


RESEARCH ARTICLE

Modelling migratory waterfowl stopover habitat while accounting for ephemeral environmental conditions

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Handling Editor: Marc-André Villard**Abstract**

1. Migratory species depend on ephemeral environmental conditions; thus, species distribution modelling (SDM) must incorporate phenological changes along migratory routes. Our overarching goal was to model habitats for three waterfowl species migrating through Eurasian grasslands (red-breasted goose [*Branta ruficollis*], taiga bean goose [*Anser fabalis fabalis*] and Bewick's swan [*Cygnus columbianus bewickii*]) while accounting for ephemeral environmental conditions. Our objectives were (a) to develop a workflow of mapping ephemeral environmental conditions, (b) model habitats for the three species and (c) evaluate the protection status of habitats in natural and agricultural landscapes. We expected water availability, particularly ephemeral spring waterbodies, to strongly influence these species' distributions.
2. We utilized MODIS data for phenological synchronization of Landsat images to create species- and season-specific metrics and land cover maps. We used Landsat-derived environmental variables, elevation and bird GPS locations in Maxent SDM. We compared locations of modelled habitats, protected areas and Ramsar sites.
3. Our land cover maps had an overall accuracy of 0.92–0.95 and captured ephemeral water extent during these species' migrations. All models had AUC scores of 0.89–0.94; distance to water, land cover and elevation were the most important variables. Modelled habitats were distributed unevenly and occurred in both natural and agricultural landscapes; 40%–76% fell within croplands. Although most croplands provide a rich food supply, their value as waterfowl habitat critically depended on water availability. Approximately 22% of potential habitat in the natural landscape, but only 3% in croplands, had some level of protection.

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4. *Synthesis and applications.* We demonstrated the potential of phenological synchronization to estimate fine-scale ephemeral environmental conditions crucial for migratory species. Modelled habitats revealed key stopover sites in both natural and agricultural landscapes. The maps showed gaps in the protected area network of Eurasian grasslands, especially in agriculture. Our workflow could be easily adapted for other species and is broadly relevant for conservation.

KEYWORDS

Bewick's swan, ephemeral habitat, Landsat, Maxent, MODIS, phenology, red-breasted goose, taiga bean goose

1 | INTRODUCTION

Agricultural land use plays a dominant role in landscape simplification (Ramankutty et al., 2002) reducing the areal extent of the most productive natural habitats, although agriculture provides wildlife with new food (Fox & Abraham, 2017; Randin et al., 2020). Spilled grains not only surpass natural food in nutrient content but also remain available far longer in fall and much earlier in spring (Fox & Abraham, 2017). Agriculture is especially important for migratory birds as they pass several months every year between breeding and wintering grounds, spending this time mostly at stopover sites (Grishchenko et al., 2019). The habitat quality at stopovers determines survival during migration as well as birds' body condition upon arrival in their breeding areas, hence, reproductive success (Lei et al., 2019; Newton, 2006). Birds can also adjust their arrival time to nesting sites by changing the time they spend at stopover sites, adapting to climate warming in polar regions (Lameris et al., 2017). Human-modified resource availability can affect species distributions as strongly as natural factors (Fox & Abraham, 2017). Resource availability appears especially important for species whose migratory routes cross vast human-modified areas, since they must adapt to land cover changes (Davis et al., 2014; Reynolds et al., 2018).

Species distribution modelling (SDM) is a widely used tool for biodiversity conservation, management and risk assessment under climate change; however, many studies still rely on easily acquired predictors, such as WorldClim BIO climate data or global land cover maps (Randin et al., 2020), though more ecologically specific predictors substantially enhance model performance (Andrew & Fox, 2020; Nagy et al., 2022; Oeser et al., 2020). Remote sensing technologies offer a variety of data on environmental conditions, while cloud computing platforms, such as Google Earth Engine accelerate data set generation and reveal fine-scale spatial and temporal changes (Gorelick et al., 2017; He et al., 2015; Randin et al., 2020). The freely available imagery of Landsat, Sentinel, MODIS and radar satellites provides a wide selection of data for mapping environmental conditions tailored to reveal species ecological preferences at different stages of annual cycles and track long-term changes. Particularly, accurate cropland mapping can identify areas of available food (spilled grain etc.), while spectral indices, such as the Normalized Difference Vegetation Index (NDVI) indicate the presence of green vegetation.

Using advanced remote sensing techniques to characterize environmental conditions, while potentially complicated, could contribute substantially to SDMs—the basis of biodiversity conservation and management (He et al., 2015; Randin et al., 2020).

Developing SDMs for migratory species is challenging because the models must account for species-specific migration timing and rapid environmental changes across large areas (Andrew & Fox, 2020). Habitat availability varies greatly due to intra-annual differences in weather conditions, making it necessary to estimate which parts of habitat are available for a given year. Dynamic SDMs of migratory animals often utilize regular time intervals (such as monthly periods) or divide a study area by latitude gradients (Andrew & Fox, 2020; Gschweng et al., 2012; Li et al., 2017). Although generally sufficient, these methods may fail to account for intra-annual variability and can be difficult to implement with multidirectional migration routes (e.g. when animals travel east before turning north). Another issue of dynamic SDMs is the availability of fine-scale environmental data within short timeframes. Landsat/Sentinel data are rarely included in dynamic SDMs as cloud-free image coverage is insufficient for large areas within short migration periods (Huseby et al., 2005; Lewińska et al., 2024), while frequently used MODIS images (Andrew & Fox, 2020; Gschweng et al., 2012; Li et al., 2017) lack spatial resolution (Mertes & Jetz, 2018).

Phenological synchronization of Landsat/Sentinel data using dense MODIS time series (Isaacson et al., 2012) can account for within- and between-year variability and overcomes the scarcity of Landsat/Sentinel data. However, this approach is not commonly integrated into SDM. The main idea of the phenological synchronization is that frequent MODIS observations provide phenological references, such as snowmelt dates, and enable the delineation of zones with similar phenological stages for each study year. Combining Landsat/Sentinel data from different years with reference to phenological zones can provide enough fine-scale images covering large areas and representing similar environmental conditions, independent of actual calendar dates. Since migratory birds track major phenological changes (Wang et al., 2019), Landsat/Sentinel data combined in this way accurately reflect environmental conditions exactly at the time of migratory bird presence.

Eurasian grasslands provide a great opportunity to implement phenological synchronization for capturing ephemeral conditions

during migration, thanks to their highly diverse landscape with considerable interannual variability, season-dependent, often ephemeral, resource availability and extensive but unevenly distributed cereal-dominated croplands (Medeu, 2010, Rosstat, annual reports, n.d.). Several migratory flyways cross Eurasian grasslands, including Mediterranean/Black Sea, East Asia/East Africa, Central Asian and East Asia/Australasia (Boere & Stroud, 2006).

