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Can pikas hold the umbrella? Understanding the current and future umbrella potential of keystone species Pika (*Ochotona spp.*)

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ABSTRACT

The umbrella species concept is a frequently used concept in conservation since the conservation of an umbrella species may benefit other species. Keystone species are often suggested as potential umbrella species, but the validity of this approach remains uncertain. Moreover, climate change can have a multidirectional effect on the distribution of species, in which the distribution of umbrella species can be affected differently than that of beneficiary species. The validity of applying the umbrella species concept in conservation may thus be jeopardised by climate change. This study assessed the potential of two keystone species, the plateau pika (*Ochotona curzoniae*) and the Daurian pika (*Ochotona dauurica*), to be umbrella species for 13 potentially beneficiary species under current and future environmental conditions. Of these 13 species, five currently only co-occur with the plateau pika, five only with the Daurian pika, and three with both pika species. Current and future distributions of the pika species and potentially beneficiary species were predicted using bioclimatic and land-use variables. Range overlaps, Pearson correlations, niche similarity tests and relative suitability tests were performed to assess the umbrella potential of both pika species. Our results show that at present, both pika species may be considered to be umbrella species, benefitting several co-occurring species. However, species that currently co-occur with both pika species will not benefit from conservation of either of the pikas in the future years under climate change scenarios. The plateau pika loses its potential to act as umbrella species for two of the four species which currently may benefit. We can conclude that keystone species like pikas can act as umbrella species for carefully selected potentially beneficiary species under current conditions. Due to climate change related shifts in species distributions, they may however lose their umbrella species status in the future, which should be considered when selecting species conservation strategies.

1. Introduction

Essential goods and services, stability, and productivity of ecosystems are a few of the key functions attributed to biological diversity (Alho, 2012; Bernstein and Ludwig, 2008; Emmett Duffy, 2009; Gamfeldt et al., 2008; Turner, 2018). However, populations are declining rapidly due to pollution, overexploitation, habitat loss and degradation, invasive species, and climate change (Living Planet Report 2020, WWF). Approximately 20–30% of species are estimated to be at high risk of extinction if the temperature rises 2–3 °C

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above pre-industrial levels urging for increased conservation efforts. Unfortunately, the limited resources available to monitor the impact of anthropogenic and climatic pressures on a myriad of species complicates conservation efforts (Burnett and Roberts, 2015; Johnson et al., 2017; Warren et al., 2013).

Various approaches for management and conservation have been developed to optimise limited resource availability to conserve species (Johnson et al., 2017). One example of a resource efficient conservation strategy is the surrogate species concept, such as umbrella species (Caro and O'Doherty 1999; Johnson et al., 2017). Use of specific species, so-called umbrella species, to conserve other naturally co-occurring species, so-called beneficiary species, has gained popularity as this presents possibilities to conserve a range of species with minimal efforts and funds. This concept however has been criticised and labelled as a shortcut since umbrella species are often selected based on the known geographic distribution of a species (Roberge and Angelstam, 2004; Caro & O'Doherty, 1999; Ovando-hidalgo and Tun-garrido, 2020). Usually, species with greater spatial requirements are selected assuming that species with modest spatial needs encompassed within will receive the benefits of any conservation efforts. These are usually large bodied vertebrates with large home ranges. Although this fails to consider the ecological requirements of beneficiary species such as resource requirements, vegetation, habitat connectivity etc. (Roberge and Angelstam, 2004). Nevertheless, the umbrella species concept is still frequently used in conservation planning (Crosby et al., 2015; Hurme et al., 2008; Johnson et al., 2017; Roberge et al., 2008; Rowland et al., 2006), even though the effectiveness of the concept is still questioned (Branton and Richardson, 2014).

When implementing the umbrella species concept, it is essential that the umbrella species is chosen carefully. There are multiple selection criteria, such as based on area requirement, rarity, or sensitivity to human disturbances, and different authors have followed different criteria to select an umbrella species (Fleishman et al., 2000; Roberge and Angelstam, 2004). Keystone species may act as suitable candidates for umbrella species (Caro and O'Doherty, 1999; Johnson et al., 2017) since they have a large effect on the ecosystem relative to their abundance (Power et al., 1996). It seems only logical that conservation efforts towards keystone species would benefit naturally co-occurring species due to their large impact on their respective ecosystem. But the potential of keystone species to serve as suitable umbrella species remains largely unexplored (Branton and Richardson 2014; Caro and O'Doherty 1999; Lambeck, 1997).

In addition to ascertaining the ecological requirements, one way to assess a species' suitability to act as an umbrella for other species is to investigate the extent of overlap between the species' geographic distribution ranges (see e.g. Johnson et al., 2017). However, even if geographic distribution ranges of umbrella species overlap with that of other species at present, it is uncertain if this will remain to be the case in the future. Species distributions could shift due to climate change (Erb et al.,2011; Singh, 2008; Yoccoz et al., 2011). These shifts may be multidirectional and vary in time and in space, i.e. range shifts are predicted to be species unique (Hof et al., 2012b).

The aim of this study was to assess current and future umbrella species potential of two keystone species - plateau pika (*Ochotona*

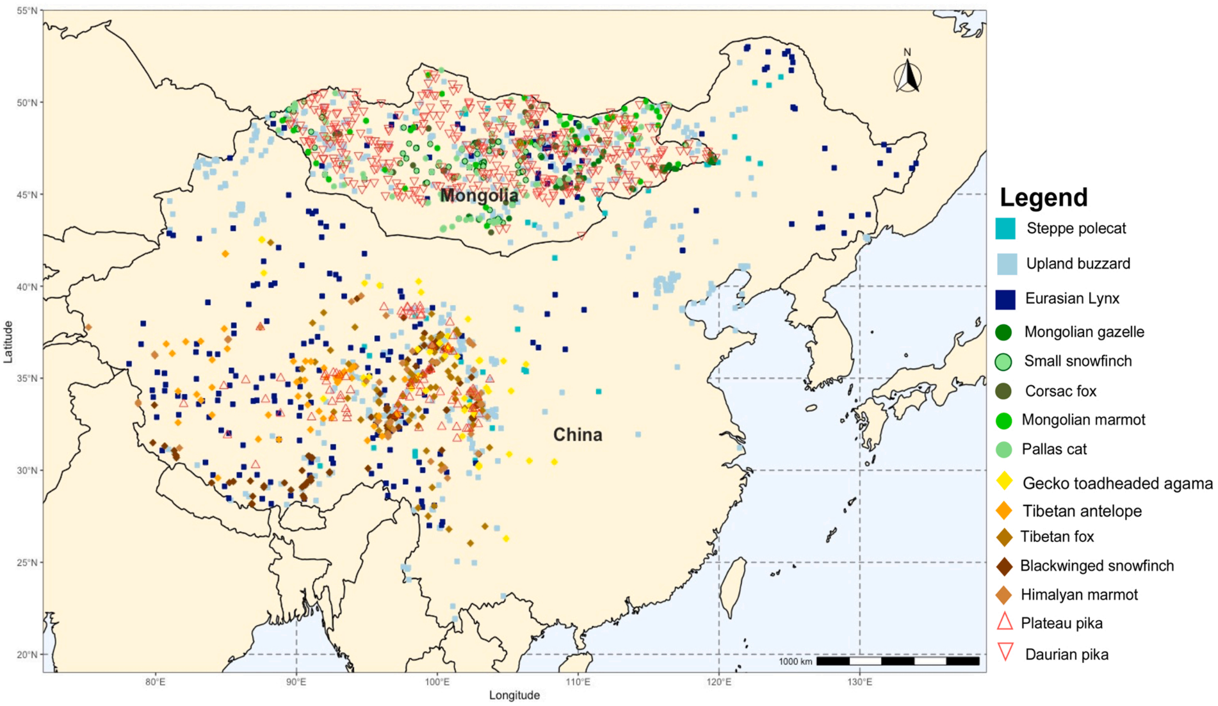

Fig. 1. Occurrences of species from suite 1, suite 2 and suite 3 along with that of keystones species in China and Mongolia. The occurrence points represent the occurrence data used to model the distribution of these species in this study. The shape of points is indicative of the suite the species belong to, such that suite 1 is represented by diamonds, suite 2 by circles and suite 3 by squares. The keystone species are represented by triangles.

Table 1
Suites of beneficiary species for both potential pika umbrella species. Numbers of occurrence locations are given as used in models, i.e. after data cleaning and thinning.

