density of functional disturbance	Influence of human activity density on selection	Core model + dCOI

proximity map based on Euclidean distance of each cell to the nearest infrastructure. We then transformed the maps to exponential decays in the form of

$$sd = 1 - e^{-\alpha d} \quad (1)$$

with sd = structural disturbance, α = 0.002 and d = distance (m) to a given linear feature (Nielsen et al., 2009). This transformation drastically reduced the effect of linear features beyond a few hundred meters, making large distances essentially irrelevant (e.g. >1500 m). The resulting values for sd range from 0 (at $d = 0$) to 1 (for large values of d). Using Eq. (1), structural disturbance layers were calculated for Distance from Human settlements (DHS), Distance from Main Roads (DMR), Distance from Forest Roads (DFR), Distance from Human Trail (DHT), and Distance from Roads and Trails (DRT) (Table S5.1). Furthermore, for both structural and functional disturbance, we computed derived spatial covariates expressing the 'density of disturbance' (cumulated disturbance per spatial unit). Specifically, we summed COI and the values of the raster layer combining all linear infrastructure features (roads and trails), both ranging (0,1), within a 11 × 11 pixel moving window (dCOI, dRTN: Table S5.1). This accounts for the spatial context around each pixel and potentially for spatial perception of disturbance by bears (~100 m; Moen et al., 2012). We performed a correlation analysis (Hinkle et al., 2003; Fig. S5.1) between all variables, thereafter building a priori models to evaluate the respective contribution of human disturbance metrics to bear habitat selection, with covariates within the same model having $|r| \leq 0.6$ (Peters et al., 2015).

2.2.4. Resource Selection Analysis

We fit a Resource Selection Function (RSF) to estimate the probability of use by bears of given resource units (Manly et al., 2002). We applied a used/available design and estimated selection within individual home ranges, i.e. third-order selection scale (Johnson, 1980). We considered GPS fixes as used locations and calculated individual bear's annual home range by Kernel Density Estimation (Worton, 1989) using the R package adehabitatHR (Calenge, 2006). We calculated 90% fixed kernel home ranges using h_{ref} as smoothing parameters (Worton, 1989). We sampled twice as many available than GPS-based used locations to have better parameter estimates while maintaining reasonable computational times (Northrup et al., 2013). We extracted all the environmental covariates described above at each of the used and available locations.

We evaluated how anthropogenic disturbance influences space use behaviour of brown bears in Western Trentino by testing five alternative hypotheses, corresponding to a set of a-priori RSF models ("Models of Disturbance", MD; Table 1). Specifically, a core environmental model with slope, TCD and CORINE land cover as predictors (to represent respectively topography, canopy cover and land use effects) was complemented by one or more variables describing different aspects of structural disturbance (DHS, DMR, DFR, DHT, DRT, dRTN; giving models MD1 to MD4, Table 1). Similarly, we complemented the core model with the index of functional anthropogenic disturbance dCOI (model MD5, Table 1). We thus fitted each RSF model using a Generalized Linear Mixed Model (GLMM) with a binomial error distribution via maximum likelihood, using a Laplace approximation. We included all the covariates as additive fixed terms and individuals as random intercept to account for autocorrelation (Gillies et al., 2006), as the purpose of this study was to quantify population-level variations as a response. We performed model selection using the Akaike Information Criterion (AIC).

We predicted the relative probability of use based on selection coefficients of the best fitting model for all pixels in the given area (Fig. 1) using the function *predict* in the R package raster (Hijmans, 2017). Afterwards, we tested the predictive capability of the RSF model via 10-fold cross-validation (Boyce et al., 2002), measuring the performance of the spatially explicit predictions with the set of random training and test subsets using Spearman's rank correlation coefficient. We managed, processed, and analysed the data entirely on the free and open-source software QGIS 3.4.4 (QGIS Development Team, 2019), GRASS 7.4 (GRASS Development Team, 2018), and R 3.4.3 (R Core Team, 2017) under Ubuntu 16.04.3 LTS (Canonical Ltd., London, United Kingdom). Results were reported in tables created with the R package stargazer (Hlavac, 2018).

3. Results

3.1. Validation of COI as an index of functional human disturbance

The camera trap survey yielded 1262 independent events of humans both as pedestrians/bikers over a period of 30 consecutive days across the 58 camera traps that functioned well. Of these events, 514 were recorded on trails and 748 on unpaved roads. The median count of people per camera was 21.76 (IQR 2.25 to 33.50, range 0 to 108), while the median of the extracted COI values per camera was 0.08 (IQR 0.00 to 0.39, range 0 to 0.71). We found a positive, statistically significant Pearson correlation between the Cumulated Outdoor activity Index and the number of human detection events ($r = +0.63$, $p < 0.001$; Fig. S6.1).

