Received: 15 January 2018 | Revised: 20 July 2018 | Accepted: 3 August 2018

DOI: 10.1111/ddi.12839

BIODIVERSITY RESEARCH

WILEY Diversity and Distributions

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

Benjamin Bleyhl[1] | Marine Arakelyan[2] | Elshad Askerov[3,4] | Hendrik Bluhm[1] | Alexander Gavashelishvili[5] | Mamikon Ghasabian[6] | Arash Ghoddousi[1] | Aurel Heidelberg[7] | Igor Khorozyan[8] | Alexander Malkhasyan[9] | Karen Manvelyan[9] | Mohammadreza Masoud[10] | Ehsan M. Moqanaki[11] | Volker C. Radeloff[12] | Mahmood Soofi[8] | Paul Weinberg[13] | Nugzar Zazanashvili[14,15] | Tobias Kuemmerle[1,16]

[1]Geography Department, Humboldt-University Berlin, Berlin, Germany

[2]Department of Zoology, Yerevan State University, Yerevan, Armenia

[3]WWF-Azerbaijan, Baku, Azerbaijan

[4]Institute of Zoology of Azerbaijan Academy of Sciences, Baku, Azerbaijan

[5]Center of Biodiversity Studies, Institute of Ecology, Ilia State University, Tbilisi, Georgia

[6]Scientific Center of Zoology and Hydroecology, NAS RA, Yerevan, Armenia

[7]WWF-Germany, Berlin, Germany

[8]Workgroup on Endangered Species, J.F. Blumenbach Institute of Zoology and Anthropology, University of Göttingen, Göttingen, Germany

[9]WWF-Armenia, Yerevan, Armenia

[10]Iranian Department of Environment, East Azerbaijan Provincial Office, Tabriz, Iran

[11]Iranian Cheetah Society (ICS), Tehran, Iran

[12]SILVIS Lab, Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, Wisconsin, U.S.A.

[13]North Ossetian Nature Reserve, Alagir, RSO-Alania, Russia

[14]WWF Caucasus Programme Office, Tbilisi, Georgia

[15]Institute of Ecology, Ilia State University, Tbilisi, Georgia

[16]Integrative Research Institute on Transformations of Human-Environment Systems (IRI THESys), Humboldt-Universität zu Berlin, Berlin, Germany

Correspondence
Benjamin Bleyhl, Geography Department, Humboldt-University Berlin, Berlin, Germany.
Email: benjamin.bleyhl@geo.hu-berlin.de

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 are 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 km^2).

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 vs. 40,270 km^2) 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).

Funding information
Federal State of Berlin, Germany; World Land Trust through the Iranian Cheetah Society

Editor: Joern Fischer

KEYWORDS
Armenian mouflon, Caucasus, Gmelin's mouflon, human–wildlife conflict, livestock, niche 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., 2015). This is worrisome as large ungulates play important roles for ecosystem functioning, for example as ecosystem engineers (Pringle, Young, Rubenstein, & McCauley, 2007) or as prey for large carnivores and scavengers (Margalida, Colomer, & Sanuy, 2011; Wolf & 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, Buuveibaatar, & Mishra, 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, Ciuti, & Apollonio, 2013; Krishna, Kumar, & Isvaran, 2016; Namgail, Fox, & Bhatnagar, 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, Van Wieren, Ketner, Heitkonig, & Prins, 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, Van Wieren, Heitkönig, & Prins, 2002; Owen-Smith, 2002; Shackleton, 1997). 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 & Rubenstein, 2016; Shackleton, 1997). 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, Glor, & Turelli, 2010). However, while there are analyses using species distribution modelling to quantify niche overlap among different wild species (e.g., Blair, Sterling, Dusch, Raxworthy, & Pearson, 2013; Wordley, Sankaran, Mudappa, & Altringham, 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 is 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, Kowalczyk, & Cromsigt, 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, Kerley, & Kowalczyk, 2012; Soga & Gaston, 2018). Similarly, mapping suitable habitat based on current habitat use might be erroneous for species pushed into marginal habitat (Braunisch, Bollmann, Graf, & Hirzel, 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 (*Capra 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 & Nebieridze, 1989). Today, poaching and overgrazing are the main threats to large ungulates in the southern Caucasus (Williams, Zazanashvili, Sanadiradze, & Kandaurov, 2006). 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., 2015; Ghoddousi et al., 2017). 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 & Danell, 2003; Iranian Department of Environment, unpubl. data; Mallon, Weinberg, & Kopaliani, 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, Weinberg, & Malkhasyan, 2009; Talibov, Weinberg, Mammadov, Mammadov, & Talibov, 2009). Identifying areas to establish new and expand existing populations, ideally so that key habitat patches are connected, is therefore important (Zazanashvili, Garforth, Jungius, & Gamkrelidze, 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 (a) to map mouflon summer and winter habitat; (b) to assess niche overlap in environmental and geographic space with domestic sheep in summer; and (c) 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 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., 2006). 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.

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 twofold in 2017 compared to the early 1990s, partly due to incentives through