Species	Scientific Name	Abbreviation	IUCN Red list category	Number of occurrences	Sites Endemic to	Relation with pika	Source
Keystone species							
Plateau Pika	*Ochotona curzoniae*	PP	Least Concern	79	QTP	–	GBIF (https://doi.org/10.15468/dl.qkaf34), Chen et al. (2017); Li et al., 2019; Qu et al., 2016
Daurian pika	*Ochotona dauurica*	DP	Least Concern	346	Russia, China, and Mongolia	–	GBIF (https://doi.org/10.15468/dl.b7gwcr), IUCN, Batbayar et al., 2015; Erbjeva et al., 2012; Liao et al., 2007
Suite 1: co-occurrence with the plateau pika							
Tibetan Fox	*Vulpes ferrilata*	TF	Least Concern	76	Tibetan plateau	Primary predator	GBIF (https://doi.org/10.15468/dl.4aq5bv), Harris et al., 2014; Liu et al., 2010; Tsukada et al., 2014; Z. Wang et al., 2007; Z. H. Wang et al., 2008.
Black-winged snowfinch	*Montifringilla adamsi*	BSWF	Least Concern	109	Tibetan plateau	Nesting in burrows	GBIF (https://doi.org/10.15468/dl.ufhk2g)
Tibetan antelope	*Pantholops hodgsonii*	TA	Near Threatened	52	QTP	Shared niche	GBIF (https://doi.org/10.15468/dl.y3g3h7), Ahmad et al., 2016; Kang & Mao, 2011; Leslie & Schaller, 2008; Lin et al., 2005; Schaller et al., 2006
Gecko toad headed agama	*Phrynocephalus vlangalii*	GLA	Least Concern	47	QTP	Nesting in burrows	GBIF (https://doi.org/10.15468/dl.qkxged), JD Murdoch et al., 2010, The reptile database (http://www.reptile-database.org)
Himalayan Marmot	*Marmota himalayana*	HM	Least Concern	53	Tibetan plateau	Shared niche	GBIF (https://doi.org/10.15468/dl.fjqh32), Gao et al., 2010
Suite 2: co-occurrence with the Daurian pika							
Corsac Fox	*Vulpes corsac*	CF	Least Concern	77	Northern and Central Asia	Predator	GBIF (https://doi.org/10.15468/dl.7dcqbe), Batbayar et al., 2015; Communication et al., 2006; Munkhzul et al., 2012; James D. Murdoch et al., 2009, 2010
Small snowfinch	*Pyrgilauda davidiana*	SSF	Least Concern	116	Mongolia, China, and Siberia	Shared niche	GBIF (https://doi.org/10.15468/dl.csqg78)
Mongolian Gazelle	*Procapra gutturosa*	MG	Least Concern	53	EMS	Shared niche	GBIF (https://doi.org/10.15468/dl.b6e988), Batbayar et al., 2015; Communication et al., 2006; Olson et al., 2005, 2009
Mongolian Marmot	*Marmota sibirica*	MM	Endangered	72	Mongolia and China	Shared niche	GBIF (https://doi.org/10.15468/dl.a2muex), Buuveibaatar & Yoshihara, 2012; Rogovin, 1992; Townsend, 2009
Pallas Cat	*Otocolobus manul*	PC	Least Concern	96	Central Asia, Tibetan plateau, and Mongolia	Predator	GBIF (https://doi.org/10.15468/dl.q469bb), Barashkova et al., 2019; Munkhtsog et al., 2004; Murdoch et al., 2006; Ross et al., 2010.
Suite 3: co-occurrence with the plateau pika and the Daurian pika							
Eurasian Lynx	*Lynx lynx*	EL	Least Concern	246	Eastern Europe and Asia	Predator and shared niche	GBIF (https://doi.org/10.15468/dl.wmcjpr), IUCN-Redlist, Bao, 2010; Tang et al., 2019
Upland Buzzard	*Buteo hemilasius*	UB	Least Concern	1067	Central Asia	Predator and shared niche	GBIF (https://doi.org/10.15468/dl.akxqae)
Steppe Polecat	*Mustela eversmanii*	SP	Least Concern	49	Central and Eastern Europe and Central Asia	Predator and shared niche	GBIF (https://doi.org/10.15468/dl.ec63de)

curzoniae) and Daurian pika (*Ochotona dauurica)* for several co-occurring species, using species distribution modelling techniques. We hypothesise that due to their keystone status, both the plateau pika and the Daurian pika will be appropriate candidates as umbrella species (Johnson et al., 2017) at present, but their status in the future is uncertain. Pikas share a multitude of relationships and dependencies with the environment and a few beneficiary species, which makes them an essential part of the ecosystem. Therefore, pikas can be considered as keystone and umbrella species (Komonen et al., 2003; Smith and Foggin, 1999; Zhang et al., 2016). Assessing the umbrella potential of a species under current as well as under the future environmental conditions could provide clarity on conservation strategies and their long-term effectiveness.

2. Methods and materials

2.1. Study species and region

Pikas are a group of small lagomorphs of which various species are considered to be keystone species. The plateau pika is considered to be a keystone species for the alpine grassland ecosystem and is endemic to the region covered largely by the Qinghai-Tibetan Plateau. The Daurian pika is considered to be a keystone species for the steppe ecosystem and is endemic to the region covered largely by the Eastern Mongolian Steppes (Fig. 1) (Komonen et al., 2003; Smith and Foggin, 1999; Zhang et al., 2016). Further, both pika species hold the status of keystone species in their respective regions due to their burrowing behaviour and the fact that they are the primary prey for a multitude of predators (Chapman and Flux, 1990, Smith et al., 2019; Smith and Foggin, 1999). Their burrows house a wide variety of lizards and birds (Smith et al., 2019; Smith and Foggin, 1999) and benefit flora by creating novel habitat in the landscape and by constructing structural diversity and microhabitat suitable for plant species (Hogan, 2010; Smith et al., 2019). It has also been observed that the burrows made by pikas can lead to a decrease in soil moisture (Chen et al., 2017; Pang and Guo, 2017; Sun et al., 2015) and an increase in soil percolation (Hogan, 2010; Wilson and Smith, 2014) thus supporting increased plant diversity as well as providing important ecosystem services (Qin et al., 2021; Wilson and Smith, 2015). As both pika species are at the centre of complex interactions with the ecosystems, they are ideal species to be considered as umbrella species to strategize effective conservation in these ecosystems. It is however uncertain if they can be considered as umbrella species considering the potential effects of climate change on their distributions.

The study region (Fig. S1) of China and Mongolia is inclusive of the Qinghai-Tibetan Plateau (QTP), which extends from 25° to 45°N to 70–105°E, and the Eastern Mongolian Steppes (EMS), which extend approximately from 40° to 60°N and 85–120°E. QTP and EMS together cover approximately 3.3 million km^2 (IUCN 2013; Royden et al., 2008). The QTP is anticipated to be highly sensitive to global climatic perturbations, threatening its biodiversity (Liu and Chen, 2000; Liu Xiaodong and Zhang Minfeng, 1998; Wang et al., 2015). Mongolia has seen a significant loss in vegetation biomass over the past few years and 60% of this loss is attributed to climate change (Liu et al., 2013). Both QTP and EMS are sites with importance in terms of ecology and global conservation where there is a need to implement efficient conservation and management strategies to tackle the threats posed by climate change in the near future (Komonen et al., 2003). Identifying suitable umbrella species in these regions may therefore greatly benefit conservation efforts.

2.2. Wildlife and environmental data

To assess the umbrella potential of both pika species, two suites of potentially beneficiary species were identified. In this paper, a suite is defined as a group of species consisting of three to five species. Suite 1 consists of five species which co-occur with the plateau pika and suite 2 consists of five species which co-occur with the Daurian pika. A suite of three potentially beneficiary species which co-occur with both pika species was also identified (Table 1, henceforth referred to as suite 3). The potentially beneficiary species were selected based on the following criteria: (a) taxa, (b) conservation status, (c) endemism, (d) availability of occurrence data and (e) specialists/generalists. The purpose of selecting species based on the above-mentioned criteria was to remove any bias towards a certain taxon as well as to explore the maximum potential of the keystone species as umbrella species for this study (Table 1).

Species occurrence data were collected from the Global Biodiversity Information Facility (GBIF) for the years 1970–2020 (GBIF 2021a-GBIF 2021o). This timeframe was chosen to be able to obtain sufficient ($n > 50$) occurrence records to build species distribution models (van Proosdij et al., 2016). The datapoints from GBIF were cross referenced in September 2020 with the International Union for Conservation of Nature (IUCN) range of the respective species to ensure the validity of the data points obtained. For species for which fewer than 50 data points were available from GBIF, additional data points were collected from the literature (Table 1). As models with < 50 data points performed poorly. Google Earth was used to extract coordinates of the locations obtained from the literature when the name of the place was available, but the coordinates were not explicitly mentioned. Distribution ranges published by the IUCN – Redlist (IUCN 2020–21) were used for the Eurasian Lynx (*Lynx lynx*) and the Daurian pika to manually extract additional occurrence data. This entailed that locations within the published IUCN range of the species were randomly selected; their coordinates served as occurrence records. The locations were selected in such a manner that they were within the IUCN distribution range, within bounds of the natural reserves as well as in proximity to known occurrence points. This step was performed to mitigate the scant availability of occurrence data in the literature and to grasp the distribution ranges of these species in the area of interest as closely as possible. The exact coordinates were extracted from Google Earth such that an additional 75 random occurrence points were selected for the Eurasian Lynx and 5 for the Daurian pika to ensure sufficient data for species distribution models. Duplicate occurrence records were removed for all the species. With help of the ArcToolbox in ArcMap (v10.8, ESRI 2011), the dataset of occurrence records was thinned manually to remove clustered occurrence records i.e., to make sure that there was only one record per 10 km^2, to obtain an as unbiased and uncorrelated species occurrence dataset as possible. Using the distance rule, where points below a certain threshold distance are deleted till the species occurrence dataset is considered as not clustered, allows to overcome any spatial sampling biases in a convenient and straightforward method to avoid overfitting of the model (Aiello-Lammens et al., 2015; Sillero and Barbosa, 2021 also see Li et al., 2022). We used 10 km^2 as a threshold as we worked on a 2.5′ scale (∼ 3.2 km, see below). The same procedure was repeated for each species. Steppe polecat (n = 49) and Gecko toad headed agama (n = 47) were the only species which were left with less than 50 occurrence points after thinning (Table 1). The datasets were randomly divided into a training and testing dataset with a ratio of 7:3.

