

Climate change-induced range shift of the endemic epiphytic lichen *Lobaria pindarensis* in the Hindu Kush Himalayan region

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Abstract: The Hindu Kush Himalayan (HKH) region harbours some of the richest and most diverse ecosystems on the planet that are now facing substantial threats through changes in climate, land use and human population growth, with serious consequences for the biodiversity in this mountainous region. In this paper we evaluated the effects of climate change on the distribution of the tripartite epiphytic macrolichen *Lobaria pindarensis*, considered to be endemic to the Himalayas. To predict the current and future distribution of this species we applied the Random Forest modelling algorithm and climatic variables with a post-processing of projected distributions using a map of habitat types in the study region. We calibrated models based on 1397 species presences within an altitudinal range of 2036–4000 m and extrapolated them according to two IPCC scenarios of climate change (RCP 2.6 and RCP 8.5). Based on the results of ensemble modelling, two new localities where *L. pindarensis* might potentially occur were predicted. Our simulations predicted a range expansion of this epiphytic lichen to the north-east and to higher altitudes in response to climate change, although the species' low dispersal abilities and the local availability of trees as a substratum will considerably limit latitudinal and altitudinal shifts. By contrast, assuming the species can migrate to previously unoccupied areas, and depending on different future climate scenarios, our models forecasted a habitat loss of 30–70% for *L. pindarensis*. The main reason for the simulated habitat loss is the expected increase in mean annual temperature (by 1.5–3.7 °C) and total annual precipitation (by 56–125 mm). Our results contribute further evidence for the high sensitivity of tripartite macrolichens, especially those from mountain areas, to climate change and particularly emphasize the vulnerability of *L. pindarensis*. Thus, we stress the need to develop and formulate conservation measures and strategies for the protection of this endemic species in the Hindu Kush Himalayan region.

Key words: climate warming, conservation, habitat loss, mountain area, Nepal, Random Forest modelling, species distribution

Accepted for publication 29 August 2018

Introduction

Globally, climate change and anthropogenic disturbance have resulted in shifts in the distributions of many species (Parmesan 2006; D'Andrea *et al.* 2009; Anderson *et al.* 2012). Particularly high rates of habitat loss are predicted for bryophytes, plants and animals in

mountain ecosystems (Parmesan & Yohe 2003; Raxworthy *et al.* 2003, 2008; Bergamini *et al.* 2009; Dullinger *et al.* 2012; Steinbauer *et al.* 2018). The Hindu Kush Himalayan (HKH) region is home to some of the richest and most varied ecosystems on the planet (Singh *et al.* 2011) that now face substantial threats from changes in climate, land use and human population dynamics (Sharma 2012). Although meteorological data for the HKH region are scarce (especially for precipitation) and collected from a limited number of weather stations, they indicate that overall there is a moderate warming trend with a more pronounced temperature increase at higher compared with lower elevations (Singh *et al.* 2011). The increase in average temperature ranged from 0.6 to 1.3 °C

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(Dimri & Dash 2012), the latter being considerably higher than the global average of 0.74 °C (IPCC 2007). In general, most of the studies on precipitation in the Himalayas show a lack of any notable trends (Shrestha *et al.* 2000; Dimri & Dash 2012). However, it is reported that heavy rainfall events have become more common in the HKH region while the frequency of moderate rainfall events has decreased (Singh *et al.* 2011). Besides the direct impact of global warming on temperature and precipitation, different climate-induced changes in Himalayan ecosystems have been reported, such as loss and fragmentation of habitats, decrease in forest biodiversity, increase in forest fire, wetland degradation and changes in land use pattern (Tse-ring *et al.* 2010). It is therefore very important to understand the impacts of climate change and subsequent climate-induced disturbances on the biodiversity and population dynamics of different taxa in the Himalayas because shifts in species distributions may increase their vulnerability to extinction (Lenoir & Svenning 2015; Allen & Lendemer 2016).

As complex symbiotic organisms, lichens are very sensitive to environmental change including global warming (van Herk *et al.* 2002; Aptroot & van Herk 2007; Ellis *et al.* 2007b; Allen & Lendemer 2016). Previous studies have shown that the effect of climate change on lichens with different functional traits, including substratum preference and photobiont type, might vary considerably. For example, Aptroot & van Herk (2007) reported the expansion of trentepohlioid epiphytic lichens in Central Europe while Ellis *et al.* (2007b) and Hauck (2009) showed that significant declines have occurred for species from cold climates (i.e. arctic-alpine, boreal and montane lichens). A recent study of future climate impact on lichens on the Iberian Peninsula suggested that large cyanobacterial macrolichens are the most threatened, and as a result of climate warming they might lose c. 70% of their current habitats (Rubio-Salcedo *et al.* 2017). Over 93% of distributional loss has also been predicted under future climate change for high-elevation

lichens, especially narrowly endemic species (Allen & Lendemer 2016).

