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Fostering large carnivore recoveries: Persian leopards and their prey in the Caucasus

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Benjamin Bleyhl

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Abstract

Large carnivore populations are threatened globally. This is worrisome because of their intrinsic value and their importance for ecosystems and humans. Finding ways to maintain and restore large carnivore populations is therefore a central goal for conservation. Interestingly, large carnivores are also returning to areas where they were extirpated before, which provides a great opportunity for conservation science to identify pathways to safeguard large carnivore populations. The overall goal of this thesis was to better understand the conditions that foster large carnivore recoveries. Gaining a better understanding of large carnivore recoveries is challenging though, because it requires working across broad areas, where data on environmental characteristics and prey species is often limited and inconsistent. Using the Persian leopard recovery in the Caucasus ecoregion as an example, the specific research questions of this thesis were: (1) Does the Caucasus ecoregion have suitable, safe, and connected habitat for Persian leopards and their prey? (2) What are effective management strategies to foster the recovery of Persian leopards in the Caucasus? Results revealed that suitable habitat for Persian leopards and their prey is widespread in the Caucasus. However, habitat patches are often not safe and conservation efforts are needed to mitigate threats and restore, protect, and connect populations of leopards and their prey. Reducing the persecution of leopards seems the most important strategy to foster leopard recovery in the Caucasus. For large carnivore recoveries in general, this thesis underpins the importance of human-carnivore conflict mitigation to prevent killings of carnivores, particularly in areas where populations are small. Further, this thesis underlines the need of improving connectivity among safe habitat patches and the value of international cooperation. Overall, this thesis provides insights into conditions that foster large carnivore recovery and outlines potential future pathways for a critically endangered apex predator in a global biodiversity hotspot.

Zusammenfassung

Weltweit sind viele Populationen großer Raubtiere bedroht. Das ist besorgniserregend aufgrund ihres intrinsischen Wertes, aber auch wegen ihrer Bedeutung für Ökosysteme und Menschen. Die Suche nach Wegen zur Erhaltung und Wiederherstellung von Populationen großer Raubtiere ist daher ein zentrales Naturschutzziel. Interessanterweise erholen sich einige Populationen dieser Tiere aber auch in einigen Regionen, in denen sie zuvor ausgerottet wurden. Dies bietet der Naturschutzwissenschaft eine hervorragende Möglichkeit, um potentielle Wege zum Schutz der Populationen großer Raubtiere zu identifizieren. Das Ziel dieser Arbeit war es, die Voraussetzungen besser zu verstehen, die eine solche Erholung von Raubtierpopulationen begünstigen. Dieses Verständnis zu erlangen erfordert jedoch einen großflächigen Ansatz und wird zudem erschwert durch wenig verfügbare und oft inkonsistente Daten zu Umwelteigenschaften und Beutetieren. Am Beispiel der sich erholenden Population des Persischen Leoparden im Kaukasus beantwortet diese Arbeit die folgenden Forschungsfragen: (1) Bietet die Ökoregion des Kaukasus einen geeigneten, sicheren und zusammenhängenden Lebensraum für Persische Leoparden und ihre Beutetiere? (2) Was sind wirksame Schutzstrategien, die eine Erholung der Population des Persischen Leoparden im Kaukasus begünstigen? Die Ergebnisse dieser Arbeit lassen den Schluss zu, dass für die Leoparden und ihre Beutetiere im Kaukasus großflächig geeigneter Lebensraum vorhanden ist. Trotz dieser günstigen Ausgangsposition für den Artenschutz zeigt diese Arbeit jedoch auch klar auf, dass Schutzmaßnahmen erforderlich sind, um direkte Bedrohungen abzumildern und Leoparden- und Beutetierpopulationen zu erhalten und aufzubauen, sowie untereinander zu vernetzen. Darüber hinaus zeigt diese Arbeit, dass die Wiederherstellung von Beutetierpopulationen die Lebensfähigkeit der Leopardenpopulation zwar steigert, dass aber der wichtigste Faktor für eine Erholung der Leopardenpopulation das Verhindern von Tötungen darstellt. Diese Arbeit verdeutlicht somit die wichtige Rolle von Konfliktminderung zwischen Menschen und Raubtieren, um die daraus resultierende Tötung von Raubtieren zu verhindern, insbesondere, wenn deren

Populationen klein sind. Darüber hinaus unterstreicht diese Dissertation die Notwendigkeit der Vernetzung sicherer Lebensräume und den Wert von internationaler Zusammenarbeit zur Förderung der Genesung von Populationen großer Raubtiere. Zusammengefasst liefert diese Arbeit Einblicke in Bedingungen, die die Genesung von Großraubtieren fördern, und umreißt mögliche zukünftige Wege eines vom Aussterben bedrohten Raubtiers in einem globalen Biodiversitäts-Hotspot.

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Chapter I:
Introduction

1 The importance of large carnivores

Humanity faces a biodiversity crisis, with species and wildlife populations being eradicated at unprecedented rates (Barnosky et al. 2011; Dirzo et al. 2014). In the past 40 years, vertebrate populations on Earth declined on average by 60% (WWF 2018) and one million species are facing extinction (IPBES 2019). Since the rise of human civilization, wild mammal biomass has decreased six-fold to the point where today it only makes up 4% of all mammalian biomass (60% is livestock, 36% humans (60% is livestock, 36% humans; Bar-On et al. 2018). An ever-growing human population uses more space to produce food and energy, leading to increasing competition for land (Chaplin-Kramer et al. 2015; Tilman et al. 2011). Nevertheless, people are linked to and depend on biodiversity, for its intrinsic and aesthetic value, but also instrumentally, for the many ecosystem services biodiversity provides (Cardinale et al. 2012). For both reasons, protecting wildlife habitat and allowing for healthy ecosystems is one of the greatest challenges for humanity (Lambin and Meyfroidt 2011; Phalan et al. 2011).

In many ecosystems, large carnivores are of exceptional importance for ecosystem functioning and health (Estes et al. 2011; Ripple et al. 2014). When large carnivores disappear, high herbivore densities can result in substantial pressure on vegetation, with negative effects on overall biodiversity (Beschta and Ripple 2009). For example, the reintroduction of wolves (*Canis lupus*) in Yellowstone National Park in the United States had profound knock-on effects on the entire ecosystem. Elk (*Cervus canadensis*) densities were reduced, with remaining populations pushed towards less predation-prone foraging grounds. This released trees from herbivory and thereby contributed to the recovery of riparian plant communities and stream morphology (Beschta and Ripple 2019; Ripple et al. 2015a). Furthermore, the presence of large carnivores can alter the behavior of mesocarnivores to the benefit of several other species in lower trophic levels (Suraci et al. 2016).

Large carnivores also provide substantial benefits to people (Ripple et al. 2014; Young et al. 2014). In West Africa, for example, leopards (*Panthera pardus*) and lions (*Panthera leo*) likely suppress high olive baboon (*Papio anubis*) densities that can pose a threat to the livelihood of local people due to losses of livestock and crops (Brashares et al. 2010). Leopards also prey on stray dogs in India, which reduces the number of people bitten by dogs and the risk of rabies transmission (Braczkowski et al. 2018). Further, large carnivores are used to promote ecotourism related to charismatic wildlife and thereby can contribute to the livelihoods of local villagers (Lindsey et al. 2005).

In terms of conservation planning, large carnivores are useful targets because they function as umbrella species, whose conservation benefits other wildlife because it requires the protection of large geographic areas (Branton and Richardson 2011). Protecting jaguar habitat across Central and South America, for example, can simultaneously protect a substantial amount of high-quality habitat for ~1,500 co-occurring mammal species (Thornton et al. 2016). Large carnivores are also important for conservation as a whole, because of their charismatic appearance as flagship species (Ray 2005). Many conservation organizations focus their publicity on large carnivores to attract funding or have them in their emblems (Clucas et al. 2008).

Finally, people often assign a high intrinsic value to large carnivores (Bruskotter et al. 2015; Lute et al. 2018). Many indigenous cultures in North America revere large carnivores such as Grizzly bears (Ursus arctos horribilis; Kellert et al. 1996). Tibetan monasteries protect snow leopards (*Panthera unica*) despite livestock depredation because of the cultural and religious value that people assign to snow leopards (Li et al. 2014). Additionally, large carnivores are frequently voted highest in polls as most charismatic species, underlining the specific intrinsic value that people connect with large carnivores (Albert et al. 2018; Macdonald et al. 2015).

2 Conservation status and protection of large carnivores

Despite their importance for ecosystems and people, many large carnivore species are threatened with extinction and are experiencing population declines (Ripple et al. 2014; Wolf and Ripple 2018). Large parts of Europe and North America lost all their large carnivore species in the 18th and 19th centuries (Figure I-1; Wolf and Ripple 2017). Where large carnivores prevailed, their populations and habitat are under high pressure today. In South America, jaguars (*Panthera onca*) lost more than 30% of their core habitat in only 30 years in the Gran Chaco region (Romero-Muñoz et al. 2019). Tigers (*Panthera tigris*) are on the brink of extinction throughout their range, and cheetahs (*Acinonyx jubatus*) and lions are predicted to face extinction if human pressures are not reduced (Bauer et al. 2015; Dinerstein et al. 2007; Durant et al. 2017).

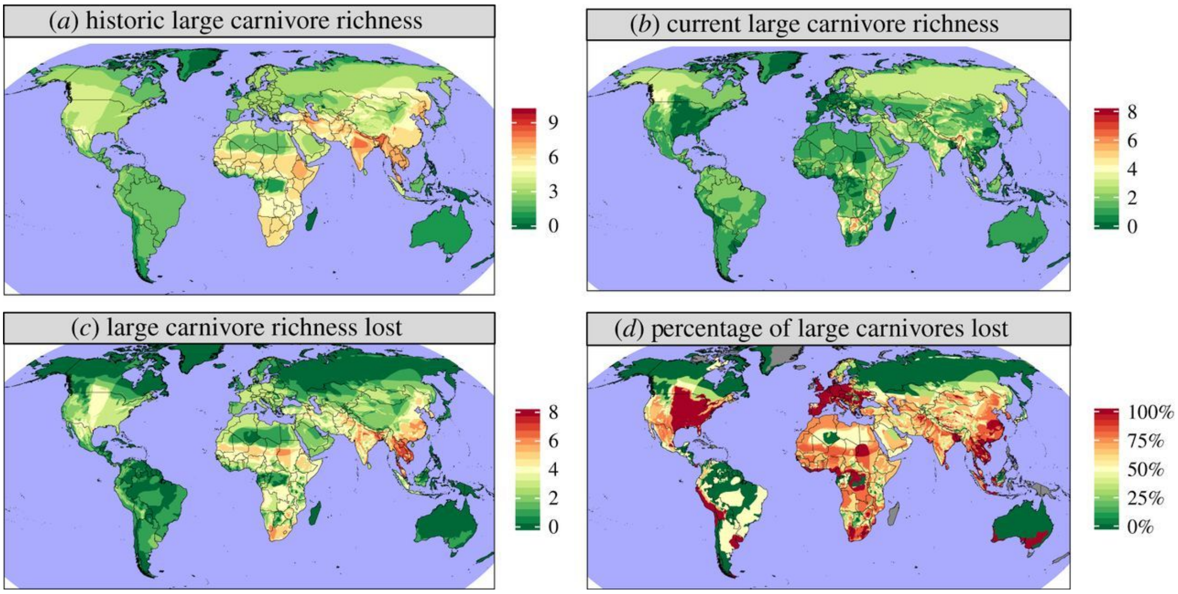

Figure I-1: Historic and current large carnivore species richness and species loss across the Earth. Source: (Wolf and Ripple 2017).

Primary threats for large carnivores are habitat loss, over-hunting and poaching, and prey depletion (Hunter 2011). In cases where habitat remains, human-caused mortality has often created so-called "empty forests", where structural and physical environmental conditions are still suitable, but high poaching pressure directly on large carnivores or indirectly on their prey does not allow for viable large carnivore populations (Datta et al. 2008; Mitchell et al. 2012). Given the disproportionate importance of large carnivores and the current threats they are facing, there is a strong need to safeguard their populations where they still exist and to restore them where they have been extirpated (Hoffmann et al. 2011; Ripple et al. 2014).

Restoring large carnivores is challenging. Large carnivores are particularly vulnerable to population declines, extirpation, and extinction (Ripple et al. 2014). This is because they require large tracts of suitable habitat, occur at low densities, and reproduce slowly (Purvis et al. 2001). Furthermore, human tolerance towards large carnivores is often low because they frequently come into conflict with people (e.g., due to livestock depredation or direct attacks on people; Bombieri et al. 2019; Dickman et al. 2014). While the international community might endorse policies targeted at integrating carnivores in rural landscapes, local communities might not want to share their landscapes with carnivores because of the real and perceived risks to human livelihood and safety (Carter and Linnell 2016). Finally, large carnivore restoration is complicated, because they are dependent on a stable prey base, which mostly consists of large herbivores that are themselves increasingly threatened (Ripple et al. 2015b; Wolf and Ripple 2016).

The challenge to large carnivore restoration is thus to find pathways that allow people, large carnivores, and their prey to coexist. Despite numerous obstacles, some encouraging examples are available. For instance, tigers successfully share the same landscapes with people in Nepal when prey species are abundant (Carter et al. 2012). Likewise, brown bears (*Ursus arctos*) and people peacefully coexist in the Romanian Carpathians, facilitated by functioning corridors and traditional livestock shepherding (Dorresteijn et al. 2014). Additionally, recent land-use trends in some regions may provide conservation opportunities. In Europe for example, farmland abandonment has become a dominant land-use change (MacDonald et al. 2000; Verburg et al. 2010) and has allowed for the population recovery and range expansion of some large carnivores (Chapron et al. 2014a; Enserink and Vogel 2006). Identifying such opportunities and understanding how they can be used to foster large carnivore recoveries with the goal of viable populations is important for guiding conservation efforts.

3 Large carnivore comeback

In contrast to the places where large carnivores are under increasingly high pressure, such as South-east Asia or South America (Di Minin et al. 2016b), parts of Europe and North America are experiencing a recovery and range-extension of their formerly extirpated large carnivore populations (Chapron et al. 2014a; Ripple et al. 2014). Wolves have returned to countries where they have been extirpated for centuries such as Germany (Reinhardt et al. 2019). Europe today hosts around 17,000 brown bears and 9,000 lynx (*Lynx lynx*) with stable or growing populations (Chapron et al. 2014a). In the US, wolves have recolonized territory from the north and cougars (*Puma concolor*) substantially extended their range towards the east (LaRue and Nielsen 2016; Linnell et al. 2001). Remarkably, most of these range expansions are happening naturally, only partly supported by reintroductions (Enserink and Vogel 2006). A range of underlying conditions might have facilitated these recoveries, but more research is needed to better understand how these conditions can be assessed across larger regions and how they might ultimately foster large carnivore recoveries.

First, recent recoveries of large carnivores in Europe and North America were likely facilitated through forest habitat that was structurally still available (i.e., “empty forests”, although sometimes hosting prey). This habitat was still available, because high hunting pressure through a government-supported policy to eradicate large carnivores together with prey depletion were primary reasons for the strong population declines in the 19th and early

20th century (Breitenmoser 1998; Linnell et al. 2001). Additionally, many western European countries and large parts of the US experienced a forest transition from declining to recurring forest cover in the 19th and early 20th century (Meyfroidt and Lambin 2011), which led to more potentially available forest habitat. Further, the quality of formerly degraded areas such as intensively grazed forests or rangelands improved through the abandonment of agricultural land and practices in many areas following industrialization (Breitenmoser 1998).

A second underlying condition of the large carnivore recovery is reduced hunting and poaching pressure on carnivores and their prey. In areas where large carnivores were once historically extirpated, human pressure on carnivores and their prey has now decreased. This is in large part thanks to a major change in policies towards more protection in the second half of the 20th century, alongside increased human tolerance, which led to substantially less human-induced mortality (Bruskotter et al. 2017; Linnell et al. 2001). Additionally, prey species of large carnivores either were already or became abundant in many forested areas, because of less livestock in the forest and because they were managed as game (Apollonio et al. 2010; Bradford and Hobbs 2008). Decreasing livestock numbers also potentially led to less retaliatory killings of large carnivores as a reaction to livestock depredation (Breitenmoser 1998). A reduction of both the direct killing of carnivores and the depletion of their prey through poaching and over-hunting, markedly improved the outlook for large carnivores (Breitenmoser 1998; Chapron et al. 2014a).

A third underlying factor of the large carnivore comeback is that large carnivore individuals from adjacent core population nuclei (i.e., source populations) were able to fill formerly inhabited areas. In the US, this was happening from wilderness areas in the west and north, including Canada (LaRue and Nielsen 2016; Linnell et al. 2001). In Europe, a recovery was fostered by larger populations in Eastern Europe (Enserink and Vogel 2006; Linnell et al. 2016). The presence of viable source populations together with functioning connectivity to suitable habitat patches is therefore an important condition to promote natural population recoveries (Chapron et al. 2008).

The recent recoveries of large carnivores are nevertheless not happening without conflict (Marshall et al. 2016). Rebounding wolf (*Canis lupus*) populations in the Yellowstone area caused high annual costs for livestock owners due to depredation on sheep (Muhly and Musiani 2009). People often do not want large carnivores regaining formerly lost areas, because they are afraid of attacks and want to protect their livestock (Carter and Linnell

2016). Illegal hunting on large carnivores is common in recovery areas (Gangaas et al. 2013; Liberg et al. 2012). In the Bohemian Forest in Europe, illegal hunting is most likely causing 15–20 % of lynx mortality, thereby preventing a further extension of the population and increasing the population extinction risk for the coming decades (Heurich et al. 2018). Studying large carnivore recoveries and better understanding recovery conditions can therefore help identifying conservation strategies and pathways to coexistence for large carnivores and people.

For a better understanding of large carnivore recoveries, conservation science is needed to identify remaining habitat with the least conflict potential for carnivores and prey, assess reasons for why the available habitat is not occupied (such as killings of large carnivores, depletion of their prey, and no connectivity to source populations or habitat patches), and finally, assess strategies that most effectively foster population recoveries of large carnivores and their prey.

4 Scaling-up conservation planning for large carnivores

Studying large carnivore populations often requires broad-scale (i.e., covering a large geographic area) modeling approaches, because of the extensive area requirements of large carnivores. The recent comeback of large carnivores in Europe for example, covers many countries, with core and frontier populations often separated by hundreds of kilometers (Scharf and Fernández 2018). Working at such broad scales is nevertheless challenging and has often been inhibited by a lack of consistent environmental and biotic data, and a scarcity of tools that are able to model range expansions with important processes such as demography and dispersal.

Consistent environmental data at fine spatial resolution are key to broad-scale ecological models (Pettorelli et al. 2014), but often such data are missing. An important way forward to provide consistent environmental data across large regions is the use of remote sensing (Pettorelli et al. 2014). Products that are derived from remote sensing such as land cover or phenology are increasingly used to describe habitat characteristics for large wildlife (Jetz et al. 2019). The Landsat sensors are of particular interest as they provide imagery at fine spatial resolution (30 m) with a global coverage and free accessibility (Turner et al. 2015; Wulder et al. 2012). Nevertheless, approaches that link fine-scale remote sensing derived products to potential drivers of large carnivore recoveries such as habitat availability and connectivity across a large area are rare.

In addition to a lack of consistent environmental data, modeling large carnivore recoveries requires consistent data on prey species (Guisan and Thuiller 2005; Hebblewhite et al. 2014). Yet, the habitat distribution of many large herbivores of conservation concern remains unclear. Further, integrating prey species into large carnivore habitat models is challenging, because the models might fail to capture the association between large carnivore habitat quality and prey availability, and characterize only an environmental characteristic such as forest distribution (Dormann et al. 2018). Given the importance of prey species for large carnivores, more studies are needed that (i) predict large herbivore habitat patterns, (ii) assess potential threats to their populations, and (iii) test how to integrate prey availability into large carnivore recovery assessments across broad areas.

Modeling large carnivore recoveries across extensive areas is also limited by a lack of tools that can incorporate important population dynamics such as demography and dispersal. Demography and dispersal are key processes to describe range expansions of populations (Bocedi et al. 2014; Kramer-Schadt et al. 2004). While species distribution models are a common tool to identify large carnivore extension sites, particularly across large areas or when data is scarce (Elith and Leathwick 2009; Scharf and Fernández 2018), they are limited in their ability to incorporate population dynamics (Franklin 2010).

Spatially-explicit metapopulation models provide a promising way forward, allowing for the prediction of potential carnivore metapopulation structures, include demography and dispersal, and allow for scenario testing when empirical data are scarce (Akçakaya et al. 2007). Such models simulate a metapopulation that consists of multiple connected sub-populations to ensure genetic exchange (Akçakaya et al. 2007), and have been widely used to assess future pathways and conservation or threat scenarios for large carnivores (e.g., Fordham et al. 2013; Tian et al. 2011). They are also particularly well suited to predict areas that carnivores will likely recolonize, which may help to prepare threat mitigation measures and inform conservation practitioners and local stakeholders (LaRue and Nielsen 2016; Maletzke et al. 2016).

Particularly for small populations, it might be beneficial to use spatially-explicit metapopulation models in an individual-based framework (Bocedi et al. 2014; Kramer-Schadt et al. 2004). Large carnivore populations at range margins are usually small, and individual demographic traits and stochasticity are likely important processes (Bocedi et al. 2014). Yet, individual-based modeling approaches are very data hungry and have therefore been predominantly applied in smaller areas and for species with good data availability (e.g., Heurich et al. 2018; Ovenden et al. 2019). Often though, areas with a high conservation priority such as biodiversity hotspots are data-scarce regions (Amano and Sutherland 2013), which limits our understanding and our possibilities of large carnivore recoveries. There is therefore a need to apply individual-based modeling approaches in data-scarce regions and across broad geographic areas. Biodiverse regions that lack detailed biodiversity data, such as the Caucasus, therefore provide great opportunities for testing such approaches.

5 The Caucasus

The Caucasus is located between the Black and the Caspian Seas and spans over Armenia, Azerbaijan, and Georgia, as well as parts of northern Iran, southern Russia, and eastern Turkey. It encompasses the mountain ranges of the Greater and Lesser Caucasus, the South Caucasus Depression separating the two mountain ranges, and the Talysh-Alborz Mountains (Figure I-2). The Caucasus is among the most biologically diverse and culturally rich regions globally (Krever et al. 2001a). It is listed as a global biodiversity hotspot with exceptional biodiversity due to its environmental heterogeneity and location at the crossroads of Europe, the Middle East, and Central Asia (Krever et al. 2001a; Mittermeier et al. 2004). Over 6,500 species of vascular plants occur in the Caucasus, of which at least 1,600 species are endemic, representing the highest level of endemism in the temperate zone (Krever et al. 2001a). Furthermore, the Caucasus is home to a diverse array of iconic large carnivores and herbivores such as the Persian leopard (*P. p. saxicolor*), brown bear, grey wolf, European lynx, striped hyena (*Hyaena hyaena*), European bison (*Bison bonasus*), Caucasian red deer (*Cervus elaphus maral*), bezoar goat (*Capra aegagrus*), Gmelin's mouflon (*Ovis orientalis*), wild boar (*Sus scrofa*), and Goitered gazelle (*Gazella subgutturosa*).

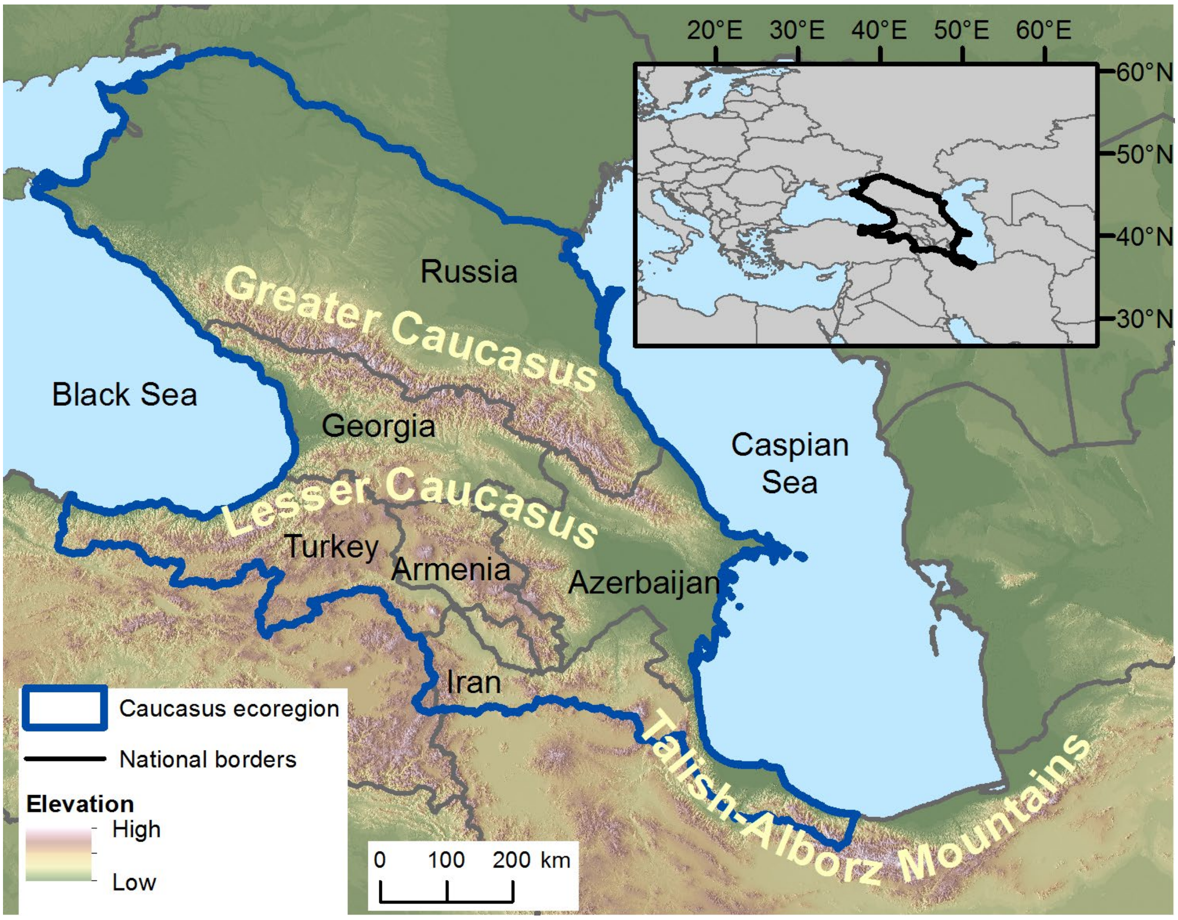

Figure I-2: The Caucasus ecoregion and the main mountain ranges.

Biodiversity in the Caucasus is threatened (Zazanashvili 2009). The construction of large-scale infrastructure for hydro-electric power plants, roads, and mining sites are destroying and fragmenting habitat throughout the region (Şekercioğlu et al. 2011; Zazanashvili et al. 2012). Widespread poaching and overgrazing as well as an increase in livestock numbers in parts of the Caucasus (e.g., in Azerbaijan) are further threatening wildlife, particularly large mammals (Williams et al. 2006a). As elsewhere in the former Soviet Union, weakening law enforcement, diminishing support for nature conservation, and economic hardships of the local population led to a poaching crisis in the 1980s and after the fall of the Iron Curtain (Bragina et al. 2015a; Zazanashvili et al. 2012). Moreover, the poaching crisis was amplified by the many armed conflicts that occurred within and between countries (Zazanashvili and Mallon 2009a). The widespread distribution of firearms among military personnel and local populations across the region led to high killing rates of wildlife (Khorozyan et al. 2009). In Iran and Turkey, which cover the southern border of the Caucasus, the situation for wildlife was not much better. The Iranian 1979 Revolution in conjunction with an increased pressure on land due to high population growth led to sharp declines in large mammal populations in

Iran (Farashi et al. 2017; Jowkar et al. 2016). Turkey's biodiversity is also under continuous high human pressure (Şekercioğlu et al. 2011).

At the same time, the conservation situation for wildlife in the Caucasus improved slightly in the last two decades. As a reaction to the multiple threats on wildlife, the Caucasus has seen a substantial expansion of its protected area network since the early 2000s (Montalvo Mancheno et al. 2016). Protective policies and an improved law enforcement further fostered a regional recovery of wildlife populations (e.g., a hunting ban in the autonomous republic of Nachikhivan, Azerbaijan, likely promoted an increase of large herbivore populations; Askerov et al. 2015). Additionally, limited access for people to military zones and abandonment of agricultural areas and settlements during political and armed conflicts might also have created refuge areas for wildlife (Baumann et al. 2014; Yin et al. 2018). Assessing where and how human induced pressure affects large mammal habitat at the ecoregional scale and identifying opportunities to make use of released pressures is therefore an important conservation goal for the region.

6 Persian leopards in the Caucasus

The Caucasus has lost most of its remaining apex predators. The Caspian tiger (*Panthera tigris virgata*) became extinct in the 1960s (in the Caucasus in the 1930s) due to a combination of habitat loss, prey depletion, and hunting (Faizolahi 2016). Asiatic lions (*Panthera leo persica*) were extirpated in Turkey in the late 19th century and in Iran in the early 20th century, and Asiatic cheetahs (*Acinonyx jubatus venaticus*) vanished from the Caucasian part of Iran in the 18th century (Farhadinia et al. 2017; Khosravifard and Niamir 2016; Mallon 2007; Nowell and Jackson 1996). Together with the brown bear and the Eurasian lynx, the Persian leopard is the last remaining large predator in the Caucasus ecoregion today.

The Persian leopard is an endangered leopard subspecies and occurred throughout the Caucasus ecoregion until at least the mid-18th century (Figure I-3; Jacobson et al. 2016; Kitchener et al. 2017). Their range and their population size declined rapidly, and already in the 1960s they were considered extirpated in most parts of the Caucasus (Zazanashvili et al. 2007). Today, Iran hosts the majority of Persian leopards (a likely optimistic estimate was 550–850 individuals for Iran, with a global population of 800–1,000) (Jacobson et al. 2016; Kiabi et al. 2002; Sanei et al. 2016). Within the Caucasus ecoregion, only some individuals survived in the border region of Armenia, Azerbaijan, and Iran (Khorozyan and Abramov

2007). Yet, leopards have slightly recovered in the last years (Breitenmoser et al. 2017). In the southern Caucasus, leopards have successfully reproduced, and further sightings throughout the region, including the northern Greater Caucasus, give hope that their population might grow (Askerov et al. 2018; Yarovenko and Zazanashvili 2016). A potential recovery of leopards in the Caucasus is strongly dependent on the Iranian source population (Breitenmoser et al. 2010). Nevertheless, without urgent management, this population itself is likely to decline and become functionally disconnected from the Caucasus (Breitenmoser et al. 2017; Moqanaki et al. 2013). Time and resources to foster a recovery are scarce, because the approximate population size is still very small (likely < 50 individuals) and poaching pressure remains high (Askerov et al. 2015; Lukarevsky et al. 2007a; Maharramova et al. 2018). Assessing what could most effectively foster the development of a viable Persian leopard metapopulation in the Caucasus is therefore of high conservation importance. Therefore, the Caucasus is a useful exemplary region to study the main factors that support large carnivore recoveries – habitat restoration, controlling human caused mortality, increased connectivity, and prey restoration.

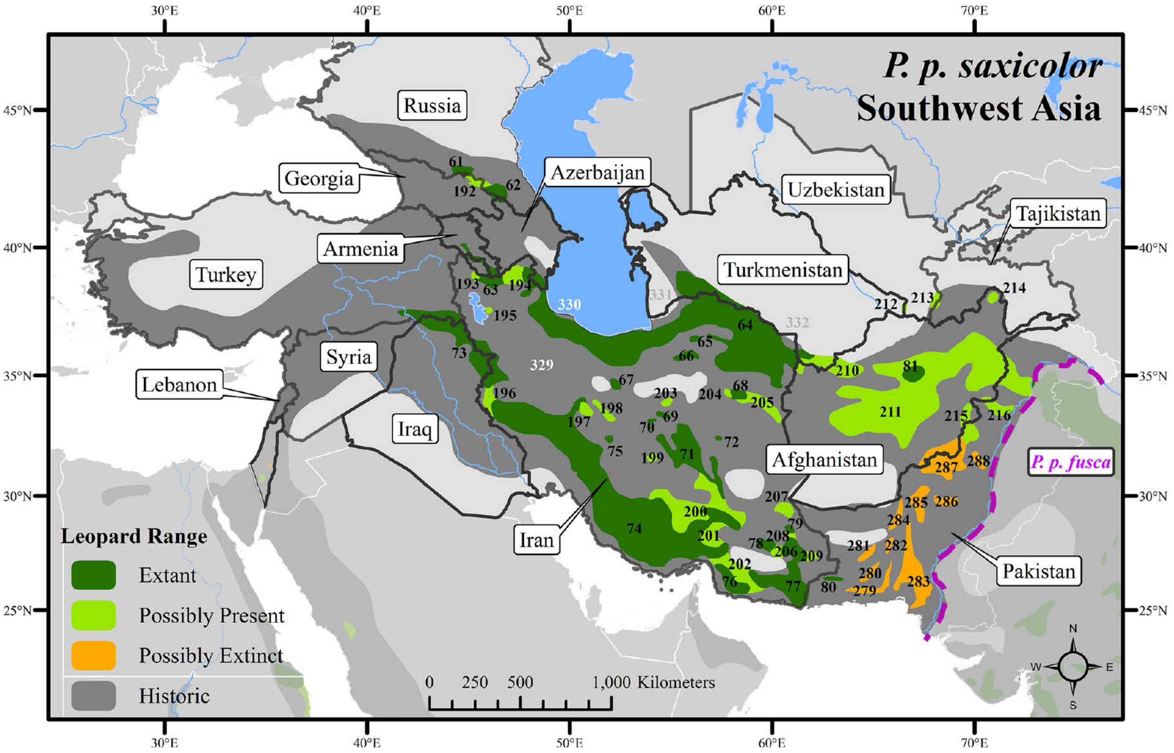

Figure I-3: Historic and extant distribution of Persian leopard in Southwest Asia. Source: (Jacobson et al. 2016).

7 Research questions and objectives

While some regions have undergone a carnivore comeback, in many other parts of the world, large carnivore populations are on the decline. Studying the conditions and barriers that lead to large carnivore population recovery is crucial to outline conservation strategies and pathways for large carnivores globally. Studying large carnivore recoveries is yet challenging, because it requires broad-scales assessments, the inclusion of large herbivore prey species, and overcoming data scarcity. Against this background, the overall goal of this thesis was to better understand the conditions that foster large carnivore recoveries. To achieve these goals, the thesis answered two main research questions.

Research question I: Does the Caucasus ecoregion have suitable, safe, and connected habitat for Persian leopards and their prey?

The Persian leopard has slightly extended its northern range from Iran and increased its populations in small numbers in the southern Caucasus. Yet, it is not well understood if this potential recovery was fostered by available habitat both for leopards and for their prey and what might prevent suitable habitat from being occupied. Consequently, the specific objectives to research question I were:

(1) To map habitat suitability and core habitat patches for Persian leopards and their prey species
(2) To identify corridors and assess the connectivity of the Caucasus at the landscape-scale and among habitat patches
(3) To identify potential threats for leopards and their prey

Research question II: What are effective management strategies to foster the recovery of Persian leopards in the Caucasus?

Fostering large carnivore recoveries is a central conservation goal, but it remains unclear how to most effectively achieve this goal. Conservation science is therefore needed to shed more light on the relative importance of conservation strategies. The Persian leopard recovery in the Caucasus provides a valuable exemplary region to assess this at a broad geographic scale and in a data scarce region. Consequently, the specific objectives to research question II were:

(4) To parameterize a spatially explicit metapopulation model for Persian leopards across the Caucasus and northern Iran

(5) To assess the relative importance of poaching control and prey restoration on leopard metapopulation viability

8 Structure of this thesis

This thesis is structured in three main chapters (Chapter II–IV) that each relate to one or more of the objectives outlined above, and four Appendix Chapters (Figure I-4). In Chapter II, I used a recently developed remote sensing approach to map land cover in the Caucasus consistently at 30-m spatial resolution based on Landsat 8 imagery. Further, I conducted an expert-survey among wildlife specialists to link the land cover to movement ability for large mammal species in the Caucasus and to identify and assess wildlife corridors and landscape connectivity across the region. In Chapter III, I assessed the habitat availability of Gmelin's mouflon, an important prey species of the Persian leopard. Further, I identified corridors among habitat patches and quantified the niche overlap of mouflons and domestic sheep to assess the potential for competition with livestock as a major conservation threat. In Chapter IV, I used an individual-based, spatially-explicit metapopulation model to identify the spatial distribution of a potential leopard metapopulation in the Caucasus and to simulate population dynamics under different conservation scenarios. Additionally, this chapter included the source population in northern Iran, and used the link between land cover and leopard connectivity derived in chapter I to further map connectivity among habitat patches and assess the potential range expansion of the leopard population towards the north. Finally, chapter V synthesizes the results derived in this dissertation and provides an overview on conservation implications and possible future research directions.

Chapters II–IV were written as stand-alone manuscripts that were either published in or submitted to international, peer-reviewed journals. Because these chapters serve as independent articles, there is a limited amount of recurring material. The chapters were published or submitted as follows:

Chapter II: **Bleyhl, B.**, Baumann, *M.* Griffiths, P., Heidelberg, A., Manvelyan, K., Radeloff, V.C., Zazanashvili, N., & Kuemmerle, T. (2017): "Assessing landscape connectivity for large mammals in the Caucasus using Landsat 8 seasonal image composites". *Remote Sensing of Environment* **193**, 193-203.

Chapter III: **Bleyhl, B.**, Arakelyan, M., Askerov, E., Bluhm, H., Gavashelishvili, A., Ghasabian, M., Ghoddousi, A., Heidelberg, A., Khorozyan, I., Malkhasyan, A., Manvelyan, K., Masoud, M., Moqanaki, E.M., Radeloff, V.C., Soofi, M., Weinberg, P., Zazanashvili, N. & Kuemmerle, T. (2019): "Assessing niche overlap between domestic and threatened wild sheep to identify conservation priority areas". *Diversity and Distributions* **25**, 129-141.

Chapter IV: **Bleyhl, B.**, Ghoddousi, A., Askerov, E., Bocedi, G., Breitenmoser, U., Manvelyan, K., Palmer, S., Shmunk, V., Soofi, M., Weinberg, P., Zazanashvili, N. & Kuemmerle, T. (under review): "Potential conservation pathways to the recovery of Persian leopards in the Caucasus". *Journal of Applied Ecology*.

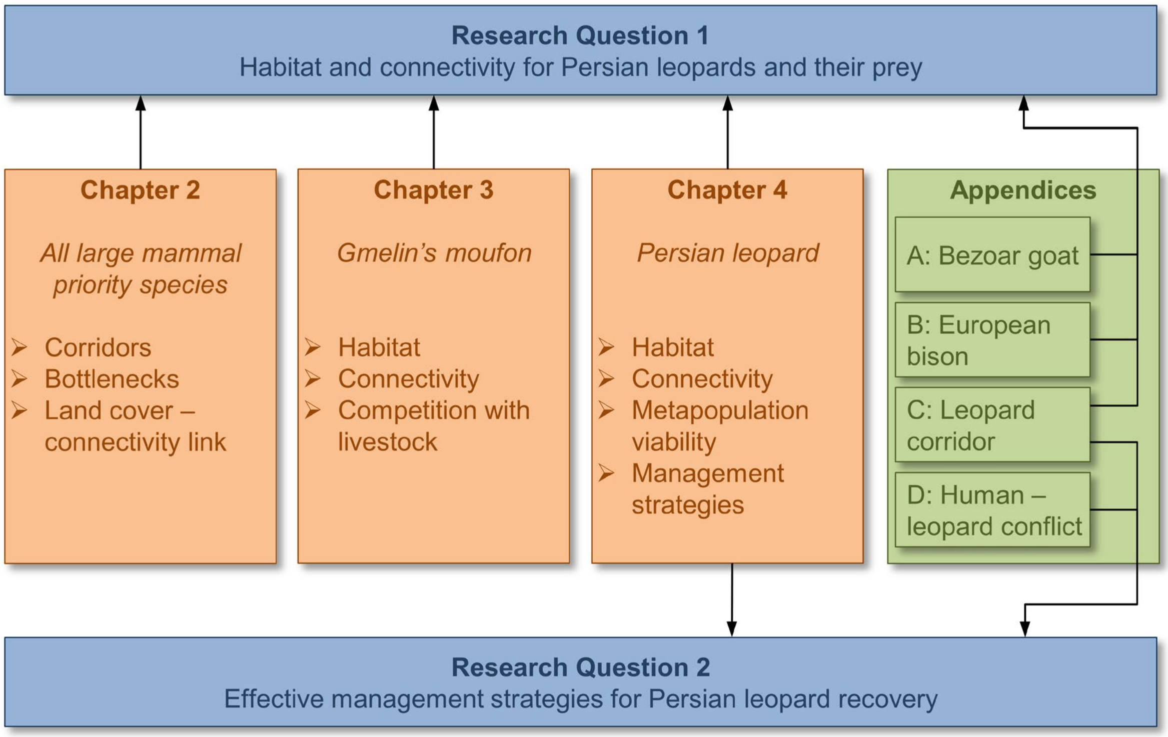

Figure I-4: Schematic overview on how the three core research chapters and the four Appendices contribute to answer the two research questions of this thesis.

Four additional appendix chapters (Appendix A–D) contribute to address the specific objectives. Appendix A and B extend the quantification and mapping of prey species habitat by further looking at bezoar goats (Appendix A) and European bison (Appendix B). Bezoar goats are one of the main prey species for leopards in the Caucasus (Mallon et al. 2007), and

Appendix A used an extensive occurrence dataset and a species distribution modeling approach to map suitable habitat. Further, it explored reasons for why suitable patches were sometimes not occupied. Appendix B used a similar approach to identify European bison habitat in the Caucasus, but extends the habitat analysis by distinguishing suitable and safe areas from areas with suitable environmental conditions but high human presence that could function as ecological traps. While European bison are not a main prey species for leopards, their calves are sometimes preyed on and they often co-occur with other prey species of leopards such as red deer and roe deer. Appendix C applied the link between land cover and connectivity that was derived in Chapter I to assess connectivity in more detail between two important protected areas for leopards in eastern Iran and extents this method with a bottom-up approach using interview data to identify areas with a high risk for human-leopard conflict. Further, this Appendix uses the land cover classification approach from Chapter I to extend the land cover map consistently towards eastern Iran (i.e., to cover the whole leopard range across the Caucasus and the Talysh-Alborz mountains), which was needed to have consistent land cover information in Chapter IV. Finally, Appendix D sheds more light on poaching as a main threat for the potential source population of leopards in Iran. This Appendix uses spatially explicit records of leopard mortality to relate poaching incidents to factors such as livestock depredation or attacks on humans. Appendices A–D were written or are prepared as stand-alone manuscripts for publication as follows:

Appendix A	Kuemmerle, T., Bluhm, H., Arakelyan, M., Askerov, E., **Bleyhl, B.**, Gavashelishvili, A., Ghasabian, M., Ghoddousi, A., Heidelberg, A., Malkhasyan, A., Manvelyan, K., Masoud, M., Soofi, M., Weinberg, P., & Zazanashvili, N. (submitted): “Identifying priority areas for restoring mountain ungulates in the Caucasus ecoregion”.
Appendix B	**Bleyhl, B.**, Sipko, T., Trepet, S., Bragina, E., Leitão, P.J., Radeloff, V.C., & Kuemmerle, T. (2015): Mapping seasonal European bison habitat in the Caucasus Mountains to identify potential reintroduction sites. *Biological Conservation*, **191**, 83–92.
Appendix C	Ghoddousi, A., **Bleyhl, B.**, Sichau, C., Ashayeri, D., Moghadas, P., Sepahvand, P., Hamidi, A.K., Soofi, M., & Kuemmerle, T. (under review): “Identifying safe corridors for Persian leopard by combining remote sensing, interview data, and conflict mapping”. *Landscape Ecology*.
Appendix D	Soofi, M., Qashqaei, A., Filla, M., Zeppenfeld, T., **Bleyhl, B.**, Ghoddousi, A., Hadipour, E., Pavey, C., Kiabi, B.H., Balkenhol, N., Khorozyan, I., & Waltert, M. (in prep.): “Human-leopard conflict outside protected areas is the main cause of leopard poaching in Iran”.

Chapter II:

Assessing landscape connectivity for large mammals in the Caucasus using Landsat 8 seasonal image composites

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Abstract

Land-use is transforming habitats across the globe, thereby threatening wildlife. Large mammals are especially affected because they require large tracts of intact habitat and functioning corridors between core habitat areas. Accurate land-cover data is critical to identify core habitat areas and corridors, and medium resolution sensors such as Landsat 8 provide opportunities to map land cover for conservation planning. Here, we used all available Landsat 8 imagery from launch through December 2014 to identify large mammal corridors and assess their quality across the Caucasus Mountains (>700,000 km²). Specifically, we tested the usefulness of seasonal image composites (spring, summer, fall, and winter) and a range of image metrics (e.g., mean and median reflectance across all clear observations) to map nine land-cover classes with a Random Forest classifier. Using image composites from all four seasons yielded markedly higher overall accuracy than using single-season composites (8% increase) and the inclusion of image metrics further improved the classification significantly. Our final land-cover map had an overall accuracy of 85%. Using our land-cover map, we parameterized connectivity models for three generic large mammal groups and identified wildlife corridors and bottlenecks within corridors with cost-distance modeling and circuit theory. Corridors were numerous (in total, 85, 131, and 132 corridors for our three mammal groups, respectively), but often had bottlenecks or high average cost along the least-cost path, indicating limited functioning. Our findings highlight the potential of Landsat 8 composites to support connectivity analyses across large areas, and thus to contribute to conservation planning, and serve as an early warning system for biodiversity loss in areas where on-the-ground monitoring is challenging, such as in the Caucasus.

1 Introduction

Increasing human domination of the Earth has resulted in rapid losses of natural ecosystems and wildlife habitat (Butchart et al. 2010). Functioning protected areas are therefore cornerstones for conservation (Bruner et al. 2001; Macdonald et al. 2012; Watson et al. 2014), particularly for large mammals which typically have large home ranges and are attractive to poachers (Di Marco et al. 2014; Ripple et al. 2014; Ripple et al. 2015b). Unfortunately, many protected areas are not large enough to support viable large mammal populations by themselves and wide-ranging species in particular depend on habitat outside protected areas (Di Minin et al. 2013; Ripple et al. 2015b). This means that the landscapes between protected areas are crucial to prevent extirpation within them and that detailed information on land cover and use around protected areas is important for large mammal conservation planning (Beier et al. 2008; DeFries et al. 2007; Jones et al. 2009).

One way to overcome some of the limitations of small protected areas is to provide connectivity between them, for example through corridors (Crooks and Sanjayan 2006; Haddad et al. 2003; Walker and Craighead 1997). Corridors are swaths of habitat that allow movement of species among habitat patches (Beier et al. 2008; Hilty et al. 2006). Increased movement and dispersal can support both genetic exchange and range shifts, thereby mitigating effects of habitat fragmentation (Brudvig et al. 2009; Gilbert-Norton et al. 2010). Thus, corridors are an important conservation management tool to increase connectivity (Crooks and Sanjayan 2006). Yet, delineating and assessing corridors at the regional or landscape scale is challenging because it requires consistent, fine-scale, and up-to date land-cover information for large areas (Sanderson et al. 2006; Wiens et al. 2009; Zeller et al. 2012).

Remote sensing plays a key role in acquiring broad-scale environmental information for conservation planning (Pettorelli et al. 2014), and particularly Landsat imagery provide a sufficiently high spatial and temporal resolution to map land cover in a way suitable for identifying corridors. Unfortunately though, using Landsat data over large areas is often difficult due to clouds, especially in mountainous regions (Wulder and Coops 2014). Landsat image compositing algorithms are a promising tool to overcome limitations of single-scene analyses, such as excessive cloud coverage, data gaps (e.g., through the failure of the scan-line corrector in Landsat 7 imagery), or limited data availability because of acquisition policies or archive consolidation issues. Landsat compositing algorithms mine all available imagery on a per-pixel basis to create a gap-free coverage of any user-defined study region at 30-m resolution (Griffiths et al. 2013b; Hansen et al. 2013; Potapov et al. 2011; Roy et al.

2010). Composites can be targeted to a user-defined time of the year (so-called seasonal best-pixel composites, BPC), that may be particularly well-suited to separate two or more land-cover classes (e.g., broadleaved and coniferous forest or cropland and grassland; Griffiths et al. 2013a; Roy et al. 2010). Seasonal composites are likely particularly beneficial for mapping land covers with strong phenology, because many land covers are similar in terms of their spectral properties in some times of the year, but differ in others (Baumann et al. 2012; Griffiths et al. 2013a). Existing studies so far have only tested the use of multi-seasonal data (e.g., Prishchepov et al. 2012; Senf et al. 2015) or used multi-seasonal composites (e.g., Baumann et al. 2016; Griffiths et al. 2013a), but no study tested the usefulness of seasonal composites to improve land-cover classifications empirically.

Using all available imagery allows to complement Landsat BPC with spectral metrics that summarize the full image record. For example, spectral metrics provide information on the average or variability of reflectance for a given time period (e.g., one year), or capture the minimum or maximum reflectance. Such metrics have the potential to greatly improve land-cover classifications (Griffiths et al. 2013b; Hermosilla et al. 2015; Potapov et al. 2011). Furthermore, metadata-layers can be produced containing, e.g., the number of available cloud-free observations, or zenith and azimuth of the observations used in the BPC. While Landsat composites have been applied to data from Landsat 4/5/7 (e.g., Griffiths et al. 2014; Potapov et al. 2015), increased image collection capacity may make Landsat 8 particularly suitable for large-area compositing (White et al. 2014; Wulder et al. 2015), but we are not aware of any prior studies that used Landsat 8 composites and metrics for land-cover classifications. Likewise, despite their advantages in addressing landscape-scale questions, image composites have not been derived to support large mammal conservation planning.

One region that harbors a range of iconic and wide-ranging large mammal species is the Caucasus at the intersection of Europe, the Middle East, and Central Asia. However, land-use pressure in the Caucasus is widespread and increasing, especially in the form of agriculture, infrastructural development, mining, logging, and tourism (Williams et al. 2006a). All this raises concern about land-use effects on wildlife populations and habitats, suggesting that conservation opportunities may be diminishing as land use intensifies (Zazanashvili et al. 2012). Many of the iconic large mammals such as the European bison, the Persian leopard, and the Eurasian lynx occurred in the past in large parts of the region, but their current distributions are only a fraction of where they occurred before, and they require conservation action (Bleyhl et al. 2015; Khorozyan and Abramov 2007; Zazanashvili et al. 2012). Moreover, conservation planning is challenging because the Caucasus extends into six countries (i.e., Russia, Georgia, Armenia, Azerbaijan, Turkey, and Iran), creating the necessity of ecoregion-wide coordination. Despite numerous local conservation initiatives and a trans-national conservation plan (Montalvo Mancheno et al. 2016; Williams et al. 2006a; Zazanashvili et al. 2012), implementing conservation planning at broad scales is currently severely hindered by a lack of up-to-date, fine-scale land-cover information that is consistent across political borders and that may be used to identify bottlenecks for connectivity (CORINE land cover, for example, only covers European Union countries). The Caucasus is therefore an interesting region to test new approaches for broad-scale land-cover mapping and how they could enable connectivity assessments.

Our goal here was to utilize the full Landsat 8 image data record from launch (April 2013) to December 2014 to assess landscape connectivity for large mammals across the entire Caucasus ecoregion. Specifically, our objectives were to (1) test the usefulness of seasonal Landsat 8 image composites and spectral metrics for land-cover classifications, (2) map land cover across the Caucasus, (3) identify potential wildlife corridors between protected areas in the Caucasus ecoregion, and (4) highlight potential bottlenecks that jeopardize landscape connectivity.

2 Methods

2.1 Study area

The Caucasus ecoregion is located between the Black and Caspian Seas. We analyzed the Caucasus ecoregion as defined by the World Wide Fund for Nature (WWF; Krever et al. 2001a) plus a buffer of 30 km to avoid edge effects (760,000 km^2; Koen et al. 2010). The ecoregion's topography includes mountain ranges (e.g., the Greater and Lesser Caucasus, the Talysh Mountains), plains, mainly north of the Greater Caucasus and in the eastern part, and upland areas in the central part. Climate varies from moist and temperate in the west (>2,000 mm precipitation) to arid in the east (<250 mm). Forests occur mainly in the mountains and are dominated by broadleaved tree species (mostly beech (*Fagus orientalis*), oak (*Quercus* spp.), hornbeam (*Carpinus betulus, Carpinus orientalis*.), and chestnut (*Castanea sativa*)). Additionally, the region harbors large steppe areas, as well as semi-deserts and arid woodlands in the drier eastern parts (Krever et al. 2001a).

Agricultural land use has a long history in the Caucasus and is economically important. During Soviet times, agriculture in Armenia, Azerbaijan, Georgia, and Russia was characterized by large state farms. Today, most farms in Armenia and Azerbaijan are private with small fields, whereas in Russia and Georgia parts remained as larger state or corporate farms (Giovarelli and Bledsoe 2001; Lerman et al. 2004). Main crops include cereals, vegetables, fruits, tea, and tobacco. In the mountainous regions, livestock production is also important (Williams et al. 2006a).

The Caucasus is a key region for the conservation of large mammals. In the late 1980s and ‘90s, large mammal populations declined dramatically, mostly due to poaching and weak law enforcement during the political and economic transition period from communism to market economies (Bragina et al. 2015a; Williams et al. 2006a; Zazanashvili et al. 2004). Since the early 2000s, wildlife populations have recovered somewhat, but land-use change, mining, and infrastructural development, as well as ongoing political and armed conflicts threaten this recovery. New protected areas have been established in the last two decades, yet it remains unknown how well protected areas are connected across the region.

2.2 Image compositing

To map the land cover of the Caucasus ecoregion, we applied pixel-based image compositing (Griffiths et al. 2013b). We acquired all available Landsat 8 images from April 12th 2013 to December 18th 2014 for the 63 Landsat footprints covering our study area. We downloaded terrain-corrected images with less than 70% cloud cover as the Landsat Surface Reflectance High Level Data Product (i.e., Landsat 8 bands 1–7), as well as the surface temperature product provided by the USGS (i.e., Landsat 8 bands 10 and 11; in total >2,000 images; downloaded in April 2015 from: https://espa.cr.usgs.gov). To create best pixel composites, we used a score-based weighing function to assess each pixel’s suitability for the final composite, based on acquisition year, day of year, distance to clouds, thermal brightness temperature, and distance to nadir for the Landsat 8 bands 2–7, resulting in 6-band composites consisting of pixels with the highest suitability score (Griffiths et al. 2013b). The thermal brightness temperature was incorporated into the scoring, assuming that warmer pixels are less likely to be affected by cloud remnants or haze. Distance to clouds was based on the cloud mask delivered with the Surface Reflectance Product (i.e., the C Language Function of Mask cloud mask or CFmask) and calculated as the number of pixels to the nearest cloud or cloud shadow. As our target year we chose 2014, meaning that pixels from that year were favored over pixels from 2013. To capture different phenological stages of the vegetation, we produced seasonal composites that were based on all available observations, but employed different target days of year for the compositing (i.e., pixels close to that day were favored). The output from the pixel-based compositing algorithm were four cloud-free image composites, one for spring, summer, fall, and winter (defined by the target days of year: 105 for spring, 196 for summer, 288 for fall, 349 for winter). Each of these composites consisted of 6 spectral bands (i.e., bands 2–7).

In addition to the best-observation composites, we calculated spectral metrics and metadata flags for each pixel. The spectral metrics were based on all clear observations and thereby contain information on phenology of the land-cover classes over time (e.g., band-wise mean and standard deviation surface reflectance; Griffiths et al. 2013b). In total, our compositing resulted in 93 bands (see Table SI II-1 for a full list).

2.3 Assessing the value of seasonal composites and spectral metrics for land-cover mapping

We classified nine land-cover classes: coniferous forest, broadleaved forest, mixed forest, rangeland (including pastures), cropland, built-up, sparse vegetation, permanent ice and snow, and water. We collected training data using current high-resolution GoogleEarth images in combination with the full set of Landsat 8 composites, digitized training data polygons, and randomly sampled 4,000 training points within these polygons for each class. Training data for built-up, permanent ice and snow, and water was gathered based on visual interpretation of the high-resolution imagery. For the forest classes, if available in GoogleEarth, we also considered imagery from leaf-off seasons. We identified cropland areas visually based on their rectangular shape, plowing patterns, homogeneous texture, and signs of bare soil in spring. Conversely, we labeled areas as rangeland that did not show rectangular shape, evidence of plowing, or bare soil in spring. The sparse vegetation class was defined as not showing a clear vegetation signal (i.e., spectral profile) in any of our Landsat composites or being clearly identified as bare areas due to the presence of rocks, cliffs, or sandy areas in the GoogleEarth high-resolution images. After initial classifications, we added additional training data iteratively in misclassified areas.

To test the usefulness of the seasonal composites, we ran initial classifications based on single-season composites and all possible combinations of seasonal composites. For the classification, we used a Random Forests classifier with 300 trees. Random Forests are a machine-learning algorithm (Breiman 2001) that consistently outperform parametric classifiers (Gislason et al. 2006) while being computationally efficient. To validate the land-cover maps of our alternative classification runs, we randomly collected 200 points per class (strata derived from the classification using all bands), and labeled them individually according to visual inspection of current (2010 or later) high-resolution GoogleEarth imagery in conjunction with our Landsat composites. We assessed composite-combinations using standard accuracy measures (Foody 2002).

To assess the extent to which the spectral metrics and metadata flags improved classification accuracy, we took the best-performing seasonal composite combination and compared it to classifications that included also the spectral metrics, the metadata flags, and both. We used the best-performing classification run to generate our final land-cover classification and applied a McNemar’s test to assess if differences in accuracy between the classifications were significant (De Leeuw et al. 2006).

For our final land-cover map, we applied a minimum mapping unit of 0.54 ha (six Landsat pixels) to remove salt-and-pepper structures that mainly represented misclassifications. Furthermore, we used point locations of settlements (i.e., one point location per settlement) from Open Street Map (OSM; http://www.openstreetmap.org/) to improve the discrimination between the built-up and sparse vegetation classes. We limited built-up to areas within one kilometer around the OSM settlement point layer and assigned built-up pixels outside this buffer to the sparse vegetation class. To validate our final land-cover map, we calculated overall accuracy and class-wise user’s and producer’s accuracy (Foody 2002). We accounted for potential sampling bias by adjusting error and area estimates according to the class distribution of our target classes (Olofsson et al. 2014).

2.4 Corridor mapping

To assess landscape connectivity and to map corridors, we converted our land-cover map into a resistance surface that measured how difficult it is for a given species to move through the landscape (Zeller et al. 2012; Ziółkowska et al. 2014). We selected all eleven large mammal species as focal species identified as priority species in the Caucasus Ecoregion Conservation Plan (Table II-1; Zazanashvili et al. 2012). A key step for assessing connectivity using resistance surfaces is setting resistance values for each land-cover class. This is best done using movement data for the species in question (Ziółkowska et al. 2016a) but such data are rarely available and expert-knowledge can be an alternative (Beier et al. 2008). To obtain expert knowledge, we conducted an email survey among 27 wildlife experts in the Caucasus, asking them to assign resistance values for each combination of focal species and land-cover class. Resistance values were allowed to range from 1 (most permeable) to 10 (least permeable). In total, we received 17 responses (return rate of 63%; Table II-1).

Our goal was to identify corridors that would benefit many species, which is why we assigned the eleven species to broad dispersal groups. To do so, we first calculated the median resistance values for each land-cover class and species based on all expert scorings. We used the median to account for variability in expert scorings (Figure SI II-1). Second, we used a k-means clustering analysis to derive three clusters of focal species that were similar in terms of their dispersal limitations. We discussed and further verified these dispersal groups in a workshop with Caucasian wildlife experts held in Berlin in February 2016. We labeled the dispersal groups according to movement traits of the species within each group as ‘forest-and-shrubland species’, ‘open-land species’, and ‘mountain species’. For each of these three groups, we delineated three resistance surfaces representing the minimum, median, and maximum resistances of the species in a specific group (Table II-2).

We further added barriers that are known to inhibit dispersal to our resistance maps. As partial barriers, we used motorway, trunk, and primary roads, as mapped in OSM, as well as elevations above 3,000 m (approximately the sub-nival zone in the Caucasus). We assigned resistance values of 100 to these barriers. We tested for sensitivity of this cost parameter by also testing cost values of 50, 200, and 500, revealing only slight changes in corridor distributions (Figure SI II-2). As total barriers (i.e., no-data in the connectivity analyses), we considered the land-cover classes built-up, permanent ice and snow, and water, as well as areas above 4,000 m (the limit of vascular plant growth; Zazanashvili et al. 2000). Although some of our species can occur above 3,000 m, and at least temporarily above 4,000 m, many areas in the Caucasus at this elevation do not foster vascular plant growth or are permanently glaciated, severely hindering the movement of most species. We therefore chose to use elevation barriers to avoid overestimating connectivity or deriving unrealistic corridors.

Table II-1: Species in the three dispersal groups.

Dispersal group	Species		Number of expert scorings
#1: Forest-and-shrubland group	Brown bear	*Ursus arctos*	16
	European bison	*Bison bonasus*	8
	Persian leopard	*Panthera pardus saxicolor*	15

	Eurasian Lynx	*Lynx lynx*	14
	Caucasian red deer	*Cervus elaphus maral*	13
#2: Open-land group	Goitered gazelle	*Gazella subgutturosa*	12
	Striped hyena	*Hyena hyena*	14
	Gmelin’s mouflon	*Ovis ammon gmelini*	13
#3: Mountain group	Bezoar goat	*Capra aegagrus*	14
	Caucasian chamois	*Rupicapra rupicapra caucasica*	10
	Caucasian tur	*Capra cylindricornis* & *Capra caucasica* *	11

Table II-2: Resistance values for the land-cover classes used to parameterize the cost surface for the connectivity analysis. Values refer to the minimum, median, and maximum resistance values per focal species cluster according to our wildlife expert survey.

		Resistance values*					
		Coniferous forest	Broadleaved forest	Mixed forest	Rangeland	Cropland	Sparse Vegetation
Forest-and-shrubland	min	1	1	1	2	5	5
	median	1	1	1	3	7	7
	max	3	2	2	4	9	8
Open-land	min	7	7	7	1	4	2
	median	7	7	8	1	5	3
	max	9	10	10	2	5	3
Mountain	min	4	4	3	2	7	2
	median	4	5	4	4	8	3
	max	6	6	6	5	8	7

* The land-cover classes built-up, permanent ice and snow, and water formed total barriers (i.e., no movement through these covers was allowed in our analysis).

We mapped corridors between Caucasian protected areas of IUCN category I and II based on the World Database on Protected Areas (IUCN and UNEP-WCMC 2019) and WWF’s Caucasus Programme Office database (wwfcaucasus.net; Figure SI II-3). We focused on only these IUCN categories because protected areas with lower protection status rarely contained any of the species we focused on in our study. Protected areas (PAs) bordering each other were considered as one PA. Disjunct patches of the same PAs were modeled as one patch if patches were <10 km apart and as separate patches otherwise (resulting in 57 PAs in total). In order to exclude PAs without forest cover for the forest-and-shrubland group, we only considered PAs with forest cover >10% for that group (resulting in 41 PAs in total; we chose 10% as our threshold because some species from that group such as Eurasian lynx or brown bear occur in areas with 11% forest cover). We calculated cumulative resistances for the closest protected area pairs using the Linkage Mapper Toolkit (McRae and Kavanagh 2011), resulting in least-cost paths (i.e., the single pixel-wide path between each PA pair with the lowest cumulative resistance) and corridors around them (i.e., those areas around least-cost paths with a cumulative resistance below a certain threshold; Ziółkowska et al. 2016b). For each path, we calculated the ratios of (a) the cost-weighted distance divided by the Euclidean distance and (b) the cost-weighted distance divided by the least-cost path distance as indicators of corridor quality (Dutta et al. 2015). High values of these indices indicate low corridor quality. To identify bottlenecks within our corridors, we applied circuit theory using the Pinchpoint Mapper tool within the Linkage Mapper Toolkit (McRae et al. 2008). This tool uses Circuitscape to model connectivity based on concepts from electric circuits where landscapes consist of nodes, resistors between them, and a current density flowing from node to node (McRae et al. 2013). This current density can be interpreted as the likelihood of a species passing through a cell, with high current indicating a lack of alternative routes and therefore a bottleneck in a corridor (McRae 2012). Although such bottlenecks can be identified well in current density maps, there is at the moment no systematic way to validate bottlenecks (Pelletier et al. 2014). We defined bottlenecks here as areas with current density of the mean plus two standard deviations. Because the connectivity modeling is computationally very demanding, and initial results for smaller sub-regions at coarser resolutions were qualitatively similar to fine resolutions, we ran all connectivity models at a 300-m resolution.