The recent historical (1970–2000) and future (2041–2060 and 2061–2080) bioclimatic variables were obtained from WorldClim version 2.1 (https://www.worldclim.org/) at a 2.5′ scale. The 2.5′ scale (∼ 3.2 km) was chosen as this is the smallest resolution at which Coupled Model Intercomparison Project Phase 6 (CMIP6) downscaled future projections for bioclimatic variables were available at the time of the study. For future projections, one global climatic model (GCM) was chosen: Beijing Climate Centre System Model (BCC-CSM2-MR) with three different shared socio-economic pathways (SSPs): SSP2–4.5, SSP3–7.0 and SSP5–8.5. BCC-CSM2-MR was developed for CMIP6 with major improvements as compared to CMIP5. BCC-CSM2-MR was the chosen GCM for future projections because large improvements are observed in this GCM in terms of model physics, reduction in biases, equilibrium climate sensitivity and vertical resolution at global and regional scale in the study area (Wu et al., 2019). SSPs represent various pathways that are based on the impact of societal, demographic, and economic changes on greenhouse emissions. SSP5–8.5 represents the worst-case scenario with an increased mean temperature of 5.1 °C above pre-industrial levels by 2100 due to increased economic and social development pushing for exploitation of fossil fuels (Riahi et al., 2017). SSP2–4.5 is a more optimistic scenario with medium challenges to ameliorate, and SSP3–7.0 represents an intermediate pathway predicting future hardships such as regional conflicts. Current and future (2041–2060 and 2061–2080) land use data for the same periods were obtained from the Land Use Harmonization^2 project (http://luh.umd.edu/data.shtml) and were downscaled from the 10′ scale to the 2.5′ scale by dividing 10′ cells into 2.5′ cells without achieving higher information so that they matched the scale of the bioclimatic variables. The future projections for land use data are based on different climate scenarios provided by Integrated Assessment Model (IAM) teams based on the Scenario Model Intercomparison Project (ScenarioMIP; O′Neill et al., 2016). Further, data on the current human population and elevation were also included. These datasets were taken from DIVA-GIS (http://diva-gis.org) and scaled up to the 2.5′ scale by taking the average of the 1′ cells to match the scale of the other variables. These variables were included as static variables in the model.

Bioclimatic variables, land use, human population, and elevation data, henceforth referred to as environmental variables (Table 2), were either cropped to match the North, East, South and West coordinates of 1) China, which encompasses the QTP, for the models of the Plateau pika and the suite 1 species, 2) Mongolia, which encompasses the EMS, for the models of the Daurian pika and the suite 2 species or 3) Mongolia and China combined for the models of the suite 3 species. Analyses were performed at the country level to help identify suitable areas for the diverse suites of wildlife species. This scale is likewise appropriate to derive practical national management suggestions, given that conservation policies are expected to differ between the two countries. Moreover, modelling for this extended area allows to account for the anticipated shifts and expansions of the species.

2.3. Species distribution modelling

The Maximum Entropy algorithm (v3.4.1, MaxEnt, Phillips et al., 2006) was used to develop species distribution models (SDMs). MaxEnt has been used to predict the impact of past and future climate change on distributions of numerous (groups of) species across the globe (Elith et al., 2011a; Hof and Allen, 2019; Hof et al., 2012; Johnson et al., 2017; Rodríguez-Castañeda et al., 2017). It is one of the most frequently used algorithms (Rodríguez-Castañeda et al., 2012) and is also considered to be one of the best performing

Table 2
Explanation of bioclimatic and land-use variables used as environmental predictors in species distribution models.

Variable	Explanation	Source	Variable	Explanation	Source
Bio 1	Annual mean temperature	WorldClim	**Primn**	Non-forested primary land	Land Use Harmonization^2 project
Bio 2	Mean diurnal range		**Primf**	Forested primary land	
Bio 3	Isothermality		**C3ann**	C3 annual crops	
Bio 4	Temperature seasonality		**C3per**	C3 perennial crops	
Bio 5	Maximum temperature of warmest month		**C4ann**	C4 annual crops	
Bio 6	Minimum temperature of coldest month		**C4per**	C4 perennial crops	
Bio 7	Temperature annual range		**Secmb**	Secondary mean biomass density	
Bio 8	Mean temperature of wettest quarter		**Secdf**	Potentially forested secondary land	
Bio 9	Mean temperature of driest quarter		**Range**	Rangeland	
Bio 10	Mean temperature of warmest quarter		**Pastr**	Managed pasture	
Bio 11	Mean temperature of coldest quarter		**Urban**	Urban land	
Bio 12	Annual precipitation		**Secdn**	Potentially non-forested land	
Bio 13	Precipitation of wettest month		**C3nfx**	C3 nitrogen fixing crops	
Bio 14	Precipitation of driest month		**Secma**	Secondary mean age	
Bio 15	Precipitation seasonality		Human pop	Human population	
Bio 16	Precipitation of wettest quarter		Elev	Elevation	DIVA-GIS
Bio 17	Precipitation of driest quarter				
Bio 18	Precipitation of warmest quarter				
Bio 19	Precipitation of coldest quarter				

algorithms when there are (a restricted number of) presence-only occurrences available (Hernandez et al., 2006). As this is the case for the species we modelled (see below), we chose to use MaxEnt. MaxEnt first identifies variables that determine most of the variation in species presence, after which it predicts the relative suitability of the study region for the species to occur, based on the predictor variables entered in the model (Phillips et al., 2006). To construct the SDMs, first the background points were set to a default of 10,000 points (Johnson et al., 2017). Then the regularisation multipliers, which help to avoid fitting too complex a model (Elith et al., 2011b), ranging between 0.5 and 2 were tested and the optimal performing multiplier per species was used in the final models with the auto features setting. The importance of species-specific tuning of regularisation multipliers for optimal complexity of models has been underlined by recent studies (Low et al., 2021; Moreno-Amat et al., 2015; Radosavljevic and Anderson, 2014). Use of appropriate regularisation multipliers reduces the need to select for feature classes and these settings have been shown to be appropriate for multispecies modelling (Aguirre-Gutiérrez et al., 2015; Low et al., 2021). Area under the curve (AUC) has been extensively used for model evaluation in SDM literature. AUC is indicative of the ability of a model to differentiate between the presences or absences of the species, ranging from 0 to 1 such that models with AUC < 0.5 have no better than random discriminatory ability, and that models with AUC > 0.75 are generally considered useful (Elith et al., 2006; Merow et al., 2013). Models with AUC < 0.5 can perform worse than random due to poor prediction even if the data fits the modelling data (Elith et al., 2006). For selecting the best model, the AUC of the testing dataset was assessed along with a binomial test in R-language (Team R Development Core, 2020) as standard threshold-independent method to assess whether the model predicts the presence of the species accurately, given the observed and predicted values. Other methods, such a partial AUC, may present a stronger alternative (Peterson et al., 2008), however there is a discord surrounding the appropriate method for MaxEnt model assessment involving large raster datasets (Johnson et al., 2017; Mas et al., 2013; Merow et al., 2013). Finally, a default prevalence of 0.5 was used for model building (Johnson et al., 2017; C. Liu et al., 2005) with logistic output format in MaxEnt. This approach was used for all species. Once the optimal regularisation multiplier was determined for each species, the variables that were highly correlated based on the jackknife test (Elith et al., 2011b) were removed ($>$0.7). The models with selected variables were replicated 30 times. Replicates are used for repeated sub-sampling and cross validation of the dataset (Phillips, 2017). Finally, a niche identity test was performed using ENMTools (v1.3) (Warren et al., 2008, 2010) to verify that each species distribution model was statistically unique. A statistically unique model represents a unique habitat and statistically bolsters the ecological differences between the habitat model of keystone species and potentially beneficiary species (Johnson et al., 2017). From the niche identity test, we obtained Schoener's D values and Identity or Hellinger's distance (I) values of all the SDMs. Schoener's D and Hellinger distance are similarity measures for niche overlap, ranging from 0 (SDMs with no overlap) to 1 (SDMs are identical) for each grid cell of the study areas (Schoener, 1968; Warren et al., 2008; Zachariah Atwater and Barney, 2021). Schoener's D has an historic ecological interpretation which can quantify the extent to which a pair of species interact in a given space whereas I deals with SDMs as probability distributions (Warren et al., 2010). If the actual Schoener's D and I values are lower than D and I values of pseudo-replicates created with ENMTools, then the SDMs are statistically unique. MaxEnt gives a logistic output which provides a close estimate of the probability that the species is present given the environment, which is interpreted as suitability of the habitat for the species to occur representing the potential distribution range (Elith et al., 2011b). These probabilities or suitability scores are obtained from the SDMs, or niche models created by MaxEnt. In this paper we refer to the habitat suitability obtained from the SDMs created by MaxEnt as suitability scores.

