Understanding habitat selection of wild yak *Bos mutus* on the Tibetan Plateau

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Abstract: This study tests a series of hypotheses on drivers of habitat selection in wild yak *Bos mutus* by combining distribution-wide sighting data with species distribution modelling approaches. Results unveil climatic conditions as being of paramount importance to shaping wild yak's distribution on the Tibetan Plateau. Habitat selection patterns were seasonal, with wild yaks appearing to select areas closer to villages during the vegetation-growing season. Unexpectedly, our index of forage quantity had a limited effect in determining the distribution of the species. Altogether, our work suggests that expected changes in climate for this region could strongly impact habitat availability for wild yaks, calling for more attention to be provided to the unique wildlife found in this ecosystem.

Keywords: Climate change, GAM, highland, large herbivore, MaxEnt, Random forest, seasonal habitats, species distribution model

Introduction

The wild yak (*Bos mutus*) is a rare yet iconic large herbivore species inhabiting one of the highest places on Earth, namely the Tibetan plateau. Being among the largest bovids on Earth, wild yaks are also the largest native animal in their range, which used to include China (Gansu, Sichuan, Xinjiang, Tibet, Qinghai), northern India (Ladak), and Nepal (Schaller & Liu, 1996). Mainly due to excessive hunting, wild yak numbers collapsed in the 20th century; the total number of mature individuals was last estimated to be around 15,000 in 1995 (Schaller, 1998). The species is currently classified as Vulnerable by the IUCN; most of the remaining individuals are found in isolated and fragmented populations in the central and northern parts of Tibetan plateau. Remnant populations face escalating threats from anthropogenic activities, such as increasing competition with livestock for good grazing areas and expanding road systems that cause degradation of their habitats (Leslie & Schaller, 2009). Climate change is also expected impact the long-term availability of suitable habitats for the species (Schaller, 1998), although little quantified and spatially-explicit information is currently available to inform discussions on potential management options. More broadly, quantitative information on the factors driving patterns in the seasonal distribution of wild yaks is still rare. Existing studies on any Tibetan herbivore species rarely include data from the entire species' distribution range (Sharma et al., 2004; Singh et al., 2009; St-louis & Côté, 2014), which prevents the identification of concrete environmental management actions to alleviate further pressures on wild yak populations at the scale relevant for large species' conservation.

The present study aims to fill this gap in knowledge by combining recent advances in species distribution modelling (SDM) with a set of sighting data collected across most of the known distribution range of the wild yak. We expect (i) the species to show distinct habitat selection patterns between seasons, a distinction that has been previously suggested to occur but that has not been assessed in a quantitative manner (Harris & Miller, 1995; Schaller, 1998). In particular, we expect preferred habitats of wild yaks during the vegetation growing season to be found at higher altitudes, in more rugged terrains, and closer to glaciers (Schaller, 1998). We then expect (ii) the species to select for forage quantity over forage quality at the distribution-range scale, given that wild yaks are non-selective grazers (Jarman, 1974). We moreover expect

(iii) predation risk, herein captured by anthropogenic disturbances due to the general lack of natural predators for wild yaks in the area (Schaller, 1998), to be a significant factor shaping habitat selection patterns, with wild yaks being expected to avoid areas near human communities (Leslie & Schaller, 2009). The knowledge derived from this study will be used to predict seasonal habitat availability in the context of climate change; this will help highlight future global conservation challenges on the Tibetan plateau.

Study Area

The considered study area (Figure 1) covers around 1.1 million km^2 on the Tibetan plateau (WGS84, 78.5°E to 95.5°E, and 29.5°N to 37.0°N). It encompasses the entire *Tibet Interior* region defined by Kunlun in the north and Gangdise and Nyainqentanglha Ranges in the south, with slight eastward extension to incorporate part of Sanjiangyuan region in the Qinghai province of China. This part of the world includes most of the known current distribution range of the wild yak (Leslie & Schaller, 2009). There, average annual precipitation follows a decreasing gradient from east to west and from south to north, ranging from around 500 mm in the South East to less than 50 mm in the North West. Average annual temperatures vary from 0 C° to -6 C°, with winter extremes < -40 C°. The *Tibetan Steppe* is the main ecoregion present in the study area. Sparsely-distributed vegetation types are common, found on the alpine meadows, alpine steppes, semi-arid steppes and cold deserts (Schaller, 1998; Miller, 2003).

Methods

Data

Presence data

Presence data were collected by the Wildlife Conservation Society (WCS) and its partners in the years 2006, 2008, 2009, 2011, 2012, and 2013. Most of the surveys were conducted within areas known to hold wild yaks; however, the surveys were not primarily designed to collect information on wild yaks and sightings were thus opportunistic. Sightings were geo-referenced by trained staff, following the field protocol established by WCS China. Ancillary data (e.g. collection of sighting data while in vehicle or on foot; number of observers; survey efforts) were not systematically collected and could therefore not be taken into account in subsequent analyses. Vehicle surveys were not based on existing road systems; however, survey effort was shaped by the local topography as well as the distribution of seasonal rivers. While conducting surveys, the speed of the vehicle was required to be below 20km per hour to avoid disturbing wildlife as much as possible.

The total number of independent occurrences within our dataset was 755. Five hundred and sixty nine of these sightings were collected during the non-growing season (October to March; Yu et al., 2012), the rest (n=186) being collected during the vegetation growing season (April to September).

Environmental variables

This study adopted a methodological framework that distinguishes *limiting factors* (i.e., climatic and topographic factors*), disturbance* (i.e., anthropogenic influence), *and resources' distribution* (i.e., forage and fresh water availability) to categorise the environmental variables to be considered when exploring habitat selection patterns

(Guisan & Thuiller, 2005; Austin, 2007). The spatial resolution of all the environmental variables considered was set to 1 km^2. All the candidate variable layers were cropped to the extent of the study area, and if necessary, resampled to a 1 km^2 spatial resolution using the 'Nearest Neighbour' method in the 'raster' library (Hijmans & Etten, 2012) in R (version 3.0.2; R Development Core Team, 2014).

Climate

The 19 Bioclim variables (representative of the years 1950 to 2000) from the WorldClim dataset (Version 1.4; Hijmans et al., 2005) were used to capture current climatic conditions in the study area. To predict future trends in habitat availability, the Bioclim layers for the year 2070 were downloaded under two Representative Concentration Pathways (RCP), namely, RCP26 and RCP85. These were derived from the 'HadGEM2-ES' climate model, an updated version of the 'HADGEM' that has been reported to adequately help predict the Tibetan climate (Hao et al., 2013).

