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Mapping seasonal 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

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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., 2012; 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, the 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 have 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 (580000 km^2), plus a buffer of 25 km to avoid edge effects in the predictors (Fig. 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., 2012; 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 × American bison (*Bison bison*) hybrids), Teberdinsky biosphere nature reserve (Teberdinsky, 22 animals), and the North-Ossetian national nature reserve (North Ossetia, 66 animals).

2.2. European bison presence data

We delineated the summer and winter ranges of the three existing populations, and a fourth that was extirpated by poachers near the city of Nalchik in the 1990s, based on information taken from the literature and our personal experience (co-authors T. Sipko, S. Trepet), and outlined them on topographic maps (1:25000) and high-resolution Google Earth images. The ranges represented 1160 km^2 of summer and 180 km^2 of winter habitat (Fig. 1). From these ranges, we randomly selected 50 location points per herd for summer and 30 location points per herd for winter grounds, while keeping a minimum distance of 500 m to avoid spatial autocorrelation. We further excluded locations on roads. In total, we used 195 locations for summer and 46 locations for winter habitat (not all ranges were large enough to contain 50 summer or 30 winter locations).

2.3. 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 (Appendix A), out of which we included six environmental and two human-disturbance predictors in our final models (Table 1).

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 Appendix A). 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,

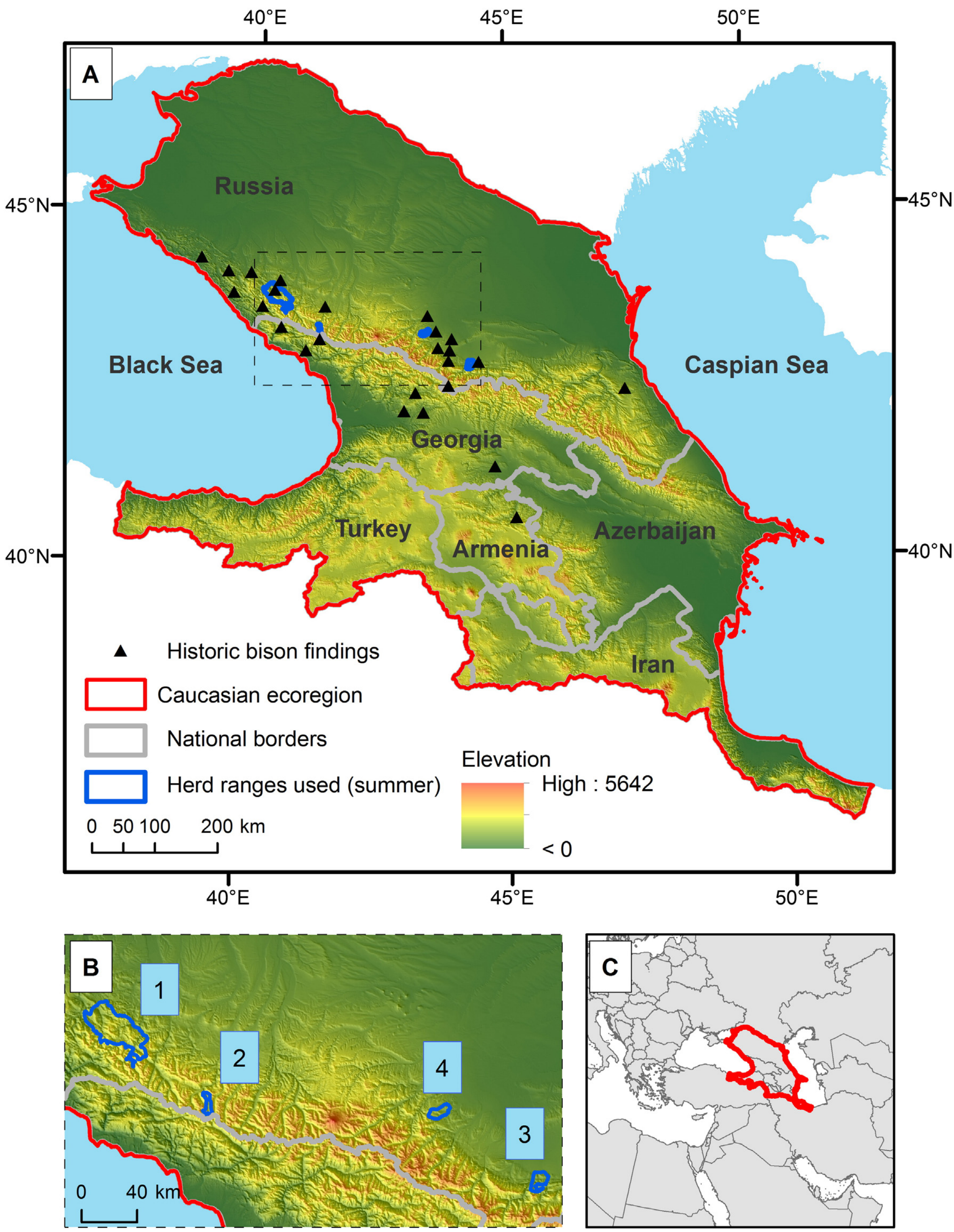

Fig. 1. (A) Overview of the Caucasus ecoregion, herd ranges and historic findings of European bison (Heptner et al., 1961; Kuemmerle et al., 2012; Nemtsev et al., 2003), mountain ranges of the Greater Caucasus (in the north) and the lesser Caucasus (in Georgia, Turkey, Armenia, and Azerbaijan in the 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). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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.

Table 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 Appendix A.

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