2.4. Understanding the umbrella potential of species

Pearson's correlation was quantified on the suitability scores of species to assess the strength of association between the distribution ranges of the keystone species and their respective suites. Pearson's correlation coefficient was calculated for every pairwise combination of the suitability scores representing the predicted distribution ranges based on the environmental variables in each grid cell for a) plateau pika and suite 1, b) Daurian pika and suite 2, c) plateau pika and suite 3 and d) Daurian pika and suite 3. Pearson's correlation coefficient was summed to identify which species had the highest overall correlation only for the common suite (suite 3) to determine which of the pika species was the best umbrella species for this suite. Range overlap was quantified to assess how much of the keystone species' predicted distribution ranges with high suitability scores ($>$0.50) overlapped with the predicted distribution range of each potentially beneficiary species such that it was quantified for a) plateau pika and suite 1, b) Daurian pika and suite 2, c) plateau pika and suite 3 and d) Daurian pika and suite 3.

2.5. Choosing the umbrella species

The Niche similarity metric, as defined by Warren et al. (2008), was used to assess the similarity between the SDMs of suites and their respective candidate umbrella species. We used this to quantify the niche shared by pika species and potentially beneficiary species. For the potentially beneficiary species from suite 3, the selected umbrella species, either the plateau pika or the Daurian pika, dependent on which of the two had the highest overall correlation as per Section 2.5, was considered for this analysis. Henceforward, all the subsequent analysis were quantified for the following combinations a) plateau pika and suite 1, b) Daurian pika and suite 2, c) Selected pika species and suite 3. Then, pairwise similarity between the suitability score in each grid cell of each predicted suitable distribution range was calculated using ENMTools. Relative suitability analysis was performed to determine the value of each species' predicted suitability in parts of the range that provided high, moderate, and low suitability for the keystone species. This analysis was performed using the spatial analyst extraction toolset in ArcMap (v10.8, ESRI 2011). A total of three geometric quantiles (grouping the grid cells of the keystone's habitat map into 3 equally sized groups based on predicted suitability scores: highest to lowest) were quantified. The percentage difference of the average suitability between the highest and the lowest quantile was calculated for all keystone and beneficiary species. The average predicted suitability score across the study area for each species in 3 quantiles – low, moderate, and high - was compared. The process of assessing which of the pika species can act as an umbrella species for their respective suites and suite 3 (Sections 2.5–2.6) was repeated for all future projections.

3. Results

3.1. Model performance of SDMs

All models predicting the suitability scores for the 15 species in total were found to be statistically unique based on the niche identity test; thus, there was a significant difference between SDMs of the potentially beneficiary species and the keystone species. The model performances were moderate to good with an AUC > 0.7 for all species (Table S1). The most important predictor variable for the plateau pika was the maximum temperature of the warmest month with a negative relationship with predicted suitability (Fig. S2a, b). For the Daurian pika it was rangeland, which positively affected the predicted habitat suitability (Fig. S2c, d). The most important explanatory variables differed for each potentially beneficiary species (Table S1).

3.2. Is the plateau pika holding the "umbrella" for suite 1?

Based on Pearson's correlation coefficient analysis, the current predicted suitable ranges of 3 out of 5 potentially beneficiary species from suite 1, namely the Tibetan fox, Tibetan antelope, and black winged snowfinch, showed moderate to high correlation (>0.6) with the current predicted suitable range of the plateau pika (Table S2). The distribution range of the plateau pika was generally predicted to decrease in the future in comparison to its current range (Figs. S3-S4). For instance, approximately 36% of the total area (in km^2) currently suitable for the plateau pika is predicted to be lost by the period 2041–2060 while an additional 5% is predicted to be lost by 2061–2080 under the SSP2.45 pathway (Fig. S3a, b). Even under the best-case scenario, the gain of new suitable area by 2061–2080 is minimal (1%). A trend of increasing loss of estimated suitable area for the plateau pika was observed as we shifted from the best case (SSP2–4.5) to the worst-case scenario (SSP5–8.5) (Table S3). The degree of association between the predicted distribution ranges of the plateau pika and of its beneficiary species declined from the best case to the worst-case scenario (SSP2–4.5 to SSP5–8.5) for both time periods (Fig. 2a, b). Similar to the current situation, the distribution ranges of the black-winged snowfinch, Tibetan fox, and Tibetan antelope were predicted to have a high correlation (>0.6) with that of the plateau pika under all scenarios and both time periods (Fig. 2a,b).

Range overlap analysis (Fig. 3a,b) revealed that there was a great overlap in the estimated future suitable areas (suitability scores >0.50) of the species from suite 1 and the plateau pika. The greatest range overlap was observed between the plateau pika and the Tibetan fox; 94% of the area that was predicted to be highly suitable for the plateau pika also was predicted to be highly suitable for the Tibetan fox. The range overlap between the estimated areas for the plateau pika and its co-occurring species increased in 2050 (Fig. S6a). This overlap remained high (> 60%) for all beneficiary species in both time frames, across all scenarios (Fig. S6b).

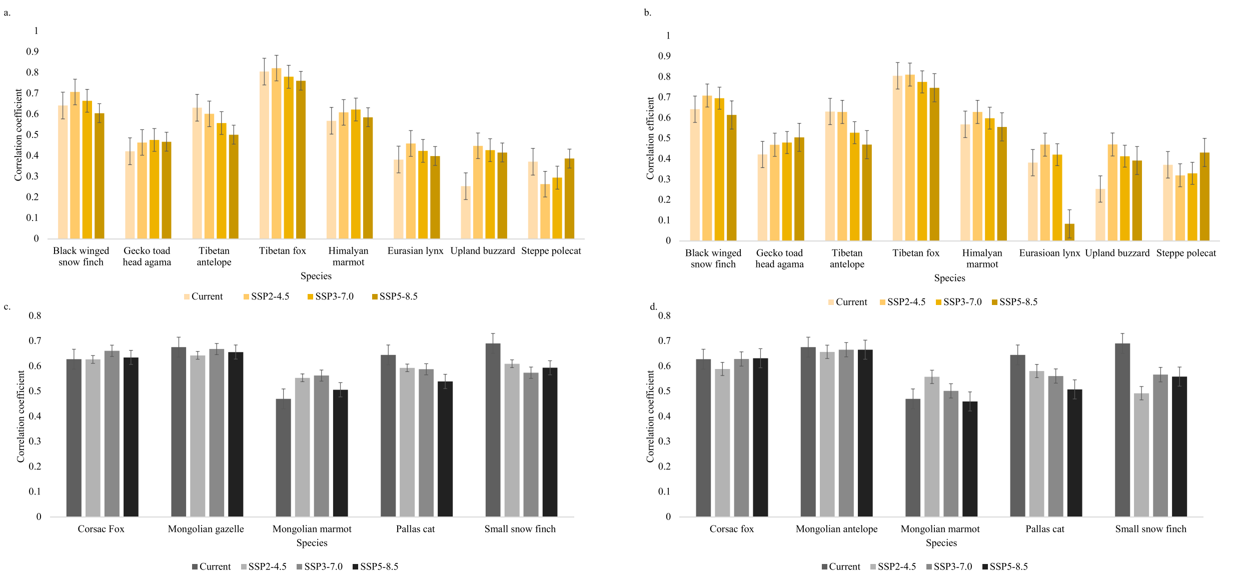

Fig. 2. The correlation coefficients between pika species and of species from suite 1, 2 and 3 in different scenarios. a. Plateau pika and suite 1 and 3 in 2041–2060 compared to the current scenario; b. Plateau pika and suite 1 and 3 in 2061–2080 compared to the current scenarios; c. Daurian pika and suite 2 in 2041–2060 compared to the current scenario and d. Daurian pika and suite 2 in 2061–2080 compared to the current scenario. The correlation coefficient represents the correlation between the predicted distribution ranges obtained from the ENMs of each beneficiary species with its respective keystone species.