We studied migratory stopover habitats of three waterfowl species of conservation concern (Environment European Commission; Directorate-General for Environment, 2022): red-breasted goose (*Branta ruficollis*), taiga bean goose (*Anser fabalis fabalis*) and Bewick's swan (*Cygnus columbianus bewickii*). The red-breasted goose is classified as 'Vulnerable' on the IUCN Red List, with a declining population trend (BirdLife International, 2017). The taiga bean goose is declining and was recently included in the Russian Red List (RDBRF, 2020), while the population status of swans migrating through Central Asia is unknown (Environment European Commission; Directorate-General for Environment, 2022; Nagy et al., 2012). All the species nest in the Arctic and migrate through northern Kazakhstan and European Russia to wintering grounds in China, Southern Europe, Central Asia and the Caspian Sea (Boere & Stroud, 2006). Understanding what areas are used as stopover sites and the main factors associated with these areas is crucial for the conservation of these species, especially because migratory bird habitats appear underprotected in Central Asia (Runge et al., 2015).

Our main goal was to model habitats for the three waterfowl species during their migration across northern Kazakhstan and European Russia, accounting for species-specific ecological preferences.

Specifically, we (a) tested Landsat image phenological synchronization to create species-relevant and season-specific environmental variables for SDM, (b) modelled potential habitats for each species during spring and fall migration, and (c) evaluated the protection status of the potential habitats. We expected agriculture to provide important habitat for migratory waterfowl because it occupies the most water-rich parts of the otherwise arid landscapes and offers spilled grain as abundant food resources. Although the croplands produce cereals nearly everywhere (Medeu, 2010, Rosstat, annual reports, n.d.), and thus provide similar food resources, we expected to find strongly uneven species distributions within agriculture, depending on fine-scale seasonal variations in water availability. Furthermore, we expected that variables associated with the spatial distribution of water and croplands would contribute most to model performance.

2 | METHODS

2.1 | Study area

Our study area encompassed the western Eurasian grasslands, including northern Kazakhstan and adjacent parts of Russia (Figure 1). It is a 3-million km² plain bordered by the Volga, Don and Manych rivers on the west and by the Altai mountains to the east. There is a northwest to southeast gradient in vegetation and agriculture. In the western and northern parts, natural vegetation is largely converted into croplands (hereafter 'the agricultural belt'), while in central and

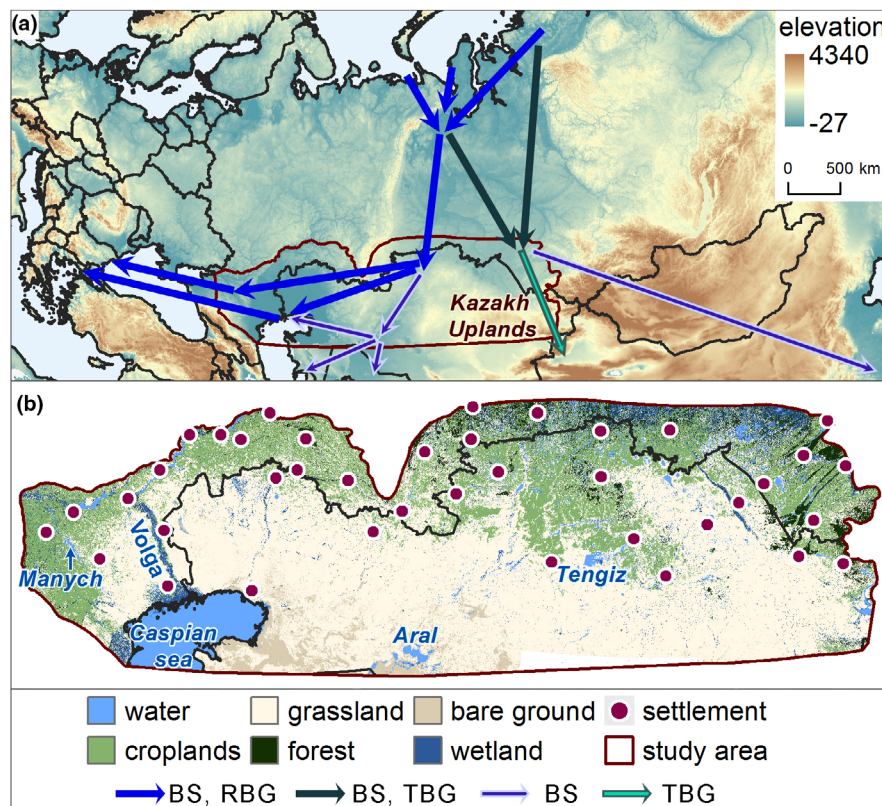


FIGURE 1 (a) Main directions of fall migrations of Bewick's swan (BS), red-breasted goose (RBG) and taiga bean goose (TBG), based on GPS tracks and literature data. Spring migrations follow the same routes in the opposite direction. (b) Land cover.

southern regions, natural grasslands persist and are used as pastures. Water resources include the Caspian and Aral seas, five major rivers, and multiple lakes and ponds. Northern lakes are mostly permanent and freshwater; southern are often temporary and saline (Kotlyakov & Kravchenko, 2007; Medeu, 2010).

Crossed by four Palearctic flyways, the study area hosts over 100 Important Bird and Biodiversity Areas. Millions of waterfowl nesting in the Arctic and Siberia migrate through the West-Siberian Plain to Kazakhstan and Altai Province in Russia (Zuban et al., 2020). The Kazakh Uplands naturally divide one route into two trajectories; the western route continues to Eastern Europe and southern Central Asia, while the eastern route traverses Mongolia towards China (Boere & Stroud, 2006). We used the watersheds of the Kazakh Uplands to define specific areas for modelling the distribution of each species.

2.2 | GPS tracker data

In 2015–2022, we tracked migrations of 6 taiga bean geese, 30 red-breasted geese and 42 Bewick's swans with various models of GPS-GSM solar-powered trackers from different manufacturers, with a mean accuracy of 12.3 ± 7.1 m. All required permits were obtained from the proper Russian, Kazakh and Bulgarian authorities (Severtsov Institute of Ecology and Evolution, the Russian Academy of Sciences, Russia; the Ministry of Environment and Water, Bulgaria; and the Forestry and Wildlife Committee, Ministry of Ecology, Geology and Natural Resources of the Republic of Kazakhstan; Appendix S1). We extracted all GPS points within the study area and estimated core areas for each bird with the R package 'track2KBA' (Beal et al., 2021). The package calculates the utilization distribution of animals based on kernel density estimation from the 'adehabitatHR' R-package (Calenge, 2006). We used core areas to separate locations during flights from those acquired during foraging and resting time because only the latter represent habitat choice (Li et al., 2017). From each core area, we randomly selected subsets of points lying at least 5000 m and 1 day apart and separated from other bird locations by a minimum of 5000 m (Table S1.2, Appendix S1.2). We created spring and fall migration point sets for red-breasted geese and Bewick's swans, but only spring sets for taiga bean geese, which had no long fall stops within the study area (Appendix S1). For each species, we divided the tracks by year into two subsets, using one for training and the other for validation (Tables S1.3–S1.7).