org/). Slope was limited to 28° maximum for the summer models, because initial results predicted increasing suitability on steeper slopes although very few occurrence points were found on slopes > 30° (see Appendix A).

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 Appendix A 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.

2.4. Mapping potential habitat

To map potential habitat, we used maximum entropy modeling (Maxent, version 3.3.3 k, 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., 2012; 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 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 km^2 (small candidate sites) plus adjacent core winter habitat of more than 6 km^2 and 5 km^2, respectively. An estimated area of 200 km^2 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 km^2. Thresholds for small candidate sites are based on the current seasonal range sizes of the smallest Caucasian herd (Teberdinsky, 22 animals, summer: 60 km^2, winter: 5 km^2). 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.

3. 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 (Fig. 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.

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 2 and Fig. 3). Potential refuges were scarce and mostly scattered (Fig. 2). Core areas and potential refuges accounted for a larger share in winter than in summer (Table 2). Among the six countries, the relative shares of the habitat categories differed greatly, but the differences between seasons remained fairly constant (Fig. 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).

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 (Appendix B). 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 km^2 in total). All summer core areas > 200 km^2 included sufficient adjacent winter habitat (core winter habitat > 6 km^2). In total, we found eleven such large candidate sites that together covered an area of 3575 km^2 (0.6% of the ecoregion). All large candidate sites were located in Russia (1930 km^2) and Georgia (1645 km^2) in the western part of the ecoregion (Fig. 5). Small candidate sites covered an additional area of 6660 km^2 (1.1% of the ecoregion) and were more widespread. Two summer core areas greater than 60 km^2 did not entail adequate winter habitat resulting in 58 small candidate sites. The largest share was located in Russia (3120 km^2) and Georgia (3050 km^2). A smaller fraction was located in Turkey (400 km^2)

Table 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 [km^2] (% 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%)