Topography

Topography is known to cause variation in forage quantity and quality for large herbivores, as well as shaping local predation risk (Brown, 1999; Illius & O'Connor, 2000). The Topographic Ruggedness Index (TRI), a measurement developed by Riley and colleagues. (1999) to quantify the total altitudinal change across a given area, was calculated based on the downloaded Digital Elevation Model layer GTOPO30 from the U.S. Geological Survey's Long Term Archive website (https://lta.cr.usgs.gov/GTOPO30). Calculations were performed in QGIS (Version 2.2.0-Valmiera; Quantum GIS Development Team, 2014).

Anthropogenic influence

Although natural predators do exist for wild yaks on the Tibetan plateau (see e.g. Schaller, 1998; Xu et al., 2006; Leslie & Schaller, 2009), human presence and activity are considered to primarily shape predation risk for this species (Leslie & Schaller, 2009). The distribution of human communities within our study area is relatively dense in the south of N33° and sparse in the north. Livestock rearing is the common livelihood. Long-distance nomadism is now seldom, whereas pastoral activities normally take place in designated grazing areas near villages (Sheehy et al., 2006). The linear distance between the centre of any given pixel and the nearest village was used as a proxy for anthropogenic disturbance and calculated for all pixels. Calculations were conducted in QGIS using the *Proximity* function. The shapefile detailing the distribution of villages in the area was provided by WCS China.

Fresh water availability

Glaciers have important effects on the hydrological cycle of high-altitude regions (Nogués-Bravo et al., 2007). The melting ice and snowpack provide seasonal fresh water and soil moisture critical to local vegetation communities (Schaller, 1998). The linear distance between the centre of any given pixel and the nearest glacier was therefore estimated for all pixels, using the *Proximity* QGIS function. The shapefile of glacier distribution was acquired from the GLIMS Glacier Database (http://nsidc.org/data/nsidc-0272).

Forage

The Normalized Difference Vegetation Index (NDVI), one of the most intensely studied and widely used vegetation indices (Pettorelli, 2013), was considered as a proxy for forage availability. MODIS Terra NDVI products (MOD13A2, monthly data of years 2001-2013) were downloaded using the USGS MODIS Reprojection Tool Web Interface (https://mrtweb.cr.usgs.gov). As the reflected light waves captured by satellite sensors can be influenced by a variety of natural phenomena (Achard & Estreguil, 1995), the downloaded data layers were processed in R to (i) convert all negative values to zeros; (ii) adjust the anomalous values, which were assumed to reflect atmospheric ‘noise’ involved in the MOD13A2 dataset (see Garonna et al., 2009 for full methdology).

Modelling approach

SDMs are numerical tools to assist in quantifying species-environment relationships; they are increasingly used for gaining ecological insights and predicting species distributions at large spatial scales (Guisan & Zimmermann, 2000). There are different types of SDMs that can be used in combination with presence data to assess habitat suitability; the predictive power of a given modelling approach can yet be context-specific and may vary depending on the study area, variables and resolution considered, as well as the amount of presence data available (Guisan & Zimmermann, 2000). To overcome uncertainties linked to the choice of SDM to be considered, we decided to conduct three different analytical approaches that have been widely employed in species distribution modelling exercises, namely, Generalized Additive Models (GAMs; Yee & Mitchell, 1991), Maximum Entropy (MaxEnt; Elith et al., 2011), and Random Forests (RF; Breiman, 2001). All models were developed in R using the package ‘biomod2’ (Version 3.1-48; Thuiller et al., 2014).

We firstly explored the importance of the climatic and topographic variables in shaping the current distribution of wild yak. Because habitat selection was expected to be seasonal, models were run 40 times for the growing (“G_I”) and non-growing (“NG_I”) season, respectively (Table 1). In a second step, current yak distribution was considered as a function of climatic conditions, topographic factors, forage availability, glacier distribution and anthropogenic influences. Again, these models were run for the growing (“G_II”) and non-growing (“NG_II”) seasons (Table 1). Multicollinearity was checked using the Variance Inflation Factor (VIF) analysis (R library 'usdm'; O’Brien, 2007). Some candidate variables were excluded to mitigate the effects of inflation caused by the high correlations amongst the predictor variables (Dormann et al., 2012).

Yak presence data was independently split into 70% for training and 30% for testing (Araújo et al., 2005). Ten thousands background points (representing pseudo-absence for GAM) were randomly selected throughout the study area. GAM was set with four degrees of freedom for smoothing (Austin, 2007). When performing MaxEnt, species prevalence was set to 0.1 (Elith et al., 2011). The maximum decision trees of RF was set to 500 (Cutler et al., 2007). Three evaluation methods, namely Kappa (Cohen 1960), TSS (Allouche et al., 2006) and AUC (Swets, 1988), were employed to assess model performance. The “Excellent” classification of model predictions were recommended to be measured by Kappa >0.75 (Fleiss, 1981), TSS >0.8 (Thuiller et al., 2009), or AUC >0.90 (Swets, 1988).

Predictions of species presence probability from the best-performing model were converted to presence-absence predictions using a transforming threshold selected as the one that maximises TSS scores (Allouche et al., 2006; Lobo et al., 2008). Variable importance was estimated using a variable permutation algorithm (Breiman, 2001). Information on altitude, terrain ruggedness, and distance to the nearest village and glacier was extracted from all predicted presence pixels for both seasons under the best model of current habitat suitability distribution for wild yaks; these values were then compared between seasons using Wilcoxon one-tailed sum rank tests (Hollander & Wolfe, 1973).

Results

RF models generally outperformed GAM and MaxEnt ones (Table 2). In accordance with our first prediction, wild yaks showed distinct seasonal patterns of habitat selection; climatic conditions were strong determinants of these patterns at the spatial scale considered (Figure 2). During the growing season, wild yaks appeared to select areas with low levels of fluctuations in monthly precipitation; they also appeared to favor areas with relatively abundant precipitations in the peak summer month (i.e., July). During the non-growing season, drier areas with greater fluctuations in monthly precipitation and less extreme winter temperatures were more likely to be preferred (Figure 2). Preferred habitats during the growing season were found at higher altitudes (W=2061875023, $p<0.001$), closer to glaciers (W=344529388, $p<0.001$) and in more rugged terrain (W=1800769226, $p<0.001$) than those used during the non-growing season (see Appendix I for details on the topographic features of suitable habitats per season). Contrary to our third hypothesis, however, wild yaks tended to be found closer to villages during the growing season than during the non-growing season (W=716972327, p<0.001). Interestingly, all the NDVI-based variables considered were comparatively of much lower importance to defining habitat selection patterns than the top climatic variables (Figure 2).