3.2. Anthropogenic disturbance effect on bear habitat selection

Within their home range (mean home range size = 259.51 km^2, with IQR 40.50 km^2 to 313.43 km^2; see Supporting information S7 for details), bears selected for steep areas and high canopy cover and strongly avoided areas with high density of functional disturbance according to the newly developed COI (most parsimonious model: MD5, Table 2; $b_{dCOI} = -5.048$, $p < 0.001$). Importantly, the effect size of dCOI was considerably larger than any other predictor in the candidate models. Still, most predictors indicating habitat disturbance showed a significant (and often strong) effect in less supported, alternative models. Bears avoided proximity to human settlements (MD1: $b_{DHS} = 2.584$, $p < 0.001$; ΔAIC = 97 with respect to the best model; Table 2) and areas with high density of structural disturbance, parameterized in the models by the density of roads and trails (dRTN) (MD4: $b_{dRTN} = -2.587$, $p < 0.001$; ΔAIC = 328 with respect to the best model; Table 2). When considering the influence of specific linear disturbance (MD3, ΔAIC = 362 with respect to the best model; Table 2), the bear showed quite different responses, avoiding areas in proximity to main roads ($b_{DMR} = 0.935$, $p < 0.001$), but selecting for human trails ($b_{DHT} = -0.198$, $p < 0.001$). Interestingly, bears did not seem to either avoid or select forest roads ($b_{DFR} = 0.057$, $p > 0.05$). The predictors of the core model maintained similar coefficients in all models (Table 2), with the exception of cultivated lands without orchards (AGR), not significant in some models and

Table 2
Output of the set of a-priori models to assess anthropogenic disturbance on brown bear habitat selection at the third-order of selection (see Table 1 for the set of models). The estimated coefficient values (b), the 90% Confidence Interval, and the *P*-values (*$p < 0.01$) are reported for each covariate. The models are sorted from left to right based on increasing AIC scores (reported at the bottom).

	Model					
	MD5	MD1	MD4	MD3	Core	MD2
Slp	2.054* (1.885, 2.223)	2.394* (2.228, 2.559)	2.316* (2.149, 2.482)	2.440* (2.273, 2.608)	2.626* (2.463, 2.789)	2.610* (2.443, 2.776)
TCD	0.831* (0.759, 0.903)	0.840* (0.768, 0.912)	0.894* (0.822, 0.966)	0.924* (0.843, 1.005)	0.813* (0.742, 0.884)	0.825* (0.749, 0.900)
AGR	0.237* (0.129, 0.345)	0.183* (0.075, 0.291)	0.028 (−0.077, 0.133)	0.225* (0.115, 0.336)	−0.078 (−0.181, 0.026)	−0.070 (−0.175, 0.035)
dCOI	−5.048* (−5.430, −4.667)					
DHS		2.584* (2.364, 2.803)				
dRTN			−2.587* (−2.856, −2.319)			
DHT				−0.198* (−0.286, −0.110)		
DFR				0.057 (−0.044, 0.158)		
DMR				0.935* (0.828, 1.042)		
DRT						0.530 (−0.608, 1.667)
Constant	−1.699* (−1.810, −1.589)	−4.438* (−4.671, −4.204)	−1.879* (−1.982, −1.776)	−2.771* (−2.925, −2.617)	−2.083* (−2.182, −1.985)	−2.099* (−2.203, −1.995)
Log likelihood	−13,122	−13,171	−13,286	−13,301	−13,421	−13,420
Akaike inf. crit.	26,257	26,354	26,585	26,619	26,852	26,853

Note.
* $p < 0.01$.

marginally significant in others (Table 2). However, the core model per se was the least supported by the data than all of Models of Disturbance but MD2 (Generic Linear Disturbance). The best fitting model (MD5; Table 2) led to robust spatial predictions of the relative probability of use by brown bear in the study area (Fig. 2; average Spearman's correlation coefficient for the 10-fold cross validation: $r = +0.98$, $p < 0.001$).