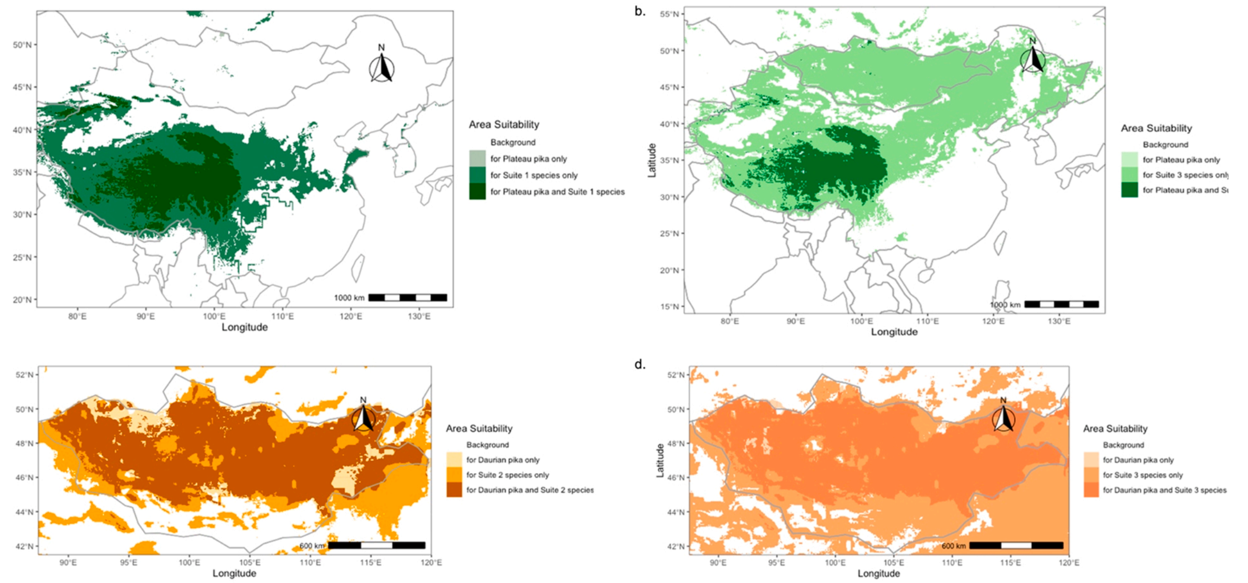

Fig. 3. The current range overlap between keystone species and their respective suite. a. Range overlap of plateau pika and suite1.; b. Range overlap of plateau pika and suite 3.; c. Range overlap of Daurian pika and suite 2.; d. Range overlap of Daurian pika and suite 3. Darker colours represent overlap between all the species from suites and pika species whereas lighter colours depict areas suitable for the pika species. Areas beyond the specified study region were not considered for analysis even though the ranges for species of suite 3 extended well beyond the study region.

Niche similarity analysis showed that there was a high degree of similarity between the environmental niche models (ENMs) of the black-winged snowfinch, Tibetan antelope and the Tibetan fox with that of the plateau pika (Schoener's *D* niche similarity scores > 0.50, Table 3). There was a moderate to high degree of similarity between the ENM of the plateau pika and the ENMs of the species from suite 1 in 2041–2060 (Schoener's *D* niche similarity scores 0.31–0.62, Table S4), but not in 2061–2080. In 2061–2080, the models of the black winged snowfinch, Tibetan fox and Himalayan marmot showed high niche similarity (>0.5) with that of the plateau pika.

Relative suitability analysis revealed that the areas providing low (<40%), moderate (40–50%), and high (>60%) predicted suitability for the pika, generally also provided low, moderate, or high suitability for the assemblage of species co-occurring with the plateau pika. In other words, when an area was predicted to be highly suitable for the pika, it was generally also highly suitable for the potentially beneficiary species. The average predicted suitability for the Tibetan fox (65%), Gecko toad headed agama (56%), Black winged snowfinch (50%), and Tibetan antelope (48%) were highest where the predicted suitability for the plateau pika was greater than 60% (Fig. 4a,b). The suitable areas which were predicted to be less suitable for the plateau pika (< 40%) generally also had a low suitability for the potentially beneficiary species of suite 1 (Fig. 4c, Fig. S7a) under the future scenarios.

3.3. Is the Daurian pika holding the "umbrella" for suite 2?

The Pearson's correlation analysis performed between the predicted suitable ranges of the Daurian pika and of the species of suite 2, consisting of the Corsac fox, Mongolian marmot, Mongolian gazelle, Pallas cat, and the small snowfinch, revealed a high degree of

Table 3
Niche Similarity between the pika species and the potentially beneficiary species in current scenario.

	Niche Similarity (*D*)	
Species	**Plateau Pika**	**Daurian Pika**
Tibetan antelope	0.535	–
Gecko toad headed agama	0.325	–
Himalayan marmot	0.493	–
Black winged snowfinch	0.547	–
Tibetan fox	0.615	–
Corsac fox	–	0.653
Mongolian gazelle	–	0.730
Mongolian marmot	–	0.594
Pallas cat	–	0.732
Small snowfinch	–	0.735
Eurasian lynx	0.320	–
Steppe polecat	0.283	–
Upland buzzard	0.261	–

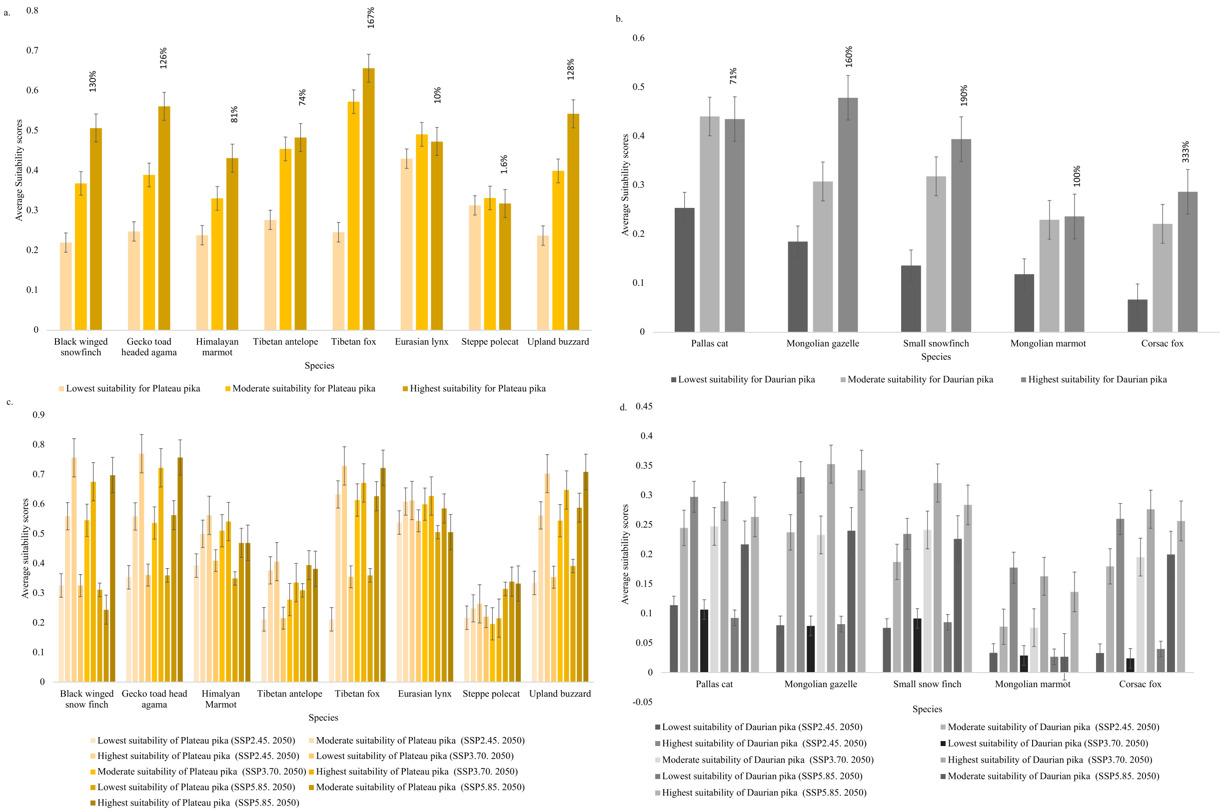

Fig. 4. Average suitability scores of each species' predicted area that occurs in lowest, moderate and highest suitability for keystone species. a. Plateau pika and suite 1 and 3. b, Daurian pika and suite 2. For e.g., the average suitability score for black-winged snowfinch increased by 130% in the highest quantile as compared to the lowest quantile. Similarly the average suitability score for Pallas cat increased by 71% in the highest quantile as compared to the lowest quantile. c. Relative suitability analysis of species from suite 1 and suite 3 with plateau pika across various scenarios; d. Relative suitability analysis of species from suite 2 and Daurian pika across various scenarios.

association with correlation coefficients > 0.6 (Fig. 2c). By 2041–2060, the Daurian pika is predicted to lose up to 20% of its current distribution range under the best-case scenario (Fig. S3c). This loss increases up to 37% by 2061–2080. There was no trend observed in the correlation between the predicted future range of the Daurian pika and the predicted future ranges of species from suite 2 across the various pathways (Fig. 2c, d). For 2 out of 5 species, the correlation coefficient between its ranges and the range of the keystone species continues to be greater than 0.6 in both time periods.

The range overlap of the predicted suitable areas for the species from suite 2 with the predicted suitable area for the Daurian pika was high (>60%) for 3 out of 5 species. Up to 68% of the area predicted to be highly suitable for the Daurian pika was also predicted to be highly suitable for the Corsac fox, Mongolian gazelle and the small snowfinch. The overlap between the predicted distribution ranges of the Corsac fox, Mongolian gazelle, and Mongolian marmot's and that of the Daurian pika continued to be high in most of the scenarios in 2041–2060 (Fig. S6 c, d). Most of the suite 2 species had a relatively lower range overlap with the predicted range of the Daurian pika (<0.6).