Based on these results, it is likely that under the RCP26 scenario, the distribution of suitable habitats for wild yaks would expand by 146% and 35% by the year 2070 in the growing and non-growing seasons, respectively. Under the RCP85 scenario, however, the distribution of suitable habitats during the growing season would expand by 194%, while the availability of suitable habitats during the non-growing season is expected to decrease by 76% (Figure 3). Shifts in the distribution of suitable habitats are also expected to occur. Based on our analyses, the present distribution of suitable habitats during the growing season could shrink by 69% (RCP26) and 74% (RCP85), respectively. Likewise, the present distribution of suitable habitats during the non-growing season could shrink by 49% (RCP26) and 98% (RCP85), respectively

(Appendix III).

Discussion

Our results largely support current expectations about the factors shaping wild yak distribution on the Tibetan plateau, showing that habitat selection patterns for the species are seasonally distinct and are largely driven by climatic factors. Yet two of our predictions were not well supported by our findings. The first pertains to the importance of forage quantity in driving habitat selection of wild yaks. Wild yaks are non-selective grazers (Schaller, 1998), and are therefore not expected to select forage quality over forage quantity (Jarman, 1974). Although we expected forage biomass to be key in determining wild yak occurrence, our results show that most NDVI-based variables play no, or very little, role in shaping wild yak distribution. Unlike the previously reported successful cases where NDVI could be linked to large herbivore distribution (see Pettorelli 2013 for a review), NDVI-based variables may have not correctly captured vegetation dynamics in our study area due to issues associated with high soil reflectance (Pettorelli et al. 2011). But these results could also suggest that wild yak select for forage quality over forage quantity to an extent beyond our initial expectation. The highly nutritious *Kobresia*-dominant moist meadows, favoured by wild yaks in summer according to empirical observations (Harris & Miller, 1995), are indeed not as productive in terms of vegetation biomass than other vegetation types such as *Stipa* grasslands, which are more widely distributed in our study area (Schaller, 1998). Pixels with higher NDVI values would thus fail to capture the distribution of these favoured, yet less productive, meadows. Interestingly, low level of fluctuations in monthly precipitation and abundant precipitations in July (the two conditions identified as being key to capture wild yak distribution during the growing period), are also key factors determining the biomass and nutrient value of *Kobresia*-dominant moist meadows (Yu et al., 2012). These meadows are indeed associated with high levels of vapor loss (Körner, 1999), therefore being strongly dependent on water availability to prevent desiccation. In July, in particular, vegetation on the *Kobresia*-dominant moist meadows is normally at its early phenological stages (Schaller, 1998); timely and abundant precipitation could thus be particularly beneficial to plant development in these meadows. Studies from other parts of the plateau on the Tibetan argali *Ovis ammon hodgsoni* (Singh et al., 2010) and kiang *Equus kiang* (St-louis & Côté, 2014) similarly suggest that forage quality can be a key factor shaping habitat selection patterns for these large herbivores. At this stage, it is difficult to conclude on the role of forage quantity and quality in driving wild yak habitat selection; further research is clearly needed.

The second prediction that our results failed to support is that wild yaks avoid human settlements, especially during the period when forage is relatively abundant and when there is thus no need to take bigger risk associated with proximity to humans (Frid & Dill, 2002; Creel et al., 2005). The low influence of anthropogenic disturbances on wild yak distribution may suggest that individuals in the area are basically unaffected by human distribution during the growing season; but this result may also be underpinned by the spatial proximity between villages and *Kobresia*-dominant moist meadows. Another potential explanation comes from the distribution of domestic yaks, found near villages. Habitat selection patterns of polygynous male herbivores is likely to be dependent on the spatio-temporal distribution of females during the mating season (Jarman, 1974; Clutton-Brock, 1989). One can expect wild male yaks to be attracted by the frequent presence of large number of domestic females without apparent competitors. This hypothesis is supported by the increasingly reported wild-domestic yak mingling and hybridization in Tibet (Leslie & Schaller, 2009).

There are a number of caveats associated with our data and modelling work. First, apart from yak sighting coordinates and group size, no other observation at the sightings are available from the survey teams (eg. topography, climatic conditions, primary productivity). Therefore, all the environmental information used for analyses are derived from global products, which have not been validated locally. We believe future research should groundtruth these products to ascertain the robustness of our conclusions. Second, our proxy of anthropogenic disturbance does not differentiate disturbance resulting from human presence from disturbance resulting from livestock. This lack of differentiation is due to the current lack of information on the spatial distribution of people and livestock in the area. As these data become available, it would be interesting to contrast the influence of humans and livestock on the distribution of wild yak. Third, the considered dataset might have been biased by the survey methods. In the growing season, in particular, limited accessibility to various areas can limit survey efforts to regions closer to villages, which means that our dataset may not capture the full range of environmental conditions where yaks can be found during that period. This sampling bias could lead to the distribution and size of suitable habitats during the growing-season being underestimated, as well as the ecological forces shaping the distribution of the species being misidentified (Syfert et al., 2013). Based on a series of correlative modelling approaches, this study moreover intrinsically assumes that wild yaks are living in equilibrium with their environment (Pearson & Dawson, 2003); the observed yak distribution may however not reflect the optimal patterns of habitat selection but rather habitat use as being constrained by a number of factors, including those associated with the presence of livestock. To address this, future large-scale studies should attempt to incorporate information on the distribution of domestic yaks while modelling wild yak distribution. Various biotic interactions and yaks' dispersal ability need to be taken into account, in order to identify scale-dependent limiting factors and consequent patterns in habitat selection (Pearson & Dawson, 2003). Another limitation to this study comes from the fact that our work did not consider the influence of sex. Dimorphic ruminants can be substantially divergent in their niche requirements (Kie & Bowyer, 1999). We were unable to explore differences in habitat selection patterns between males and females due to the gender of the individuals sighted not being reliably recorded. Our identified seasonal patterns should thus be understood as “averaged” results based on the dataset of unknown gender mixture. Finally, uncertainties associated with the modelling approaches considered should be acknowledged (Araújo et al., 2005). Predictions derived from these models vary quite substantially; for example, if we adopt GAM’s predictions (which is also acceptable in terms of AUC and TSS), the importance of factors such as altitude and mean temperature in determining suitable habitats for wild yaks in summer would be much higher than suggested by the random forest model (see Appendix II for details); suitable habitats for both seasons would also be much larger in size (Appendix III). These method-induced differences highlight the importance of interpreting model outputs with caution.

An important contribution made by this study resides in its quantification of the possible impact of climate change on the availability of suitable habitats for wild yaks.