2.3 | Environmental variables

We employed a combination of static, species-specific dynamic and hybrid environmental variables as SDM input. Static variables were the same for all species, and dynamic variables were specific to each species and migration season. Hybrid variables consisted of land cover maps with static and dynamic land cover classes (Table 1). Creating fine-scale dynamic variables required (a) evaluating which

TABLE 1 Variables used for SDM.

Variables		Type	Source
Elevation		Static	Copernicus DEM (30m)
Distance from settlements		Static	Open Street Maps
NDVI		Dynamic	Landsat8
Bare Soil Index		Dynamic	Landsat8
Brightness		Dynamic	Landsat8
Distance from water		Dynamic	Land cover maps
Water area		Dynamic	Land cover maps
Land cover maps		Hybrid	
Land cover maps classes	Forest	Static	Landsat8
	Grassland	Static	Landsat8
	Cropland	Static	Landsat8
	Bare ground	Dynamic	Landsat8
	Water	Dynamic	Landsat8
	Ice	Dynamic	MODIS
	Wetland	Dynamic	Landsat8

part of habitats within a migratory corridor is available at each migration step in a given year; (b) a sufficient number of satellite images, covering areas available to birds. Due to the limited availability of Landsat imagery, we utilized phenological synchronization (Isaacson et al., 2012) to combine images from different years (Oeser et al., 2020) while accounting for phenological variability. First, we mapped phenological zones across the entire study area for each study year. Specifically, we identified the first day without snow cover ('snowmelt') for spring migration (Wang et al., 2019) and the first day with a surface temperature of 0°C ('frost') for fall migration (Xu & Si, 2019) as the 'reference phenology'. To delineate phenological zones, we used MODIS snow cover and land surface temperature data (Riggs et al., 2019; Wan, 2013), assigning each pixel a value referring to 'snowmelt' or 'frost' day of the year. We applied X-means clustering (Pelleg & Moore, 2000) to determine the number of phenological zones for each year and Jenks Natural Breaks (de Smith et al., 2018) to delineate phenologically similar zones. Second, we determined the period, from first to last day, when each species was within each phenological zone. For each zone in each year, we selected Landsat8 images that matched each species' presence time. Then, for each species and season, we combined all selected images and calculated mean, median, 20 and 80 percentiles, and standard deviation for a set of spectral indices commonly used in remote sensing and SDM. We used Normalized Difference Vegetation Index (NDVI) as a proxy of vegetation, vegetation water content (Normalized Difference Moisture Index [NDMI]), amount of bare ground (Bare Soil Index [BSI]), and brightness, greenness, and wetness from the Tasseled Cap Transformation (representing ground and vegetation reflectance, and soil moisture, respectively) (Oeser et al., 2020). Since all remote sensing indices were derived

from Landsat8 bands, autocorrelation was a potential concern. We calculated Spearman correlation coefficients and from any pair of environmental variables with $r > 0.75$, we removed one of them (Appendix S2). The final set of predictors included brightness, BSI, NDVI, distance to the closest open water and settlements, waterbody areas, elevation and land cover maps. We repeated these steps for each species and each season. Using these metrics, we created the dynamic land cover classes and used median values as the species-specific dynamic environmental variables.

To generate the hybrid land cover maps, we first created a static land cover map and a set of dynamic maps for each species and season. We then merged the static land cover map with each dynamic map, prioritizing the values from the dynamic maps (Appendix S3). We used this approach because different land cover classes require different sets of satellite images for best results. For instance, grasslands and croplands have similar spectral reflectance, so their correct classification requires satellite images taken throughout the active vegetation growing season (Dara et al., 2018), making it impossible to identify seasonal changes. Our approach kept static classes well-separated while adding necessary season-dependent information. We created all maps in Google Earth Engine (Gorelick et al., 2017) using Random Forest classifications (Appendix S3). To evaluate the accuracy of the final hybrid maps, we created sets of 100 random points for each land cover class on each map and visually interpreted Landsat images and high-resolution images from Google Earth to label the validation samples. Using these validation points, we calculated overall, user's, and producer's accuracy (Olofsson et al., 2014). Finally, we computed the distance from the closest open water and waterbody areas separately for each hybrid map. In the waterbody area layer, each pixel within a given waterbody was assigned the value of that waterbody's area, while all pixels outside the water class were assigned a value of 0.

2.4 | Species distributions models

We used the Maxent algorithm (Phillips et al., 2006) because it requires presence data only, and provides accurate estimation of habitats even for a low number of tracked individuals (Gschweng et al., 2012). We created specific modelling areas for each species based on literature, field observations collected by the authors and shared by Russian and Kazakh ornithological societies, analyses of bird ring recoveries, and our GPS tracking data. A preliminary analysis of the GPS data showed that the maximum distance between stopover sites ranged 500 to 1200 km, while birds of our species can fly 1400 to 2300 km without stops longer than 1 day. This suggests that theoretically available areas are much larger than the areas used. Consequently, we restricted our modelling areas to those that: (1) were identified by experts or in literature as presence locations of our species, (2) fell within the western Eurasian grasslands, where both agricultural and natural habitats occur, and (3) encompassed our GPS tracking data. For each species-specific modelling area, we created 10,000 random background points (Merow et al., 2013)

and then used all features in Maxent, including the threshold. We trained, tuned and validated our models in Maxent (version 3.4.4) using 'samples with data' format; however, we created habitat maps in Google Earth Engine (Gorelick et al., 2017) with the same settings (including default Maxent beta regularization parameters). We used the equal training sensitivity and specificity threshold to convert probability maps into binary ones and compare spring and fall stopover habitats. We evaluated models using the validation point sets as independent data. Furthermore, we used presence locations from literature (Appendix S6) in empirical validation. Although the literature-based data do not represent the full extent of bird migration, and their availability differs among species, they helped us to assess whether modelled habitats reflected empirical patterns of the species distributions.

2.5 | Protection status of potential habitats

To determine the proportion of stopover habitats in natural versus transformed landscape, we assigned all habitats to either 'cropland' or 'natural' (i.e. any non-cropland) classes using our static land cover maps. Specifically, pixels within the static cropland category were counted as cropland even if updated to seasonal water in our dynamic maps. We used the World Database on Protected Areas (UNEP-WCMC and IUCN, 2023, including Ramsar sites) to determine protection status, regardless of protection level. Then, we calculated proportions of the 'cropland' and 'natural' modelled habitats within and outside of protected areas.

