Identifying priority areas for restoring mountain ungulates in the Caucasus ecoregion

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

**KEYWORDS**

*Capra*, conservation planning, corridors, habitat restoration, megafauna, poaching, reintroductions, species distribution models

## 1 | INTRODUCTION

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

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

Restoring mountain ungulates relies on identifying suitable habitat, ideally in places that would increase and link existing populations (Bleyhl et al., 2017; Kuemmerle et al., 2011). Current land-use trends in many mountain areas might create a favorable environment for restoration, as rural population density declines, labor-intensive agriculture is abandoned, and transhumant livestock systems are in decline (Kuemmerle et al., 2008; MacDonald et al., 2000). These trends will likely continue (Stürck et al., 2018), suggesting substantial opportunities for restoring mountain ungulate populations, and the predators that depend on them (Ripple et al., 2015).

Once suitable, but currently unoccupied habitat patches are found, a key question is why these habitats are not colonized (Davies et al., 2017; Louvrier et al., 2018). The answer to this question has important implications for restoration planning (Ferreras, Gaona, Palomares, & Delibes, 2001; Ziółkowska, Perzanowski, Bleyhl, Oستапович, & Kuemmerle, 2016). For instance, where unoccupied habitat patches are isolated from extant populations, yet contain well-managed protected areas, reintroductions can be an important measure to re-establish locally extirpated populations (Hoffmann et al., 2015). Where physical barriers prevent dispersal, restoring corridors can functionally link populations (Bleyhl et al., 2017; Ziółkowska et al., 2016). If, however, unoccupied habitat patches are well-connected to extant populations, high poaching pressure might prevent colonization. Reducing mortality (e.g., via upgrading
Bezoar goats, ancestors of domestic goats, once ranged across the region (Weinberg et al., 2008). The species is tightly linked to steep cliffs and rocky outcrops, on which they critically depend for escaping from predators (Esfandabad, Karami, Hemami, Riazi, & Sadoughi, 2010; Weinberg, 2001), making their populations naturally patchy. This also makes bezoar goats highly vulnerable to poaching (Krever et al., 2001), with males especially at risk due to their sought-after trophies (Damm & Franco, 2014). Bezoar goats were still relatively common before the Iranian Islamic Revolution (1979) and the breakdown of the Soviet Union (1991), but plummeted after these events (Ghoddousi et al., 2019; Magomedov, Omarov, & Nasrulaev, 2001; Weinberg, 2001). Despite some recent recovery, bezoar goats today are largely confined to protected areas (Karami, Ghadrian, & Faizolahi, 2016; Krever et al., 2001; Weinberg et al., 2008). This is worrisome as the species forms the main prey for the endangered Persian leopard (Panthera pardus tulliana), the region's top predator (Ghoddousi et al., 2016). A broad-scale habitat and threat assessment for bezoar goats across the ecoregion is urgently needed to guide restoration efforts (Krever et al., 2001).

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

We assessed the following research questions:

1. What is the distribution of suitable habitat for bezoar goats across the Caucasus ecoregion?
2. Where are currently unoccupied habitat patches, and which factors likely prevent bezoar goats from colonizing them?
3. Where are priority sites for different restoration scenarios for bezoar goats across their former range?

## 2 | METHODS

### 2.1 | Study region

The Caucasus ecoregion harbors high levels of biodiversity, including many endemic species (Mittermeier et al., 2004; Zazanashvili et al., 2012). The ecoregion is located between the Black and Caspian Seas, elevations range up to 5,600 m and climate varies from moist, temperate in the west (1,200–4,000 mm precipitation) to arid in the east (<250 mm). Lowland natural vegetation ranges from steppes in the western plains to semi-deserts and arid woodlands in the east. Mountains cover about 65% of the region...
and are mainly covered by broadleaved forests (mostly beech [Fagus spp.], oak [Quercus spp.], hornbeam [Carpinus spp.], and chestnut [Castanea sativa]), mixed and pure coniferous forests (mainly Caucasian fir [Abies nordmanniana], Oriental spruce [Picea orientalis], and pines [Pinus spp.], Juniper woodlands (Juniperus spp.), mountain meadows, and bare rock and ice (Krever et al., 2001). We used the Caucasus ecoregion boundary as delineated by the Ecoregion Conservation Plan for the Caucasus (Williams, Zazanashvili, Sandaridze, & Kandaurov, 2006) as our study area (580,000 km²), plus a buffer of 25 km to avoid border effects in our analyses (Figure 1; hereafter: Caucasus).