According to our current knowledge, wild yaks are mostly found between 33°N-36°N; these regions are likely to be severely impacted by climate change. In terms of conservation priorities for the species, suitable habitats for wild yaks in autumn and winter appear to be more susceptible to climate change than suitable habitats in spring and summer. Yet the total area of suitable habitats during the non-growing season can be far smaller than the total area of suitable habitats during the growing season; a lower winter to summer habitat ratio may represent a high risk to population stability owing to the "bottle neck effect" (Illius & O'Connor, 2000). Interestingly, the distribution of future suitable habitat during the growing season is more likely to be threatened by anthropogenic activities than by climate change. Any increase in the distribution of suitable habitats can represent an interesting set of economic opportunities for domestic yak herders. This could create serious resource competition between wild and domestic yaks at local scales, while increasing the potential for disease transmission between groups (Hardin, 1960; Leslie & Schaller, 2009). The increased frequency of hybridization cases could moreover heighten genetic contamination of wild populations (Leslie & Schaller, 2009).

Altogether, our results suggest that increasing dispersal opportunities for local yak populations should be a key component of any conservation scheme aiming to mitigate the impact of climatic change, helping them to “track” shifting climatic zones and colonise new suitable territories. They also suggest that the number of domestic yak holdings should be more strictly controlled in communities adjacent to the known wild yak populations. The livestock grazing activities should be limited to designated areas that compete for winter resources of wild yaks to the minimum level. These two points are especially relevant for two regions that include parts of the Ali (81.7°E, 83°E, 30.5°E, 31.3°N) and Naqu prefectures (87.7°E, 88.8°E, 32.1°E, 33.2°N), where high densities of wild yak populations can currently be found. The regions are likely to remain suitable for the species under both RCP scenarios during the growing season; however, they may not remain so during the non-growing season. These areas are beyond any extant Protected Area borders, and experience high levels of human activities. Conservation interventions in these areas could be necessary, and we suggest establishing monitoring systems as soon as possible in these areas, to assess any direct threats, such as illegal hunting. In addition, current patterns of land use (e.g., grazing sites for domestic yaks) within these regions should be evaluated and, possibly, re-arranged in a manner that takes wild yaks' habitat needs into consideration. Lastly, we recommend the rapid definition and implementation of a plan to connect these regions to the nearest protected areas that contain other wild yak populations.

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References

Achard, F. & Estreguil, C. (1995) Forest Classification of Southeast Asia Using NOAA AVHRR Data. *Remote Sensing Environment*, 54, pp.198–208.

Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, 43(6), pp.1223–1232.

Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. (2005) Validation of species–climate impact models under climate change. *Global Change Biology*, 11, pp.1–10.

Austin, M. (2007) Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling*, 200(1-2), pp.1–19.

Breiman, L.E.O.(2001) Random Forests. *Machine Learning*, 45, pp.5–32.

Brown, J.S. (1999) Vigilance, patch use and habitat selection: Foraging under predation risk. *Evolutionary Ecology Research*, 1, pp.49–71.

Clutton-Brock, T.H. (1989) Mammalian mating system. In *Proceedings of the Royal Society of London, B. Biological Sciences*. p. 236: 339–372.

Cohen, J. (1960) A coefficient of agreement for nominal scales. *Educ. Psychol. Meas.*, 20, pp.37–46.

Creel, S., Winnie J.J., Maxwell, B., Hamlin, K. & Creel, M. (2005) Elk alter habitat selection as an antipredator response to wolves. *Ecology*, 86(12), pp.3387–3397.

Cutler, D.R., Edwards, T.C., Beard, K.H., Cutler, A., Hess, K.T., Gibson, J. & Lawler, J.J. (2007) Random forests for classification in ecology. *Ecology*, 88(11), pp.2783–92.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2012) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1), pp.27–46.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. & Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, 17(1), pp.43–57.

Fleiss, J.L. (1981) *Statistical methods for rates and proportions.* 2nd ed., New York: John Wiley.

Frid, A. & Dill, L. (2002) Human-caused Disturbance Stimuli as a Form of Predation Risk. *Conservation Ecology*, 6(1).

Garonna, I., Fazey, I., Brown, M.E., & Pettorelli, N. (2009). Rapid primary productivity changes in one of the last coastal rainforests: the case of Kahua, Solomon Islands. *Environmental Conservation*, 36(03), pp.253–260.

Guisan, A., Edwards, T., Jr, & Hastie, T. (2002) Generalized linear and generalized additive models in studies of species distributions : setting the scene. *Ecological Modelling*, 157, pp.89–100.

Guisan, A., Broennimann, O., Engler, R.,Vust, M., Yoccoz, N.G., Lehmann, A., & Zimmermann, N.E. (2006) Using Niche-Based Models to Improve the Sampling of Rare Species. *Conservation Biology*, 20(2), pp.501–511.

Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8(9), pp.993–1009.

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, 135(2-3), pp.147–186.

Hao, Z., Ju, Q., Jiang, W., & Zhu, C. (2013) Characteristics and scenarios projection of climate change on the Tibetan Plateau. *The Scientific World Journal*, 2013, pp.1–9.

Hardin, G. (1960) The Competitive Exclusion Principle. *Science (New Series)*, 131(3409), pp.1292–1297.

Harris, R.B. & Miller, D.J. (1995) Overlap Summer Habitats and diets of Tibetan Plateau ungulates. *Mammalia*, 59, 197–212.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, (25), pp.1965–1978.

Hijmans, R.J. & Etten, J. van (2012) Raster: Geographic analysis and modeling with raster data. R package version 2.0-12. http://cran.r-project.org/package=raster.

Hollander, M. & Wolfe, D.A.(1973) *Nonparametric Statistical Methods.*, New York: John Wiley & Sons.

Illius, A.W. & O'Connor, T.G. (2000) Resource heterogeneity and ungulate population dynamics. *Oikos*, 89(2), pp.283–294.

Jarman, P.J. (1974) The social organisation of antelope in relation to their ecology. *Behaviour*, 48, pp.215–266.

Kie, J. & Bowyer, R. (1999) Sexual segregation in white-tailed deer: Density-dependent changes in use of space, habitat selection, and dietary niche. *Mammalogy*, 80(3), pp.1004–1020.

Körner, C. (1999) *Alpine Plant Life-Functional Plant Ecology of High Mountain Ecosystems*, Springer, Verlag Berlin Heidelberg.

Leslie, D.M. & Schaller, G.B. (2009) Bos grunniens and Bos mutus (Artiodactyla: Bovidae). In *Mammalian Species*. the American Society of Mammalogists, pp. 1–17.

Lobo, J.M., Jiménez-Valverde, A. & Real, R. (2008) AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, 17(2), pp.145–151.

Miller, D. (2003) *Tibet Environmental analysis*, Background paper in preparation for USAID's program, http://www.case.edu/affil/tibet

Nogués-Bravo, D., Araújo, M.B., Errea, M.P. & Martínez-Rica, J.P. (2007) Exposure of global mountain systems to climate warming during the 21st Century. *Global Environmental Change*, 17(3-4), pp.420–428.