3 | RESULTS

3.1 | Land cover maps

We created a set of land cover maps and environmental metrics representing conditions specific to three species and migration seasons. The land cover maps had an overall accuracy of 0.919 ± 0.033 to 0.952 ± 0.024 , with user's and producer's accuracy of the water class 0.910 ± 0.056 to 0.970 ± 0.034 and $0.7-0.95$ (Appendix S4). As the fall land cover maps were similar for Bewick's swan and red-breasted goose, we selected the higher-accuracy map and used it for both species. In spring, however, water extent was unique for each species, depending on region and migration timing. With Bewick's swan and red-breasted goose, water extent also varied between spring and fall, so distance to water was specific to each species and season.

3.2 | Species distribution modelling

The contribution of variables to models varied among species and seasons. However, a negative association with distance to water and NDVI, a positive association with distance to settlements and

a non-linear association with elevation were found for all three species, and these variables were most important for each species. For Bewick's swan, distance to water was the most important variable in spring and fall models; for red-breasted goose, distance to water and land cover were the most important variables in spring and fall models, respectively. For taiga bean goose, land cover was the most important variable. Distance to settlements contributed notably only to the taiga bean goose model and was of little importance in other species and seasons. Remote sensing indices contributed moderately to all models, NDVI being the most important one. Among land cover classes, water, wetlands and croplands provided the highest quality habitats. Elevation ranged from -26 to 1000m a.s.l. and had a non-linear relationship with habitat quality, with peaks at low and middle altitudes where larger waterbodies and croplands are located. These peaks were species-specific, yet all shared the same general pattern (Figure 2, Appendix S5).

Modelled habitats for all species and seasons were mainly located either within the agricultural belt or inside the Caspian, the Aral and the Manych depressions with large waterbodies. Notably smaller areas appeared suitable in natural grasslands. Habitat spatial patterns varied among species and seasons (Figure 3), reflecting different ecological requirements of the species and fluctuations in resource availability, depending on seasons and migration timing. Remarkably, large lakes were not predicted as habitats in spring for Bewick's swan and taiga bean goose. The overlap between spring

and fall habitats was small for red-breasted goose and Bewick's swan (22% and 28%, respectively).

All the models had training AUC scores of 0.934–0.967 and test AUC scores of 0.886–0.939, demonstrating high discrimination power (Appendix S5). Comparing our maps with literature data (Appendix S6) showed that areas noted as consistently used by the study species were within our predicted habitats. Moreover, areas mentioned as rarely visited by our species fell within areas we classified as non-habitats.

3.3 | Spatial distribution and protection status of modelled habitats

Croplands constituted around 20% of our study area; however, they contained 48% of modelled habitats, though this proportion varied greatly between species and seasons. Within agriculture, stopover habitats were distributed unevenly (Figure 4), located mainly in central and eastern parts. In natural landscapes, the habitats were predictably found at permanent waterbodies, in ephemeral wetlands, and, in the north-east, along the transition to the boreal zone.

Approximately 13% of modelled habitats fell within protected areas or Ramsar sites (hereafter 'protected habitats' regardless of their actual protection status). Most protected habitats occurred in natural landscapes, mainly in the Caspian Sea. We found that 22%

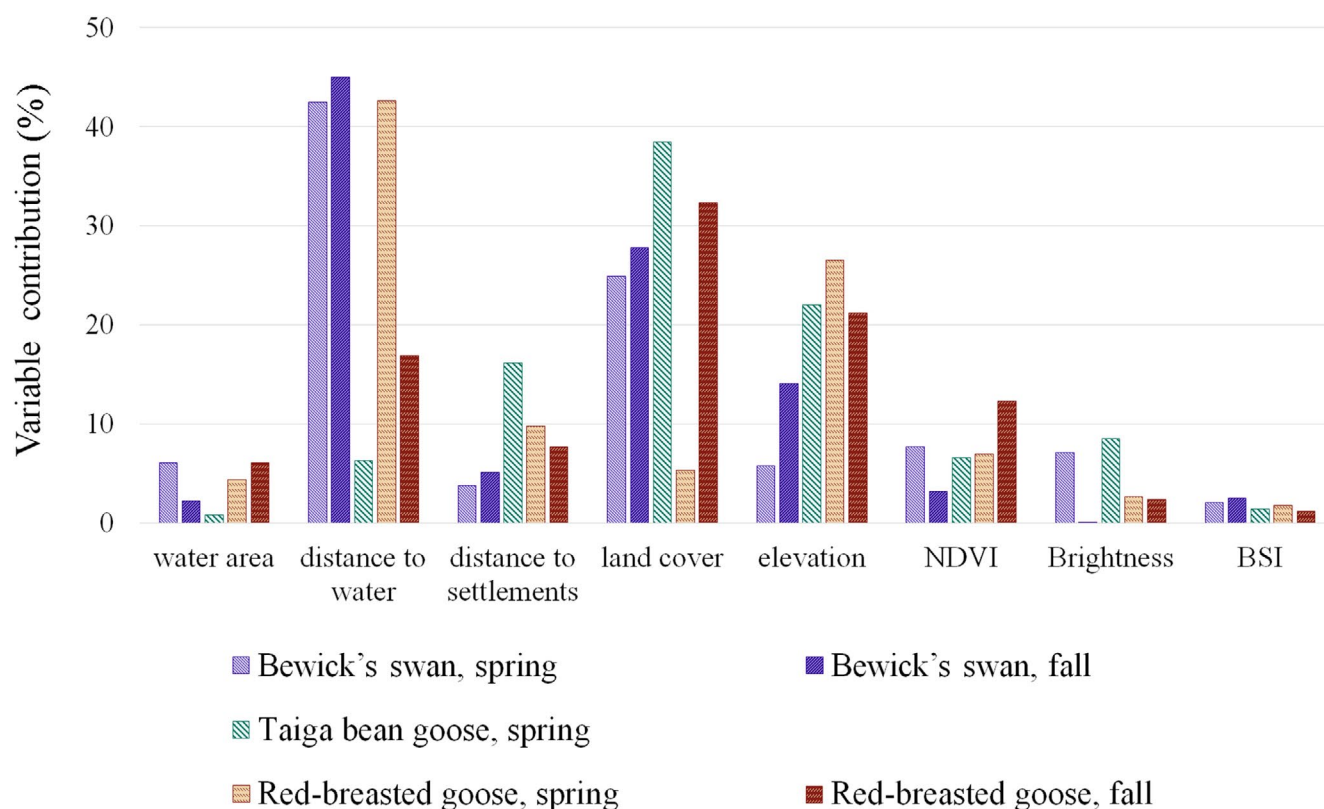


FIGURE 2 Variable contribution to distribution models (according to percent contribution of each variable in the output from Maxent) of three species during spring and fall migration. Normalized Difference Vegetation Index (NDVI) quantifies vegetation greenness, brightness quantifies ground reflectance, Bare Soil Index (BSI) identifies bare soil.

of habitats in natural landscapes were protected, but only 3% of protected habitats occurred in agriculture. For each species, the proportion of protected habitats was positively associated with habitat proportion in natural landscape. For Bewick's swan, the amount of natural habitats, and of protected habitats, was highest for the fall migration. Taiga bean goose showed the greatest proportion of habitats located in agriculture and thus a very low proportion was protected. Red-breasted goose used natural habitats in spring more than in fall, which resulted in a larger proportion of protected habitats during spring migration (Figure 5).