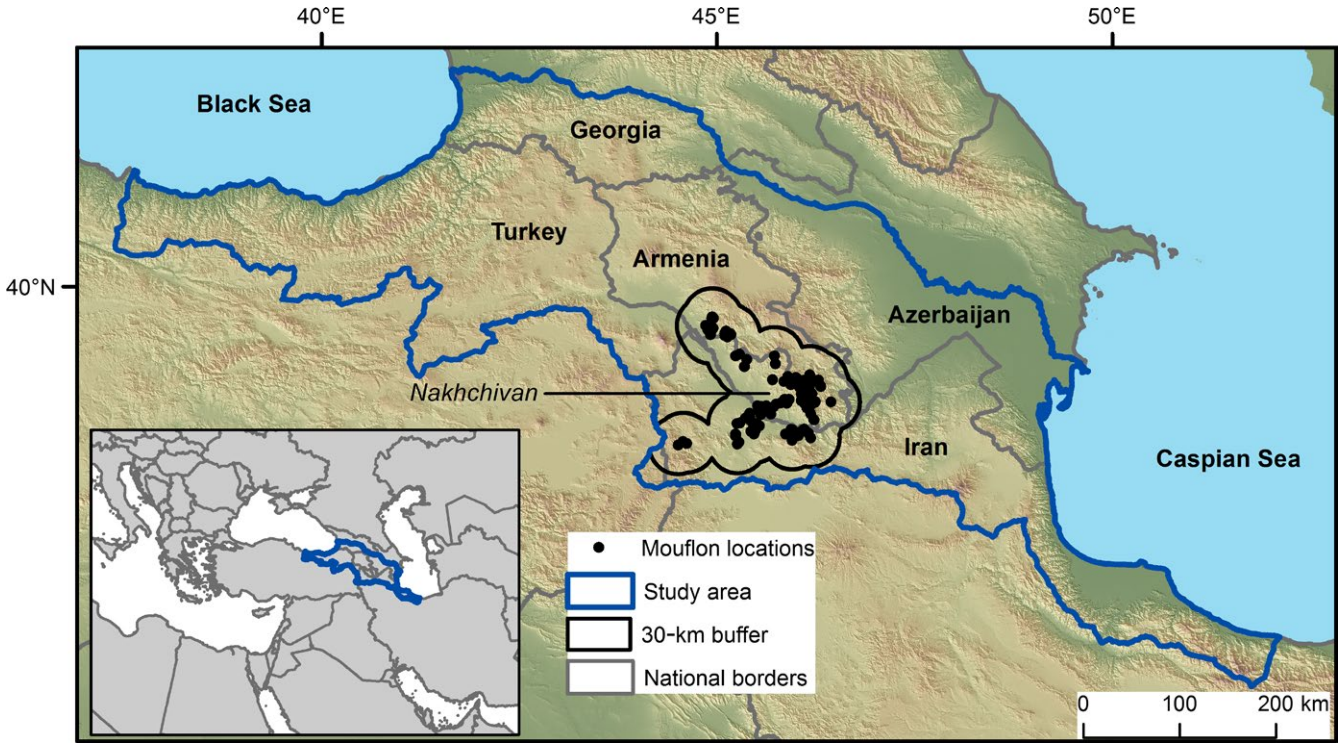

FIGURE 1 Study area and mouflon occurrence locations in the southern Caucasus [Colour figure can be viewed at wileyonlinelibrary.com]

privatization and agricultural reforms (FAOSTAT, 2017; Kosayev & 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., 2006). 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 & 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, 2009; 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, Ghadirian, & Faizolahi, 2016). 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., 2016).

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, Anderson, & Schapire, 2006), a species distribution modelling algorithm that is well-suited for presence-only data and outperforms concurrent algorithms (Elith et al., 2006). 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 & 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, Shoo, Graham, & Williams, 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 per cent 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 Supporting Information Appendix S1 for a-priori hypotheses on their relations to habitat suitability). For topography, we derived aspect (flat, north, east, south, and west), local terrain ruggedness (using a 90-m neighbourhood rule; Sappington, Longshore, & Thompson, 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 & 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 Supporting Information Appendix S1).

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, Ekhvaia, & Asanidze, 2012), mouflon might have adapted through resource partitioning (Schoener, 1974; Voeten & Prins, 1999). Competition with livestock might have pushed mouflon into marginal habitat, possibly rendering them a refugee species (Fritz, De Garine-Wichatitsky, & Letessier, 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 whether 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, 200, 500, 1,000 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, White, & Newell, 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 (van der 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 whether 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 whether the score is significantly lower (at the α = 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 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 3,600–4,800 individuals, assuming a density of 12–16 individuals per km^2 (based on studies of *Ovis vignei*, a closely related wild sheep in Iran; Farhadinia, Moqanaki, & Hosseini-Zavarei, 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 and 11) and roads as partial barriers (resistance value 100; Bleyhl et al., 2017). 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 & 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

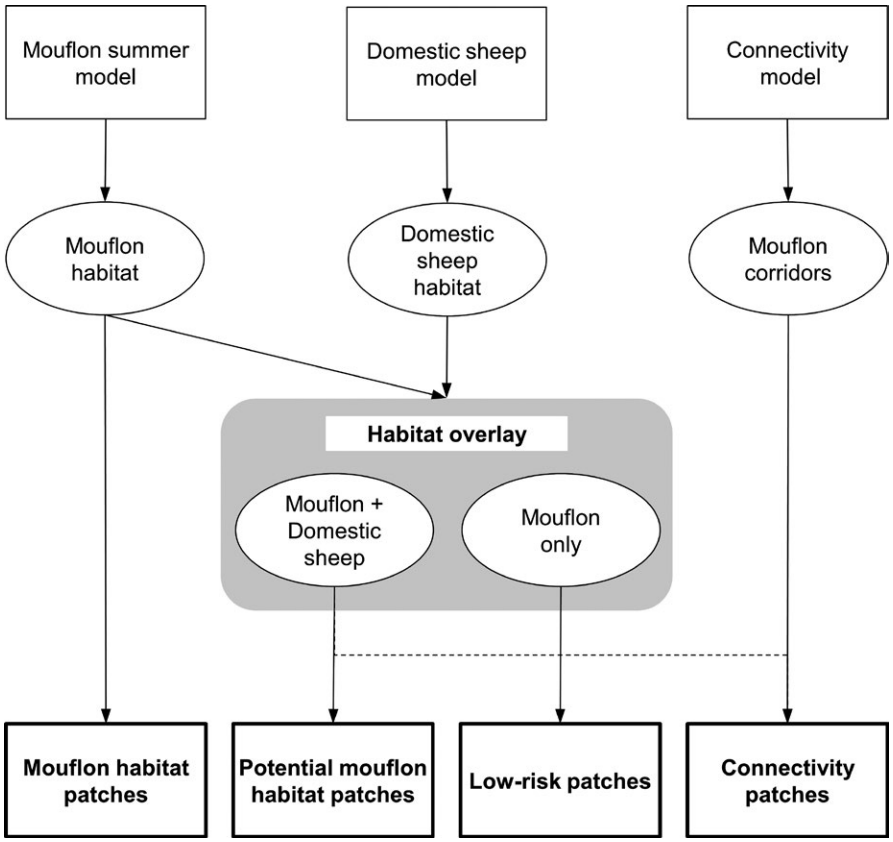

FIGURE 2 Flowchart of our analyses to identify priority habitat patches. Dashed line is only dashed to distinguish it from other crossing lines

to international borders (which might be related to poaching pressure from border patrols; Khorozyan et al., 2009).