O'brien, R.M. (2007) A Caution Regarding Rules of Thumb for Variance Inflation Factors. *Quality & Quantity*, 41(5), pp.673–690.

Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, 12(5), pp.361–371.

Pettorelli, N., 2013. *The Normalized Difference Vegetation Index*, OUP Oxford.

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M. & Kausrud, K. (2011) The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. *Climate Research*, 46(1), pp.15–27.

Quantum GIS Development Team, 2014. Quantum GIS Geographic Information System. *Open Source Geospatial Foundation Project.* http://qgis.osgeo.org.

R Development Core Team, 2014. *R: A language and environment for statistical computing.*, http://www.r-project.org.

Riley, S.J., DeGloria, S.D. & Elliot., R. (1999) A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain. *Intermountain Journal of Sciences*, 5, pp.1–4.

Schaller, G.B. (1998) *Wildlife of the Tibetan Steppe*, The University of Chicago.

Schaller, G.B. & Liu, W. (1996) Distribution, status, and conservation of wild yak Bos grunniens. *Biological Conservation*, 76(1), pp.1–8.

Sharma, B.D., Clevers, J., Graaf, R.D. & Chapagain, N.R. (2004) Mapping Equus kiang (Tibetan Wild Ass) Habitat in Surkhang, Upper Mustang, Nepal. *Mountain Research and Development*, 24(2), pp.149–156.

Sheehy, D.P., Miller, D. & Johnson, D.A. (2006) Transformation of traditional pastoral livestock systems on the Tibetan steppe. *Secheresse*, 17, pp.142–151.

Singh, N.J., Yoccoz, N. G., Lecomte, N., Côté, S. D. & Fox, J. L. (2010) Scale and selection of habitat and resources: Tibetan argali (Ovis ammon hodgsoni) in high-altitude rangelands. *Canadian Journal of Zoology*, 88(5), pp.436–447.

Singh, N.J., Yoccoz, N.G., Bhatnagar, Y.V. & Fox, J.L. (2009) Using habitat suitability models to sample rare species in high-altitude ecosystems: a case study with Tibetan argali. *Biodiversity and Conservation*, 18(11), pp.2893–2908.

St-louis, A. & Côté, S.D. (2014) Resource selection in a high-altitude rangeland equid , the kiang (Equus kiang): influence of forage abundance and quality at multiple spatial scales. *Canadian Journal of Zoology*, 92, pp.239–249.

Swets, J.A. (1988) Measuring the accuracy of diagnostic systems. *Science*, 240(4857), pp.1285–1293.

Syfert, M.M., Smith, M.J. & Coomes, D.A. (2013) The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PloS one*, 8(2), p.e55158.

Thuiller, W., Georges, D. & Engler, R. (2014) biomod2: Ensemble platform for species distribution modeling. R package version 3.1-64. http://cran.r-project.org/package=biomod2.

Thuiller, W., Lafourcade, B., Engler, R., & Araújo M.B. (2009) BIOMOD - a platform for ensemble forecasting of species distributions. *Ecography*, 32, 369–373

Xu, A., Jiang, Z., Li, C., Guo, J., Wu, G. & Cai, P. (2006) Summer food habits of brown bears in Kekexili Nature Reserve , Qinghai-Tibetan plateau , China. *Ursus*, 17(2), pp.132–137.

Yee, T.W. & Mitchell, N.D. (1991) Generalized additive models in plant ecology. *Veg. Sci.*, 2, pp.587–602.

Yu, H., Luedeling, E. & Xu, J. (2012) Seasonal response of grasslands to climate change on the Tibetan Plateau. *PloS one*, 7(11), p.e49230.

Table 1. Predictor variables used in this study. G_I (growing season) and NG_I (non-growing season) groups used only topographic and climatic variables; G_II (growing season) and NG_II (non-growing season) also included variables capturing information on anthropogenic influence, glacier distribution, and forage availability.

Variable	**Group**		**Range** Min ~ Max (mean)	**Definition** (unit)
Alt	G_I G_II	NG_I NG_II	242 ~ 7423 (4775)	Altitude (m)
TRI	G_I G_II	NG_I NG_II	0 ~ 1080 (76)	Topographic Ruggedness Index (m)
Bio3	G_I G_II	NG_I NG_II	28 ~ 46 (38)	Isothermality (The mean diurnal range divided by the Annual Temperature Range *100)
Bio15	G_I G_II	NG_I NG_II	35 ~ 154 (105)	Precipitation Seasonality (Coefficient of Variation*100)
Bio8	G_I G_II		-84 ~283 (65)	Mean Temperature of Wettest Quarter (°C * 10)
Bio13	G_I G_II		6 ~ 618 (69)	Precipitation of Wettest Month (mm)
Bio11		NG_I NG_II	-282 ~ 160 (-136)	Mean Temperature of Coldest Quarter (°C * 10)
Bio14		NG_I NG_II	0 ~ 38 (1.7)	Precipitation of Driest Month (mm)
V_distance	G_II	NG_II	0 ~ 412 (57)	Nearest village distance (km)
G_distance	G_II	NG_II	0 ~ 259 (53)	Nearest glacier distance (km)
Change_AM	G_II		-1503 ~ 3975 (100)	Changes in NDVI values between April and May
Change_MJ	G_II		-2122 ~ 5164 (442)	Changes in NDVI values between May and June (* 10,000)
Change_JA	G_II		-3156 ~ 2549 (95)	Changes in NDVI values between July and August (* 10,000)
Change_AS	G_II		-3232 ~ 3835 (-367)	Changes in NDVI values between August and September (* 10,000)
Ave_allmon	G_II		0 ~ 8521 (1237)	Averaged NDVI values across years (* 10,000)

Table 2. Model performance. This study makes use of three analytical approaches that have been widely employed in species distribution modelling exercises, namely, Generalized Additive Models (GAMs), Maximum Entropy (MaxEnt), and Random Forests (RF). Each model considered was run 40 times for each season; model performance was evaluated independently for each run.

	Growing season Mean (Standard deviation)			**Non-growing season** Mean (Standard deviation)		
	AUC	TSS	KAPPA	AUC	TSS	KAPPA
RF	0.985 (0.01)	0.91 (0.04)	0.87 (0.03)	0.95 (0.007)	0.77 (0.02)	0.62 (0.03)
GAM	0.98 (0.007)	0.90 (0.02)	0.68 (0.04)	0.92 (0.005)	0.73 (0.01)	0.39 (0.02)
MaxEnt	0.97 (0.01)	0.82 (0.03)	0.63 (0.05)	0.92 (0.006)	0.74 (0.02)	0.38 (0.02)

Figures

Figure 1. Study area. The considered area covers around 1.1 million km2 on the plateau, encompassing the entire Tibet Interior region defined by Kunlun in the north and Gangdise and Nyainqentanglha Ranges in the south, with slight eastward extension to incorporate part of Sanjiangyuan region in the Qinghai province of China.