4. Discussion

We demonstrated the possibility of using human movement data, as extracted from Strava Global Heatmap, to quantify functional human disturbance for wildlife over the landscape. We have provided empirical evidence that the cumulated outdoor activity influenced the space use behaviour of a Critically Endangered brown bear population (Huber, 2018). Previously, large carnivores have been shown to fear the human 'super predator' (sensu Smith et al., 2017) so that the spatial pattern of human-derived risk perception (Gaynor et al., 2019) can influence large carnivore space use (Cristescu et al., 2013; Ladle et al., 2018) and foraging behaviour (Ordiz et al., 2017). A recent human-carnivore coexistence model (Chapron et al., 2014) put forward a community ecology framework where humans are considered as an integral part of the community (Chapron and López-Bao, 2016). Our results support and integrate such a view by demonstrating that carnivore space use is not accurately portrayed when using disturbance metrics that are based solely on structural proxies of human presence (infrastructure per se). We showed that the functional use of human structures and presence (i.e. human mobility) provides a more realistic way to address the interplay between carnivore and human use of space.

4.1. Functional disturbance outperforms structural variables to predict brown bear habitat selection in Trentino

Peters et al. (2015) showed that bears selected mountainous habitat with forest cover within the home range, and avoided urban areas and linear features linked to human recreation. In this work, we integrated those results by demonstrating that bears avoided specific forms of structural disturbance, as both density (MD4; Table 2) and proximity of man-made infrastructures (MD1, MD3; Table 2) negatively affected bear's space use. Human settlements (e.g. Nellemann et al., 2007; Martin et al., 2010; Peters et al., 2015) and paved roads (e.g. Gibeau et al., 2002; Whittington et al., 2019) had the strongest negative effect as single factors (MD1, MD3; Table 2), whereas trails were mildly attractive (MD3; Table 2), likely because they can be used by animals in moments of low human presence (i.e. night; Tattoni et al., 2015; Oberosler et al., 2017; Ladle et al., 2018). However, it was the cumulative use of landscape by people which drove bear habitat selection within their home ranges (MD5; Table 2). We referred to this effect as *functional anthropogenic disturbance*, i.e. actual human presence in the landscape. In a community ecology framework (Chapron and López-Bao, 2016), in which humans act as 'super predators' (Tenan et al., 2016; sensu Smith et al., 2017), large carnivores are expected to avoid areas with human-derived risk. If however disturbance occurs in an area of reintroduction, where a newly-established population is still at high risk of local extinction (i.e. Critically Endangered; IUCN, 2001), carnivores may not be able to avoid such risky areas. Bears in our study have demonstrated a good spatial perception of human-derived risk (sensu Gaynor et al., 2019) at the home range scale, scarcely tolerating and thus avoiding large volumes of outdoor non-motorized activities. On the other side, our findings indicate that brown bear is shrinking its ecological niche locally as a result of functional anthropogenic disturbance.

4.2. From functional disturbance to functional connectivity: landscape fragmentation from the wildlife's perspective

Metrics of structural disturbancemight not be enough to fully understand the implications of human pervasiveness on animal spatial behaviour. Not only do humans consume and change the environment, but they also compete directly for space and resources. As a result, their active presence over the landscape could trigger animals' avoidance for suitable spaces (e.g. niche partitioning; Squires et al., 2019). If species have low plasticity or space is limited, direct human competition for space may have serious implications for conservation. Our application of