3 Results

3.1 Comparison among seasonal composites and spectral metrics

We generated four seasonal best-pixel composites (spring, summer, fall, and winter 2014) at 30-m resolution over a heterogeneous area of 760,000 km^2. Although using more than 2,000 images with at least 10 images per footprint, there were a few areas without any clear-sky observation (0.17% of all pixels). These areas were excluded from further analyses.

Our comparison of different composite combinations revealed highest overall accuracy (OA; 69.9%) when using all four seasonal composites together (Figure II-1). The spring and the summer composite resulted in the highest accuracies when using only one season for the classification (62.0% and 62.3%, respectively). When we used two seasons, combinations that included the summer and fall composite performed best (Figure II-1), and the McNemar's tests showed that these differences to other two-season combinations were significant ($p < 0.05$) except to the spring-fall combination. When using three seasons, the spring-summer-fall combination outperformed other combinations ($p < 0.05$). Despite having the highest overall accuracy, using all four seasons together was not significantly better than using a three-season combination that included the summer and fall composites ($p > 0.05$; see Tables SI-2–4 for full McNemar's test results).

To assess the value of spectral metrics and metadata layers for our land-cover classification, we added them to the four season composites. Adding the spectral metrics improved accuracy significantly (Figure II-1; OA from 69.9% to 76.4%; $p < 0.001$). Accuracy of the land-cover maps based on all seasons plus the metadata was slightly, but not significantly, higher than for the four seasons by themselves. Similarly, adding the metadata layers to the four seasons plus spectral metrics led to a higher accuracy but not to a significant change. Because the land-cover map based on the four seasons plus spectral metrics and metadata layers yielded the highest overall accuracy (77.5%), we chose this combination as our final land-cover map.

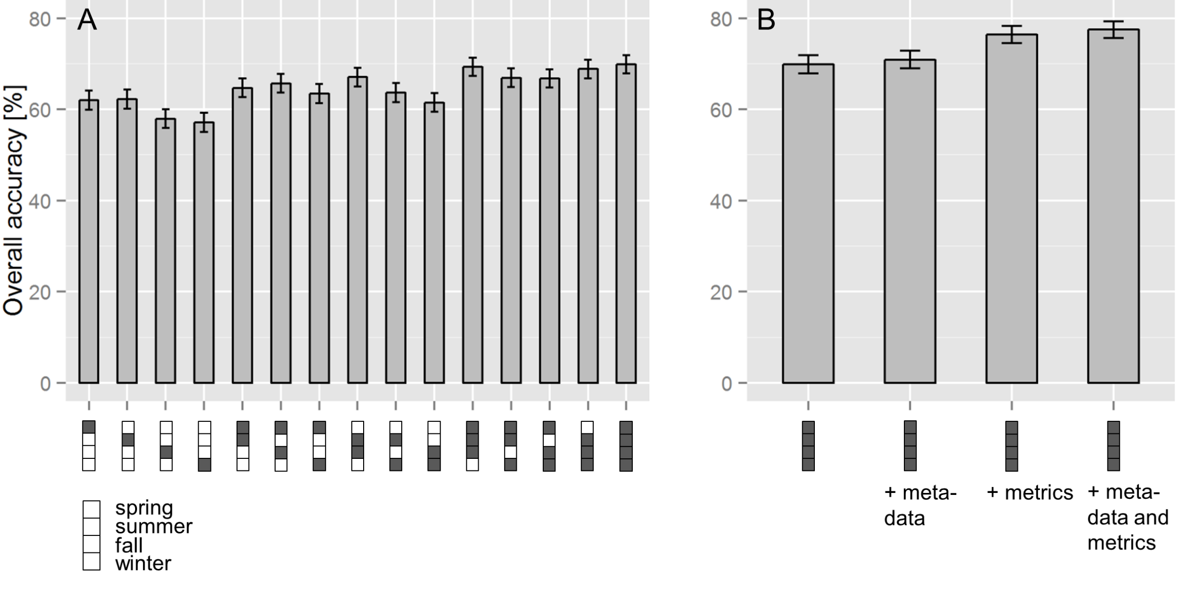

Figure II-1: Overall accuracies of different composite combination: (A) across all combinations and (B) comparing the four seasons plus metadata and metrics. Filled boxes indicate the seasonal composites that were used. Error bars show the 95% confidence interval.

3.2 Land cover mapping

After applying our post-classification steps (minimum mapping unit and built-up area correction), the overall accuracy of this map was 84.8% (Table II-3). Single-class user's accuracy ranged from 71.8% to 100% (for the sparse vegetation and the water class, respectively) and producer's accuracy from 20.5% to 97.4% (for the built-up and the water class, respectively). Our land-cover map highlighted extensive cropland areas, mainly in Russia, north of the Greater Caucasus (Figure II-2). Rangeland was the most widespread class (300,000 km² or 39% of the study area; numbers are rounded, see Table II-3 for exact numbers) followed by cropland (190,000 km²; 25%), water (100,000 km²; 13%), and broadleaved forest (90,000 km²; 12%; Table II-3). All three forest classes together covered an area of 120,000 km². Forest was mainly found in mountainous regions (72% of forest >500 m) and primarily consisted of broadleaved trees (74% of all forest). Coniferous forest was mainly found above 1,500 m. About 8% of the forest in the ecoregion was protected. In general, protected areas were mainly composed of forest and rangeland (each class covered 39% of the total protected land). Croplands were concentrated at lower elevations (72% <500 m).

Table II-3: Overall and class-wise accuracies, adjusted for potential sampling bias.

Overall accuracy [%]	Land-cover classes	Class-wise accuracies [%]		Adjusted area estimation [km²]
		Producer's accuracy	User's accuracy	
84.8	Coniferous forest	60.2	83.8	15,574
	Broadleaved forest	84.6	79.8	89,504
	Mixed forest	56.9	76.2	16,023
	Rangeland	84.1	87.6	300,751
	Cropland	90.4	78.2	192,782
	Built-up	20.5	91.3	13,254
	Sparse vegetation	66.3	71.8	26,036
	Ice & permanent snow	92.0	89.0	2,104
	Water	97.4	100.0	101,133

3.3 Wildlife corridors

Using the three large mammal dispersal groups that emerged from our expert survey and subsequent clustering, we generated three resistance surfaces for each dispersal group, corresponding to the minimum, median, and maximum resistance values per group. These maps did not result in substantially different corridors and we here therefore only show results for the median value (see Figure SI II-4 for the other values). In total, we identified 348 potential wildlife corridors linking protected areas (Figure II-3). Euclidean distances among protected areas ranged from 0.6 to 333 km (mean: 60 km, standard deviation: 52 km). Corridor length also varied substantially (e.g., least-cost path length ranging from 0.9 to 410 km; Table II-4). Corridors for the forest-and-shrubland and for the open-land dispersal groups were on average shorter than for the mountain group (73 km and 67 km mean least cost path length, respectively, versus 78 km for the mountain group) and of better quality. Quality was on average highest for the forest-and-shrubland group (Table II-4). While low-quality corridors for the forest-and-shrubland group were mainly located in the eastern part of the study region, there was no such pattern for the other groups (Figure II-4).

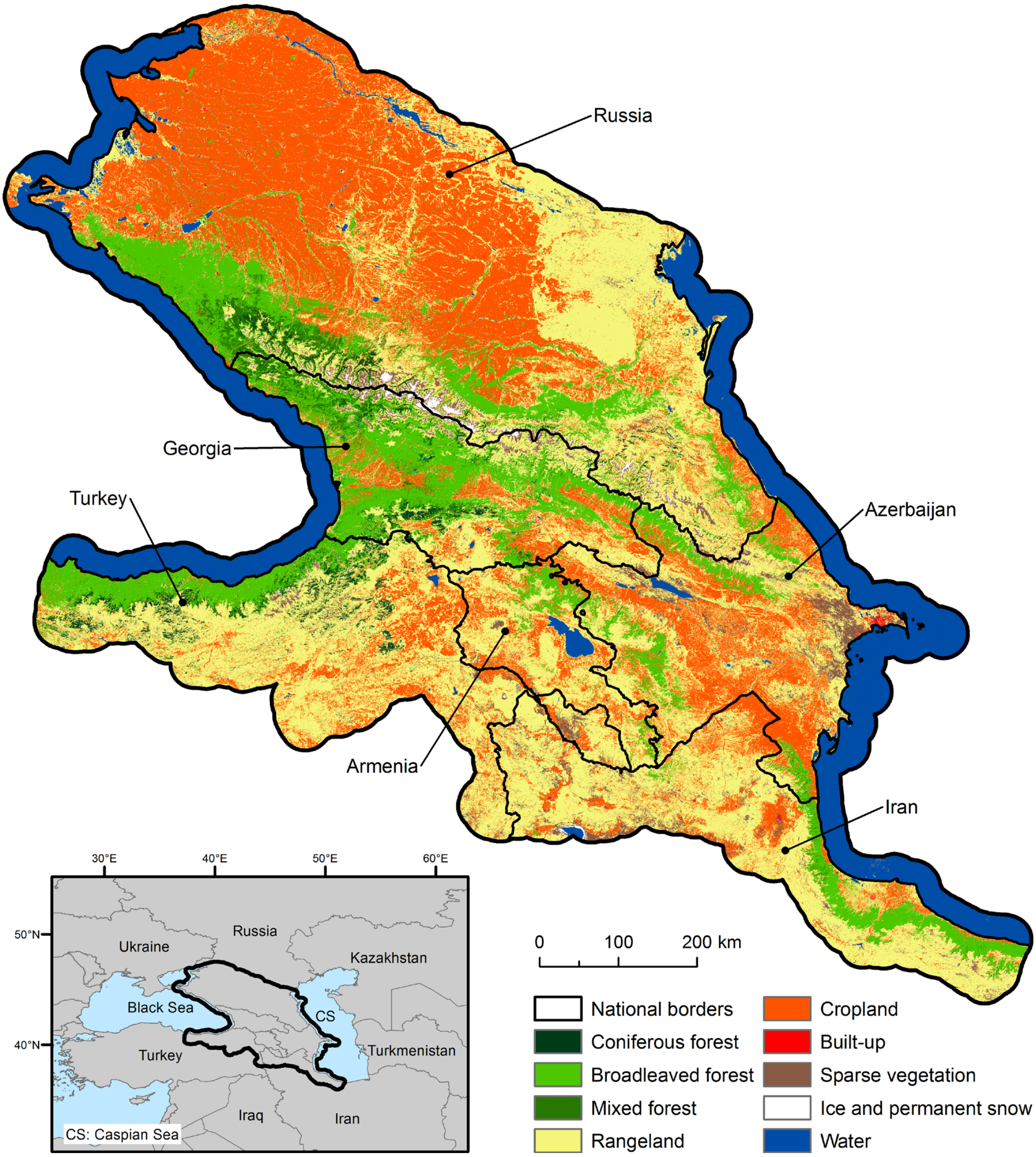

Figure II-2: Land cover of the Caucasus region. Inset shows the location of the study area between the Black Sea and the Caspian Sea.

Bottlenecks were common within our corridors (Figure II-3). Some narrow corridors were almost entirely classified as bottlenecks indicating that these corridors may have limited ecological functionality. For example, the corridors between Prielbrusie National Park and Severo-Osetinsky Zapovednik and Alania National Park entailed bottlenecks for all dispersal groups (inserts A, C, and E in Figure II-3). Additionally, many corridors had very narrow swaths of relatively low travel costs (e.g., some of the north-south leading corridors for the open-land and mountain groups).

Table II-4: Corridor properties for the three generic dispersal groups.

	Least-cost path length [km]		Cost-weighted distance [km]		Ratio of cost-weighted divided by Euclidean distance		Ratio of cost-weighted distance divided by least-cost path length	
	Range	Mean (± sd)	Range	Mean (± sd)	Range	Mean (± sd)	Range	Mean (± sd)
Forest-and-shrubland group	0.9–409	73 ± 74	0.9–946	143 ± 192	1.07–6.85	2.32 ± 1.25	1.00–4.13	1.72 ± 0.75
Open-land group	2–384	78 ± 63	5–883	127 ± 118	1.02–21.41	2.62 ± 2.23	1.00–7.00	1.75 ± 1.00
Mountain group	0.9–368	67 ± 58	5–1,595	298 ± 261	3.45–40.92	5.57 ± 3.43	3.19–9.20	4.54 ± 0.83
All groups combined	0.9–409	72 ± 64	0.9–1,595	195 ± 215	1.02–40.92	3.67 ± 2.98	1.00–9.20	2.80 ± 1.62

4 Discussion

Land-use and land-cover change is a main cause of biodiversity loss globally, and conservation planning depends on up-to-date and fine-scale land-cover maps from remote sensing. This is particularly the case for large mammals, which require large core habitats, and functioning corridors between them to persist in increasingly human-dominated landscapes. The launch of Landsat 8, with its improved radiometric resolution and imaging capacity, along with new algorithms that allow making best use of all available imagery, provide opportunities to support conservation planning with remote sensing. We demonstrate this by deriving, to our knowledge, the first seasonal large-area image composite from Landsat 8 imagery, which we used to map land cover and wildlife corridors across the Caucasus ecoregion, a global biodiversity hotspot.

Our results highlight the value of temporal information for mapping land cover across complex landscapes. Multiple seasonal composites resulted in better classifications than using only a single-season composite, and adding spectral metrics that capture information from all available clear observations further improved the accuracy of our land-cover classifications.

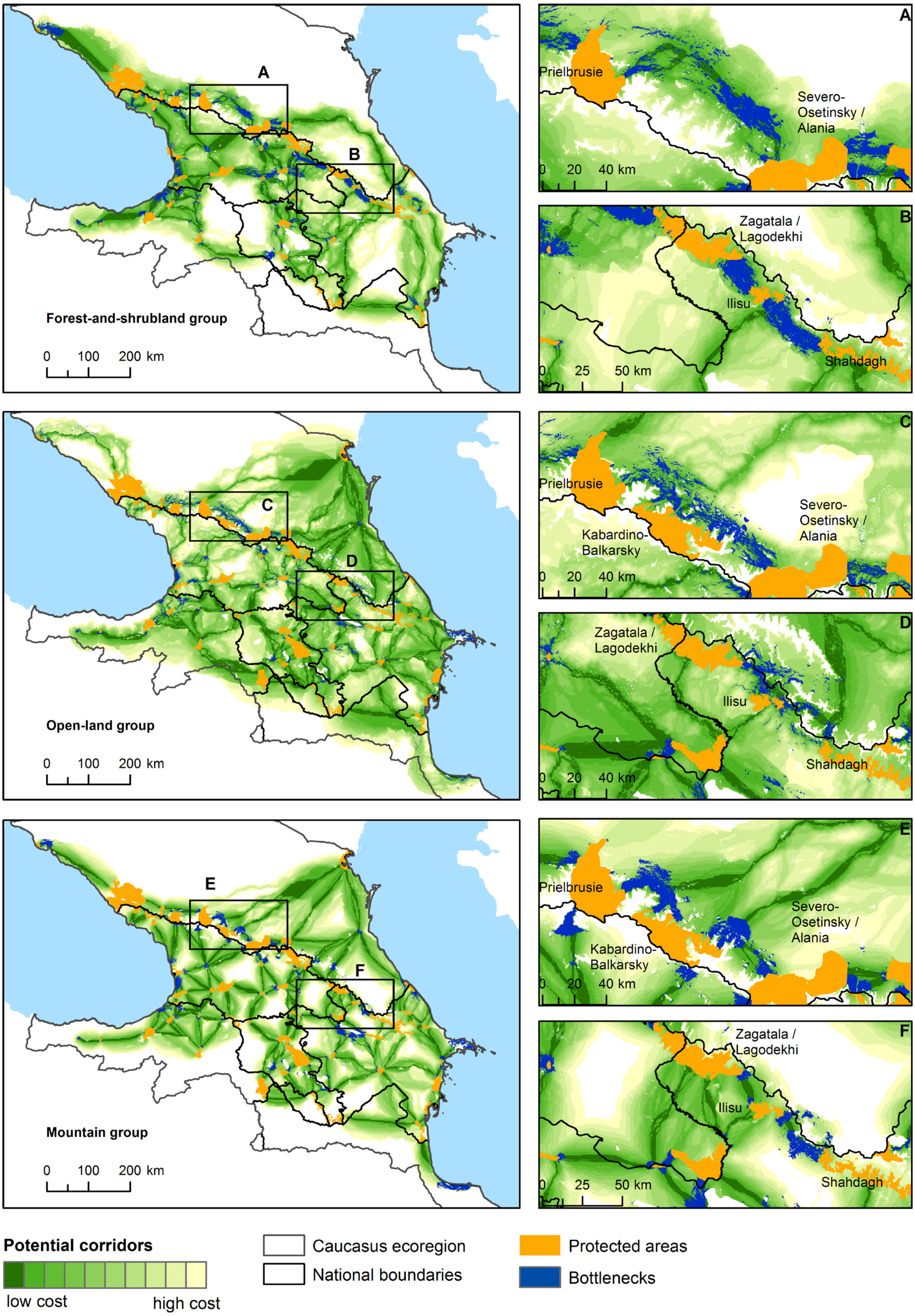

Figure II-3: Least cost corridors and bottlenecks among protected areas with IUCN category I and II. Corridors were normalized to the respective least-cost path and therefore low cost refers to areas of low travel cost. For visualization purposes, corridors were clipped to a cutoff width of 100 km (i.e., the maximum corridor width is set at cells with a 100-times higher cumulative cost-distance than that of the respective least-cost path (McRae and Kavanagh 2011)). Bottlenecks in the map were identified as areas with current density higher than the mean plus 2 standard deviations (see Figure SI II-5 for maps showing the continuous current density).

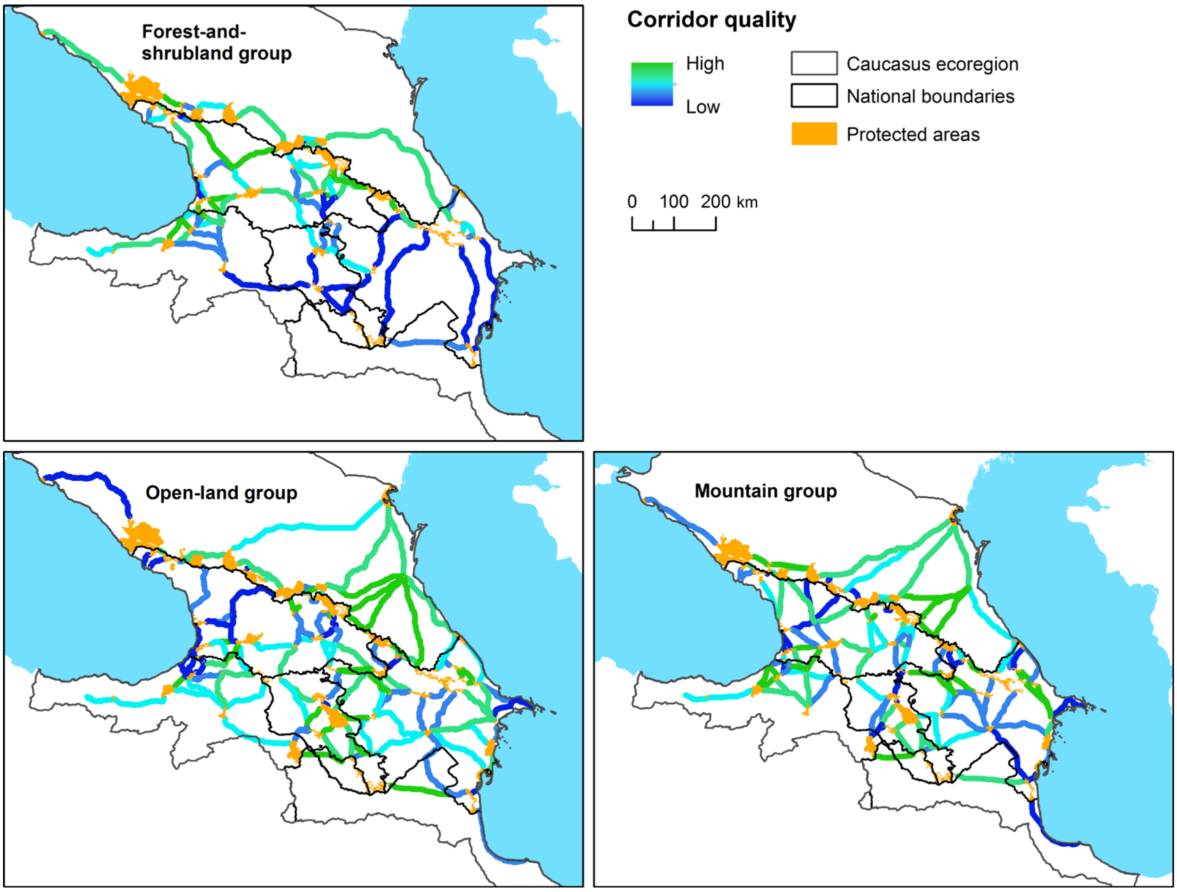

Figure II-4: Corridor quality calculated as the ratio of cost-weighted and Euclidean distance. Low quality indicates a high cost-weighted compared to the Euclidean distance between two protected areas. Our second quality index showed similar patterns (Figure SI II-6).

Based on our land-cover classes and expert scorings we derived three large mammal dispersal groups for which we mapped corridors among protected areas. Corridors were widespread but often had bottlenecks indicating limited functioning and a high threat to loosing connectivity without adequate protection and restoration measures. Because large mammals require extensive habitats, conservation planning requires identifying and safeguarding corridors between core habitat areas that are typically located inside protected areas. Our analysis thus demonstrates how Landsat 8 compositing can contribute to such broad-scale conservation planning by providing key environmental information to map corridors at fine scale across large areas.

4.1 Mapping land cover using seasonal Landsat 8 composites

We achieved the highest overall accuracy using image composites from all four seasons (i.e., spring, summer, fall, and winter). This underlines the importance of multi-temporal imagery and therefore considering different phenological vegetation stages when classifying land cover (Griffiths et al. 2014; Müller et al. 2015; Senf et al. 2015). Composite combinations that included summer and fall composites always yielded higher overall accuracies than other combinations, suggesting that important phenological characteristics are captured in these seasons. For example, cropland might show bare soil in fall after being harvested while high reflectance in summer likely further helps to distinguish it from rangeland and other classes. Additionally, using images from different seasons is well suited to separate between forest and cropland (Baumann et al. 2012). Combinations with the winter composite did only marginally improve classification accuracy, likely due to higher similarity among some classes (e.g., less green vegetation on rangeland and cropland).

Studies mapping land uses such as farmland abandonment have previously pointed out the usefulness of jointly using Landsat images from summer, fall, and spring (e.g., Baumann et al. 2011; Prishchepov et al. 2012), and our test of phenological composites supported this finding.

Similarly, adding spectral metrics to the seasonal composites further improved classification accuracy significantly. Spectral metrics capture information on the variability and distribution of imagery *within* a phenological cycle, complementing the information entailed in the seasonal composites (Griffiths et al. 2013b; Potapov et al. 2011). Higher variability might for example help to distinguish rangeland areas from built-up areas that contain green spaces. Additionally, image metrics are useful to compensate for compositing artifacts and to reduce salt-and-pepper patterns in classifications since they are based on all clear observations (Griffiths et al. 2013b). Conversely, adding the metadata flags led only to a minor, and in our case insignificant, increase in accuracy which may indicate that spectral features alone contained sufficient information to separate the classes of interest well. For our classification problem, the metadata information, such as the number of clear observations or the day of year of image acquisition, did thus not add additional information that helps to discriminate land cover, which could be different though in more data-sparse situations. In sum, given that compositing algorithms and the calculation of spectral metrics are highly automated, we recommend to analyze at least three seasonal composites, and to include spectral metrics that capture distributional features of the imagery, when mapping land-cover for large areas based on Landsat-like sensors.

Our classification resulted in a reliable land-cover map despite the high heterogeneity of our study area. Nevertheless, a few sources of uncertainty need mentioning. First, despite having at least ten images per footprint available, there were areas without any clear-sky observation. Because these areas were clustered in the very high mountain areas (i.e., areas which we mostly masked out later because they do not allow for movement of large mammals due to harsh conditions), we do not expect strong effects on our analyses. Nevertheless, more data might have helped to better distinguish between sparse vegetation and built-up areas based on phenology differences between the classes. Second, the spectral similarity of the built-up and sparse vegetation classes led to a high commission error of the built-up class in initial classification runs. Settlements often entail areas of open soil and building materials can spectrally be similar to bare areas such as rocks, leading to confusion between built-up and sparse vegetation classes. In our case, using a masking approach for built-up areas (i.e., limiting classified built-up areas to within 1 km distance to the Open Street map settlement point layer), solved this problem and improved accuracy. In situations where ancillary data are unavailable, generating composites for multiple years or longer time periods (1.5 years in our case) may result in a higher spectral separability of built-up and sparse vegetation classes. Third, for our seasonal composites, we chose the target days of year to approximate different phenological stages of the vegetation. Because the timing of seasons (i.e., the day of year) varies across years, identifying key phenological dates such as the minimum and maximum peaks of vegetation greenness beforehand instead of using day of year approximations may further improve land-cover classifications (Estel et al. 2015a; Senf et al. 2015).

4.2 Mapping wildlife corridors

Based on our land-cover map, we delineated resistance surfaces for three large mammal species groups (labeled as forest-and-shrubland, open-land, and mountain group) to identify corridors among protected areas in the Caucasus. Clustering species with similar dispersal ability reduced the number of individual assessments necessary to derive corridors. This means that our corridors are largely generic, and thus potentially valuable for more species than those that were explicitly included in our dispersal groups.

Corridor properties differed among the three dispersal groups. Corridor length was on average shorter for the forest-and-shrubland and the open-land groups and quality was highest for the forest-and-shrubland group. The short length and better quality of corridors for the forest-and-shrubland group suggests that protected areas are relatively well connected through forest. This is also highlighted by the low corridor quality for the forest-and-shrubland group in eastern and southern parts of the study area, where forest cover is naturally lower. Nevertheless, many corridors are substantially longer than the distances that single movement events of our species typically would cover. Our corridors should be interpreted as starting points for managing towards a better connected network of protected areas and more detailed analyses would be needed to assess if corridors do facilitate movement of individuals, and where conservation action such as habitat restoration is needed (Beier et al. 2008).

While we found numerous corridors, bottlenecks were common in most of them. Many of the corridors that connected protected areas in close proximity to each other had such bottlenecks. Bottlenecks can be a result of limited availability of permeable land-cover, of passages severed by roads, or a combination of both factors. Nevertheless, current density (i.e., the unit to identify bottlenecks with Circuitscape) is commonly higher between protected areas in close proximity (Dickson et al. 2013) which might lead to wider bottlenecks so that additional measures are needed to assess corridor quality, particularly for short corridors (e.g., corridor width or our quality indices). Bottleneck areas are candidates for immediate conservation actions, because the loss of them can lead to a collapse of connectivity in habitat networks (Dutta et al. 2015). Only about half of the corridors that we mapped were of high quality, further stressing that connectivity between many protected areas might already be limited.

Integrating information across focal species to derive general wildlife corridors is a challenging task. Our expert-based clustering approach showed how general corridors can be derived when available data are scarce. However, our method has a few drawbacks. First, least-cost analyses always identify the best corridor between protected areas regardless of their potential functionality (Beier et al. 2008). Thus, our corridors will have to be validated on the ground, for example with trail cameras. Third, land cover was our main variable in determining the resistance surface. This greatly simplifies the complex decisions related to animal movement, which are also affected, for example, by fine-scale resource availability, predation, or human disturbance. Fourth, expert scorings of resistance values varied markedly for some land-cover classes and for some species. We used median values for each scoring to reduce subjectivity, but we cannot fully rule out bias on our corridors due to the expert scoring. Finally, while analyses based on expert scorings are common (Beier et al. 2009; Zeller et al. 2012), it would be better to have actual movement data. However, such data do not exist for the Caucasus. We tried to minimize subjectivity by surveying many experts, and by grouping species (Beier et al. 2008), but we cannot fully rule out remaining biases.

5 Conclusions

Seasonal Landsat 8 image composites allowed us to reliably map land cover across a large and highly heterogeneous area, an important prerequisite for broad-scale connectivity analyses. Testing different combinations of best-pixel image composites and spectral metrics, based on all available observations, highlighted the strength of using multiple seasons in combination with spectral metrics for land-cover classifications. The Landsat 8 data record is thus very promising for up-to-date, large-area, yet fine-grained connectivity assessments. This highlights the value of the Landsat archives for large mammal conservation, and conservation planning, and suggests that these archives are currently an underused resource in conservation science and application (Turner et al. 2015). For the Caucasus, our results suggest that protected areas are structurally connected through forests, but widespread bottlenecks and low corridor quality stress the need for immediate conservation planning and action to both, protect existing corridors and restore their quality. We identified corridors for three large mammal groups based on all Caucasian large mammals of high conservation priority, and this can be a useful starting point for such ground-based assessments (Beier et al. 2011), for example in the upcoming revision of the Caucasus Ecoregional Conservation Plan (Williams et al. 2006a).

Habitat fragmentation is one of the main causes of global biodiversity loss. Therefore, monitoring habitat connectivity consistently over large areas can provide an important mechanism to track threat to biodiversity and potentially biodiversity change, and contribute to the standardized monitoring proposed under the essential biodiversity variable framework (Skidmore et al. 2015). Our approach demonstrates how Landsat 8 composites can contribute to such a global biodiversity monitoring strategy (Pettorelli et al. 2016).

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Supplementary Information

Table SI II-1: For our final land-cover classification we used a random forests classifier parameterized on the following outputs from the compositing:

Composite outputs	Description
Spring composite	Best pixel composite centered on DOY 105, 6 spectral bands
Summer composite	Best pixel composite centered on DOY 196, 6 spectral bands
Fall composite	Best pixel composite centered on DOY 288, 6 spectral bands
Winter composite	Best pixel composite centered on DOY 349, 6 spectral bands
Metrics	Band-wise mean, median, standard deviation, 25th percentile (Q25), 50th percentile (Q50), 75th percentile (Q75), median based on Q25–Q50, median based on Q50–Q75, slope (slope of the linear regression between the DOYs and the band-wise reflectance values multiplied by 10,000), Interquartile range Calculated using all clear-sky observations 6 bands per metric
Metadata flags	Path/row, year, DOY, month, day, # of clear observations, # of clouded observations, sun zenith angle, sun azimuth angle

Table SI II-2: McNemar’s test p-values for comparison of single season composites.

	Spring	Summer	Fall	Winter
Spring	0	0.864	0.003	<0.001
Summer		0	0.001	<0.001
Fall			0	0.578
Winter				0

Table SI II-3: McNemar’s test p-values for three season settings compared to all seasons setting(Sp = Spring, Su = Summer, F = Fall, W = Winter).

	Sp-F-W	Sp-Su-F	Sp-Su-W	Su-F-W	All seasons
Sp-F-W	0	0.008	0.916	0.051	<0.001
Sp-Su-F		0	0.015	0.008	0.456
Sp-Su-W			0	0.916	<0.001
Su-F-W				0	0.188
All seasons					0

Table SI II-4: McNemar's test p-values for all season settings compared to adding image metrics and metadata flags(Sp = Spring, Su = Summer, F = Fall, W = Winter).

	All seasons	All seasons + metadata	All seasons + metrics	All seasons + metadata + metrics
All seasons	0	0.278	<0.001	<0.001
All seasons + metadata		0	<0.001	<0.001
All seasons + metrics			0	0.146
All seasons + metadata + metrics				0

Table SI II-5: Confusion matrix from the validation of our final land cover classification (CF = coniferous forest, BF = broadleaved forest, MF = mixed forest, RL = rangeland, CL = cropland, BU = built-up, SV = sparse vegetation, IS = ice and permanent snow, WA = water).

	Reference									
Classification	CF	BF	MF	RL	CL	BU	SV	IS	WA	Sum
CF	140	11	9	7	-	-	-	-	-	167
BF	9	194	13	24	3	-	-	-	-	243
MF	3	29	125	6	1	-	-	-	-	164
RL	2	3	1	205	12	3	6	-	2	234
CL	-	7	-	34	169	5	1	-	-	216
BU	-	-	-	-	3	84	5	-	-	92
BG	-	-	-	28	29	20	206	2	2	287
IS	-	-	-	3	-	-	16	178	3	200
WA	-	-	-	-	-	-	-	-	197	197
Sum	154	244	148	307	217	112	234	180	204	1800

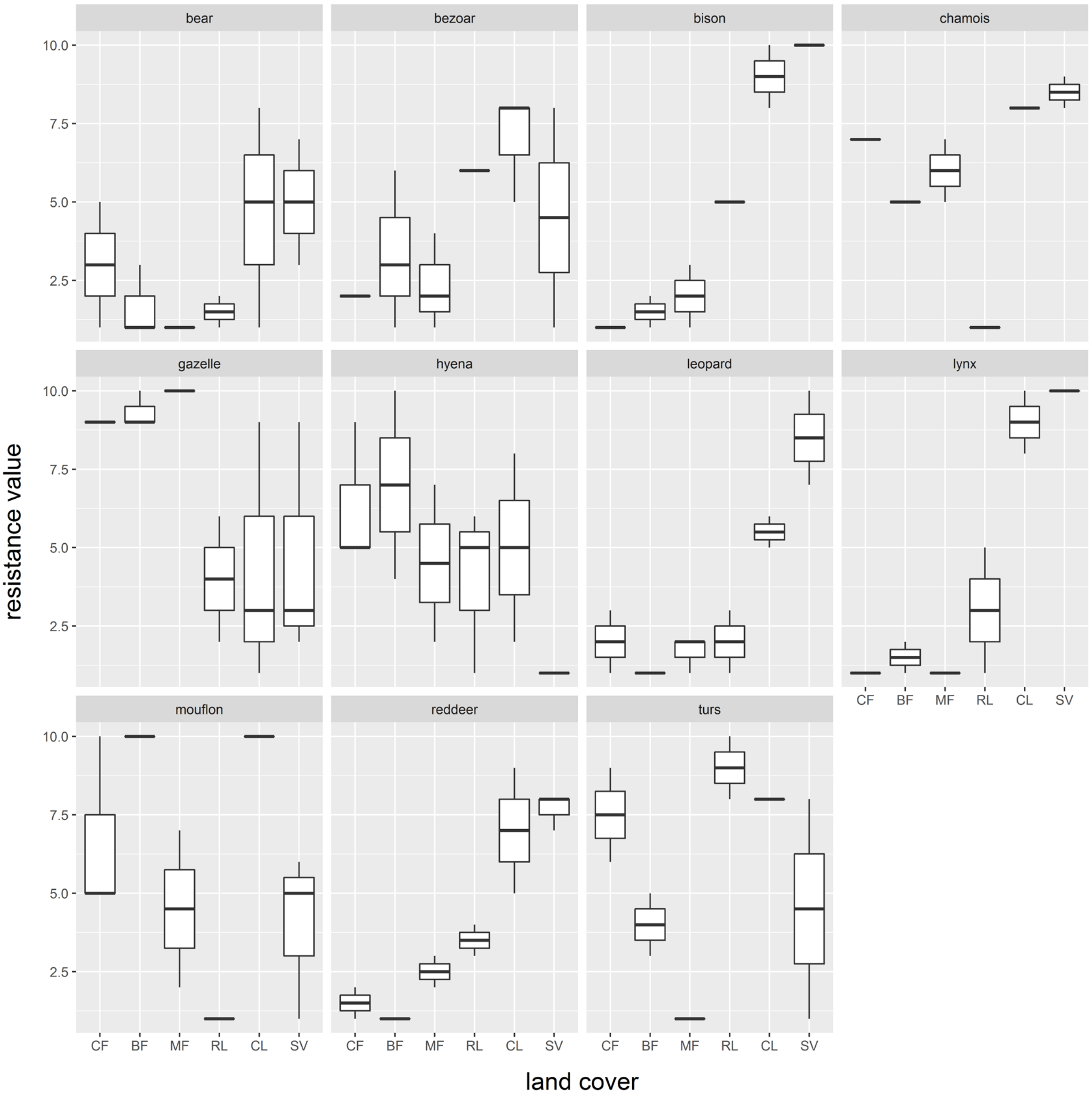

Figure SI II-1: Variation of expert estimations for each species and land cover (CF = coniferous forest, BF = broadleaved forest, MF = mixed forest, RL = rangeland, CL = cropland, SV = sparse vegetation.

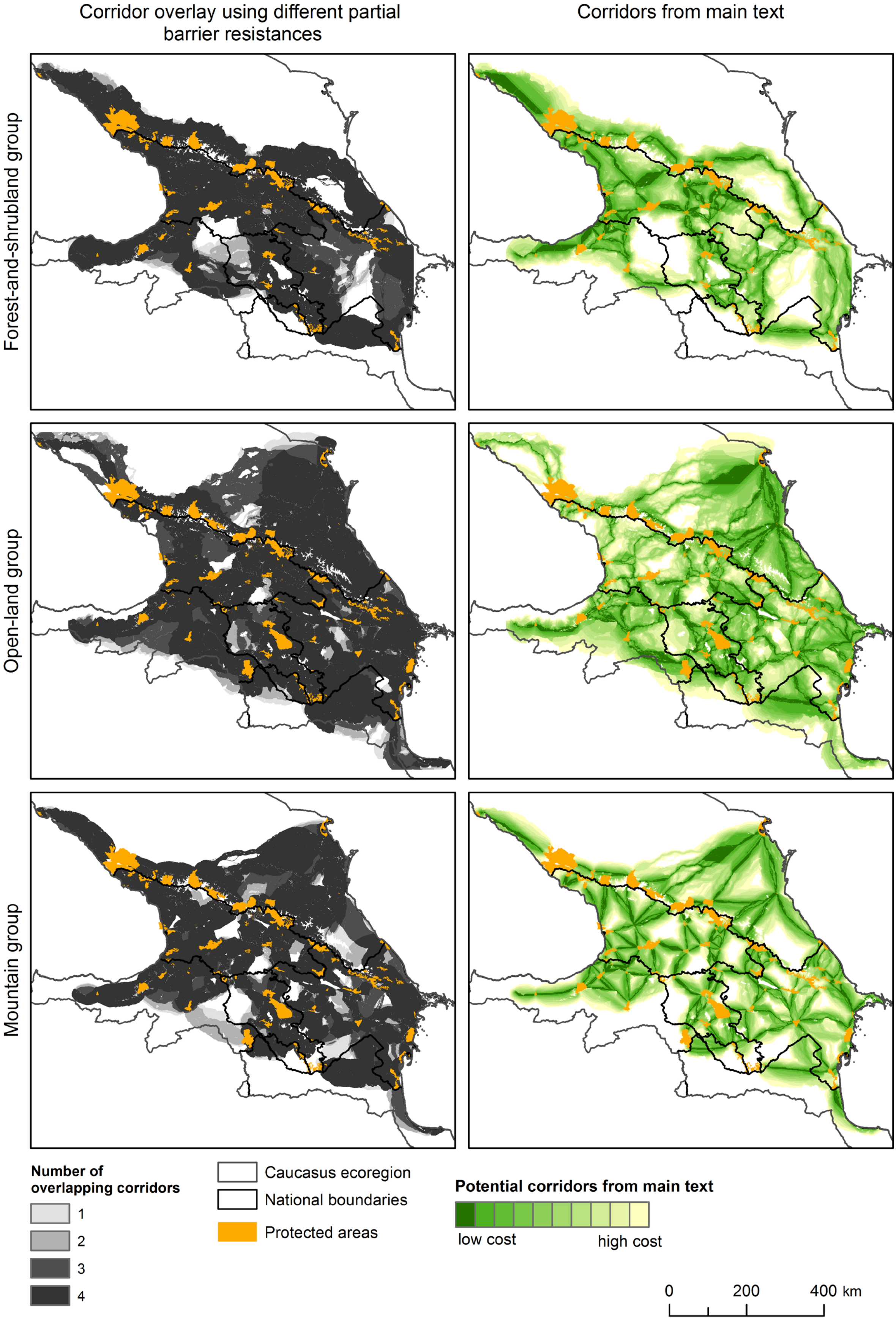

Figure SI II-2: Comparison of corridor results using different resistance values for the partial barriers (high order roads derived from Open Street map with type motorway, trunk, and primary as well as areas with elevation between 3000–4000 m). We compared resistance values of 50, 100, 200, and 500. Corridors in the main text use a resistance value of 100 and are shown here for comparison.

Figure SI II-3: Location of the study area and the protected areas used for the connectivity analysis.

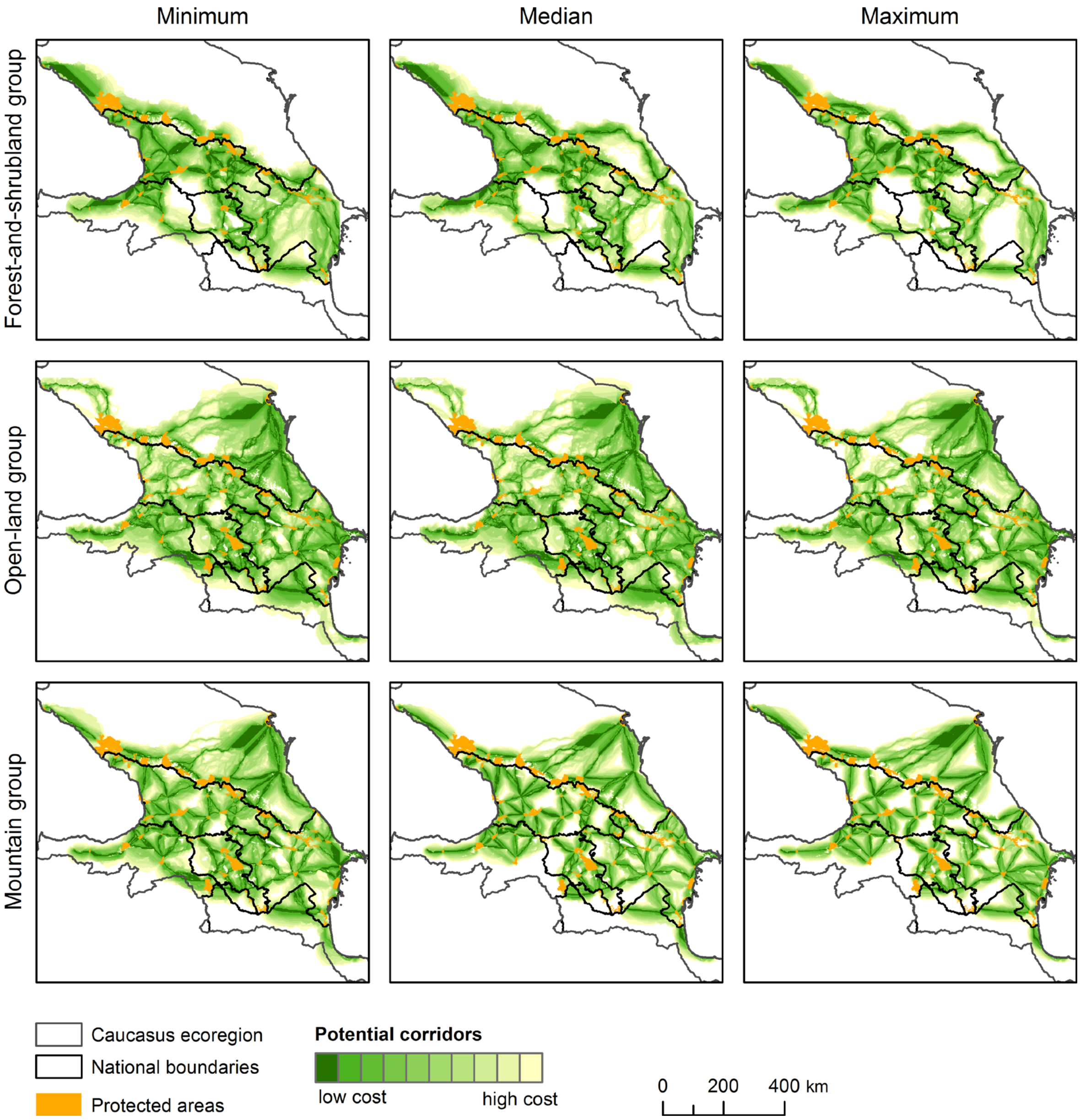

Figure SI II-4: Corridors for the three dispersal groups based on minimum, median, and maximum resistance values from all species within the group.

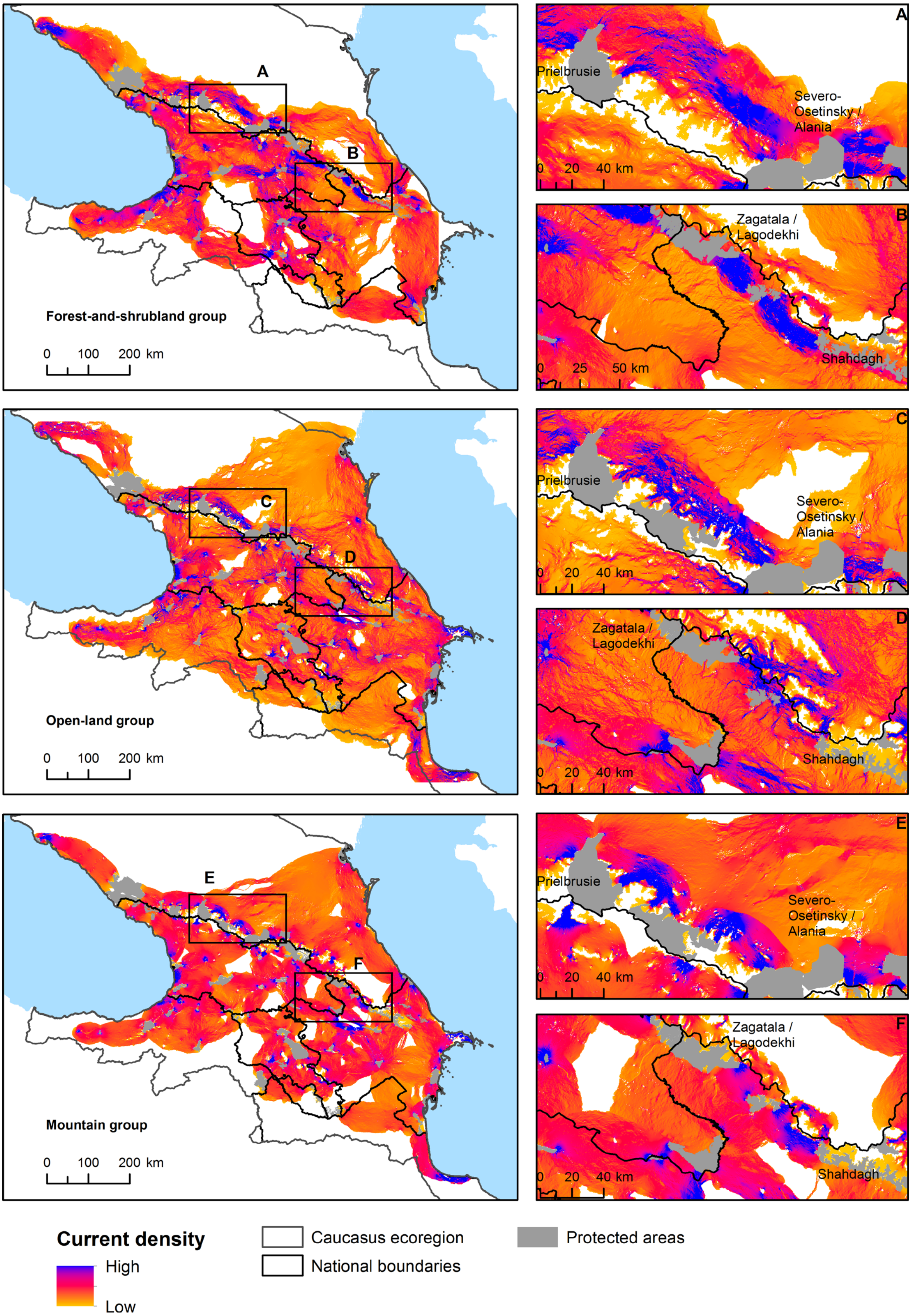

Figure SI II-5: Continuous output of current density used to identify bottlenecks within the corridors.

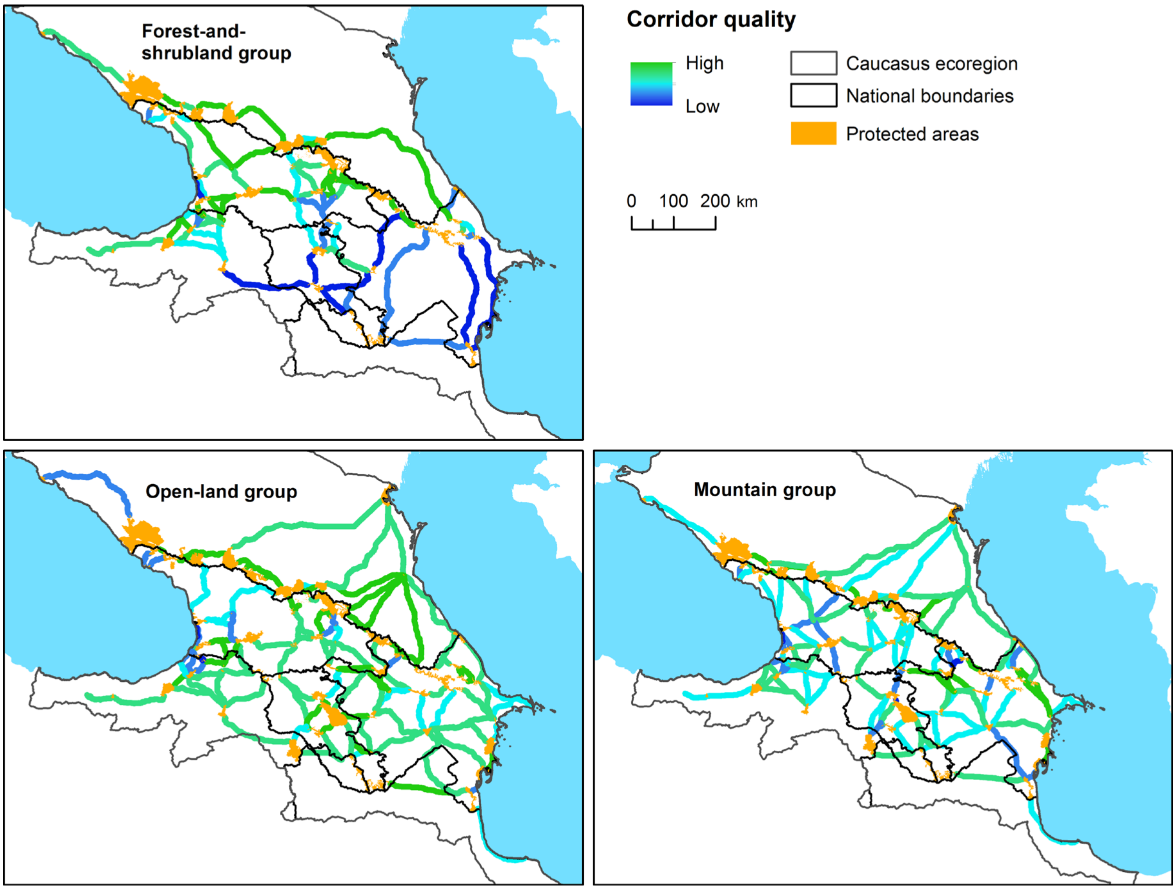

Figure SI II-6: Corridor quality calculated via the ratio of the cost-weighted distance divided by least-cost path length. Low quality indicates a high average cost along the least-cost path.

Chapter III:
Assessing niche overlap between domestic and threatened wild sheep to identify conservation priority areas

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Abstract

Aim: Populations of large ungulates are dwindling worldwide. This is especially so for wild sheep, which compete with livestock for forage, are disturbed by shepherds and their dogs, and exposed to disease transmissions from livestock. Our aim was to assess spatial patterns in realized niche overlap between wild and domestic sheep to better understand where potential competition might arise, and thus to identify priority areas for wild sheep recovery.

Location: Southern Caucasus (220,000 km²).

Methods: We studied Gmelin's mouflon (*Ovis orientalis gmelinii*), an ancestor of domestic sheep, to investigate seasonal habitat use and niche overlap with domestic sheep. To map habitat, we analysed mouflon occurrences collected during 2006–2016, and domestic sheep occurrences from shepherd camp locations digitized on high-resolution satellite imagery. We mapped areas of potential competition between mouflon and domestic sheep and assessed potential habitat displacement.

Results: Mouflon and domestic sheep niches overlapped substantially (overlap index I = 0.89, where 1 means perfect overlap) but were not identical. Mouflon habitat was less widespread than domestic sheep habitat (14,000 km² vs. 40,270 km²) and tended to be located in more rugged areas with less vegetation cover. We identified 51 priority patches as reintroduction candidates if grazing pressure and poaching were reduced.

Main conclusions: Our results suggest that competition with domestic sheep might have pushed mouflon into marginal habitat. Thus, conservation efforts focusing on current mouflon habitat might miss suitable reintroduction sites. We demonstrate that a combined habitat model for wild and domestic sheep can identify general sheep habitat, which might be more useful for conservation planning than understanding current mouflon habitat selection. Our results highlight that considering competition with livestock is important for large ungulate conservation, both in terms of reactive (e.g. lessening livestock pressure in prime habitat) and proactive strategies (e.g. reintroduction in areas with low contemporary overlap).

1 Introduction

Large ungulates are threatened throughout the world and their numbers have declined precipitously during recent decades (Di Marco et al. 2014; Ripple et al. 2015b). This is worrisome as large ungulates play important roles for ecosystem functioning, for example as ecosystem engineers (Pringle et al. 2007) or as prey for large carnivores and scavengers (Margalida et al. 2011; Wolf and Ripple 2016). Therefore, understanding threats to large ungulates and ensuring that their populations are viable is an important conservation goal (Ripple et al. 2016).

A key factor contributing to large ungulate declines is conflict with people, often through competition with livestock. More than a quarter of the Earth's land surface is used for grazing, with livestock outnumbering wild ungulates by several orders of magnitude (Berger et al. 2013; Robinson et al. 2014). Livestock grazing affects large ungulate populations in many ways, including the degradation of food resources, displacement of ungulates from suitable habitats, disease transmission, and direct mortality from shepherds and their dogs (Chirichella et al. 2013; Krishna et al. 2016; Namgail et al. 2006). While certain pastoral systems allow for coexistence and maintain open-land habitats for wild grazers, more commonly, competition with livestock threatens large ungulates, particularly in resource-scarce regions such as drylands or mountainous areas (Ekernas et al. 2017; Mishra et al. 2004; Riginos et al. 2012).

Generally, competition between species occurs when they depend on the same limiting resources, which is likely the case for domestic livestock and their wild ancestors (Madhusudan 2004). With more than one billion domestic sheep worldwide (Ovis aries; FAOSTAT 2017), most of which are pastured, wild sheep are likely particularly negatively affected by competition with livestock (Mishra et al. 2002; Owen-Smith 2002; Shackleton 1997a). Wild sheep also often occur in areas with low productivity and may therefore be particularly prone to competition and conflicts with shepherds and their dogs (Ekernas et al. 2017; Schieltz and Rubenstein 2016; Shackleton 1997a). Conservation planning to protect and restore wild sheep populations thus requires understanding where and to what extent domestic and wild sheep may compete.

Species distribution models help to understand niche characteristics and to identify habitat patterns (Franklin 2009). These models combine occurrence data and environmental factors to describe species' niches in environmental space. Analysing multiple species allows to assess the degree of realized niche overlap between them (Warren et al. 2010). However, while there are analyses using species distribution modelling to quantify niche overlap among different wild species (e.g. Blair et al. 2013; Wordley et al. 2015), to our knowledge, this has not yet been done between livestock and wild ungulates. Broad-scale studies might benefit especially from such an approach, because detailed information on grazing pressure or the location of domestic animals are often not available across larger geographic areas, which is limiting their use as predictors in wildlife habitat models.

Given the high ecological and biological similarity of domestic and wild sheep, their fundamental niches should overlap substantially (Gordon 2009). If realized niche overlap is low, however, then this may indicate niche partitioning and possibly that wild sheep are a so-called refugee species that is confined to marginal habitat (i.e. habitat where fitness might be decreased due to, for example, lower resource availability or higher mortality; Caughley 1994; Kerley et al. 2012). This marginalization would have likely occurred over long time periods, resulting in shifting baselines that might lead conservationists to regard the current habitat of this species as optimal, which would lead to misguided conservation effort (Cromsigt et al. 2012; Soga and Gaston 2018). Similarly, mapping suitable habitat based on current habitat use might be erroneous for species pushed into marginal habitat (Braunisch et al. 2008; Kerley et al. 2012). Assuming similar habitat use by domestic and wild sheep (Hofmann 1989), quantifying realized niche overlap would be a way to test for a possible refugee status of wild sheep. Jointly assessing potential habitat for wild and domestic sheep could then provide a better assessment of optimal wild sheep habitat.

The Caucasus Mountains at the crossroads of Europe, Central Asia and the Middle East are a global Biodiversity Hotspot and home to many iconic large ungulates, including European bison (*Bison bonasus*), bezoar goat (*C. aegagrus*), and Gmelin's or Armenian mouflon (*Ovis orientalis gmelinii*) (Mittermeier et al. 2004). The Caucasus, particularly its southern part, has a long history of livestock husbandry, dating back to around 9,000 BC (Kalandadze and Nebieridze 1989). Today, poaching and overgrazing are the main threats to large ungulates in the southern Caucasus (Williams et al. 2006a). Most wild ungulate populations experienced drastic population declines due to poaching after and during the Iranian 1979 Revolution and the breakdown of the Soviet Union and are in dire need of broad-scale conservation planning and action (Bragina et al. 2015a; Ghoddousi et al. 2019). This makes the Caucasus an interesting and relevant region to explore potential effects of coexistence and competition between wild and domestic sheep.

The southern Caucasus is a stronghold for Gmelin's mouflon. This species, one of the seven subspecies of Asiatic mouflon, the ancestor of domestic sheep, is listed as vulnerable in the IUCN Red List of Threatened Species (Alberto et al. 2018; Rezaei et al. 2010; Valdez 2008). Gmelin's mouflon only persists in very small populations of a few hundred individuals each in Armenia and Azerbaijan, and around 1,200–1,400 in the Iranian part of the Caucasus (Baskin and Danell 2003; Iranian Department of Environment, unpubl. data; Mallon et al. 2007). These populations are severely threatened by livestock grazing and often occur close to international borders with high military presence, fragmenting their range and increasing poaching risk (Khorozyan et al. 2009; Talibov et al. 2009). Identifying areas to establish new and expand existing populations, ideally so that key habitat patches are connected, is therefore important (Zazanashvili et al. 2012).

Our goal was to assess realized niche overlap between domestic sheep and Gmelin's mouflon in the southern Caucasus to better understand where potential competition might arise, and thus to identify suitable habitat for mouflon recovery. Specifically, our objectives were (1) to map mouflon summer and winter habitat, (2) to assess niche overlap in environmental and geographic space with domestic sheep in summer, and (3) to use this information to identify mouflon conservation priority areas.

2 Methods

2.1 Study area

Our study area covers large parts of the southern Caucasus and stretches over Armenia and parts of Azerbaijan, Georgia, Iran, and Turkey (Figure III-1). It is limited in the north by the Rioni River Lowlands (Georgian black sea region) and the Kura river, and in the south (in Turkey and Iran) by the Caucasus Ecoregion as delineated by the Ecoregion Conservation Plan for the Caucasus (Williams et al. 2006a). Most parts of the study area are mountainous including the entire Lesser Caucasus and the southern Caucasus volcanic uplands with Mt. Ararat as the highest peak (5,137 m). The vegetation is characterized by open juniper woodlands, steppes, mountain steppes, subalpine and alpine grasslands, and broadleaved forests with some mixed and coniferous forests in more humid areas. The areas that mouflon occupy include grasslands and open shrub communities of rolling steppes and of the subalpine and alpine zones.

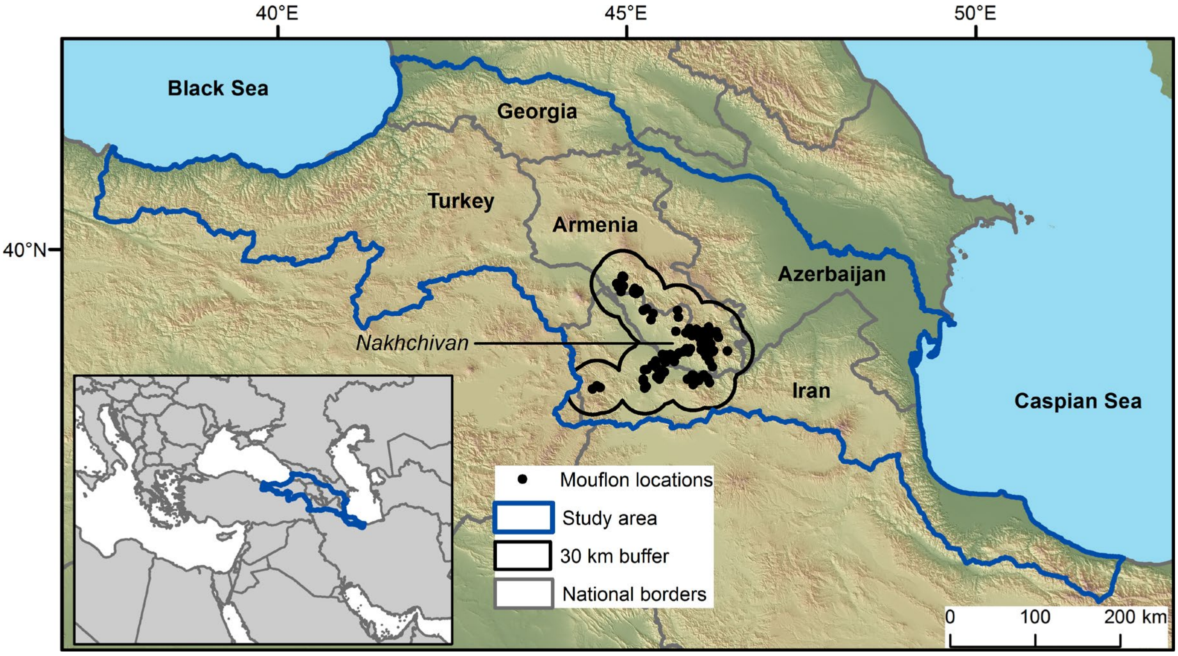

Figure III-1: Study area and mouflon occurrence locations in the southern Caucasus.

Livestock husbandry is widespread in the southern Caucasus. After the breakdown of the Soviet Union domestic sheep numbers declined substantially and in 2017 were still at lower levels in Georgia and Armenia than in the early 1990s (FAOSTAT 2017). In contrast, livestock numbers in Azerbaijan were almost two-fold in 2017 compared to the early 1990s, partly due to incentives through privatization and agricultural reforms (FAOSTAT 2017; Kosayev and Guliev 2006). In Iran, sheep numbers almost doubled after the 1979 Revolution until the early 2000s, but have been decreasing since then (FAOSTAT 2017). Nevertheless, sheep production in the Iranian Caucasus is among the highest in the region with over 6 million heads (Statistical Center of Iran 2017). The pastoral livestock system in the study area is mostly based on transhumance, utilizing summer pastures in the mountains and winter pastures in the steppe lowlands (Williams et al. 2006a). On average, one to three shepherds accompany herds of several hundred sheep, and almost all herds have dogs (normally between one and four dogs per 100 sheep).

2.2 Mouflon ecology and occurrence data

While the exact historic range of mouflons is somewhat unclear, the species was widespread in the region and occurred in larger numbers. Today, it is restricted to small herds in southern Armenia, Nakhchivan (autonomous exclave of Azerbaijan), and north-western Iran (Baskin and Danell 2003; Dinnik 1910). In the Caucasus, mouflon inhabit mountain grasslands and shrublands on dry and mainly open slopes with a preference for slightly rugged terrain

(Gavashelishvili 2009a; Khorozyan et al. 2009; Zazanashvili et al. 2012). In our study, we refer to habitat as encompassing all types in which mouflon occur and survive. Mouflon feed mainly on grasses and shrubs but sometimes also on grain (Valdez 2008). In summer, mouflon usually migrate towards higher elevations for fresh and nutritious fodder. Socially, mouflon live in groups with adult males separate from adult females and the young (Karami et al. 2016a). However, during the rut (i.e. mating season; November to December) dominant males establish groups with several females and defend them from other males (Karami et al. 2016a).

We analysed 211 mouflon occurrence locations from populations in Armenia, Azerbaijan, and Iran, collected in the field during 2006–2016. Mouflon occurrence locations were collected by walking transects and through point counts and opportunistic direct observations. We split the data into summer (May–September) and winter (October–April) sightings. Further, we used only locations with a minimum distance of 500 m between them to reduce spatial autocorrelation that could lead to inflated accuracy measures or biased parameter estimations (Dormann et al. 2007; Veloz 2009), resulting in 91 summer and 97 winter locations (46 of which were repeated sightings from both seasons and from the same location).