2.2 | Bezoar goat data

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

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

2.3 | Habitat predictor variables

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

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

To characterize resource availability for bezoar goats, we calculated the share of forest, rangeland, and sparse vegetation at the 300 m grid level, based on the 30 m land-cover map (Bleyhl et al., 2017). Further, we calculated the average Normalized Difference Vegetation

### Table 1

| Predictor variables | Data source | Description | Assumed influence |
|---------------------|-------------|-------------|-------------------|
| Refuges             | Elevation   | Shuttle radar topography Mission elevation model (30 m resolution) | median elevation of each 300 m gridcell | +/- |
|                     | Median slope third quartile of slope | See above | Median and 75th percentile of slope distribution in each 300 m gridcell | + |
|                     | Ruggedness  | See above | Standard deviation of slope in each 300 m gridcell | + |
|                     | Share of cliffs | See above | Area share of slope larger than x (x = 30 to 50°, in 5° steps) in a gridcell | + |
|                     | Distance to cliffs | See above | Average distance of non-cliff areas to cliffs | - |
| Resource availability | Share of forest | Land-cover map by Bleyhl et al., 2017 (30 m resolution) | Area share in a gridcell | +/- |
|                     | Share of rangeland | See above | Area share in a gridcell | + |
|                     | Share of sparse vegetation | See above | Area share in a gridcell | - |
|                     | Distance to forest | See above | Average distance of non-forested pixels to closest forest edge | - |
|                     | Peak NDVI | MODIS NDVI time series based on MOD/MYD13Q1 | Average NDVI value at peak productivity over the years 2001–2012 (Estel et al., 2015) | +/- |
|                     | Length of growing season | See above | Average length of growing season over the years 2001–2012 (Estel et al., 2015) | + |
|                     | Average snow cover | MODIS snow cover time series based on MOD/MYD10A | Average days with snow cover | - |
|                     | Variation in snow cover | See above | Standard deviation of days with snow cover | +/- |
| Human dist.         | Distance to roads | OpenStreet map | Euclidean distance to nearest road | +/- |
|                     | Distance to settlements | WWF Caucasus program database | Euclidean distance to nearest settlement | +/- |
2.4 | Map potential habitat patches

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

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

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

2.5 Assess barriers to colonization

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

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

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

Bezoar goats compete with other mountain ungulates, particularly Caucasian tur, and are typically not sympatric with them (Gavashelishvili, 2009). To identify patches where bezoar goats might face high competition with turs, we modelled tur habitat using the same predictors and Maxent parameterization as for the final bezoar goat model (see Figure S1.1 in the Supporting Information). After obtaining a tur habitat map, we calculated the similarity statistic $I$ (Warren, Glor, Turelli, & Funk, 2009) between Caucasian tur and bezoar goat habitat suitability. We did this individually for each bezoar goat habitat patch that was at least partly inside the IUCN range for Caucasian tur (see Appendix S2 in the Supporting Information), resulting in an index ranging from 0 (high similarity of habitat suitability values) to 1 (low similarity).

2.6 Identify priority patches for restoration

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

3 | RESULTS

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

Predicting this model across the region highlighted large areas of potentially suitable bezoar goat habitat throughout the Caucasus (Figure 3). These potentially suitable areas occurred in the western part of the Greater Caucasus (Karachay-Cherkessia and Kabardino-Balkaria in Russia, and Svaneti in Georgia), as well as in Chechnya and particularly Dagestan in the eastern Greater Caucasus. In the Lesser Caucasus, notable areas occurred in Georgia (Samtskhe-Javakheti), eastern Turkey (Artvin and Erzurum), western Azerbaijan (Gadabay, Dashkasan, and Goygol), southern Armenia, and northern Iran (Kiamaky and Alborz Mountains). Converting the continuous habitat suitability map into discrete habitat patches (TSS threshold = 0.28) resulted in 153 individual patches of suitable habitat >30 km$^2$ (Figure 3), together covering an area of about 30,960 km$^2$ (mean patch size =202 km$^2$, median = 86 km$^2$, $SD = 392$ km$^2$).

Out of these patches, we identified 29 patches as occupied by bezoar goats, while 124 patches did not have confirmed presence of a permanent bezoar goat population. Occupied patches occurred in all Caucasus countries, as well as in both the Greater and the Lesser Caucasus. We identified four distinct clusters of extant bezoar goat populations: (a) in the Greater Caucasus (Chechnya and Dagestan in Russia, as well as in neighboring Tusheti in Georgia), (b) in eastern Turkey (HatilaVadisi National Park and Borçka Karagöl Nature Park, plus surroundings), (c) southern Armenia (Koshrov State Nature Reserve, Zangezur range, Arevik National Park), as well as neighboring regions (e.g., Nakhichevan, Kiamaky Wildlife Refuge in Iran), and (d) the Alborz Mountains in northern Iran (Figure 3, inset). The largest individual patch of suitable habitat, partly occupied by bezoar goats, occurred in Dagestan (about 3,120 km$^2$).