Figure 2. Variable importance in predicting wild yak distribution, under the best model. (a) Growing season results. (b) Non-growing season results. The best model was run 40 times for each season; variable importance was evaluated independently for each run.

Figure 3. Predicted distributions of suitable habitats for wild yaks. (a) and (b) show current distributions in the growing season and non-growing season, respectively; (a1) and (b1) were potential distributions under RCP26 scenario for both seasons; (a2) and (b2) showed potential distributions under RCP85 scenarios for both seasons.

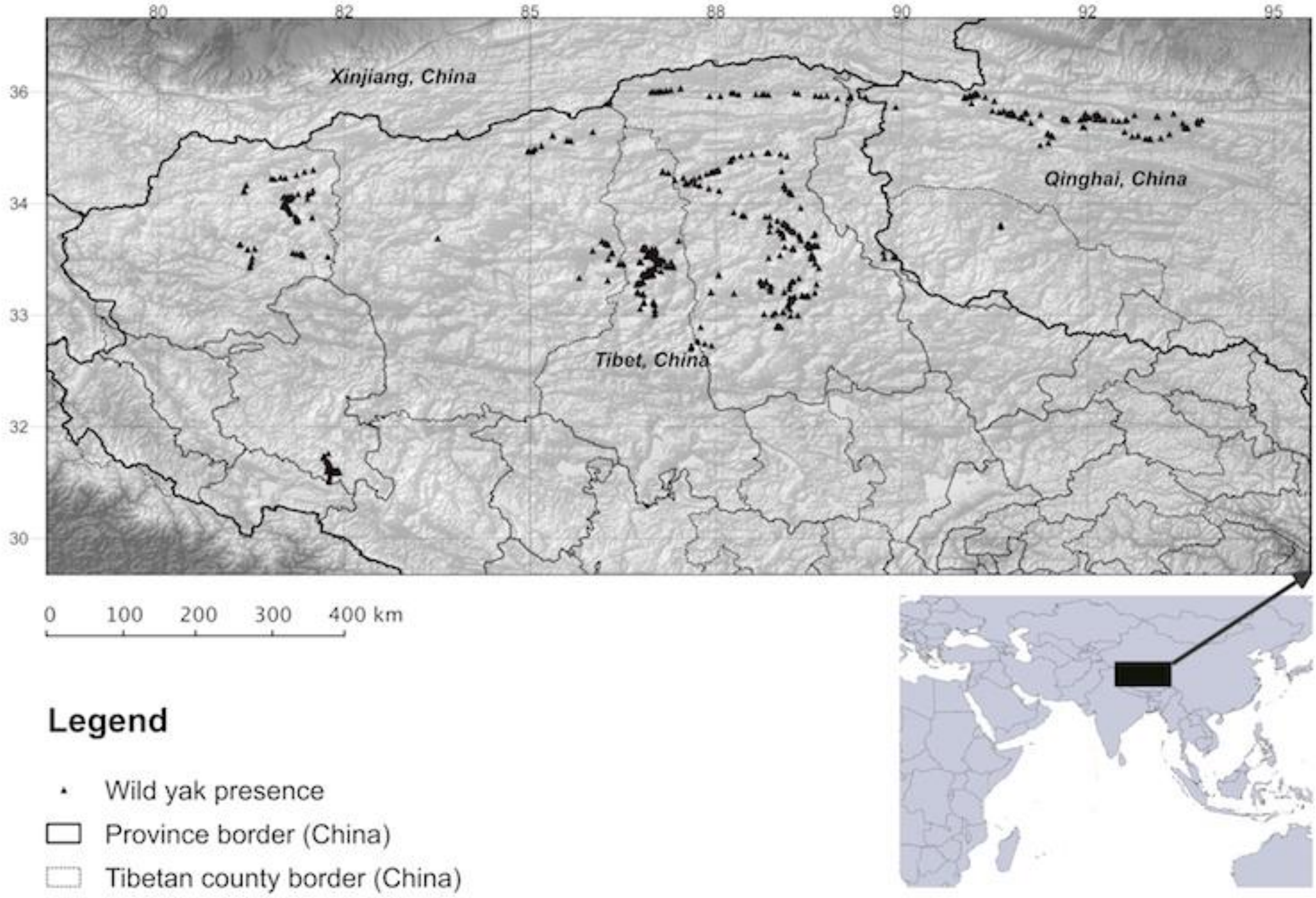
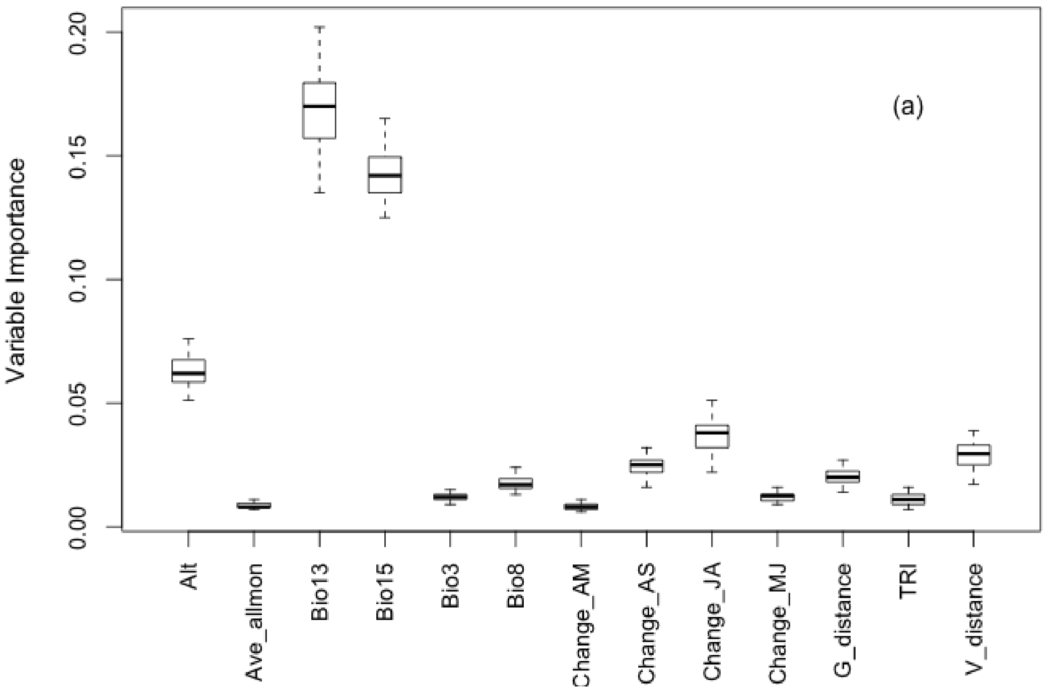
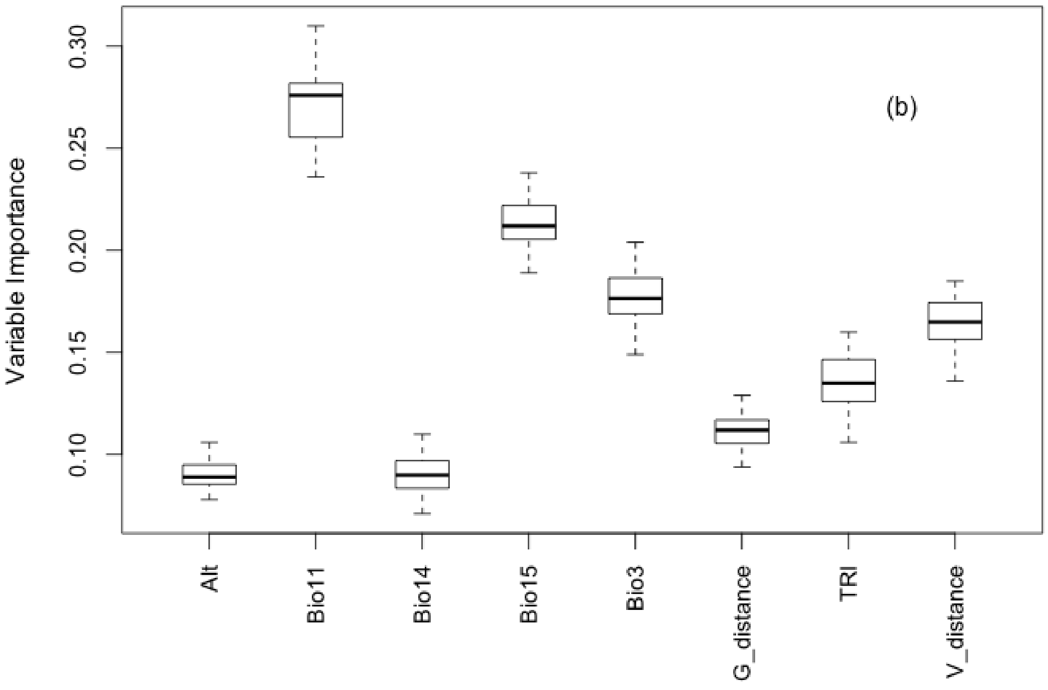
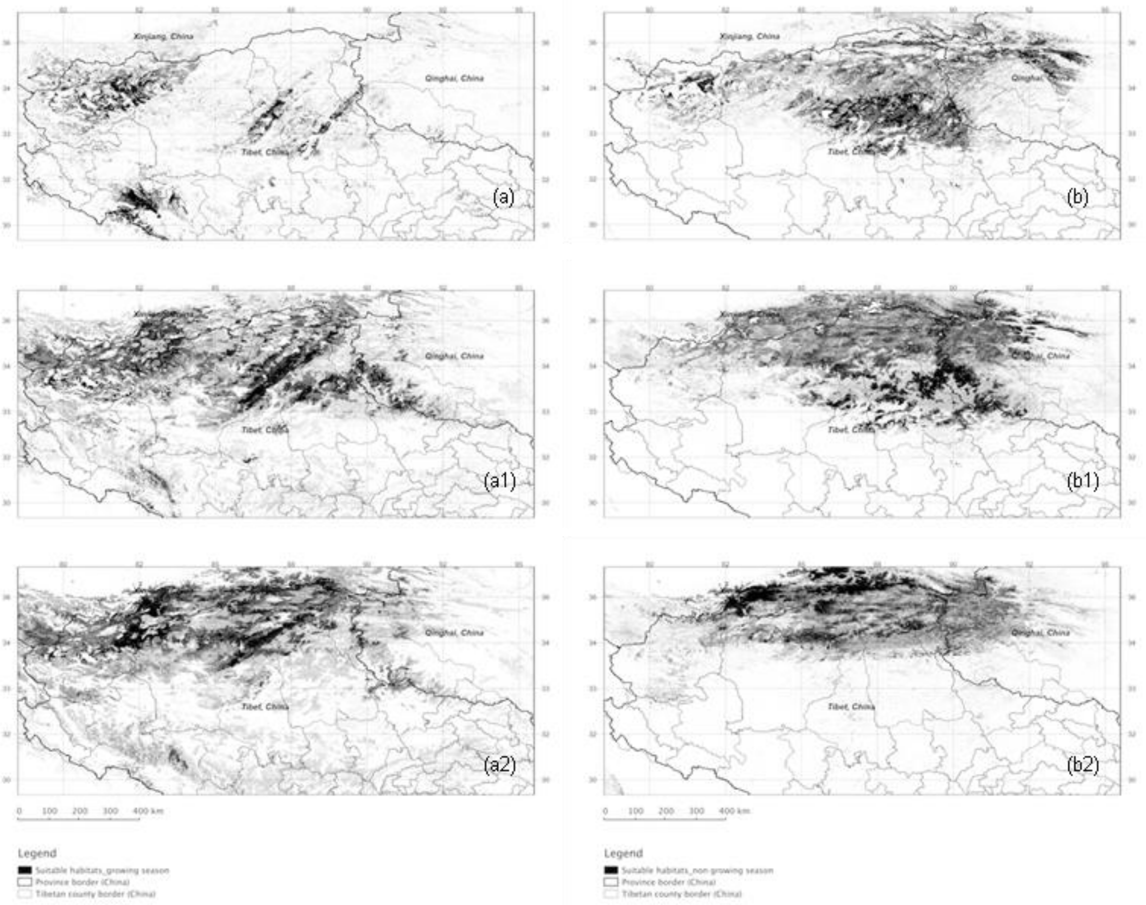