2.3 Mouflon habitat mapping

We mapped suitable mouflon summer and winter habitat with maximum entropy modelling (Maxent; Phillips et al. 2006), a species distribution modelling algorithm that is well-suited for presence-only data and outperforms concurrent algorithms (Elith et al. 2006b). We ran the models with a maximum of 2,500 iterations, quadratic and hinge features only, and default settings for convergence thresholds and regularization (Phillips and Dudik 2008). Because sampling background data from too broad areas can result in overly simplistic models, we sampled 10,000 points as background in a 30-km buffer around all mouflon locations (VanDerWal et al. 2009). We validated our models with a 10-fold cross validation and the mean area under the curve (AUC) of the receiver operating characteristic (ROC) curve. To assess variable importance, we used the percent gain contribution of each variable and a jackknife test measuring the AUC for single variable models and models without this variable (Phillips et al. 2006). We further compared differences in model predictions with and without the clamping function, which avoids extrapolation by restricting features to range between values covered by the training data.

To characterize habitat suitability, we used seven predictors related to topography, landscape composition, resource availability, and human disturbance (see Supplementary Information for *a-priori* hypotheses on their relations to habitat suitability). For topography, we derived aspect (flat, north, east, south, west), local terrain ruggedness (using a 90-m neighborhood rule; Sappington et al. 2007), and landscape ruggedness (mean slope within 2 km) based on Shuttle Radar Topography Mission data (SRTM; NASA JPL 2013). We defined local ruggedness to characterize the direct surroundings of a cell (i.e. at pixel level) and landscape ruggedness to characterize the general topographic setting in which a cell was embedded (i.e. a 2 km window surrounding the cell). We tested other neighbourhoods (30 and 210 m for local, and 0.3, 1 and 3 km for landscape ruggedness), which resulted in models with very similar, but lower AUC values (results not shown). To capture landscape composition, we used a recent, high-resolution land-cover map with the classes coniferous forest, broadleaved forest, mixed forest, rangeland, cropland, built-up, ice and permanent snow, and water (Bleyhl et al. 2017). Additionally, we acquired Vegetation Continuous Fields data (VCF, MOD44B, years 2000–2010) from the MODerate Resolution Imaging Spectroradiometer (MODIS) to calculate mean fractional woody vegetation cover. We measured human disturbance as the Euclidean distances to roads and settlements, using data from Open Street Map (OSM; http://www.openstreetmap.org/) and the World Wide Fund for Nature's Caucasus Programme Office (WWF CauPO). Distances were limited to a maximum of 8 km for roads and 6 km for settlements because initial models predicted less suitable habitat for higher distances. We considered decreasing habitat suitability at higher distances to be an artefact of our presence data because mouflon are currently not colonizing all available remote and suitable areas and because very remote areas might not have been surveyed equally intensively as more accessible areas (Bleyhl et al. 2015). We further tested climatic variables (annual mean temperature, minimum temperature of the coldest month, annual precipitation, and precipitation of coldest quarter; WorldClim 2; Fick and Hijmans 2017) but these did not improve model performance and were therefore dropped in our final models. We resampled all predictor variables to a 100 m resolution and reprojected them to the Albers Equal Area projection. Correlation among our predictor variables was generally low ($r<0.65$; see Supplementary Information).

2.4 Quantifying niche overlap between domestic sheep and mouflon

Because domestic sheep and mouflon are closely related, fundamental niche overlap (as well as functional similarity) is likely high, but realized niche overlap may or may not be high. On the one hand, realized niche overlap might be high, because the species rely on the same resources. On the other hand, because domestic sheep have been reared in the Caucasus for millennia (Akhalkatsi et al. 2012), mouflon might have adapted through resource partitioning (Schoener 1974; Voeten and Prins 1999). Competition with livestock might have pushed mouflon into marginal habitat, possibly rendering them a refugee species (Fritz et al. 1996; Kerley et al. 2012). Both scenarios would result in a lower overlap of realized niches than the close phylogenetic relationship of the two species suggests. We tested the hypothesis that realized niche overlap between mouflon and domestic sheep was lower than expected, either because the species adapted to coexistence through adapting their niche or because mouflon is a refugee species.

To assess the habitat use of domestic sheep in the same way as the mouflon's niche, we captured the summer distribution of domestic sheep by mapping all shepherd camps within 30 km of our mouflon occurrences. Camps appeared as homogeneous open-soil patches within otherwise heterogeneously textured grassland in high-resolution imagery in GoogleEarth and BingMaps. Often, these camps had tent-like structures making the identification easy. We digitized 977 shepherd camps and excluded locations with an elevation <1,500 m because these are likely not related to summer shepherding that mostly takes place at high elevations (we repeated our niche overlap analysis with all shepherd camps and did not find substantial differences; results not shown). To reduce spatial autocorrelation, we applied a minimum distance of 500 m between camps, resulting in 586 locations. To test if niche overlap changes when using likely domestic sheep locations (rather than camp locations), we also assessed overlap based on randomly sampled (i.e. simulated) sheep occurrences within set distances around the camps (100 m, 200 m, 500 m, 1,000 m, and 2,000 m). Because domestic sheep are kept on winter grazing sites at lower elevations, sometimes several hundred kilometres away from the summer camps and predominantly outside current mouflon areas, we did not expect winter niches to overlap and mapped only summer habitat for domestic sheep.

First, to map the spatial overlap of the realized niches of sheep and mouflon, we overlaid suitable mouflon and sheep summer habitat. We delineated habitat using the maximum training sensitivity plus specificity threshold (Liu et al. 2013). We also calculated Euclidean distances of all mouflon summer locations to the closest shepherd camp. Second, to quantify realized niche overlap between mouflon and domestic sheep, we used the similarity statistic

I (Vaart 1998) calculated by ENMTools (Warren et al. 2010). This similarity statistic ranges from 0 (no overlap) to 1 (complete overlap). We ran Maxent models with the same settings and predictor variables for domestic sheep and compared them to our mouflon summer model using the 30 km buffer area to project the models as a basis for the comparison. To test if an overlap existed between domestic sheep summer habitat and mouflon winter habitat, we also quantified the similarity using our mouflon winter model. Additionally, we also calculated niche overlap based on models that used only environmental predictors (i.e. excluding human disturbance predictors). Finally, to test our hypothesis that wild and domestic sheep have identical realized niches, we used the identity test in ENMTools (Warren et al. 2010). For this test, we derived a distribution of the overlap index from 100 replicates based on random partitioning of a pooled dataset of occurrence locations (i.e. treating the data as if mouflon and domestic sheep occurrences were from the same species). Subsequently, we tested the actual overlap index score against this distribution under the null hypothesis of niche identity to assess if the score is significantly lower (at the $\alpha = 0.05$ level; Warren et al. 2010).

2.5 Priority habitat patches for mouflon

We identified four types of priority habitat patches based on habitat suitability using the training sensitivity plus specificity threshold (Liu et al. 2013) and a minimum area rule (Figure III-2). First, we identified suitable areas based on currently occupied mouflon habitat (i.e. our mouflon summer model), that were larger than 300 km^2 (*mouflon habitat patches*). A patch of 300 km^2 could harbour approximately 3,600 to 4,800 individuals, assuming a density of 12–16 individuals per km^2 (based on studies of O. vignei, a closely related wild sheep in Iran; Farhadinia et al. 2014; Ghoddousi et al. 2016). Second, we identified areas with suitable habitat for both mouflon or domestic sheep (*potential mouflon habitat patches*), because mouflon might use suboptimal habitat due to competition with domestic sheep and a combination of both habitat areas potentially better describes suitable habitat. Third, we identified habitat patches where competition potential with domestic sheep is likely lowest (*low-risk patches*), by selecting suitable mouflon habitat that does not entail suitable domestic sheep habitat. Finally, to assess which new areas could best foster connectivity among current *mouflon habitat patches*, we highlighted *potential mouflon patches* located within a corridor connecting *mouflon habitat patches* (*connectivity patches*). We identified these corridors with a least-cost analysis using our summer habitat suitability map as a cost surface (highest suitability = lowest cost to travel through a cell; resistance values between

1–11) and roads as partial barriers (Bleyhl et al. 2017; resistance value 100). We used summer habitat because we were interested in dispersal corridors and not in migration corridors from summer to winter habitat, which would require a more fine-scale assessment. We derived least-cost corridors using the Linkage Mapper Toolkit (McRae and Kavanagh 2011). For all priority patches, we calculated the area that is currently protected based on protected area layers from WWF CauPO (wwfcaucasus.net), the share of suitable winter habitat based on the maximum training sensitivity plus specificity threshold (Liu et al. 2013), and the distances from each patch to international borders (which might be related to poaching pressure from border patrols; Khorozyan et al. 2009).

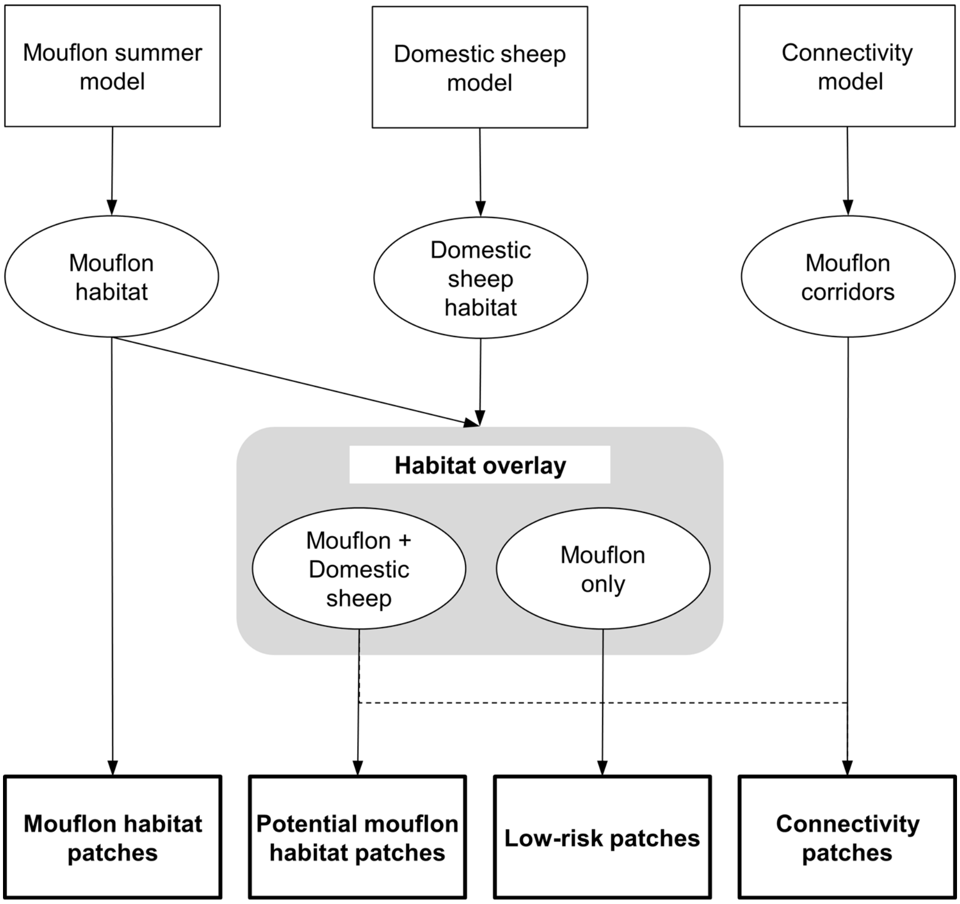

Figure III-2: Flowchart of our analyses to identify priority habitat patches. Dashed line is only dashed to distinguish it from other crossing lines.

3 Results

3.1 Mouflon habitat modelling

Our mouflon model predicted widespread areas of suitable but currently unoccupied habitat across the southern Caucasus, mainly in the border region of Armenia, Azerbaijan and Iran. Suitable mouflon summer habitat generally overlapped with suitable winter habitat, but winter habitat was more widespread (Figure III-3). Our Maxent models had high AUC values of 0.89 for summer and 0.83 for winter. Variable importance was similar for both seasons. Mouflon habitat occurred far away from human settlements and roads, and in medium-rugged terrain with low woody vegetation cover. Rangeland was the land-cover class with highest suitability in both seasons. Aspect had only a minor influence on summer habitat suitability (least important variable), but south facing slopes were important in winter. Further, restricting features to ranges covered by the training data showed that our results were not affected by extrapolation.

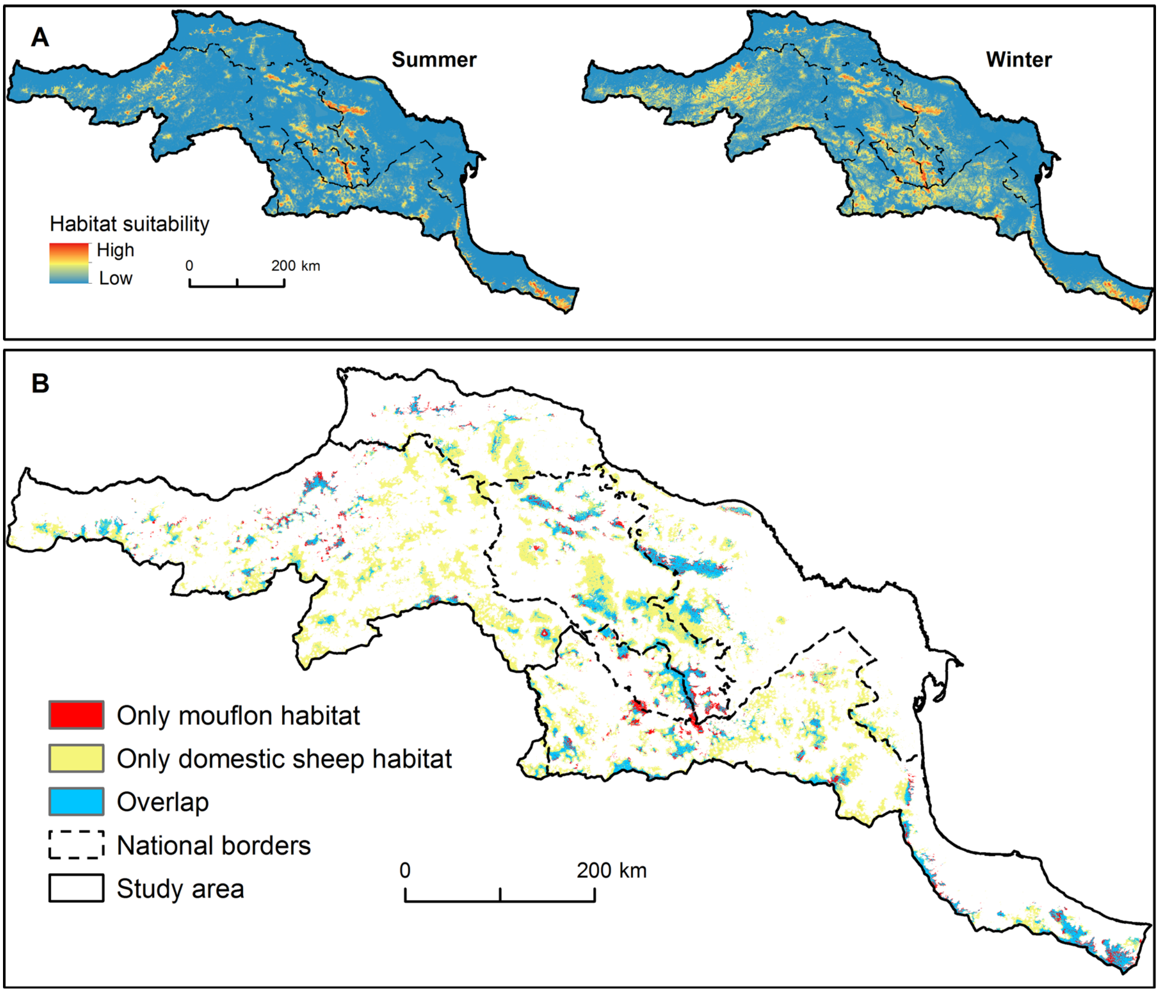

Figure III-3: (A) Mouflon summer and winter habitat suitability and (B) areas with suitable mouflon and domestic sheep habitat, as well as areas where both habitats overlap.

3.2 Niche overlap between domestic sheep and mouflon

Mouflon occurrence locations differed markedly from shepherd camp locations in geographic space and regarding some of our predictor variables. Mouflon locations were far from shepherd camps in both seasons (distances ranged from 0.4–22 km, median: 5 km, standard deviation: 4 km). Further, mouflon habitat was more rugged and characterized by higher distances to settlements and by higher shares of sparse vegetation (see Supplementary Information Figure SI III-1).

We found substantial overlap between the realized niches of domestic sheep and mouflon during summer, particularly based on models without the human disturbance predictors (I = 0.89). The niche overlap did not change markedly for winter mouflon locations (I = 0.88). Overlap index values increased slightly with buffer distance around shepherd camps that we used to sample domestic sheep locations (Table III-1). However, the two realized niches were not identical according to the niche identify test (i.e. our empirical similarity indices were significantly lower than indices from the pooled model).

Despite the differences in location and niche characteristics, we found that the majority of suitable mouflon habitat was also suitable for domestic sheep (77%; Figure III-3). In general, domestic sheep habitat was much more widespread than mouflon habitat (40,270 km² compared to 14,000 km² for mouflon) and only a few areas that were suitable for mouflon were not suitable for domestic sheep (3,280 km² or 23% of all suitable mouflon habitat). The combination of both mouflon and domestic sheep habitat revealed widespread areas (43,560 km²) potentially suitable as general *Ovis* habitat across the southern Caucasus (Figure III-3).

Table III-1: Niche overlap indices between mouflon summer habitat and domestic sheep habitat across a range of buffer areas used to derive the domestic sheep occurrences.

Domestic sheep locations	Overlap index I	
	Without human disturbance	With human disturbance
Camp	0.89	0.82
100 m buffer	0.89	0.82
200 m buffer	0.89	0.83
500 m buffer	0.90	0.83
1000 m buffer	0.90	0.83
2000 m buffer	0.90	0.82

3.3 Priority habitat patches

We identified four types of priority patches for mouflon conservation: (1) *mouflon habitat patches* are the most suitable patches based on current mouflon habitat use only, (2) *potential mouflon habitat patches* are based on the assumption that mouflon could also thrive in areas suitable for domestic sheep, (3) *low-risk patches* are those patches with least potential for competition with domestic sheep, and (4) *connectivity patches* are potential mouflon patches that would foster connectivity among mouflon habitat patches (i.e. among category (1) patches).

We found eleven *mouflon habitat patches* with high habitat suitability and an area exceeding 300 km² (Figure III-4). All of these patches had at least 73% suitable winter habitat. In total, these habitat patches covered 6,830 km² (mean patch size: 620 km²). We found *mouflon habitat patches* in all countries except Georgia, and the majority of them was in Iran (six areas, in total 3,000 km²). Of the total area covered by such patches, 18% was protected (9% in reserves with IUCN category I or II; see Supplementary Information for an overview of all priority patches). Six of the eleven patches were close to international borders (<10km) and three extended across borders. Further, 77% of the total area was also suitable for domestic sheep. The combination of mouflon and domestic sheep habitat, i.e. potential mouflon habitat, resulted in markedly more and larger priority patches. In total, we found 51 *potential mouflon habitat patches* >300 km² distributed across all countries and covering an area of 40,400 km² (mean patch size: 790 km²). However, some of them did not have much winter habitat inside (five patches had less than 10% suitable winter habitat) and only 14% of the total area was protected. Additionally, we only identified two *low-risk patches* larger than 300 km², one in the border triangle of Armenia, Nakhchivan, and Iran, and one in Iran, together covering an area of 740 km² (Figure III-4). Both of these patches had also suitable winter habitat (96% of their area), but only the northern patch at the border triangle was partly protected (87% of its area).

We identified 25 *connectivity patches* that were >300 km² and located within the corridors linking *mouflon habitat patches* (Figure III-5). Corridor length ranged from 8–320 km. All corridors crossed at least one major road, and five corridors crossed international borders. Resistance along the least-cost path ranged between 7.1–12.1 (mean: 9.5, standard deviation: 1.5), which is high given that our resistance values ranged between 1 and 11 (with 100 only used for partial barriers). We found at least one *connectivity patch* in each corridor. On average, *connectivity patches* were large (mean patch size: 980 km²) and covered a total area of 24,000 km².

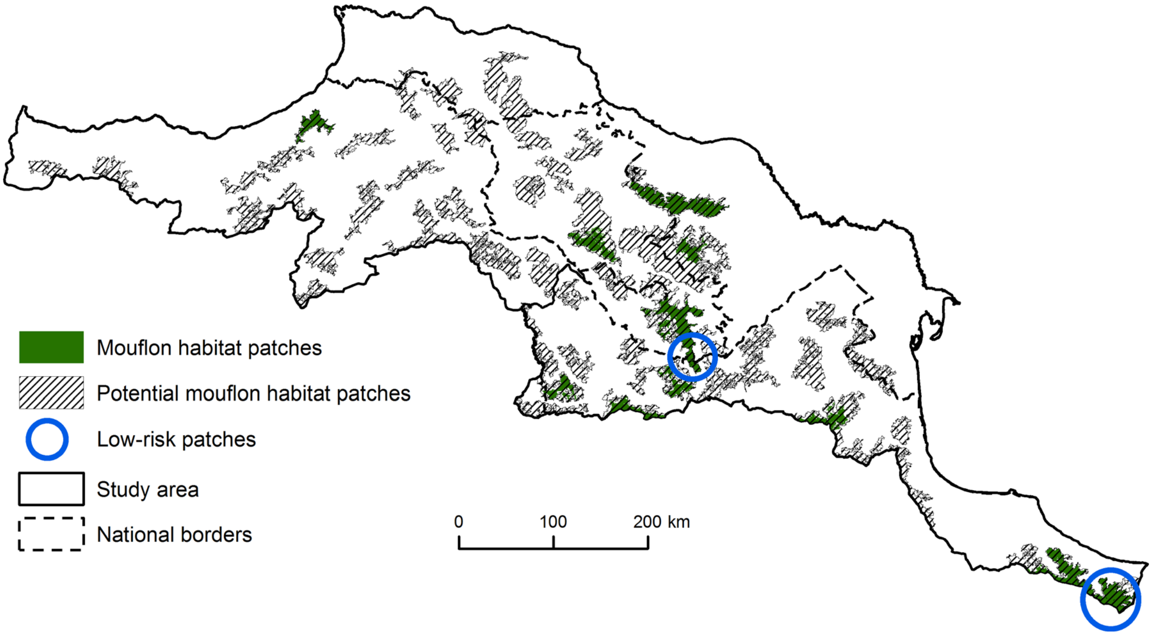

Figure III-4: Distribution of mouflon habitat patches (based on the mouflon summer model), potential mouflon habitat patches (based on the combination of mouflon and domestic sheep habitat), and patches with low risk for competition with livestock.

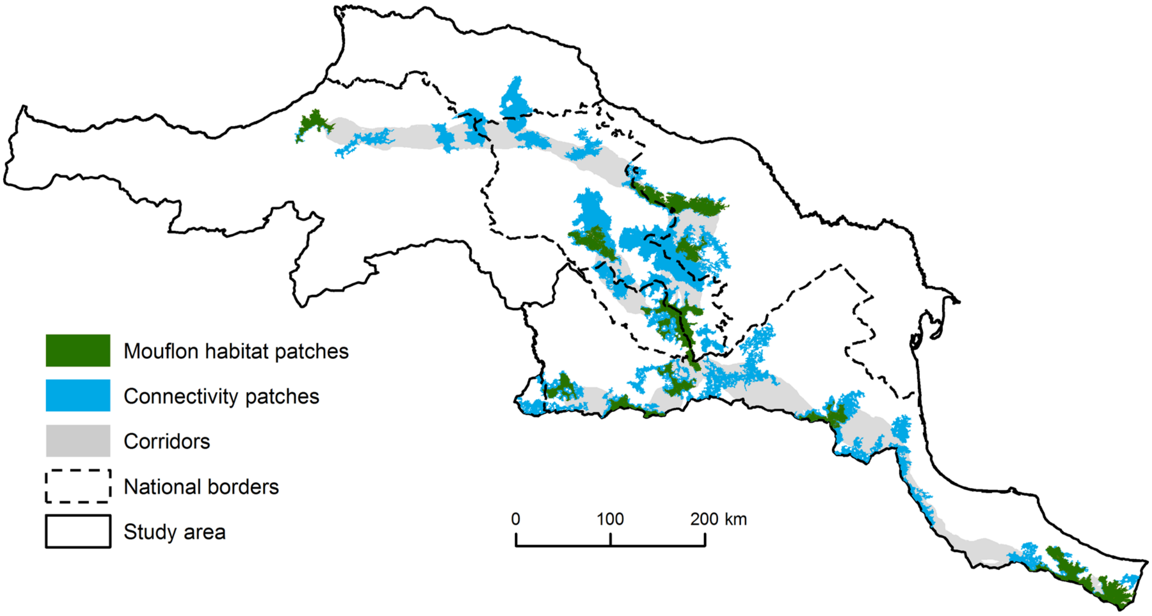

Figure III-5: Least-cost corridors among mouflon habitat patches (i.e., patches based on current habitat patterns) and connectivity patches that would foster connectivity if new herds were established.

4 Discussion

Large ungulates and particularly wild sheep are threatened by competition with livestock. Competition can lead to the displacement of wildlife to marginal habitats, which might compromise conservation efforts based on assessing current habitat. In our study, we analysed Gmelin's mouflon habitat, and investigated seasonal habitat patterns and the potential for competition with domestic sheep using species distribution modelling and a niche overlap analysis. We identified widespread habitat that is currently unoccupied. However, our niche overlap assessment also revealed that despite a considerable overlap, realized niches of mouflon and domestic sheep differed and mouflon habitat was associated with less productive areas. Our study is, to our knowledge, the first that uses niche modelling to spatially assess the niche overlap between a wild ungulate and its domestic relative, thereby highlighting opportunities for restoring wild ungulate populations in landscapes shared with livestock.

We found widespread suitable mouflon summer and winter habitat across the southern Caucasus. Much of this habitat is currently not occupied by mouflon, potentially providing space for reintroduction and herd expansions. Suitable habitat was mostly located in mountainous areas, which we expected, given the species' preference for medium ruggedness and areas afar from human settlements (Gavashelishvili 2009a). The spatial distribution of summer and winter habitat was very similar, suggesting that seasonal habitat preferences do not differ substantially. It might be that the resolution of our predictor variables was not fine enough to capture fine-scale seasonal migrations along the elevation gradient. However, in the past, mouflon occasionally migrated over longer distances to lower elevations in winter, for example from Armenia to Nakhchivan and to Iran (Baskin and Danell 2003; Khorozyan et al. 2009). Border patrols that limit migrations and overgrazing of mouflon wintering areas by domestic sheep may have stopped these migrations (Linnell et al. 2016; Talibov et al. 2009).

Our niche overlap assessment revealed that most suitable mouflon habitat was also suitable for domestic sheep. A high niche overlap is not surprising given that the species are closely related (Gordon 2009; Madhusudan 2004), but highlights the need to limit negative effects of sheep on mouflon populations (Khorozyan et al. 2009; Talibov et al. 2009). Niche overlap was higher for models without human disturbance, which indicates that mouflon utilize areas close to human infrastructure, where shepherd camps are often located, less than domestic sheep.

In general, our analyses provide more support for differences in mouflon and domestic sheep realized niches due to either a displacement of mouflon to marginal habitats or to niche partitioning (which in turn could also lead to diverging fundamental niches over time). First, despite high overlap, realized niches differed significantly. Second, mouflon occurrences differed from shepherd camp locations regarding several of our predictor variables. Differences in habitat use might arise from niche partitioning as a strategy to coexist. Domestic sheep are herded in the area for millennia (Akhalkatsi et al. 2017) and mouflon could have adapted to avoid competition. Mouflon were found in terrain that is more rugged and with only sparse vegetation, both of which are generally associated with decreased forage availability (Chirichella et al. 2013). Similar habitat-use patterns have been found for other wild ungulates that compete with livestock and have been displaced into marginal habitat. For example, when livestock was present, Argali sheep (*O. ammon*) were pushed to steeper slopes with less vegetation cover (Namgail et al. 2006) and ibex (*C. pyrenaica*) and chamois (*Rupicapra rupicapra*) to areas with decreased resource availability (Acevedo et al. 2007a; Chirichella et al. 2013). Likewise, a displacement of mouflon from middle to higher elevations with less resources due to livestock grazing has occurred in Nakhchivan (Talibov et al. 2009). Such a displacement to areas with less resource availability might in turn indicate that mouflon are a refugee species (Kerley et al. 2012).

Based on our habitat suitability analysis and the niche overlap assessment, we identified mouflon conservation priority patches. Using current mouflon locations, we identified eleven *mouflon habitat patches*. Yet, only 18% of their area was protected. Additionally, the majority of the patches was also highly suitable for domestic sheep (77%) or located within 10 km from international borders, which might be inaccessible to shepherds and provide havens for mouflon, but sometimes might also entail high poaching pressure from border patrols (Khorozyan et al. 2009). When combining mouflon and domestic sheep habitat, we identified 51 *potential mouflon habitat patches* that cover a substantially larger area than the *mouflon patches*. Since our niche overlap analysis suggested a shift to marginal habitat for mouflon, these 51 patches may include better habitat. Yet, due to their high suitability for domestic sheep, we would expect strong potential for competition with livestock. Indeed, we found only two areas that were >300 km² and had a low-risk for competition with livestock, underlining the need for conservation efforts that limit negative effects of grazing in the southern Caucasus (Shackleton 1997a; Soofi et al. 2018).

Connectivity among *mouflon habitat patches* was low. We found at least one high-level road crossing each of the eleven corridors, five corridors crossing international borders, and high average cost along the least-cost paths. To increase connectivity, we highlighted those *potential mouflon habitat patches* that were located within corridors. All corridors had *connectivity patches*. However, some of the corridors were very long (up to 320 km), suggesting that an active dispersal management including translocations might be needed to avoid the loss of genetic diversity (Bouzat et al. 2009; Ptak et al. 2002). Additionally, the exact historic distribution of mouflon is unclear and therefore patches in northern Armenia, Georgia, and Turkey might be outside the former mouflon range and never been functionally connected.

We successfully gained more knowledge on potential niche overlap, consequences of competition, and spatial habitat patterns of a threatened large ungulate and livestock. Nevertheless, a few drawbacks remained. First, to model the domestic sheep niche, we used locations from shepherd camps that we derived from high-resolution satellite imagery instead of actual sheep locations. Further, areas where domestic sheep graze are to a large degree driven by shepherd's decisions instead of the animals themselves. However, niche overlap indices were similar for random locations in buffers around the camps, which are more likely the areas the sheep graze. We might have missed some camps, but this should not affect our models unless there was a systematic omission bias. Second, high niche overlap among species translates into competition only when shared resources become limited, which we did not test (de Boer and Prins 1990; Putman 1996). Yet, high mountain regions are generally resource scarce, which is why we assumed that at least high stocking rates do deplete resources for mouflon. Additionally, physical disturbance by herders and dogs is a key factor of competition and displacement (Chirichella et al. 2013; Young et al. 2011) and may be more detrimental for mouflon than forage competition (Talibov et al. 2009). Finally, we did not assess if livestock grazing in some areas could be beneficial for mouflon by keeping formerly forested areas open. It is unlikely though that such high grazing pressure would leave substantial resources for mouflon.

5 Conclusions

Competition with livestock is a major threat to wild sheep (Shackleton 1997a) necessitating new approaches to identify where to restore wild sheep populations in human-dominated landscapes. Our study makes progress towards that in two main points. First, our approach is applicable to assess competition potential and displacement from optimal habitats. Second, we highlight how potential bias in current occurrence data due to competition with livestock and associated displacement can be overcome when identifying priority conservation areas. We suggest that conservation planning should consider competition with livestock both reactively (lessening livestock pressure in suitable ungulate habitat) and proactively (reintroduction in areas with low competition potential).

For mouflon conservation, our results point out that large areas of suitable habitat exist in the southern Caucasus where the mouflon population could be enlarged. This is urgently needed to safeguard the species in the Caucasus (Zazanashvili et al. 2012). However, competition with livestock is very likely in most of these areas and connectivity among them is low. Further, poaching might be a severe threat to existing and new populations, as well as to dispersing animals. Thus, conservation efforts should focus on (1) lessening conflict with livestock, particularly in key mouflon patches, and (2) improving connectivity among priority habitat patches and between seasonal habitat through protection of stepping stones and/or translocations. Promoting private or community-based reserves with small-scale livestock production may help establish mouflon populations with local landowners potentially co-benefiting from wildlife (e.g. tourism, trophy hunting once populations are viable) while reducing poaching risk for mouflon (Allan et al. 2017).

Acknowledgements

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Supplementary Information

Predictor variables

Table SI III-1: *A-priori* hypotheses on how predictor variables are related to mouflon habitat suitability.

Predictor variable	Hypotheses on relation to habitat suitability
Aspect	Highest habitat suitability on south facing slopes, because mouflon prefer warm areas and resource availability on south facing slopes is higher at least in spring.
Human disturbance (distance to roads and to settlements)	Higher habitat suitability with increasing distance because of less human disturbance.
Land cover	Highest habitat suitability in the rangeland class.
Local ruggedness	Highest habitat suitability at low to medium index values because mouflon need relatively flat areas to escape from predators.
Landscape ruggedness	Highest habitat suitability at medium index values, because mouflon in the Caucasus prefer slightly rugged landscapes that provide sheltering opportunities on varying slopes.
Mean fractional woody vegetation cover	Decreasing habitat suitability with increasing woody vegetation because mouflon prefer open areas.

Table SI III-2: Correlation (Pearson's R) among the continuous predictor variables.

	Distance to settlements	Local ruggedness	Landscape ruggedness	Percent woody vegetation
Distance to roads	0.49	0.12	0.22	-0.01
Distance to settlements		0.00	0.05	-0.03
Local ruggedness			0.61	0.36
Landscape ruggedness				0.50

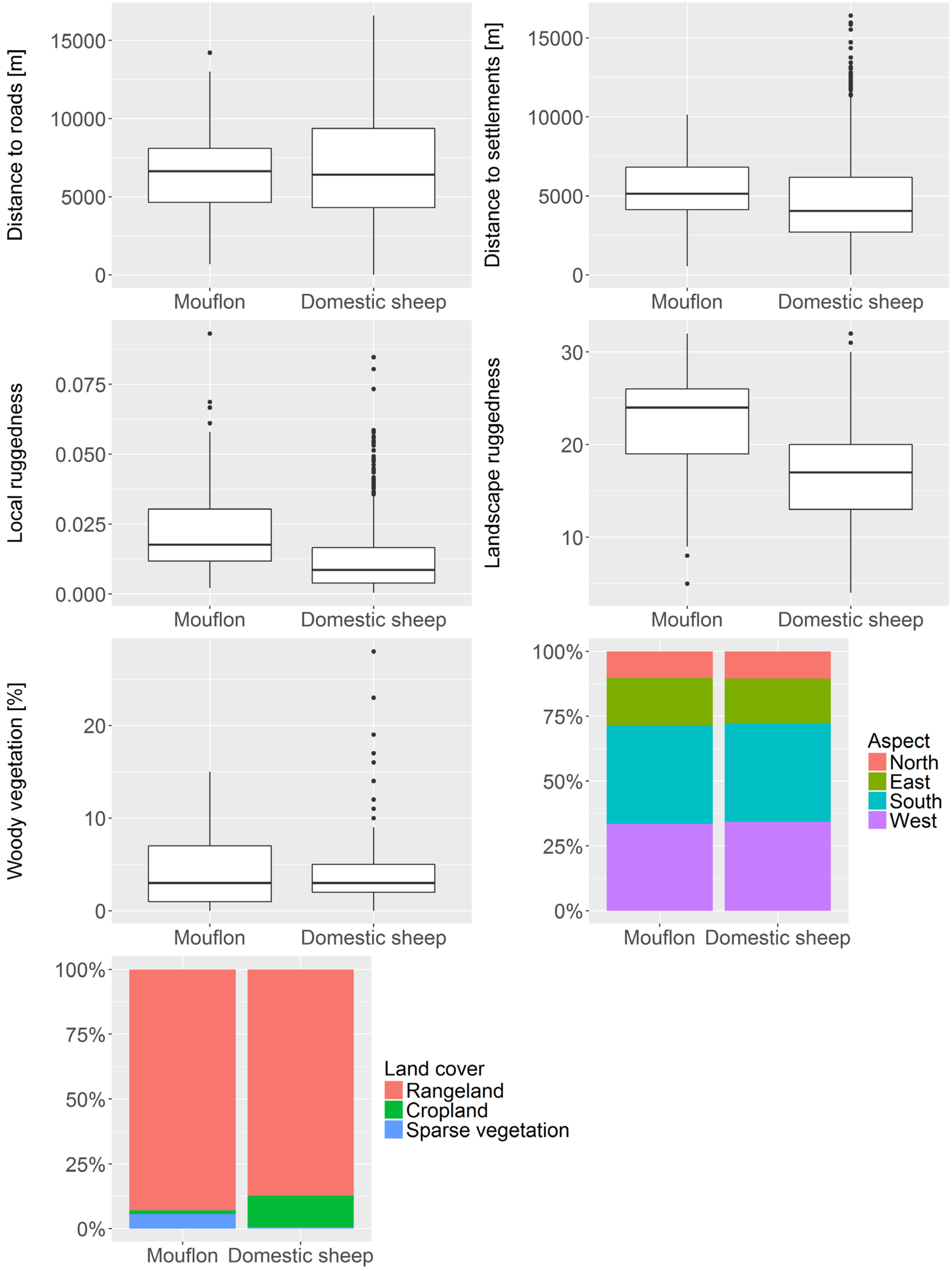

Figure SI III-1: Distribution of predictors at mouflon summer and domestic sheep locations.

Description of the priority habitat patches

Mouflon habitat patches

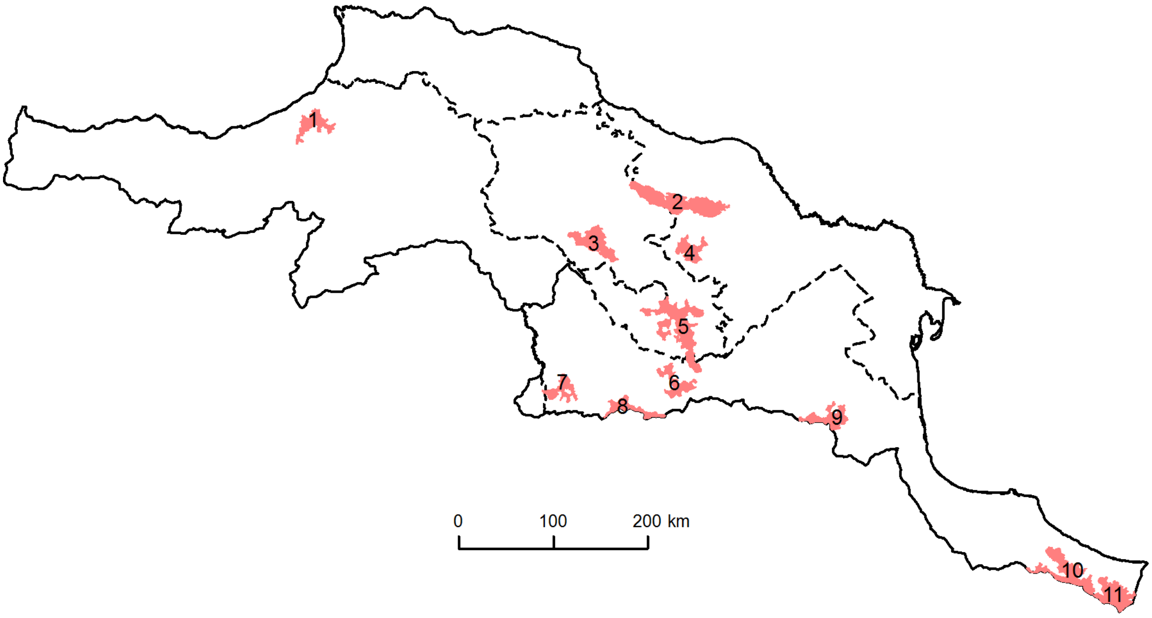

Table SI III-3: Mouflon habitat patches.

Patch ID	Area [km²]	Winter habitat [km²]	% winter habitat	Protected area [km²]	% protected area
1	412	397	96	29	7
2	1271	1159	91	92	7
3	626	481	77	156	25
4	358	260	73	15	4
5	1262	1154	91	771	61
6	364	295	81	93	26
7	322	285	89	0	0
8	334	302	90	0	0
9	432	360	83	63	15
10	816	751	92	14	2
11	646	615	95	9	1

Potential mouflon habitat patches

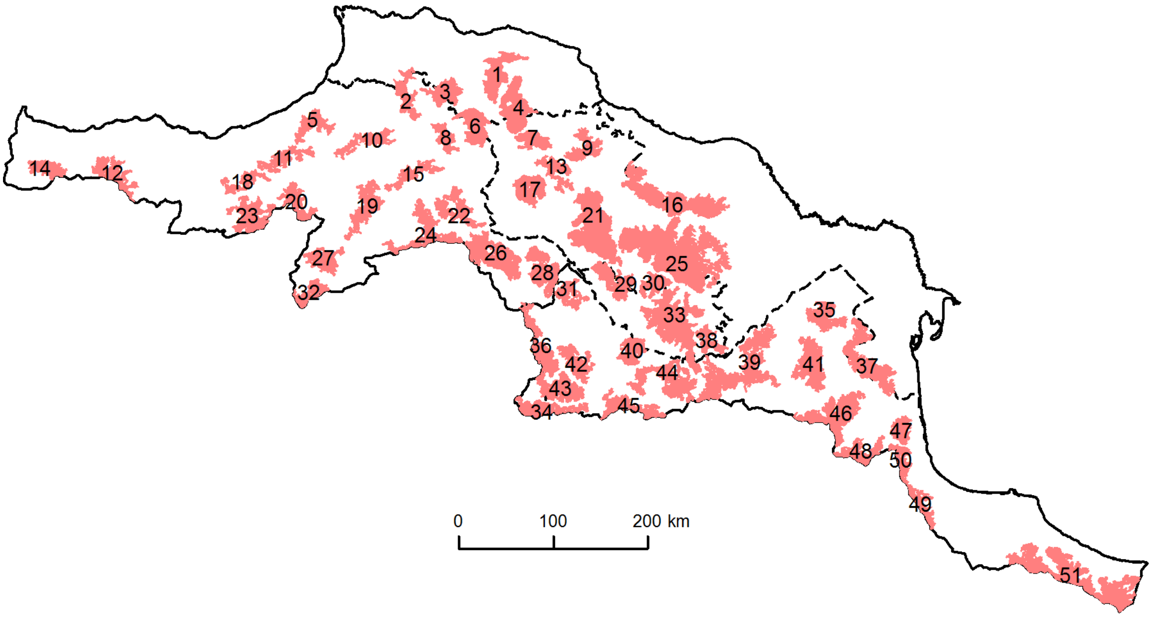

Table SI III-4: Potential mouflon habitat patches.

Patch ID	Area [km²]	Winter habitat [km²]	% winter habitat	Protected area [km²]	% protected area
1	773	208	27	115	15
2	479	51	11	120	25
3	526	86	16	31	6
4	1041	103	10	54	5
5	459	434	95	31	7
6	720	23	3	209	29
7	396	276	70	0	0
8	356	69	19	0	0
9	463	286	62	40	9
10	433	158	36	9	2
11	438	381	87	259	59
12	615	321	52	43	7
13	451	299	66	68	15
14	411	96	23	0	0
15	403	10	3	37	9
16	1737	1243	72	102	6
17	642	89	14	2	0
18	348	222	64	0	0
19	697	120	17	8	1
20	485	101	21	0	0
21	2082	598	29	183	9
22	633	21	3	0	0

23	760	301	40	0	0
24	817	344	42	142	17
25	3900	951	24	289	7
26	1099	151	14	0	0
27	506	123	24	0	0
28	849	214	25	636	75
29	656	412	63	466	71
30	399	203	51	85	21
31	353	134	38	0	0
32	353	14	4	0	0
33	1963	1344	68	941	48
34	570	194	34	0	0
35	564	105	19	192	34
36	692	192	28	0	0
37	1136	158	14	136	12
38	315	268	85	150	48
39	1638	416	25	374	23
40	462	352	76	392	85
41	934	322	35	0	0
42	516	120	23	0	0
43	769	423	55	0	0
44	1052	637	61	262	25
45	610	353	58	0	0
46	1205	467	39	64	5
47	357	157	44	47	13
48	449	13	3	0	0
49	313	258	82	0	0
50	315	168	53	2	1
51	2239	1606	72	29	1

Low-risk patches

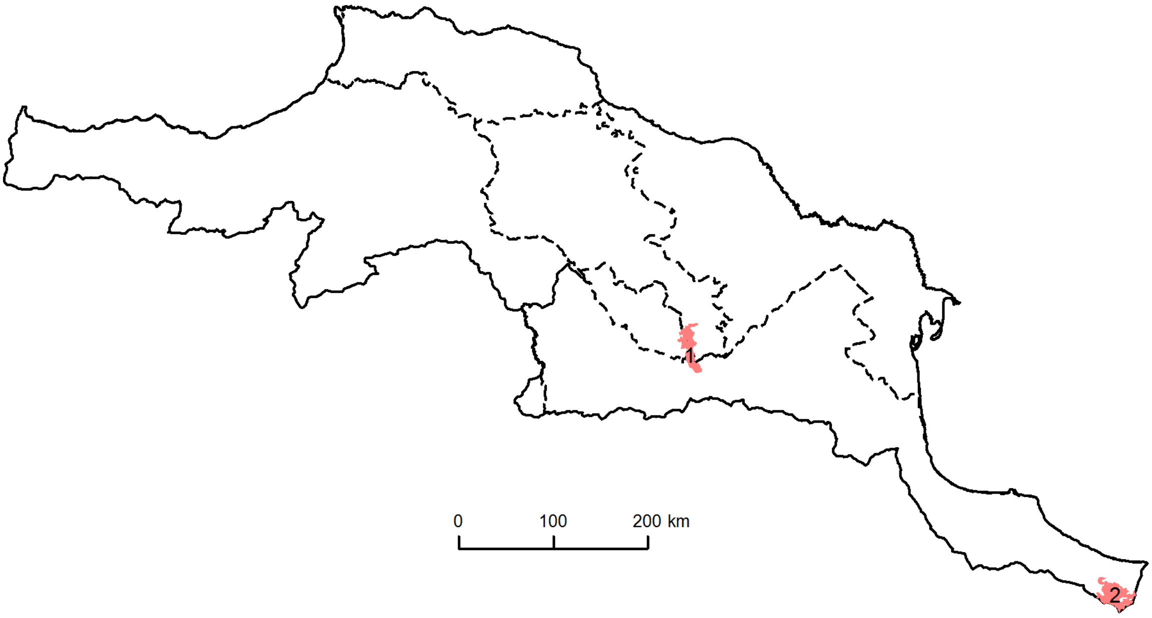

Table SI III-5: Low-risk patches.

Patch ID	Area [km²]	Winter habitat [km²]	% winter habitat	Protected area [km²]	% protected area
1	345	333.01	96	301	87
2	393	377.61	96	9	2

Connectivity patches

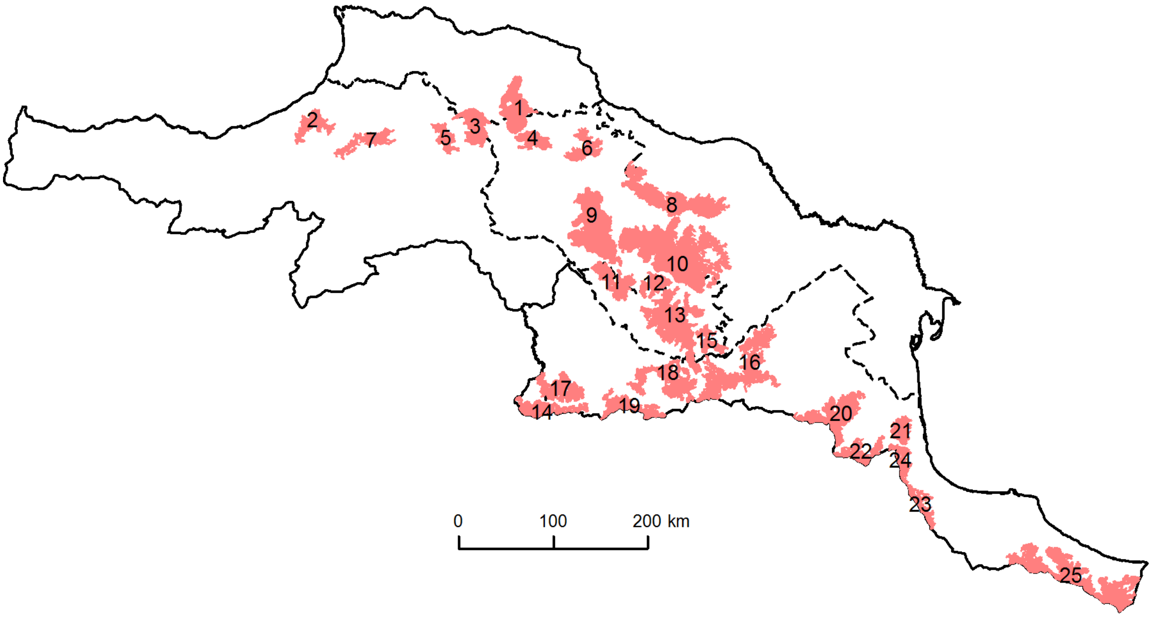

Table SI III-6: Connectivity patches.

Patch ID	Area [km²]	Winter habitat [km²]	% winter habitat	Protected area [km²]	% protected area
1	1041	103	10	54	5
2	459	434	95	31	7
3	720	23	3	209	29
4	396	276	70	0	0
5	356	69	19	0	0
6	463	286	62	40	9
7	433	158	36	9	2
8	1737	1243	72	102	6
9	2082	598	29	183	9
10	3900	951	24	289	7
11	656	412	63	466	71
12	399	203	51	85	21
13	1963	1344	68	941	48
14	570	194	34	0	0
15	315	268	85	150	48
16	1638	416	25	374	23
17	769	423	55	0	0
18	1052	637	61	262	25
19	610	353	58	0	0
20	1205	467	39	64	5
21	357	157	44	47	13
22	449	13	3	0	0
23	313	258	82	0	0
24	315	168	53	2	1
25	2239	1606	72	29	1

Chapter IV:
Reducing persecution is more effective for restoring large carnivores than restoring their prey

submitted

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Abstract

Large carnivores are currently disappearing from many world regions due to habitat loss, prey depletion, and persecution. Ensuring large carnivore persistence requires safeguarding and sometimes facilitating the expansion of their populations. Understanding which conservation strategies, such as reducing persecution or restoring prey, are most effective to help carnivores to reclaim their former ranges is therefore important. Here, we systematically explored such alternative strategies for the endangered Persian leopard (*Panthera pardus saxicolor*) in the Caucasus. We combined a rule-based habitat suitability map and a spatially explicit leopard population model to identify potential leopard sub-populations (i.e., breeding patches), and to test the effect of different levels of persecution reduction and prey restoration on leopard population viability across the entire Caucasus ecoregion and northern Iran (about 737,000 km²). We identified substantial areas of potentially suitable leopard habitat (~120,000 km²), most of which is currently unoccupied. Our model revealed that leopards could potentially recolonize these patches and increase to a population of > 1,000 individuals in 100 years, but only in scenarios of medium to high persecution reduction and prey restoration. Overall, reducing persecution had a more pronounced effect on leopard metapopulation viability than prey restoration: without conservation strategies to reduce persecution, leopards went extinct from the Caucasus in all scenarios tested. Our study highlights the importance of persecution reduction in small populations, which should hence be prioritized when resources for conservation are limited. We show how individual-based, spatially explicit metapopulation models can help in quantifying the recolonization potential of large carnivores in unoccupied habitat, designing adequate conservation strategies to foster such recolonizations, and anticipating the long-term prospects of carnivore populations under alternative scenarios. Our study also outlines how data scarcity, which is typical for threatened range-expanding species, can be overcome with a rule-based habitat map. For Persian leopards, our projections clearly suggest that there is a large potential for a viable metapopulation in the Caucasus, but only if major conservation actions are taken towards reducing persecution and restoring prey.

1 Introduction

Large carnivores have been extirpated or are declining in many world regions, owing to the combined effects of habitat loss, prey depletion, and persecution (Ripple et al. 2014). As a consequence, large carnivore populations today are small, and restricted to isolated fragments of their former range (Wolf and Ripple 2017). This is concerning, given the important role that large carnivores play in food webs and ecosystems (Estes et al. 2011; Ripple et al. 2014). Protecting and restoring large carnivore populations are therefore central goals for conservation globally, yet doing so in increasingly human-dominated landscapes is extremely challenging (Di Minin et al. 2016b).

Ensuring the persistence of large carnivores requires maintaining and sometimes increasing the number and sizes of their populations (Ripple et al. 2014). Past habitat transformation and fragmentation typically does not accommodate contiguous large populations today, and protected areas are generally too small to host viable populations (Akçakaya et al. 2007; Linnell et al. 2005). One conservation approach is therefore to promote the establishment of metapopulations comprising multiple, connected sub-populations to ensure genetic exchange in patchy landscapes and allow for recolonizations of suitable but abandoned patches (Akçakaya et al. 2007). Understanding the potential of landscapes to maintain such metapopulations, the connectivity between available patches, and the factors determining population viability is therefore key to large carnivore conservation.

Persecution and prey depletion (and interactions between them) threaten population viability of large carnivores in many regions (Ripple et al. 2014). Large carnivore persecution has been reported as a major cause of population declines, and can lead to local extinctions (Balme et al. 2009; Newby et al. 2013). Despite being mostly legally protected, large carnivores are persecuted for their fur and body parts, through conflict over livestock, or because they are perceived as a danger (Liberg et al. 2012; Ripple et al. 2014). Reducing persecution has allowed carnivore populations to recover in many cases (Balme et al. 2009; Persson et al. 2015). However, prey depletion is also indirectly threatening large carnivores (Wolf and Ripple 2016). In areas with declining prey biomass, large carnivores tend to have larger home range sizes and lower net reproduction, which often leads to declining populations (Fuller and Sievert 2001; Hayward et al. 2007). Additionally, without sufficient prey, large carnivores increasingly prey on livestock, which leads to retaliatory killings (Khorozyan et al. 2015).

Spatial information on persecution and prey abundance could help to understand better which conservation strategies are effective to promote large carnivore metapopulations. Nevertheless, such information is lacking for most regions. At the same time, implementing conservation strategies for large carnivores is costly because protection must cover large areas, often across international borders. Thus, large carnivore conservation needs to be well-targeted, while typically being based on scarce data. Spatially explicit metapopulation models provide a promising opportunity, and have been used to assess the effect of conservation strategies on large carnivore metapopulation viability (LaRue and Nielsen 2016; Ovenden et al. 2019; Robinson et al. 2015). Moreover, such models are highly informative in assessing which conservation strategies, such as reducing persecution or restoring prey, have a larger impact on metapopulation viability (Chapron et al. 2008).

Here, we systematically explore the relative importance of persecution reduction and prey restoration on determining metapopulation viability of the endangered Persian leopard (*Panthera pardus saxicolor*; recently revised as *P. p. tulliana* by Kitchener et al. 2017) across the entire Caucasus ecoregion. The Caucasus, located between the Black and the Caspian Seas, is a global biodiversity hotspot, and once hosted widespread populations of the Persian leopard and its prey (Krever et al. 2001a; Mittermeier et al. 2004). Diminishing support and enforcement of nature conservation, economic hardships, and armed conflicts led to a poaching crisis and extensive wildlife declines after the breakdown of the Soviet Union and the Iranian Revolution (Bragina et al. 2015a; Ghoddousi et al. 2019; Zazanashvili et al. 2012). Yet, since 2000, the Caucasus has seen a substantial expansion of its protected area network and a slight recovery of some wildlife populations, highlighting a window of opportunity for large carnivore conservation (Breitenmoser et al. 2017; Montalvo Mancheno et al. 2016).

Recent habitat models suggest potential for a larger leopard metapopulation in the Caucasus (Gavashelishvili and Lukarevskiy 2008; Zimmerman et al. 2007). If conservation measures to restore such a metapopulation were initiated, many other species could potentially benefit (e.g., through expanding protected areas, or attracting conservation funding). Such a recovery would very likely depend on source populations in Iran (Breitenmoser et al. 2010; Caucasus Leopard Working Group 2017). In the southern Caucasus, leopards successfully reproduce, and sightings throughout the region, including the northern Greater Caucasus, may indicate that the population is expanding its range (Askerov et al. 2018; Yarovenko and Zazanashvili 2016). The small population size (< 20 individuals, excluding Iran) nevertheless requires swift and targeted conservation actions to encourage range expansion. Yet, it remains unclear which conservation strategies are more effective for doing so.

In this study, our goal was to assess possible conservation strategies such as reducing leopard persecution and restoring the wild prey base for leopards to secure a viable leopard metapopulation in the Caucasus. More specifically, we asked:

(1) What is the potential spatial structure and size of a future Persian leopard metapopulation in the Caucasus?

(2) How do persecution reduction and prey restoration affect leopard metapopulation viability in the Caucasus?

Exploring these questions is widely relevant, as many other species of large carnivores face similar challenges to Persian leopards in the Caucasus. For example, Amur tiger (*P. tigris altaica*) recovery is challenging because tigers come into conflict with livestock owners and suffer from wild prey depletion (Li et al. 2019). Likewise, jaguars (*P. once)* are rapidly disappearing from the Gran Chaco in South America, one of their strongholds until recently, owing to conflicts with ranchers, probably an indirect effect of a depleted prey base and habitat destruction (Romero-Muñoz et al. 2019). Yet, how to halt these losses effectively and how best to support large carnivore populations given limited conservation funding remains unclear (Ripple et al. 2014). Additionally, data on large carnivores are often lacking because of their elusive nature and small populations, which makes it challenging to assess alternative conservation strategies (Amano and Sutherland 2013; Schadt et al. 2002). Our study aims to answer such questions for a species and region with limited data and of high conservation concern.

2 Material and methods

2.1 Persian leopards in the Caucasus and northern Iran

Our study region comprised the Caucasus ecoregion, as delineated by the Ecoregion Conservation Plan for the Caucasus (Williams et al. 2006a), and extended across the Talysh-Alborz Mountains in northern Iran (Figure IV-1). The natural vegetation of the region comprises temperate, mainly broadleaf and mixed forests along the mountain ranges, but includes large areas of steppe drylands as well as arid woodlands and semi-deserts in the East. Most parts of our study region are mountainous, and elevations can reach more than 5,500 m.

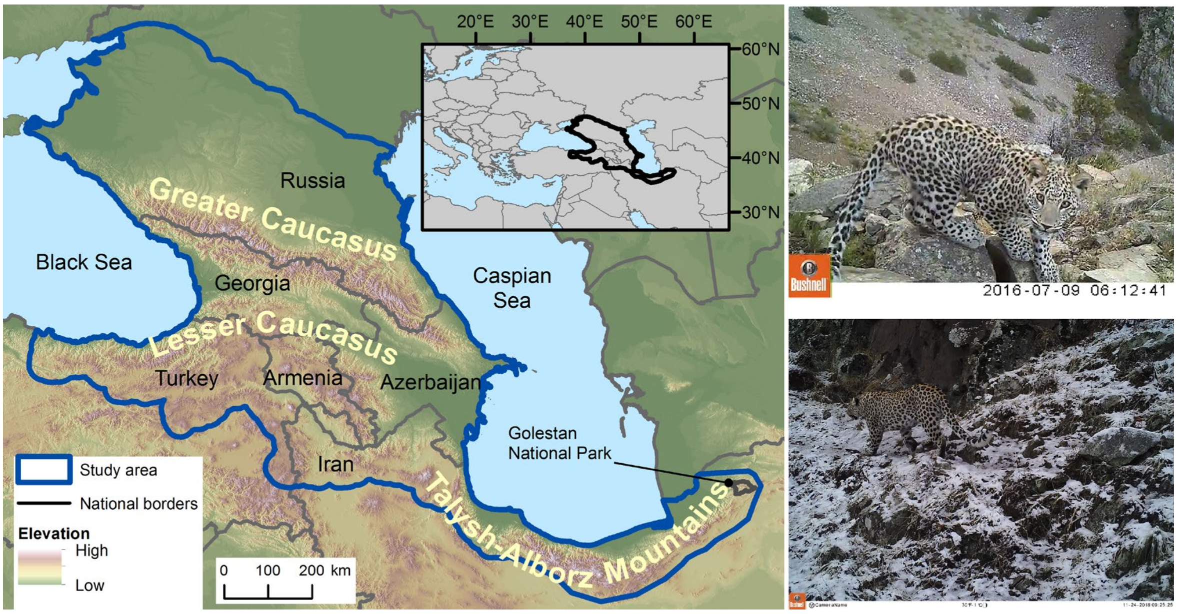

Figure IV-1: Study area, main mountain ranges, and the location of Golestan National Park in north-eastern Iran. The right panel shows two camera trap pictures of the same leopard from the Zangezur region in Nakhchivan, Azerbaijan (top) and the Khosrov Forest State Reserve in Armenia (bottom). The locations are separated by a ~170 km straight-line distance. Photo credit: WWF-Caucasus.

Until at least the mid-18th century, Persian leopards occurred throughout the entire Caucasus (Jacobson et al. 2016). Today, resident population nuclei are restricted to the southern rim of the Lesser Caucasus (Askerov et al. 2018; Khorozyan and Abramov 2007; Stein et al. 2016). This population is severely threatened and dependent on the Iranian source population, which itself is likely to decline (Moqanaki et al. 2013). Leopards in the Caucasus prey mainly on large ungulates, which are nevertheless also under pressure from poaching and competition with livestock (Bleyhl et al. 2019; Mallon et al. 2007). In the Greater Caucasus, no leopard reproduction has been detected recently (Caucasus Leopard Working Group 2017), but since 2016, six leopards have been reintroduced to the Russian Greater Caucasus (see Supplementary Information).

2.2 Spatial structure of a potential leopard metapopulation

To assess the structure of a potential leopard metapopulation, we first mapped suitable habitat. Leopards can thrive in a range of environments if prey is available (Gavashelishvili and Lukarevskiy 2008; Nowell and Jackson 1996). We developed a rule-based habitat suitability model on a 5 km x 5 km grid (mean maximum leopard movement distance between recaptures in a camera trap study; Ghoddousi et al. 2010). We used a range of predictors related to shelter and ambushing habitat, human-induced mortality risk, and snow cover, which characterize leopard habitat suitability (Breitenmoser et al. 2007; Lukarevsky et al. 2007b). Specifically, we assumed increasing habitat suitability with increasing ruggedness or increasing forest cover in areas that are distant from roads and human settlements and have a low proportion of surrounding croplands (Gavashelishvili and Lukarevskiy 2008; Zimmerman et al. 2007). Further, we excluded areas with a very high snow cover in winter (see Supplementary Information for details on the specific rules used to derive the habitat suitability map). We purposefully did not use a correlative species distribution model, because only very few leopards are left in the Caucasus, and the species is far from being in equilibrium with its environment, which could introduce substantial bias in such models (Guisan and Thuiller 2005). To validate our habitat model, we used 36 leopard locations from camera traps and 53 locations from indirect signs such as scrapes or scats from WWF's Caucasus Programme Office and from other surveys (Soofi et al. 2018). We then calculated the continuous Boyce index (Hirzel et al. 2006) and the area under the ROC curve (AUC; using 10,000 random pseudo-absence points) as a measure of accuracy (Fielding and Bell 1997). The continuous Boyce index measures the correlation between the habitat suitability prediction and the predicted to expected ratio of the frequency of validation points using a moving window of differing widths (negative values indicating an inverse model, values around zero a random model, and one a perfect model; Boyce et al. 2002; Hirzel et al. 2006). The AUC value contrasts sensitivity and specificity across all possible thresholds, with values ranging from 0 to 1 (1 indicating a perfect model; Jiménez-Valverde 2012).

To identify potential sub-populations, we first selected those cells with a habitat suitability above the 25th percentile of values at our known leopard locations (Pitman et al. 2017). We then selected continuous suitable areas of at least 250 km² (i.e., ~ 2.5 home ranges and large enough to host breeding populations; Farhadinia et al. 2015; Farhadinia et al. 2018). Although home range sizes for female leopards are known to be smaller (Fattebert et al. 2016), no study has assessed this specifically for Persian leopards. Before applying the minimum area threshold, we split sub-population patches to exclude potential barriers such as roads and very high ridges within sub-populations because we did not model movement within patches. Accordingly, we split sub-population patches using main roads (categories motorways, trunk, and primary, derived from Open Street Map) and the Russian border, which roughly follows the main ridge of the Greater Caucasus and is therefore typically at high elevations (~2,700 m). We assessed the protection status of each patch using terrestrial protected areas from the World Database on Protected Areas (IUCN and UNEP-WCMC 2019) and WWF's Caucasus Programme Office database (wwfcaucasus.net; Figure SI IV-2).