4 | DISCUSSION

Phenological synchronization made it possible to combine multi-year satellite images, while accounting for intra-annual variability, and to map fine-scale ephemeral land cover. Habitat distribution was strongly uneven, with a high proportion (40% to 75%) of modelled

habitats within croplands. There was also considerable difference in habitat use by each species between seasons, and among species during spring, mainly due to changes in water availability. Our results represent the first successful attempts to map habitat for Bewick's swan, taiga bean goose, and red-breasted goose in northern Kazakhstan and European Russia. We found that habitat protection is minimal for all three species, especially in agricultural landscapes.

Agricultural landscapes are well-known as habitats for migratory waterfowl in North America and Europe, where natural biomes are largely transformed or degraded (Davis et al., 2014), while croplands provide abundant high-quality food (Fox & Abraham, 2017). Regardless of food availability, habitats in agriculture depend on fine-scale landscape features affecting water availability. In Europe, habitats in croplands are associated with seashore, lakes or wetlands (Davis et al., 2014; Harrison et al., 2018). Flooded harvested rice fields are typical waterfowl habitat in California (Reynolds et al., 2018), while in the Southern Great Plains, waterfowl use seasonally flooded playas (Davis et al., 2014).

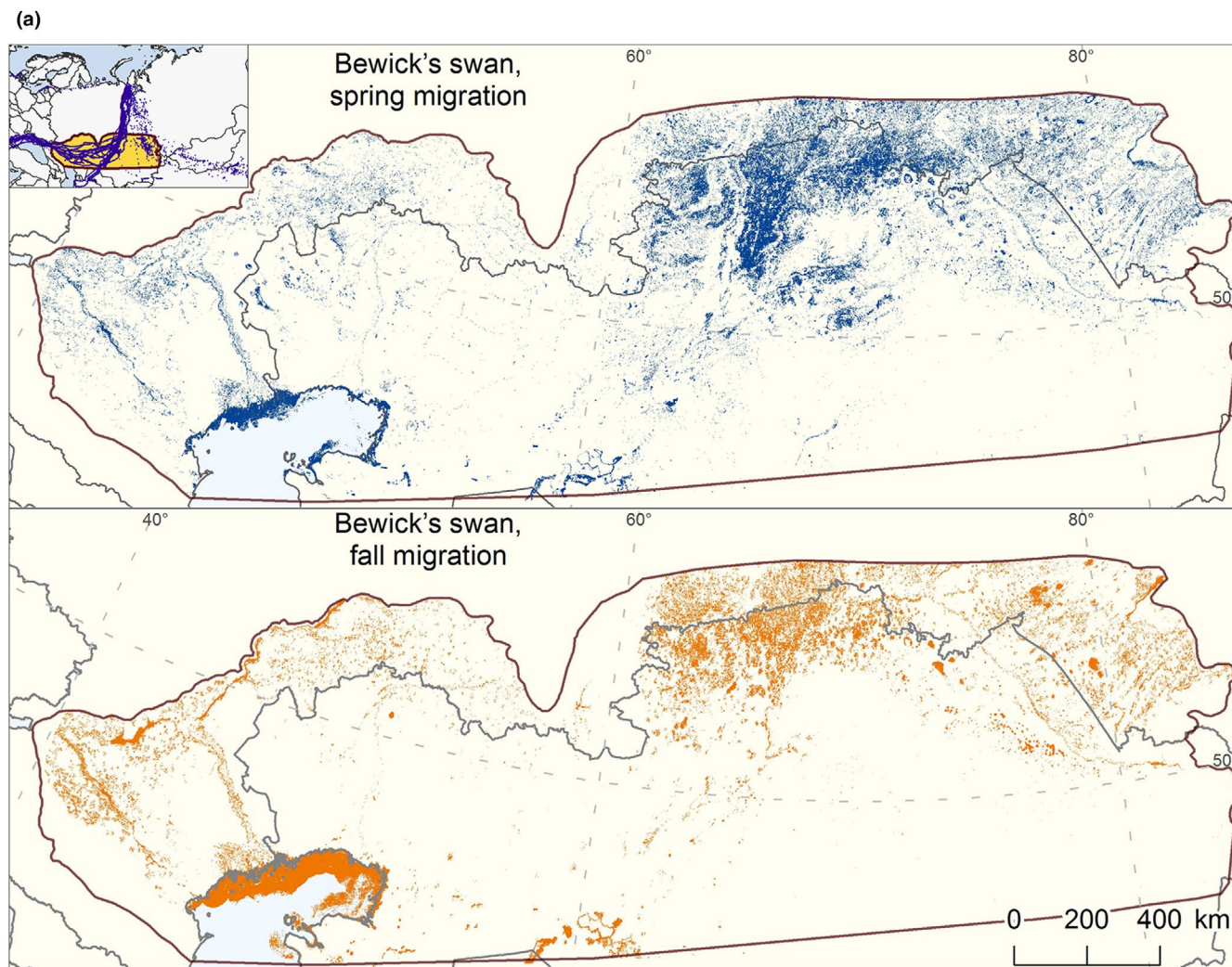


FIGURE 3 Modelled habitat for three species (a—Bewick's swan, b—red-breasted goose and c—taiga bean goose) during migration. For the taiga bean goose, only spring migration habitats are represented, as this species does not make long stops in the study area during fall migration. Inserts show species' GPS tracks and the areas of modelling (yellow).