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

Ranking patches according to these indices identified candidate patches for specific restoration scenarios.

**FIGURE 3** Habitat suitability for bezoar goats across the Greater and Lesser Caucasus. Inset: Occupied and unoccupied habitat patches of at least 30 km$^2$
patches were sometimes highlighted under our scenarios 1 and 3. The top-ranking 15 patches per scenario covered substantial areas in the Caucasus, with priority patches in scenario 1 covering the highest (>3,800 km²) and patches in scenario 2 the lowest area (1,400 km²). The top-three patches of scenarios 1 and 2 had a cumulative area of under 300 km².

4 | DISCUSSION

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

Our habitat suitability model had a robust model fit and response types were generally in line with our a-priori hypotheses (Table S1, Supporting Information), as well as with prior work on bezoar goats. Specifically, our model confirmed the overwhelming importance of cliffs as refuges from predators (Esfandabad et al., 2010; Ghoddousi et al., 2016; Weinberg, 2001). Bezoar goats preferred areas with intermediate productivity, longer growing seasons, moderate to low forest cover, and high shares of rangeland (Table S1, Supporting Information), in line with a reported preference of the species for warmer and more arid conditions (Heptner, Nasimovich, & Bannikov, 1961;
Interestingly, human-pressure variables (in our case proxied by distance to settlements and roads) were less important in our models. Explanations could be that these variables do not effectively proxy key human threats to bezoar goats, such as poaching pressure, that the pressure associated with roads varies seasonally (high in summer but low in winter), or that other variables, such as the cliff variables, partly capture (low) human pressure. Similarly, the relationship between such pressures and our variables likely varies across the region and over time, which we could not take into account. Indeed, mountain ungulates in the region occur close to people if they are not poached (Ghoddousi et al., 2015; Weinberg & Malkhasyan, 2013).

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

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

Much of the currently unoccupied habitat was well-connected to extant bezoar goat populations (Figure 4). We suggest that high human pressures, and particularly poaching, likely explain why bezoar goats are not colonizing these seemingly suitable habitat patches in many parts of the Caucasus. As elsewhere, spatial data on poaching is unavailable in the Caucasus, preventing us from including poaching directly in our models. Yet poaching is a key threat to mountain ungulates in this region (Ghoddousi et al., 2019; Soofi et al., 2019; Zazanashvili & Mallon, 2009), as these species are preferred by poachers and easy to hunt (Ghoddousi et al., 2019), and because poaching is linked to transhumance grazing still found across large areas in the Caucasus (Gavashelishvili et al., 2018). Most extant bezoar goat populations we identified are confined to protected areas, even within otherwise larger patches of habitat (Figure 3, Figure S1, Supporting Information). High poaching pressure outside protected areas would render successful colonization of new patches through dispersal an unlikely scenario. Moreover, many protected areas are underfunded, particularly regarding anti-poaching patrols (Ghoddousi et al., 2019; Holden et al., 2019). If poaching extends into protected areas, dispersal events might be rare as these events typically become common only at high population densities (McCullough, 1999). High bezoar goat densities are rare throughout the Caucasus. Indeed, where bezoar goats are slowly expanding their ranges, it is in areas where stricter law enforcement has reduced poaching levels, leading to population increases, such as in eastern Nakhichevan (authors’ own observation). Yet, for most places in the Caucasus, translocations and/or anti-poaching measures will be key to foster recolonization of unoccupied habitat patches.

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

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

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

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CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHORS’ CONTRIBUTIONS
T.K., H.B., and A.G. conceived the idea and designed the study. M.A., E.A., M.G., A.M., K.A., M.S. Y.Y., P.W., and N.Z. collected and processed the raw data. H.B., T.K., and B.B. implemented the data analysis. T.K. led the writing. All co-authors critically contributed to interpretation and manuscript drafts.

ETHICS STATEMENT
This manuscript is solely the work of the authors. This study did not involve any experiments on animal or human subjects. No ethical approval was required for this research.

DATA ACCESSIBILITY STATEMENT
The final habitat map, the priority ranking of patches and the occurrence data used in the modelling are available at DRYAD (https://doi.org/10.5061/dryad.xpnvxökcv).

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**SUPPORTING INFORMATION**

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

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