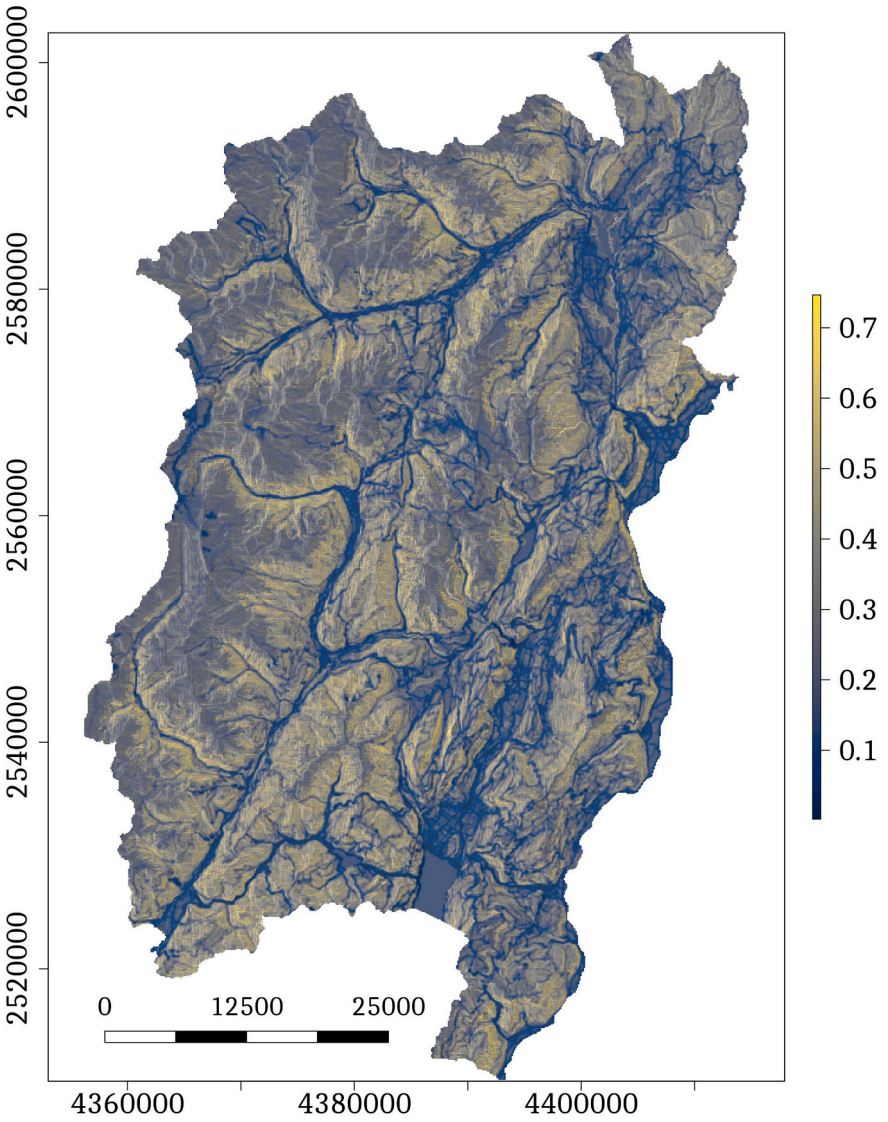


Fig. 2. Predicted relative probability of use by brown bears in Western Trentino, based on third-order (within home range) resource selection coefficients (MD5: slope, tree cover density, cultivated without orchards, density of Cumulative Outdoor activity Index). The map has a resolution of 20 m pixel size.

the community ecology-based human-carnivore coexistence model (Chapron et al., 2014; Chapron and López-Bao, 2016) by using a novel metric of functional anthropogenic disturbance indicates that conclusive conservation planning - especially in areas with high human density - should necessarily take into account human mobility. Future applications to other contexts and/or other sensitive large carnivore species (e.g. Amur Tiger, Kerley et al., 2002; Asiatic leopard, Ngoprasert et al., 2007; Iberian lynx, Fernández et al., 2003) could further generalise our findings and their implications for carnivore conservation in a world where human presence is increasingly pervasive, and the community ecology coexistence model will likely be the only viable alternative for their persistence (Chapron and López-Bao, 2016).

We were able to take and demonstrate these concepts into a concrete case of conservation concern. The predictive map (Fig. 2) showed the relative probability of brown bear habitat selection in the area of prime establishment of the reintroduced population. In general, when compared with Peters et al. (2015; Fig. 2a), areas of high probability of use seem to be more distributed, yet more fragmented. Indeed, most of the core habitat patches and linking corridors identified in Peters et al. (2015) correspond in our map to a matrix of suitable, but very small fragments. Our results seem to confirm a certain level of connectivity at the small scale, as previously predicted, but also an important contraction of large suitable areas when we accounted for functional human disturbance. Portions with greater probability of presence were found only in the Central-South Western and Central-Northern sectors of the area, and along some narrow secondary Alpine valleys, whereas extensive human activity and large infrastructures limited the suitability of the main valley bottoms, including Adige valley (Fig. 2).

In light of these findings, the establishment of a long-term, viable Alpine-Dinaric brown bear metapopulation (Kaczensky et al., 2012) may be difficult to achieve, as potential expansion eastwards is still severely limited by both structural and functional anthropogenic disturbance. As bears continue to search for space in this increasingly complex and expanding matrix of anthropogenic disturbance, long term population viability is at risk. To facilitate this expansion, specific measures could be adopted to spatially reduce functional anthropocentric disturbance. Temporal trail/road closure, as well as seasonal restriction of areas, have shown to improve habitat quality for wildlife while still providing opportunities for human use (Lamb et al., 2018, Whittington et al., 2019). On the other hand, measures such as the establishment of recreational areas, including protected areas, could have an opposite effect to that desired, as more people would be locally drawn to outdoor activities (e.g. Fredman et al., 2007). The availability of a reliable, yet easy-to-obtain metric of functional anthropogenic disturbance, like the index we

developed, is paramount for the effective planning of such mitigation measures.

Declaration of competing interest

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

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CRediT authorship contribution statement

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Luca Pedrotti: Conceptualization, Resources, Supervision, Funding acquisition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108818.

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