(b)

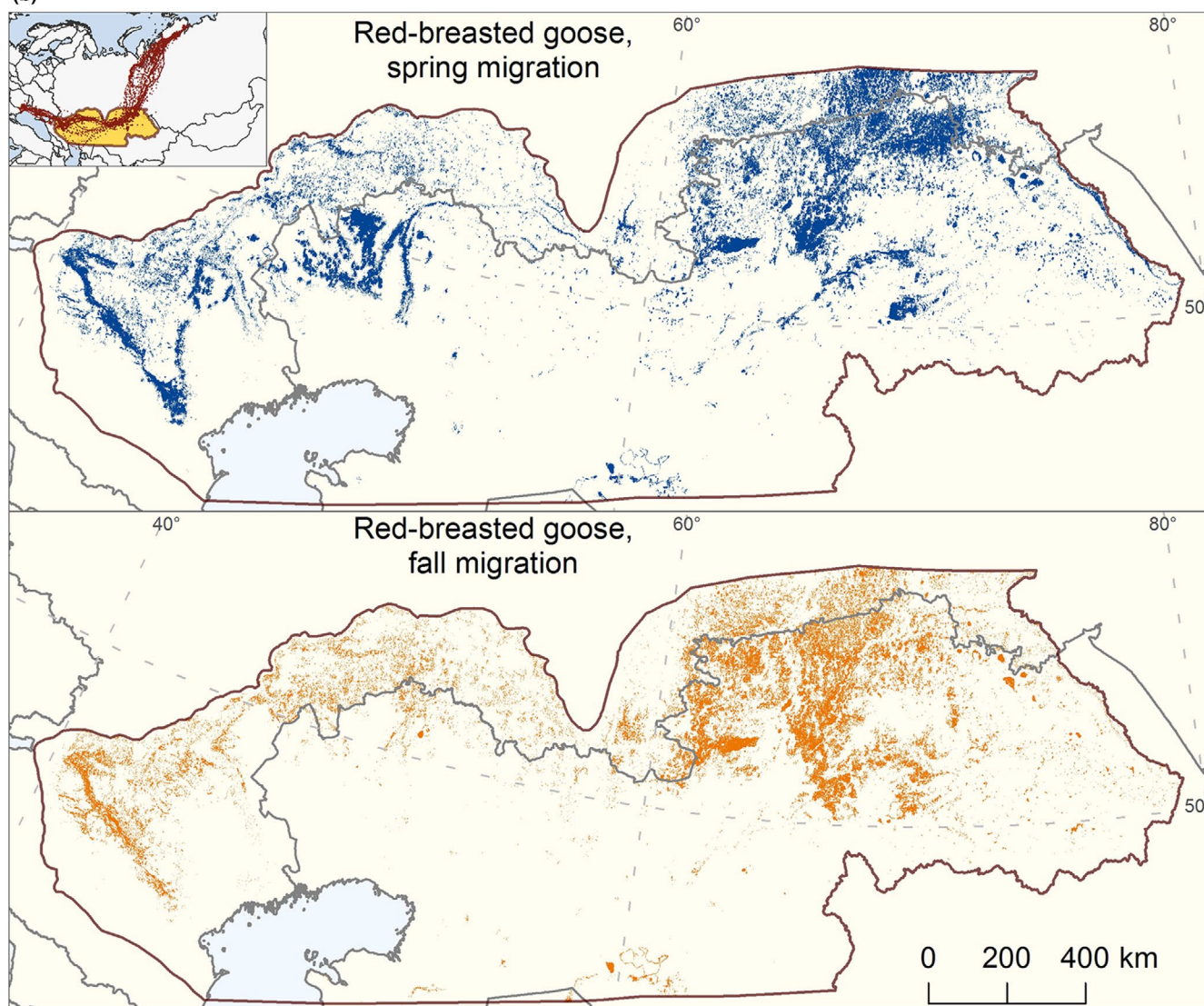


FIGURE 3 (Continued)

In our study area, spring water availability depends on ice and snow accumulation, melting rates and drying of ephemeral waterbodies. In early spring, larger waterbodies and wetlands are covered with ice and unavailable to birds. Ephemeral pools emerge as soon as snow begins to melt, but they dry out within weeks (Appendix S7). In some parts of north Kazakhstan, numerous shallow depressions scattered across croplands and grasslands rapidly accumulate melt water, providing habitats 10–15 days before ice melts on permanent lakes. In the easternmost area, forest belts planted between fields accumulate snow; when it melts, fresh pools become widespread, even on flat surfaces, but for a very short time. Thus, even a small difference in migration timing leads to major changes in water availability (Appendix S7)—a reason for within-season differences in habitat extent. In the western portion of the agricultural belt, no landscape features favour the occurrence of shallow temporary waterbodies, while permanent lakes and ponds become ice-free rather late in spring, making these areas less suitable for migratory waterfowl.

In fall, only larger permanent waterbodies remain, which explains the similarity in the fall land cover maps for Bewick's swan and red-breasted goose. Potential habitats for these two species are generally concentrated in croplands around permanent lakes. Habitats available in both seasons are thus limited to areas where shallow depressions/forest belts and permanent lakes co-occur.

The main portion of modelled habitats in natural landscapes was predictably associated with the two largest permanent waterbodies. Manych Lake, with surrounding croplands and grasslands, can accommodate the entire population of red-breasted goose, while the Caspian Sea is a key stopover for Bewick's swan. Moreover, both remain largely unfrozen, allowing birds to wait for good migration conditions, or even stay all winter if the weather is favourable. Outside Manych Lake and the Caspian Sea basins, only a few habitats were found in natural grasslands because in Kazakhstan and Russia they mostly remain where water bodies are scarce.

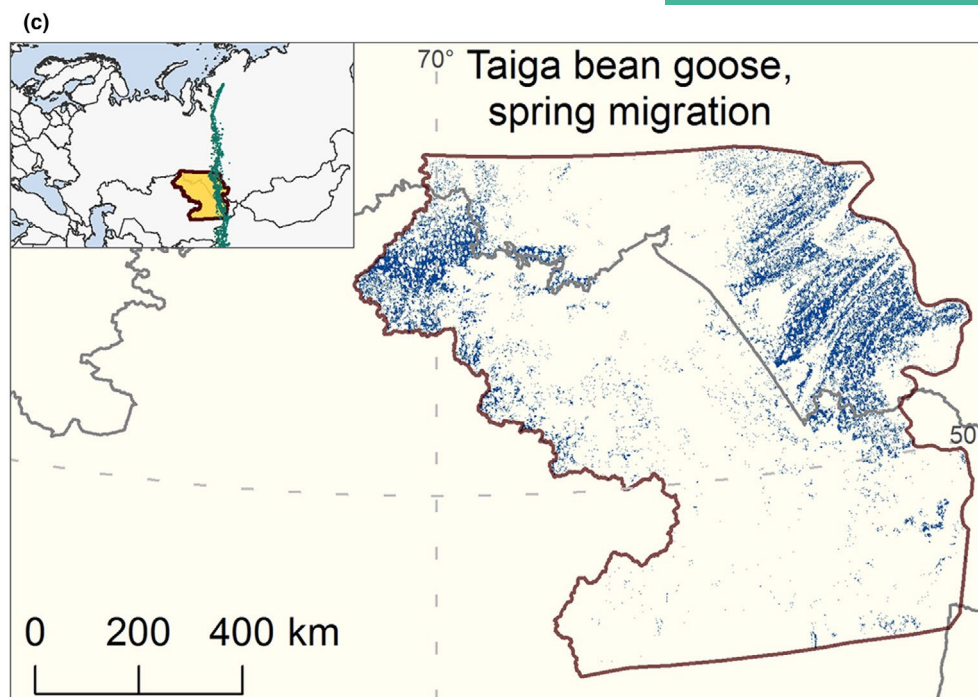


FIGURE 3 (Continued)