2.3 Metapopulation parameterization

We parameterized a spatially explicit metapopulation model using the software RangeShifter (Bocedi et al. 2014). RangeShifter is an individual-based modelling platform, which integrates a demographic and a dispersal model to predict metapopulation dynamics. We developed a stage-structured model with four stages and annual time steps (Caswell 2001). Survival rates were based on all known age-structured estimates for leopard populations anywhere in the world (i.e., studies from Botswana, Namibia, and South Africa; Table IV-1 and Table SI IV-1). Mean fecundity (i.e., number of offspring per female per year) was set to 1.92 (Daly et al. 2005) and modelled as negatively density-dependent (i.e., decreasing fecundity with increasing density; Table IV-2). Further, males could mate with up to three females, and only adults (older than 2 years) were allowed to breed (Lukarevsky et al. 2007b). Females in our model paused for one year between reproductions (Daly et al. 2005). To consider environmental stochasticity (i.e., the effects of year-to-year variation in environmental conditions on demography), we applied random variation to mean fecundity so that it fluctuated between 1 and 4 (i.e., range of number of cubs reported from captivity; Lukarevsky et al. 2007b; eqn. S2-S3). We assumed an initial population of 352 individuals for our study area (based on a population size estimate of northern Iran; Kiabi et al. 2002). Because abundance of leopards in the area is not well known, we distributed these individuals randomly amongst patches with known leopard occurrence (i.e., patches with locations matching our presence dataset or a neighboring cell, and patches that overlapped with a protected area that is known to host leopards) and proportionally to patch size. We distributed individuals with equal sex ratio and drew initial ages from a Poisson distribution with a mean of seven years so that individuals were no older than 19 years (Balme et al. 2013). Since survival rates were higher for females than for males, the adult sex ratio in our models was slightly female-biased (1:1.10 – 1:1.39 m/f).

We modelled dispersal of sub-adults among patches using the Stochastic Movement Simulator implemented in RangeShifter, a step-based model that accounts for interaction between individual movements and landscape structure (Palmer et al. 2011; see Supplementary Information). We set our maximum dispersal distance to 170 km, based on the Euclidean distance between the Zangezur Range in southern Azerbaijan and Khosrov Forest State Reserve in Armenia – a distance that was recently completed by an identified sub-adult leopard, presenting the longest documented dispersal event in the region (Askerov et al. 2018). Individuals died if they reached this distance without settling in a patch. Further, we modelled the probability for each sub-adult individual to disperse from a patch and to settle in a patch as a density-dependent function (see Supplementary Information and Table IV-2 for equations and an overview of all RangeShifter parameters used in our models). To estimate cell-wise resistance to movement, we used a leopard-specific cost surface based on the land cover of each cell from Bleyhl et al. (2017). We also tested our inverted habitat map as a cost surface (Fattebert et al. 2015b), which did not result in substantial differences in regard to our model outcomes.

We ran 100 model replicates and calculated the mean total number of individuals and 99% confidence intervals annually up to 100 simulated years. We chose 100 years, because we wanted to assess possible conservation strategies and population prospects in the long run, and initial models indicated that (sub-)population extinction sometimes occurred after more than 60 years. Further, we calculated metapopulation extinction probability as the proportion of model replicates with no individuals after 100 years. Finally, we calculated the probability of each patch being occupied by at least one leopard after 100 years, by dividing the number of times a patch was occupied after 100 years by the total number of replicate runs.

2.4 Persecution reduction scenarios

To assess the effect of persecution reduction on leopard metapopulation viability, we increased leopard survival rates of all stages (Chapron et al. 2008; Liberg et al. 2012). We therefore used minimum, mean, and maximum values from our survival rate estimates as high, medium, and low persecution reduction scenarios (Table IV-1 and Table SI IV-1; Balme et al. 2009; Balme et al. 2017; Daly et al. 2005; Swanepoel et al. 2015).

Table IV-1: Female and male leopard survival ratesthat were used to characterize the three persecution reduction scenarios in our metapopulation model (based on Balme et al. (2009); Balme et al. (2017); Daly et al. (2005); Swanepoel et al. (2015)).

Stage	Survival rate (female / male)		
	Persecution reduction scenario		
	Low	Medium	High
Juvenile (0–1 years)	0.39 / 0.39	0.52 / 0.53	0.71 / 0.71
Sub-adult (1–3 years)	0.79 / 0.54	0.90 / 0.79	0.98/ 0.94
Adult (3+ years)	0.86 / 0.67	0.89 / 0.85	0.95 / 0.94

2.5 Prey restoration scenarios

Prey availability is an important factor in determining leopard density (Fuller and Sievert 2001; Ghoddousi et al. 2017; Hayward et al. 2007). Therefore, we simulated different prey restoration scenarios by altering possible leopard densities in relation to available prey biomass (Hayward et al. 2007). To calculate the available prey biomass, we used past and present estimates for bezoar goat (*Capra aegagrus*) and urial sheep (*Ovis vignei*) from Golestan National Park in north-eastern Iran (see Supplementary Information; Ghoddousi et al. 2019). From the available prey biomasses, we estimated that the leopard sub-population patches could sustain 0.856 individuals/100 km² in a low prey restoration scenario, 3.817 individuals/100 km² in a medium prey restoration scenario, and 6.778 individuals/100 km² in a high prey restoration scenario using the following equation from Hayward et al. (2007):

$$log_{10}(leopard\ density) = -2.455 + \ 0.456 * (log_{10}(prey\ biomass)) \qquad \text{(eqn. 1)}$$

2.6 Sensitivity analysis

First, we assessed model sensitivity to survival rates, fecundity, and strength of density dependence. Using the medium persecution reduction and medium prey restoration scenario, we conducted a sensitivity analysis assessing how decreasing and increasing each parameter by 5% changed our two main model outcomes: extinction probability and leopard abundance after 100 years. Second, we tested how altering the maximum dispersal distance from 170 km to 47 km and 353 km (maximum dispersal distances in Fattebert et al. (2015a) and in Fattebert et al. (2013), respectively) and the initial population size from 352 individuals to 200 and 500 individuals would affect model outcomes. Third, the sex ratio in leopard populations is often female biased, because males tend to have larger home ranges and are territorial (Bailey 1993; Kittle et al. 2017; Kumar et al. 2019). Additionally, sub-adult males tend to have lower survival rates than females due to human-caused mortality, which can lead to female-biased sex ratios (Thapa 2014). Therefore, we also tested altering the sex ratio of our initial population from 1:1 to 1:2 and 1:3 (male/female). Fourth, female leopards often tend to be more philopatric than males (Fattebert et al. 2015a). We therefore tested decreasing the maximum emigration probability (at high densities) for females incrementally from 1.0 to 0.1 (in steps of 0.1). Finally, we assessed sensitivity of our model towards the ongoing reintroductions of leopards to the Russian Greater Caucasus by having additional individuals at model initialization in Russia (see Supplementary Information for further detail on the sensitivity analyses).

Table IV-2: RangeShifter equations and parametersused to model the stage-structured leopard metapopulation. For details on the equations refer to the Supplementary Information.

Demographic parameters	**Value**	
# of stages	4 (1 juvenile, 2 sub-adults, 1 adult)	
Survival rates	Scenario dependent, see Table IV-1	
Fecundity	1.92	
Density dependence in fecundity	$\phi_i = \phi_{0,i} * e^{-b\sum_{j=1}^{S}\omega_{ij} N_{j,t}}$ ϕ_i = fecundity of stage *i*; $\phi_{0,i}$ = maximum fecundity of stage *i* at low densities; *S* = number of stages; ω_{ij} = contribution of stage *j* to the density dependence in the fecundity of stage *i*; $N_{j,t}$ = number of individuals at time *t* in stage *j*	(eqn. 2)
Strength of density dependence (b)	Scenario dependent, see Table SI IV-2	
# of reproductive seasons before subsequent reproduction (in our case, one season = one year)	1	
Maximum age	19	
Initial population size	352	
Dispersal parameters (limited to sub-adults)	**Value**	
Density-dependent emigration probability	$d = \frac{D_0}{1+e^{-(bN_{i,t} - \beta)\alpha}}$ D_0 = maximum emigration probability, β = inflection point, α = slope, *b* = strength of density dependence, $N_{i,t}$ = number of individuals in patch *i* at time *t*	(eqn. 3)
Maximum emigration probability D_0	1.0	
α (slope)	10.0	
β (inflection point)	0.5	
Density-dependent settlement probability	$p_s = \frac{S_0}{1+e^{-(bN_{i,t} - \beta_s)\alpha_s}}$ S_0 = maximum settlement probability, β_s = inflection point, α = slope, *b* = strength of density dependence, $N_{i,t}$ = number of individuals in patch *i* at time *t*	(eqn. 4)
Maximum settlement probability S_0	1.0	
α_s (slope)	-10.0	
β_s (inflection point)	0.5	
Perceptual range	1 cell (5 km)	
Maximum number of steps	28	
Directional persistence	2.5	
Environmental stochasticity parameters	**Value**	
Noise value ε	$\varepsilon_{t+1} = \kappa\varepsilon_t + \omega_t\sqrt{1-\kappa^2}$ κ = the autocorrelation coefficient, ω = a random variable	(eqn. 5)

Environmental stochasticity in fecundity	$\phi_{i,t+1} = \phi_{0,i}(1 + \varepsilon_{t+1})$	(eqn. 6)
Minimum and maximum fecundity	1 and 4	
Temporal autocorrelation κ	0.0	
Random variable ω	$N(0, 0.25)$	

3 Results

Our habitat suitability map had a high accuracy in predicting known leopard occurrences (continuous Boyce index of 0.73 and an AUC of 0.86). Suitable leopard habitat was widespread across the study area (Figure IV-2). In total, we identified 74 potential sub-population patches that together covered 119,552 km². Patches varied greatly in size (range 250–18,478 km², mean: 1,616 km², standard deviation 2,779 km²). We identified potential sub-population patches in all six countries of the Caucasus ecoregion. Russia had the largest total patch area (40,534 km²), followed by Iran (34,757 km²) and Georgia (16,978 km²; Table IV-3). Several large patches were located in the Greater Caucasus (in total 58,930 km²) and along the Talysh-Alborz Mountains in southern Azerbaijan and northern Iran (31,995 km²). Almost one quarter (23%) of the total sub-population patch area is currently protected. The proportion of protected area differed among countries with Russia having the highest (32%) and Turkey the lowest proportion protected (8%; Table IV-3).

Table IV-3: Breeding patch numbers and areas and their area under protection across the countries.

Country	# of breeding patches*	Breeding patch area [km²]	Area under protection [%]
Armenia	6	3,467	14
Azerbaijan	9	13,084	27
Georgia	13	16,978	15
Iran	22	34,757	19
Russia	12	40,534	32
Turkey	15	10,732	8
Total	74	119,552	23

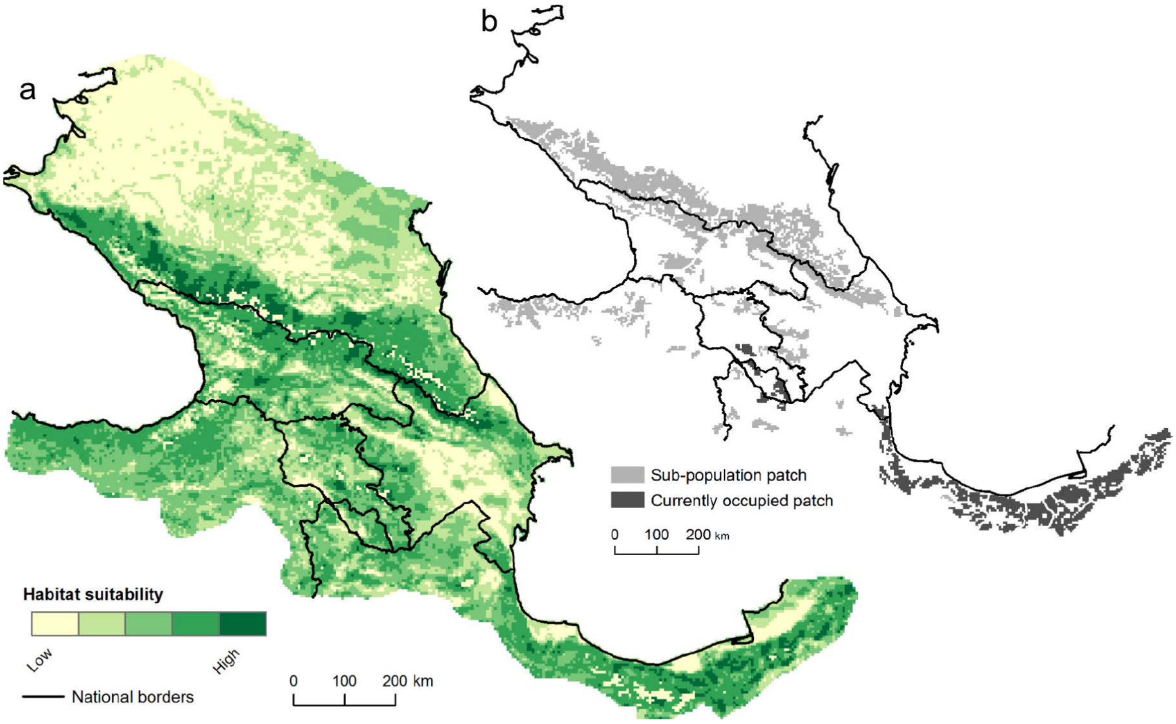

Figure IV-2: (a) Distribution of suitable leopard habitat and (b) potential leopard sub-population patchesand currently occupied patches across the Caucasus ecoregion and northern Iran (see Supplementary Information Figure SI IV-3 for details).

Our metapopulation model showed that we could expect the establishment of a stable population given the current initial population size under a scenario of medium persecution reduction and medium prey restoration (Figure IV-3). High prey restoration (with medium persecution reduction) resulted in moderate population increases, with up to 537 individuals on average after 100 years (53% increase over initial abundance). For the high persecution reduction scenarios, substantial population increases were only possible when combined with medium to high levels of prey restoration. Specifically, high persecution reduction led to mean population increases of up to 1,048–2,288 individuals (3-fold to 6.5-fold increase after 100 years) for medium and high prey restoration, respectively. Additionally, extinction probability after 100 years was 0% for all high persecution reduction scenarios and for medium persecution reduction paired with medium prey restoration. However, extinction probability increased to 86% for low prey restoration under medium persecution reduction. Low persecution reduction led to sharp population declines and the metapopulation went extinct after at most 60 years, regardless of prey restoration.

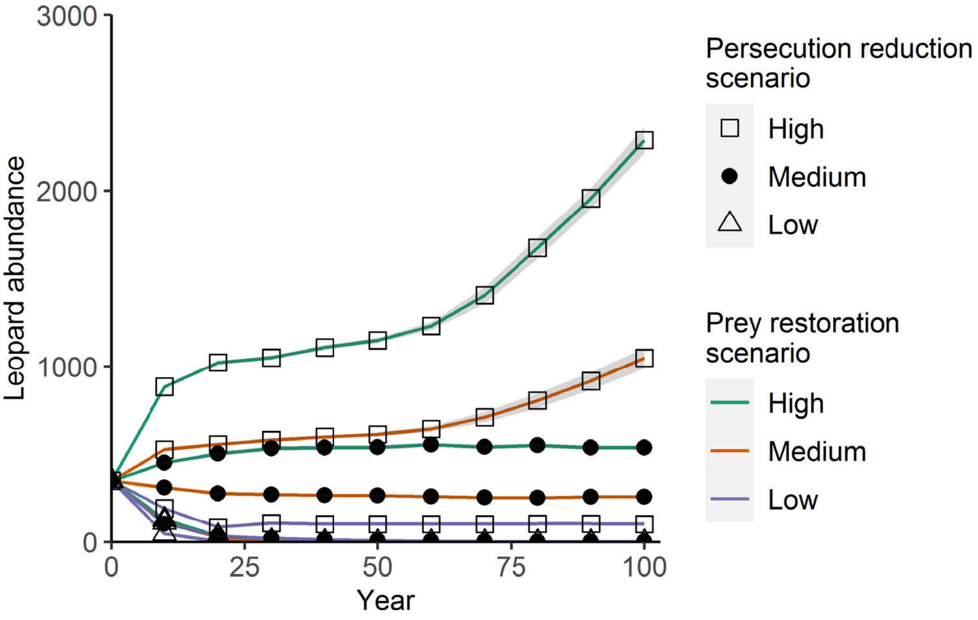

Figure IV-3: Leopard total population size across the nine conservation scenariosfor 100 years.The solid lines show mean estimates and the shaded bands 99% confidence intervals. The Caucasus leopard metapopulation went extinct within 60 years for all three scenarios with little investment into reducing persecution and therefore, those results are not visible in the graph.

The mountain range of the Greater Caucasus (northern part of our study area, Figure IV-1) was colonized within 100 years only in the high persecution reduction scenarios, assuming medium to high prey availability (Figure IV-4). Nevertheless, the currently occupied patches in the Lesser Caucasus and Iran remained occupied after 100 years also for the medium persecution reduction scenarios if prey restoration was medium or high.

Our metapopulation model was relatively robust to variations in survival rates, fecundity, and the strength of density dependence (Figure IV-5). Changing the adult female survival rate had the strongest effect on mean leopard abundance after 100 years (5% decrease in survival rate led to 53% decrease in abundance, while 5% increase in survival rate led to 34% increase in abundance). Altering the maximum dispersal distance (to 47 km and 353 km) did not affect extinction probability but had an effect on the resulting leopard abundance after 100 years (Figure SI IV-4). Altering the initial population size (to 200 and 500 individuals) did not affect model outcomes markedly (Figure SI IV-4). Initial sex ratios of 1:2 and 1:3 (m/f) did not lead to notable differences in leopard abundance and extinction probability (260 individuals after 100 years on average for sex ratios of 1:2 and 1:3 instead of 258 individuals for the mean persecution reduction and prey restoration scenario and no change in extinction probability). Decreasing the maximum emigration probability for females did also not lead to marked changes of our model outcomes (Table SI IV-4). Adding additional individuals at model initialization to the Greater Caucasus to test model sensitivity to ongoing reintroductions in that area did not affect our high and low persecution reduction scenarios (no change in extinction probability, only slight changes in leopard abundance). However, we detected some effect on model outcomes for the medium persecution reduction scenarios, where 5–50 additional leopards in the Greater Caucasus led to a 10%–90% higher abundance after 100 years and a decreased extinction probability (Table SI IV-4 and Figure SI IV-8).

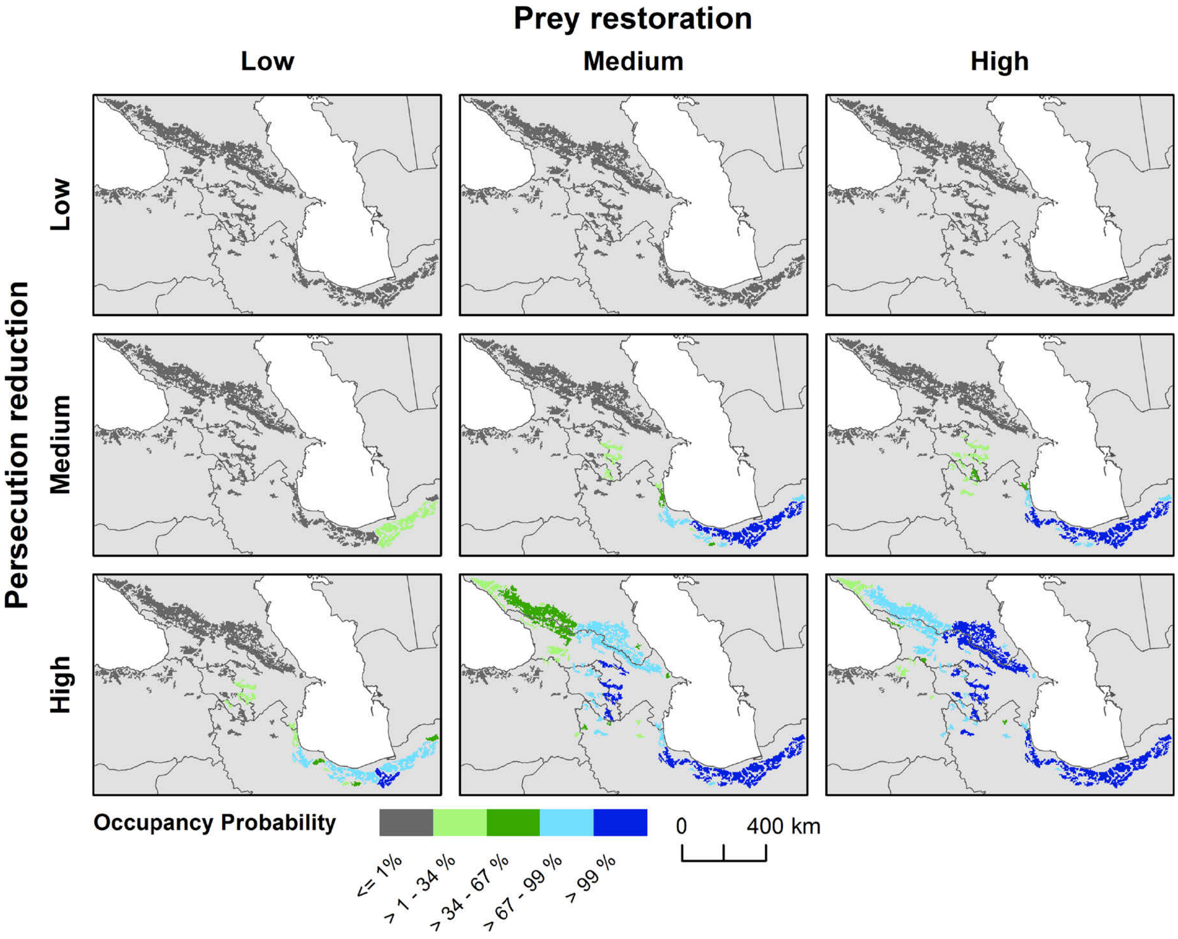

Figure IV-4: Probability of leopard occurrence after 100 years in a patch (the proportion of replicate simulations in which a patch was occupied after 100 years) for all combinations of persecution and prey restoration scenarios.

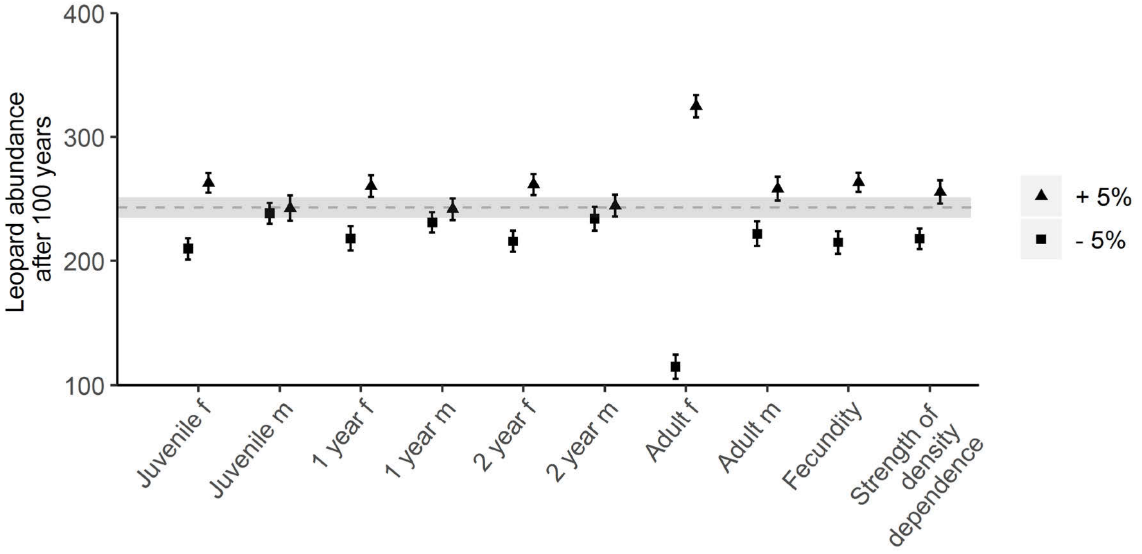

Figure IV-5: Sensitivity of leopard abundance after 100 years towards increasing and decreasing survival rates (first eight parameters), fecundity, and strength of density dependence of the medium direct killing control and prey restoration scenario by 5% (f = female, m = male). Symbols indicate mean values, error bars show 99 percent confidence intervals. The dashed grey line and the shaded area show the mean value and 99 percent confidence interval for the medium persecution reduction and prey restoration scenario.

4 Discussion

Given the wide-ranging nature of large carnivores, ensuring their persistence and fostering their recovery can be a colossal task: where should conservation action start, and which strategies are most effective? In our study, conservation measures to reduce persecution, and thus the killing of leopards, had a much higher impact on the long-term viability of the leopard population than that of prey restoration, underlining the often devastating effect of losing individuals in small populations and suggesting a high sensitivity of large carnivore populations to increased levels of mortality. Using the case of the endangered Persian leopard in the Caucasus, we investigated three key issues of relevance for many situations where information on large carnivore population dynamics is scarce, thereby hindering the identification of promising conservation strategies. First, we explored the relative importance of conservation actions that target human persecution of large carnivores and depletion of their prey base, which are central drivers of large carnivore decline globally. Second, we show how an individual-based, spatially explicit simulation framework can be used to assess potential pathways for restoring large carnivores. Third, we outline an approach that works for data-deficient regions and species, which is a typical situation for large carnivores worldwide. For the Caucasus, our study clearly suggests a large potential for leopards to recolonize unoccupied habitat and establish a viable metapopulation – if conservation measures are ramped up.

Using a rule-based habitat assessment, we identified ample leopard habitat across the mountain ranges of our study area (i.e., Greater and Lesser Caucasus, Talysh-Alborz Mountains). This is in line with previous studies mapping leopard habitat suitability in parts of our study area (Ebrahimi et al. 2017; Farhadinia et al. 2015; Gavashelishvili and Lukarevskiy 2008; Zimmerman et al. 2007). Our assessment highlights the importance of the Lesser Caucasus, the only region where leopard reproduction currently occurs in the Caucasus. Moreover, the Greater Caucasus could play a major role in leopard recovery, because it contains almost half of the area of all potential sub-population patches we identified. Parts of these sub-population patches are already under protection (32% and 15% in Russia and Georgia, respectively). However, it is unlikely that leopards are currently breeding in the Greater Caucasus, and considering the characteristics of felid populations in recolonizing their historical range, it is likely that only long-range dispersing males will arrive there from the Lesser Caucasus in the near future.

Our metapopulation analysis clearly suggests that high mortality is the principal reason for why the leopard population is not growing. Only high persecution reduction led to a substantial population increase, whereas low persecution reduction led to sharp population decreases. All prey depletion scenarios had smaller effects on our model outcomes. While some studies and historic hunting bags indicate that large carnivores are fairly resilient to high rates of offtake and thus low survival rates (Karanth and Stith 1999; Lindzey et al. 1992), our results suggest that leopard populations are susceptible to high mortality, at least when persecution is not sex-biased (which we did not test). This corroborates studies highlighting low survival rates as a main determinant of large carnivore declines (Balme et al. 2009; Dalerum et al. 2008; Williams et al. 2017). Historically, larger population sizes or nearby source populations could have contributed to buffer high mortality rates (Chapron et al. 2008). Today, many large carnivores occur in small and isolated populations, where the death of only a few individuals can substantially increase the extinction probability of the population, underlining the importance of effective law enforcement and conflict mitigation measures to reduce persecution (Bisht et al. 2019; Heurich et al. 2018).

Persian leopards are under marked pressure from persecution, particularly outside protected areas (Kiabi et al. 2002; Naderi et al. 2018). Several leopards have been killed in the Lesser Caucasus or observed missing a limb, indicating the use of snare and gin traps (Memarian et al. 2018), and the only confirmed transboundary leopard in the Talysh Mountains was poached in 2014 (Maharramova et al. 2018). Positive effects of persecution reduction on large carnivore populations have been shown also for other regions. For example, leopard population growth rates increased by about 15% after implementing conflict mitigation measures such as promoting alternative husbandry methods to prevent livestock depredation in South Africa (Balme et al. 2009). Likewise, preventing persecution lowered the modelled extinction probability of a lynx (*Lynx lynx)* population in the Bohemian Forest in Europe from up to 74% to less than 1% (Heurich et al. 2018). While our analyses highlight avenues to lower leopard mortality in the Caucasus, it is worrying that three quarters of the sub-population patch area we found are unprotected, making the implementation of measures to effectively reduce persecution challenging.

Despite the importance of persecution reduction, our results suggest that prey restoration is also needed to increase the carrying capacity for leopards, and hence their abundance and density, and to decrease their population extinction probability. The situation we found for Persian leopards is likely exemplary for many threatened large carnivores. Prey depletion is a major threat to large carnivores globally, because large herbivores that are mostly threatened themselves constitute the majority of large carnivore prey (Wolf and Ripple 2016). For example, decreases in ungulate densities likely led to the absence of tigers (*P. tigris*) in a reserve in India (Ramakrishnan et al. 1999). Likewise, in Central Asia, an increase in livestock numbers reduced native ungulate densities, which promoted human retaliatory killings of snow leopards (Berger et al. 2013). Additionally, even our medium prey restoration scenario was based on prey abundances from a relatively prey-rich and strictly protected area in Iran (Ghoddousi et al. 2019). Therefore, current potential leopard densities are likely to lie closer to our lowest prey restoration scenario, underlining that sufficient prey is essential to prevent population declines (Zimmerman et al. 2007). Often, it is indeed a combination of persecution reduction and prey restoration that fosters population increase of large carnivores (Jędrzejewski et al. 2017).

We used all available data on leopards from the Caucasus and elsewhere to parameterize a spatially explicit metapopulation model across a large and heterogeneous biodiversity hotspot. Our findings are in line with other large carnivore studies, while providing new insights into the relative impact of persecution reduction and prey restoration. Nevertheless, some challenges remain. First, persecution reduction of leopards and their prey can be synergistic. Therefore, effective prevention of persecution would likely reduce both leopard and prey mortality (Ramesh et al. 2017). Second, neither persecution reduction nor prey restoration will act consistently across space and stage classes. For example, low survival rates of some sub-populations might be compensated by immigration from neighboring populations, which we did not consider (Chapron et al. 2008). Third, variability in survival rates, for example due to extreme weather events, disease outbreaks, or periods of heavy poaching can have large impacts on population viability, particularly in small populations (Melbourne and Hastings 2008). Because RangeShifter does not currently allow for variability in survival rates, we could not account for this in our model, and might therefore partly underestimate the extinction risk of leopards in the Caucasus. Finally, our habitat map possibly overestimated sub-population patches in areas that encompass small-scale agriculture or tree-crops (e.g., northern Turkey), because these were not differentiated from forest in our land-cover map (Bleyhl et al. 2017). Leopards are highly adaptable and persist well in such landscapes, but we caution that human-leopard conflict might be high (Navya et al. 2014).

Limited resources require conservation efforts to be targeted towards the most effective strategies. Three general insights for large carnivore conservation may be derived from our work. First, our study highlights the importance of preventing the loss of individuals in small populations. Reducing persecution had a much higher impact on the long-term population survival than prey restoration, making a case for actions to reduce human-carnivore conflicts that might lead to carnivore killings (e.g., compensation schemes, adapted livestock husbandry practices, promoting tolerance, and awareness raising). Second, our work shows the value of individual-based, spatially explicit metapopulation models to assess where large carnivores may recolonize suitable habitat, compare conservation strategies to promote such recolonizations, and quantify the long-term prospects of carnivore populations under alternative scenarios. Finally, our study outlines how data-sparse situations can be overcome, which are typical for threatened range-expanding or recovering species that are far from occupying all suitable areas (Fechter and Storch 2014; Guisan and Thuiller 2005). Our rule-based habitat map validated favorably against known leopard presence locations, highlighting the value of such a relatively simple approach for assessing and predicting large carnivore recolonizations when combined with a mechanistic population model.

For Persian leopards, our results contribute to the implementation of the objectives outlined in the Strategy for the Conservation of the Leopard in the Caucasus Ecoregion (Caucasus Leopard Working Group 2017). We clearly show that the Caucasus can indeed host a viable leopard metapopulation if appropriate conservation measures are augmented, and we highlight the patches that are likely important for establishing such a metapopulation.

Measures to reduce persecution should be targeted at carnivore-adapted livestock husbandry, and compensation schemes for livestock losses (e.g., corralling vulnerable animals at night, guards during the day; Balme et al. 2009). Particularly since the early 2000s, many protected areas have been established in the Lesser Caucasus to prevent leopard persecution more effectively and restore prey populations (Zazanashvili et al. 2020). Further, through the active involvement of local people, leopard and prey species monitoring has substantially increased, allowing for better predictions of population trends and conflict hotspots (Zazanashvili et al. 2020). Our results can thereby assist in identifying areas that are likely to be recolonized, and we suggest pro-active actions such as improving awareness and tolerance amongst local people, and prey restorations in those patches to support leopard range expansion.

Acknowledgements

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Supplementary Information

Assessing spatial metapopulation structure

Habitat suitability model

To assess the structure of a potential leopard metapopulation, we first mapped suitable leopard habitat based on shelter and ambushing habitat, human-induced mortality risk, and snow cover in winter using six predictor variables (Figure SI IV-1). We captured shelter and ambushing habitat with topographic ruggedness and the proportion of forest per grid cell. We calculated ruggedness as the standard deviation of slope within each cell, where slope was based on Shuttle Radar Topography Mission data (NASA JPL 2013). We then normalized ruggedness linearly between 0 and 1 after dropping the highest 5% values. The proportion of forest per grid cell was based on a recent high-resolution land-cover map (Bleyhl et al. 2017). Finally, to derive an index for shelter and ambushing habitat, we used the maximum of ruggedness and forest proportion, because both high ruggedness and high proportions of forest are associated with good shelter and ambush opportunities (Gavashelishvili and Lukarevskiy 2008).

To capture human-induced mortality risk, we used distance to roads, distance to settlements, and the proportion of cropland per grid cell. We derived roads and settlements from Open Street Map (www.openstreetmap.org) and cropland from the land-cover map (above). We assumed decreasing human-induced mortality risk with increasing distance to roads and settlements (linear decrease scaled between 0 and 1, after dropping the highest 5% distances) and with decreasing proportion of cropland. To derive an index for human-induced mortality risk, we then averaged the three predictors (distance to roads, distance to settlements, and cropland proportion; Gavashelishvili and Lukarevskiy 2008; Zimmerman et al. 2007).

To exclude areas with high snow depth in winter, a key limitation for leopards (Lukarevsky et al. 2007b), we derived climate data at ~1 km spatial resolution from the CHELSA dataset Version 1.2 (Karger et al. 2017). We calculated a snow cover index as the proportion of cells with a mean temperature of the coldest quarter of ≤ 0 °C and precipitation in the coldest quarter of ≥ 400 mm. We further assigned a habitat suitability of 0 to all cells with a mean elevation > 3,000 m.

To derive our final habitat suitability map, we averaged the shelter and ambush habitat index and the human-induced mortality risk index to derive a habitat suitability index ranging between 0 and 1. We then multiplied this habitat suitability index raster with the inverted snow cover index, which effectively reduced habitat suitability in areas with high snow depth in winter.

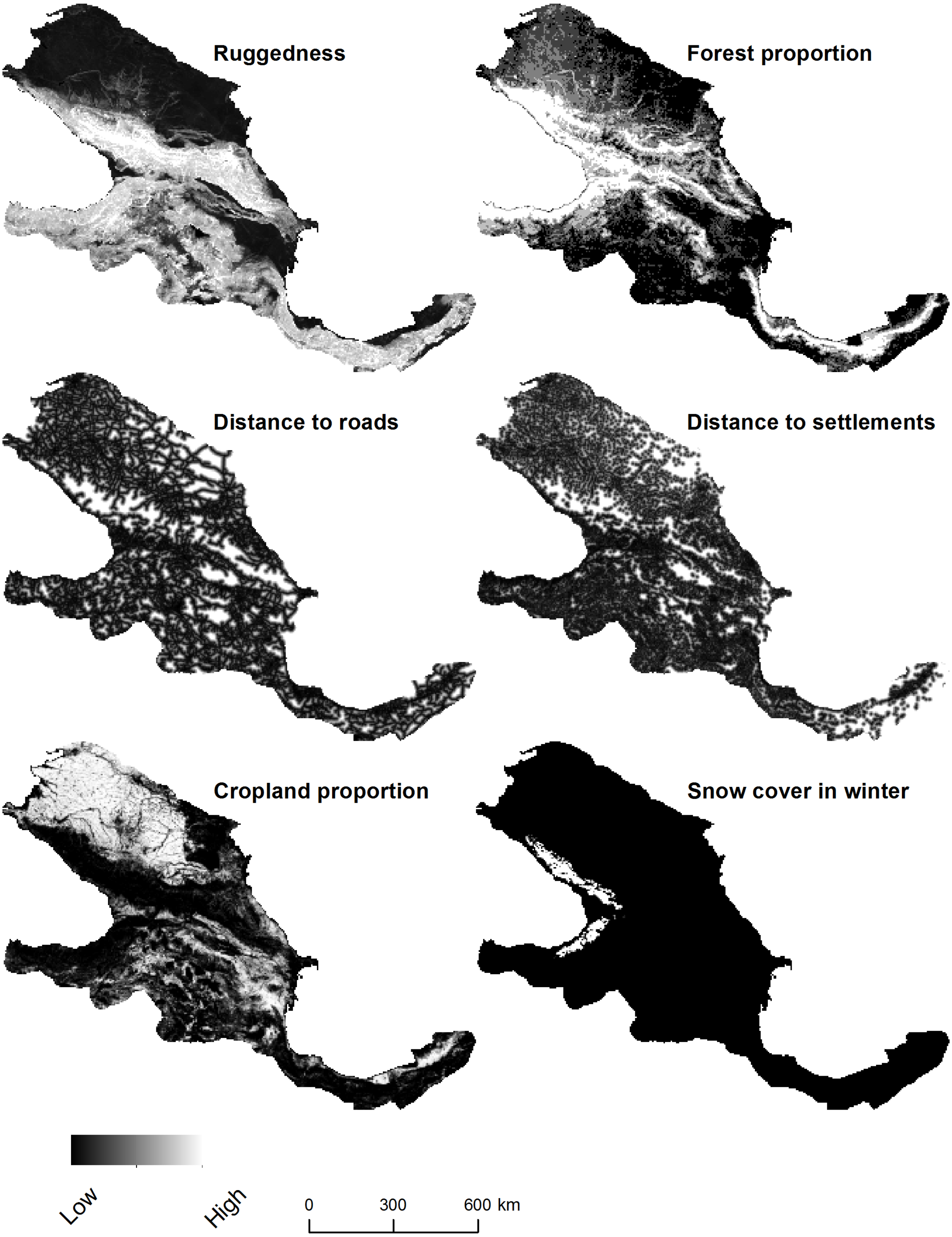


Figure SI IV-1: Maps of the individual variables used in our leopard habitat suitability model.

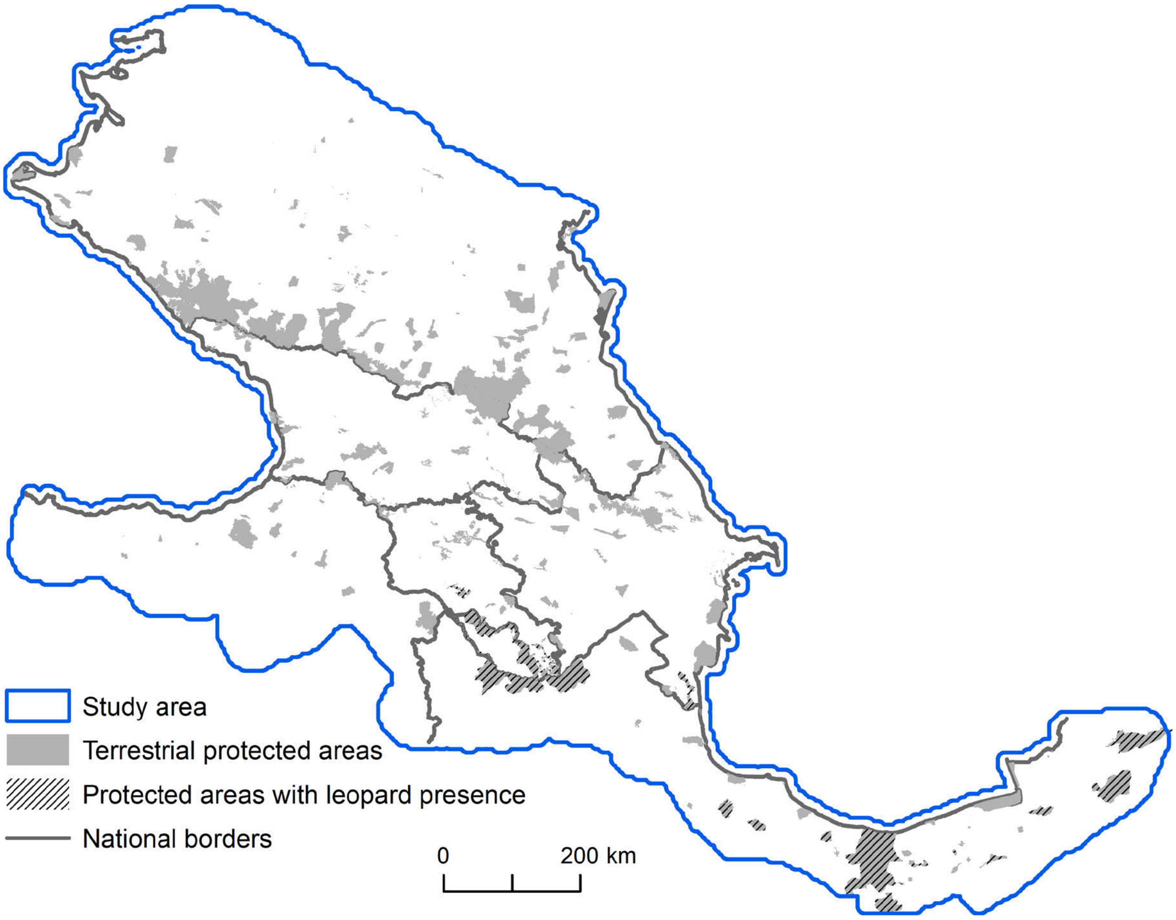


Figure SI IV-2: Terrestrial protected areas within the study area, based on the World Database on Protected Areas (IUCN and UNEP-WCMC 2019) and WWF Caucasus Programme Office database (wwfcaucasus.net). Protected areas with leopard presence in the last 5 years are highlighted (hatched) based on expert delineation and our leopard presence dataset.

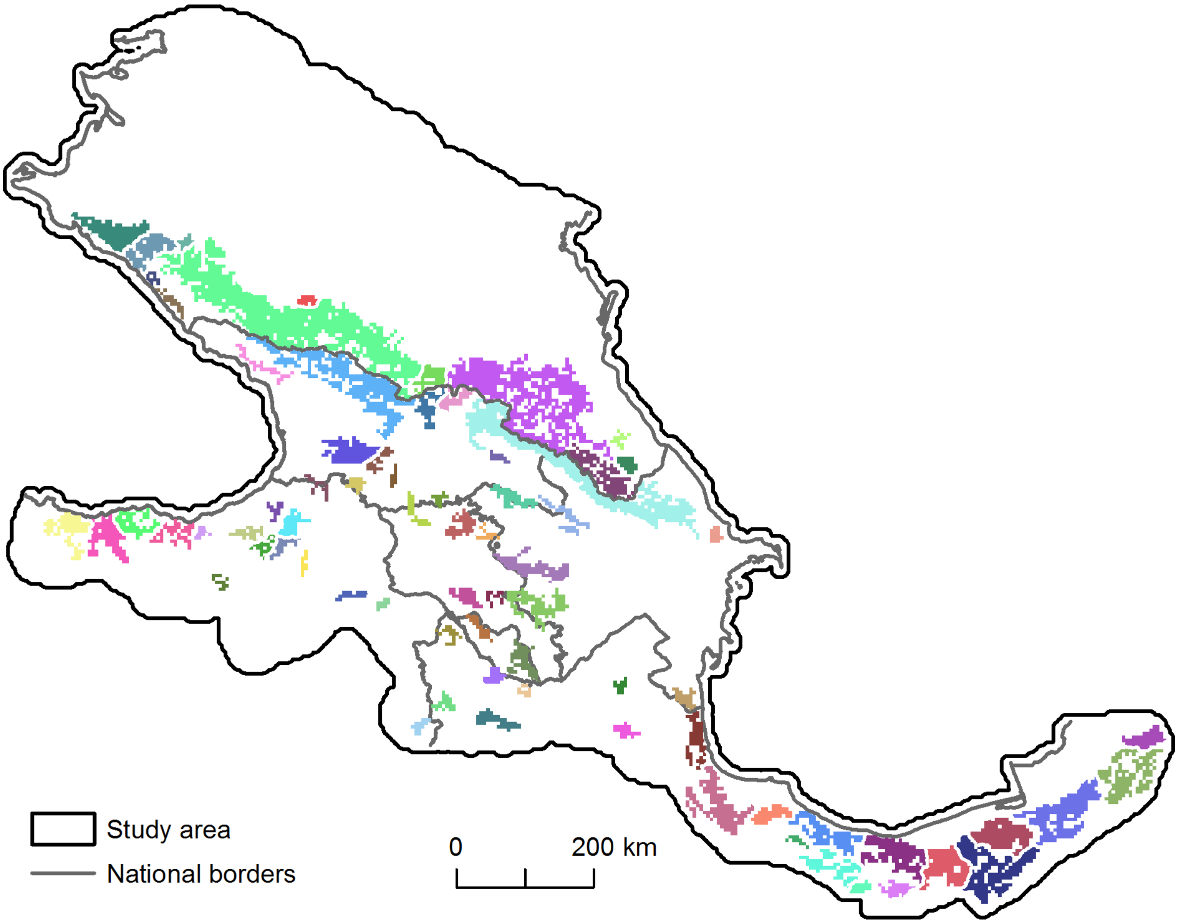


Figure SI IV-3: The distribution of individual potential leopard breeding patches. Colors are used to distinguish the individual patches.

Model parameterization

Demographic model

We used leopard survival rates from the literature, derived from several hundred leopard individuals, to parameterize our demographic model (Table SI IV-1) and ran sensitivity analyses for each rate. We used the fecundity estimate from Daly et al. (2005) and modelled fecundity as density-dependent using the equation:

$$\phi_i = \phi_{0,i} * e^{-b\sum_{j=1}^{S}\omega_{ij}N_{j,t}} \qquad \text{(eqn. S1)}$$

where ϕ_i is the fecundity of stage i, $\phi_{0,i}$ its maximum fecundity at low densities, b the strength of density dependence, S the number of stages, ω_{ij} the contribution of stage j to the density dependence in the fecundity of stage i, and $N_{j,t}$ the number of individuals at time t in stage j. Females paused for one year between reproductions (Daly et al. 2005). Males were allowed to mate with up to three females and only individuals older than 2 years were allowed to breed (Lukarevsky et al. 2007b). Further, mean fecundity was weighted by environmental stochasticity and constrained to known litter sizes of 1 to 4 (i.e. range of litter size reported from captivity; Lukarevsky et al. 2007b). To do so, RangeShifter implements a first-order autoregressive process to generate time series of the weighting noise value ε:

$$\varepsilon_{t+1} = \kappa\varepsilon_t + \omega_t\sqrt{1 - \kappa^2} \qquad \text{(eqn. S2)}$$

where κ is the autocorrelation coefficient and ω is a random normal variable drawn from the normal distribution N(0, σ) (Ruokolainen et al. 2009). We assumed no temporal autocorrelation in environmental stochasticity (i.e. $\kappa = 0$) and used an amplitude of the fluctuation of 0.25 (i.e. $\sigma = 0.25$). At each time step, mean fecundity was then modified using equation S3 before applying density-dependence (equation S1):

$$\phi_{i,t+1} = \phi_{0,i}(1 + \varepsilon_{\ t+1}) \qquad \text{(eqn. S3)}$$

Table SI IV-1: Overview of studies used to derive leopard survival rates.

Study	Location	# leopards studied	Characteristics
Balme, Slotow & Hunter (2009)	South Africa	35	This study compared leopard survival rates in Phinda Private Game Reserve, South Africa, before and after a conservation treatment. Leopards were protected inside the reserve, but faced high legal and illegal hunting outside Phinda. We used mean survival rates across the whole study period because survival rates reached up to 100% for some age classes, which we considered as extremely high (similar to Di Minin et al. (2013).
Balme et al. (2017)	South Africa	355	This study estimated survival rates based on leopards monitored over six years in Sabi Sand Game Reserve, South Africa. Leopards were protected in the reserve.
Daly et al. (2005)	South Africa	-	This study used an expert-based approach to estimate survival rates for ten different sites across South Africa.
Swanepoel et al. (2015)	Botswana, Namibia, South Africa	162	This study collated data from 18 studies across southern Africa and compared survival rates inside and outside protected areas. We used only survival rates from leopards within protected areas (n = 128), because the recorded survival rates outside protected areas were characterized by very high standard errors (we still compared our results to these rates).

Dispersal model

Dispersal allows for gene flow and is recognized as an important aspect of a functioning metapopulation (Clobert et al. 2012). Leopards are wide-ranging and cryptic, solitary animals, which can disperse over very long distances, often unnoticed by humans (Fattebert et al. 2013). The maximum recorded distance a leopard moved within a year was 562.1 km (Fattebert et al. 2013). From our study area, a sub-adult leopard recently dispersed from the Zangezur Range in southern Azerbaijan to Khosrov Forest State Reserve in Armenia, which is a Euclidean distance of 170 km (Askerov et al. 2018). We therefore set our maximum dispersal distance to 170 km. This led to a mean dispersal distance of 66 km (SD: 35 km) across all scenarios modelled. In RangeShifter, maximum dispersal distance is expressed through the maximum number of steps (one step = moving from one cell to a neighboring cell), and we therefore set the maximum number of steps to 28 (i.e., accounting for half of the steps being diagonal across our 5 km x 5 km cells). Individuals died if they reached 28 steps without settling in a patch. Additionally, dispersal seems to be density-dependent, meaning that the emigration rate increases with increasing leopard density and that the immigration probability decreases with increasing leopard density in a patch, most likely due to intraspecific competition and because leopards are territorial (Fattebert et al. 2013; Fattebert et al. 2015a). We therefore modelled the probability of individuals emigrating from a patch and the probability of individuals settling in a patch as density-dependent. On average, leopards start to disperse with an age of about 14 months and become territorial as adults (Fattebert et al. 2015a). We therefore limited dispersal to our sub-adult age classes.

RangeShifter models three phases of dispersal: emigration, transfer, and settlement (Clobert et al. 2012). Emigration is the first phase of dispersal and refers to an individual leaving its natal patch. For each individual, the density-dependent emigration probability is given by:

$$d = \frac{D_0}{1 + e^{-(bN_{i,t} - \beta)\alpha}} \qquad \text{(eqn. S4)}$$

where D_0 is the maximum emigration probability, β the inflection point of the function, α the slope at the inflection point, b is the strength of density dependence (as used in eqn. S1), and $N_{i,t}$ is the number of individuals in patch i at time t. We used $D_0 = 1$, $\beta = 0.5$, and $\alpha = 10$ (i.e. emigration probability is 1 if the relative leopard density in a patch is 1).

Transfer is the second phase of dispersal and refers to the movement through the landscape in search of a new suitable patch. Because movement between potential sub-population patches is affected by the structure of the landscape, we used the Stochastic Movement Simulator (SMS; Palmer et al. 2011), implemented in RangeShifter, as a mechanistic movement model to simulate leopard transfer among potential sub-population patches. SMS uses a cell-based cost surface, or resistance to movement. Individual dispersers decide, probabilistically, on the direction of each step by taking into account the cost values of the cells within their perceptual range. We defined the perceptual range as one grid cell (i.e., 5 km). At each step, the probability of moving to each of the neighboring cells is calculated first by taking the arithmetic mean of the cost values of the surrounding cells that are within the perceptual range, and secondly by weighting this average by the directional persistence parameter, which quantifies the tendency to follow a correlated path. We applied a directional persistence of 2.5, meaning that, for example, in a homogenous landscape, individuals are 39 times more likely to continue in the same direction rather than making a 180° turn (Coulon et al. 2015; Palmer et al. 2011). We used a leopard-specific cost surface from our own prior research (Bleyhl et al. 2017) and calculated average costs for each 5 km x 5 km grid cell. Because dispersing individuals might favor habitat used by resident adults (Fattebert et al. 2015b), we also tested our inverted habitat suitability map as a cost surface, and did not find substantial differences in metapopulation structure and viability.

Settlement is the last phase of dispersal and refers to the immigration of a disperser to a new patch. For each individual, the density-dependent settlement probability p_s is:

$$p_s = \frac{S_0}{1 + e^{-(bN_{i,t} - \beta_s)\alpha_s}} \qquad \text{(eqn. S5)}$$

Where S_0 is the maximum settlement probability, β_s the inflection point of the function, α_s the slope at the inflection point, b is the strength of density dependence, and $N_{i,t}$ is the number of individuals in patch i at time t. We used $S_0 = 1$, $\beta_s = 0.5$, and $\alpha_s = -10$ (i.e. settlement probability is 1 if relative leopard density in a patch is 0; see **Error! Reference source not found.** for an overview of all RangeShifter parameter values).

Prey restoration scenarios

Leopard density is positively correlated with prey availability (Fuller and Sievert 2001; Hayward et al. 2007). Therefore, we parameterized our low, medium, and high prey restoration scenarios reflecting low, medium, and high leopard densities. We derived those leopard densities (number of individuals per km²) based on known prey abundances from Golestan National Park using the following equation from Hayward et al. (2007):

$$log_{10}(leopard\ density) = -2.455 + \ 0.456 * (log_{10}(prey\ biomass) \qquad \text{(eqn. S6)}$$

Prey biomass (kg / km²) refers to prey species within the preferred weight range for leopards (10–40 kg; Hayward et al. 2006) and we therefore used estimates for bezoar goat *Capra aegagrus* and urial sheep *Ovis vignei*. Compared to most protected areas in our study region, Golestan National Park shows high prey abundance (Soofi et al. 2018). Nevertheless, some of the park's prey species declined by 66–89% since the 1970s (Ghoddousi et al. 2019). We therefore used prey abundances from the 1970s to calculate our high prey restoration leopard density and prey abundances from 2011–2014 for our medium prey restoration leopard density. Prey abundances and mean body mass were available from the literature (Decker and Kowalski 1972; Ghoddousi et al. 2016; Ghoddousi et al. 2019; Kiabi 1978). Because we had no prey abundance for a low prey restoration scenario, we reduced leopard density by the same interval as from the high to the medium scenario. We used the resulting three leopard densities to calculate target carrying capacities for Golestan National Park that correspond to the leopard densities by multiplying the densities with the park area (874 km²). In RangeShifter, patch carrying capacity is further determined by the mean habitat suitability of a patch and the strength of density dependence parameter 1/b (i.e., multiplying mean habitat suitability of a patch with patch size and the strength of density dependence parameter). Therefore, to derive our three strength of density dependence parameter values for the prey restoration scenarios, we decreased the originally calculated potential leopard densities until we reached the three target carrying capacities for Golestan National Park (Table SI IV-2).

Table SI IV-2: Potential leopard densities with resulting strength of density dependence for our three prey restoration scenarios based on prey biomass estimated for Golestan National Park in the 1970s (i.e. high prey availability) and in 2011–2014 (i.e. medium prey availability). Prey biomass was based on Decker & Kowalski (1972), Kiabi (1978), Ghoddousi et al. (2016), and Ghoddousi et al. (2019). For our low prey restoration scenario we decreased medium leopard density by the same interval as between the medium and high density.

Prey restoration scenario	Prey biomass [kg/km²]	Possible leopard density (# / 100 km²)	Target carrying capacity for Golestan National Park (874 km²)	Resulting strength of density dependence (1/b) for RangeShifter
Low	-	0.856	7	0.000086
Medium	188	3.817	33	0.000370
High	661	6.778	59	0.000670

Sensitivity analysis

We assessed model sensitivity using a local sensitivity analysis assessing how altering model parameters changed our two main model outcomes, extinction probability and leopard abundance after 100 years. First, we varied all survival rates, the strength of density dependence parameter (1/b), and the fecundity by ± 5% while keeping other parameters constant, resulting in 20 extra model runs. Additionally, we tested our inverted habitat suitability map as cost surface. Third, we tested maximum dispersal distances of 47 and 353 km (maximum dispersal distances in Fattebert et al. (2015a) and in Fattebert et al. (2013), respectively) instead of the original 170 km, and initial populations of 200 and 500 individuals instead of the original 352. For maximum dispersal distance, we also tested the effect on patch occupancy after 100 years.

In addition to the results shown in the main text (survival rates, fecundity, strength of density dependence, and sex ratio), we found that our model was relatively robust towards altering the initial leopard population size (Figure S4). Extinction probability further remained 0% when altering the maximum dispersal distance, but leopard abundance after 100 years decreased 45% with a maximum dispersal distance of 47 km and increased 20% with a maximum dispersal distance of 353 km, indicating that population growth is more likely if longer dispersal distances are also more likely. Additionally, higher maximum dispersal distances led to higher probabilities of patches in the Greater Caucasus to be occupied after 100 years (Figure SI IV-5). Using the inverted habitat suitability as a cost surface in our dispersal model had no substantial effect on model outcomes (results not shown).

Decreasing the female maximum emigration probability from 1.0 to 0.1 led to no changes in extinction probability and to a slight increase in the mean leopard abundance after 100 years (Table SI IV-3). A reason for the slight increase in abundance with lower female emigration probability could be that lower numbers of emigrating females (i.e., a lower maximum emigration probability and therefore a higher tendency for females for philopatry) might stabilize the population in the currently already occupied patches, given the high importance of females for viable populations. If more females disperse, they might end up in empty patches without the chance to reproduce or die after reaching the maximum dispersal distance. Additionally, we observed slightly lower probabilities for patches in the northern study area to be occupied if females had a high tendency for philopatry (i.e., for a maximum emigration probability of 0.1; Figure S6). This is likely also related to the fact that for successful reproduction both sexes need to colonize a patch, and with fewer females leaving their natal patch, the range expansion takes more time.

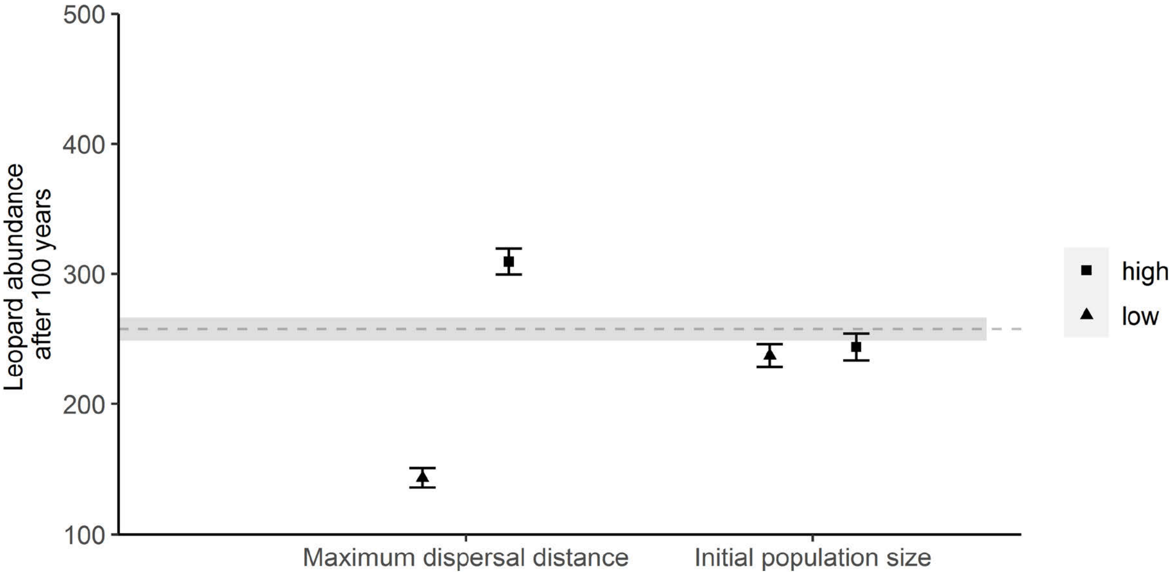


Figure SI IV-4: Sensitivity of leopard abundance after 100 years towards altering the maximum dispersal distance from 170 km to 353 km (high) and to 47 km (low) and the initial population size from 352 to 500 (high) and to 200 (low), shown for the medium poaching control and prey restoration scenario. Symbols indicate mean values, error bars show 99% confidence intervals. The grey line and the shaded area show the mean value and 99% confidence interval for the medium persecution reduction and prey restoration scenario. We also tested sensitivity towards extinction probability, which remained 0% for all sensitivity levels (results not shown).

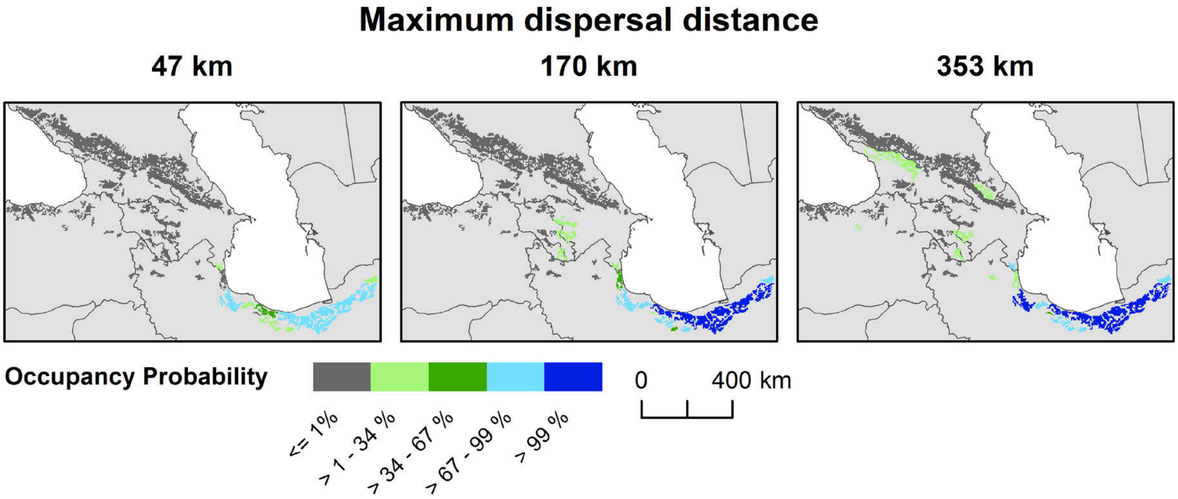


Figure SI IV-5: Sensitivity of the occupancy probability after 100 years towards increasing and decreasing the maximum dispersal distance.

Table SI IV-3: Sensitivity of the outcomes “extinction probability” and “mean leopard abundance after 100 years” to decreasing the maximum emigration probability for females incrementally from 1.0 to 0.1 (in steps of 0.1).

Max. emigration probability females	Extinction probability after 100 years	Mean leopard abundance after 100 years
1.0	0%	258
0.9	0%	268
0.8	0%	277
0.7	0%	287
0.6	0%	296
0.5	0%	308
0.4	0%	305
0.3	0%	325
0.2	0%	329
0.1	0%	334

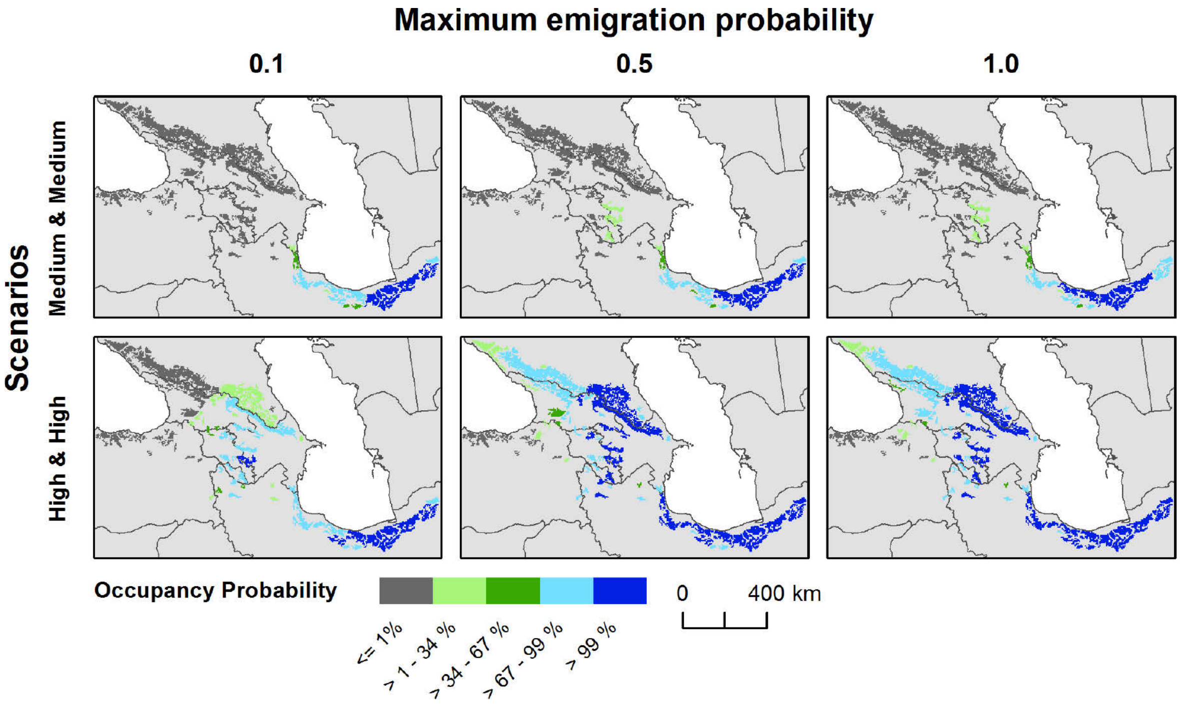


Figure SI IV-6: Sensitivity of the occupancy probability after 100 years towards decreasing the maximum emigration probability for females from 1.0 (base model) to 0.5 and 0.1, exemplified for the scenario combinations medium & medium and high & high (poaching reduction & prey restoration).