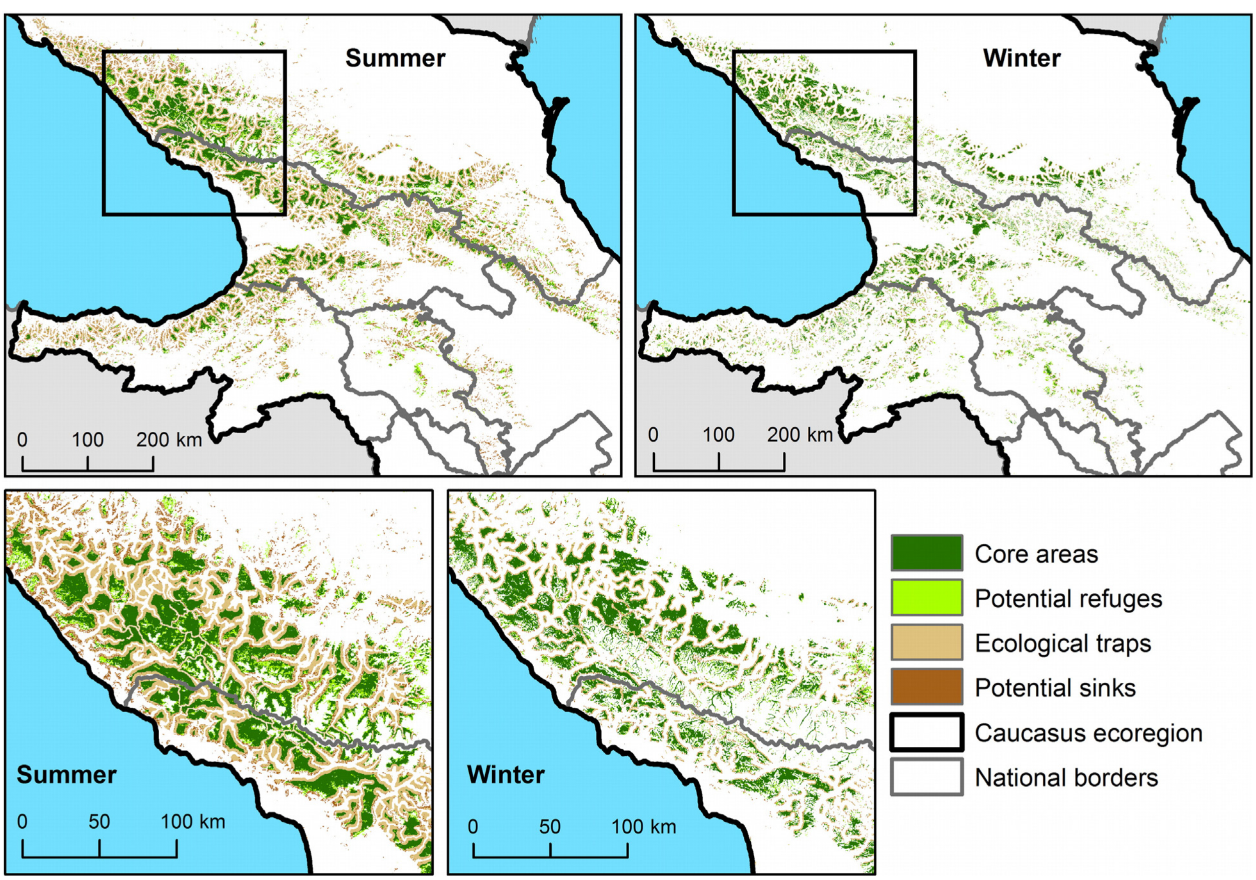

Fig. 2. Habitat refinement maps for summer and winter (top) with a detailed view of the western Greater Caucasus (bottom). White areas indicate the matrix between habitat patches.