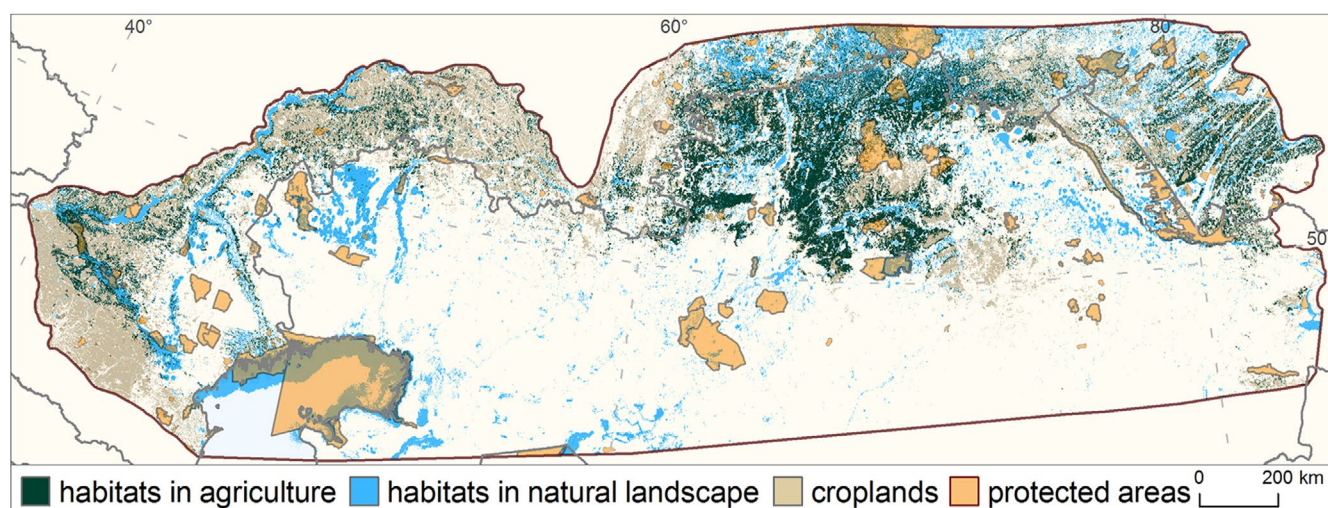


FIGURE 4 Modelled habitats of three species in natural and agricultural landscapes, with protected areas overlaid.

Stopover site protection is critically important because the loss of even a small part of *en-route* habitats could negatively affect the whole population (Runge et al., 2015). Particularly, climate change could cause flyway collapse due to phenological mismatch in green food availability between stopover sites and breeding grounds (Nagy et al., 2022; Wei et al., 2024). Habitats within croplands are especially important as they provide abundant resources when snowmelt begins—several weeks before the start of a 'green wave' of vegetation productivity. Cropland supplementation allows waterfowl to migrate earlier, helping mitigate phenological mismatch. Our findings agree with models demonstrating that waterfowl track snow melt (Li et al., 2020; Wang et al., 2019).

Revealing fine-scale landscape features affecting ephemeral conditions required by species is essential for management actions. Most conservation efforts focus on natural habitats (Nagy et al., 2022), yet protecting agricultural sites with particular landscape features is also important (Davis et al., 2014; Reynolds et al., 2018). For instance, shallow depressions in croplands are prone to soil erosion and sedimentation. In the US Playa Lakes area (a landscape similar to our study area), such degradation negatively impacts the hydrological regime of surrounding areas and compromises waterfowl habitats (Davis et al., 2014). Preventing excessive sedimentation by preserving natural vegetation around depressions and promoting snow

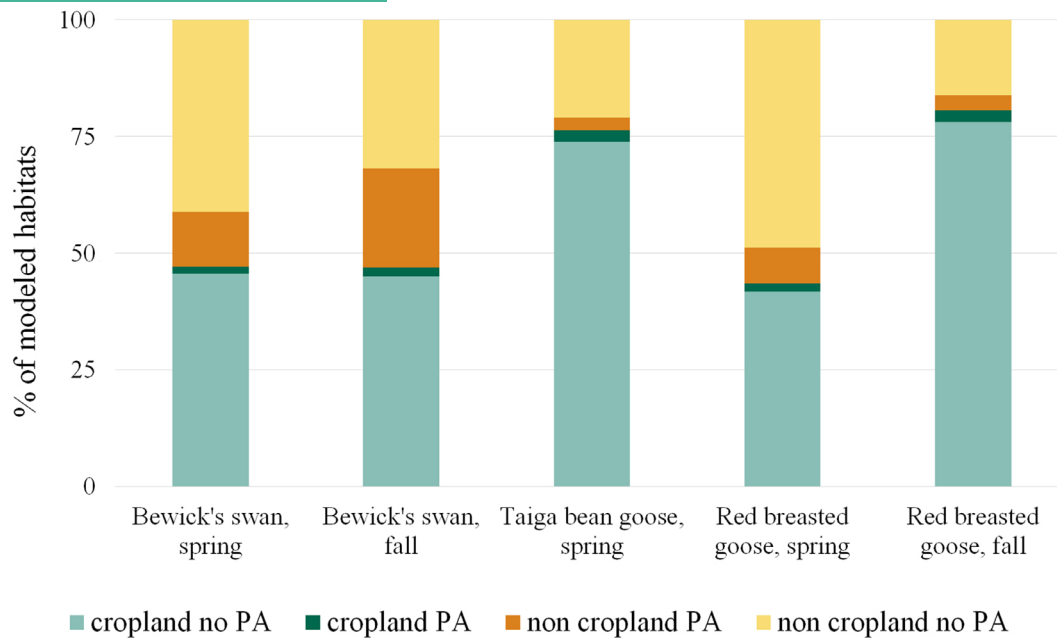


FIGURE 5 Proportions of modelled 'agricultural' and 'natural' habitats for three waterfowl species during migration within and outside of protected areas and Ramsar sites.

accumulation could maintain the conditions necessary for waterfowl stopover habitat (Joint Venture Playa Lakes, 2014). Besides important habitats, these measures would also support the overall hydrological regime, securing future agricultural production.

Given the importance of water to waterfowl (Li et al., 2017), we expected that distance to water would be the most important variable in our SDMs. However, in two of five models, land cover was the most important variable (red-breasted goose, fall migration, taiga bean goose, spring migration), while elevation was the second most important variable (Figure 2). The importance of land cover is easily understood since all three species prefer water and croplands but avoid forests and bare ground. The importance of elevation is less straightforward to interpret as differences in elevation in our study area are relatively modest. We suggest that elevation influences the spatial distribution of agriculture, large water bodies and human pressure. Notably, NDVI, our proxy for green vegetation, was not among the most important variables in any models. The negative relationship between NDVI and habitat suitability indicates that migrating waterfowl do not depend on green food availability. Since negative NDVI values indicate water, the negative relationship also highlights the importance of water as a critical stopover resource.