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 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.

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 to 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 Supporting Information Appendix S1).

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 1). However, the two realized niches were not identical according to the niche identity 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 3). In general, domestic sheep habitat was much more widespread than mouflon habitat (40,270 km^2 compared to 14,000 km^2 for mouflon) and only a few areas that were suitable for mouflon were not suitable for domestic sheep (3,280 km^2 or 23% of all suitable mouflon habitat). The combination of both mouflon and domestic sheep habitat revealed widespread areas (43,560 km^2) potentially suitable as general *Ovis* habitat across the southern Caucasus (Figure 3).

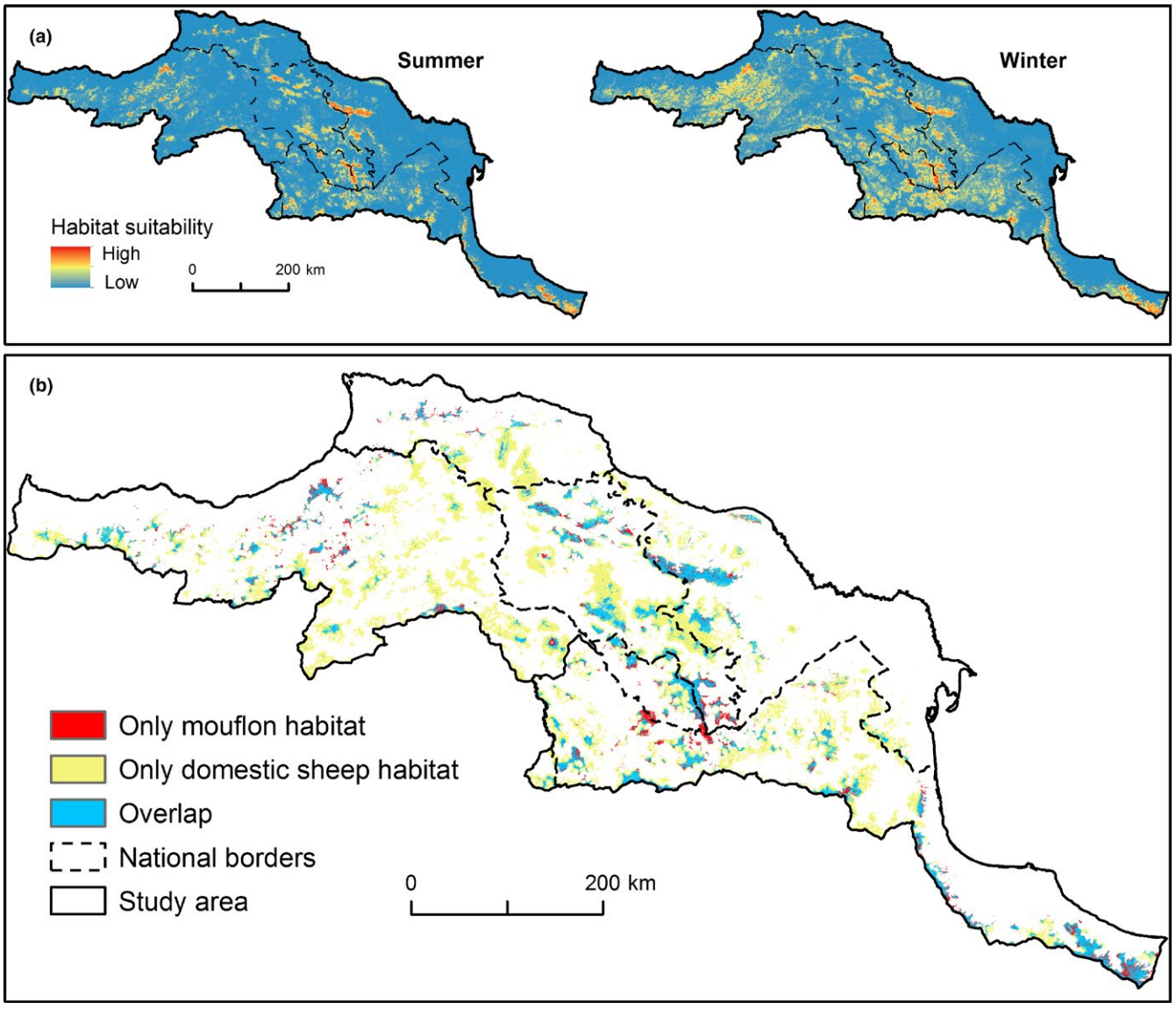

FIGURE 3 (a) Mouflon summer and winter habitat suitability and (b) areas with suitable mouflon and domestic sheep habitat, as well as areas where both habitats overlap [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Priority habitat patches

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

We found eleven *mouflon habitat patches* with high habitat suitability and an area exceeding 300 km^2 (Figure 4). All of these patches had at least 73% suitable winter habitat. In total, these habitat patches covered 6,830 km^2 (mean patch size: 620 km^2). We found *mouflon habitat patches* in all countries except Georgia, and the majority of them was in Iran (six areas, in total 3,000 km^2). Of the total area covered by such patches, 18% was protected (9% in reserves with IUCN category I or II; see Supporting Information Appendix S2 for an overview of all priority patches). Six of the eleven patches were close to international borders (<10 km) 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, that is potential mouflon habitat, resulted in markedly more and larger priority patches. In total, we found 51 *potential mouflon habitat patches* >300 km^2 distributed across all countries and covering an area of 40,400 km^2 (mean patch size: 790 km^2). 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 km^2, one in the border triangle of Armenia, Nakhchivan, and Iran, and one in Iran, together covering an

area of 740 km^2 (Figure 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 km^2 and located within the corridors linking *mouflon habitat patches* (Figure 5). Corridor length ranged from 8 to 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 and 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 km^2) and covered a total area of 24,000 km^2.