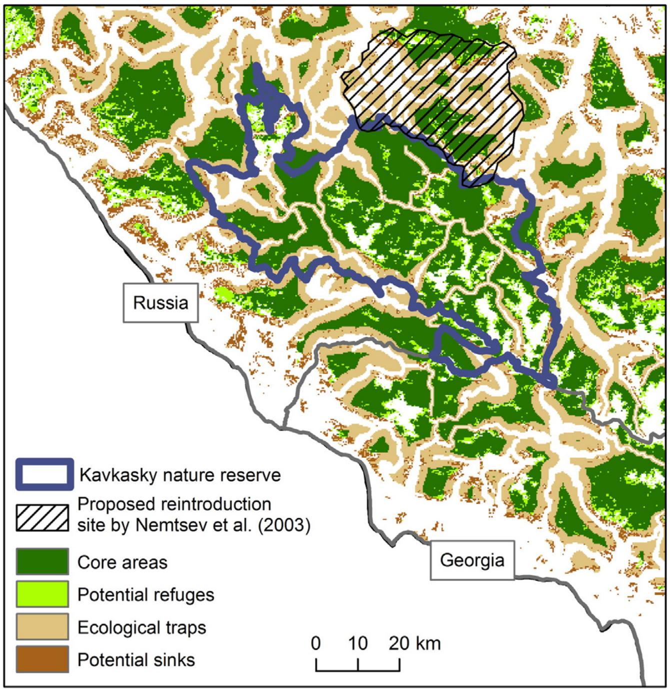

Fig. 3. Summer habitat categories around Caucasus biosphere nature reserve in the western Greater Caucasus.

whereas only one area was found in Azerbaijan (90 km^2). 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 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 (Fig. 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).

4. 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 (Fig. 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 (Fig. 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 (Fig. 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 (Fig. 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, 2011) as well as of studies of historical habitat use of European bison (Bocherens et al., 2015; Kuemmerle et al., 2012). 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

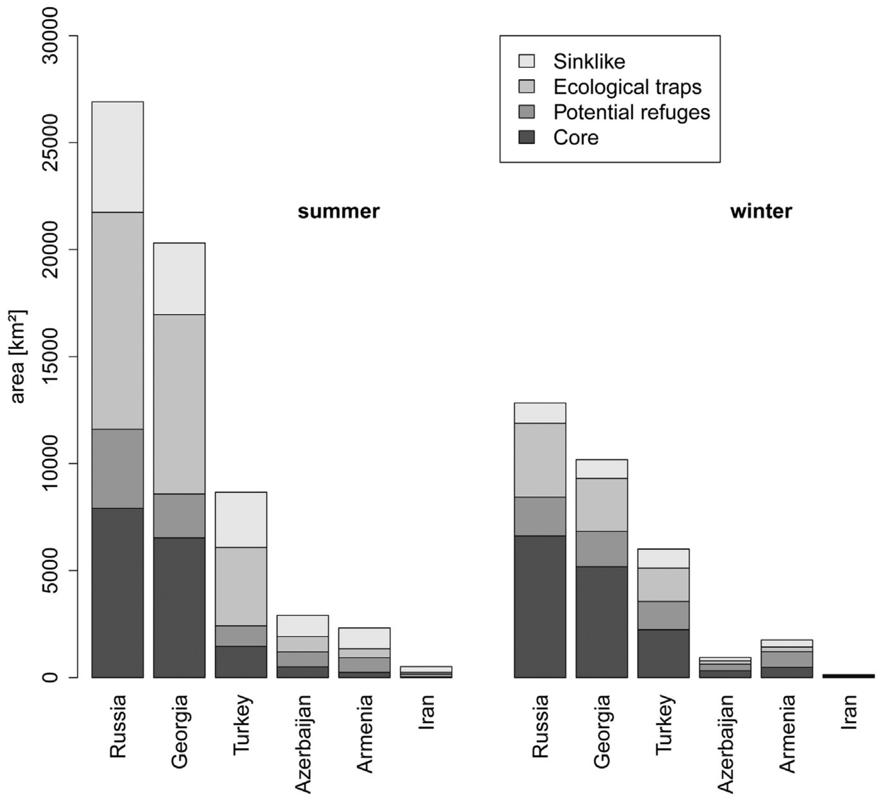

Fig. 4. Distribution of the four habitat categories inside the countries containing parts of the Caucasus ecoregion.

these candidate sites (61%) were not protected, and in Georgia only 15% of the area was protected. With a total area of 10 200 km^2, and assuming a potential bison density of 0.9–1.0 animals/km^2 (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 Appendix C 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 × 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 (Fig. 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 transboundary 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).