All the ENMs of species from suite 2 showed a high degree of niche similarity with the Daurian pika model (Schoener's *D* niche similarity scores > 0.59, Table 3). The niche similarity between the models for the years 2041–2060 and 2061–2080 models of the Daurian pika and the models for the years 2041–2060 and 2061–2080 for all suite 2 species was predicted to rise. Schoener's *D* values remained in the same range (± 0.05) across all scenarios for most species (Table S4).

The relative suitability analysis indicated that in the areas that were predicted to be highly suitable for the Daurian pika, the Mongolian gazelle on average had a large area predicted to be highly suitable (48%) (Fig. 4b, d). Further, the percentage difference between the mean suitability scores of the Daurian pika in the highest quantile (> 60%) as compared to the lowest quantile (< 40%) increased by 579%. The suitability of the areas for the suite 2 species incremented with the suitability of the area for the Daurian pika in 2041–2060 and 2061–2080, irrespective of the SSPs (Fig. 4d, Fig. S7b).

3.4. Who is holding the "umbrella" for suite 3?

The predicted current distribution ranges of the potentially beneficiary species from suite 3, namely Eurasian Lynx, steppe polecat, and upland buzzard, had a poor correlation (<0.4) with the predicted current ranges of both pika species (Table S2). The correlation remained poor in 2041–2060 and 2061–2080 and declined across the various SSPs (Fig. 2a, b). However, the overlap between the predicted current suitable areas for species of suite 3 was higher with the predicted current range of the plateau pika than with that of the Daurian pika (Fig. 3c, d). Thus, the plateau pika was chosen as the umbrella candidate for further analysis. More than 60% of the predicted ranges of the lynx and the buzzard continued to overlap with that of the plateau pika across most of the SSPs in 2041–2060 and 2061–2080 (Fig. S6a, b).

There was a low niche similarity between the plateau pika model and the models for the suite 3 species (Schoener's *D* 0.26–0.31), both at present and in the future (Table 4). For both the lynx and the polecat, the predicted current suitability of the area was highest when the area had at present a moderate suitability for the plateau pika (Fig. 4a). Generally, areas predicted to be less suitable for the keystone species in the future were likely to be less suited for the potentially beneficiary species of this suite as expected (Fig. 4c).

4. Discussion

Climate change is likely to impact numerous species and ecosystems, hence it is critical to account for the impact of climate change in conservation planning. With the availability of frugal budgets for biodiversity conservation and management, assessing impacts of climate change on surrogate species, such as keystone or umbrella species, represents an optimal approach (Carroll, 2010; Oliver et al., 2012; Simberloff, 1998). This study is one of the few studies that analyses current and future potential of keystone species as candidates for umbrella species (Caro & O'Doherty, 1999; Johnson et al., 2017) and that quantitatively compares and predicts the habitat suitability of species using a multi-species approach across various landscapes (Braunisch et al., 2008; Duflot et al., 2018; Johnson et al., 2017; Maslo et al., 2016). Furthermore, it is first of its kind to extend this analysis to future projections. Here we analyzed the potential of two keystone species as umbrella species while accounting for bioclimatic as well as habitat needs of the beneficiary species and not limiting the assessment to the pre-existing criteria of spatial overlap. The focus of the study was not only on the spatial overlap of the distribution ranges but was also to consider the similarity and association of the models created using the predictor variables.

4.1. Pikas as potential umbrella species

Based on the studied indicators to assess the potential to act as umbrella species, the plateau pika can act as an umbrella species for the black winged snowfinch and the Tibetan fox at present as well as in the future, irrespective of the SSPs, as both species share a strong positive relationship with the plateau pika in terms of space and niche. This finding is not surprising since the black winged snowfinch primarily nests in the burrows dug by the plateau pika (Lai & Smith, 2003), and the Tibetan fox is known to be an obligate predator of the plateau pika and hence relies greatly on them (Harris et al., 2014). Although the results of this study suggest that the plateau pika can also act as an umbrella species for the Tibetan antelope at present, they also suggest it will most likely not be able to hold this status in the future. We speculate that the loss of umbrella potential of the plateau pika for the Tibetan antelope in the future may be because the shifts in the distribution ranges are likely to mismatch (IPCC 2013; Liang et al., 2021). However, further investigation is required to comprehend the factors altering the umbrella potential of the pika for these ungulates. The Himalayan marmot can also potentially benefit from the plateau pika as an umbrella species under current circumstances which may be due to the similar food niche of these small mammals (Qu, Ji, et al., 2016). Whether it continues to benefit from the umbrella status of the plateau pika in the future is uncertain. The marmots are hibernating mammals highly adapted to low temperatures and the summer activity is severely restricted by high temperatures (Armitage, 2013). Additionally, drought has been recorded to seriously affect marmot growth and survival as during the active season marmots obtain water from their food plants. However, it is threatened when drought overlaps with marmots' active season (Armitage, 2013). This results in marmots being highly susceptible to perturbations in temperatures whereas pikas, being non-hibernating mammals, can successfully forage and obtain water throughout the year. This difference in sensitivity to temperature of the two species may explain the loss of the umbrella potential of pika for the Himalyan marmot. The Gecko toad headed agama will not be able to benefit from the plateau pika as an umbrella species at present nor will it be able to benefit in the future. This may be because the Gecko toad headed agama occupies burrows from the plateau pika opportunistically rather than out of necessity (Lambert et al., 2020).

At present, the Daurian pika was found to be able to act as an umbrella species for 3 out of 5 species from suite 2 apart from the Mongolian marmot and Pallas cat. The Mongolian gazelle is thought to forage on similar resources as the Daurian pika, which may explain the potential benefit for the Mongolian gazelle (Yoshihara et al., 2008). Although both the Corsac fox and the Pallas cat rely on pika as prey (Murdoch et al., 2010; Ross et al., 2010), we found that only the Corsac fox may benefit from the Daurian pika as an umbrella species. The Pallas cat is identified as a dietary specialist with the Daurian pika as main prey (Ross et al., 2010), so the reason for this lack of potential benefit remains uncertain. Depending on the SSP, the Daurian pika is generally predicted to still be able to act as an umbrella species for these three species in the future. The fact that the Mongolian marmot is unlikely to benefit from the Daurian pika as an umbrella species can be attributed to the potential niche segregation between the marmot and the pika (Barrio & Hik, 2013). This explanation is in line with our findings that the Mongolian marmot and the Daurian pika had a high range overlap but a moderate niche similarity index. However, the small snowfinch may be able to benefit only in the best-case scenario (SSP2–4.5). That it is unlikely to benefit under the other scenarios may be explained by the fact that even though this finch is known to utilise the burrows of the Daurian pika for nesting, excavation activity by the Daurian pika can also hinder burrow entrance, especially for small birds (Li et al., 2013). However, our analysis did not provide any insights into how climate change may alter the relationship between these two species. Such insights may be gained using approaches that directly account for trophic interactions at local scales.

Neither the plateau pika or the Daurian pika would be a suitable umbrella species for the species from suite 3 that co-occurred both with the plateau pika and the Daurian pika. One reason for this may be because all these species had a vast distribution range in comparison to the plateau pika and the Daurian pika. Their ranges extend far beyond the study region (Bao, 2010; Šálek et al., 2013). Moreover, although both pika species make up some part of their diet, it is not a limiting prey for species from suite 3 (Bao, 2010; Mengüllüoğlu et al., 2018; Shengmei et al., 2006; Xianfeng, 2005).

Evidence from this study suggest that the Daurian pika is a stronger candidate as an umbrella species for its respective suite than its Tibetan counterpart. Although the Daurian pika currently benefits 3 out of 5 species whilst the plateau pika benefits 4 out of 5 species, we predicted that the Daurian pika will continue to benefit those species in the future whilst the plateau pika will only benefit 2 species in the future, losing its umbrella potential for the other two. This loss of umbrella potential could be due to climate change related loss of suitable areas in the future for both keystone species and the beneficiary species. The pika poisoning programmes (Badingqiuying et al., 2016) may add an additional burden on the pikas' potential to act as an umbrella species and should be considered for any future studies. Our results also highlight the fact that smaller mammals (e.g., Otters, American marten) can indeed act as umbrella species (Bifolchi and Lodé, 2005; Delibes-Mateos et al., 2011; Mortelliti et al., 2022).

4.2. Challenges

This study supports the school of thought that keystone species, such as pikas, can be potential umbrella species (Johnson et al., 2017). But the paradox that we see is that even though the pikas hold ecological importance, they are considered pests. Since the pikas tend to consume fodder for domestic livestock, there have been widespread poisoning programmes in place (H. Liu et al., 2013; Smith and Foggin, 1999; Zhang et al., 2016). The ability of the pikas to reach high abundance adds to their image as pest. Further, the burrowing nature of pikas has also been blamed for increasing soil erosion and changing the fundamental plant community, although evidence is lacking (Smith et al., 2019). Nevertheless, areas where pikas have been subjected to poisoning have lower abundance of carnivores such as Tibetan foxes, red foxes, and upland buzzards (Badingqiuying et al., 2016). A similar pattern is observed for bird species richness, with lower bird sightings in areas where pikas were poisoned (Smith et al., 2019). The view that pikas are indicators of rangeland degradation rather than the cause is however increasing (Choying, 2016; Sun et al., 2015; Zhao et al., 2019). Thus, implementation as well as acceptance of the pikas as umbrella species will require a shift in social and scientific paradigms towards the pikas and their roles as umbrella species in the ecosystems.