TABLE 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

	Overlap index *I*	
Domestic sheep locations	**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
1,000-m buffer	0.90	0.83
2,000-m buffer	0.90	0.82

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, 2009). The spatial distribution of summer

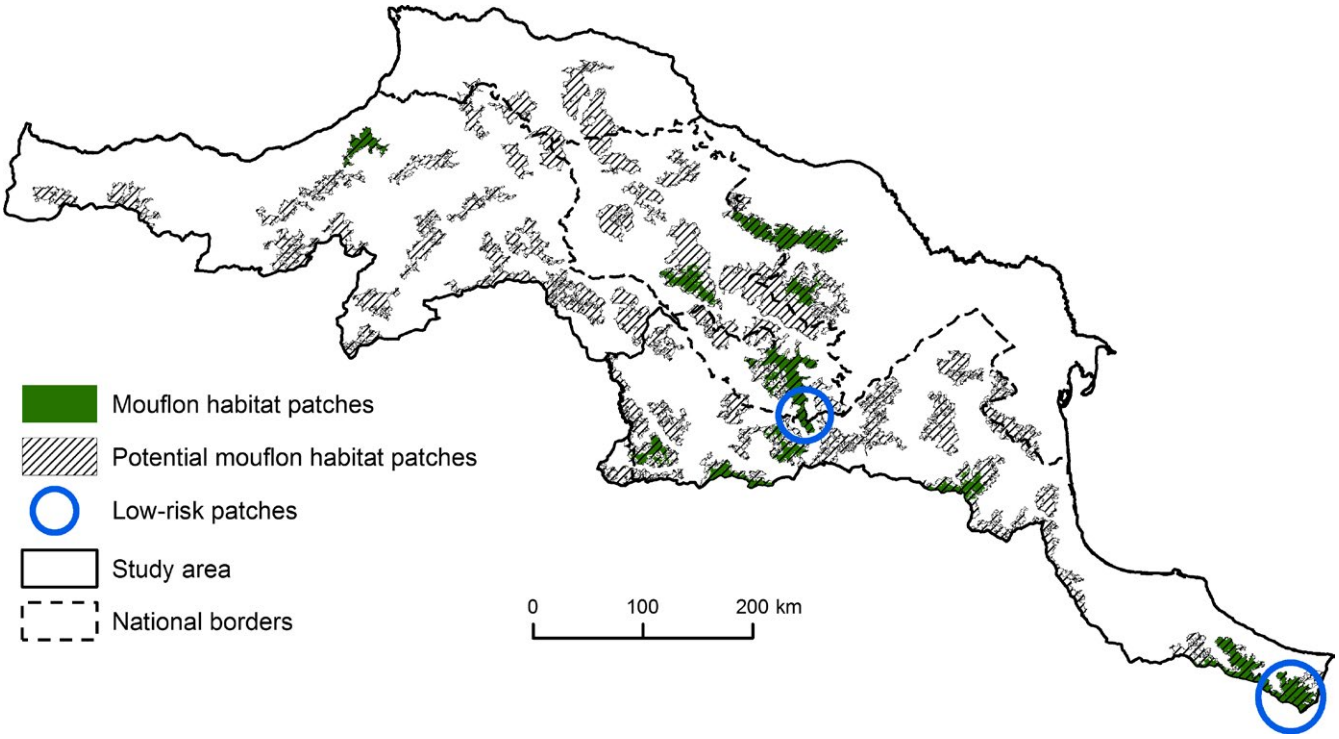

FIGURE 4 Distribution of mouflon habitat patches (based on the mouflon summer model), potential mouflon habitat patches (based on the combination of mouflon and domestic sheep habitat), and patches with low risk for competition with livestock [Colour figure can be viewed at wileyonlinelibrary.com]