Ongoing reintroductions to the Russian Greater Caucasus

In 2016, three leopard individuals (1 female, 2 males) were reintroduced to the Caucasus Biosphere Reserve and in 2018 one additional male was added to that population and two individuals (1 female, 1 male) were released to Alaniya National Park, both located in the

Russian Greater Caucasus (Figure SI IV-7). The Greater Caucasus seems to be functionally disconnected from the Persian leopard sub-populations in the Lesser Caucasus, although sightings of individual leopards suggest that at least long-range dispersers occasionally appear (Caucasus Leopard Working Group 2017). More reintroductions are planned to the Greater Caucasus (e.g. WWF Russia and the Russian Academy of Science aim for a self-sustaining leopard population of at least 50 individuals; https://www.worldwildlife.org/stories/persian-leopards-return-to-caucasus). Nevertheless, the effect of the reintroductions on the Persian leopard metapopulation across the Caucasus is not well-understood.

To get a better understanding of how such a new leopard population in the Greater Caucasus could affect our model outcomes, we tested how incrementally adding 5–50 individuals (in steps of 2 females, 3 males, each three years old) to the breeding patch overlapping with the recent reintroductions (Figure SI IV-7) changed extinction probability and leopard abundance after 100 years. We found that 5–50 additional leopards in the Russian Greater Caucasus had a small effect on our results for the high and low persecution reduction scenarios (extinction probability after 100 years remained 0% for all high persecution reduction scenarios and 100% for the low persecution reduction scenarios; Table SI IV-4). While leopard abundance changed only marginally for high and medium prey restoration, it increased about 50% for the low prey restoration scenarios (Table SI IV-4). Reintroductions predominantly affected our medium poaching control by a 35–161% increase in leopard abundance after 100 years compared to our no-reintroduction model (Table SI IV-4). Nevertheless, variation among model repetitions increased (Figure SI IV-8).

Generally, these results suggest that our models were robust against adding individual leopards to the Greater Caucasus. Nevertheless, adding initial leopard individuals had some impact on our medium persecution reduction scenarios (decreasing extinction probability, increasing leopard abundance). High variability across model repetitions suggests that the impact of reintroductions is dependent on whether the initial individuals manage to sustain a population in the Greater Caucasus, which is less likely with only few individuals. Thereby, our results highlight that connectivity to the Lesser Caucasus and Iran is most likely key to support the reintroduced populations and successfully recolonize the Greater Caucasus. The recent mortality of one reintroduced female and one reintroduced male further underline the unpredictable outcome of reintroductions in the Greater Caucasus at present.

Table SI IV-4: Sensitivity of extinction probability and mean leopard abundance after 100 years towards having 5–50 additional leopards in the Greater Caucasus at initialization.

Scenario		Extinction probability after 100 years				Mean leopard abundance after 100 years			
		Additional leopard individuals				Additional leopard individuals			
Persecution reduction	Prey restoration	0	5	25	50	0	5	25	50
High	High	0%	0%	0%	0%	3,701	3,721	3,727	3,686
High	Medium	0%	0%	0%	0%	2,062	2,047	2,077	2,055
High	Low	0%	0%	0%	0%	270	402	407	411
Medium	High	0%	0%	0%	0%	739	1,056	1,517	1,582
Medium	Medium	0%	0%	0%	0%	360	485	727	805
Medium	Low	77%	37%	5%	3%	18	35	49	47
Low	High	100%	100%	100%	100%	0	0	0	0
Low	Medium	100%	100%	100%	100%	0	0	0	0
Low	Low	100%	100%	100%	100%	0	0	0	0

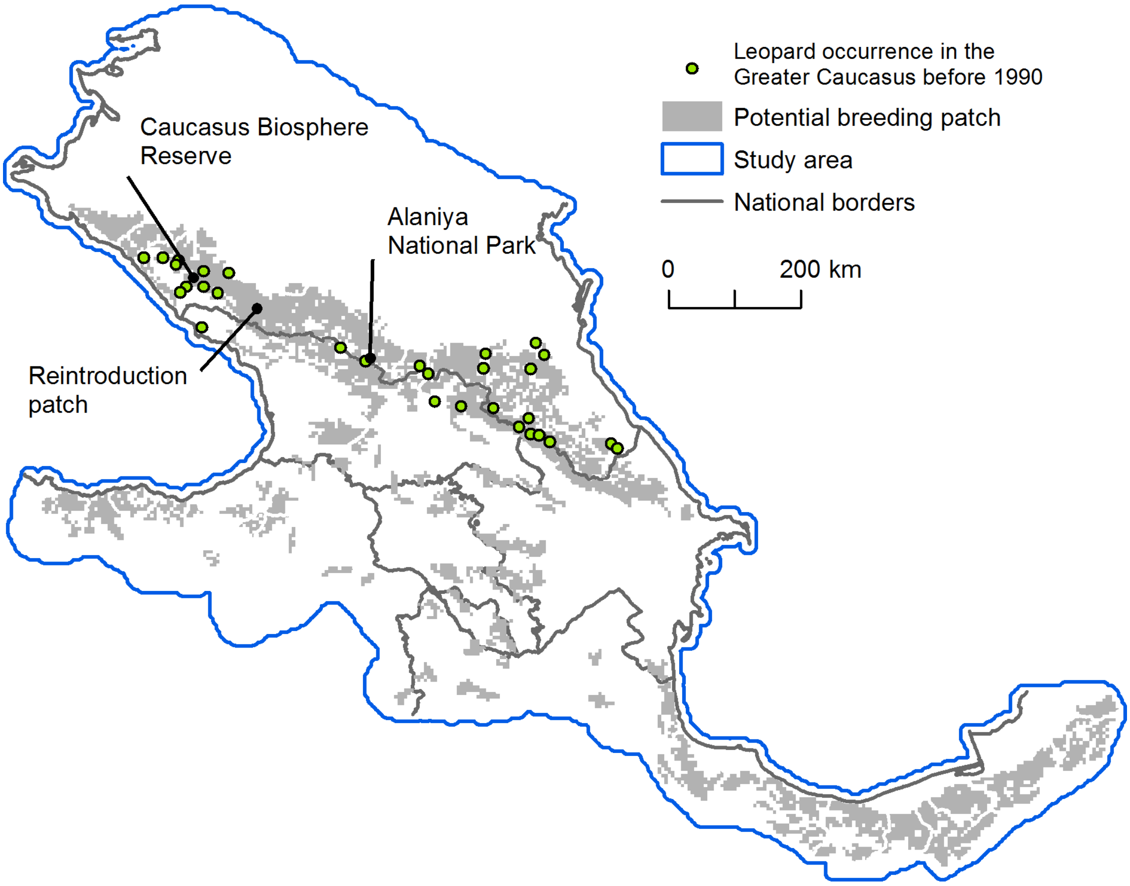


Figure SI IV-7: Locations of the recent reintroductions in the Greater Caucasus and the patch to which we added leopards at model initialization (reintroduction patch). Additionally, leopard occurrence records from before 1990 from the Greater Caucasus are shown (Heptner and Sludskij 1972; Nasimovich 1941; Vereshchagin 1959; Yarovenko 2010).

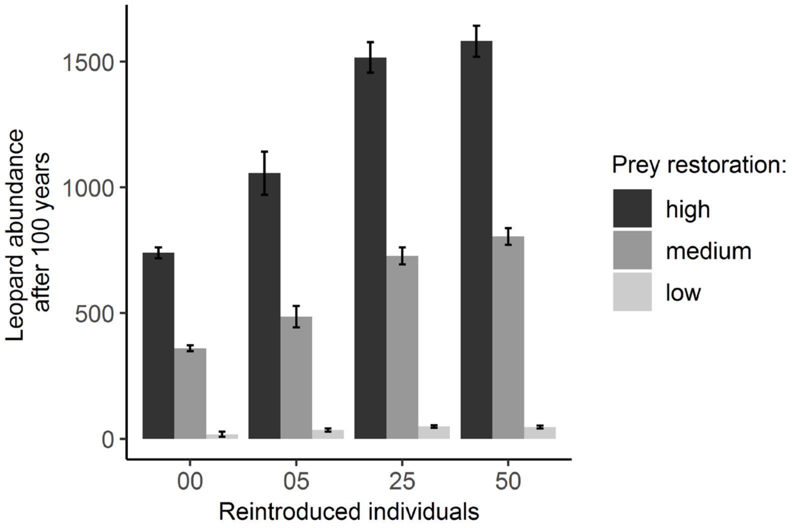


Figure SI IV-8: Effects of reintroductions on leopard abundance after 100 years for the medium poaching control scenarios (effect was only marginal on the low and high poaching scenarios). Bars show the mean leopard abundance across 100 model repetitions, error bars show the 99 percent confidence intervals.

Chapter V:
Synthesis

1 Research challenge

Many large carnivores are endangered and occur only in small and isolated populations (Ripple et al. 2014). The decline of large carnivore populations is worrisome because of the intrinsic value of these charismatic species and because of the increasing recognition of the major importance of large carnivores in ecosystems (Estes et al. 2011). Interestingly, large carnivores are also returning to some areas where they were previously extirpated (Chapron et al. 2014a; Enserink and Vogel 2006). Studying the conditions under which large carnivore populations are recovering is a great opportunity for conservation science to identify pathways for sustaining viable populations in the future. Yet, gaining a better understanding of large carnivore recoveries is still challenging. First, assessing recovery conditions requires working across broad geographic areas, which is often hampered by either inconsistent data (i.e., incomparable inventories) and/or a lack of detail when using global data products. Second, large carnivores depend on prey species that should be included in recovery assessments. However, this is hardly ever done across large geographic extents. Third, data availability for recovering and range-expanding species is often scarce, a problem that multiplies when working across large geographic extents. Hence, modeling approaches that require extensive input data, such as species distribution models, are difficult to calibrate across large geographic areas.

A perfect example of a large carnivore species that is showing signs of recovery in parts of its range, but where knowledge is limited, is the Persian leopard (*Panthera pardus saxicolor*) in the Caucasus. The Caucasus is one of the few regions globally with a high conservation value and an apex predator that is expanding its range from a nearby source population. The conditions that underlay their recovery are however not well understood, and systematic data on leopard and prey occurrence and abundance are missing for large parts of the Caucasus. This hampers conservation efforts for this important species and region. In this thesis, I studied Persian leopard recovery in the Caucasus to better understand what fosters large carnivore recoveries, and how to assess large carnivore recovery conditions in data-scarce situations.

2 Summary and main conclusions

2.1 Persian leopards in the Caucasus

Persian leopards are slowly extending their range in the Caucasus from Iran northwards, where they were widespread until the early 20th century (Breitenmoser et al. 2017). In this thesis, a broad-scale perspective on Persian leopards and their prey species across the Caucasus highlighted conditions and strategies that foster the recovery of an apex predator in a data-scarce region of high conservation concern. To achieve this, I used different habitat suitability modeling approaches to identify habitat for the Persian leopard and its prey. I then assessed which factors might constrain or promote the colonization of suitable habitat using connectivity models (Chapters II and III), threat analyses (Chapter III), and a spatially-explicit individual-based metapopulation model (Chapter IV). The results described in these three core research chapters outline and assess potential pathways to overcome constraints to colonize suitable leopard and prey habitat, including the identification of potential reintroduction sites, options for habitat and corridor protection, population restorations, and reducing competition with livestock or direct persecution. The insights gained during this thesis thus answer the two main research questions:

Research question I: Does the Caucasus ecoregion have suitable, safe, and connected habitat for Persian leopards and their prey?

The results of this thesis suggest that the Caucasus has widespread areas of suitable habitat for Persian leopards and their prey but much of this habitat is under threat. Chapter II and Appendices A and B used correlative species distribution models to identify such habitat for bezoar goat (*Capra aegagrus*), European bison (*Bison bonasus*), and Gmelin's mouflon (*Ovis orientalis*). All three prey species had at least 14,000 km² of habitat throughout the Caucasus. Further, chapter III used a rule-based habitat suitability modeling approach to identify suitable leopard habitat (in total 120,000 km², including northern Iran). Hence, there is little evidence that habitat availability is a limiting factor for the distribution of leopards and their prey species in the Caucasus.

While habitat seems not to be a limiting factor, this thesis highlighted a range of threats that likely render large proportions of the identified habitat unsafe. First, leopards and their prey species were threatened by livestock farming. For example, the majority of mouflon habitat overlapped with suitable domestic sheep habitat (77%), which might cause competition over forage and space, disease transmission and poaching. High persecution risk for leopards was linked to areas with livestock, indicating that leopards face high mortality rates in regions with high livestock numbers, despite otherwise suitable habitat. Such high persecution is mainly due to retaliatory killings from livestock depredation. Second, poaching and persecution threatened leopards and their prey. For European bison, 38% of habitat was classified as an ecological trap, where bison are likely to gravitate towards because of good environmental conditions, but face high poaching risk. On average, only 25% of suitable habitat was protected for all species studied herein. Third, infrastructural development was a threat to suitable habitat identified in this study. In the Greater Caucasus, ski resorts are planned and built in close proximity to remote wilderness areas that include some of the key European bison habitat patches, as well as a reintroduced Persian leopard sub-population. Fourth and finally, the border areas between the countries in the Caucasus often follow mountain ranges, and these are mostly remote areas highlighted as suitable habitat for the species studied here. A range of armed conflicts such as the Nagorno-Karabakh conflict between Armenia and Azerbaijan or the Russo-Georgian war continues to resurge in such border areas, which likely threatens wildlife and further complicates the implementation of conservation interventions (Gaynor et al. 2016). Despite the opportunity that habitat availability provides, the results of this thesis underpin the need for conservation efforts to mitigate threats and restore and protect wildlife populations within these suitable areas to reach the goal of viable populations (Zazanashvili et al. 2012).

Connections between suitable areas is also crucial to leopard recovery. Nevertheless, the results of this thesis indicate that wildlife corridors are likely not functional. Chapters II, III and Appendices A–C identified and assessed connectivity between habitat patches and protected areas for different large mammal species. While corridors were prevalent, their functionality to provide connectivity on the ground was severely hampered. Numerous bottlenecks were located within corridors (i.e., narrow passages that species have to pass with no alternatives routes), and many corridors were of low quality (i.e., had a high average cost related to movement). For leopards, corridors might be particularly dangerous if they pass through agricultural lands, which increases the risk of conflict with people. The results from this thesis thus indicate that key habitat patches of the studied species are not well connected.

Research question II: What are effective management strategies to foster the recovery of Persian leopards in the Caucasus?

Chapter IV provided answers to this question by comparing the relative importance of two commonly applied conservation strategies – persecution reduction and prey restoration. For Persian leopards in the Caucasus, reducing persecution was the most effective strategy to foster a viable population. Nevertheless, reducing persecution alone was not sufficient to lead to marked population size increases or range expansions, and prey restoration was required to support management efforts. Persecution is driven by a range of different reasons and a management strategy to reduce persecution therefore has to be case-specific (Carter et al. 2017). Appendix D highlights that one of the main reasons for leopard persecution was livestock depredation, and often this happened outside protected areas. Mitigating human-carnivore conflicts such as livestock depredation, particularly in corridors between key habitat patches, is thus likely a very effective management strategy to foster Persian leopard recovery. In sum, the results of this thesis emphasize that conservation strategies that are targeted towards reducing leopard persecution are effective to foster leopard population recovery and should be combined with strategies to restore prey species.

2.2 Cross-cutting insights

The results of the research chapters and Appendices provided answers to the two research questions of this thesis. Based on these results, five cross-cutting insights emerged that address the overarching goal of this thesis to better understand the conditions that foster large carnivore recoveries.

First, the results of this thesis underpin the importance of mitigating human-carnivore conflicts in unprotected lands to foster large carnivore comebacks (Broekhuis et al. 2017). Human-carnivore conflict is one of the main drivers of carnivore declines globally (Woodroffe et al. 2005). Often, human-carnivore conflicts lead to carnivores being killed (Treves and Karanth 2003). Illegal killings are widespread, for example in Europe, where they limit population recoveries of wolves (*Canis lupus*) in Scandinavia (Liberg et al. 2012), or brown bears (*Ursus arctos*) in the Alps (Kaczensky et al. 2011). In the Caucasus, conflicts with people were the main reason for leopard persecution, and mostly happened outside protected areas. While persecution reduction would effectively allow Persian leopards to establish sub-populations in suitable habitat patches, most of these areas were not protected, which makes conservation efforts cumbersome. Conflict mitigation has been highlighted as a key strategy to increase human tolerance for large carnivores (Carter and Linnell 2016), and the results of this thesis underline the need for such measures to foster large carnivore comebacks.

Second, this thesis highlights that losing individuals can be detrimental when populations of large carnivores are small (Heurich et al. 2018; Mech 2017). While some studies indicate that large carnivores might sustain high persecution (e.g., Karanth and Stith 1999; Lindzey et al. 1992), the leopard metapopulation model in this thesis indicates that high persecution rates will lead to the extinction of leopards in the Caucasus. High persecution rates on small populations lead to decreasing population growth rates in areas where large carnivores could otherwise recover, and can amplify other threats of small populations such as decreasing genetic diversity (Liberg et al. 2012). For the European lynx (*Lynx lynx*), for example, a population in the border region of Austria, Czech Republic, and Germany might go extinct if only a few more individuals are killed per year (Heurich et al. 2018). Tigers (*Panthera tigris*) require large populations to persist and have a high extinction probability under high persecution rates (Chapron et al. 2008). All in all, persecution can lead to the extinction of small populations (Kaczensky et al. 2011) and prevent the recovery of large carnivores in range expansion areas, where their populations are typically small (Kaczensky et al. 2011; Mech 2017) , which is underpinned by the results of this thesis.

Third, the results underline the importance of functional connectivity in fragmented landscapes to foster large carnivore comebacks (Crooks Kevin et al. 2011; Kanagaraj et al. 2011). Large carnivore habitat is fragmented in many parts of the world (Crooks Kevin et al. 2011). Habitat fragmentation was also a characteristic for the species studied in this thesis, where most habitat patches were not large enough to host viable populations. Without connectivity, isolated sub-populations are prone to extinction (Crooks et al. 2017; Jansson et al. 2012). For instance, the leopard individuals that were reintroduced in the Greater Caucasus had only a low chance of persistence in the metapopulation model due to their isolated location. Moreover, connectivity promotes the re-colonization of suitable areas (Kramer-Schadt et al. 2004). Increased connectivity to source populations in Eastern Europe, for example through the fall of the Iron Curtain, played an important role in the comeback of large carnivores in Europe (Linnell et al. 2016). Fostering large carnivore comebacks therefore likely depends on increasing connectivity among safe habitat patches (Lyons et al. 2018), which is supported by the results of this thesis.

Fourth, the results of this thesis reinforce the importance of ecoregion-wide conservation planning across international borders (Linnell et al. 2016). Border areas might retain core habitat for large wildlife from alteration because of lower human impact, and are therefore important conservation targets (Romero-Muñoz et al. 2019). This became evident also for the Caucasus, where widespread habitat and corridors were often located close to international borders. Large carnivores further depend on transboundary cooperation, because they are wide-ranging and often move across international borders (Bartoń et al. 2019; Linnell et al. 2016). Particularly in the case of different law enforcement, conservation statuses, and attitudes of people to wildlife, crossing borders can increase persecution risk for large carnivores (Linnell et al. 2016). In Europe, for example, a brown bear was shot from an expanding Italian population after entering Germany (Rosen and Bath 2009). In the Caucasus, a leopard was recently shot in Abkhazia, Georgia, after crossing the border from a protected area in Russia (WWF Russia 2019). Another leopard was shot in Iran after entering the country from a National Park in Azerbaijan (Maharramova et al. 2018). The results of this thesis emphasize that international cooperation is key to make full use of the conservation opportunity of large carnivore recoveries and avoid population sinks across borders.

Fifth, a common characteristic of all chapters of this thesis was that they outlined approaches for scaling up analyses for large mammals in data-scarce regions. Broad-scale approaches that overcome data scarcity are important to assess large carnivore recoveries. Large carnivore populations often consist of only a few individuals, which limits the use of data from these populations to derive generalizable model outcomes (Martin et al. 2012). Moreover, in areas with high conservation value, such as biodiversity hotspots, data scarcity is very common (Amano and Sutherland 2013; Collen et al. 2008). Chapter II highlighted a remote sensing approach to support broad-scale conservation planning of landscape connectivity at ecologically-relevant spatial resolution. This Chapter developed a relatively simple approach that linked land cover with connectivity (without the need for empirical data) and used a cluster analysis to map general large mammal corridors. The link between land cover and connectivity was then successfully used in Chapter IV and Appendix C as a tool for characterizing connectivity among leopard habitat patches. Chapter III further demonstrated how species distribution modelling combined with a niche overlap analysis can be used to map conflict potential of a threatened large herbivore with livestock across large areas. This chapter further outlined how data scarcity could be overcome using freely available, high-resolution satellite imagery from GoogleEarth to digitize shepherd camp locations as a proxy for domestic sheep occurrence. Finally, Chapter IV highlighted a rule-based approach to map leopard habitat. This chapter provided a suitability map with high accuracy across all the Caucasus ecoregion and northern Iran. Species that extend their range do not necessarily occupy all suitable areas and data on them is often scarce (Poor et al.

2012; Schadt et al. 2002). This thesis represents such a case and exemplifies possible ways forward.

3 Conservation implications

3.1 Persian leopard conservation in the Caucasus

Persian leopard recovery in the Caucasus will likely depend on conservation interventions because persecution and habitat fragmentation are threatening their populations (Breitenmoser et al. 2017). The spatially-explicit estimations of land cover, habitat suitability, connectivity, threats to wildlife, and metapopulation viability developed in this thesis provide powerful information for conservation planners to implement conservation strategies that safeguard leopards, restore their ecological role as a top predator, and mitigate human-wildlife conflict. More specifically, three implications for broad-scale leopard conservation interventions can be drawn from the results of this thesis.

First, the results of this thesis suggest that suitable habitat and corridors for leopards and their prey seem to be available, but conservation measures are needed to counteract the original reasons for extirpations and make habitat and corridors safe and functional. Persecution reduction is likely to be a very effective strategy. Compensation schemes for livestock depredation, improved husbandry practices, and awareness raising are promising tools that have been shown to be effective in reducing persecution (Krafte Holland et al. 2018; Marchini and Macdonald 2012; van Eeden et al. 2018). Moreover, measures to promote private or community-based reserves with small-scale livestock production as well as providing communities with benefits from wildlife conservation such as ecotourism could promote alternative income for local communities, thereby releasing wildlife from competition with livestock and poaching (Allan et al. 2017; Redpath et al. 2017).

Second, this thesis highlights areas of high conservation importance for leopards and their prey across the Caucasus. Wherever possible, these areas should be protected from infrastructural developments such as new roads, surface mining, or skiing resorts. Moreover, areas that will likely be recolonized by leopards should be high-priority targets for pro-actively mitigating conflicts with people (LaRue and Nielsen 2016; Schadt et al. 2002).

Third, resurging armed conflicts are threatening areas of high conservation value in the Caucasus. The effective implementation of conservation strategies is almost impossible in areas of high conflict. Nevertheless, interventions in times of peace might help to prevent local extinctions of species (Daskin and Pringle 2018). Further, negative impacts on wildlife from border controls (e.g., poaching through military personnel) and border fences (e.g., fragmentation) should be avoided (Linnell et al. 2016). To achieve that, international conservation organizations could promote a dialogue between hostile countries to implement protected areas (e.g., peace parks) along country borders (Vasilijević et al. 2015).

Some results of this thesis have already been used in local conservation plans in the Caucasus. For example, WWF's Caucasus Programme Office mapped leopard connectivity between key conservation areas in the Lesser Caucasus using the approach and data developed in Chapter II. With the resulting map, areas to increase survey efforts were located with the goal to detect dispersal paths of leopards and to identify important regions to ensure connectivity between conservation areas. Further, Chapter IV contributes to the implementation of objectives outlined in the Strategy for the Conservation of the Leopard in the Caucasus Ecoregion (Caucasus Leopard Working Group 2017). Particularly, the leopard metapopulation model will allow for the prioritization and selection of the most effective conservation strategies and the most important locations. For example, a metapopulation model was outlined as a required tool for assessing reintroduction scenarios in the Caucasus to support natural leopard recovery (Caucasus Leopard Working Group 2017). Finally, the suitable European bison habitat patches outlined in Appendix B were used as candidate sites for a reintroduction project in Azerbaijan.

3.2 Fostering large carnivore recoveries

In light of predominantly declining population trends, the recent natural population recoveries and range expansions of large carnivores provide some reason for cautious hope (Wolf and Ripple 2018). Based on the cross-cutting insights of this thesis, some general conservation strategies can be drawn that foster large carnivore recoveries. First, strategies to prevent persecution are needed to allow large carnivore populations to grow and expand across their potential range. Given that persecution can have many different reasons, these strategies should be developed in concordance with local assessments of the context specific drivers of persecution (Carter et al. 2017). Second, identifying corridors and areas of high conservation concern within corridors such as bottlenecks or human-wildlife conflict hotspots are important to make use of the conservation opportunity of widespread available habitat patches. Despite their potential to expand populations even through a network of dense roads, for example in Europe (Trouwborst 2010), measures to reduce roadkill such as wildlife passages might be an effective tool to prevent mortalities of dispersing individuals

(Kramer-Schadt et al. 2004; Parchizadeh et al. 2018; Sawaya et al. 2013). Third, the importance of international cooperation that was found in this thesis underlines the need for conservation planning across borders at biologically relevant scales for large carnivores (Linnell and Boitani 2012). In Europe, broad directives such as the Council Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora or the Bern Convention are good examples for how cooperative legislation can contribute to large carnivore recovery (Redpath et al. 2017; Trouwborst 2015). Finally, this thesis highlights how individual-based population models can be used to identify areas that large carnivores might recolonize and to assess conservation strategies to foster their comeback. Importantly, this has been outlined under data-scarce conditions, which is typical for recovering species.

4 Follow-up work and outlook

This thesis gained new knowledge on the conditions of large carnivore recoveries, and importantly did so in a data-scarce region that has not yet lost all of its apex predators. During the course of this thesis, additional important topics for follow-up research emerged.

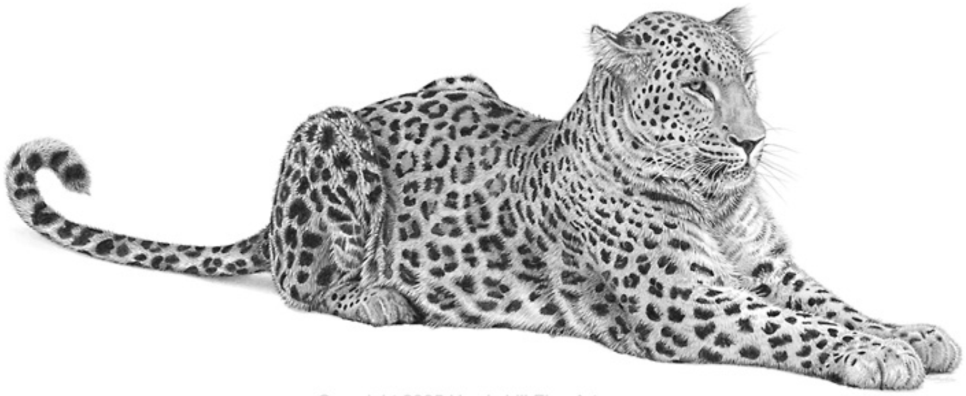
Within this thesis, I mapped current land-cover patterns and used present patterns of human infrastructure without including potential future change. This static perspective allowed me to work across a large geographic area, and with only limited data. Nevertheless, it is likely that land-use change will also affect the distribution and extent of large mammal habitat throughout space and time. New infrastructural projects are planned in the Caucasus, such as new roads and touristic facilities, and surface mining sites are threatening particularly remote areas (Zazanashvili et al. 2012). In contrast, the Caucasus is also experiencing land-use trends that may provide conservation opportunities, such as farmland abandonment (Yin et al. 2018). Climate change will most certainly also affect habitat, and might be particularly threatening to mountain wildlife (Parmesan 2006). More research that incorporates future land-use and climate change scenarios in habitat, connectivity, and population models can be an interesting addition to expand on the insights generated in this thesis. The individual-based metapopulation modeling approach used in chapter IV, for instance, offers promising ways forward by simulating dynamic landscapes that change in space and time (Synes et al. 2019).

Chapter IV used a scenario analysis to compare persecution reduction and prey restoration as two important conservation strategies. More data on prey abundances and patterns of human persecution would have allowed for a more in-depth mechanistic assessment of the impact of these strategies on population viability. For example, the habitat maps of prey species could have been linked to actual and projected prey abundances and used in a resource-selection function approach to estimate leopard habitat suitability (Hebblewhite et al. 2014). Further, large carnivore persecution happens for a range of reasons that most likely differs between regions (Ripple et al. 2014). Including varying levels of persecution across regions and population features, such as age or sex classes, could shed more light onto how to most effectively design conservation responses to persecution. Appendix D shows an approach to link persecution patterns to other variables, such as livestock densities, which might be an interesting way forward to overcome the current data scarcity.

This thesis highlighted the importance of functioning connectivity in fragmented landscapes. Different approaches were used to model connectivity, including least-cost corridors based on habitat suitability and on an expert-based approach, electric-circuit tools, and a mechanistic movement simulator. While these approaches are frequently used to assess landscape connectivity across large areas and with limited empirical information, wildlife tracking data has become more available in recent years (Kays et al. 2015). Wildlife tracking data likely facilitates the parameterization of complex connectivity modeling approaches (Palmer et al. 2014; Travis et al. 2012), thus offering an innovative approach for enhancing future models. More empirical data that links the movement of species to certain landscape elements, or includes more complexity such as individual dispersal behavior, or mortality rates would be better to predict range expansions of large carnivores (Ovenden et al. 2019; Ziółkowska et al. 2016a).

This thesis mainly focused on the ecological aspects of large carnivore recoveries and reduced the social dimension to a threat component. Yet, it is predominantly more a social-ecological than a pure ecological question if large carnivores will survive in an increasingly human-dominated world (Carter and Linnell 2016; López-Bao et al. 2017). Human tolerance towards large carnivores remains a major condition for their recovery (Bruskotter and Wilson 2014). Often, human tolerance is low for people who live close to large carnivores, and persecution remains a factor that likely hinders range expansions (Mech 2017). Providing science-based information to a broader audience can play a key role to promote more tolerance (Arbieu et al. 2019). Further, aspects such as poverty, education, and the proportion of people that rely on subsistence farming have been frequently linked to human tolerance towards large carnivores (Bruskotter et al. 2017), and could therefore be a starting point to add the critical social dimensions into otherwise ecological models (Behr et al. 2017).

Ultimately, the fate of large carnivores depends on human decisions. In an increasingly human-dominated world, humans and large carnivores must adapt to find ways to successfully coexist (Carter and Linnell 2016). The results of this thesis suggest that from an environmental perspective, there might be an opportunity to increase the population of a threatened large carnivore in a global biodiversity hotspot. Reducing persecution, for example through mitigating human carnivore conflicts, increasing connectivity, and promoting international cooperation are important to foster the recovery of large carnivore populations. The insights from this thesis shed light on conditions that underlay natural comebacks of large carnivores and inform strategies that foster coexistence of large carnivores and humans. With timely conservation action, these charismatic species, and the important role they play for ecosystems and humans can be restored and preserved.



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Appendix A:
Identifying priority areas for restorating mountain ungulates in the Caucasus ecoregion

submitted

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Abstract

Mountain ungulates around the world have been decimated to small, fragmented populations. Restoring these species often is limited by inadequate information on where suitable habitat is found, and which restoration measures would help to increase and link existing populations. We developed an approach to spatially target threat-specific restoration actions and demonstrate it for bezoar goats (*Capra aegagrus*) in the Caucasus. Using a large occurrence dataset, we identified suitable habitat patches and evaluate them in terms of connectivity, protection status, and competition with other mountain ungulates. We found extant bezoar goat populations to be highly isolated, yet with widespread areas of suitable, unoccupied habitat between them. Many unoccupied habitat patches were well-connected to extant populations, were at least partly protected, and have low potential for competition with other *Capra* species. This signals substantial pressure on bezoar goats, likely due to poaching, which currently prevents natural recolonization. Our study shows how restoration planning is possible in the face of multiple threats and scarce data. For bezoar goats in the Caucasus, we pinpoint priority patches for specific restoration measures, including reintroductions and anti-poaching action. We highlight that many patches would benefit from multiple interventions and that transboundary restoration planning is needed, a situation likely similar for many mountain ungulates around the world.

1 Introduction

Defaunation is a characteristic of the Anthropocene and has been particularly drastic for the world's largest mammals (Dirzo et al. 2014). Large ungulates are especially impacted, because they are wide-ranging, often compete with livestock, come otherwise into conflict with people, or are sometimes unsustainably hunted for their meat or trophies (Cardillo et al. 2005; Ripple et al. 2015c). As a result, many large ungulates have disappeared from large portions of their historical ranges (Di Marco et al. 2014; Gordon and Loison 2009). Given the importance of these species as ecosystem engineers, in food webs, and as conservation flagships, restoring their populations is a conservation priority (Malhi et al. 2016; Ripple et al. 2015c).

Mountain ungulates are often particularly threatened. These species often naturally occur in fragmented populations, because they depend on specific elevation belts, such as alpine grasslands, or landscape features, such as cliffs on which they rely as refuges to be safe from predators (Acevedo et al. 2007b; Bleich et al. 1990; Gavashelishvili 2004; Gross et al. 2002). Because of these clear habitat associations, mountain ungulates are relatively easy to locate and hunt (Damm and Franco 2014; Shackleton 1997b). This is highly relevant because mountain sheep and goats provide highly sought-after trophies, especially if they are rare (Bhatnagar et al. 2009). While controlled, scientifically-grounded hunting of these species can contribute to their conservation (IUCN 2016; Michel et al. 2015), poaching (i.e., illegal, uncontrolled and often unsustainable offtake) threatens these species, particularly during times of institutional instability, such as armed conflicts, of which there have been many in mountain regions (e.g., Kashmir, Pamir, Dinaric Mountains, Caucasus; Matloff 2017). Mountain ungulates face additional threats from competition with livestock (Bleyhl et al. 2019), surface mining (Ripple et al. 2015c; Shackleton 1997b), and climate change (Grotan et al. 2008). As a result, many species today hold out only in small, isolated populations, often solely inside protected areas (Damm and Franco 2014).

Restoring mountain ungulates relies on identifying suitable habitat, ideally in places that would increase and link existing populations (Bleyhl et al. 2017; Kuemmerle et al. 2011). Current land-use trends in many mountain areas might create a favorable environment for restoration, as rural population density declines, labor-intensive agriculture is abandoned, and transhumant livestock systems are in decline (Kuemmerle et al. 2008; MacDonald et al. 2000). These trends will likely continue (Stürck et al. 2015), suggesting substantial opportunities for restoring mountain ungulate populations, and the predators that depend on them (Ripple et al. 2015c).

Once suitable, but currently unoccupied habitat patches are found, a key question is why these habitats are not colonized (Davies et al. 2017; Louvrier et al. 2018). The answer to this question has important implications for restoration planning (Ferreras et al. 2001; Ziółkowska et al. 2016b). For instance, where unoccupied habitat patches are isolated from extant populations, yet contain well-managed protected areas, reintroductions can be an important measure to re-establish locally extirpated populations (Hoffmann et al. 2015). Where physical barriers prevent dispersal, restoring corridors can functionally link populations (Bleyhl et al. 2017; Ziółkowska et al. 2016b). If, however, unoccupied habitat patches are well-connected to extant populations, high poaching pressure might prevent colonization. Reducing mortality (e.g., via upgrading protection status, anti-poaching measures, awareness raising) inside suitable habitat patches or in corridors between them can be effective restoration measures in such situations (Jachmann 2008; Kuemmerle et al. 2011; Leader-Williams and Milner-Gulland 1993). Thus, understanding where unoccupied but suitable habitat patches occur, how they are linked into the wider habitat network, and which threats prevail in these patches are all key for deciding where to implement restoration measures. Mountain regions are generally hard to survey and many areas where mountain ungulates of conservation concern occur are notoriously data-sparse, particularly regarding data on threats. A major challenge is thus how to jointly map potential habitat and multiple threats in such regions across larger geographic extents in order to facilitate restoration planning.

Here, we develop and demonstrate such an approach for bezoar goats (*Capra aegagrus*) in the Caucasus ecoregion, a global biodiversity hotspot (Krever et al. 2001b). This region harbors several species of mountain ungulates, all of which are of conservation concern: two species of Caucasian tur (*Capra caucasica* and *C. cylindricornis*), chamois (*Rupicapra caucasica*), bezoar goat, and Armenian mouflon (*Ovis gmelini*). Most of the ecoregion was part of the former Soviet Union, where the collapse of the Soviet Union in 1991 led to declining human pressure in rural areas (Meyfroidt et al. 2016). This, in turn, translated into increasing habitat quality for many large mammals (Sieber et al. 2015; Weinberg 2001). On the other hand, weakening law enforcement, diminishing support for nature conservation, and economic hardships resulted into a severe poaching crisis in the 1990s (Bragina et al. 2015b). In the Caucasus, this was further amplified by several armed conflicts, occurring especially in regions harboring mountain ungulates (Baumann et al. 2015; Weinberg 2001;

Zazanashvili and Mallon 2009b). Also in Iran and Turkey, poaching has increased substantially in the last decades (Ghoddousi et al. 2019; Şekercioğlu et al. 2011). As a result, populations of mountain ungulates have collapsed in many parts of the Caucasus (Gavashelishvili 2004; Weinberg 2001), their distributions are today only a fraction of what they were, and many species are in urgent need of conservation action (Bleyhl et al. 2015; Zazanashvili et al. 2012).

Bezoar goats, ancestors of domestic goats, once ranged from the Balkans to Pakistan, but today only occupy small pockets of habitat within this region (Naderi et al. 2008; Weinberg et al. 2008). In the Caucasus ecoregion, bezoar goats only occur in small, isolated populations scattered across the region (Weinberg et al. 2008). The species is tightly linked to steep cliffs and rocky outcrops, on which they critically depend for escaping from predators (Esfandabad et al. 2010; Weinberg 2001), making their populations naturally patchy. This also makes bezoar goats highly vulnerable to poaching (Krever et al. 2001b), with males especially at risk due to their sought-after trophies (Damm and Franco 2014). Bezoar goats were still relatively common before the Iranian Islamic Revolution (1979) and the breakdown of the Soviet Union (1991), but plummeted after these events (Ghoddousi et al. 2019; Magomedov et al. 2001; Weinberg 2001). Despite some recent recovery, bezoar goats today are largely confined to protected areas (Karami et al. 2016b; Krever et al. 2001b; Weinberg et al. 2008). This is worrisome as the species forms the main prey for the endangered Persian leopard (*Panthera pardus tulliana*), the region's top predator (Ghoddousi et al. 2016). A broad-scale habitat and threat assessment for bezoar goats across the ecoregion is urgently needed to guide restoration efforts (Krever et al. 2001b).

Restoring mountain ungulates is a conservation priority in many regions, but how to spatially prioritize restoration measures in the face of scarce data typical for mountain regions is often unclear. Here, we exemplify for bezoar goats in the Caucasus, an approach to (1) identify potential habitat patches, (2) assess main factors inhibiting colonization of unoccupied patches, and (3) prioritize patches for particular restoration scenarios, including reintroductions and anti-poaching measures. We assessed the following research questions:

(1) What is the distribution of suitable habitat for bezoar goats across the Caucasus ecoregion?

(2) Where are currently unoccupied habitat patches, and which factors likely prevent bezoar goats from colonizing them?

(3) Where are priority sites for different restoration scenarios for bezoar goats across their former range?

2 Methods

2.1 Study region

The Caucasus ecoregion harbors high levels of biodiversity, including many endemic species (Mittermeier et al., 2004; Zazanashvili et al., 2012). The ecoregion is located between the Black and Caspian Seas, elevations range up to 5,600 m and climate varies from moist, temperate in the west (1,200–4,000 mm precipitation) to arid in the east (<250 mm). Lowland natural vegetation ranges from steppes in the western plains to semi-deserts and arid woodlands in the east. Mountains cover about 65% of the region and are mainly covered by broadleaved forests (mostly beech (*Fagus* spp.), oak (*Quercus* spp.), hornbeam (*Carpinus* spp.), and chestnut (*Castania sativa*)), mixed and pure coniferous forests (mainly Caucasian fir (*Abies nordmanniana*), Oriental spruce (Picea orientalis), and pines (*Pinus* spp.)), Juniper woodlands (*Juniperus* spp.), mountain meadows, and bare rock and ice (Krever et al. 2001b). We used the Caucasus ecoregion boundary as delineated by the Ecoregion Conservation Plan for the Caucasus (Williams et al. 2006b) as our study area (580,000 km^2), plus a buffer of 25 km to avoid border effects in our analyses (Figure A 1; hereafter: Caucasus).

2.2 Bezoar goat data

The known populations of bezoar goat in the Greater Caucasus are in Dagestan, Chechnya and Ingushetia (Russia), and Tusheti (Georgia). In the Lesser Caucasus they occur on the Murovdag, Karabakh uplands and Nehramdag ridge in Azerbaijan, Shahdag and Zangezur ranges (between Armenia and Nakhichevan, Azerbaijan), in Khosrov Forest State Reserve and on the Urts, Vardenis, Sevan, Hayots Dzor, Bargushat and Meghri mountain ridges (Armenia), in Goygol National Park (Azerbaijan) and in the Kaçkar mountains and surroundings in Eastern Turkey. On the Iranian side, the species persists mainly in a number of protected areas in Qaradag and the Alborz mountains, with the largest populations in Marakan Protected Area, Kiamaky Wildlife Refuge and Arasbaran Protected Area (Karami et al. 2016b; Krever et al. 2001b, Iranian Department of Environment, unpub. reports; Weinberg et al. 2008).

We compiled a comprehensive set of bezoar goat occurrence points, collected in the field across the Caucasus. No comprehensive and systematic bezoar goat monitoring system exists at the ecoregional level, and our dataset therefore comprised data from several field campaigns. In most cases, data were collected by trained field ecologists using transect walks or point counts, but we also used opportunistically collected data if coordinates were available. In total, we gathered 902 independent observations of bezoar goats, both from the Greater and the Lesser Caucasus, as well as the Alborz and Qaradag mountain ranges, and Kaçkar Mountains (164 points from Russia, 586 from Armenia, 89 from Georgia, 14 from Iran, 18 from Azerbaijan, and 31 from Turkey). Most points were collected after 2000 (92%), but we also used some points from the 1990s for populations that have since declined or become extirpated (Zazanashvili and Mallon 2009b). These points were roughly equally distributed among sexes and surveys took place in winter and summer. To homogenize our dataset and to minimize pseudo-replication due to clustering, we rarefied our occurrence dataset (Kramer-Schadt et al. 2013) by applying a minimum Euclidean distance of 500 m between points. This yielded a total number of 491 independent occurrence points that were roughly evenly distributed between sexes.

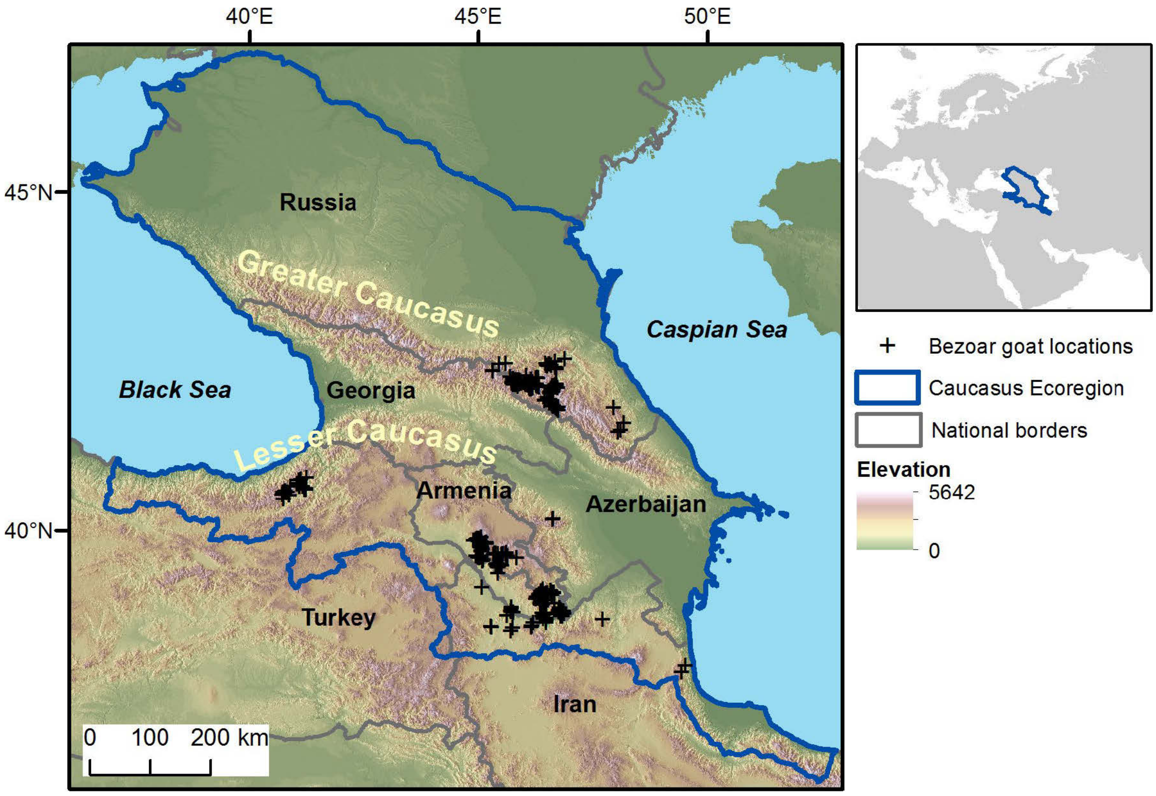

Figure A 1: Caucasus ecoregion, with the Greater Caucasus mountain range in the north and the Lesser Caucasus mountain range in the south.

2.3 Habitat predictor variables

To model bezoar goat habitat suitability, we compiled predictor variables related to (1) landscape elements that function as refuges, (2) resource availability, and (3) human disturbance. We generated all variables at a resolution of 300m for the entire study region (Table A 1). All predictors were projected to an Albers equal-area coordinate system.

Landscape elements such as cliffs provide important refuges to bezoar goats to avoid predation (Esfandabad et al. 2010; Ghoddousi et al. 2016). To proxy such refuges, we derived six variables based on the 30m topography model (from the Shuttle Radar Topography Mission, SRTM) and summarized them to the 300m target resolution: median elevation, median slope, 3rd quartile of slope, ruggedness (measured as the standard deviation of slope), share of cliffs, and the average Euclidean distance to cliffs. For the latter two variables, we tested a range of slope thresholds to separate cliffs from less steep areas, ranging from 30 to 50 degrees (in 5-degree steps). Because bezoar goats use forested areas in proximity to cliffs in some parts of the Caucasus as a refuge, we used a 30m land-cover map derived from Landsat imagery (Bleyhl et al. 2017) to calculate the Euclidean distance of each non-forested pixel to the closest forest edge in that map, and then averaged distances to gridcells at our 300m target resolution.

To characterize resource availability for bezoar goats, we calculated the share of forest, rangeland, and sparse vegetation at the 300m grid level, based on the 30m land-cover map (Bleyhl et al. 2017). Further, we calculated the average Normalized Difference Vegetation Index (NDVI) for the time of peak productivity and over the entire growing season, as well as the average length of the growing season, based on MODIS time series analyses from 2001 to 2012 (Estel et al. 2015b). For the latter, the growing season was defined as the period with NDVI values >0.01 and land surface temperature >5 °C (see Estel et al. 2015 for details). Finally, we calculated two snow cover variables, average days with snow cover and the standard deviation of days with snow cover, using the MODIS snow cover product from 2001 to 2012.

As measures of human disturbance, we derived the Euclidean distance to settlements of every 300 m gridcell using a settlement layer developed by the WWF Caucasus Programme Office on the basis of topographic maps (1:500,000) and OpenStreetMap data (www.openstreetmap.org). Second, we derived the distance of every 300 m gridcell to major roads using the OpenStreetMap road data (categories motorway, trunk, primary, secondary, and tertiary).

Table A 1: Predictor variables used in the bezoar goat habitat suitability models, including data sources and hypothesized influence (+ = positive correlation, – = negative correlation, +/– = non-linear relationship or unclear *a-priori* hypothesis).

	Predictor variables	Data source	Description	Assumed influence
Refuges	Elevation	Shuttle Radar Topography Mission elevation model (30 m resolution)	Median elevation of each 300 m gridcell	+/–
	Median slope 3rd quartile of slope	See above	Median and 75th percentile of slope distribution in each gridcell	+
	Ruggedness	See above	Standard deviation of slope in each gridcell	+
	Share of cliffs	See above	Area share of slope larger x (x = 30 to 50 degrees, in 5-degree steps) in a gridcell	+
	Distance to cliffs	See above	Average distance of non-cliff areas to cliffs	–
Resource availability	Share of forest	Land-cover map by Bleyhl et al. 2017 based on Landsat 8 imagery (30 m resolution)	Area share in a gridcell	+/–
	Share of rangeland	See above	Area share in a gridcell	+
	Share of sparse vegetation	See above	Area share in a gridcell	–
	Distance to forest	See above	Average distance of non-forested pixels to closes forest edge	–
	Peak NDVI	MODIS NDVI time series from Estel et al. 2015 based on MOD/MYD13Q1 (~232 m resolution)	Average NDVI value at peak productivity over the years 2001-2012	+
	Length of growing season	See above	Average length of growing season over the years 2001-2012	+
	Average snow cover	MODIS snow cover time series based on MOD/MYD10A (~500 m resolution)	Average days with snow cover	–
	Variation in snow cover	See above	Standard deviation of days with snow cover.	+/–
Human dist.	Distance to roads	OpenStreet Map & ESRI's Data and Maps Kit Europe 2012	Euclidean distance to nearest road	+/–
	Distance to settlements	See above	Euclidean distance to nearest settlement	+/–

2.4 Map potential habitat patches

Our general approach consisted of three main steps: (1) map habitat suitability for bezoar goats and identify potential habitat patches, (2) assess factors inhibiting patch colonization, and (3) prioritize patches for particular restoration scenarios (Figure A 2).

To map bezoar goat habitat suitability across the Caucasus, we used maximum entropy (Maxent) modeling (Phillips et al. 2006). Maxent models habitat suitability by contrasting distributions of environmental predictors at occurrence locations with the overall distribution of these predictors, while using regularization parameters to prevent overfitting (Elith et al. 2011; Merow et al. 2013). Maxent is well-suited for presence-only data, often outperforms concurrent algorithms and works well with small datasets (Elith et al. 2006a). We used Maxent v3.4.1 with a maximum of 2,500 iterations, quadratic and hinge features only, and default settings for convergence thresholds and regularization (Merow et al. 2013; Phillips and Dudik 2008). Given the clustered nature of our occurrence data, we sampled 10,000 background points in a 20km buffer around our bezoar goat locations, with a minimum distance of 500m between points (VanDerWal et al. 2009). We validated our models with a 10-fold cross validation and the mean area under the curve (AUC) of the receiver operating characteristics (ROC) curve. To assess variable importance, we calculated the percent gain contribution per variable and compared the AUC for single variable models and models without this variable (Phillips et al. 2006). We checked variable collinearity and compared alternative models for all variable pairs with $|r|>0.7$, retaining the variable with a higher model fit and/or with an ecologically more meaningful response curve. Likewise, for the variables share of cliffs and distance to cliffs, we compared models for all slope thresholds and selected the best-fitting variable combination.

We converted the resulting habitat suitability map (average map across 10 replicate runs) into a binary patch vs. matrix map using the maximum training sensitivity plus specificity (TSS) threshold (Liu et al. 2013). We split patches when barriers to dispersal (i.e., major roads) ran through them (according to Bleyhl et al. 2017). We then aggregated polygons into single patches if they were closer than 1km and only retained patches >30km^2 (a patch size allowing for about 125 individuals (Frisina et al. 2003; Ghoddousi et al. 2016; Gundogdu 2011)).

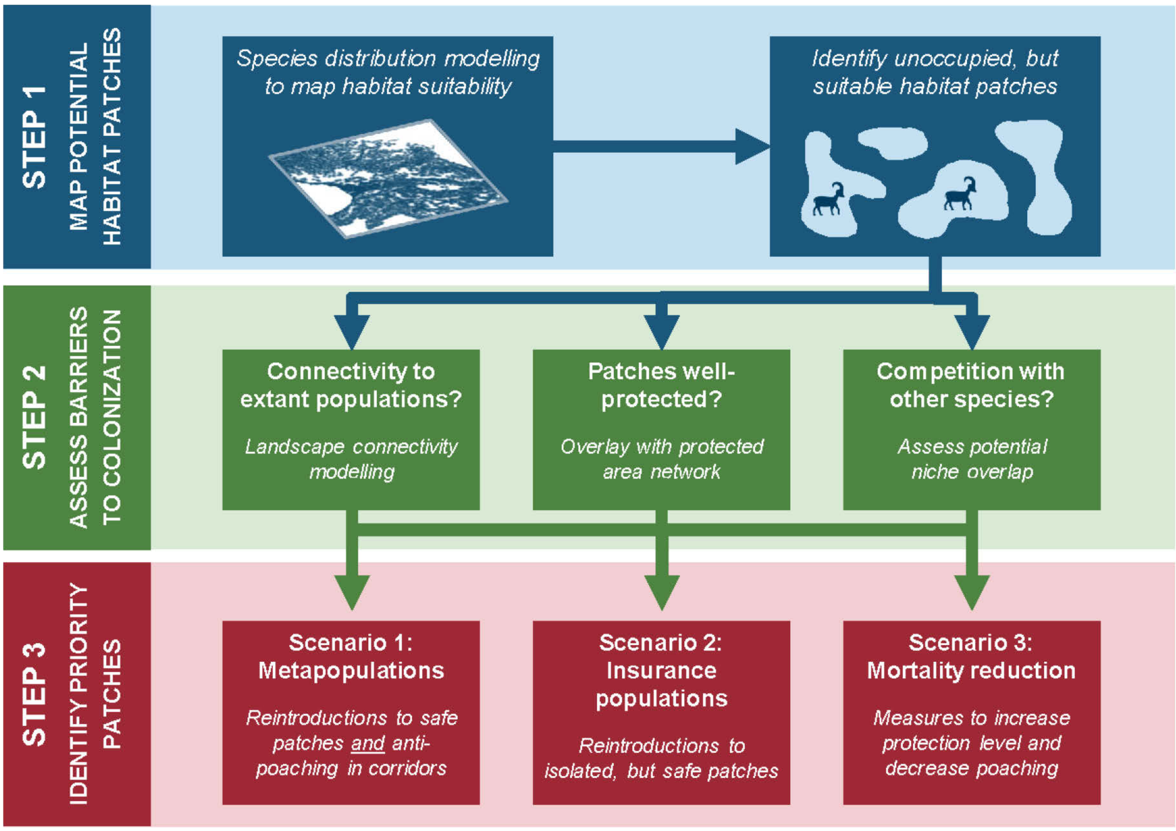

Figure A 2 General workflow to identify priority patches for different bezoar goat restoration scenarios.

3 Assess barriers to colonization

To separate occupied from unoccupied patches, we first selected all patches that had any occurrence point(s) in them based on our (unfiltered) database. Second, we identified patches for which bezoar goat presence has been reported after 2010 (but for which no geotagged occurrence points were available). We considered information as valid when it came from (a) personal field observation of the authors, (b) official reports (e.g., by protected area administrations) or (c) photographic evidence with a clear geographic origin. We considered patches unoccupied if no bezoar goat population has been reported for a given patch.

To assess whether or not unoccupied patches are well-connected to extant populations, we used least-cost path modelling (Adriaensen et al. 2003; Ziółkowska et al. 2016b). We used a cost surface describing the cost of movement of bezoar goats through each cell, parameterized by a wide range of regional wildlife experts (Bleyhl et al. 2017). We then calculated least-cost paths (i.e., cumulative costs along a corridor) from every unoccupied patch to all occupied patches and selected the corridor with the shortest cost-distance for each pair of patches. We then scaled these cost distances between 0 (high degree of isolation from occupied patches) and 1 (well-connected to occupied patches).

To assess whether patches represent safe habitat, we calculated the proportion of each habitat patch that was inside a protected area of IUCN category Ia, Ib or II. In all these protected areas, hunting is prohibited, other land-uses, including livestock herding, are forbidden or highly restricted. Most extant bezoar goat populations today reside in such protected areas. This resulted in an index of protection level, ranging from 0 (patch entirely outside strictly protected areas) to 1 (patch entirely inside strictly protected areas). Note that other factors (e.g., poaching pressure, protected area effectiveness) might influence how safe a patch is, but area-wide data for these indicators is not available for the Caucasus.

Bezoar goats compete with other mountain ungulates, particularly Caucasian tur, and are typically not sympatric with them (Gavashelishvili 2009). To identify patches where bezoar goats might face high competition with turs, we modelled tur habitat using the same predictors and Maxent parameterization as for the final bezoar goat model (see Figure SI A 2 in the Supplementary Information). After obtaining a tur habitat map, we calculated the similarity statistic *I* (Warren et al. 2009) between Caucasian tur and bezoar goat habitat suitability. We did this individually for each bezoar goat habitat patch that was at least partly inside the IUCN range for Caucasian turs (see Supplementary Information), resulting in an index ranging from 0 (high similarity of habitat suitability values) to 1 (low similarity).

4 Identify priority patches for restoration

Once all three indices were available (i.e., connectivity, protection level, competition with turs), we used these indices to identify candidate patches for specific bezoar goat restoration measures. Specifically, we considered three restoration scenarios. Scenario 1 *"Metapopulations"* focused on well-connected patches with a high level of protection. These patches offer potential for establishing new populations via reintroductions, and working towards reducing mortality in corridors (e.g., via anti-poaching measures) to functionally link these herds to existing ones in order to establish bezoar goat metapopulations. Scenario 2 *"Insurance populations"* focused on isolated patches with a high protection level as potential reintroduction sites. Such patches will not make a contribution towards establishing larger, linked populations but could serve as reservoir or 'insurance' populations, from which other populations can be restocked in case of population collapse elsewhere (Perzanowski et al. 2019). Scenario 3 *"Mortality reduction"* focused on well-connected patches with a currently low level of protection. Here, restoration should prioritize measures to reduce poaching of bezoar goats (e.g., educational programs, community-based management, law enforcement) and/or on establishing additional protected areas. For each scenario, instead of using absolute thresholds, we identified the top-ranking patches by calculating average ranks across the three indices (we always prioritized patches with low levels of competition with turs).

5 Results

Our final Maxent model contained 11 variables, three variables describing refuges (distance to cliffs, share of cliffs, 3rd quartile of slope), six variables related to resource availability (share of forest, share of rangeland, distance to forest, maximum NDVI, length of vegetation period, variation in snow cover), and two variables related to human disturbance (distance to settlements, distance to roads). This model had a cross-validated AUC of 0.86 (SD= 0.02). Topographic variables were most important, especially distance to cliffs (35% relative contribution) and share of cliffs (20%), followed by productivity-related variables (vegetation period and maximum NDVI, 11% and 9%, respectively). Human-disturbance variables were of lower importance in our final model (<5% cumulative contribution).

Predicting this model across the region highlighted large areas of potentially suitable bezoar goat habitat throughout the Caucasus (Figure A 3). These potentially suitable areas occurred in the western part of the Greater Caucasus (Karachay-Cherkessia and Kabardino-Balkaria in Russia, Svaneti in Georgia), as well as in Chechnya and particularly Dagestan in the eastern Greater Caucasus. In the Lesser Caucasus, notable areas occurred in Georgia (Samtskhie-Javakheti), eastern Turkey (Artvin, Erzurum), western Azerbaijan (Gadabay, Dashkasan, Goygol), southern Armenia, and northern Iran (Kiamaky, Alborz Mountains). Converting the continuous habitat suitability map into discrete habitat patches (TSS threshold = 0.28) resulted in 153 individual patches of suitable habitat >30km² (Figure A 3), together covering an area of about 30,960 km² (mean patch size =202 km², median =86 km², SD = 392km²).

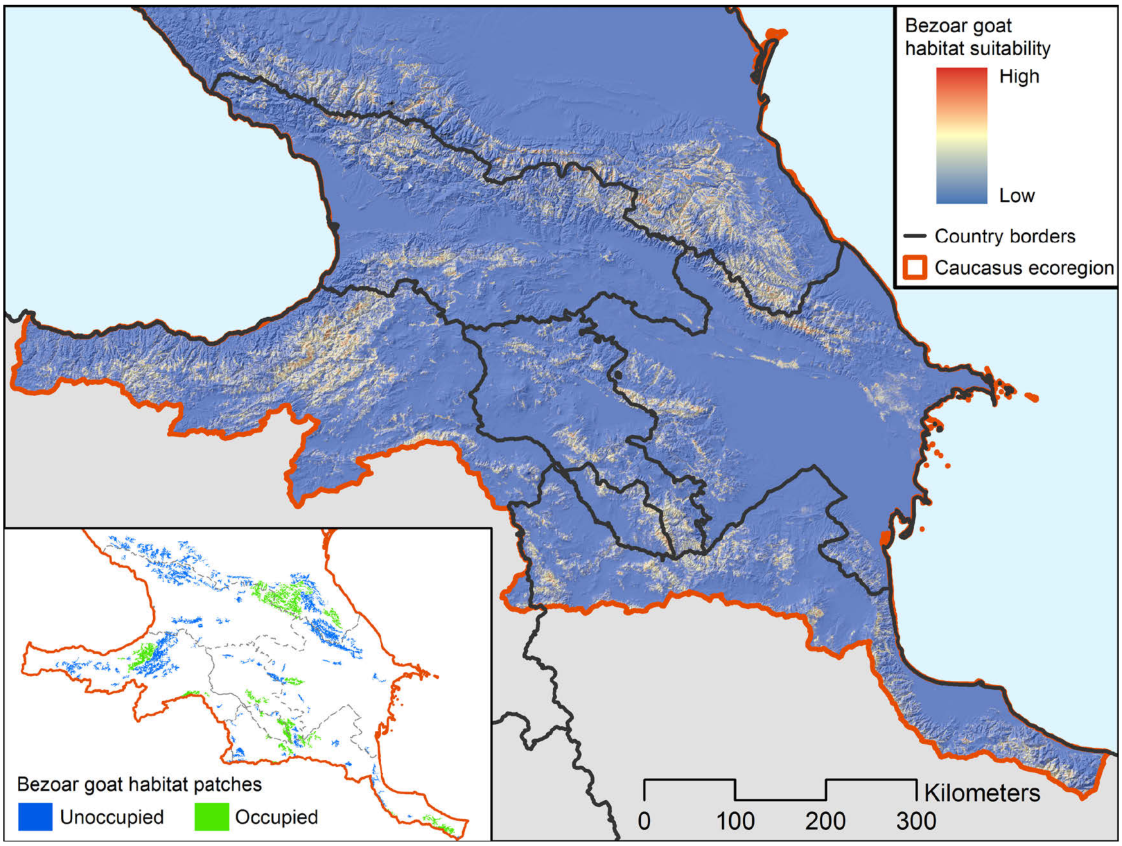

Figure A 3: Habitat suitability for bezoar goats across the Greater and Lesser Caucasus. Inset: Habitat patches of at least 30 km² of suitable habitat, differentiated by whether patches harbor extant bezoar goat populations or not.