80
82
85
88
90
92
95
36
34
33
32
30
Xinjiang, China
Qinghai, China
Tibet, China
0 100 200 300 400 km
Legend
Wild yak presence
Province border (China)
Tibetan county border (China)

Figure 1


(a)
Variable Importance
0.00
0.05
0.10
0.15
0.20
Alt
Ave_allmon
Bio13
Bio15
Bio3
Bio8
Change_AM
Change_AS
Change_JA
Change_MJ
G_distance
TRI
V_distance

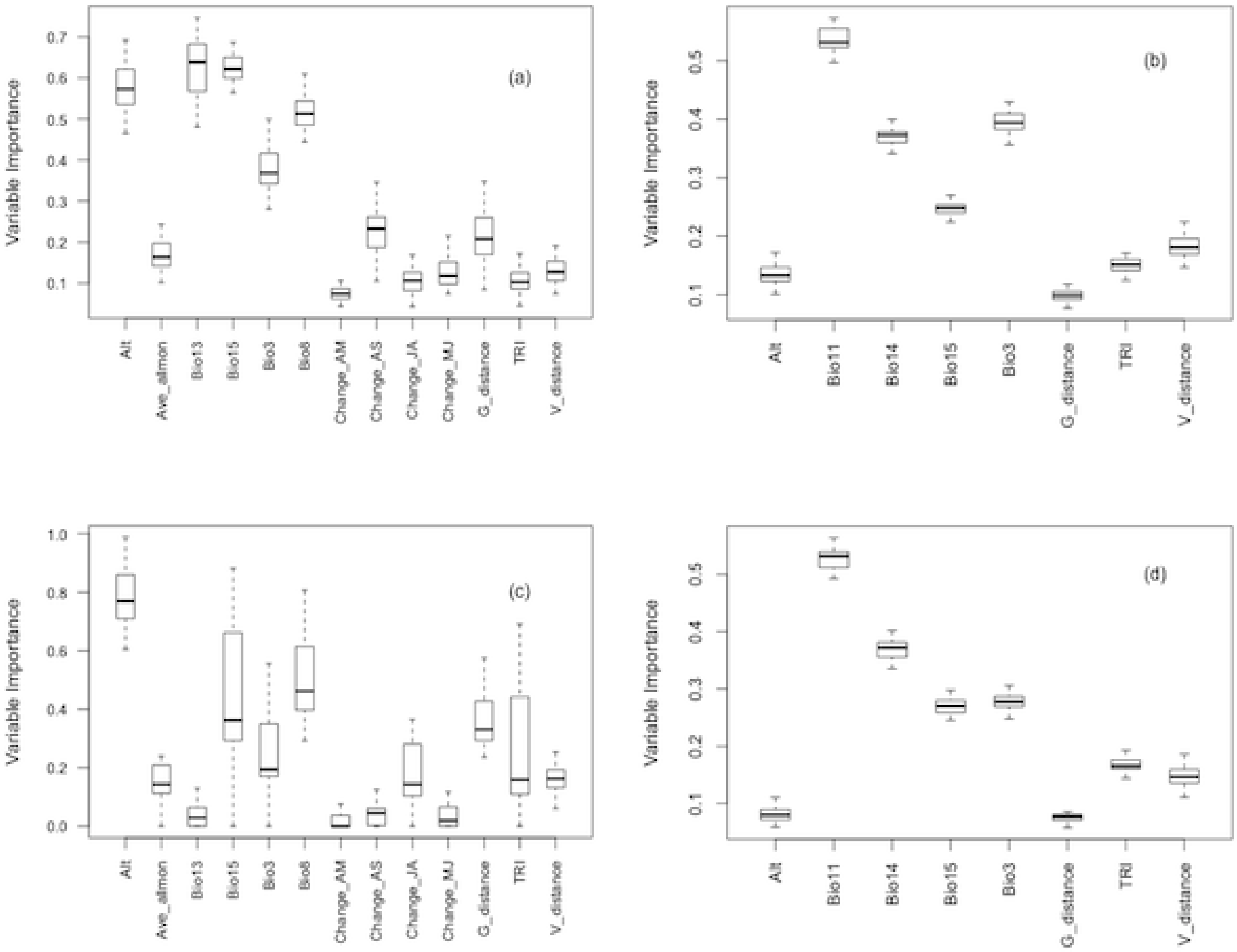

(b)
Variable Importance
0.10
0.15
0.20
0.25
0.30
Alt
Bio11
Bio14
Bio15
Bio3
G_distance
TRI
V_distance


Xinjiang, China
Qinghai, China
Tibet, China
(a)
(b)
(a1)
(b1)
(a2)
(b2)
0 100 200 300 400 km
0 100 200 300 400 km
Legend
■ Suitable habitats_growing season
□ Province border (China)
□ Tibetan county border (China)
Legend
■ Suitable habitats_non growing season
□ Province border (China)
□ Tibetan county border (China)

Appendix I: Topographic features of suitable habitats of wild yaks

Habitat features	**Growing season** Min - Median - Max	**Non-growing season** Min - Median - Max
Altitude (m)	2783 - 5243 - 6215	4001 - 4990 - 6142
Ruggedness (TRI; m)	0 - 48 - 428	0 - 23 - 571
Distance to nearest glacier (km)	0 - 13 - 181	0 - 54 - 245
Distance to nearest village (km)	0 - 32 - 290	0 - 70 - 377

Appendix II: Variable importance derived from different modelling approaches. (a) and (b) are the GAM outputs for the growing season and non-growing season; respectively; (c) and (d) are the MaxEnt outputs for the growing season and non-growing season; respectively.



Appendix III: Changes in habitat distribution for wild yaks on the Tibetan Plateau under two climate change scenarios (RCP26 & RCP85), by the year 2070. Three analytical approaches were considered, namely, Generalized Additive Models (GAMs), Maximum Entropy (MaxEnt), and Random Forests (RF). Models were run independently for the growing (G) and non-growing (NG) season.

RCP scenario	Seasons	Total area of suitable habitat (pixels)			Habitat gain			
		RF	GAM	MaxEnt	RF	GAM	MaxEnt	RF
Current	Growing	24,222	81,092	745,463	/	/	/	/
	Non-growing	169,539	266,793	445,140	/	/	/	/
RCP26	Growing	59,610	94,527	612,210	146%	17%	-18%	-69%
	Non-growing	228,776	294,194	407,691	35%	10%	-8%	-49%
RCP85	Growing	71,252	156,422	522,930	194%	93%	-30%	-74%
	Non-growing	40,306	46,803	102,947	-76%	-82%	-77%	-98%

Appendix IV: Topographic features of suitable habitats of wild yaks by 2070（RF predictions）.

		Growing seasonal habitats					Non-growing season habitats				
RCP26	Alt	Min	25%	Median	75%	Max	Min	25%	Median	75%	Max
		2913	5059	5152	5289	6175	4159	4949	5076	5194	6272
	TRI	Min	25%	Median	75%	Max	Min	25%	Median	75%	Max
		0.00	21.25	33.88	52.75	457.75	0.00	16.63	30.13	47.75	373.28
RCP85	Alt	Min	25%	Median	75%	Max	Min	25%	Median	75%	Max
		3800	5088	5162	5283	6091	542	5068	5150	5245	6343
	TRI	Min	25%	Median	75%	Max	Min	25%	Median	75%	Max
		0.00	20.75	32.63	49.75	382.13	0.00	25.25	36.88	50.50	336.50