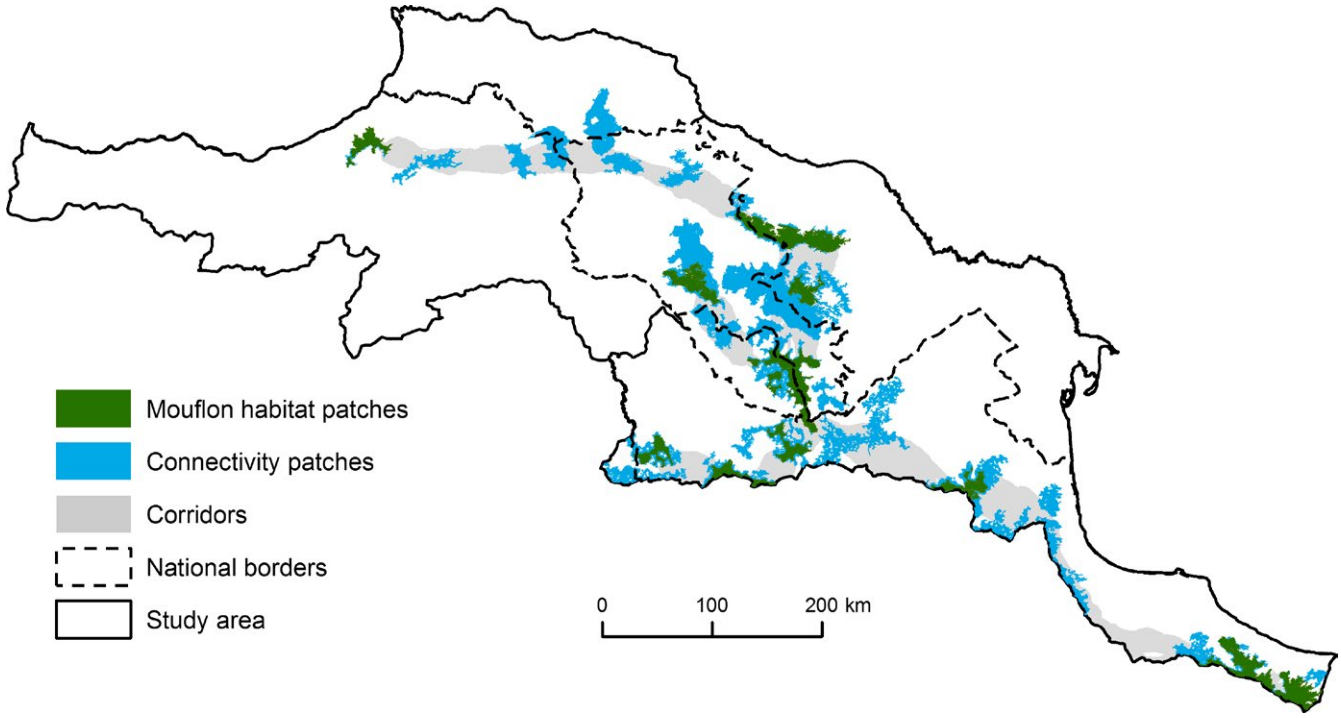

FIGURE 5 Least-cost corridors among mouflon habitat patches (i.e., patches based on current habitat patterns) and connectivity patches that would foster connectivity if new herds were established [Colour figure can be viewed at wileyonlinelibrary.com]

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 & 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 (*Ovis ammon*) were pushed to steeper slopes with less vegetation cover (Namgail et al., 2006) and ibex (*Capra pyrenaica*) and chamois (*Rupicapra rupicapra*) to areas with decreased resource availability (Acevedo, Cassinello, & Gortazar, 2007; 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*. As 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 km^2 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, 1997; 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 shepherds' 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 & 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, Olson, Reading, Amgalanbaatar, & Berger, 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, 1997) 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 (a) lessening conflict with livestock, particularly in key mouflon patches; and (b) 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

B. Bleyhl gratefully acknowledges funding through an Elsa-Neumann Scholarship from the Federal State of Berlin, Germany. We thank D. Frantz and M. Baumann for support in processing the data. We also thank WWF-Armenia, WWF-Azerbaijan, WWF Caucasus Programme Office Georgia, and WWF-Germany for logistic support during field trips. E. M. Moqanaki was supported by a research grant from World Land Trust through the Iranian Cheetah Society. We are grateful for the help and constructive comments of two reviewers.

DATA ACCESSIBILITY

We will make habitat maps available via Humboldt University Berlin's cloud storage system (HU-Box).

ORCID

Benjamin Bleyhl http://orcid.org/0000-0002-4858-950X
Ehsan M. Moqanaki http://orcid.org/0000-0001-7968-0210
Volker C. Radeloff http://orcid.org/0000-0001-9004-221X

REFERENCES

Acevedo, P., Cassinello, J., & Gortazar, C. (2007). The Iberian ibex is under an expansion trend but displaced to suboptimal habitats by

the presence of extensive goat livestock in central Spain. *Biodiversity and Conservation*, *16*, 3361–3376. https://doi.org/10.1007/s10531-006-9032-y

Akhalkatsi, M., Ekhvaia, J., & Asanidze, Z. (2012). Diversity and genetic erosion of ancient crops and wild relatives of agricultural cultivars for food: Implications for nature conservation in Georgia (Caucasus). In J. Tiefenbacher (Ed.), *Perspectives on nature conservation-patterns, pressures and prospects*. Rijeka, Croatia: InTech.

Akhalkatsi, M., Otte, A., Togonidze, N., Bragvadze, T., Asanidze, Z., Arabuli, G., … Mazanishvili, L. (2017). Agrobiodiversity and genetic erosion of crop varieties and plant resources in the Central Great Caucasus. *Annals of Agrarian Science*, *15*, 11–16. https://doi.org/10.1016/j.aasci.2016.12.002

Alberto, F. J., Boyer, F., Orozco-terWengel, P., Streeter, I., Servin, B., de Villemereuil, P., … Pompanon, F. (2018). Convergent genomic signatures of domestication in sheep and goats. *Nature Communications*, *9*, 813. https://doi.org/10.1038/s41467-018-03206-y

Allan, B. F., Tallis, H., Chaplin-Kramer, R., Huckett, S., Kowal, V. A., Musengezi, J., … Keesing, F. (2017). Can integrating wildlife and livestock enhance ecosystem services in central Kenya? *Frontiers in Ecology and the Environment*, *15*, 328–335. https://doi.org/10.1002/fee.1501

Baskin, L., & Danell, K. (2003). Mouflon—*Ovis aries*. In L. Baskin & K. Danell (Eds.), *Ecology of ungulates: A handbook of species in Eastern Europe and Northern and Central Asia* (pp. 277–283). Berlin, Heidelberg, Germany, New York, NY: Springer. https://doi.org/10.1007/978-3-662-06820-5

Berger, J., Buuveibaatar, B., & Mishra, C. (2013). Globalization of the cashmere market and the decline of large mammals in Central Asia. *Conservation Biology*, *27*, 679–689. https://doi.org/10.1111/cobi.12100

Blair, M. E., Sterling, E. J., Dusch, M., Raxworthy, C. J., & Pearson, R. G. (2013). Ecological divergence and speciation between lemur (Eulemur) sister species in Madagascar. *Journal of Evolutionary Biology*, *26*, 1790–1801. https://doi.org/10.1111/jeb.12179