Out of these patches, we identified 29 patches as occupied by bezoar goats, while 124 patches did not have confirmed presence of a permanent bezoar goat population. Occupied patches occurred in all Caucasus countries, as well as in both the Greater and the Lesser Caucasus. We identified four distinct clusters of extant bezoar goat populations: (1) in the Greater Caucasus (Chechnya and Dagestan in Russia, as well as in neighboring Tusheti in Georgia), (2) in eastern Turkey (HatilaVadisi National Park and Borçka Karagöl Nature Park, plus surroundings), (3) southern Armenia (Koshrov State Nature Reserve, Zangezur range, Arevik National Park), as well as neighboring regions (e.g., Nakhichevan, Kiamaky Wildlife Refuge in Iran), and (4) the Alborz Mountains in northern Iran (Figure A 3, inset). The largest individual patch of suitable habitat, partly occupied by bezoar goats, occurred in Dagestan (about 3120 km²).

In a next step, we assessed possible reasons why suitable habitat patches might be unoccupied (Figure A 2). Connectivity to extant populations was, as expected, high in the immediate surrounding of occupied patches; but not always. For instance, strong barriers separate unoccupied patches from nearby extant populations in eastern Turkey, the Greater Caucasus in Georgia (i.e., Tusheti), and northern Iran. There was also remarkably low connectivity along the Greater Caucasus ridge, with patches in the western part seemingly isolated from the populations in the eastern part and a clear connectivity bottleneck in Ossetia (Figure A 4A). Our index of protection level (i.e., share of a patch inside protected areas of IUCN category II or higher) signaled generally high levels of protection in and around patches with extant bezoar goat populations in the Greater Caucasus and in southern Armenia (Figure A 4B). Yet the share of patches under protection did not differ noticeably between patches containing extant populations (0.10±0.23) and unoccupied patches (0.11±0.21). Regarding competition with Caucasian tur, potential competition was highest for potential bezoar goat patches along the main ridge of the Greater Caucasus, particularly in the westernmost region, as well as in Chechnya and Dagestan, and adjacent areas in Azerbaijan (Figure A 4C).

Ranking patches according to these indices identified candidate patches for specific restoration scenarios (Figure A 5). Patches fitting our scenario 1 "metapopulations" (i.e. well-connected to extant populations, at least partly protected, low level of competition with turs) occurred in eastern Turkey, and Dagestan in Russia, the Murovdag range in Azerbaijan and Shahdag ridge between Armenia and Azerbaijan, as well as in southern Armenia (Figure A 5A). Priority patches for our second scenario "insurance populations" (isolated, but protected patches from which other populations could be restocked in case of population collapse) occurred on a range of smaller mountain chains between the Greater and the Lesser Caucasus (e.g., Borjomi-Kharagauli National Park in Georgia), as well as in the western Greater Caucasus in Russia (e.g., Mt. Elbrus National Park; Figure A 5B). Finally, our third scenario "mortality reduction" focused on restoring bezoar goat populations outside protected areas (i.e., well-connected patches nearby extant populations). Priority patches for this scenario were highlighted in Dagestan, southern Armenia, as well as eastern Turkey (Figure A 5C). Interestingly, the same patches were sometimes highlighted under our scenarios 1 and 3. The top-ranking 15 patches per scenario covered substantial areas in the Caucasus, with priority patches in scenario 1 covering the highest (>3,800 km^2) and patches in scenario 2 the lowest area (1,400km^2). The top-three patches of scenarios 1 and 2 had a cumulative area of under 300km^2.

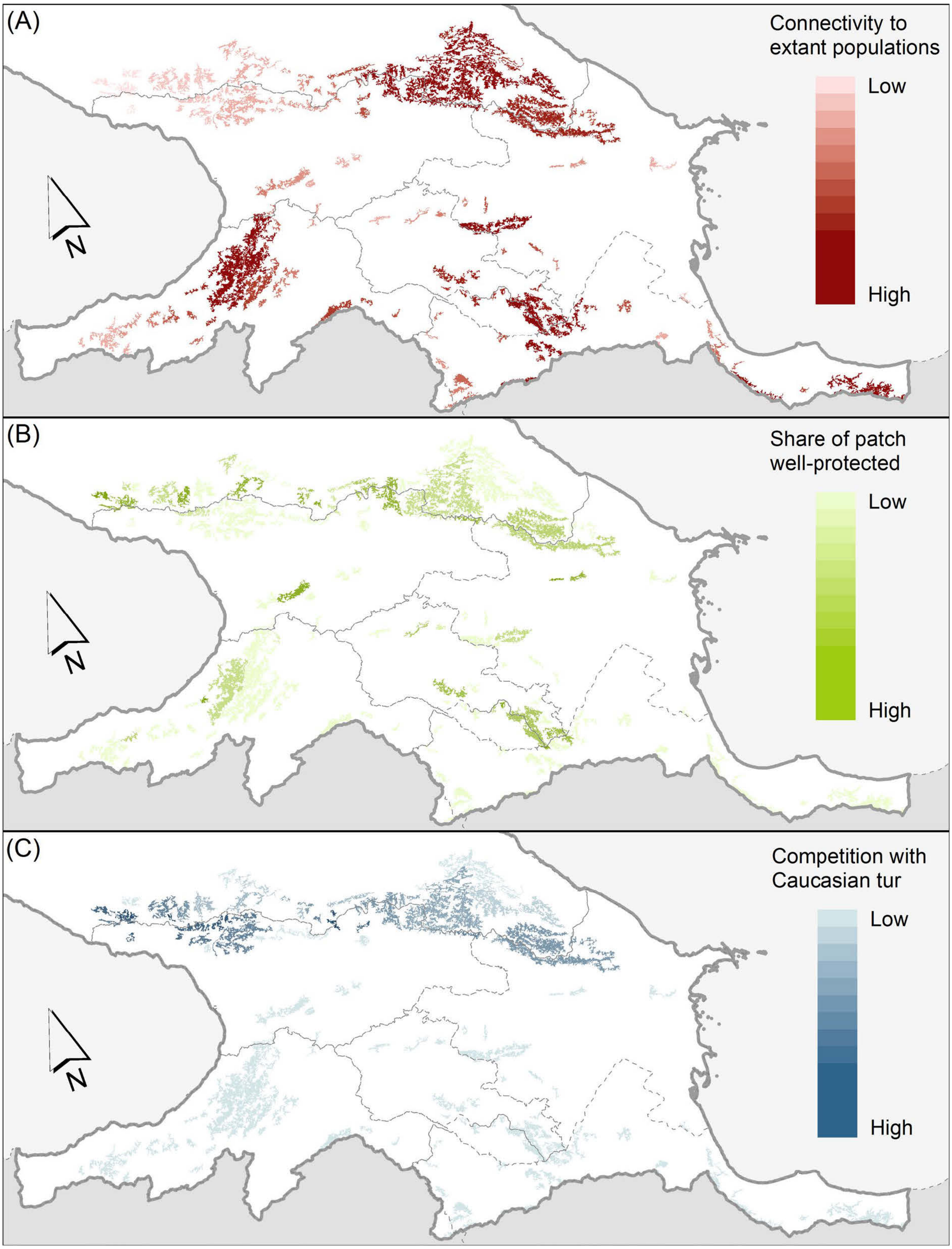

Figure A 4: Potential factors explaining unoccupied bezoar goat habitat patches in the Caucasus. (A) Connectivity of patches to the closest extant bezoar goat population, based on least-cost path modeling. (B) Share of patch protected (inside protected areas of at least IUCN category II). (C) Level of potential competition with Caucasian turs, based on niche overlap analyses (only habitat patches inside the Caucasian tur range were included).

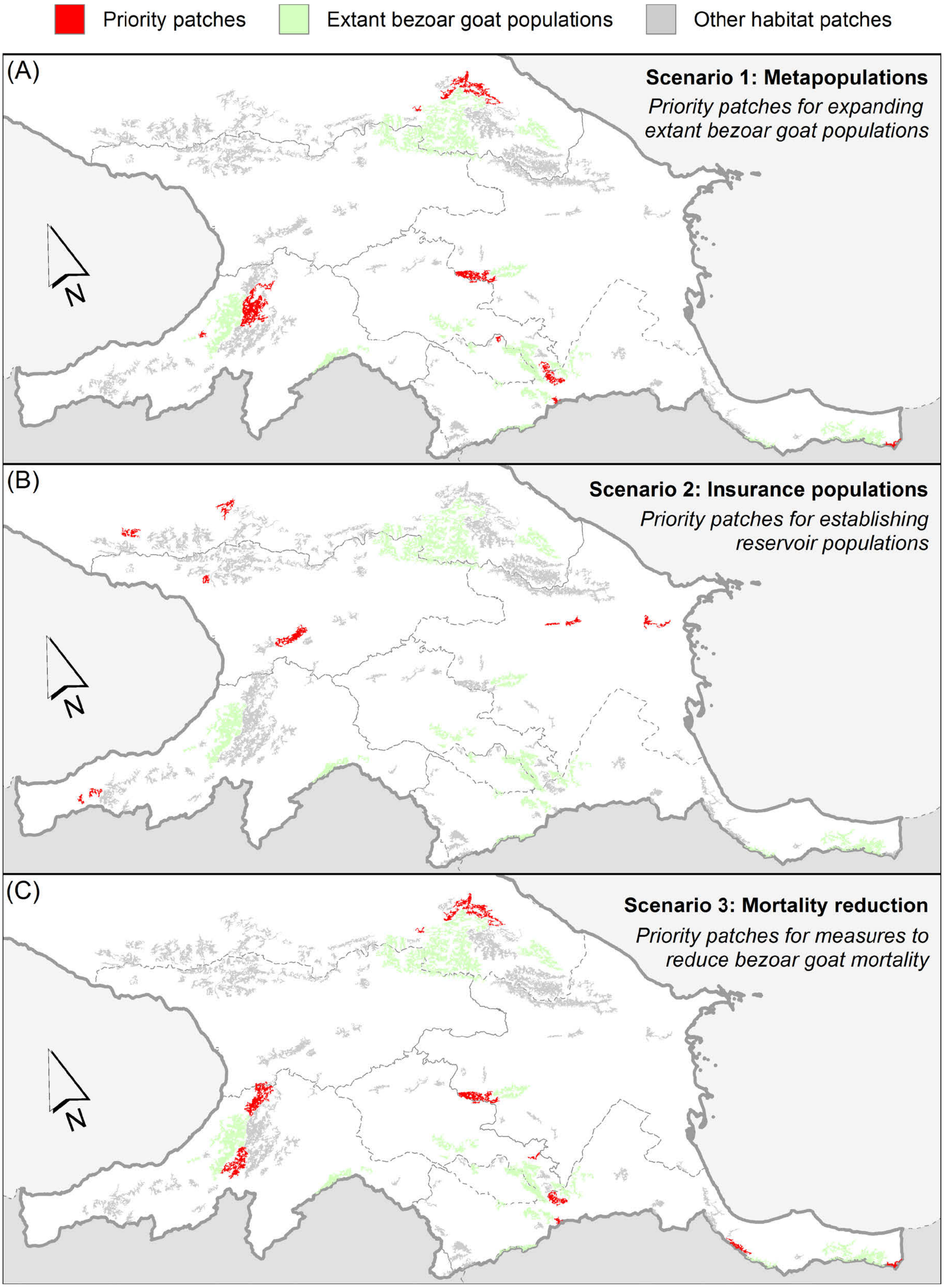

Figure A 5: Priority patches for different scenarios of potential conservation interventions. (A) Scenario 1: candidate sites for reintroductions to expand extant populations. (B) Scenario 2: candidate sites for reintroductions to establish reservoir populations. (C) Scenario 3: candidate sites for conservation measures to lower bezoar goat mortality (e.g., increasing protection-level, anti-poaching actions).

6 Discussion

Mountain regions harbor rich and unique biodiversity (Rahbek et al. 2019), but are also places where strong threats act on biodiversity (Kehoe et al. 2017; Myers et al. 2000). Mountain ungulates are often particularly vulnerable and in decline in many regions. (Damm and Franco 2014; Shackleton 1997b). Restoring their populations is therefore a conservation priority (Bleyhl et al. 2019; Ripple et al. 2015c; Shackleton 1997b). Focusing on bezoar goats in the Caucasus ecoregion, we demonstrate an approach to assess (1) where suitable habitat occurs, (2) why habitat might be unoccupied, and (3) where particular restoration actions would be most beneficial. Collectively, our results highlight widespread unoccupied but suitable habitat for bezoar goats across the Caucasus ecoregion, often near and well-connected to extant populations. This suggests that anthropogenic factors currently prevent natural recolonization of suitable habitat, and that active restoration measures are therefore needed. We identify priority patches for specific restoration interventions, highlighting that many patches would benefit from multiple interventions, and that transboundary, ecoregion-wide conservation planning is needed. Mountain ungulates in many parts of the world are in peril, and our simple and transferable approach can help to guide restoration planning in the face of multiple threats, despite the data-sparse situation typical for remote mountain areas.

Our habitat suitability model had a robust model fit and response types were generally in line with our *a-priori* hypotheses (Table SI A 1), as well as with prior work on bezoar goats. Specifically, our model confirmed the overwhelming importance of cliffs as refuges from predators (Esfandabad et al. 2010; Ghoddousi et al. 2016; Weinberg 2001). Bezoar goats preferred areas with intermediate productivity, longer growing seasons, moderate to low forest cover, and high shares of rangeland (Table SI A 1), in line with a reported preference of the species for warmer and more arid conditions (Heptner et al. 1961; Weinberg et al. 2008). Interestingly, human-pressure variables (in our case proxied by distance to settlements and roads) were less important in our models. Explanations could be that these variables do not effectively proxy key human threats to bezoar goats, such as poaching pressure, that the pressure associated with roads varies seasonally (high in summer but low in winter), or that other variables, such as the cliff variables, partly capture (low) human pressure. Similarly, the relationship between such pressures and our variables likely varies across the region and over time, which we could not take into account. Indeed, mountain ungulates in the region occur close to people if they are not poached (Ghoddousi et al. 2015; Weinberg and Malkhasyan 2013).

Overall, our habitat model resulted in plausible spatial patterns of potential bezoar goat habitat (Figure A 3). A surprising result was the relatively large area of moderately suitable habitat we predicted for the northwestern Caucasus, where the species has historically not been recorded (Heptner et al. 1961). Bezoar goats are thought to be linked to more arid climates than those found in the wet and snow-rich northwestern Caucasus (Weinberg et al. 2008). We purposefully did not include downscaled, modelled climate variables, but instead used observational variables more directly linked to resource availability. Aridity proxies, such as ‘share of rangelands’, support the idea that bezoar goats prefer warmer climates (Table S1). Yet including other climate variables might reduce habitat suitability in the northwestern Caucasus further. Alternatively, other ecological factors, particularly dispersal limitations and competition, might prevent bezoar goats from colonizing moderately suitable areas in this region. There is a possible dispersal bottleneck along the main ridge in the Greater Caucasus (Figure A 3; Bleyhl et al. 2017), west of which bezoar goats have not been recorded. Likewise, competition with other mountain ungulates, particularly tur and chamois, could prevent colonization. These species are better adapted to wetter and snowier conditions (Gavashelishvili et al. 2018), and we indeed found many moderately suitable bezoar goat habitat patches in the western Greater Caucasus to be highly suitable for turs (Figure A 4B). While the complex relationship of competition between multiple mountain ungulates and the resulting niche partitioning and distributions remains weakly understood (Bleyhl et al. 2019; Gavashelishvili et al. 2018), competition is a plausible explanation for the absence of bezoar goats in the western Greater Caucasus. Thus, although we find potentially suitable habitat for bezoar goats in the northwestern Caucasus, we explicitly caution against restoration projects there (e.g., reintroductions) until the biogeographic history and ecology of interactions with other mountain ungulates are better understood.

Across the confirmed historical range of bezoar goats in the Caucasus, our habitat map highlighted vast areas of currently unoccupied yet suitable habitat. Recent population declines can explain this pattern. As elsewhere in the former Soviet Union, large mammal populations in the Caucasus crashed in the 1990s due to high poaching levels (Berger et al. 2013; Bragina et al. 2015b), leading to substantial range contractions and local extirpation (Zazanashvili and Mallon 2009b). Consequently, the four clusters of extant bezoar goat populations we identified are now isolated from each other (i.e., eastern Greater Caucasus, southern Armenia and surroundings, eastern Turkey, and Iranian Alborz Mountains; Figure A 3). Even within these areas, bezoar goats only occupy a fraction of the suitable habitat we found there. Whereas large mammal populations rebounded after 2000 elsewhere in the former Soviet Union, due to better protection and declining human pressure (Bragina et al. 2015b; Chapron et al. 2014b), such trends have not yet materialized across larger areas in the Caucasus. This underpins the persistently high level of threats to large mammals in this region (Bleyhl et al. 2019; Burton et al. 2018).

Much of the currently unoccupied habitat was well-connected to extant bezoar goat populations (Figure A 4). We suggest that high human pressures, and particularly poaching, likely explain why bezoar goats are not colonizing these seemingly suitable habitat patches in many parts of the Caucasus. As elsewhere, spatial data on poaching is unavailable in the Caucasus, preventing us from including poaching directly in our models. Yet poaching is a key threat to mountain ungulates in this region (Ghoddousi et al. 2019; Soofi et al. 2019; Zazanashvili and Mallon 2009b), as these species are preferred by poachers and easy to hunt (Ghoddousi et al. 2019), and because poaching is linked to transhumance grazing still found across large areas in the Caucasus (Gavashelishvili et al. 2018). Most extant bezoar goat populations we identified are confined to protected areas, even within otherwise larger patches of habitat (Figure A 3, Figure SI A 1). High poaching pressure outside protected areas would render successful colonization of new patches through dispersal an unlikely scenario. Moreover, many protected areas are underfunded, particularly regarding anti-poaching patrols (Ghoddousi et al. 2019; Holden et al. 2019). If poaching extends into protected areas, dispersal events might be rare as these events typically become common only at high population densities (McCullough 1999). High bezoar goat densities are rare throughout the Caucasus. Indeed, where bezoar goats are slowly expanding their ranges, it is in areas where stricter law enforcement has reduced poaching levels, leading to population increases, such as in eastern Nakhichevan (authors' own. obs.). Yet, for most places in the Caucasus, translocations and/or anti-poaching measures will be key to foster recolonization of unoccupied habitat patches.

Our ecoregion-wide priority patches under different restoration scenarios provide a spatial template for targeting possible restoration interventions. Importantly, as with any top-down conservation planning, a next step would be to complement our assessment with bottom-up components to explore local site conditions, socio-demographic factors, feasibility, and costs, before deciding on where to implement restoration interventions. Two main insights emerge from our prioritization exercise. First, bezoar goat restoration would benefit from, and in many cases will likely require, the parallel implementation of multiple actions, as similar patches were highlighted by two of our restoration scenarios (Scenario 1 and 3; Figure A 5). Eastern Turkey and southern Armenia and surrounding areas stand out as regions where translocations to new patches and anti-poaching measures in corridors (i.e., scenario 1), as well as ramping up protection (new reserves, anti-poaching patrols) in currently unoccupied patches (scenario 3) would provide substantial restoration opportunities. This would likely not only benefit bezoar goats, but also other mountain ungulates and the predators that depend on them, such as the endangered Persian leopard. Likewise, restored bezoar goat populations might create co-benefits for local communities via legal, controlled hunting and/or income from trophy hunting (Di Minin et al. 2016a; IUCN 2016; Michel et al. 2015). This can reduce poaching incentives and pressure, but also entails risks as trophy hunting can lead to undesirable evolutionary and fitness outcomes (Coltman et al. 2003; IUCN 2016). We caution that legal hunting can only become an option once bezoar goats have attained (much) larger populations and any offtake quotas would have to be scientifically grounded. Currently, bezoar goats are strictly protected in all Caucasus countries. Second, many of the priority patches we found occur close to international borders (one third of all patches occur closer than 5km to international borders or are extend across them). This highlights the urgent need for transboundary cooperation and planning to restore and safeguard populations of mountain ungulates in the Caucasus and elsewhere. Our second restoration scenario identified isolated patches that are comparatively well-protected. While establishing populations there would not contribute to establishing larger metapopulations, such additional populations would still be important as reservoirs from which to translocate individuals to other areas (Perzanowski et al. 2019).

A few limitations need mentioning. We used a large occurrence dataset, tested a wide range of variables determining habitat suitability for bezoar goats, and our species distribution models performed well. Still, additional variables that were unavailable for the ecoregion, such as a snow depth or local water availability, would have likely improved the model further. Also, our measure of protection level (share of patch strictly protected) was quite simplistic. Indeed, some officially strictly protected areas are not functioning well, whereas some protected areas of lower IUCN categories, such as wildlife refuges or sanctuaries provide safe habitats for wildlife. Incorporating measures of protected area effectiveness once available across the region, such as data collected through the Protected Area Management Effectiveness (PAME) tools, would be beneficial and might provide a more direct measure of poaching pressure and what constitutes a safe habitat. Likewise, incorporating data on the presence of shepherds in the landscape would be beneficial for the same purpose. Direct competition between bezoar goats and livestock is likely lower than for other mountain ungulates (Bleyhl et al. 2019), due to bezoar goats clear connection to steep cliffs. However, shepherds can exert substantial poaching pressure (Gavashelishvili et al. 2018). Likewise, incorporation of other potential threats, such as mining and infrastructure development, would improve our models. However, region-wide spatial data on these threats is lacking. Importantly, once such data become available, they can be easily incorporated in our approach (step 2, Figure A 2). We considered competition with Caucasian turs which have considerable niche overlap with bezoar goats (Gavashelishvili 2009), but did not consider chamois, another potential competitor. However, chamois typically prefer more humid habitats, and turs are considered the main native competitor for bezoar goats (Gavashelishvili 2009b; Gavashelishvili et al. 2018; Weinberg 1983). Nevertheless, repeating our assessment for the full suite of mountain ungulates in the Caucasus can be an interesting next step, but would require substantial additional data on species' occurrences. Finally, we used a wide range of available occurrence data and reports to identify patches with extant bezoar goat populations. Yet some regions, such as Chechnya, are poorly surveyed and we cannot rule out that higher survey effort would reveal additional bezoar goat populations in the region.

Mountain ungulates in many parts of the world are in decline, and many only persist today in small and fragmented populations, mostly confined to protected areas (Berger et al. 2013; Luo et al. 2014; Shackleton 1997b; Zazanashvili and Mallon 2009b). Restoring them across their historical ranges is therefore a conservation priority, but restoration planning is often inhibited by inadequate data on threats and on where to prioritize which restoration measures. Here, we show how relatively simple biodiversity models and geospatial analyses can be brought together to detect unoccupied but potentially suitable habitat, assess potential barriers to recolonization, and spatially prioritize restoration interventions, including reintroductions and anti-poaching interventions. For bezoar goats in the Caucasus, this highlighted that multiple restoration measures would often be beneficial to address interacting threats, a situation likely similar for many mountain ungulates. Addressing these threats, particularly poaching, would benefit bezoar goats and many other threatened large mammals in the Caucasus. Likewise, our work highlights the importance of border regions as havens for mountain ungulates, translating into an urgent need for transboundary, ecoregion-wide restoration planning in the Caucasus biodiversity hotspot (Farhadinia et al. 2015; Zazanashvili and Mallon 2009b) as well as other mountain regions of the world (Gavashelishvili et al. 2018).

Supplementary Information

Protected areas in the Caucasus

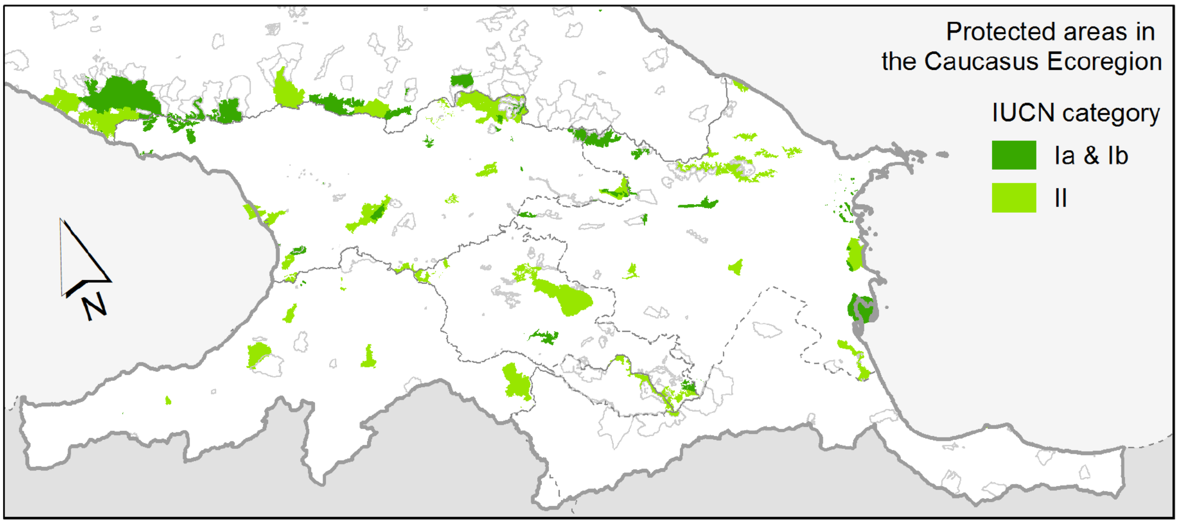

Figure SI A 1: Protected areas in the Caucasus. Only protected areas of IUCN category Ia, Ib or II are shown. Other protected areas are outlined.

Tur habitat suitability modelling

To assess possible niche overlap between bezoar goats (*Capra aegagrus*) and Caucasian turs (*C. caucasica* and *C. cylindricornis)*, we modelled the habitat suitability of Caucasian tur using the same Maxent parameterization as our final bezoar goat model. While other parameterizations and predictor variables would possibly approximate tur habitat even better, using the same model parameterization maximizes comparability and provides a conservative measure of niche overlap.

We treated the two tur species (Western and Eastern) as one as they are ecologically equivalent (Weinberg 2008a, b). For Eastern tur, we used occurrence data from Gavashelishvili et al. (2018) (n= 80) gathered in the field using transect and point counts. For Western tur, we used opportunistic field sightings (n=7) and home ranges of tur groups identified during a field census in Kavkasky Nature Reserve, Russia. Within these home ranges, we randomly sampled 30 points, relative to the size of the home range. This yielded a total of 117 occurrence points. As background points, we used 10,000 randomly drawn points from within the IUCN tur ranges, with a minimum distance of 10 km between points.

As predictors, we used 11 variables: three variables describing refuges (*distance to cliffs, share of cliffs, 3rd quartile of slope*), six variables related to resource availability (*share of forest*, *share of rangelands*, *distance to forest*, *maximum NDVI, length of vegetation period*, *variation in snow cover*), and two variables related to human disturbance (*distance to settlements*, *distance to roads*). This Maxent model had a cross-validated AUC of 0.903. Vegetation period and variability in snow cover, both climate proxies, were the most important variables in this model, followed by human disturbance variables and topographic variables.

Niche overlap between bezoar goats and Caucasian turs

To assess potential competition between bezoar goats and Western and Eastern Caucasian tur, we calculated Warren's I, which measures niche overlap between two species based on the probability distributions of occurrence, as generated by species distribution models (Warren et al. 2008). We calculate *I* individually for each bezoar goat habitat suitability patch that was at least partly in the range of Caucasian turs according to the IUCN range of the two species. Warren's *I* was calculated according to:

$$I(p_{Bezoar}, p_{Tur}) = 1 - \frac{\left(\sqrt{\Sigma_i\left(\sqrt{p_{Bezoar,i}} - \sqrt{p_{Tur,i}}\right)^2}\right)^2}{2} \qquad \text{(Eq. 1)}$$

where p_{bezoar} and p_{tur} denote habitat suitability values for bezoar goats and Caucasian tur, respectively. Note that p was normalized so that the sum of p equals 1 across all gridcells i in a given bezoar goat habitat patch. For our calculation, we used the corrected formula (http://enmtools.blogspot.com/2010_09_01_archive.html).

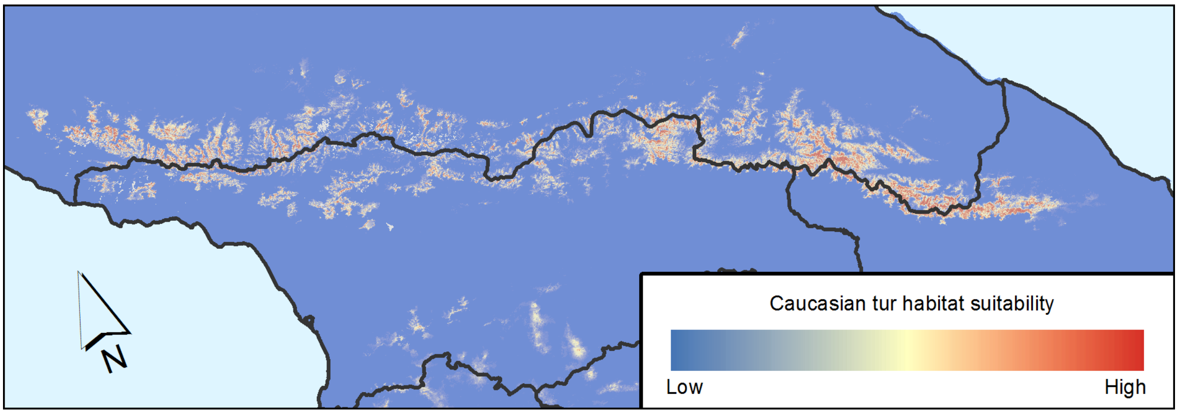

Figure SI A 2: Caucasian tur habitat suitability.Note that Caucasian tur are endemic to the Greater Caucasus *(Weinberg 2008a, b)*.

Variable response types in the final habitat model

Table SI A 1: Predictor variables in the final bezoar goat habitat suitability model. Variable contribution: relative contribution of a variable to the regularization gain. Permutation importance: relative change in training AUC when randomly permuting the input data. A-priori hypothesis: + = positive relationship, – = negative relationship, +/– = unclear *a-priori* hypothesis. HD = Human disturbance.

	Predictor variables	Variable contribution	Permutation importance	A-priori hypothesis	Response type found
Refuges	Distance to cliffs	31	27.8	–	╲
	Share of cliffs	21.3	3.4	+	╱
	3rdquartile of slope	8.1	5.2	+	╱
Resource availability	Peak NDVI	13.4	12	+/–	∩
	Length of growing season	8.9	15.2	+	╱
	Variation in snow cover	7.5	17.4	+/–	∩
	Share of forest	1.4	4.6	+/–	∩
	Distance to forest	0.8	1.6	–	∪
	Share of rangeland	0.5	3.6	+	╱
HD dist.	Distance to roads	3.6	3.7	+/–	∩
	Distance to settlements	3.5	5.5	+/–	∩

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Appendix B:
Mapping European bison habitat in the Caucasus mountains to identify potential reintroduction sites

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Abstract

In an increasingly human-dominated world, conservation requires the mitigation of conflicts between large mammals and people. Conflicts are particularly problematic when resources are limited, such as at wintering sites. Such conflicts have fragmented many large mammal populations, making reintroductions in suitable sites necessary. Broad-scale habitat suitability mapping can help to identify sites for species' reintroductions. The European bison is a good example of a large mammal that is restricted to only a fraction of its former range. The goal of our study was to identify and assess potential habitat for European bison in the Caucasus Mountains, which is a part of its former range and has the potential to harbor larger populations. Specifically, we used seasonal presence data from four reintroduced European bison populations and two sets of predictor variables to: (i) map habitat suitability for summer and winter, (ii) characterize habitat based on management-relevant categories that capture the potential for conflicts with people, and (iii) identify candidate sites for reintroductions. We found substantial areas of suitable habitat. However, areas of potential conflicts with people were widespread and often near highly suitable areas. We identified 69 potential reintroduction sites (10 230 km^2, 1.8% of the ecoregion) that have suitable summer and winter habitat with relatively low risk of human-wildlife conflict. These results can guide conservation efforts in establishing a viable European bison metapopulation in the Caucasus ecoregion. More broadly, our results highlight the need to map large mammal habitat suitability for different seasons in order to derive meaningful conservation recommendations.

1 Introduction

Large mammals are threatened in many parts of the world, mainly because of habitat loss, over-hunting, and conflicts with people and their land use (Cardillo et al. 2005; Hoffmann et al. 2011; Ripple et al. 2015). Many large mammal populations are therefore small and isolated, making them prone to extirpation (Di Marco et al. 2014). This is worrisome, because large mammals play key roles in ecosystem functioning (Jaroszewicz et al. 2013; Pringle et al. 2007), often serve as umbrella species (Branton and Richardson 2011), and are iconic flagships for conservation. Identifying ways to protect large mammal species in increasingly human-dominated landscapes is thus a key priority for conservation science (Hoffmann et al. 2011; Ripple et al. 2015).

Conservation planning for large mammals requires mapping suitable habitat for protecting and enlarging existing populations, for identifying corridors between them, and for locating candidate sites for future reintroductions (Hebblewhite et al. 2011; Schadt et al. 2002). Species distribution modeling is an important tool to understand habitat selection and predict habitat patterns (Elith and Leathwick 2009; Engler et al. 2004; Guisan and Thuiller 2005). In human-dominated landscapes, habitat models must include measures of potential conflicts with people (e.g., Hebblewhite et al. 2014; Kuemmerle et al. 2014; Zhou and Zhang 2011), and if spatially explicit data on underlying threats, such as poaching, is lacking, then proxy variables, such as distance to roads or settlements, are typically used. However, when proxy variables for conflict are immediately combined with resource-related variables in habitat models, then it becomes more difficult to assess what ultimately drives habitat suitability. Moreover, habitat models that include conflict variables are ill-suited to identify areas that may act as population sinks because they offer attractive but risky habitat (i.e., ecological traps, Delibes et al. 2001; Naves et al. 2003). That makes it advantageous to parameterize models characterizing environmental and human conflicts separately (Naves et al. 2003), but such a two-step modeling approach has only been applied a few times, and mainly for large carnivores (e.g., De Angelo et al. 2013; Kanagaraj et al. 2011; Martin et al. 2012).

Another important issue when modeling habitat of large mammals arises from the fact that their habitat needs can vary considerably among seasons. However, most modeling applications so far have modeled large mammal habitat for a single season, usually summer. This is problematic for two reasons. First, summer habitat is typically more widespread than winter habitat, especially for large ungulates, but survival rates are typically lower in winter

(Mysterud et al. 2007). Second, summer and winter habitat may differ in location and spatial pattern, meaning the protection of the species' full annual range is necessary to ensure its survival and thus to achieve conservation goals (Gavashelishvili 2009; Kuemmerle et al. 2014; Martin et al. 2007).

European bison (*Bison bonasus*), Europe's largest terrestrial mammal, is a great example of a species restricted to a few small and isolated populations (Kuemmerle et al. 2012a; Pucek et al. 2004). European bison went extinct in the wild in the early 20th century and the last free-ranging individual was poached in 1927 in the western Caucasus (Krasińska and Krasiński 2007). A small number of European bison survived in zoos though, and a reintroduction program began after World War II. Today, about 3220 animals live in 40 wild, but small and isolated populations (Raczyński 2013). The Caucasus is one of the species' strongholds, with three herds harboring together more than 500 bison (Sipko et al. 2010). Yet, effective population size (N_e) of European bison in the region is too small to be viable (i.e., $N_e > 400$–500 individuals, Olech and Perzanowski 2002; Pucek et al. 2004; Tokarska et al. 2011) and there is no natural exchange among the herds, which is especially problematic because of the genetic bottleneck that the species went through (only 12 captive founders). Furthermore, a suite of human threats has caused population declines for bison and other wildlife after the collapse of the Soviet Union (Bragina et al. 2015a; Di Marco et al. 2014; Krasińska and Krasiński 2007). Poaching was the main reason and may continue in some parts of the Caucasus (Sipko 2009; Trepet and Eskina 2012). Other threats include illegal logging, pollution, armed conflicts, and infrastructural development (Cheterian 2008; Zazanashvili and Mallon 2009).

The Caucasus contains some of the last remaining wilderness areas in Europe where apex predators and large ungulates still exist in large enough numbers to shape ecosystem processes (Estes et al. 2011; Zazanashvili and Mallon 2009), making it a prime candidate site for further bison reintroductions (Sipko et al. 2010). Indeed, a trans-national conservation plan for the Caucasus lists European bison as one of 26 priority species with the target to achieve a healthy and safe population by 2025 (Williams et al. 2006; Zazanashvili et al. 2012). Identifying suitable habitat, especially winter habitat, with low risk for human-wildlife conflict is critical to reach this target. However, prior studies focused either on very small study sites (Klich and Perzanowski 2012; Nemtsev et al. 2003) or covered the Caucasus in a coarse-scale habitat suitability analysis as part of the species' former range (Kuemmerle et al. 2011). A detailed habitat analysis for different seasons and for the entire region is still lacking.

Our first objective was to map potential European bison habitat in both winter and summer for the Caucasus region. Our second objective was to distinguish suitable habitat that is safe, from suitable habitat with high potential for human-bison conflicts (i.e., ecological traps), and safe but only marginally suited habitat (i.e., potential refuges). Finally, our third objective was to identify patches with sufficient winter and summer habitat and low human impact as candidate sites for potential future reintroductions.

2 Data and Methods

2.1 Study area

The Caucasus harbors high levels of biodiversity, including many endemics (Mittermeier et al. 2004; Myers et al. 2000; Zazanashvili et al. 2012). The ecoregion is located between the Black and Caspian Seas, elevations range up to 5600 m and climate varies from moist, temperate in the west (1200–2000 mm precipitation) to arid in the east (< 250 mm). Lowland natural vegetation ranges from steppes in the western plains to semi-deserts, and arid woodlands in the east. Mountains cover about 65% of the region and are dominated by broadleaf forests (mostly beech, oak, hornbeam, and chestnut) with some dark coniferous and pine forests (Krever et al. 2001), mountain meadows, and bare rock and ice. We selected the Caucasus ecoregion, as delineated by the World Wide Fund for Nature (WWF, Krever et al. 2001) as our study area (580 000 km^2), plus a buffer of 25 km to avoid edge effects in the predictors (Figure B 1).

The exact historic range of European bison in the Caucasus is not known, but archeozoological findings suggest historic occurrences throughout the Greater Caucasus (Kuemmerle et al. 2012a; Nemtsev et al. 2003; Sipko et al. 2010). Bison today occur in three reintroduced herds in Russian protected areas: the Caucasus biosphere nature reserve (Kavkasky, 830 animals, consisting of European bison x American bison (*Bison bison*) hybrids), Teberdinsky biosphere nature reserve (Teberdinsky, 22 animals), and the North-Ossetian national nature reserve (North Ossetia, 66 animals).

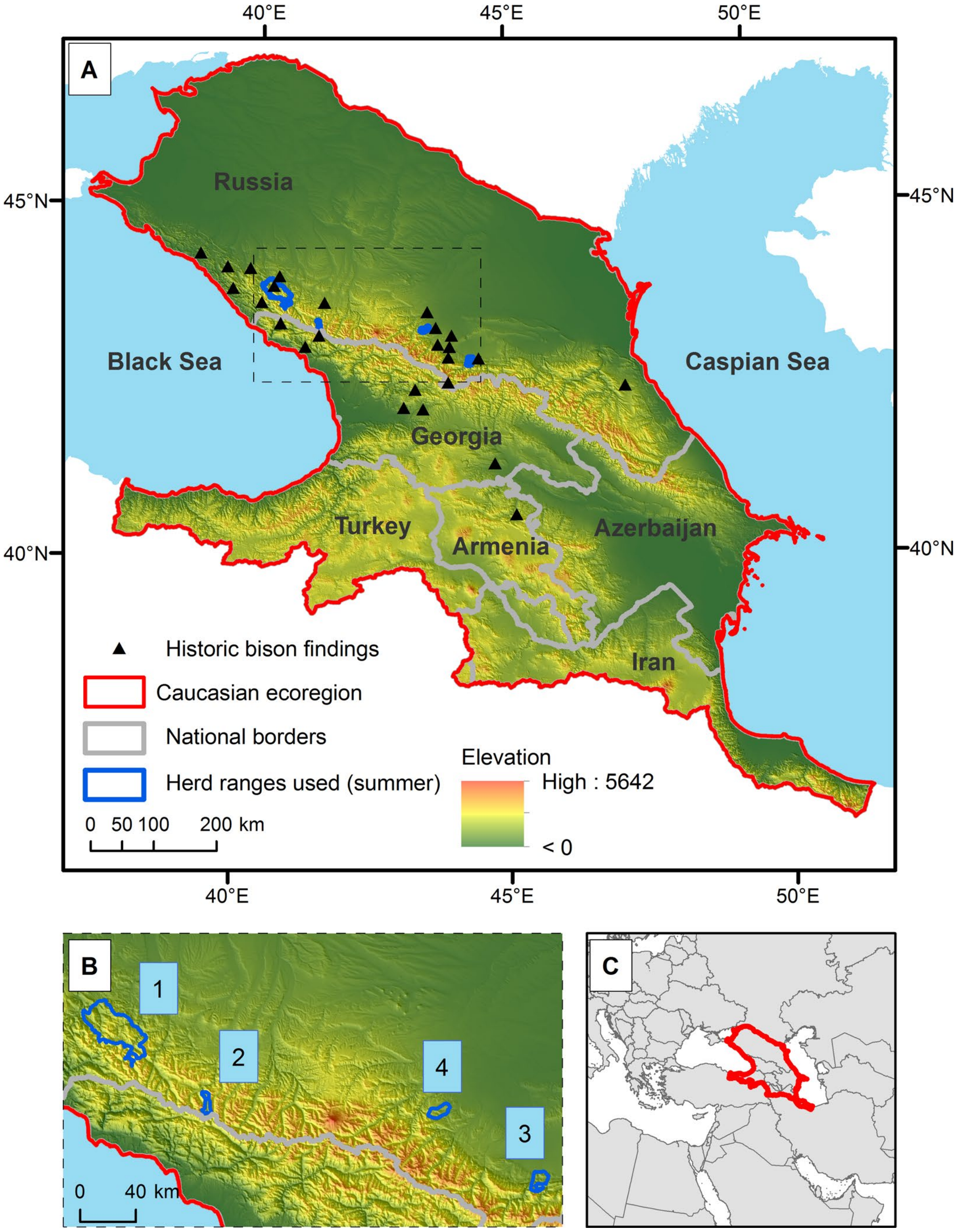

Figure B 1: (A) Overview of the Caucasus ecoregion, herd ranges and historic findings of European bison (Heptner et al. 1961; Kuemmerle et al. 2012a; Nemtsev et al. 2003), mountain ranges of the Greater Caucasus (in the north) and the lesser Caucasus (in Georgia, Turkey, Armenia, and Azerbaijan in the south); (B) herd ranges, shown in blue, of the four European bison populations: 1 = Kavkasky, 2 = Teberdinsky, 3 = North Ossetia, 4 = Nalchik; (C) Location of the Caucasus ecoregion (red).

3 Predictor variables

To parameterize our habitat suitability models, we used a candidate set of eleven predictors characterizing landscape composition, topography, vegetation productivity, and human disturbance (see Supplementary Information), out of which we included six environmental and two human-disturbance predictors in our final models (Table B 1).

Table B 1: Summary of predictor variables used in the final Maxent models.A detailed rationale and description of these variables, including full data sources, is provided in the Supplementary Information.

Category	Predictor	Source	Spatial resolution
Environmental	Land cover	Globcover 2009	300 m
	Forest fragmentation		
	Distance to forest		
	Percent tree cover	MODIS Vegetation continuous field product	250 m
	Length of the vegetation period	MOD13Q1v5 and MYD13Q1v5	250 m
	Slope	SRTM	90 m
Human disturbance	Distance to roads	WWF CauPO, WWF Armenia, Open Streetmap, ESRI Data and Maps Kit 2012	100 m
	Distance to settlements	WWF	100 m

To capture land-cover, we used the 2009 Globcover dataset (300 m resolution, Bontemps et al. 2011, http://due.esrin.esa.int/globcover/). We aggregated the 22 Globcover land-cover categories into ten classes: coniferous forest, mixed forest, broadleaved forest, open forest, grass- and shrubland, cropland, mosaic vegetation / cropland, bare and sparsely vegetated areas, settlements, and water (for details see Supplementary Information). To capture forest fragmentation, we used morphological image segmentation applied to the combined forest classes as the focal class (Vogt et al. 2007). We stratified all forest gridcells into (i) core forest (forest neighbors), (ii) edge forest (outer margin of core forest), (iii) islet (forest patches too small to contain core forest), and (iv) perforation (interior edges, Kuemmerle et al. 2010; Vogt et al. 2007), using an eight-neighbor rule and 300-m edge width. We also calculated the Euclidean distance of each pixel to the closest forest edge. In addition, we acquired the Vegetation Continuous Fields product (VCF, MOD44B, collection 5, version 1, years 2000–2010) from the MODerate Resolution Imaging Spectroradiometer (MODIS) to calculate fractional tree cover data with 250-m resolution as the VCF average for 2000, 2006, 2008, 2009 and 2010 (the other years had too much missing data).

To capture vegetation productivity, we calculated the mean Normalized Difference Vegetation Index (NDVI) for summer (June–August) and the length of the vegetation period for each year, and then averaged them across all years (2000–2012, see Estel et al. 2015). Length of the vegetation period was defined as the period with NDVI values > 0.01 and a land surface temperature > 5 °C. Additionally, we used the MODIS snow cover product (MOD10A2) from 2001–2012 to calculate the number of days with snow cover per year which we then averaged across all years. All MODIS data (including VCF) were acquired from the Land Processes Distributed Active Archive Center (http://lpdaac.usgs.gov).

To capture topography, we derived elevation and slope from the Shuttle Radar Topography Mission data (SRTM, http://srtm.csi.cgiar.org/). Slope was limited to 28 degrees maximum for the summer models, because initial results predicted increasing suitability on steeper slopes although very few occurrence points were found on slopes > 30 degrees (see Supplementary Information).

Human disturbance was measured as the Euclidean distances to roads and settlements. We obtained the roads and settlements layer from WWF Caucasus Programme Office (CauPO) and WWF Armenia. Both datasets are based on topographic maps (scale: 1:500 000). We included major roads, minor roads and forest roads to cover potential human disturbance. Roads can act as effective barriers even if traffic is comparatively low (Perzanowski et al. 2007). Moreover, even small roads may amplify human disturbance due to easier access for poachers or ongoing logging. Distance to roads was limited to a maximum of 5.4 km in summer and 2.4 km in winter because initial models predicted less suitable habitat for higher distances (see Supplementary Information for further detail).

We resampled all predictors to a 300-m resolution with bilinear interpolation, and reprojected these grids to the Albers Equal Area coordinate system. The snow cover and elevation predictors were both highly correlated to the length of the vegetation period ($r > 0.7$, Dormann et al. 2013), and the mean summer NDVI was highly correlated to the fractional tree cover. Ultimately, snow cover, elevation, and mean summer NDVI were therefore not included in our final models because corresponding alternative models yielded higher model accuracy.

4 Mapping potential habitat

To map potential habitat, we used maximum entropy modeling (Maxent, version 3.3.3k, Phillips et al. 2006). Maxent is a machine-learning technique that estimates the unknown distribution of habitat suitability by contrasting the values of predictors at occurrence locations with the overall distribution of these predictors (Merow et al. 2013). Maxent chooses the distribution that fulfills the given constraints inferred from the presence data and minimizes the relative entropy for the model derived from the overall distribution of the predictors (the background, Elith et al. 2011). Maxent requires only presence data, which is advantageous in the case of European bison that currently only use a part of their historical range. Moreover, Maxent performs well with small sample sizes (Wisz et al. 2008) and frequently outperforms other presence-only modeling techniques (Elith et al. 2006).

We parameterized the models with 10 000 background points, 2500 iterations maximum, and default settings for convergence thresholds and regularization (Phillips and Dudik 2008). We used only quadratic and hinge features to prevent overfitting (Kuemmerle et al. 2014). Sampling background points from very broad areas may result in overly simplistic model predictions (Anderson and Raza 2010; VanDerWal et al. 2009), which is why we took background samples only from the minimum convex polygon of historic European bison locations in the Caucasus (Heptner et al. 1961; Kuemmerle et al. 2012a; Nemtsev et al. 2003) and elevations below 4000 m while maintaining a minimum distance of 900 m between individual points. Our minimum convex polygon covered an area of about 100 000 km^2.

After parameterization, we projected the model over the whole study region and used a logistic link function to derive a relative habitat suitability index (HSI) between zero and one (Phillips and Dudik 2008). We parameterized two models for each season. The first model captured environmental conditions only (environmental model) and the second model captured human disturbance only (human disturbance model, Table B 1). We validated our models through ten-fold cross-validation using the mean area under the curve (AUC) of the receiver operating characteristics (ROC) curve. To measure variable importance, we used a jackknife procedure by measuring the test AUC for single variable models and models without the variable as well as gain changes in the Maxent function (Phillips et al. 2006). To test if model outputs were influenced by the random sampling of occurrence records from the range maps, we compared five different sets of presence points.

The resulting HSI-maps from both the environmental and the human disturbance models were categorized as matrix and potential habitat with the latter being areas with HSI-values equal or higher to those where 5% of the presence locations occurred. In addition, we used the maximum training sensitivity plus specificity threshold (Jiménez-Valverde and Lobo 2007; Liu et al. 2013) to subdivide potential habitat into marginal (HSI < threshold, sub-optimal conditions) and good habitat (HSI > threshold, good conditions). By combining the suitability maps, we identified four habitat categories, following Naves et al. (2003) and De Angelo et al. (2013): (1) core areas (good habitat in both, the environmental and the human disturbance model), (2) potential refuges (sub-optimal habitat in the environmental model, good habitat in the human disturbance model), (3) potential sinks (sub-optimal habitat in both models), and (4) ecological traps (good habitat in the environmental model, sub-optimal habitat in the human disturbance model). We then summarized the area of each habitat category in each of the six Caucasian countries.

To identify potential candidate sites for reintroductions, we selected all summer core areas > 200 (large candidate sites) or > 60 km² (small candidate sites) plus adjacent core winter habitat of more than 6 km² and 5 km², respectively. An estimated area of 200 km² is necessary to sustain a population of 50–60 animals (Pucek et al. 2004) and the current winter range of the North Ossetia herd with 50 animals is around 6 km². Thresholds for small candidate sites are based on the current seasonal range sizes of the smallest Caucasian herd (Teberdinsky, 22 animals, summer: 60 km², winter: 5 km²). Lastly, we obtained data about armed conflicts from the PRIO Conflict site dataset (Hallberg 2012) and for new or planned ski resorts (Northern Caucasus Resorts, http://www.ncrc.ru/ru/resort) to identify candidate sites with potential threats.

5 Results

Our models and predictive maps of bison habitat identified 69 habitat patches for potential reintroductions. Generally, our results suggested substantial potential for increased bison numbers especially in Georgia and Russia, but also widespread risk for conflicts with people. In total, 10.6% of the study area provided potential summer and 5.5% potential winter habitat. Summer and winter habitat occurred in similar areas, but potential winter habitat was more restricted (Figure B 2). Particularly the western part of the Greater Caucasus contained large areas of suitable habitat in our predictions. The lowland areas of the ecoregion had only low suitability. In general, suitable habitat was mainly found in Russia, Georgia, and Turkey and was scarce in Armenia, Azerbaijan, and Iran.

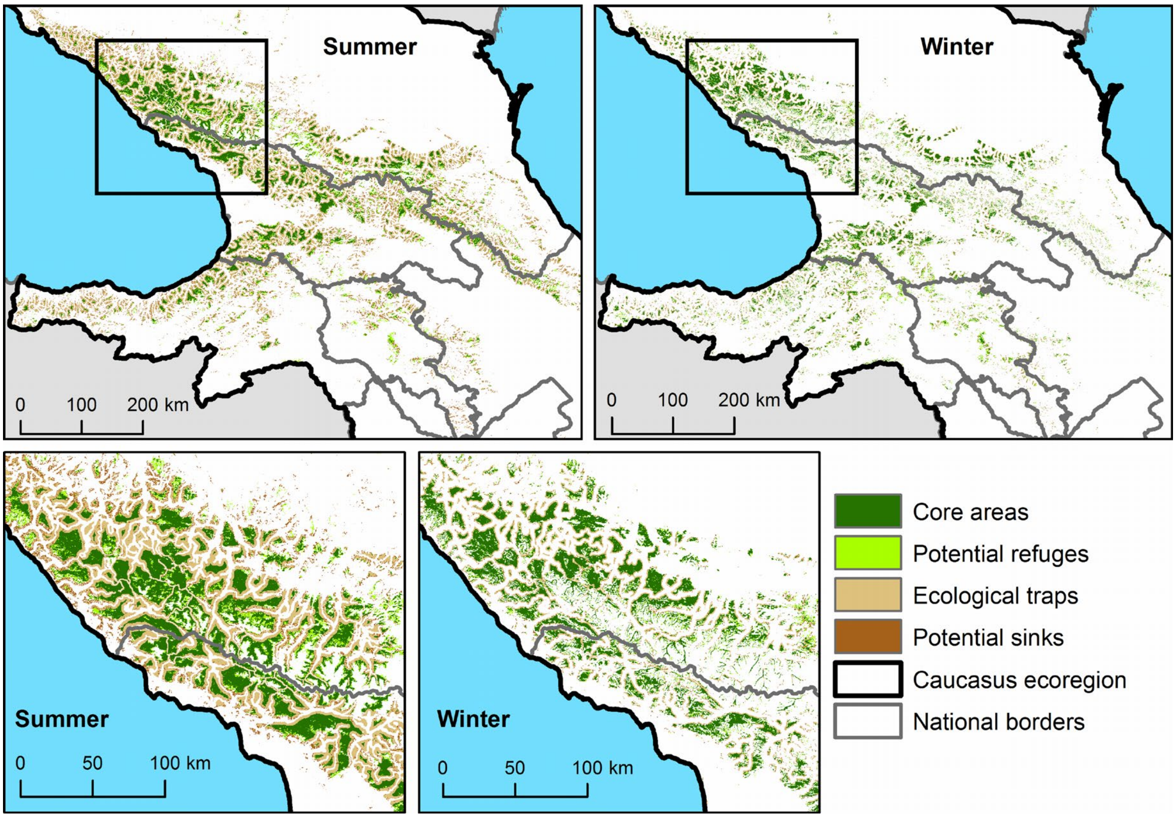

Figure B 2: Habitat refinement maps for summer and winter (top) with a detailed view of the western Greater Caucasus (bottom). White areas indicate the matrix between habitat patches.

A substantial share of all potential habitat was core area (27% in summer and 47% in winter). However, most core areas were surrounded by ecological traps in both seasons and ecological traps accounted for the largest fraction in summer (38%, Table B 2 and Figure B 3). Potential refuges were scarce and mostly scattered (Figure B 2). Core areas and potential refuges accounted for a larger share in winter than in summer (Table B 2). Among the six countries, the relative shares of the habitat categories differed greatly, but the differences between seasons remained fairly constant (Figure B 4). Russia and Georgia had the largest fractions of core areas (30% in summer, 50% in winter), but also high fractions of ecological traps (40% in summer, 25% in winter).

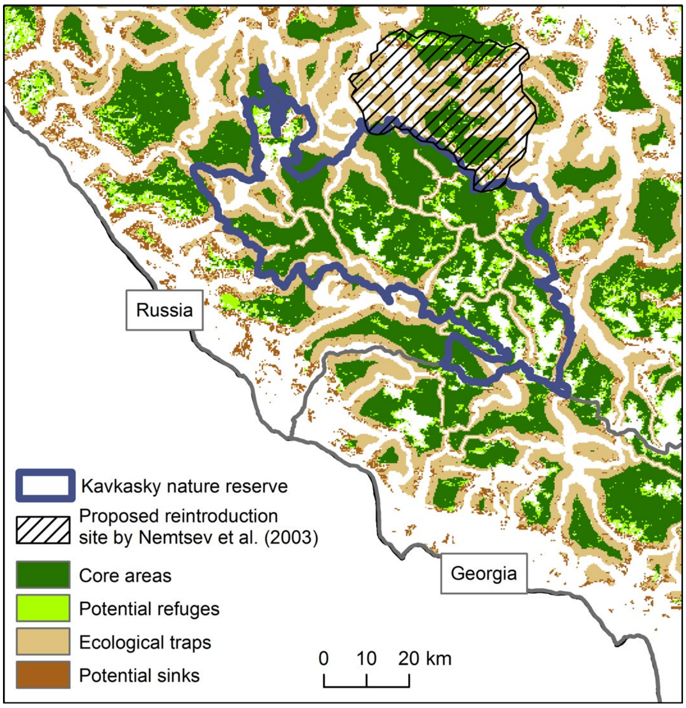

Figure B 3: Summer habitat categories around Caucasus biosphere nature reserve in the western Greater Caucasus.

Table B 2: Area contributions of the four habitat categories derived from the two-step modeling approach (environmental model vs. human-disturbance model) for winter and summer habitat.

Habitat category	Area [km²] (% of total habitat)	
	Summer	Winter
Core	16 665 (27%)	14 885 (47%)
Potential refuges	8210 (13%)	5860 (18%)
Potential sinks	13 325 (22%)	3235 (10%)
Ecological traps	23 395 (38%)	7890 (25%)
Total	61 595 (100%)	31 870 (100%)

Model variable importance and response functions were similar for summer and winter. The length of the vegetation period together with the fractional tree cover and land cover were the most important environmental predictors, accounting for > 90% and > 80% gain contributions in summer and winter respectively, and decreased test AUC substantially when omitted. European bison avoided areas near roads and settlements and preferred landscapes with intermediate to high tree cover. Mixed and coniferous forests showed intermediate suitability whereas broadleaved and open forest yielded lower scores. Habitat suitability showed high values for different lengths of the vegetation period but decreased substantially for areas with a vegetation period throughout the year (see Supplementary Information). All four models had cross-validated AUC values > 0.75. Furthermore, the environmental models predicted high suitability values for two areas highlighted in independent, field-based assessments of reintroduction sites in the northern Caucasus for summer and winter habitat (Klich and Perzanowski 2012; Nemtsev et al. 2003).

Based on our stratification, we identified 69 candidate sites for potential bison herd reintroductions (10 200 km² in total). All summer core areas > 200 km² included sufficient adjacent winter habitat (core winter habitat > 6 km²). In total, we found eleven such large candidate sites that together covered an area of 3575 km² (0.6% of the ecoregion). All large candidate sites were located in Russia (1930 km²) and Georgia (1645 km²) in the western part of the ecoregion (Figure B 5). Small candidate sites covered an additional area of 6660 km² (1.1% of the ecoregion) and were more widespread. Two summer core areas greater than 60 km² did not entail adequate winter habitat resulting in 58 small candidate sites. The largest share was located in Russia (3120 km²) and Georgia (3050 km²). A smaller fraction was located in Turkey (400 km²) whereas only one area was found in Azerbaijan (90 km²). No candidate sites existed in Armenia and Iran.

Almost two-thirds of the area of the candidate sites (61%) was not protected and only 13% were located inside strict nature reserves or national parks (IUCN categories I and II). The protection status of the candidate sites differed among countries (Table B 3). For example, only 15% of the area of Georgia's candidate sites was protected compared to 33% in Russia. Six candidate sites crossed international boundaries.

Several candidate sites were located where new ski resorts have been built recently or are planned (16 candidate sites were within 25 km distance to an existing or planned skiing resort). Further, the majority of all candidate sites (52 out of 69) were in 100 km distance to the center of a site that experienced armed conflicts since 1989, highlighting potential threats for reintroductions (Figure B 5). The clustered candidate sites in the western Greater Caucasus were especially at risk, containing three current or planned ski resorts and one past conflict zone (i.e., the 2008 conflict in Abkhazia).

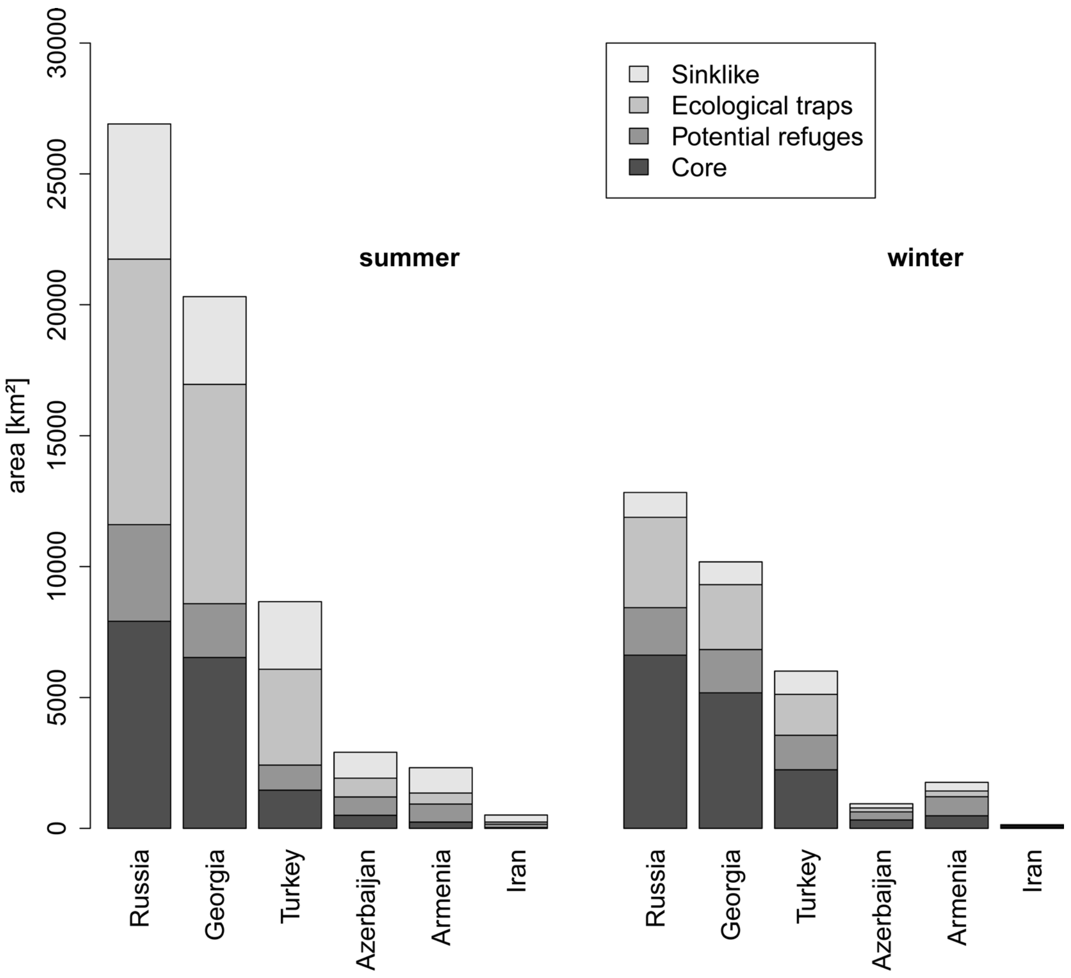

Figure B 4: Distribution of the four habitat categories inside the countries containing parts of the Caucasus ecoregion.

Table B 3: Area of currently protected candidate sites for reintroductions.