5. 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

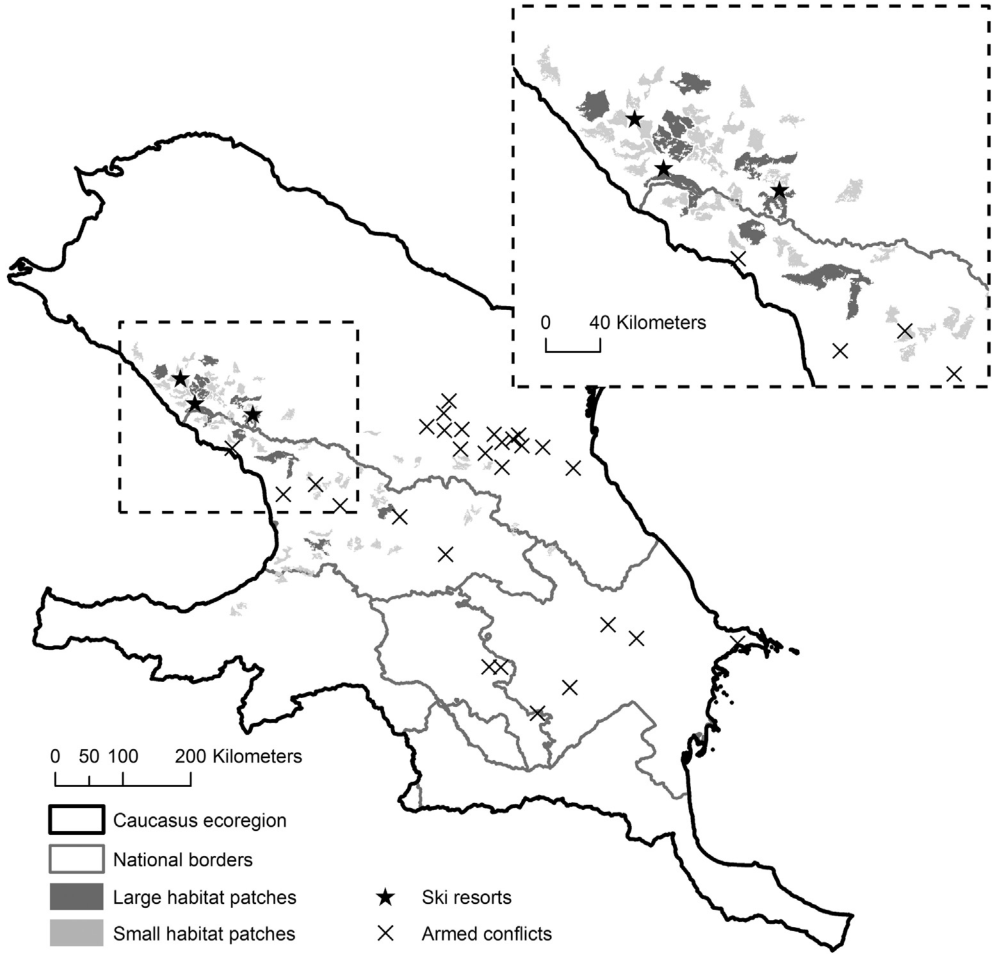

Fig. 5. Candidate sites for potential reintroductions with new or planned ski resorts (Northern Caucasus Resorts, http://www.ncrc.ru/ru/resort) and past armed-conflict sites (Hallberg, 2012).

the establishment of a functioning bison metapopulation, seem 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.

Table 3
Area of currently protected candidate sites for reintroductions.

IUCN category	Area of candidate sites that is protected [absolute in km^2] (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%)

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Appendix A. Supplementary data

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