Bleyhl, B., Baumann, M., Griffiths, P., Heidelberg, A., Manvelyan, K., Radeloff, V. C., … 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. https://doi.org/10.1016/j.rse.2017.03.001

Bleyhl, B., Sipko, T., Trepet, S., Bragina, E., Leitao, 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. https://doi.org/10.1016/j.biocon.2015.06.011

Bouzat, J. L., Johnson, J. A., Toepfer, J. E., Simpson, S. A., Esker, T. L., & Westemeier, R. L. (2009). Beyond the beneficial effects of translocations as an effective tool for the genetic restoration of isolated populations. *Conservation Genetics*, *10*, 191–201. https://doi.org/10.1007/s10592-008-9547-8

Bragina, E. V., Ives, A. R., Pidgeon, A. M., Kuemmerle, T., Baskin, L. M., Gubar, Y. P., … Radeloff, V. C. (2015). Rapid declines of large mammal populations after the collapse of the Soviet Union. *Conservation Biology*, *184*, 456–464. https://doi.org/10.1016/j.biocon.2015.02.013

Braunisch, V., Bollmann, K., Graf, R. F., & Hirzel, A. H. (2008). Living on the edge—Modelling habitat suitability for species at the edge of their fundamental niche. *Ecological Modelling*, *214*, 153–167. https://doi.org/10.1016/j.ecolmodel.2008.02.001

Caughley, G. (1994). Directions in conservation biology. *Journal of Animal Ecology*, *63*, 215–244. https://doi.org/10.2307/5542

Chirichella, R., Ciuti, S., & Apollonio, M. (2013). Effects of livestock and non-native mouflon on use of high-elevation pastures by Alpine chamois. *Mammalian Biology – Zeitschrift für Säugetierkunde*, *78*, 344–350. https://doi.org/10.1016/j.mambio.2013.04.005

Cromsigt, J. P. G. M., Kerley, G. I. H., & Kowalczyk, R. (2012). The difficulty of using species distribution modelling for the conservation of refugee species – The example of European bison. *Diversity and Distributions*, *18*, 1253–1257. https://doi.org/10.1111/j.1472-4642.2012.00927.x

de Boer, W. F., & Prins, H. H. T. (1990). Large herbivores that strive mightily but eat and drink as friends. *Oecologia*, *82*, 264–274. https://doi.org/10.1007/BF00323544

Di Marco, M., Boitani, L., Mallon, D., Hoffmann, M., Iacucci, A., Meijaard, E., … Rondinini, C. (2014). A retrospective evaluation of the global decline of carnivores and ungulates. *Conservation Biology*, *28*, 1109–1118. https://doi.org/10.1111/cobi.12249

Dinnik, N. (1910). *Mammals of the Caucasus*, *vol. 1*. Tbilisi, Georgia: K.P. Kozlovsky's Press.

Dormann, C. F., McPherson, J. M., Araujo, M. B., Bivand, R., Bolliger, J., Carl, G., … Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, *30*, 609–628. https://doi.org/10.1111/j.2007.0906-7590.05171.x

Ekernas, L. S., Sarmento, W. M., Davie, H. S., Reading, R. P., Murdoch, J., Wingard, G. J., … Berger, J. (2017). Desert pastoralists' negative and positive effects on rare wildlife in the Gobi. *Conservation Biology*, *31*, 269–277. https://doi.org/10.1111/cobi.12881

Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., … Zimmermann, N. E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, *29*, 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

FAOSTAT. (2017). *FAOSTAT database (online)*. Retrieved from http://www.fao.org/faostat/en/#home.

Farhadinia, M. S., Moqanaki, E. M., & Hosseini-Zavarei, F. (2014). Predator–prey relationships in a middle Asian Montane steppe: Persian leopard versus urial wild sheep in Northeastern Iran. *European Journal of Wildlife Research*, *60*, 341–349. https://doi.org/10.1007/s10344-013-0791-y

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*, 4302–4315. https://doi.org/10.1002/joc.5086

Franklin, J. (2009). *Mapping species distributions: Spatial inference and prediction*. Cambridge, UK; New York, NY: Cambridge University Press.

Fritz, H., De Garine-Wichatitsky, M., & Letessier, G. (1996). Habitat use by sympatric wild and domestic herbivores in an African savanna woodland: The influence of cattle spatial behaviour. *Journal of Applied Ecology*, *33*, 589–598. https://doi.org/10.2307/2404987

Gavashelishvili, A. (2009). GIS-based habitat modeling of mountain ungulate species in the Caucasus hotspot. In N. Zazanashvili & D. Mallon (Eds.), *Status and protection of globally threatened species in the Caucasus* (pp. 74–82). Tbilisi, Georgia: Contour Ltd.

Ghoddousi, A., Soofi, M., Hamidi, A. K., Ashayeri, S., Egli, L., Ghoddousi, S., … Waltert, M. (2017). The decline of ungulate populations in Iranian protected areas calls for urgent action against poaching. *Oryx*, 1–8. https://doi.org/10.1017/S003060531600154X

Ghoddousi, A., Soofi, M., Hamidi, A. Kh., Lumetsberger, T., Egli, L., Khorozyan, I., … Waltert, M. (2016). Assessing the role of livestock in big cat prey choice using spatiotemporal availability patterns. *PLoS One*, *11*, e0153439. https://doi.org/10.1371/journal.pone.0153439

Gordon, I. J. (2009). What is the future for wild, large herbivores in human-modified agricultural landscapes? *Wildlife Biology*, *15*, 1–9. https://doi.org/10.2981/06-087

Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: A comparative view of their digestive system. *Oecologia*, *78*, 443–457. https://doi.org/10.1007/BF00378733

Kalandadze, A. N., & Nebieridze, L. D. (1989). Neolithic age. In G. Melikishvili & O. Lortkipanidze (Eds.), *Essays on the History of Georgia*, *Vol. 1: Georgia from ancient time to the 4th century BC* (pp. 56–66). Tbilisi, Georgia: Metsniereba.