IUCN Category	Area of candidate sites that is protected [absolute in km²] (relative to the area of all candidate sites in the country in %)			
	Russia	Georgia	Turkey	Azerbaijan
I	9.5 (0.2 %)	309.4 (6.6%)	4.2 (1.0%)	76.4 (86.6%)
II	587.8 (11.6%)	297.9 (6.4%)	73.2 (18.2%)	-
III	-	-	-	-
IV	1065.2 (21.1%)	102.6 (2.2%)	25.3 (6.3%)	-
V	-	4.7 (0.1%)	-	-
I–V	1662.5 (32.9%)	713.9 (15.3%)	102.7 (25.5%)	76.4 (86.6%)

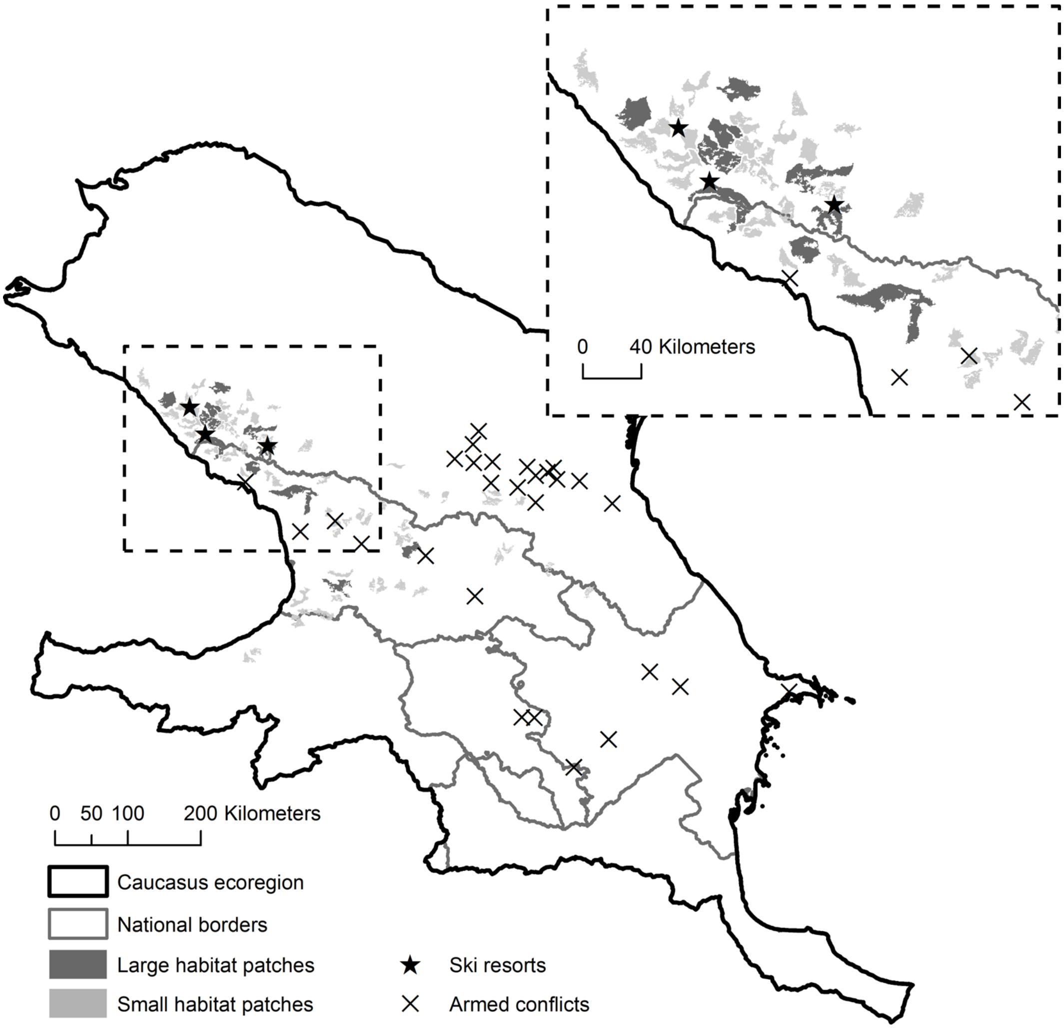

Figure B 5: Candidate sites for potential reintroductions with new or planned ski resorts (Northern Caucasus Resorts, http://www.ncrc.ru/ru/resort) and past armed-conflict sites (Hallberg 2012).

6 Discussion

The Caucasus once harbored large herds of European bison, but current herds are small and isolated, requiring both the enlargement of current and the establishment of new herds. We mapped seasonal habitat for European bison throughout the Caucasus, based on data from all current Caucasian herds, and showed that the Caucasus Mountains harbor substantially more habitat than is currently occupied. Much of the suitable habitat is surrounded by areas of risk for human-bison conflict, but we identified 69 candidate sites for potential reintroductions that have both adequate summer and winter habitat and a low risk for conflict with people. Yet, only 13% of the candidate site's area is strictly protected and new skiing sites or potentially resurging armed conflicts could further threaten bison populations established in these sites.

Our two-step habitat modeling approach, adapted from Naves et al. (2003), allowed us to base the identification of habitat and reintroduction candidate sites on a finer assessment than would have been possible with a combined modeling approach. Particularly the distribution of locations with high risk for human-wildlife conflicts (i.e., ecological traps) is of high importance since human pressure is one of the main determining factors for large mammal survival (Gordon 2009; Zhou and Zhang 2011), and has led to marked wildlife decline in the Caucasus in the past (Sipko et al. 2010; Trepet and Eskina 2012).

Our second major advancement was to map habitat for different seasons, i.e., summer and winter. Many large mammals have different habitat needs in different seasons (e.g., vertical migrations are known for a range of mountain ungulates, Nemtsev et al. 2003; Tilton and Willard 1982), and enough suitable winter habitat is a particularly limiting factor for large ungulates (Gaillard et al. 2000; Mysterud et al. 2007). Yet, most habitat models have so far focused on summer habitat only, or use data from all seasons jointly. Our winter habitat modeling allowed us to account for a critical aspect of the survival of bison herds, and we showed that some areas with ample summer habitat would be ill-suited for reintroductions because there is no winter habitat in the vicinity. In general, winter habitat was scarcer than summer habitat and both often overlapped (Figure B 2), as is the case for the extant populations (Krasińska and Krasiński 2007). Winter habitat was largely determined by forest, where snow is less deep and sprouts and bark can provide forage.

Suitable habitat occurred mainly in mountainous areas. Although bison also used to inhabit the plains (Sipko et al. 2010), human presence there is too high today (e.g., Gracheva et al. 2012). Moreover, the mountains entail the largest share of forest in the region (Krever et al. 2001) and forest was one of the main factors characterizing the habitat utilized by extant European bison populations (see below). Georgia and Russia harbored most of the potential habitat (Figure B 2). This suggests a high potential for the enlargement of existing herds or the establishment of new herds in areas where bison cannot disperse to due to natural barriers (e.g., high elevation, steep slopes, or gorges).

Our models also identified potential refuges and ecological traps that could have crucial management implications. For example, the area proposed as range extension in Nemtsev et al. (2003) was predicted highly suitable by the environmental models but entailed substantial parts of ecological traps (Figure B 3). Further, many core areas were surrounded by ecological traps in summer and winter, which may increase mortality (Woodroffe and Ginsberg 1998). However, whether ecological traps are actually sinks for bison has to be assessed in detail on the ground and will depend on a range of factors such as levels of enforcement and poaching. Potential refuges were scattered and rare (13% and 18% of all potential habitat in summer and winter, respectively) but could play an important role as buffers around large core areas (Figure B 3; DeFries et al. 2010).

Variable importance and response curves were similar for summer and winter. European bison were closely associated with forest cover which was also the case in other broad-scale habitat suitability assessments for European bison (Kuemmerle et al. 2010; Kuemmerle et al. 2011) as well as of studies of historical habitat use of European bison (Bocherens et al. 2015; Kuemmerle et al. 2012a). However, we caution that the strong forest association we found may at least partly reflect that forests were the last refuges for bison, and the species may thrive in more open landscapes as well (Kerley et al. 2012). Broadleaved forests were less important in our assessment than elsewhere (Kuemmerle et al. 2010; Pucek et al. 2004). This may be a consequence of the spatial distribution of our herd ranges, which are equally composed of both coniferous and broadleaved forest. The extensive presence of broadleaved forest in our study area (and therefore in Maxent's background sample) may have led the models to underestimate the suitability of this class.

We identified 11 large and 58 small candidate sites for potential reintroductions that could be used as a starting point for further, more local assessments (covering e.g., fodder quality, access to drinking water but also road-building plans). Almost two thirds of the area of these candidate sites (61%) were not protected, and in Georgia only 15% of the area was protected. With a total area of 10 200 km², and assuming a potential bison density of 0.9–1.0 animals/km² (as has been observed for Caucasian mountain forests, Nemtsev et al. 2003), the candidate sites could harbor up to 10 200 bison (up to 690 bison in the largest single candidate site, see Supplementary Information for an overview of all candidate sites). While more detailed assessments are needed to determine the actual carrying capacity of these sites (and a likely much lower socially acceptable carrying capacity, Balciauskas and Kazlauskas 2014), these numbers highlight the potential of the Caucasus to harbor a viable European bison population. Effective conservation of the species, including anti-poaching measures, should nevertheless be a main focus, since poaching led to the extirpation of several bison herds in the Caucasus and elsewhere after their reintroduction, even within protected areas (Khoyetskyy 2011; Krasińska and Krasiński 2007). Additionally, we emphasize that the largest current Caucasian herd, the Kavkasky population, contains European bison x American bison hybrids and there is an ongoing debate about whether this herd should be kept separate from the other herds, which are pure European bison, or even be eliminated and rebuilt (Pucek et al. 2004; Sipko et al. 2010). Therefore, detailed reintroduction assessments should include and draw implications from analyses on potential connectivity to the Kavkasky population.

Armed conflicts and tourism development could further endanger European bison and should be incorporated into future conservation planning. For example, 52 of 69 candidate sites were located within 100 km distance to the center of a conflict site (Figure B 5, based on the PRIO Conflict site dataset, years 1989–2008, Hallberg 2012). This could potentially lead to habitat destruction, fire outbreaks, higher poaching rates, and disregard of environmental legislation (Dudley et al. 2002; Witmer and O'Loughlin 2011). While the location of future conflicts is hard to predict, some areas in the Caucasus have been historically more prone than others, and this should be considered when planning future reintroductions. Moreover, three large skiing resorts are being developed in close proximity to highly suitable areas. Such large scale construction projects are often related to habitat loss through deforestation, sometimes even within protected areas as in the case of the Olympic Games sites in Sochi National Park (Bragina et al. 2015b), suggesting a focus on other candidate sites first. Finally, six candidate sites crossed international boundaries, indicating a need for trans-boundary cooperation that may be difficult given political realities (Zazanashvili et al. 2012).

Model predictive power was relatively high for all models (AUC 0.77–0.90). Nevertheless, some uncertainties remain. First, we predicted areas similar to the ones currently occupied by bison herds in the Caucasus. Current herds are small and have been reintroduced. It could therefore be that current herds do not utilize the most optimal habitat (Kerley et al. 2012), and that our models thus underestimated habitat suitability for other sites. Nevertheless, herds have been reintroduced in those areas where European bison prevailed longest globally, and the Caucasus has been a stronghold for the reintroduced bison herds for many decades (Sipko et al. 2010). Furthermore, none of the herds receive supplementary winter feeding, highlighting the suitability of current herd ranges (Sipko 2009).

7 Conclusions and management implications

Broad-scale species distribution modeling allowed us to identify and assess potential seasonal habitat for European bison in the Caucasus Mountains. The two-step seasonal approach accounted for two main determinants of large mammal survival: human disturbance and winter habitat. Our results showed that there is sufficient habitat available to achieve the goal of a healthy bison population by 2025 set in the Caucasus Conservation plan, as long as conservation efforts lead to the establishment of new and enlargements of extant bison populations (Zazanashvili et al. 2012). Connectivity among bison herds, and thus the establishment of a functioning bison metapopulation, seems essential to achieve a large enough effective population size, because our analysis suggests single candidate sites are too small to harbor a viable bison population. Managing for connectivity of large mammals is a challenging task, but encouragingly, several core areas were connected by marginal habitat which may function as corridors, or ecological trap areas, which could be protected to foster dispersal. Conservation efforts should therefore (1) identify and protect potential corridors between candidate sites (2) target poaching and habitat destruction within the identified candidate sites and their surroundings, and (3) develop strategies to link bison populations across national borders.

Strengthening bison populations in one of the species' strongholds would contribute substantially to its overall conservation (Kuemmerle et al. 2011) and other species of conservation concern could benefit both directly (e.g., through seed dispersal, Jaroszewicz et al. 2013) and indirectly (e.g., as species under bison's conservation umbrella, Branton and Richardson 2011), especially if the habitat requirements of these species are similar such as in the case of the Caucasian red deer (i.e., Maral). Our approach can further help to prioritize and bundle conservation efforts such as the establishment of protected areas and the protection of existing herds from poachers.

Acknowledgements

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Supplementary Information

Description of Predictor variables

Environmental variables

Landscape composition – The composition of land cover is an important determinant of suitable European bison habitat. European bison are generally thought to prefer forest-dominated, yet mosaic-type landscape with patches of open grassland that bison use for foraging (Krasińska and Krasiński 2007; Kuemmerle et al. 2010). Particularly in winter, forest cover is important, as bison tend to feed on bark and sprouts if grass is covered by a deep snow layer, and snow depth is often higher outside than inside forests (Krasińska and Krasiński 2007). The preference of bison for semi-open landscapes with a substantial share of forest emerges from studies on habitat selection of contemporary bison herds in Eastern Europe at local (Hofman-Kaminska and Kowalczyk 2012; Krasińska and Krasiński 2007; Perzanowski et al. 2011) and broad scales (Kuemmerle et al. 2010; Kuemmerle et al. 2011) as well as from paleo-ecological work on historical habitat use of bison (Bocherens et al. 2015). At the same time, it remains unclear which level of openness constitutes optimal habitat for European bison (Cromsigt et al. 2012; Kerley et al. 2012; Kuemmerle et al. 2012b).

To characterize land cover, we used ESA's Globcover 2009 dataset (http://due.esrin.esa.int/globcover/), the most fine-scale global land-cover map currently available (300 m). Globcover is an initiative of the European Space Agency (ESA) and is based on data from the Medium Resolution Imaging Spectrometer (MERIS). The 2009 global map product contains 22 classes (an earlier version of the GlobCover map for 2005, also included continental, more detailed class catalogues). We aggregated both the global and continental land-cover maps to 10 broad land-cover categories (Table SI B 1) and compared these alternative land-cover maps, but found only marginal differences. Maxent model runs were also not improved by using the continental product. We therefore used the global 2009 version for all final models.

To complement our land cover map and to include continuous information on the degree of woody vegetation (and thus landscape openness), we used the MODIS Vegetation Continuous Field (VCF) product (MOD44B, 250 m resolution, years 2000–2010, tiles h20v04, h20v05, h21v04, h21v05, h22v05). The VCF provides fractional woody vegetation cover and we calculated mean tree cover values across all available years. We excluded years with missing values in this calculation.

Forest fragmentation is an important determinant of European bison habitat selection, with bison preferring open, edge forests over core forest (Kuemmerle et al. 2010). We derived forest fragmentation by first aggregating all forest-related classes (coniferous forest, mixed forest, and broadleaved forest) into one forest class, and assigning all other classes to a non-forest class. We then assigned all forest pixels to one of the classes core forest, islet forest, perforation forest (i.e., edge forest inside larger forest patches), and edge forest (i.e., edge forest at the outside of larger forest patches) using morphological image segmentation (Vogt et al. 2007). To segment the forest class into the four fragmentation classes, we used the software Guidos 1.4 (Vogt et al. 2007). As an additional measure of forest fragmentation, we calculated the Euclidean distance of each non-forest pixel to the nearest forest pixel.

Table SI B 1: Reclassification of the Globcover 2009 land-cover classes.

Pixel Value	Label	Area in the ecoregion [km²]	Our class	Our label
14	Rainfed croplands	118 000	6	Cropland
20	Mosaic cropland (50-70%) / vegetation (grassland / shrubland / forest) (20-50%)	169 000	7	Mosaic vegetation / cropland
30	Mosaic vegetation (grassland / shrubland / forest) (50-70%) / cropland (20-50%)	98 000	7	Mosaic vegetation / cropland
50	Closed (> 40%) broadleaved deciduous forest (> 5m)	81 400	3	Broadleaved forest
70	Closed (> 40%) needleleaved evergreen forest (> 5m)	15 900	1	Coniferous forest
90	Open (15–40%) needleleaved deciduous or evergreen forest (> 5m)	66	4	Open forest
100	Closed to open (> 15%) mixed broadleaved and needleleaved forest (> 5m)	6500	2	Mixed forest
110	Mosaic forest or shrubland (50–70%) / grassland (20–50%)	15 000	4	Open forest
120	Mosaic grassland (50–70%) / forest or shrubland (20–50%)	8900	4	Open forest
130	Closed to open (> 15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (< 5 m)	23 700	5	Grassland and Shrubland
140	Closed to open (> 15%) herbaceous vegetation (grassland, savannas or lichens / mosses)	1360	5	Grassland and Shrubland
150	Sparse (< 15%) vegetation	30 800	8	Vegetation < 15%

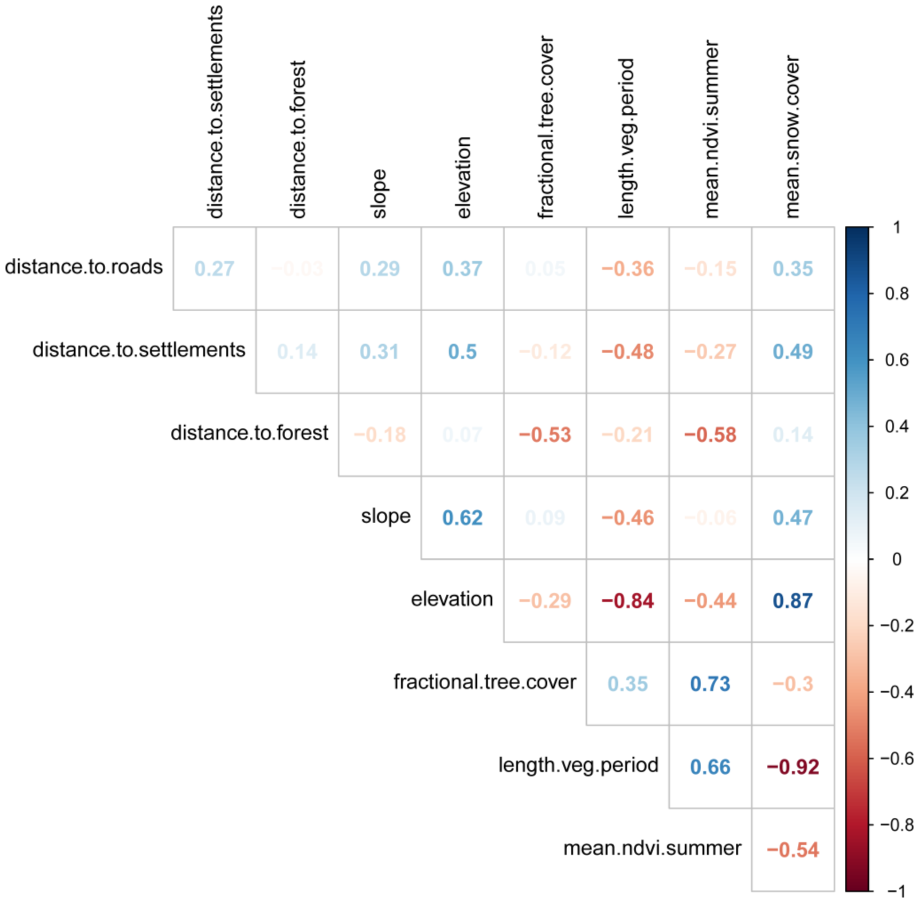
180	Closed to open (>15%) grassland or woody vegetation on regularly flooded or waterlogged soil - Fresh, brackish or saline water	2030	5	Grassland and Shrubland
190	Artificial surfaces and associated areas (Urban areas > 50%)	900	9	Settlements
200	Bare areas	6380	8	Vegetation < 15%
210	Water bodies	8030	10	Water
220	Permanent snow and ice	1300	8	Vegetation < 15%
230	No data (burnt areas, clouds…)	0.4	-9999	No data

Additionally, we used the snow cover product (MOD10A2) at 500 m resolution, which measures the number of days a pixel was covered with snow for every eight-day period over the year. Snow cover is also one of the most important constraints for ungulate survival in general, as it limits mobility and access to food (Krasinska et al. 2000; Mysterud et al. 2007). Although bison can deal with snow to considerable depths reasonably well (Okarma et al. 1995), for example by scooping snow off to reach the underlying vegetation, moving and foraging in deep snow is comparably energy intensive and therefore avoided by bison if possible (Pucek et al. 2004). To derive a measure of snow cover (and thus winter severity), we calculated the mean annual days with snow cover across the years 2001–2012 for each pixel in our study region.

In our final models, mean NDVI of the summer months and mean days of snow cover were not used since these variables were highly correlated to the fractional tree cover and to the length of the vegetation period, respectively (Figure SI B 1). Alternative models suggested that fractional tree cover and the length of the vegetation period had higher explanatory power and we therefore used these variables.

Topographical variables – Topography is an important factor shaping habitat quality, directly through influencing resource availability (e.g., lower productivity during summer and more snow during winter on higher elevations) and indirectly via, for example, lower levels of human disturbance in more rugged terrain (Sipko et al. 2010; Sipko 2009). While bison tend to avoid the steepest slopes, they can use relatively steep and rugged terrain because human access to such areas is constrained (Sipko 2009). Extant bison populations occupy areas up to 3000 m above sea-level in summer, which may still not be the upper limit of where bison can survive. During winter, most herds migrate into valleys, but bison have also been witnessed using alpine meadows above the tree line in winter when storms are blowing away snow and grass is accessible (Sipko 2009).

Elevation and slope were derived from the Shuttle Radar Topography Mission (SRTM, http://srtm.csi.cgiar.org/) with 90 m spatial resolution. Slope was limited to 28 degrees for the summer models (i.e., the 90th percentile of the presence locations), to avoid extrapolating into areas with few or no occurrence points. Also, some bison herds (e.g., Teberdinsky) may currently occupy steeper areas than they would if bison were in equilibrium with their environment (which is currently unlikely as all herds were introduced). Initial models showed a positive relationship between slope and habitat suitability, but we do not assume that habitat quality would increase at slopes steeper above 28 degrees (apart from being related to potential lower human impact, which we captured in other variables). Therefore, our results should not be impaired by using a maximum slope cutoff value. Elevation was not used in the final models because it was correlated strongly to the length of the vegetation period (Figure SI B 1).



	distance.to.settlements	distance.to.forest	slope	elevation	fractional.tree.cover	length.veg.period	mean.ndvi.summer	mean.snow.cover
distance.to.roads	0.27	−0.03	0.29	0.37	0.05	−0.36	−0.15	0.35
distance.to.settlements		0.14	0.31	0.5	−0.12	−0.48	−0.27	0.49
distance.to.forest			−0.18	0.07	−0.53	−0.21	−0.58	0.14
slope				0.62	0.09	−0.46	−0.06	0.47
elevation					−0.29	−0.84	−0.44	0.87
fractional.tree.cover						0.35	0.73	−0.3
length.veg.period							0.66	−0.92
mean.ndvi.summer								−0.54

Figure SI B 1: Correlation Matrix showing collinearity among predictor variables (only continuous predictors). Values are Pearson's correlation coefficients calculated and plotted using R (v2.15.1, R Development Core Team 2013).

Human disturbance

Human disturbance, through hunting or land use, is a key determinant for the survival of large mammals (Woodroffe and Ginsberg 1998). This is particularly true in the Caucasus, where high poaching rates led to huge population declines of European bison after the breakdown of the Soviet Union in 1991 (Pucek et al. 2004; Sipko 2009). To capture human disturbance, we calculated Euclidean distances to roads and settlements based on digital layers obtained from WWF Caucasus Programme Office (CauPO) and WWF Armenia. Initial model runs showed a hump-shaped relationship between distance to roads and habitat suitability, likely due to bison not occupying all suitable areas in the Caucasus (as shown by our results). To account for this, distance to roads was capped to a maximum of 5.4 km in summer and 2.3 km in winter, representing thresholds with maximum habitat suitability according to the hump-shaped response functions in the initial models. Ecologically it is not reasonable to assume that habitat suitability decreases with increasing distance after these maximum values (i.e., choosing these values for all distances beyond is conservative for modelling habitat suitability).

Response curves

We here show the marginal variable response curves of the best-performing models for summer and winter. In the graphs, we use the following abbreviations for the forest fragmentation categories: C = Core; I = Islet; P = Perforation; E = Edge; B = Background; as well as the following abbreviations for the land cover types: CF = Coniferous forest; MF = Mixed forest; BF = Broadleaved forest; OF = Open forest; GR = Grass- and shrubland; MOS = Mosaic vegetation / cropland; Veg. < 15% = Vegetation cover < 15%; ST = Settlements; WA = Water.

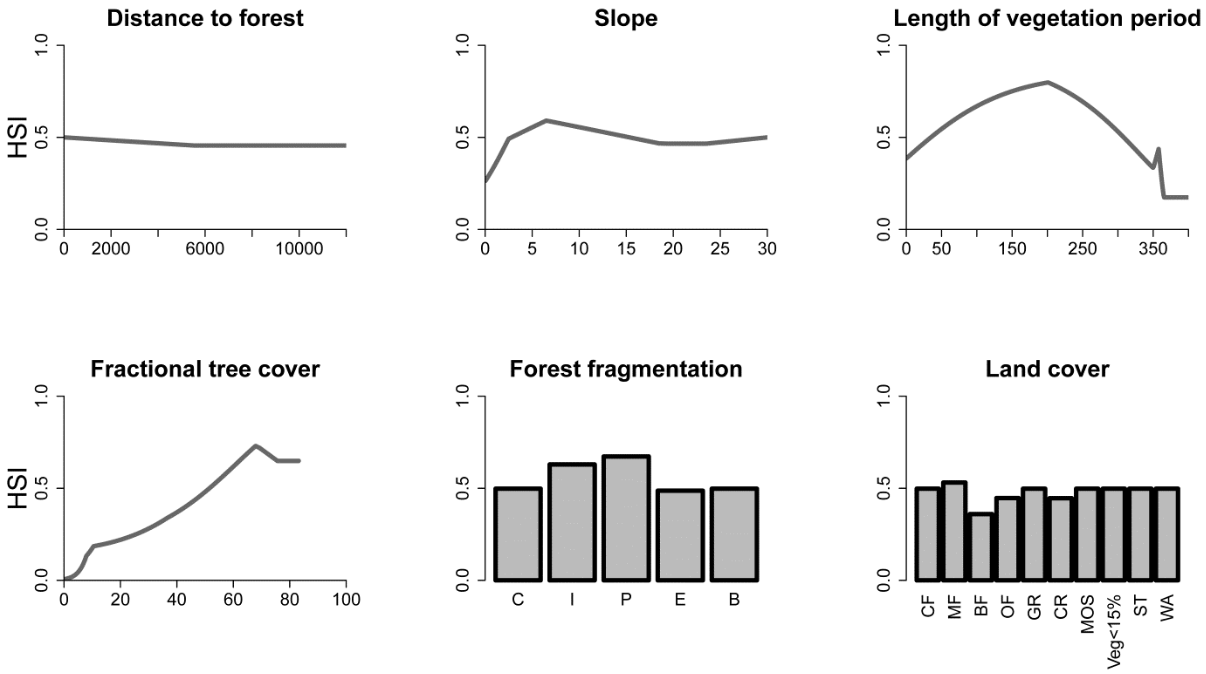


Figure SI B 2: Response curves of the environmental summer model.

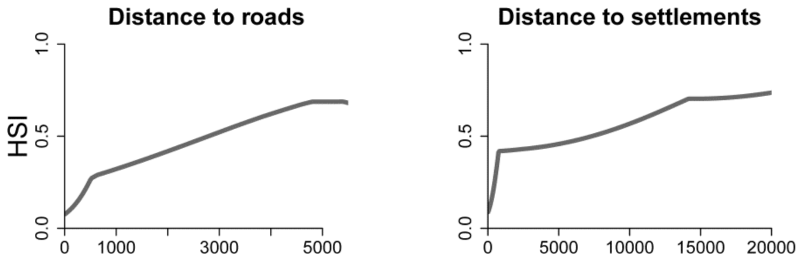


Figure SI B 3: Response curves of the human disturbance summer model.

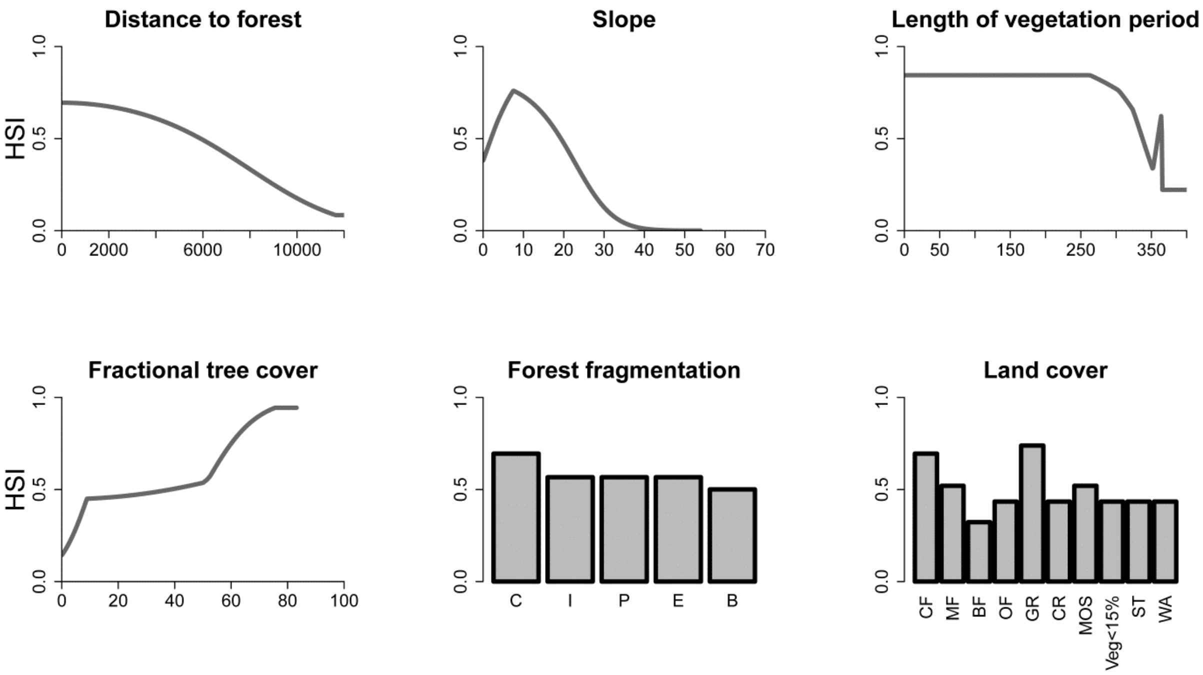


Figure SI B 4: Response curves of the environmental winter model.

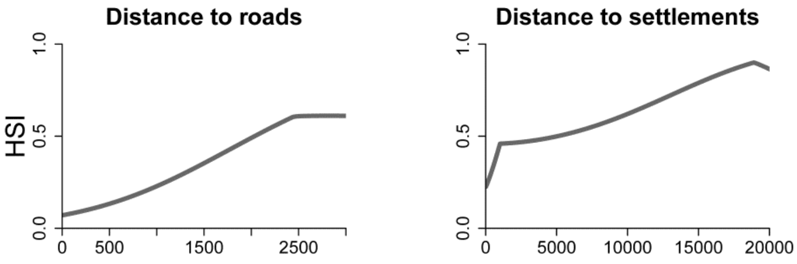


Figure SI B 5: Response curves of the human disturbance winter model.

Overview of Candidate sites for reintroductions

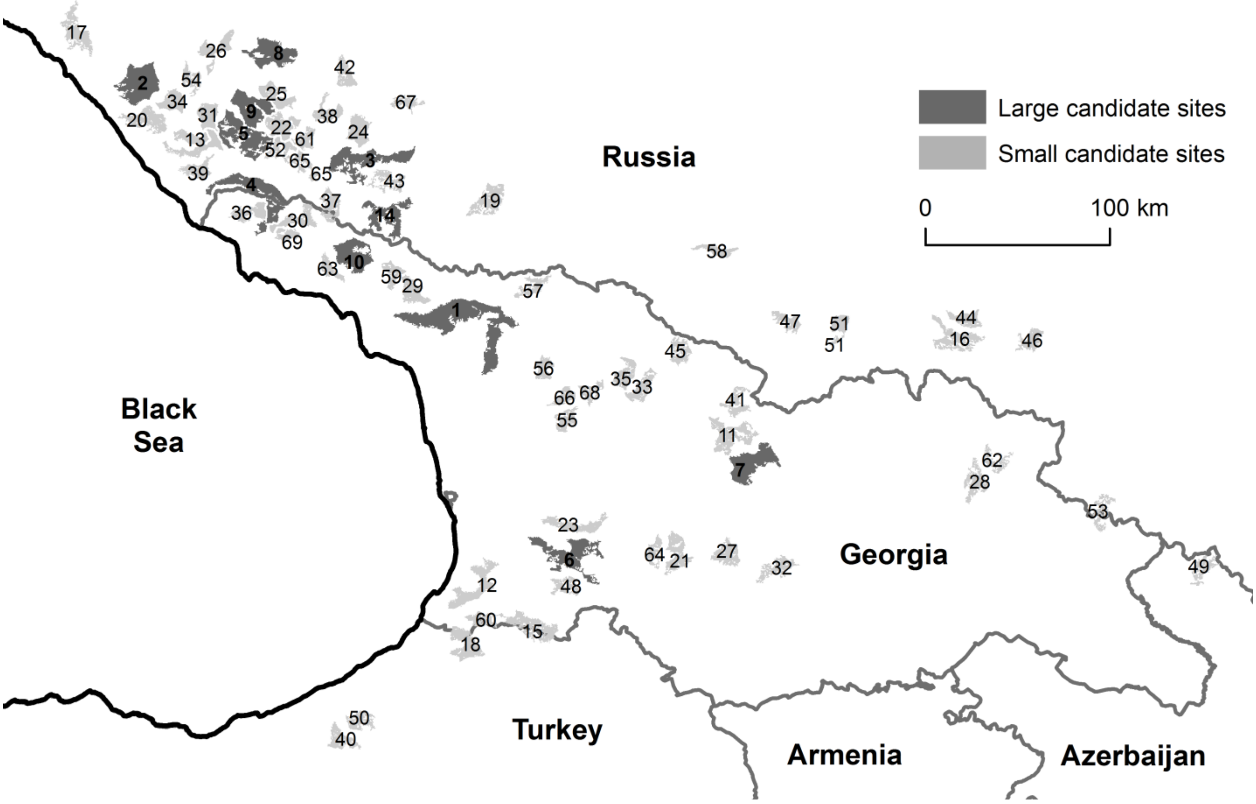


Figure SI B 6: Summary of the candidate sites for potential reintroductions of European bison populations in the Caucasus.Labels are sorted according to patch size (smallest numbers for the largest patches).

Table SI B 2: Summary of the large (in bold font) and small candidate sites for potential reintroductions. Note that the potential carrying capacity is only a first-order estimation, based on European bison densities observed in the Caucasus at the time when bison were most abundant in the 20th century (Nemtsev et al. 2003).

Candidate site	Area [km²]	Potential carrying capacity (0.9–1.0 bison/km², Nemtsev et al., 2003)
1	**691**	**622–691**
2	**335**	**302–335**
3	**335**	**301–335**
4	**332**	**299–332**
5	**325**	**292–325**
6	**317**	**285–317**
7	**295**	**266–295**
8	**252**	**227–252**
9	**243**	**218–243**
10	**234**	**211–234**
11*	222	200–222
12*	217	195–217

13*	215	194–215
14	**214**	**192–214**
15*	201	181–201
16	195	176–195
17	183	164–183
18	178	160–178
19	172	155–172
20	172	155–172
21	156	140–156
22	151	135–151
23	146	131–146
24	146	131–146
25	135	121–135
26	131	118–131
27	131	118–131
28	129	116–129
29	124	112–124
30	123	111–123
31	121	108–121
32	119	107–119
33	117	105–117
34	116	104–116
35	114	102–114
36	111	100–111
37	111	100–111
38	105	95–105
39	104	94–104
40	103	93–103
41	102	92–102
42	101	91–101
43	98	88–98
44	96	87–96
45	96	86–96
46	93	84–93
47	90	81–90
48	88	79–88
49	88	79–88
50	88	79–88
51	88	79–88
52	86	78–86

53	86	77–86
54	83	74–83
55	82	74–82
56	82	74–82
57	82	73–82
58	81	73–81
59	81	73–81
60	80	72–80
61	77	69–77
62	76	69–76
63	75	67–75
64	74	67–74
65	72	65–72
66	71	64–71
67	67	60–67
68	66	59–66
69	60	54–60

* Small candidate sites that have a total area (suitable summer plus winter habitat) of more than 200 km^2.

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Appendix C:
Joint connectivity and conflict risk mapping for identifying safe corridors for the Persian leopard

Landscape Ecology (under review)

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Abstract

Context Many large carnivores depend on habitat patches outside protected areas as well as safe corridors between them. However, corridor assessments typically ignore potential conflicts between carnivores and people, which can undermine corridor effectiveness and thus conservation success.

Objectives We identified habitat patches, safe dispersal corridors and conflict-prone movement bottlenecks for Persian leopard (*Panthera pardus saxicolor*) between protected areas in the Alborz Mountains, Iran, by combining habitat assessment, structural connectivity, and conflict risk mapping. We then identified priority areas for conservation interventions according to the intensities of different threats.

Methods We mapped land cover using Landsat satellite images, and gathered data on leopard distributions, prey distributions, and livestock depredation events via interview surveys. We then used occupancy modeling to identify habitat patches, derived corridors using a least-cost pathway and circuit theory modeling, and assessed human-leopard conflict risk using generalized linear models.

Results Leopard habitat use increased with prey availability and decreased with elevation. Prey distribution, in turn, was mostly negatively influenced by agricultural lands. Conflict risk (i.e. probability of leopard depredation on livestock) was high in landscapes where agriculture was widespread and historical forest loss high, and the risk was particularly pronounced inside corridors between habitat patches. Not accounting for conflicts overestimated connectivity substantially.

Conclusions Human-carnivore conflicts are an important constraint to connectivity and should be considered in corridor assessments. Our study shows how habitat analysis, corridor assessment, and conflict risk mapping can be combined to guide conservation planning for identifying habitat networks and safe corridors for carnivores in human-dominated landscapes.

1 Introduction

Landscapes across the globe are increasingly human-dominated (Tilman et al. 2017). This is particularly perilous for large carnivores, which are wide-ranging and require large tracts of suitable and well-connected habitat (Crooks et al. 2011; Ripple et al. 2014). Across the globe, these species are currently disappearing over large extents of their historical range as a result of habitat loss and fragmentation, as well as high mortality in human-dominated landscapes (Bruskotter et al. 2017; Di Marco et al. 2014). This is worrisome given that large carnivores play key roles in ecosystems (Ripple et al. 2014). Many protected areas are not large enough to host viable carnivore populations, driving large carnivores to seek habitat and dispersal corridors in surrounding landscapes (Crooks et al. 2011; Di Minin et al. 2016). Therefore, conservation planning to protect large carnivores and the ecological functions they provide, must look beyond protected areas and identify strategies so these species can persist in human-dominated landscapes (Goswami and Vasudev 2017; Sanderson et al. 2002).

A central approach in this regard is to maintain connectivity between protected areas and habitat patches, commonly through retaining and establishing corridors (Kramer-Schadt et al. 2011; Tischendorf and Fahrig 2000). Corridors are landscape features that connect two or more habitat patches (or populations) so that individuals are able to move between the two without encountering major barriers (Tischendorf and Fahrig 2000). Therefore, identifying effective corridors requires an understanding of the key factors limiting connectivity (Vasudev et al. 2015). Corridor identification typically focusses on landscape features only, such as roads, high elevation, or the inhospitable matrix surrounding habitat patches (Kramer-Schadt et al. 2011; Tischendorf and Fahrig 2000). However, ecological factors such as predation, competition, prey availability (Cushman et al. 2010), as well as species' intrinsic characteristics, such as avoidance of unsafe landscapes (Ciuti et al. 2012; Gehr et al. 2017; LaPoint et al. 2013), both affect the behavioral responses of organisms to landscape structure in major ways and thus play important roles in connectivity (Vasudev et al. 2015). Ignoring ecological and behavioral constraints to dispersal might result in overestimation of corridor functionality and turn these corridors into 'ecological traps' where mortality is high, potentially undermining conservation efforts (Chetkiewicz et al. 2006; Northrup et al. 2012; Scharf et al. 2018). Approaches that consider mortality risks when deriving corridors are therefore urgently needed.

For large carnivores, a key cause of mortality is conflict with humans (Lennox et al. 2018; Treves and Karanth 2003). This conflict usually occurs in the form of livestock depredation (Chapron et al. 2014; van Eeden et al. 2018), which in turn may result in the persecution and killing of carnivores, and ultimately elevate extinction risk (Jędrzejewski et al. 2017; Michalski et al. 2006). The effects of human-carnivore conflict are more far-reaching than directly increasing mortality though. For instance, large predators in landscapes where human-related mortality is high may change their space and resource use (Bleicher 2017; Gehr et al. 2017) and may no longer exert a top-down control in the food webs (Atkins et al. 2019; Dorresteijn et al. 2015). Likewise, high conflict risk can act as a barrier to movement (Goswami and Vasudev 2017; Vasudev et al. 2015). Therefore, ignoring human-carnivore conflict risk when identifying corridors may result in funneling dispersing individuals to 'unsafe' landscapes (Little et al. 2002) and thus overestimating the effectiveness of corridors for carnivore movement (Goswami and Vasudev 2017). Planning for functioning meta-populations of large carnivores in human-dominated landscapes should, therefore, consider the risk of human-wildlife conflict (Cushman et al. 2018; Festa-Bianchet 2018).

We know of only a single study (Cushman et al. 2018) that considered conflict risk when assessing corridors for species of conservation concern. This is mainly because approaches to estimate mortality risk in space have only recently gained attention, demonstrating the potential of such tools to provide insights into drivers of human-wildlife conflict, to identify conflict hotspots, and understand which types of landscapes are more prone to conflict than others (Miller 2015). All of this can provide worthwhile information for designing conservation strategies that mitigate conflict (Miller 2015) and could be incorporated in corridor planning (Goswami and Vasudev 2017). We advance this approach (Cushman et al. 2018) by using empirical data on livestock depredation events and applying conflict risk modeling to identify conflict-prone landscapes in corridors that link habitat patches of large carnivores.

Our goal here was to identify safe dispersal corridors between habitat patches for the Persian leopard (*Panthera pardus saxicolor*), a wide-ranging large carnivore that critically depends on areas outside protected areas (Kiabi et al. 2002). We focused on the eastern Alborz Mountains in Iran, that contain two of the most important (sub)populations of this subspecies in Golestan National Park on the one hand, and Jahan Nama Protected Area on the other. In between, no protected areas exist, but leopard occurrence has been reported (Kiabi et al. 2002). The area between these protected areas is also among the most fertile agricultural regions in notoriously drought-prone Iran, resulting in a human-dominated landscape and a high potential for further land-use changes and habitat fragmentation (Ghoddousi et al. 2017). Moreover, leopards are responsible for frequent livestock depredation in the area (Ghoddousi et al. 2016), causing widespread conflict and retaliatory killings by local people. This likely affects the survival of the leopard population in this region in major ways, which is highly problematic because the entire, critically endangered Caucasus population of Persian leopard strongly depends on immigrations from Iran (Askerov et al. 2015). Assessing where both permeable and safe corridors are found will thus contribute to leopard conservation beyond the study region, in the entire Caucasus-Hyrcanian Biodiversity Hotspot. Specifically, our objectives were to:

(1) identify habitat patches from estimated leopard and prey habitat uses;
(2) assess structural connectivity across the study region;
(3) estimate human-leopard conflict probabilities using spatial risk modeling; and
(4) identify safe corridors, movement bottlenecks, and possible conservation interventions.

2 Methods

2.1 Study area

Our study area (ca. 3132 km²) is situated in the eastern Alborz Mountains, northeast of Iran (Figure C 1). The area connects the Golestan National Park complex (including Golestan National Park and its buffer zones Loveh Protected Area and Zav Protected Area) and Jahan Nama Protected Area, two strongholds of the Persian leopard in southwest Asia (Kiabi et al. 2002). No protected areas exist between Golestan National Park and Jahan Nama Protected Area; however, some parts of this range receive occasional patrols from the rangers of Golestan provincial office of Department of Environment. The main prey species of leopard in this area are bezoar goat (*Capra aegagrus*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) (Ghoddousi et al. 2016). The study area is part of the Caucasus-Hyrcanian Biodiversity Hotspot and is covered by Hyrcanian temperate mixed forest. We focused on the mountainous part of the region (up to >3200 m a.s.l.), as leopard occurrence in the lowlands is very rare and the landscape there has almost entirely been transformed into urban and agricultural areas. Moreover, there is a sharp environmental difference between the northern and southern slopes of the Alborz Mountains, with the southern slopes receiving less precipitation and thus being arid and without forests. We here focused only on the northern slopes, which are more similar to the landscapes in western Golestan National Park and Jahan Nama Protected Area.

We used a grid system of 36 km^2, superimposed over the study area to identify 74 sampling units (hereafter: cells) with at least 50% natural vegetation based on Landsat 8 satellite images with 30-m spatial resolution. We chose this cell size to represent the typical travel distance covered by foot by interviewees (see below), as well as logistical constraints (MacKenzie et al. 2017; Petracca et al. 2018). We used a 50% threshold for the natural vegetation coverage in each cell since highly transformed areas may function as strong barriers to the movement of leopard and its prey (Bleyhl et al. 2017).

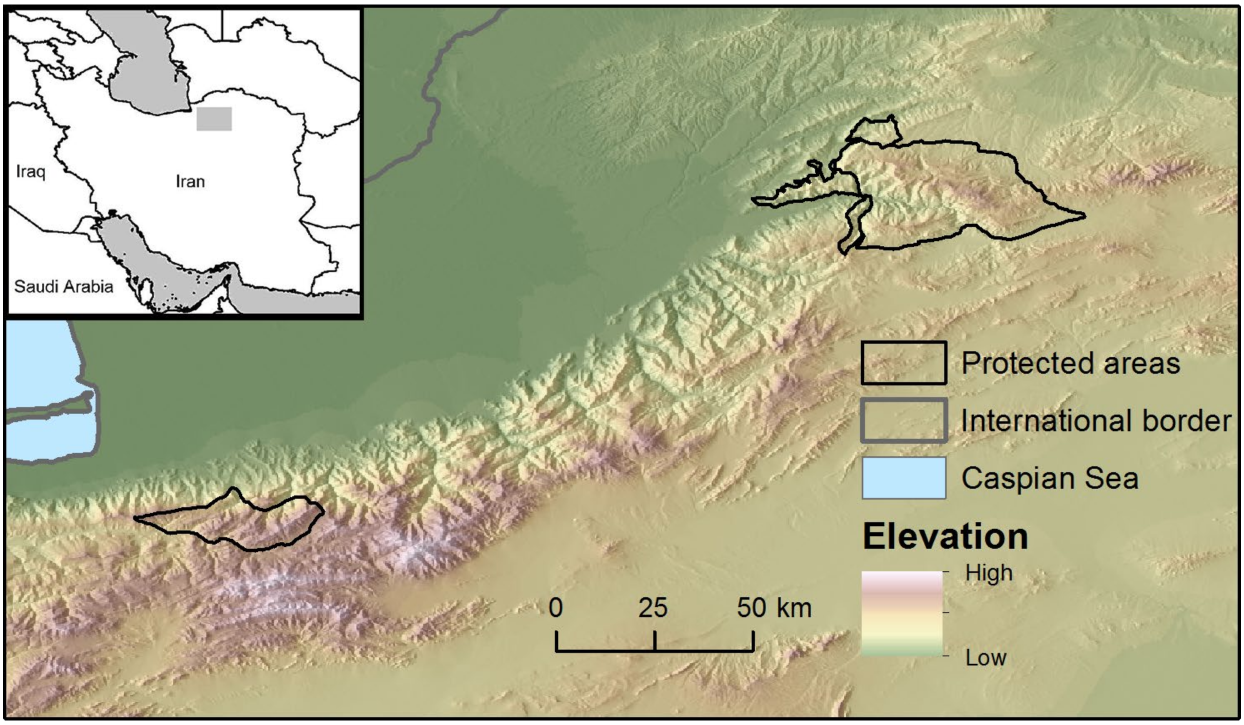

Figure C 1: Study area in the eastern Alborz Mountains, Iran, and the location of Golestan National Park complex (including Golestan National Park, Loveh Protected Area and Zav Protected Area; right) and Jahan Nama Protected Area (left).

2.2 Interview survey

We collected data on the presence of leopard, other wildlife, and leopard depredation on livestock, using interviews with local communities. Surveys across larger landscapes can be very costly and difficult to implement using field observations of wildlife or camera trapping, and interview surveys can be a viable alternative in such situations (Ghoshal et al. 2017; Martinez-Marti et al. 2016; Pillay et al. 2014; Zeller et al. 2011). The use of interview data for wildlife surveys is especially successful when applied for relatively rare species with large body size, given appropriate statistical methods are used (Steger et al. 2017). We conducted interviews in one or two randomly chosen villages in each cell and aimed to collect information from at least four interviewees. Each interviewee represented a replicate, providing information for the cell surrounding his/her village (Zeller et al. 2011), and if other neighboring cells were visited often by the interviewee, we conducted a separate interview related to that cell (Taubmann et al. 2015). We conducted interviews only with individuals who were knowledgeable about wildlife (e.g. regularly working outdoor), lived in the area for at least one year and with a minimum residence of three months in the prior year. We gathered information from the interviewees on direct sightings of leopard and main prey species (i.e. bezoar goat, red deer, roe deer, and wild boar), as well as cases of leopard depredation on livestock in the prior year (Zeller et al. 2011). We only included sightings when the interviewee was able to distinguish the species from the presented pictures. Only direct observations by the interviewee were included, as we considered sightings by others or of species' signs (e.g. tracks) unreliable. Moreover, we asked interviewees about their age, occupation, the period he/she has lived in the cell and the proportion of the prior year resided in the cell (Zeller et al. 2011). We received verbal consent from all interviewees before conducting the interviews and assured them about the confidentiality and anonymity of their data.

2.3 Occupancy modeling

We assessed leopard and prey habitat use in the study area using occupancy modeling (MacKenzie et al. 2017; Zeller et al. 2011). As the assumption of population closure within the survey, required for occupancy states, could not be met due to the long period of sightings (i.e. one year prior to the interview), we assumed that the occupancy states represent the habitat use (MacKenzie and Nichols 2004). We arranged the detection/non-detection histories for leopard and prey species in different cells based on interviewees' sightings. We incorporated potential false-positive bias from interviewee responses into our modeling approach to minimize chances of misidentifications (Chambert et al. 2015; Miller et al. 2011;

Petracca et al. 2018). We considered sightings by rangers and hunters as having lower probability of false positive bias compared to other interviewees (Ghoshal et al. 2017; Johnston et al. 2018; Martinez-Marti et al. 2016; Miller et al. 2011) and marked the detections by this observer category as ‘certain’ in the detection matrix (Chambert et al. 2015; Pillay et al. 2014).

We developed *a-priori* hypotheses regarding factors that could affect species’ detection (ρ), habitat use (ψ) and false positives detections (ρ_{10}). We assumed effort (days of the prior year spent in the cell) and residence (proportion of years lived in the cell to age) covariates to influence ρ (Zeller et al. 2011). Regarding ψ, we hypothesized potential influence by land cover, elevation, road density, prey availability (only in leopard models), ruggedness and distance to protected areas (Abade et al. 2018; Athreya et al. 2015; Petracca et al. 2014). Regarding, ρ_{10}, we tested the possible influence of occupation of interviewees. A detailed description of each covariate and their hypothesized effects on ρ, ψ and ρ_{10} are provided in

We tested different scenarios to calculate prey availability (bezoar goat, red deer, roe deer, and wild boar) per cell: (1) prey richness (number of prey species reported by interviewees); (2) single-species and (3) cumulative habitat use (from occupancy model estimates); and (4) cumulative catch-per-unit-effort (CPUE; multiplying the number of independent detections by the species’ average biomass, divided by the number of interviewees) (Abade et al. 2018; Petracca et al. 2018). We obtained prey biomass figures from (Lumetsberger et al. 2017). Using univariate occupancy models, CPUE performed best in explaining leopard habitat use (Table C 2), and therefore, we used this covariate as prey availability in the leopard models. We tested all covariates for autocorrelation using the Pearson correlation test (cut-off point r = 0.60). Moreover, we scaled all the covariates prior to the analyses to have a unit variance and minimize overdispersion (MacKenzie et al. 2017).

Table C 1: Covariates used in the occupancy models, with the hypothesized effect of each covariate on detection probability (ρ), habitat use (ψ) or false positive detections (ρ_{10}) of leopard and prey species.

Model process	Covariate	Description	Data source	Hypothesized influence
Detection (ρ)	Effort	Proportion of the prior year spent in the cell	Interview data	+
	Residence	Proportion of years lived in the cell to the interviewee's age	Interview data	+
Habitat use (ψ)	Prey availability[a]	The cumulative catch per unit effort for three large prey species in cell[b]	Interview data	+
	Distance to protected areas	Nearest distance (km) to protected area borders from cell centroid	World Database on Protected Areas [c]	-
	Forest[d]	Proportion of forest in cell	Land-cover map	+
	Cropland[d]	Proportion of cropland in cell	Land-cover map	-
	Road density	Length (km) of primary roads in cell	Google Earth	-
	Elevation	Average elevation (m) in cell	SRTM[e]	+/-
	Ruggedness	Average ruggedness index in cell	SRTM[e]	+
False positives (ρ_{10})	Occupation	Coded as "1" if the interviewee was a hunter or ranger "0" otherwise	Interview data	-

[a] Only considered in the leopard models

[b] Biomass of prey species based on (Lumetsberger et al. 2017): bezoar goat 36 kg, roe deer 20 kg, red deer 99 kg

[c] Source: www.protectedplanet.net

[d] Due to the high correlation between forest and cropland layers, we only used either of them in each model

[e] Source: Shuttle Radar Topography Mission (https://search.earthdata.nasa.gov)

We fitted single-species, single-season occupancy models for leopard and four prey species using the Unmarked package in R (Fiske and Chandler 2011). We used a multi-step approach by first building models using covariates influencing ρ and ρ_{10} while maintaining ψ as constant. Then, we held the covariates in the top ρ and ρ_{10} models constant and built models that influenced ψ (MacKenzie et al. 2017). We evaluated univariate occupancy models based on *a-priori* hypotheses and then made combinations of covariates to assess their influence on ψ. We ranked models based on their Akaike Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002) and calculated Akaike weights to determine the relative goodness-of-fit per model. We used ΔAICc<2 criteria to select the best models (Burnham and Anderson 2002). We also compared naïve model ($\psi_{naïve}$; proportion of cells with at least one detection) with and without ρ_{10} to assess the impact of false positive bias on occupancy estimates (Petracca et al. 2018).

Table C 2: Comparison of model performance of different prey covariate scenarios in explaining leopard habitat use (ψ).Scenarios: *CPUE*, cumulative catch-per-unit-effort for all prey species (prey biomass data from (Lumetsberger et al. 2017); *cumulative prey*, cumulative habitat use estimates from occupancy models; *roe deer*, *red deer*, *bezoar goat*, single-species habitat use estimates from occupancy models; *prey richness*, number of prey species reported by interviewees per cell; *null*, null model.

Prey covariate scenarios	K[a]	AICc[b]	ΔAICc[c]	AICc weight	Log-likelihood
CPUE	6	370.57	0	0.54	-178.61
Cumulative prey	6	373.83	3.27	0.11	-180.25
Roe deer	6	373.93	3.36	0.10	-180.29
Red deer	6	374.00	3.43	0.10	-180.32
Prey richness	6	374.02	3.46	0.10	-180.33
Bezoar goat	6	375.53	4.96	0.05	-181.09
Null	4	379.16	8.59	0.01	-185.27

[a] Number of parameters in the model

[b] Akaike Information Criterion corrected for small sample size

[c] Difference in AICc value relative to the best model

2.4 Connectivity analysis

To assess structural connectivity in our study region, we mapped six land-cover classes using Landsat 8 satellite images with 30-m spatial resolution: forest, rangeland, cropland, built-up, sparse vegetation, and water (see Supplementary Information for details on the land-cover mapping). We translated our land-cover map into a surface characterizing resistance to leopard movement (Zeller et al. 2012) by assigning resistance values per land-cover class based on a survey among 27 wildlife experts (Bleyhl et al. 2017). Resistance values were allowed to range from 1 (most permeable) to 10 (least permeable). We calculated median resistance values across expert estimations per land-cover class to create a resistance surface (Bleyhl et al. 2017). Additionally, we treated roads as partial barriers, assigning a resistance value of 100 to each 30-m cell that contained a major road, and considered the land-cover classes built-up and water as total barriers (Bleyhl et al. 2017). We averaged resistance values for each 36 km^2 cell.

To identify bottlenecks across the landscape, we applied circuit theory using the Linkage Mapper Toolkit (McRae et al. 2008). This method measures the current (i.e. likelihood of a species passing) between nodes (i.e. source populations) across the landscape, considering the resistance of the landscape (McRae et al. 2008). High currents indicate a lack of alternative paths, and therefore, potential bottlenecks within a corridor. We defined bottlenecks as areas with a current density higher than the mean plus two standard deviations (Bleyhl et al. 2017). Finally, we calculated the number of bottlenecks for each 36 km^2 cell.

2.5 Conflict risk modeling

To quantify and map associations between human-leopard conflict and landscape characteristics, we used generalized linear models (GLMs) (Miller 2015). We derived the binomial presence or absence of conflict (i.e. leopard depredation of livestock) in each cell from our interview data. In addition to the environmental covariates used in the occupancy modeling, we calculated variables reflecting forest type and fragmentation in each cell, as we hypothesized these variables to affect leopard depredation risk (Acharya et al. 2017; Carvalho et al. 2015; Miller 2015). We used Morphological Spatial Pattern Analysis (MSPA) (Vogt and Riitters 2017) on our land-cover map to measure the share of core forest as well as connecting forest patches per cell. Core forest was defined as patches larger than 2 km^2 with an adjacent forest edge of <300m (10 forest pixels). The connecting forest was assigned to those patches (>2 km^2) that were >300m from the nearest forest patch. Additionally, we calculated the median forest patch area per cell using FRAGSTATS (McGarigal et al. 2012) as an indicator of forest fragmentation. We tested for collinearity among all covariates using the Pearson correlation test ($r<0.60$). We applied a similar model selection procedure as in our occupancy modeling. We evaluated model results using the area under the receiver-operating curve (AUC) with 10-fold cross-validation.

2.6 Identification of habitat patches and safe corridors

We used a multi-criteria approach to identify habitat patches and corridors (Figure C 2; Cushman et al. 2018; Rödder et al. 2016). We used Jenk's natural breaks as the classification method for the habitat use of leopard and prey, landscape resistance, bottleneck numbers, and human-leopard conflict intensity. We classified each into three categories (i.e. low, medium, high) by finding points where between-group variability was highest while within-group variability was minimized. We defined 'habitat patches' as areas where leopard and/or prey are prevalent and can be the origin or destination of dispersers (Kramer-Schadt et al. 2011). We identified habitat patches as cells with high habitat use of leopard and/or high sum of habitat use of all prey species (Zeller et al. 2011). All other cells were classified as 'matrix', that is cells where leopard and prey likely do not permanently occur (Kramer-Schadt et al. 2011; Rödder et al. 2016). We used the Wilcoxon signed-rank test to assess differences in the levels of landscape resistance and conflict probabilities between the habitat patches and the matrix.

We identified ‘safe corridors’ by relabeling matrix cells characterized by low or medium levels of landscape resistance and low or medium levels of conflict risk. All remaining cells were relabeled as ‘severed corridors’ (Riggio and Caro 2017). Finally, within the severed corridors, we identified cells with the highest number of bottlenecks, which require urgent conservation intervention due to the absence of alternative dispersal paths, high landscape resistance and conflict risk (Taubmann et al. 2015). To assess the sensitivity of our classification, we also did a re-classification using geometrical intervals (a classifier algorithm that minimizes the square sum of element per class) instead of natural breaks and quantified the differences.

3 Results

We conducted 231 semi-structured interviews in 69 cells from August to September 2015 and from February to October 2016. We were unable to collect data from five cells due to inaccessibility or lack of settlements, and therefore, those cells were removed from the analysis. Within the sampled cells, on average around 3.07 questionnaires were completed. Interviewees were all male and between 17 and 80 years old with a mean age of 41.12 years. Interviewees spent on average 309 days of the year within their respective cells and had on average 38.85 years of living experience in the area. The interviewees were mostly shepherds (44.87%), but also farmers (26.82%), rangers (12.19%), foresters (6.34%), hunters (6.34%) and porters (3.41%). From 69 cells, leopard was sighted in 51 (73.91%) and leopard depredation on livestock was reported in 24 cells (34.78%). The most often-sighted wild prey was wild boar, which occurred in all cells, followed by roe deer (63.77%), red deer (42.02%) and bezoar goat (26.08%). We removed wild boar from the analyses due to their ubiquitous distribution.

None of the detection (ρ) covariates were selected in our top models but the false positive (ρ_{10}) covariate of occupation (if the interviewee was a hunter/ranger or from another category) was present in the top models of leopard and red deer (Table C 3). This covariate negatively influenced ρ_{10} and dropped the naïve occupancy ($\psi_{naïve}$) by around 16% and 17% for leopard and red deer, respectively, showing the potential false positive bias in our interview data. The most parsimonious habitat use (ψ) model for leopard included prey availability and elevation covariates (Table C 3). Agriculture was the main factor limiting ψ for red deer and roe deer (Table C 3). In addition, ψ of red deer and roe deer was influenced by elevation and distance from protected areas, respectively (Table C 3). The ψ of bezoar goat was associated with the ruggedness of the cells and the distance from protected areas (Table C 3). Projecting our final model to all cells showed that high leopard habitat use (>0.55) occurred in 15 cells (22% of all cells; Figure C 3). High cumulative prey habitat use (>1.87) occurred in 13 cells (19%; Figure C 3). We identified 22 cells (32%) as habitat patches based on combined high leopard and prey habitat use, and considered the remaining cells (n = 47) as matrix (Figure C 4). The results indicated a habitat gap of around 100 km between Golestan National Park and the nearest continuous habitat patch in the western part of the study area (Figure C 4).

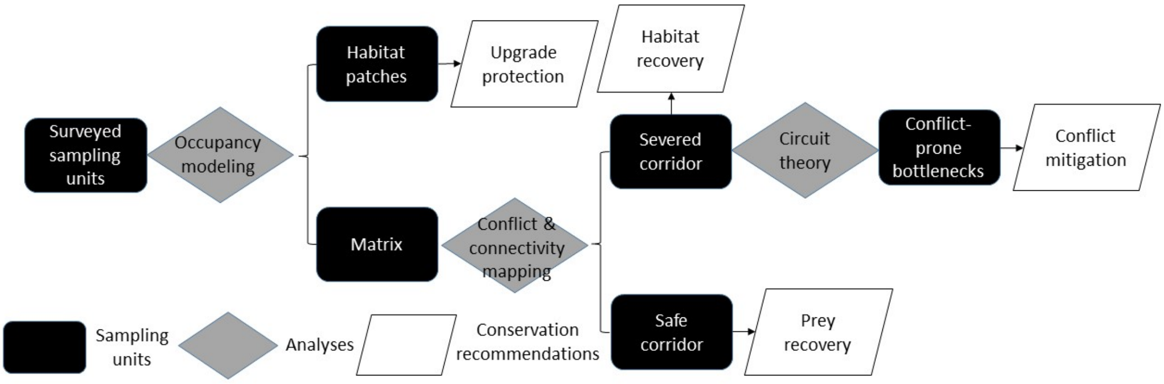

Figure C 2: Flowchart of the step-wise multi-criteria approach to identify habitat patches, safe corridors and conflict-prone movement bottlenecks, and their respective conservation recommendations.

Table C 3: Top occupancy models of leopard and prey species with habitat use (ψ), detection probability (ρ) and probability of false positives (ρ10) covariates.The habitat use (ψ) covariates: prey, the cumulative catch per unit effort for three large prey species; elev., average elevation (m) in cell; PA, distance (km) to protected areas from cell centroid; crop, proportion of cropland in cell; rugged, average ruggedness index in cell; job: coded as "1" if the interviewee was a hunter or ranger "0" otherwise.

Species	Model	Intercept (SE[a])	Prey (SE[a])	Elev. (SE[a])	PA (SE[a])	Crop (SE[a])	Rugged (SE[a])
Leopard	Ψ (prey + elev.), $\rho(.)$, ρ_{10}(job)	-0.67 (0.53)	1.79 (0.83)	-1.27 (0.72)	-	-	-
Red deer	Ψ (crop + elev.), $\rho(.)$, ρ_{10}(job)	-3.26 (1.30)	NA	0.93 (0.52)	-	-4.96 (2.19)	-
Roe deer	Ψ (crop + PA), $\rho(.)$, $\rho_{10}(.)$	1.03 (0.59)	NA	-	-2.15 (0.89)	-1.99 (0.68)	-
Bezoar goat	Ψ (PA + rugged), $\rho(.)$, $\rho_{10}(.)$	- 9.03 (6.54)	NA	-	-7.92 (5.98)	-	4.74 (4.66)

[a] Standard error

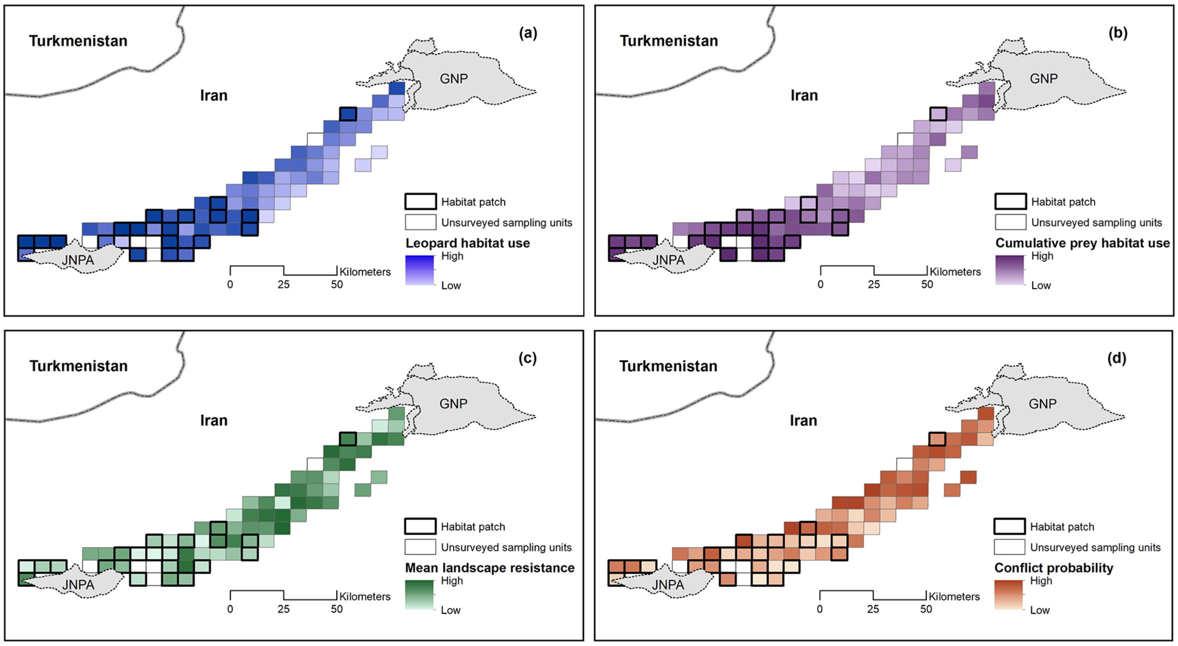

Figure C 3: Estimated leopard (a) and prey (b) habitat uses, mean landscape resistance (c) and human-leopard conflict risk (d) between Golestan National Park (GNP) and Jahan Nama Protected Area (JNPA), Iran.