Predictive modelling is a great conservation tool, especially when resources such as occurrence data and time are limiting, but it is also important to acknowledge that these predictions cannot capture complete ecological complexities that exist in reality (Pimm, 2008). Occurrence and environmental data may not accurately represent the complete ecological requirements of a species. Thus, assumptions from predictive modelling studies like ours should be carefully made, and the limitations should be clearly acknowledged. Pertaining to this study, the results gained are also subject to the set of species chosen as beneficiary species and their role in the ecosystem. Hence, results may have been different if a different set of species would have been chosen with the same candidate species. The use of the umbrella species concept should thus be used with caution and grounded on empirical evidence. In this study, we decided to model umbrella and potential beneficiary species separately rather than using a joint species distribution modelling approach since the coarse resolution of environmental and occurrence data that we relied on here is rarely able to capture trophic interactions (Descombes and Golay, 2011). Such inadequacy of capturing trophic interactions can be clearly seen in the case of Pallas cat, a predator with Daurian pika as main prey (Ross et al., 2010). We acknowledge that inclusion of trophic interactions in our study would be able to provide a higher precision of the predicted future distributions, however to achieve such precision requires data at a local scale such as ground temperature and spatial locations of trophic interactions (Descombes and Golay, 2011; Trainor et al., 2014). The joint distribution modelling approach is currently under active development to increase its practical usability to resolve issues surrounding the potential confounding factors associated with occurrence data (Tikhonov, 2019) and any conclusions about the associations between species predicted by such an approach should hitherto be used with caution. Inclusion of biotic interaction in modelling can also provide additional information to the argument we present here (Hof, Jansson, and Nilsson, 2012a). However, local processes, such as biotic interactions at small scales, are not to thought to have a similar dominant role in governing large scale species distributions as climatic processes at macroecological scales (Araújo and Luoto, 2007; Pearson and Dawson, 2003). Biotic interactions are complex and dynamic and obtaining such data that can parameterise these interactions might be arduous. Additionally, including such interactions requires a priori knowledge of the biology of the species included and the community itself (Araújo and Luoto, 2007; Hof et al., 2012a). Since our study is one of the few studies combining multiple species from the steppe ecosystems and only one with this specific set of species, we need to be well informed before incorporating these interactions. Alternatively, a hierarchical modelling framework is a useful approach such that factors are addressed based on the hierarchy of its operation for e.g., at a continental scale climate is considered the dominant factor whereas at local scales factors like topography become more important (Pearson and Dawson, 2003). Additional factors like microclimatic conditions and biotic interactions are also included eventually. However, modelling the species distributions to identify the important predictor climatic variables is the first step for a multi-level modelling framework (Araújo and Luoto, 2007), as such, our study provides in this need. We suggest that studies like ours can be used as a guide for local data collection that can be incorporated in future studies.

The rationale behind selecting a species as umbrella species is debated (Maslo et al., 2016). Here, we addressed the issue by providing a quantitative approach with explicit criteria for selection of potential umbrella species and potential beneficiary species. We recognise that it is unrealistic to create a "one shoe fits all" strategy that will effectively conserve all species. However it is possible to formulate actions that can be complemented with broader strategies for conservation, ultimately benefiting multiple species (Maslo et al., 2016).

5. Conclusions

There is compelling evidence that many species ranges will shrink with global warming (Pimm, 2008). Without climate change mitigation, large climatic range contractions can be expected, amounting to a substantial global reduction in biodiversity and ecosystem services by the end of this century. Modelling approaches like those presented in this study can be used to create species' habitat networks to identify areas which can be prioritised for conservation by conservation and landscape planners, optimising the limited resources available (Duflot et al., 2018). This study provides a potential avenue to explore various theoretical concepts during the pre-implementation phase of conservation planning. It is possible to identify areas retaining biodiversity in the current and the future circumstances where conservation efforts targeted towards the umbrella species can benefit multiple species. Thus, we stress that species distribution modelling can be a powerful conservation tool for assessing species' current and future umbrella potential as well as integrating climate change into conservation management and strategies. We also highlight the importance of considering the impact of climate change and species distribution shifts while formulating conservation policies and plans. We extend a fairly simple method here, which requires presence-only data with basic information on environmental requirements which can be widened for other species and ecosystems. As the concept of umbrella species is likely to persist as an appealing cost effective measure in conservation planning, selecting ecologically well linked species such as keystone species can help to improve the efficiency of this theoretical concept drastically. However, it is important to recognise that species from different taxa may not benefit each other, as we see in the case of vertebrates and invertebrates (Daniel, 2001; Suter et al., 2002). We provide evidence that keystone species, here the plateau pika and the Daurian pika, can be potential candidates for umbrella species in their respective ecosystems at present as well as in the future. The uncertainty in forecasts of species' distributions underline the urgency of exploring and integrating novel modelling approaches for biodiversity conservation management and planning.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02247.

References

Aguirre-Gutiérrez, Jesús, et al., 2015. Similar but not equivalent: ecological niche comparison across closely-related Mexican white pines. Divers. Distrib. 21 (3), 245–257.

Aiello-Lammens, Matthew E., et al., 2015. SpThin: an r package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38 (5), 541–545. https://doi.org/10.1111/ecog.01132.

Alho, Cleber J.R. 2012. "The Importance of Biodiversity to Human Health: An Ecological Perspective." *Estudos Avançados*.

Araújo, Miguel B., Luoto, Miska, 2007. The importance of biotic interactions for modelling species distributions under climate change. Glob. Ecol. Biogeogr. 16 (6), 743–753.

Armitage, Kenneth B., 2013. Climate change and the conservation of marmots. Nat. Sci. 05 (05), 36–43.

Bernstein, Aaron S., Ludwig, David S., 2008. The Importance of Biodiversity to Medicine."J. Am. Med. Assoc.

Bifolchi, Aline, Lodé, Thierry, 2005. Efficiency of conservation shortcuts: an investigation with otters as umbrella species. Biol. Conserv. 126 (4), 523–527.

Branton, Margaret A., Richardson, John S., 2014. A test of the umbrella species approach in restored floodplain ponds. J. Appl. Ecol.

Burnett, Ryan D., Roberts, L. Jay, 2015. A quantitative evaluation of the conservation umbrella of spotted owl management areas in the Sierra Nevada. PLoS One 10 (4), e0123778. https://doi.org/10.1371/journal.pone.0123778.

Caro, T.M., O'Doherty, Gillian, 1999. On the use of surrogate species in conservation biology. Conserv. Biol. 13 (4), 805–814.

Chen, Jianjun, Yi, Shuhua, Qin, Yu, 2017. The contribution of plateau pika disturbance and erosion on patchy alpine grassland soil on the qinghai-tibetan plateau: implications for grassland restoration. Geoderma.

Crosby, Andrew D., Dwayne Elmore, R., Leslie, David M., Will, Rodney E., 2015. Looking beyond rare species as umbrella species: northern bobwhites (Colinus virginianus) and conservation of grassland and shrubland birds. Biol. Conserv. 186, 233–240.

Delibes-Mateos, Miguel, Smith, Andrew T., Slobodchikoff, Con N., Swenson, Jon E., 2011. The paradox of keystone species persecuted as pests: a call for the conservation of abundant small mammals in their native range. Biol. Conserv. 144 (5), 1335–1346.

Descombes, Patrice, Golay, Joaquim. 2011. "Trophic Interactions Impact Butterflies ' Future Distribution under Climate Change." 1–20.

*Elith, Jane, et al., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29 (2), 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x.

Elith, Jane, et al., 2011a. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 17 (1), 43–57.