Karami, M., Ghadirian, T., & Faizolahi, K. (2016). *The atlas of mammals of Iran*. Karaj, Iran: Jahad Daneshgahi, Kharazmi.

Kerley, G. I. H., Kowalczyk, R., & Cromsigt, J. P. G. M. (2012). Conservation implications of the refugee species concept and the European bison: King of the forest or refugee in a marginal habitat? *Ecography*, *35*, 519–529. https://doi.org/10.1111/j.1600-0587.2011.07146.x

Khorozyan, I., Weinberg, P., & Malkhasyan, A. (2009). Conservation strategy of Armenian mouflon (*Ovis [orientalis] gmelini* Blyth) and bezoar goat (*Capra aegagrus* Erxleben) in Armenia. In N. Zazanashvili & D. Mallon (Eds.), *Status and protection of globally threatened species in the Caucasus* (pp. 37–45). Tbilisi, Georgia: Contour Ltd.

Kosayev, E., & Guliev, Y. (2006). *Country pasture/forage resource profiles Azerbaijan*. Rome, Italy: Food and Agriculture Organization of the United Nations (FAO).

Krishna, Y. C., Kumar, A., & Isvaran, K. (2016). Wild ungulate decision-making and the role of tiny refuges in human-dominated landscapes. *PLoS One*, *11*, e0151748. https://doi.org/10.1371/journal.pone.0151748

Linnell, J. D. C., Trouwborst, A., Boitani, L., Kaczensky, P., Huber, D., Reljic, S., … Breitenmoser, U. (2016). Border security fencing and wildlife: The end of the transboundary paradigm in Eurasia? *PLoS Biology*, *14*, e1002483. https://doi.org/10.1371/journal.pbio.1002483

Liu, C., White, M., & Newell, G. (2013). Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography*, *40*, 778–789. https://doi.org/10.1111/jbi.12058

Madhusudan, M. D. (2004). Recovery of wild large herbivores following livestock decline in a tropical Indian wildlife reserve. *Journal of Applied Ecology*, *41*, 858–869. https://doi.org/10.1111/j.0021-8901.2004.00950.x

Mallon, D., Weinberg, P., & Kopaliani, N. (2007). Status of the prey species of the leopard in the Caucasus. *Cat News*, *2*, 22–27.

Margalida, A., Colomer, M. À., & Sanuy, D. (2011). Can wild ungulate carcasses provide enough biomass to maintain avian scavenger populations? An empirical assessment using a bio-inspired computational model. *PLoS One*, *6*, e20248. https://doi.org/10.1371/journal.pone.0020248

McRae, B. H., & Kavanagh, D. M. (2011). *Linkage Mapper user guide*. Seattle, WA: The Nature Conservancy.

Mishra, C., Van Wieren, S. E., Heitkönig, I. M. A., & Prins, H. H. T. (2002). A theoretical analysis of competitive exclusion in a Trans-Himalayan large-herbivore assemblage. *Animal Conservation*, *5*, 251–258. https://doi.org/10.1017/S1367943002002305

Mishra, C., Van Wieren, S. E., Ketner, P., Heitkonig, I. M. A., & Prins, H. H. T. (2004). Competition between domestic livestock and wild bharal *Pseudois nayaur* in the Indian Trans-Himalaya. *Journal of Applied Ecology*, *41*, 344–354. https://doi.org/10.1111/j.0021-8901.2004.00885.x

Mittermeier, R. A., Robles Gil, P., Hoffmann, M., Pilgrim, J., Brooks, T., Goettsch Mittermeier, C., … Da Fonseca, G. A. B. (2004). *Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions*. Mexico City, Mexico: Cemex.

Namgail, T., Fox, J. L., & Bhatnagar, Y. V. (2006). Habitat shift and time budget of the Tibetan argali: The influence of livestock grazing. *Ecological Research*, *22*, 25.

NASA JPL. (2013). *NASA Shuttle Radar Topography Mission Global 1 Arc Second*. N.L. Daac.

Owen-Smith, R. N. (2002). *Adaptive herbivore ecology: From resources to populations in variable environments*. Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/CBO9780511525605

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Phillips, S. J., & Dudik, M. (2008). Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography*, *31*, 161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x

Pringle, R. M., Young, T. P., Rubenstein, D. I., & McCauley, D. J. (2007). Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *Proceedings of the National Academy of Sciences*, *104*, 193–197. https://doi.org/10.1073/pnas.0609840104

Ptak, G., Clinton, M., Barboni, B., Muzzeddu, M., Cappai, P., Tischner, M., & Loi, P. (2002). Preservation of the wild European mouflon: The first example of genetic management using a complete program of reproductive biotechnologies. *Biology of Reproduction*, *66*, 796–801. https://doi.org/10.1095/biolreprod66.3.796

Putman, R. J. (1996). *Competition and resource partitioning in temperate ungulate assemblies*. London, UK: Chapman & Hall. https://doi.org/10.1007/978-94-009-1517-6

Rezaei, H. R., Naderi, S., Chintauan-Marquier, I. C., Taberlet, P., Virk, A. T., Naghash, H. R., … Pompanon, F. (2010). Evolution and taxonomy of the wild species of the genus *Ovis* (Mammalia, Artiodactyla, Bovidae). *Molecular Phylogenetics and Evolution*, *54*, 315–326. https://doi.org/10.1016/j.ympev.2009.10.037

Riginos, C., Porensky, L. M., Veblen, K. E., Odadi, W. O., Sensenig, R. L., Kimuyu, D., … Young, T. P. (2012). Lessons on the relationship between livestock husbandry and biodiversity from the Kenya Long-term Exclosure Experiment (KLEE). *Pastoralism: Research, Policy and Practice*, *2*, 10. https://doi.org/10.1186/2041-7136-2-10