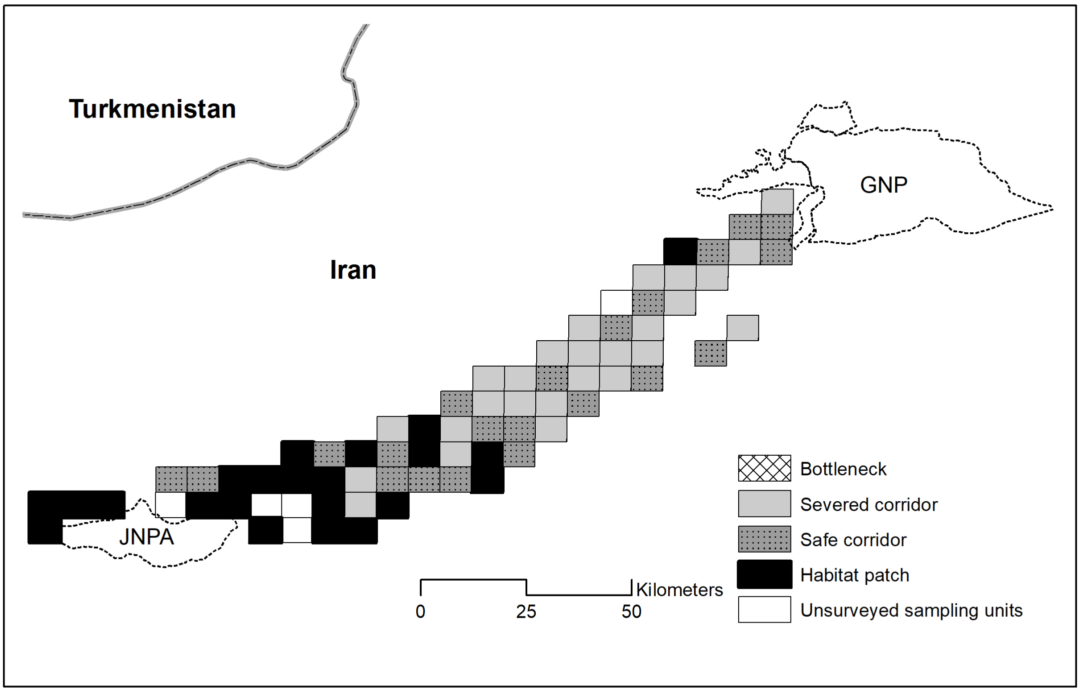

Figure C 4: Location of habitat patches, safe and severed corridors and conflict-prone movement bottlenecks between Golestan National Park (GNP) and Jahan Nama Protected Area (JNPA), Iran.

Our land-cover map had an overall accuracy of 85.8%. User’s accuracy ranged from 71.0% for the sparse vegetation class to 100% for the water class. Producer’s accuracy ranged from 42.0% (built-up) to 98.7% (forest). Forest was the most widespread land-cover class (66.7%)

followed by rangeland (18.6%), cropland (12.8%), sparse vegetation (1%), built-up (0.9%) and water (<0.05%; Figure SI C 1 in the Supplementary Information). The mean landscape resistance in each cell based on our land-cover maps ranged from 1 to 5.05. Our structural connectivity analysis revealed high landscape resistance in the eastern part of the study area (Figure C 3). The landscape resistance ($Z = 285$, $p<0.01$) was significantly lower in the habitat patches compared to the matrix.

The top conflict risk models included cropland, connecting forest and median forest patch area (Table C 4). These models revealed a positive association of cropland with conflict intensity, whereas median forest patch area and connecting forest were associated with lower conflict rates. The AUC for the best model was 0.73. The conflict risk ($Z = 315$, $p<0.01$) was significantly lower in the habitat patches compared to the matrix.

We relabeled 21 matrix cells (45% of all matrix cells) with low or medium conflict risk (<0.56) and low or medium landscape resistance (<3.47) as safe corridor and identified the remaining cells (n=26) as severed corridor. The identified safe corridor cells could fill the connectivity gap between some of the habitat patches but were absent from the eastern parts of the study area (Figure C 4). When not accounting for the conflict risk and using the same landscape resistance threshold, the safe corridor cells were overestimated by 52.38%. We identified four cells with a high number of bottlenecks (>1377) in the severed corridors, indicating priority areas for conflict mitigation measures (Figure C 4). The results of the sensitivity analysis showed that habitat patches and safe corridors identified based on geometrical intervals had 88% and 95% overlap with the results of the Jenk's method, respectively.

Table C 4: Parameters of the best-performing generalized linear models of human-leopard conflict.Covariates: connecting forest, forest patches larger than 2 km^2 with >300 m distance from the nearest forest in the land-cover map; cropland, proportion of cropland in cell; forest patch area, median forest patch area in cell from land-cover map.

Coefficient	Estimate	SD[a]	z-value	p-value	Odds	95%CI[b]
Intercept	0.32	0.61	0.52	0.59	-	-
Connecting forest	-0.13	0.05	-2.51	0.01	0.87	0.77–0.95
Cropland	0.11	0.05	2.23	0.02	1.12	1.02–1.26
Forest patch area	-0.24	0.11	-2.14	0.03	0.78	0.60–0.96

[a] Standard deviation

[b] Confidence intervals

4 Discussion

Large carnivores in human-dominated landscapes typically cannot persist inside protected areas alone and critically depend on habitat outside them as well as functioning corridors between habitat patches. We here show how assessments of habitat, landscape connectivity, and human-carnivore conflict risk can be combined to identify safe corridors for large carnivores, and ultimately to guide conservation planning for maintaining wide-ranging species outside protected areas. Our analyses, using the example of Persian leopards in northern Iran, provide three main insights.

First, ignoring human-leopard conflict in connectivity assessments may lead to a substantial overestimation of the extent of the corridor. Many leopard dispersal bottlenecks in the eastern Alborz Mountains were located in areas with high conflict risk (i.e. severed corridors), where the persecution of leopard is likely (Kiabi et al. 2002; Lennox et al. 2018), and local extinction risk is high (Jędrzejewski et al. 2017). These landscapes may act as 'ecological traps' when animals are funneled through them (Kramer-Schadt et al. 2011; Little et al. 2002; Northrup et al. 2012) and consequently, undermine corridor functionality. Moreover, the behavioral constraints to dispersal, such as avoidance of unsafe landscapes (Gehr et al. 2017) may limit the permeability of these bottlenecks (Goswami and Vasudev 2017). Therefore, our study reinforces other calls (Festa-Bianchet 2018; Goswami and Vasudev 2017; LaPoint et al. 2013), for more deeply considering ecological as well as intrinsic constraints for corridor identification in human-dominated landscapes, some of which might be difficult to measure with remote sensing and conventional habitat assessment techniques (Scharf et al. 2018). Our study shows how a rapid and low-cost assessment based on local interviews can alleviate this issue and help in identification of conflict-prone landscapes.

A second insight from our analyses was better understanding the influence of agricultural lands and forest fragmentation on human-carnivore conflicts in human-dominated landscapes. In our study, conflict probability was clearly associated with the share of croplands in each cell, which has been reported in other human-dominated landscapes (Northrup et al. 2012). Agricultural lands offer domestic prey as a food source and increase the probability of livestock depredation by leopard (Abade et al. 2018). Moreover, the prey depletion in these landscapes from habitat loss and/or poaching may trigger a higher rate of livestock depredation by big cats, as suggested in a global review (Khorozyan et al. 2015). Our results also showed a negative association between forest fragmentation and the probability of livestock depredation. Other studies (Acharya et al. 2017; Carvalho et al.

2015; Michalski et al. 2006), similarly showed that forest fragmentation leads to the creation of heterogeneous landscapes and higher presence of livestock, both of which increase the probability of conflict between humans and large carnivores.

A third key finding of our work was the marked negative impact of human land uses on the habitat use and connectivity of the studied species. Only about a third of the study area between Golestan National Park and Jahan Nama Protected Area could be considered as highly used by the leopard and three prey species. The absence of high-quality habitat patches in the eastern part of the study area, which has experienced a higher rate of land-use change, suggests that these areas are likely devoid of resident leopard and prey species (except wild boar). This result contradicts previous studies (Kshettry et al. 2017; Odden et al. 2014), showing that leopards may use modified landscapes and agroecosystems as habitat. Prey availability, as the most important driver of leopard habitat use in our study, may explain this as it may be the true limiting factor in modified landscapes. In our study, the habitat use of prey species was mostly negatively affected by agricultural landscapes. This reflects the importance of habitat loss from the land-use change as a threat to the existence of ungulate species, especially when it coincides with poaching (Benitez-Lopez et al. 2017; Romero-Muñoz et al. 2019), which ultimately impacts large carnivores. In other human-dominated landscapes, however, prey can be abundant (Chapron et al. 2014) and this can explain the diverging results of the impact of agricultural extent on large carnivore existence.

Despite the absence of habitat patches in the modified landscape, these areas may still be valuable as dispersal corridors (Vanbianchi et al. 2018). However, high levels of landscape resistance due to the existence of roads and residential areas pose major barriers to leopard dispersal in the eastern part of the study area. The high potential in agricultural expansion and intensification in this fertile region (Ghoddousi et al. 2017), may further isolate the habitat patches, impacting the habitat connectivity of leopard and prey species. These results highlight the effect of structural landscape changes on habitat use and connectivity of wide-ranging species, especially where they interplay with other threats such as poaching.

In this study, we strived to improve connectivity assessments by considering ecological and behavioral constraints to dispersal, such as human-carnivore conflict. To our knowledge, only one study has considered conflict risk in corridor planning (Cushman et al. 2018). By using empirical data on livestock depredations and spatial risk modeling, we here for the first time incorporated conflict risk directly in connectivity assessments. With the recent developments in conflict risk mapping (Miller 2015), we advocate that future corridor assessments should consider ecological and behavioral constraints to the dispersal of wide-ranging species (Goswami and Vasudev 2017; LaPoint et al. 2013). This study may be used as the scientific basis for such corridor planning outside protected areas by combining habitat assessment, structural connectivity, and conflict risk mapping.

Some possible drawbacks and room for improvement of our approach need mentioning. First, integrating different methodologies across various scales is challenging and we acknowledge simplifications in the classification of habitat patches and safe corridors. However, using different classification methods, we showed that the influence of this issue on our final results was minor. Second, the approach used in dealing with probabilities of false positives in occupancy modeling is not ideal (Johnston et al. 2018). However, the effects of false positive probabilities on naïve occupancies showed the necessity of considering this bias in the analysis of interview data (Petracca et al. 2018). Finally, the prey species in our study may use smaller areas than our cell size, which may bias our inferences by overestimating the habitat use of these species. However, such cell size has been successfully tested in multi-species settings of large carnivores and prey in previous studies (Petracca et al. 2014; Zeller et al. 2011).

Our results indicate a range of concrete conservation and landscape planning recommendations based on the intensities of species' habitat use, landscape resistance, and conflict risk. First, we recommend upgrading the protection measures in the habitat patches due to the higher habitat use of leopard and prey species. Present protected areas in Golestan Province are insufficient for the protection of the ungulate species (Momeni Dehghani et al. 2013), and the identified habitat patches in our study may represent suitable candidates for the expansion of the protected area network. Second, safe corridors, as areas with low conflict risk and landscape resistance but with low prey availability, require conservation interventions related to poaching mitigation, prey recovery, and protection from development (Cushman et al. 2018). Third, movement bottlenecks within the severed corridors require urgent conflict mitigation measures to reduce the actual and perceived risk of human-leopard conflict in these landscapes (Broekhuis et al. 2017; Cushman et al. 2018), which are critical for the long-term persistence of leopards in the Caucasus-Hyrcanian ecoregion. The compensation schemes and/or preventive measures such as improved husbandry methods are recommended to reduce the chance of depredation and lethal control (Krafte Holland et al. 2018; van Eeden et al. 2018). Finally, the remaining cells identified as severed corridors require habitat recovery and prevention of further land-use change and forest fragmentation. For the persistence of threatened wide-ranging carnivores in the human-dominated landscapes, retaining certain levels of native habitat within the agroecosystems is crucial (Ferreira et al. 2018). While we derive these recommendations for our case study of Persian leopards in northern Iran, these recommendations are likely equally valid for other regions where large carnivores depend on corridors in human-dominated landscapes, and where human-carnivore conflict may undermine the effectiveness of these corridors. More broadly, our study highlights a low-cost and effective way of combining bottom-up and top-down approaches for incorporating conflict risk assessments in corridor planning.

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Supplementary Information

Land-cover mapping

We mapped land cover using pixel-based image compositing and Landsat 8 satellite imagery (Griffiths et al. 2013b). Pixel-based image compositing, instead of using individual images, is rapidly emerging as a new standard for mapping land cover and changes therein, including for assessing forest dynamics, agricultural land change, and wildlife connectivity over large areas (Bleyhl et al. 2017; Griffiths et al. 2013a; Hansen et al. 2013; Potapov et al. 2015). Compositing is advantageous over single scene approaches mainly by overcoming data gaps from cloud cover or missing imagery in the Landsat archives (Roy et al. 2010). Landsat compositing algorithms use all available imagery on a per-pixel basis to create a gap-free coverage of any user-defined study region at 30-m resolution (Griffiths et al. 2013b; Hansen et al. 2013; Potapov et al. 2011; Roy et al. 2010). To create best pixel composites, we acquired all available Landsat 8 images from April 12th 2013 to 31st December 2015 with less than 70% cloud cover. We then used a score-based weighing function to assess each pixel's suitability for the final composite, based on acquisition year, day of year, distance to clouds, and distance to nadir (Griffiths et al. 2013b). We thereby derived four cloud-free seasonal image composites targeted on different seasons of the year 2014 to approximate different phenological stages of the vegetation (i.e. spring, summer, fall, and winter). Additionally, we calculated spectral-temporal metrics for each pixel that summarize the full image record and have the potential to greatly improve land-cover classifications (Bleyhl et al. 2017; Hermosilla et al. 2015). These metrics were based on all clear observations and thereby contained further phenological information for the land-cover classes over time (e.g. mean and standard deviation of the surface reflectance for each Landsat band (Griffiths et al. 2013b).

Using the four seasonal image composites and the spectral metrics, we classified six land-cover classes: forest, rangeland, cropland, built-up, sparse vegetation, and water (Figure SI C 1). To collect training data, we used high-resolution GoogleEarth images and our seasonal composites, and digitized polygons for each land-cover class. We then randomly selected 1000 points within each class as training data. For our final land-cover map, we applied a minimum mapping unit of 0.54 ha (i.e. six Landsat pixel) to remove salt-and-pepper structures that mainly represented misclassifications. We further used settlement point locations from Open Street Map (OSM) to improve discrimination between the built-up and the sparse vegetation class and limited built-up class to areas within two kilometers around OSM settlements (Bleyhl et al. 2017). We assigned built-up pixels outside this buffer to the sparse vegetation class. For validating our final land-cover map, we randomly collected 100 points per class and labeled them according to visual inspection of high-resolution GoogleEarth imagery together with our Landsat composites. We then calculated overall accuracy, class-wise user's and producer's accuracy and accounted for potential sampling bias by adjusting error and estimate according to the class distributions (Foody 2002; Olofsson et al. 2014).

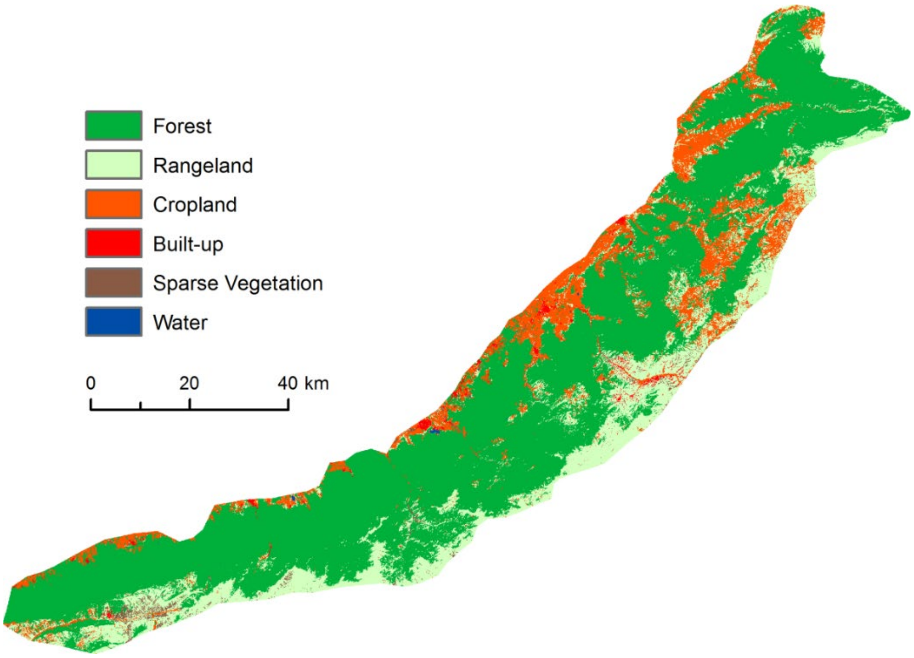

Figure SI C 1: Land-cover map of the study area in eastern Alborz Mountains between Golestan National Park and Jahan Nama Protected Area, Iran.

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Appendix D:

Human-leopard conflict outside protected areas is the main cause of leopard poaching in Iran

Manuscript in preparation

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Abstract

Globally, many large mammalian carnivores are facing population declines due to overexploitation (e.g. poaching) and farming (e.g. livestock rearing). An important impact of increasing livestock numbers is the occurrence of human-carnivore conflict due to livestock depredation. Additionally, retaliation against livestock depredation leads to human injuries or deaths from carnivore attacks. Thus, retaliatory or precautionary poaching of large carnivores as a result of conflicts over livestock depredation is becoming a great concern for their conservation. However, due to the cryptic nature of poaching, the relationship between carnivore poaching over livestock depredation and attacks on humans has rarely been assessed. We gathered 115 records of leopard mortality and 41 attacks on humans throughout Iran using national website articles produced between 2007 and 2017. Over 62% of leopard poaching records were related to traditional beliefs (as indicated by the removal of body parts) and livestock depredation events indicating only indirect commercial incentives. In contrast, direct commercial motivation (e.g. selling pelt) were less commonly indicated (31%). Over 97% of poaching cases occurred outside protected areas. We used occupancy modelling within a Bayesian framework to assess the relationship between leopard poaching and livestock density, and between leopard poaching and attacks on people. Our results explicitly show that leopard poaching increases with attacks on humans. Likewise, leopard poaching also increased with livestock density and mostly occurred in forested areas reflecting the preferred habitat of leopards. Although the distinction between leopard mortalities driven by commercial interests and depredation could potentially be biased against reports of commercial poaching, our data shows that there are high levels of leopard poaching and that often they are causally related to increased and unregulated livestock grazing and leopard attacks on shepherds. We, therefore, underline the need for improved management of livestock grazing to mitigate leopard-livestock conflicts and reduce poaching of leopards.

1 Introduction

Globally, many large mammalian carnivores (>50 kg) are experiencing population declines, range loss and local extinctions as a result of overexploitation, direct persecution, habitat degradation and prey reduction (Woodroffe & Frank 2005; Ripple et al. 2014; Wolf & Ripple 2016; Jędrzejewski et al. 2017). Large home range sizes, requirements for high densities of wild prey and competitive behaviors of large carnivores direct their movements into unprotected lands, where law enforcement measures are often lacking and the risk of livestock depredation and human-caused mortality is high (Ripple et al. 2014; Durant et al. 2017). Thus, carnivores have been predisposed to various mortality risks such as intentional human-caused mortality (e.g. poisoning, snaring, and shooting) and incidental human-caused mortality (e.g. rail/road kills; Woodroffe & Frank 2005; Dobson & Lynes 2008; Jędrzejewski et al. 2017). Here, we define intentional mortality as 'poaching' if the mortality shows signs of being caused by direct economic intentions (e.g. selling pelt) and/or traditional beliefs (e.g. removal of body parts).

Conflicts between large carnivores and local people over livestock depredation have been widely recognized as one of the most significant threats to the survival of large carnivores (Ghoddousi et al. 2016; Babrgir et al. 2017; Jędrzejewski et al. 2017; Ekernas et al. 2017). Over one-third of the global land area is currently utilized to graze livestock (Otte et al. 2012). Due to flexibility in habitat use (Ebrahimi, Farashi & Rashki 2017), carnivores often compete with rural people for resources and space and trigger human-carnivore conflict (HCC; Treves & Karanth 2003). However, HCC does not only cause mortality of carnivores but also causes injuries and fatalities of local people from carnivore attacks (Kshettry, Vaidyanathan & Athreya 2017; Jędrzejewski et al. 2017), which may aggravate hostility towards carnivores and pose a serious challenge to their conservation (Treves & Bruskotter 2014). Livestock are a reliable food source for large carnivores (Ekernas et al. 2017) and high trophic dependence of carnivores on livestock may create an 'ecological trap' (Durant et al. 2017).

It has been suggested that retaliatory killings may seriously affect populations of large carnivores (Carter et al. 2016; Jędrzejewski et al. 2017). For instance, Jędrzejewski et al. (2017) demonstrated that retaliatory killing of jaguars (*Panthera onca*) in South America was the main driver of their local extirpation. Prey recovery plans are unable to sustain carnivore populations if mortality rates caused by poaching are high (Chapron et al. 2008). Additionally, if mortality rates of large carnivores in their core populations are high, then the sink effects from the core populations to subpopulations might be interrupted or discontinued (Durant et al. 2017).

Due to the cryptic nature of poaching, data on poaching is rarely available and, thus, assessing the impacts of poaching on wildlife populations is difficult (Duffy et al. 2015). For instance, deriving poaching data from law enforcement (e.g. ranger logbooks) may underestimate the actual poaching pressure as it is constrained by efforts (Carter et al. 2016; Critchlow et al. 2016; Ghoddousi et al. 2016). Thus, special attention is required to assess poaching rates with the use of methods that account for imperfect detection (Critchlow et al. 2016).

To our knowledge, the relationships between poaching of large carnivores, their attacks on people and HCC over livestock depredation have rarely been assessed. Such an assessment is essential to contribute to a better understanding of the principal drivers of carnivore poaching and possible mitigation measures (Suryawanshi et al. 2017). Having empirical evidence of complexities around poaching can help decision-makers prioritize their conservation efforts effectively (Treves & Karanth 2003).

In this study, we assessed the poaching patterns of the endangered Persian leopard (*Panthera pardus saxicolor* Pocock 1927) in its stronghold country of Iran (Stein et al. 2016). Currently, a precise estimate of the population size of Persian leopards is not available across the country, but is tentatively estimated to be around 550–850 individuals (Kiabi, Dareshouri, Ghaemi & Jahanshahi, 2002). This subspecies had once been widespread across southwest and central Asia and the Caucasus Ecoregion (Breitenmoser et al. 2007), but has lost 72–84% of its range due to human pressures (Jacobsen et al. 2016). Retaliatory killing has been recognized as the crucial factor causing local extirpation of leopards (Kiabi et al. 2002; Breitenmoser et al. 2007). Human-leopard conflicts are frequently reported in Iran (Kiabi et al. 2002; Babrgir et al. 2017; Khorozyan et al. 2017) and wildlife poaching is widespread in the country (Ghoddousi et al. 2019). During the past decades Iran's human population has exponentially increased, which has resulted in a sharp increase in livestock numbers (FAO Stats). Widespread and often freely grazing livestock increases the potential for human-carnivore conflicts with large carnivores. Thus, the situation in Iran provides a unique opportunity to examine the relationships between leopard poaching, leopard depredation on livestock and leopard attacks on humans (Kiabi et al. 2002). Specifically, we applied Bayesian occupancy modelling to assess the role of poaching for leopard mortality risk across Iran. We hypothesized that: (1) higher levels of poaching occur in areas with higher livestock density and (2) higher levels of poaching occur in areas with more attacks on humans.

2 Materials and Methods

2.1 Study area

Iran is one of the most biologically diverse countries in southwest Asia (Firouz, 2005). The country covers 1,648 million km^2, of which 54% is rangeland including steppe, 20% is desert with only 8% is covered by forest (Sagheb-Talebi, Sajedi & Pourhashemi 2014). It has a human population of 80 million (Statistic Center of Iran 2016; www.amar.org). Elevations range from below sea level to 5670 m. The Hyrcanian relic temperate forest stretching along the southern coastline of the Caspian Sea and the Zagros semi-arid oak forest in western Iran are the biodiversity hotspots (Olson & Dinerstein 2002).

About 10.3% of the Iranian land surface is designated as protected areas (PA) managed by the Iranian Department of Environment (DoE). We used PA to refer to all IUCN categories of protected areas in Iran, but specify the category V (which is also called “protected area” in Iran) separately wherever necessary. The main wild prey of Persian leopard includes the wild boar (*Sus scrofa*), bezoar goat (*Capra aegagrus*), urial (*Ovis vignei*), mouflon (*Ovis orientalis*), roe deer (*Capreolus capreolus*) and Caspian red deer (*Cervus elaphus maral*) (Firouz, 2005).

2.2 Study design

To gather information on leopard poaching and leopard attacks on humans across Iran, we relied on national public website articles published from 2007 to 2017, which reported occurrences of leopard poaching in Persian language. To find these cases, we used the following keywords in the Google search engine in Persian: “leopard poaching”, ”leopard mortality”, “leopard road kill”, “leopard rail kill” and “leopard kill” plus province names, and “leopard kill”, “leopard pelt” and “leopard attack”. Furthermore, we also searched for attacks by leopards on humans using the keywords “leopard attack” and “leopard attacks on humans”. We superimposed a grid consisting of 50 x 50 km cells over the entire land surface of Iran in ArcGIS 10.3 (ESRI, Redlands, USA). This grid cell size accounts for detectability and logistics (MacKenzie et al. 2018).

We faced a choice between using smaller grid cells that would increase spatial autocorrelation and reduce the numbers of replicates (mortality cases) per cell, and larger grid cells that would include high proportions of habitats not occupied by leopards. Since our study sample consisted of immobile organisms (cases of leopard mortality), it is unlikely that they would move between cells and produce pseudoreplication (Steenweg et al. 2018). Also, the period of repeated sampling occasions (one year) was long enough to account for the assumption of geographical closure (Steenweg et al. 2018). As a consequence, we chose the larger grid cell size for our analysis.

We excluded the cells containing <40% of land from the analysis (Soofi et al. 2018a). To minimize zero-inflation and to account for the actual leopard distribution, we further restricted our analysis to the cells that partially or fully overlapped with the range map of Persian leopards in Iran (IUCN categories of “extant” and “extant or possibly extant”) (Figure D 1; Stein et al. 2016). We also included cells that were not located in the leopard range but contained cases of intentional leopard killing. For occupancy modelling, we considered surveyed cells (i.e. searched using websites) as sites and defined each year as a survey occasion. Thus, we assigned poaching observations y_{ij} (detection 1, non-detection 0) reported by the websites in a particular grid cell (i) during each survey year (j) between 2007 and 2017 (MacKenzie et al. 2018). We grouped various causes of leopard poaching into four categories, depending on delinquents and incentives (Figure D 2). We defined a specific case of leopard mortality as an incident of poaching if it showed signs of direct economic intentions (e.g. to sell the leopard’s pelt) or traditional beliefs that may also entail economic incentives (e.g. the use of a leopard’s body parts such as skull, claws, tail, paw and teeth). In some cases, however, leopard mortality was reported that involved the use of poison and gin traps after livestock depredation events. These types of mortality records were classified as precautionary or retaliatory killings (Supplementary Information). As these are the non-targeted techniques upon which leopards might be killed. These records were not considered in our analysis. Particularly, we differentiated between intentional and incidental human-caused leopard poaching, natural deaths and unknown mortality causes (see Supplementary Information).

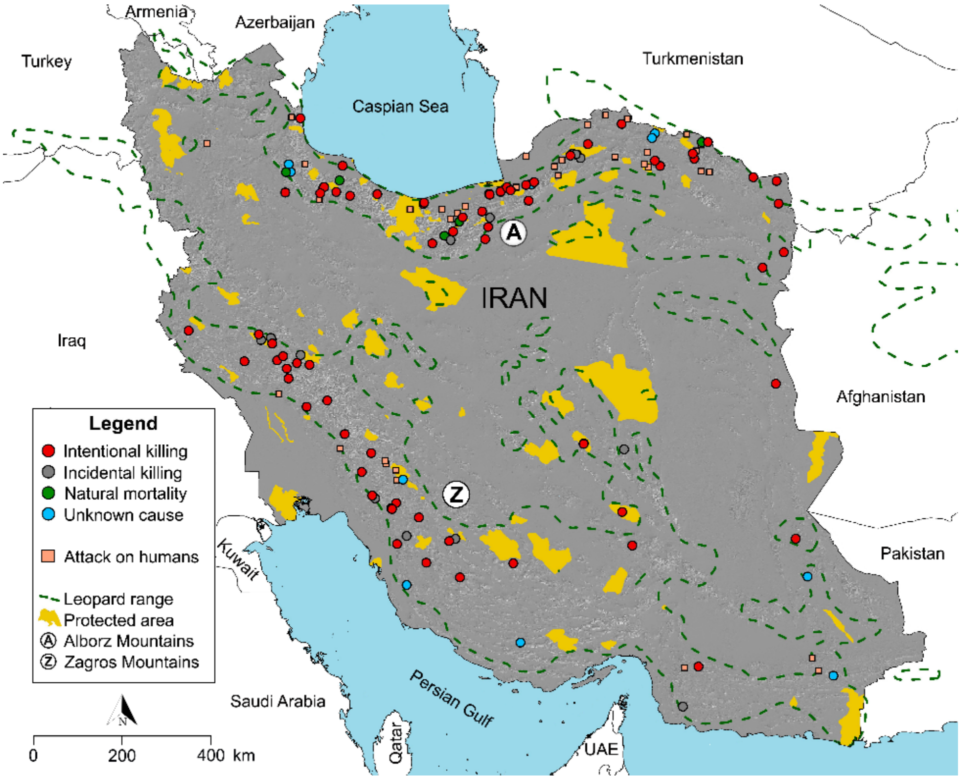

Figure D 1: Distribution of locations of Persian leopard mortality and leopard attacks on humans in Iran from 2007 to 2017.

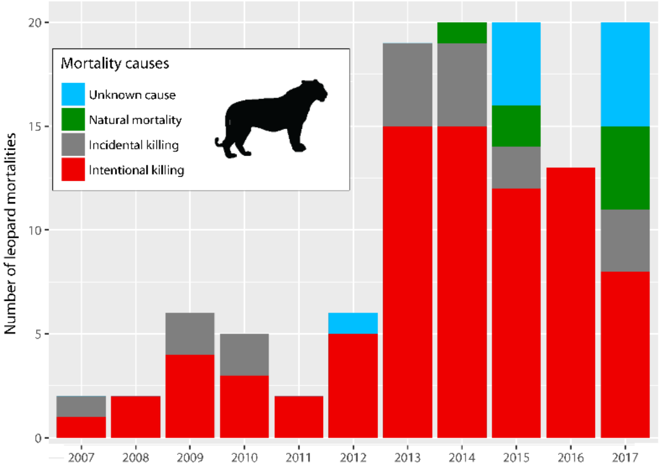

Figure D 2: Distribution of causes of Persian leopard mortality in Iran as reported by national website articles from 2007 to 2017.

2.3 Predictor variables

We derived data on livestock (cattle, sheep and goats) densities from the Food and Agriculture Organization, FAO (http://www.fao.org; 2005). We also discarded mortality cases without location data (n = 7). For each grid cell, we measured the proportion covered by PAs of all IUCN categories (excluding marine PAs), which we derived from the World Database on Protected Areas (WDPA; http://www.protectedplanet.net). To account for the effects of terrain characteristics on occupancy and detection probabilities of leopard poaching, we included the mean elevation and the mean slope from the digital elevation model of 30-m resolution from the data of the NASA Shuttle Radar Topography Mission (SRTM, https://search.earthdata.nasa.gov) (Jędrzejewski et al. 2017). Data on human population density were obtained from the NASA Socio-economic Data and Applications Center (SEDAC; http://sedac.ciesin.columbia.edu) with 1-km resolution. As roads ease site accessibility to poachers, we measured the total road length per grid cell from Open Street Map data (motorways, primary roads, secondary roads, tertiary roads, trunks and corresponding link roads from http://download.geofabrik.de/ and https://extract.bbbike.org/; Table D 1).

Table D 1: GIS-based predictor variables, data sources and associated hypotheses regarding their effects on leopard poaching in Iran.

Covariates	Source	Hypothesis	Reference
Livestock density	www.fao.org, 2005	Leopard attacks on livestock occur mainly in locations with high density of livestock, which also increases leopard mortality risk	Jędrzejewski et al. 2017
Proportion of forest cover	Forest Rangeland Watershed Organization (FRWO, Iran)	As leopards prefer complex habitats for ambush hunting, which may also represent suitable grazing places for livestock, leopard mortalities are likely to be more detected/reported in forest than in other landscapes	Jędrzejewski et al. 2017
Proportion of protected areas	www.protectedplanet.net	Protection reduces mortality of leopards. Also, detectability of leopard mortality is higher inside protected areas due to regular patrols by rangers	Kshettry et al. 2017
Mean human density	SEDAC - http://sedac.ciesin.columbia.edu	Higher human density is associated with higher leopard mortality	
Mean road density	http://download.geofabrik.de/; https://extract.bbbike.org/	Roads increase leopard mortality by increasing site accessibility to poachers	Kshettry et al. 2017
Mean elevation and mean slope	SRTM - https://search.earthdata.nasa.gov	Distribution of leopard mortality is representative for leopard occupancy and distribution in Iran	Kshettry et al. 2017

2.4 Analysis

In many cases, the exact locations of leopard mortalities were unknown but indicated by the names of the villages nearby. In these cases, we spatially assigned poaching cases to the nearest village and assumed that this procedure did not bias the accuracy of cases due to the large cell size used in this analysis. We standardized each site covariate by subtracting its mean and dividing by two times its standard deviation (Gelman 2008) to have unit variance and minimize overdispersion (MacKenzie et al. 2018). We tested for differences in the numbers of newspaper articles per case of leopard poaching and attacks on humans over years using the Kruskal-Wallis test. Hence, we accounted for the unequal reporting intensity (i.e. effort) as an offset in our occupancy models by incorporating the median number of articles per case as an annual observation covariate (Kery 2010). We checked for multicollinearity of the covariates and excluded variables if their Spearman's rank correlation $|r_s| \geq 0.7$ (Hosmer & Lemeshow 2000). Because of perfect correlation ($r_s = 1.00$) among sheep/goat and cattle densities, we kept only cattle as a representative of livestock. For preliminary modelling, we conducted a single-season occupancy analysis (MacKenzie et al. 2018) with the frequentist approach incorporating all predictors. For the final model, we then continued the modelling only with statistically significant predictors in a Bayesian framework (Kery 2010). We considered only mortality cases due to poaching as the response variable because it represented the greatest portion of leopard mortality.

For leopard mortality, we quantified the effects of predictors on the occupancy of leopard mortality ψ while simultaneously accounting for imperfect detection and sampling efforts using the logit link. Specifically, ψ of each leopard mortality in cell *i* was described as:

$$\text{logit}\,(\psi_i) = \alpha_\psi + \beta_{\psi,livestock}\, x_{livestock,i} + \beta_{\psi,attack\ on\ humans}\, x_{attack\ on\ humans,i} + \beta_{\psi,forest\ cover}\, x_{forest\ cover,i}$$

where x_i is the vector of occurrence-related covariates measured at the *i*-th site and α and β are the coefficients to be estimated. We modeled the true occurrence state z of leopard mortality in the cell i as a random variable drawn from the Bernoulli distribution with probability ψ:

$$z_i \sim Bernoulli\,(\psi_i)$$

Single-season occupancy models treat the observed detection (or non-detection) y as an outcome of a detection process, i.e. a random Bernoulli variable is defined by z and the mortality case detection probability p:

$$y_i \sim Bernoulli\,(z_i \times p_i)$$

Quantification of detection probability p allows including possible impacts of a bias arising from variability in the sampling effort. In our study, the effort is a count of websites that reported the mortality cases in each cell i per year. We used effort as an 'offset', a covariate for which no coefficient is estimated, along with the other covariates in the description of detection probability p:

$$\mathrm{logit}(p) = \alpha_p + \beta_{p,livestock}\, x_{livestock,i} + \beta_{p,attack\ on\ humans}\, x_{attack\ on\ humans,i} + \beta_{p,forest\ cover}\, x_{forest\ cover,i} + effort_{ij}$$

The model was fitted in JAGS (Plummer 2003) and R (R Core Team 2018) using R2Jags (Su & Yajima 2012). We ran three Markov chains with 200,000 iterations each. The first 150,000 steps of the burn-in were discarded. The rest was thinned to every 100th value to avoid autocorrelation among samples. The effective sample size of the posterior distribution for the coefficients was 1,500. We selected non-informative priors: a normal distribution ($\mu = 0$, $\sigma = 0.01$) for α and a uniform distribution with the boundaries from −10 to 10 for β (Kery 2010; Soofi et al. 2018a). After fitting the model, we first ensured mixing of the three chains by inspecting the Markov Chains visually and by ensuring that the Brooks-Gelman-Rubin statistic *Rhat* is less than 1.1 for convergence (Gelman & Hill 2007). Secondly, we evaluated the goodness-of-fit of the models by using posterior predictive checks and the Bayesian p-value for the χ^2 test statistic computed from the total number of occasions per cell. The values of ill-fitting models are defined by the statistic $\hat{c}$ to vary from 0 to 1 (Kery, 2010; Kery & Royle 2016). We considered the effect size as significant if the 95% credible interval (CI) of the posterior distribution did not overlap 0 (Kery & Royle 2016).

3 Results

We obtained 115 cases of leopard mortality, which were confirmed by DoE experts and thus regarded as definite records. Mortality events were caused by poaching (n = 61), poisoning (n = 12), kills by dogs/lancer (n = 7), road kills (n = 15), rail kills (n = 1), snares (n = 2), conspecifics (n = 4), starvation (n = 3), and unknown reasons (n = 10). Leopard poaching was significantly and positively influenced by occurrence of attacks on humans with a probability of ≥0.5 (i.e. 0.98), but this did not apply for detection probability (Table D 2). Leopard poaching occurrence significantly and positively increased with livestock density with a probability of 0.69, but this remained uncertain in respect to detection probability (Table D 2). Forest cover had a significant and positive effect on detection probability of leopard poaching with a probability of 0.99, but it was insignificant in terms of poaching occurrence (Table D 2; Figure D 3). The goodness-of-fit assessment of our model yielded a Bayesian p-value of 0.31 and the ratio of the test statistic for the observed and the expected dataset was $\hat{c} = 1.15$, which indicates that our model performed well (MacKenzie et al. 2018). For leopard poaching, we found more articles per case in recent years, but this difference in numbers of articles was not significant ($\chi^2 = 17.29$, df = 10, p = 0.068). For leopard attacks on humans, however, the difference was significant ($\chi^2 = 18.04$, df = 7, p = 0.012). Since 2013, all types of leopard mortality have notably increased, especially for intentional and natural mortalities (Figure D 2). Human density was significantly correlated with livestock density ($r_s = 0.72$, $p < 0.001$).

Over 62% (n = 42) of leopard poaching cases were caused by traditional beliefs (as indicated by e.g. the uses of leopards' body parts) and livestock depredation that may be considered as cases of indirect commercial incentives. By comparison, direct commercial motivation was identified as the cause of leopard mortality in 31% of cases (n = 19). Additionally, leopard mortality cases were distributed almost equally between females (n = 26) and males (n = 24), but most cases (n = 65) were of unknown sex. Of 80 leopard poaching cases, 56 were adults. By contrast, juveniles (n = 11) and cubs (n = 6) were less frequently killed, and in seven cases age was unknown. About 93% of leopard poaching cases occurred outside PAs and only 6.8% occurred inside PAs throughout the country (or 6.2% when referring to the IUCN leopard range in Iran; Figure D 1). In contrast, the road/rail kills occurred mostly inside PAs (43.8% in all the country and 46.7% in the leopard range in Iran). With regard to attacks on humans, we recorded 38 injuries and three fatalities. Only 7.3% and 8.1% of attacks on humans occurred inside PAs in relation to the country and the leopard range, respectively.

4 Discussion

Despite the elusive nature of poaching that makes it extremely difficult to detect (Milner-Gulland et al. 2003), we recorded a large number of leopard poaching events throughout Iran. Our results suggest that retaliatory or precautionary killings in response to leopard predation of livestock were the most common cause of leopard mortality. However, a caveat to our data is that direct poaching related mortalities might be under-reported as this type of kills may often go undetected (Soofi et al. 2018b).

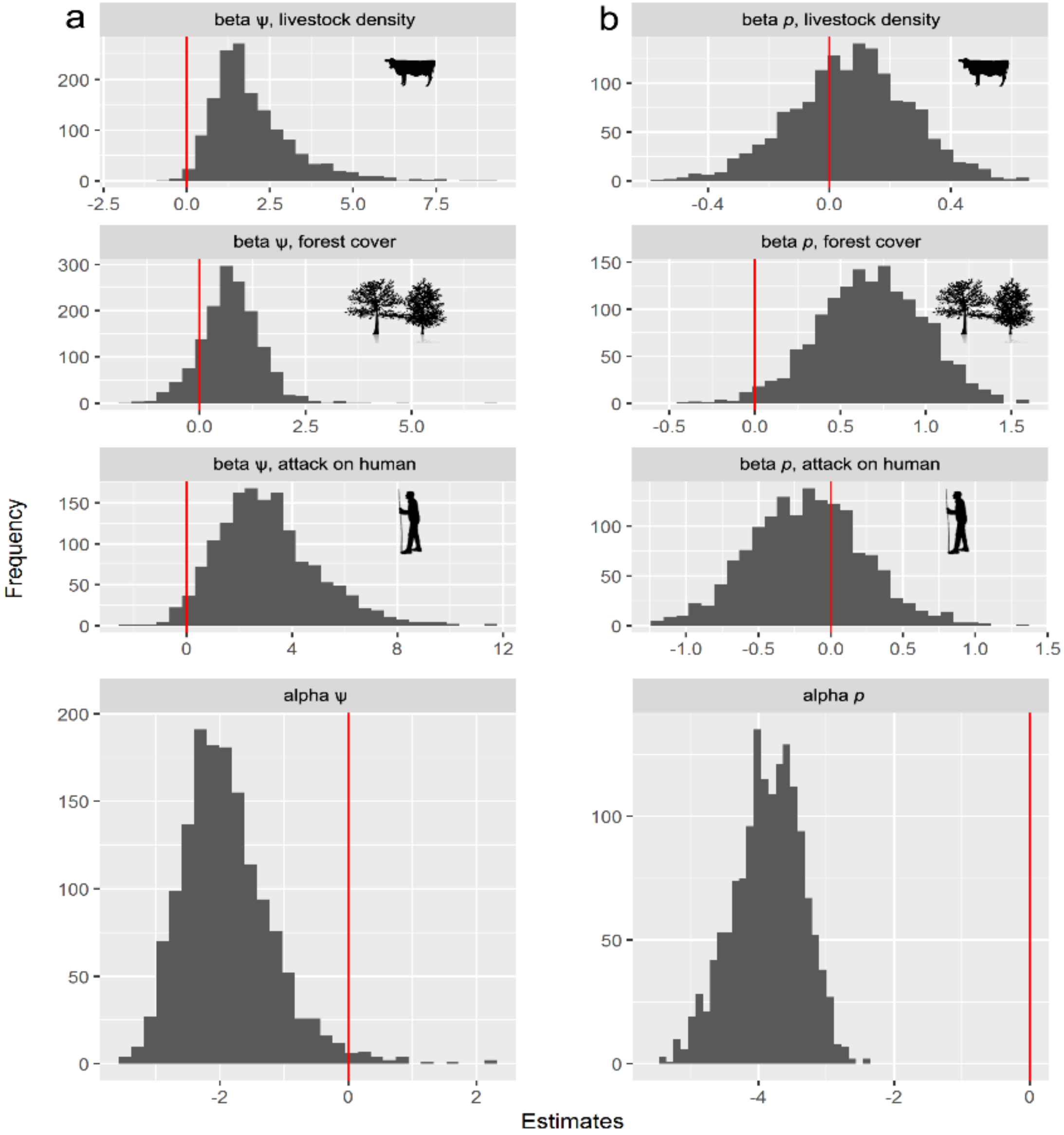

Figure D 3: The beta and alpha estimates of occupancy ψ (a) and detection probability *p* (b) with their 95% credibility intervals to assess the Persian leopard poaching risks in Iran. Alpha (α) is the intercept and beta (β) is the slope of the Bayesian single-season occupancy models. The mean credibility intervals intersecting the red line of zero are insignificant.

Over two-thirds of poaching cases were caused by traditional beliefs but were associated with livestock depredation events. Ultimately, such conditions may also carry commercial incentives and thus provoke leopard poaching. However, clear direct commercial intentions (e.g. selling pelt) were less commonly found. Although, the distinction between leopard mortalities driven by commercial interests and depredation can be gloomy because there could be a bias against reports of commercial poaching.

Table D 2: Summary of the posterior distribution of the single-season occupancy model of Persian leopard poaching. Abbreviations: CI – credible interval, SD – standard deviation. Probability signifies the proportion of the posterior outcome on the same side of zero as the mean. The effect sizes (CI 95%) are provided in logit scale.

Parameter	Posterior mean	SD	Range of CI 95%		Probability
			min	max	
alpha p	-3.81	0.51	-4.91	-2.92	1.00
alpha ψ	-1.79	0.72	-2.94	-0.11	0.98
beta $p_{livestock}$	0.09	0.20	-0.30	0.47	0.69
beta p_{forest}	0.72	0.31	0.08	1.30	0.99
beta p_{attack}	-0.12	0.39	-0.89	0.68	0.62
alpha $\psi_{livestock}$	2.16	1.26	0.49	5.38	1.00
alpha ψ_{forest}	0.88	0.72	-0.54	2.20	0.90
alpha ψ_{attack}	3.31	1.91	0.15	7.58	0.98

We underline that retaliatory killings of leopards over livestock depredation is most widespread and numerous and eventually the main threat to leopards (Kiabi et al. 2002), especially outside protected areas. Despite existing legal protection and a compensation payment system introduced in 2016, mortality of leopards has tripled during the past few years (Figure D 2). Only about 7% of leopard kills were inside protected areas. The proportion of leopards killed inside protected areas is similar to the proportion of the leopard's range in Iran (9%) that is protected. It may seem surprising that almost half of road/rail kills occurred inside protected areas, but this might result from a small sample size of cases from these areas. Alternatively, other authors also mention that road/rail kills still make a significant contribution to leopard mortality in some high-density protected areas (Kiabi et al. 2002; Naderi et al. 2018). Leopard poaching did not depend on particular times of the year and widely occurred in areas where leopards exist.

We found that leopard poaching significantly increased with the density of livestock in an area. Currently, the total livestock number in Iran is over 124 million animals. These animals either graze freely or are accompanied by pastoralists (Amiraslani & Dragovich, 2011). The Iranian law prohibits grazing only in national parks and the core areas of protected areas of other IUCN categories (Makhdoum 2008), but grazing is commonplace outside protected areas and occurs illegally even in national parks.

Presumably, high rates of leopard poaching outside protected areas are triggered by leopard predation on livestock resulting from a combination of high availability of livestock and the low abundance of wild prey (Soofi et al. 2018b). Retaliatory killings in response to livestock predation can occur because of low levels of law enforcement and a lack of awareness of people about both the importance of the species and the fact that killing leopards is illegal.

Our findings revealed that leopard poaching significantly increased with more frequent attacks on humans, especially herders. Herders are the most vulnerable group and leopard attacks on livestock or on herders that guard them may equally result in retaliatory killings. Generally, when herders are confronted with livestock losses or when they are wounded by carnivores, their decisions on why and how to kill a carnivore can depend on a complex array of drivers (Duffy et al. 2015), such as individual behaviours and economic motivations and beliefs (Carter et al. 2017). Based on website articles we analysed in this study, all victims of leopard attacks were herdsmen who were severely wounded (killed in three cases) or psychologically affected. In most cases, leopards did not originally target herders but attacked them when herders attempted to deter leopards by throwing stones and chasing them with dogs. Based on article contents, a common practice of using a group of guard dogs for chasing leopards seems to increase the rates of leopard killing (Khorozyan et al. 2018).

We found that leopard poaching is much more likely to be detected in forest than in other habitats. This higher detectability in forest may reflect the habitat choice of leopards; forested and scrubland habitats at higher altitudes in the Alborz and Zagros Ranges are the most suitable habitats for leopards.

We found no evidence of leopard mortality in the areas lying between the two source populations for the species in the Alborz and the Zagros mountain ranges. This may indicate that the connectivity between leopard populations in these two regions have been disrupted (Breitenmoser et al. 2017), potentially threatening the long-term viability of leopard subpopulations in adjacent transboundary areas via sink effects. This information is highly relevant for leopard survival in the Lesser Caucasus and Kurdistan regions, which poaching that occurs there, mitigation of human-leopard conflicts should be an urgent may strongly rely on source populations in the Alborz and Zagros Ranges, respectively (Breitenmoser et al. 2017). Because of the importance of these source populations and the high rate of leopard poaching that occurs there, mitigation of human-leopard conflicts should be an urgent conservation priority (Breitenmoser et al. 2017).

We do not have evidence for international leopard trade operating in Iran, but apparently, there are some undercover local markets, which may motivate poachers to kill leopards for financial profits. Our records contained some cases of leopard skins confiscated by Iranian

Department of Environment in Tehran but those originated from the Alborz Range (Figure D 1). This may indicate a need for further studies on the main commercial motivations to kill leopards. However, the distinction between leopard mortalities driven by commercial interests and depredation can be obscure as poachers can kill leopards due to livestock losses, but then take advantage of this opportunity to sell the skin or utilize body parts for traditional beliefs. Understanding the principal incentives for poaching is critical, as each incentive requires specific corrective actions (Milner-Gulland et al. 2003; Duffy et al. 2016). Due to incomplete data on leopard demographic structure, it was not possible for us to assess the impacts of poaching on different age classes. However, both sexes appeared to be equally vulnerable to poaching, a finding that indicates a potential serious threat to leopard survival in Iran as the survival of adult females is an important determinant of population stability in big cats (Chapron et al. 2008).

The usefulness of our poaching risk maps was constrained by the lack of a time-series dataset of livestock density, which could match annual changes in poaching cases (MacKenzie et al. 2018). However, spatially explicit annual databases of livestock numbers and densities are not available in Iran. Moreover, another bias may be due to an increasing number of websites covering wildlife news; hence, there may be uncertainties in online reporting of leopard poaching, which may affect the patterns we describe here.

To our knowledge, this study is the first that applies occupancy modelling to describe the spatial patterns of leopard poaching, attacks on herders and livestock density at a large spatial scale in southwest Asia. Our study's approach can also be applied to examine the effects of poaching risks on other large carnivore species. We conclude that high levels of leopard poaching can be a result of unregulated and increased density of livestock grazing, and frequent attacks on humans, both of which may lead to retaliatory poaching. Obviously, existing anti-poaching efforts seem to be insufficient to alleviate leopard poaching pressures. We further highlight that conservation actions should critically consider management options of livestock grazing as a conservation priority and train local shepherds on how to react and behave upon carnivore encounters. We recommend to conservation authorities in Iran that the current compensation payment system should be accompanied by scientifically based leopard monitoring efforts, at least in areas with high human-leopard conflicts. All these efforts should consider local participation and be tackled within the professional credentials of two national organizations responsible for natural resource management and conservation in Iran: Department of Environment and Forest Rangeland Watershed Organization.

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Supplementary Information

For leopard mortalities, we considered each individual killed as one ‘event’, even if mother and cub(s) were killed during one incident. However, for attacks on humans, we regarded each attack per se as one ‘event’ independent of how many persons were injured. We grouped the various causes of leopard mortality into four broader categories dependent on perpetrator and incentives. Thereby, we differentiated between intentional and unintentional human-caused leopard mortality as well as between ‘natural’ deaths and unknown mortality causes. For the analysis of leopard mortalities inside and outside protected landscapes, we neglected marine/wetland protected areas. For the occupancy analysis, we only considered intentional human-caused leopard mortalities that involved direct commercial intentions (e.g. selling pelt) as well as cases of kills that were linked with traditional beliefs e.g. use of leopard body parts (e.g. tail, claw, paw, skull). These types of kills also potentially involve commercial incentives but they differ in that they were facilitated by livestock depredation events. We still define these events as poaching. Therefore, our definition of poaching refers to leopard mortality cases which involve direct or indirect economic benefits. The exact location of leopard mortality events were unknown in many cases; however, usually the location of nearby villages was provided. In these cases, we located mortality events to the nearest village and considered this procedure not to bias our results due to the large cell size used in this analysis.

Table SI D 1: Online reports of mortality causes of Persian leopard (2007–2017) in Iran. Abbreviations: LD – livestock depredation; TB – Traditional beliefs; DCI – direct commercial Intentions; CI – commercial incentives.

No	**Mortality cause**	**Sex**	**Age**	**Date of death**
1	Road collision	Male	Adult	May 2007
2	Shot (LD, CI, TB, pelt)	Unknown	Adult	August 2007
3	Shot (LD, CI, pelt, TB)	Unknown	Adult	August 2008
4	Shot (DCI, pelt)	Unknown	Juvenile	October 2008
5	Road collision	Unknown	Adult	April 2009
6	Shot (LD, pelt, CI, S)	Unknown	Adult	April 2009
7	Shot (LD, TB, CI, pelt)	Unknown	Adult	May 2009
8	Shot (LD, CI, TB, pelt)	Unknown	Unknown	July 2009
9	Road collision	Unknown	Juvenile	November 2009
10	Shot (LD, CI, TB)	Unknown	Adult	December 2009
11	Shot (LD, CI, TB)	Unknown	Adult	March 2010
12	Rail collision	Unknown	Adult	April 2010
13	Shot (LD, CI, TB, pelt)	Male	Adult	November 2010

14	Road collision	Male	Adult	2010
15	Shot (LD, CI, TB)	Male	Juvenile	2010
16	Shot (LD, TB, CI, pelt)	Unknown	Unknown	August 2011
17	Poisoned (LD)	Unknown	Adult	September 2011
18	Killed by dogs and darts (LD)	Male	Adult	April 2012
19	Shot (LD, CI, TB)	Unknown	Adult	October 2012
20	Shot (LD, CI, TB)	Unknown	Juvenile	October 2012
21	Shot (LD, CI, Taxidermy)	Unknown	Juvenile	November 2012
22	Poisoned (LD)	Unknown	Adult	November 2012
23	Unknown	Male	Adult	November 2012
24	Shot (LD, CI, Taxidermy)	Unknown	Adult	January 2013
25	Shot (LD, TB, CI, pelt)	Male	Adult	June 2013
26	Road collision	Female	Adult	June 2013
27	Shot (DCI, pelt)	Unknown	Adult	June 2013
28	Shot (DCI, pelt)	Unknown	Juvenile	July 2013
29	Poisoned (LD)	Unknown	Adult	July 2013
30	Shot (LD, CI, TB)	Unknown	Adult	August 2013
31	Shot (LD, TB, CI, Taxidermy)	Unknown	Juvenile	September 2013
32	Shot (LD, CI, pelt)	Unknown	Unknown	October 2013
33	Killed by dogs and lancer (LD)	Unknown	Juvenile	October 2013
34	Shot (LD, TB, CI, pelt)	Unknown	Unknown	October 2013
35	Shot (LD, CI, Taxidermy)	Unknown	Adult	October 2013
36	Poisoned (LD)	Unknown	Juvenile	November 2013
37	Road collision	Female	Juvenile	December 2013
38	Road collision	Female	Adult	December 2013
39	Poisoned (LD)	Unknown	Unknown	December 2013
40	Killed by dogs and lancer (LD)	Female	Adult	December 2013
41	Road collision	Unknown	Cub	December 2013
42	Shot (LD, CI, TB)	Unknown	Adult	December 2013
43	Shot (LD, TB, CI, pelt)	Male	Adult	January 2014
44	Shot (LD, CI, TB)	Unknown	Adult	January 2014
45	Shot (LD, TB, CI, Taxidermy)	Unknown	Adult	February 2014
46	Shot (LD, CI, TB, Nails, Tail)	Unknown	Adult	February 2014
47	Shot (DCI, pelt)	Unknown	Cub	March 2014
48	Road collision	Unknown	Adult	March 2014
49	Shot (LD, TB, CI)	Unknown	Adult	April 2014
50	Road collision	Unknown	Cub	April 2014
51	Shot (DCI, pelt)	Male	Adult	April 2014
52	Road collision	Female	Adult	May 2014
53	Killed by conspecific	Unknown	Juvenile	May 2014

54	Poisoned (LD)	Unknown	Adult	June 2014
55	Shot (DCI, pelt)	Unknown	Adult	July 2014
56	Shot (DCI, pelt)	Unknown	Adult	July 2014
57	Shot (DCI, pelt)	Female	Adult	July 2014
58	Shot (LD, CI, pelt)	Unknown	Adult	November 2014
59	Shot (LD, CI, TB, pelt)	Unknown	Juvenile	December 2014
60	Killed by dogs and lancer (LD)	Female	Juvenile	December 2014
61	Shot(DCI, pelt)	Unknown	Adult	December 2014
62	Road collision	Female	Adult	December 2014
63	Killed by conspecific	Female	Adult	February 2015
64	Shot (DCI, pelt)	Unknown	Adult	February 2015
65	Road collision	Female	Adult	March 2015
66	Poisoned (LD)	Unknown	Adult	March 2015
67	Killed by shepherd (LD, run over with a vehicle)	Male	Adult	March 2015
68	Shot (LD, CI, TB)	Unknown	Adult	March 2015
69	Road collision	Male	Adult	March 2015
70	Shot (LD, CI, TB)	Unknown	Unknown	April 2015
71	Poisoned (LD)	Male	Juvenile	April 2015
72	Poisoned (LD)	Unknown	Cub	May 2015
73	Unknown	Male	Adult	May 2015
74	Killed by dogs & lancer (LD)	Unknown	Cub	May 2015
75	Unknown	Unknown	Cub	June 2015
76	Killed by conspecific	Unknown	Adult	June 2015
77	Unknown	Unknown	Unknown	July 2015
78	Shot (LD, TB, CI, Taxidermy)	Unknown	Unknown	August 2015
79	Shot (DCI, pelt)	Unknown	Adult	September 2015
80	Unknown	Unknown	Unknown	September 2015
81	Shot (DCI, pelt)	Unknown	Unknown	November 2015
82	Killed by dogs & lancer (LD)	Male	Juvenile	December 2015
83	Shot (DCI, pelt)	Unknown	Adult	January 2016
84	Shot (LD, CI, TB)	Unknown	Unknown	February 2016
85	Poisoned (LD, LD)	Female	Adult	March 2016
86	Shot (LD, CI, TB)	Unknown	Adult	March 2016
87	Shot (LD, CI, TB, pelt)	Unknown	Cub	July 2016
88	Poisoned (LD)	Unknown	Adult	July 2016
89	Shot (DCI, pelt)	Unknown	Adult	August 2016
90	Shot (DCI, pelt)	Unknown	Adult	September 2016
91	Shot (DCI, pelt)	Unknown	Adult	September 2016
92	Shot (LD, pelt)	Unknown	Adult	September 2016
93	Shot (LD, CI, pelt)	Male	Adult	October 2016

94	Shot (LD, CI, pelt)	Unknown	Unknown	November 2016
95	Shot (LD, CI, TB, pelt)	Female	Adult	December 2016
96	Road collision	Male	Juvenile	January 2017
97	Killed by conspecific	Unknown	Juvenile	January 2017
98	Shot (LD, CI, pelt)	Male	Juvenile	January 2017
99	Shot (LD, CI, TB)	Unknown	Cub	January 2017
100	Shot (LD, CI, TB)	Unknown	Adult	January 2017
101	Trapped in wild boar snare	Unknown	Adult	February 2017
102	Unknown	Unknown	Adult	March 2017
103	Shot (DCI, pelt)	Unknown	Adult	April 2017
104	Starvation	Male	Cub	April 2017
105	Unknown	Unknown	Unknown	April 2017
106	Unknown	Unknown		May 2017
107	Unknown	Unknown	Adult	May 2017
108	Trapped in wild boar snare	Unknown	Adult	May 2017
109	Starvation	Female	Cub	June 2017
110	Starvation	Unknown	Juvenile	June 2017
111	Unknown	Unknown	Juvenile	July 2017
112	Shot (DCI, pelt)	Female	Adult	August 2017
113	Shot (DCI, pelt)	Unknown	Cub	August 2017
114	Poisoned (LD)	Unknown	Adult	October 2017
115	Shot (LD, CI, TB)	Female	Adult	November 2017

Table SI D 2: Online reports of leopard attacks on human (2007–2017) in Iran.

No	Characteristics of humans attacked				Date
	Number	Sex	Age	Consequence	
1	1	Male	Unknown	Killed	July 2008
2	1	Male	Unknown	Killed	2008
3	2	Male	Unknown	Injured	May 2009
4	6	Male	Unknown	Injured	July 2009
5	1	Male	28	Injured	February 2012
6	1	Male	28	Injured	February 2012
7	2	Male	Unknown	Injured	May 2012
8	2	Male	Unknown	Injured	September 2012
9	1	Male	62	Killed	November 2012
10	1	Male	Unknown	Injured	June 2013
11	2	Male	25 and 40	Injured	October 2013
12	1	Male	22	Injured	April 2014
13	1	Male	Unknown	Injured	December 2014

14	1	Male	22	Injured	December 2014
15	1	Male	Unknown	Injured	January 2015
16	1	Male	38	Injured	March 2015
17	1	Male	Unknown	Injured	March 2015
18	1	Male	15	Injured	April 2015
19	1	Male	Unknown	Injured	May 2015
20	1	Male	Adolescent	Injured	July 2015
21	1	Male	50	Injured	August 2015
22	1	Male	30	Injured	September 2015
23	1	Male	Unknown	Injured	January 2016
24	1	Male	63	Injured	January 2016
25	1	Male	45	Injured	February 2016
26	1	Male	55	Injured	February 2016
27	3	Male	Unknown	Injured	March 2016
28	1	Male	Adolescent	Injured	June 2016
29	3	Male	Unknown	Injured	October 2016
30	1	Male	23	Injured	October 2016
31	1	Male	Unknown	Injured	December 2016
32	1	Male	41	Injured	January 2017
33	1	Male	Unknown	Injured	January 2017
34	1	Male	Unknown	Injured	March 2017
35	1	Male	Adolescent	Injured	April 2017
36	1	Male	Unknown	Injured	April 2017
37	1	Male	60	Injured	June 2017
38	1	Male	51	Injured	July 2017
39	1	Male	Unknown	Injured	July 2017
40	1	Male	48	Injured	August 2017
41	1	Male	26	Injured	September 2017

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Eidesstattliche Erklärung

Hiermit erkläre ich, die vorliegende Dissertation selbstständig und ohne Verwendung unerlaubter Hilfe angefertigt zu haben. Die aus fremden Quellen direkt oder indirekt übernommenen Inhalte sind als solche kenntlich gemacht. Die Dissertation wird erstmalig und nur an der Humboldt-Universität zu Berlin eingereicht. Weiterhin erkläre ich, nicht bereits einen Doktortitel im Fach Geographie zu besitzen. Die dem Verfahren zu Grunde liegende Promotionsordnung ist mir bekannt.

Benjamin Bleyhl

Berlin, den 01.07.2019