Human activity can force birds to concentrate in the least disturbed areas (Davis et al., 2014). Kazakhstan has several strictly protected private areas where hunting is limited (Rozenfeld et al., 2012). Such sites attract up to a million geese during spring migration (Rozenfeld et al., 2012), making naturally uneven waterfowl distribution even stronger. The Russian part of the study area has no well-protected refuges, which probably explains why the taiga bean

goose makes no long stops there in fall (Appendix S1). Incorporating human pressure patterns into SDMs is complicated because the necessary information is generally unavailable. However, the high importance of variables that cannot directly affect species distributions, like elevation in generally flat country, suggests hidden factors at work.

Spring hunting has strong negative effects on waterfowl populations (Juillet et al., 2012). Strictly limited in Kazakhstan (MARK, 2015) but allowed in Russia (MNRFF, 2020), it could explain why distance to settlements has notably higher importance for taiga bean goose whose habitats mainly occur in Russia. Precise species distribution modelling can reveal small differences in preferred habitats in vulnerable and game species (Piironen et al., 2022). This information can be used to limit hunting pressure in critical areas.

Fine-scale environmental maps could greatly improve SDM, although creating them is challenging (He et al., 2015; Huseby et al., 2005) due to limited availability of medium-resolution satellite observations. Although image availability has increased since the launches of Landsat 8, 9 and Sentinel-2, it still might not suffice for areas with frequent clouds or for mapping short-lived environmental states. Furthermore, only Landsat 4, 5 and 7 provide data for 1984–2015, which makes them irreplaceable for studies of that period. Phenological synchronization of satellite images is a useful approach to map ephemeral environmental conditions regardless of intra-annual differences in weather. We used transitions in snow cover and surface temperature for phenological synchronization; yet frequent MODIS/VIIIRS data can also be used to calculate other phenological events relevant for different target species (Andrew & Fox, 2020).

5 | CONCLUSIONS

We demonstrated that fine-scale maps representing ephemeral environmental conditions at the time of bird presence are crucial for SDM performance because they reveal landscape features affecting resource availability. Our workflow based on combining MODIS and Landsat data and integrating different maps is flexible and easily adjustable to a wide range of wildlife studies. Knowing seasonal resource dynamics is critical for understanding habitat suitability in the migratory phase of the annual cycle. Quantifying the role of fine-scale landscape features in resource availability is essential for effective habitat management, as well as planning new protected areas and developing species conservation strategies, especially in human-developed landscapes.

AUTHOR CONTRIBUTIONS

Natalia Rogova conceptualized the ideas, conducted the data analysis, created the maps and led the writing of the manuscript. Mikhail Iliev, Nikolai Petkov, Sonia Rozenfeld, Alexey Timoshenko, Didier Vangeluwe and Ivan A. Zuban conducted the fieldwork and edited the manuscript. Anna M. Pidgeon and Volker C. Radeloff conceptualized the ideas, contributed to writing the manuscript and supervised the research.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the SILVIS Lab website <https://silvis.for-est.wisc.edu/webmaps/eurasian-grassland-waterfowl-habitats/> (Rogova et al., 2025).

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SUPPORTING INFORMATION

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

Appendix S1. General information on species and GPS tracking.

Figure S1. GPS data filtering. (a) Extracting stopover sites and core areas. Area outlined in green—a stopover site; I—long migration paths; II—core areas; III—short-distance movements between core areas. (b) Example of a core area. Blue buffers around points indicate resting sites; yellow buffers indicate foraging sites (resting and foraging sites were distinguished based on time of day); points without buffers represent bird movements between resting and foraging sites.

Table S1.1. List of tracked birds.

Table S1.2. Amount of training and verification points for SDM.

Table S1.3. List of tracked Bewick's swans assigned to training and validation datasets for species distribution modelling during spring migration.

Table S1.4. List of tracked Bewick's swans assigned to training and validation datasets for species distribution modelling during fall migration.

Table S1.5. List of tracked Red-breasted geese assigned to training and validation datasets for species distribution modelling during spring migration.

Table S1.6. List of tracked Red-breasted geese assigned to training and validation datasets for species distribution modelling during fall migration.

Table S1.7. List of tracked Taiga bean goose assigned to training and validation datasets for species distribution modelling during fall migration.

Appendix S2. Spearman correlation matrices.

Figure S2.1. Spearman correlation matrix for Bewick's swan spring distribution predictors.

Figure S2.2. Spearman correlation matrix for Bewick's swan and red-breasted goose fall distribution predictors.

Figure S2.3. Spearman correlation matrix for red-breasted goose spring distribution predictors.

Figure S2.4. Spearman correlation matrix for taiga bean goose spring distribution predictors.

Appendix S3. Land cover mapping.

Appendix S4. Accuracy of the land cover maps used for species distribution modelling.

Table S4.1. Overall accuracy of the land cover maps.

Table S4.2. Accuracy of the land cover maps and area proportions for Bewick's swan, spring.

Table S4.3. Accuracy of the land cover maps and area proportions for Bewick's swan and red-breasted goose, fall.

Table S4.4. Accuracy of the land cover maps and area proportions for red-breasted goose, spring.

Table S4.5. Accuracy of the land cover maps and area proportions for taiga bean goose, spring.

Appendix S5. Variables contributions and permutation importance.

Table S5.1. Relative contributions of the variables to the Maxent models.

Table S5.2. Permutation importance of the variables for the Maxent models.

Table S5.3. Area under the receiver-operator curve.

Figure S5.1. Jackknife of AUC for Bewick's swan, spring migration.

Figure S5.2. Jackknife of AUC for Bewick's swan, fall migration.

Figure S5.3. Jackknife of AUC for red-breasted goose, spring migration.

Figure S5.4. Jackknife of AUC for red-breasted goose, fall migration.

Figure S5.5. Jackknife of AUC for taiga bean goose, spring migration.

Figure S5.6. Response curves for Bewick's swan, spring migration.

Figure S5.7. Response curves for Bewick's swan, fall migration.

Figure S5.9. Response curves for Red-breasted goose, fall migration.

Figure S5.10. Response curves for Taiga bean goose, fall migration.

Appendix S6. Empirical validation.

Appendix S7. Changes in water availability in agricultural landscape.

Figure S7. Changes in water availability in the North Kazakhstan (top) and in Altai province, Russia (bottom) during spring.

Appendix S8. Annual variability in spring snow cover.

Figure S8.1. Annual spring phenological zones based on the first day without snow cover. Colour gradient indicates day of year.

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