Elith, Jane, et al., 2011b. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 17 (1), 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x.
Emmett Duffy, J. 2009. Why Biodiversity Is Important to the Functioning of Real-World Ecosystems. Front. Ecol. Environ.
Erb, Liesl P., Ray, Chris, Guralnick, Robert, 2011. On the generality of a climate-mediated shift in the distribution of the American Pika (Ochotona princeps). Ecology 92 (9), 1730–1735.
Fleishman, Erica, Dennis D.Murphy, and Peter F.Brussard. 2000. "A New Method for Selection of Umbrella Species for Conservation Planning." *Ecological Applications*.
Gamfeldt, Lars, Helmut Hillebrand, and Per R. Jonsson. 2008. "Multiple Functions Increase the Importance of Biodiversity for Overall Ecosystem Functioning." *Ecology*.
Hernandez, Pilar A., Catherine, H.Graham, Master, Lawrence L., Albert, Deborah L., 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29 (5), 773–785. https://doi.org/10.1111/j.0906-7590.2006.04700.x.
Hof, Anouschka R., Jansson, Roland, Nilsson, Christer, 2012a. How biotic interactions may alter future predictions of species distributions: future threats to the persistence of the Arctic Fox in Fennoscandia. Divers. Distrib. 18 (6), 554–562.
Hof, Anouschka R., Allen, Andrew M., 2019. An uncertain future for the endemic Galliformes of the Caucasus. Sci. Total Environ. 651, 725–735.
Hof, Anouschka R., Jansson, Roland, Nilsson, Christer, 2012b. Future climate change will favour non-specialist mammals in the (sub)arctics. PLoS One 7 (12), e52574. https://doi.org/10.1371/journal.pone.0052574.
Hogan, Brigitte Wieshofer. 2010. Education "The Plateau Pika: A Keystone Engineer on the Tibetan Plateau."
Hurme, Eija, et al., 2008. Role of the Siberian flying squirrel as an umbrella species for biodiversity in northern boreal forests. Ecol. Indic. 8 (3), 246–255.
Johnson, Shelly A., Ober, Holly K., Adams, Damian C., 2017. Are keystone species effective umbrellas for habitat conservation? A spatially explicit approach. J. Nat. Conserv. 37, 47–55. https://doi.org/10.1016/j.jnc.2017.03.003.
Komonen, Minna, Komonen, Atte, Otgonsuren, Avirmed, 2003. Daurian Pikas (Ochotona Daurica) and grassland condition in Eastern Mongolia. J. Zool. 259 (3), 281–288.
Lambeck, Robert J., 1997. Focal species: a multi-species umbrella for nature conservation. Conserv. Biol.
Li, Ying, et al., 2022. Prediction of range expansion and estimation of dispersal routes of water deer (Hydropotes inermis) in the transboundary region between China, the Russian Far East and the Korean Peninsula. PLoS One 17 (4), e0264660. https://doi.org/10.1371/journal.pone.0264660.
Liu, Xiaodong, Chen, Baode, 2000. Climatic warming in the Tibetan Plateau during recent decades. Int. J. Climatol.
Liu Xiaodong, and Zhang Minfeng. 1998. "Contemporary Climatic Change over the Qinghai-Xizang Plateau and Its Response to the Green-House Effect." *Chinese Geographical Science*.
Liu, Yi.Y., et al., 2013. Changing climate and overgrazing are decimating Mongolian Steppes. PLoS One.
Living Planet Report 2020 | Official Site | WWF." ⟨https://livingplanet.panda.org/en-gb/⟩.
Low, Bi. Wei, Zeng, Yiwen, Tan, Heok Hui, Yeo, Darren C.J., 2021. Predictor complexity and feature selection affect maxent model transferability: evidence from global freshwater invasive species. Divers. Distrib. 27 (3), 497–511. https://doi.org/10.1111/ddi.13211.
Mas, Jean François, et al., 2013. A suite of tools for ROC analysis of spatial models. ISPRS Int. J. Geo-Inf. 2 (3), 869–887.
Merow, Cory, Smith, Matthew J., Silander Jr., John A., 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36 (10), 1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x.
Moreno-Amat, Elena, et al., 2015. Impact of model complexity on cross-temporal transferability in maxent species distribution models: an assessment using paleobotanical data. Ecol. Model. 312, 308–317.
Mortelliti, Alessio, Brehm, Allison M., Evans, Bryn E., 2022. Umbrella effect of monitoring protocols for mammals in the Northeast US. Sci. Rep. 12 (1), 1893. https://doi.org/10.1038/s41598-022-05791-x.
Ovando-hidalgo, Natalia, and Juan Tun-garrido. 2020. "Revista Mexicana de Biodiversidad Especies Clave En La Vegetación de Duna Costera En La Península de Yucatán, México." 91.
Pang, Xiao Pan, Guo, Zheng Gang, 2017. Plateau Pika disturbances alter plant productivity and soil nutrients in alpine meadows of the Qinghai-Tibetan Plateau, China. Rangel. J.
Pearson, Richard G., Dawson, Terence P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob. Ecol. Biogeogr. 12 (5), 361–371.
Peterson, A.Townsend, Papeş, Monica, Soberón, Jorge, 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecol. Model. 213 (1), 63–72.
Phillips, Steven J. 2017. "A Brief Tutorial on Maxent."
Power, Mary E., et al., 1996. Challenges in the quest for keystones. BioScience 46 (8), 609–620.
Qin, Yu, et al., 2021. Pikas burrowing activity promotes vegetation species diversity in alpine grasslands on the Qinghai-Tibetan Plateau. Glob. Ecol. Conserv. 31, e01806.
Radosavljevic, Aleksandar, Anderson, Robert P., 2014. Making better maxent models of species distributions: complexity, overfitting and evaluation. J. Biogeogr. 41 (4), 629–643. https://doi.org/10.1111/jbi.12227.
Roberge, Jean-Michel, Mikusiński, Grzegorz, Svensson, S.ören, 2008. The white-backed woodpecker: umbrella species for forest conservation planning. Biodivers. Conserv. 17 (10), 2479–2494. https://doi.org/10.1007/s10531-008-9394-4.
Roberge, Jean Michel, Angelstam, Per, 2004. Usefulness of the umbrella species concept as a conservation tool. Conserv. Biol. 18 (1), 76–85.
Rodríguez-Castañeda, Genoveva, Hof, Anouschka R., Jansson, Roland, 2017. How bird clades diversify in response to climatic and geographic factors. Ecol. Lett. 20 (9), 1129–1139. https://doi.org/10.1111/ele.12809.
Rowland, Mary M., Wisdom, Michael J., Suring, Lowell H., Meinke, Cara W., 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. Biol. Conserv. 129 (3), 323–335.
Royden, Leigh H., Burchfiel, B.Clark, van der Hilst, Robert D., 2008. The geological evolution of the Tibetan Plateau. Science 321 (5892), 1054 LP – 1058. ⟨http://science.sciencemag.org/content/321/5892/1054.abstract⟩.
Schoener, Thomas W., 1968. The anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49 (4), 704–726. https://doi.org/10.2307/1935534.
Sillero, Neftalí, Barbosa, A.M.árcia, 2021. Common mistakes in ecological niche models. Int. J. Geogr. Inf. Sci. 35 (2), 213–226. https://doi.org/10.1080/13658816.2020.1798968.
Singh, C.P., 2008. Alpine ecosystems in relation to climate change. ISG Newsl. 14 (1–4), 54–55.
Smith, Andrew T., Badingqiuying, Maxwell C. Wilson, and Brigitte W. Hogan. 2019. "Functional-Trait Ecology of the Plateau Pika Ochotona curzoniae in the Qinghai–Tibetan Plateau Ecosystem." *Integrative Zoology*.
Smith, Andrew T., Foggin, J.Marc, 1999. The Plateau Pika (Ochotona curzoniae) is a keystone species for biodiversity on the Tibetan Plateau. Anim. Conserv. 2 (4), 235–240.
Sun, Feida, et al., 2015. Effects of Plateau Pika activities on seasonal plant biomass and soil properties in the alpine meadow ecosystems of the Tibetan Plateau. Grassl. Sci.
Team R Development Core. 2020. "R: A Language and Environment for Statistical Computing."
Tikhonov, Gleb. 2019. Bayesian Latent Factor Approaches for Modeling Ecological Species Communities Doctoral Programme in Wildlife Biology Academic Dissertation To Be Presented for Public Examination with the Permission of the Faculty Of.
Trainor, Anne M., Schmitz, Oswald J., Ivan, Jacob S., Shenk, Tanya M., 2014. Enhancing species distribution modeling by characterizing predator-prey interactions. Ecol. Appl. 24 (1), 204–216.
Turner, C. 2018. Climate Change and Biodiversity. EDTECH. ⟨https://books.google.nl/books?id=A-PEDwAAQBAJ⟩.
Wang, Xuexia, et al., 2015. A comparison of biodiversity-ecosystem function relationships in alpine grasslands across a degradation gradient on the Qinghai-Tibetan Plateau. Rangel. J.

Warren, Dan L., Glor, Richard E., Turelli, Michael, 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62 (11), 2868–2883.

Warren, Dan L., Richard E.Glor, and Michael Turelli. 2010. "ENMTools: A Toolbox for Comparative Studies of Environmental Niche Models." Ecography 33(3): 607–11.

Warren, R., et al., 2013. Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. Nat. Clim. Change 3 (7), 678–682. ⟨http://www.nature.com/natureclimatechange⟩.

Wilson, Maxwell C., and Andrew T. Smith. 2014. "The Pika and the Watershed: The Impact of Small Mammal Poisoning on the Ecohydrology of the Qinghai-Tibetan Plateau." *Ambio*.

Wilson, Maxwell C., Smith, Andrew T., 2015. The Pika and the watershed: the impact of small mammal poisoning on the ecohydrology of the Qinghai-Tibetan Plateau. Ambio 44 (1), 16–22. ⟨https://pubmed.ncbi.nlm.nih.gov/25331028⟩.

Yoccoz, Nigel G., Delestrade, Anne, Loison, Anne, 2011. Impact of climatic change on alpine ecosystems: inference and prediction. Mach. Des. 83 (3), 42–44.

Zachariah Atwater, Daniel, Barney, Jacob N., 2021. Climatic niche shifts in 815 introduced plant species affect their predicted distributions. Glob. Ecol. Biogeogr. 30 (8), 1671–1684.

Zhang, Yong, et al., 2016. Responses of alpine vegetation and soils to the disturbance of Plateau Pika (Ochotona curzoniae) at burrow level on the Qinghai-Tibetan Plateau of China. Ecol. Eng. 88, 232–236. https://doi.org/10.1016/j.ecoleng.2015.12.034.