Ripple, W. J., Chapron, G., López-Bao, J. V., Durant, S. M., Macdonald, D. W., Lindsey, P. A., … Zhang, L. (2016). Saving the world's terrestrial megafauna. *BioScience*, *66*, 807–812. https://doi.org/10.1093/biosci/biw092

Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., … Van Valkenburgh, B. (2015). Collapse of the world's largest herbivores. *Science Advances*, *1*, e1400103. https://doi.org/10.1126/sciadv.1400103

Robinson, T. P., Wint, G. R. W., Conchedda, G., Van Boeckel, T. P., Ercoli, V., Palamara, E., … Gilbert, M. (2014). Mapping the global distribution of livestock. *PLoS One*, *9*, e96084. https://doi.org/10.1371/journal.pone.0096084

Sappington, J. M., Longshore, K. M., & Thompson, D. B. (2007). Quantifying landscape ruggedness for animal habitat analysis: A case study using bighorn sheep in the Mojave Desert. *Journal of Wildlife Management*, *71*, 1419–1426. https://doi.org/10.2193/2005-723

Schieltz, J. M., & Rubenstein, D. I. (2016). Evidence based review: Positive versus negative effects of livestock grazing on wildlife. What do we really know?. *Environmental Research Letters*, *11*, 113003. https://doi.org/10.1088/1748-9326/11/11/113003

Schoener, T. W. (1974). Competition and the form of habitat shift. *Theoretical Population Biology*, *6*, 265–307. https://doi.org/10.1016/0040-5809(74)90013-6

Shackleton, D. M. (1997). *Wild sheep and goats and their relatives. Status survey and conservation action plan for Caprinae*. Gland, Switzerland and Cambridge, UK: IUCN.

Soga, M., & Gaston, K. J. (2018). Shifting baseline syndrome: Causes, consequences, and implications. *Frontiers in Ecology and the Environment*, *16*, 222–230. https://doi.org/10.1002/fee.1794

Soofi, M., Ghoddousi, A., Zeppenfeld, T., Shokri, S., Soufi, M., Jafari, A., … Waltert, M. (2018). Livestock grazing in protected areas and its effects on large mammals in the Hyrcanian forest, Iran. *Biological Conservation*, *217*, 377–382. https://doi.org/10.1016/j.biocon.2017.11.020

Statistical Center of Iran. (2017). Livestock; Statistical Survey. Retrieved from https://www.amar.org.ir/.

Talibov, T. H., Weinberg, P., Mammadov, I. B., Mammadov, E. N., & Talibov, S. T. (2009). Conservation strategy of the Asiatic mouflon (*Ovis [orientalis] gmelini* Blyth) and the Bezoar Goat (*Capra aegagrus* Erxleben) in Azerbaijan. In N. Zazanashvili & D. Mallon (Eds.), *Status and protection of globally threatened species in the Caucasus* (pp. 46–52). Tbilisi, Georgia: Contour Ltd.

Valdez, R. (2008). *Ovis orientalis*. *The IUCN Red List of Threatened Species 2008*. Retrieved from http://www.iucnredlist.org

van der Vaart, A. W. (1998). *Asymptotic statistics*. Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/CBO9780511802256

VanDerWal, J., Shoo, L. P., Graham, C., & Williams, S. E. (2009). Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? *Ecological Modelling*, *220*, 589–594. https://doi.org/10.1016/j.ecolmodel.2008.11.010

Veloz, S. D. (2009). Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *Journal of Biogeography*, *36*, 2290–2299. https://doi.org/10.1111/j.1365-2699.2009.02174.x

Voeten, M. M., & Prins, H. H. T. (1999). Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia*, *120*, 287–294. https://doi.org/10.1007/s004420050860

Warren, D. L., Glor, R. E., & Turelli, M. (2010). ENMTools: A toolbox for comparative studies of environmental niche models. *Ecography*, *33*, 607–611.

Williams, L., Zazanashvili, N., Sanadiradze, G., & Kandaurov, A. (Eds.) (2006). *Ecoregional conservation plan for the Caucasus*. Tbilisi, Georgia: WWF, KfW, BMZ, CEPF, MacArthur Foundation.

Wolf, C., & Ripple, W. J. (2016). Prey depletion as a threat to the world's large carnivores. *Royal Society Open Science*, *3*, 160252. https://doi.org/10.1098/rsos.160252

Wordley, C. F. R., Sankaran, M., Mudappa, D., & Altringham, J. D. (2015). Landscape scale habitat suitability modelling of bats in the Western Ghats of India: Bats like something in their tea. *Biological Conservation*, *191*, 529–536. https://doi.org/10.1016/j.biocon.2015.08.005

Young, J. K., Olson, K. A., Reading, R. P., Amgalanbaatar, S., & Berger, J. (2011). Is wildlife going to the dogs? Impacts of feral and free-roaming dogs on wildlife populations. *BioScience*, *61*, 125–132. https://doi.org/10.1525/bio.2011.61.2.7

Zazanashvili, N., Garforth, M., Jungius, H., & Gamkrelidze, T. (Eds.) (2012). *Ecoregion conservation plan for the Caucasus. 2012 revised updated edition*. Tbilisi, Georgia: WWF, KfW, BMZ.

BIOSKETCH

Benjamin Bleyhl is a PhD student in the Conservation Biogeography group at the Geography Department of Humboldt-University Berlin. He is interested in questions regarding large mammal habitat distribution that can inform conservation planning.

Authors' contributions: B.B., H.B., T.K. and V.C.R. conceived the ideas; B.B., M.A., E.A., H.B., A.G., M.G., A.G., A.H., I.K., A.M., K.M., M.M., E.M.M., M.S., P.W. and N.Z. gathered and analysed the data; B.B. and T.K. led the writing; and all authors approved and edited the manuscript.

SUPPORTING INFORMATION

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

How to cite this article: Bleyhl B, Arakelyan M, Askerov E, et al. Assessing niche overlap between domestic and threatened wild sheep to identify conservation priority areas. *Divers Distrib*. 2019;25:129–141. https://doi.org/10.1111/ddi.12839