As a model species to evaluate the effect of climate change on the distribution of tripartite lichens (i.e. containing cyanobacterial and green-algal photobionts) in mountain areas, we chose *Lobaria pindarensis* Räsänen (*Peltigerales*; *Lobariaceae*), which is considered to be endemic to the Himalayas. This large foliose lichen is associated with a cyanobacterial photobiont in the genus *Nostoc* and the green-alga *Symbiochloris reticulata* (Škaloud *et al.* 2016). The lichen reproduces mainly through vegetative propagules, cylindrical isidia formed at the margin of the thallus (Scheidegger *et al.* 2010; Devkota *et al.* 2014). This epiphytic lichen grows on selected phorophyte species including *Abies spectabilis*, *Viburnum erubescens*, *Ribes takare*, *Tsuga dumosa* and *Rosa sericea*, though host species vary at different altitudes from temperate to subalpine zones (Devkota *et al.* 2017). *Lobaria pindarensis* was first described from the Pindar Valley in Kashmir, India (Joshi & Awasthi 1982) and was subsequently reported from several regions in eastern Nepal (Joshi & Awasthi 1982; Devkota *et al.* 2014), Bhutan (Upreti & Ranjan 1988; Upreti & Negi 1996; Aptroot & Feijen 2002) and China (Wang & Qian 2013). However, there is limited knowledge about its distribution pattern, substratum and habitat requirements (Devkota *et al.* 2017).

Species distribution models (SDMs) are being widely used in ecological studies and conservation biology to predict the potential distribution of different species under current and future climates and to evaluate the impact of climate warming on species distributions (Guisan & Thuiller 2005; Hernandez *et al.* 2008; Elith & Graham 2009; Merow *et al.* 2013). This approach has also been successfully applied to lichen-forming fungi (Engler *et al.* 2004; Bolliger *et al.* 2007; Ellis *et al.* 2007a, b; Waser *et al.* 2007; Wiersma & Skinner 2011; Braidwood & Ellis 2012; Szczepańska *et al.* 2015; Allen & Lendemer 2016; Dymytrova *et al.* 2016; Nascimbene *et al.* 2016). In this study, we hypothesize that future climate change in the Himalayas will result in habitat loss for *L. pindarensis*. To

test this hypothesis, we first mapped the present distribution of this epiphytic lichen based on extensive field studies in Nepal. We then used these locality data and the Random Forest algorithm to model the current distribution of *L. pindarensis* throughout the HKH region. Finally, we evaluated the loss of *L. pindarensis* habitats based on different climate scenarios in 2050 and 2070. The results of this study provide useful practical information on the distribution and substratum preferences of this endemic lichen, which is essential for further monitoring and effective conservation strategies.

Materials and Methods

Study area

The study area comprised the Hindu Kush Himalayan (HKH) region for the range-wide modelling. The HKH region extends for a distance of 3500 km over eight Asian countries from Afghanistan in the west to Myanmar in the east, encompassing four global biodiversity hotspots, 60 ecoregions and 488 protected areas. This mountainous region provides ecosystem services to more than 200 million people (Sharma & Tsering 2009; Chettri *et al.* 2010). The Nepal Himalaya lies within the phytogeographical transition zone between the dry western Himalaya and the wet eastern Himalaya, and is characterized by a rich regional biodiversity (Ohsawa *et al.* 1986).

In the districts of Nepal which were sampled, the climate ranges from temperate to alpine along an altitudinal gradient. The temperate zone (2000–3000 m) is characterized by lower-temperate mixed broadleaved forests (1700–2200 m), temperate mixed evergreen forests (2100–2700 m), and upper temperate mixed broadleaved forests (2400–3000 m). Silver fir (2900–3850 m) and birch-*Rhododendron* forests (3300–3800 m) are dominant in the subalpine zone (3000–4000 m). The alpine zone (above 4000 m) contains *Juniperus-Rhododendron* bush (4000–4300 m), *Caragana-Lonicera* bush (4000–4800 m) and alpine meadows (Chaudhary 1998).

Field work and species data

Specimens of *L. pindarensis* were collected during fieldwork between 2009 and 2014 in six valleys of three mountainous districts of Nepal (Fig. 1): Taplejung (Olangchung Gola and Ghunsa Valleys), Solukhumbu (Dudhkunda and Dudhkoshi Valleys) and Gorkha (Nubri and Tsum Valleys). Additional surveys were made in the Rasuwa (Gosaikunda and Kyanjin Valleys), Manang and Myagdi districts along the walking trails. The surveyed districts covered 16 655 km² in Nepal. In total, 13 field surveys, each of 13–45 days, were organized from the mid-hills to very remote mountain areas, representing the temperate (2000–3000 m) to the alpine zones

(5000 m and above) of Nepal. We searched for the presence of *L. pindarensis* along altitudinal and vertical gradients. In each valley, five elevation bands were selected at different locations (around 2200, 2400, 2800, 3200, 3800 m a.s.l.) (Scheidegger *et al.* 2010; Katuwal *et al.* 2016; Rai *et al.* 2016). At the “local level” (i.e. in each region and at each of the five locations), transects up to the highest elevation band were established at every 200 m to collect samples. In addition to our collections, earlier reports of *L. pindarensis* from Nepal (Joshi & Awasthi 1982; Devkota *et al.* 2014) and other countries of the HKH region (Joshi & Awasthi 1982; Upreti & Ranjan 1988; Aptroot & Feijen 2002) were also included in our analysis.

One presence point per 1 km² from the original data set was randomly selected in order to minimize the spatial autocorrelation and to match the resolution of environmental data in the species distribution modelling. We used the ‘spThin’ package for random subsampling of our species data. The procedure was repeated 10 times resulting in 90 species occurrences to be used for further modelling.

Environmental variables

The altitude variable was derived from the Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM). The SRTM DEM was obtained from <http://srtm.usgs.gov/index.php> in 3 arc seconds (*c.* 90 m resolution). The SRTM DEM features absolute vertical and relative vertical accuracies of ±16 m and ±10 m respectively, whereas absolute horizontal accuracy is ±20 m (Walker *et al.* 2007).

Bioclimatic data for both current and future climates were obtained from WorldClim in 30 arc seconds (*c.* 1 km resolution) (Hijmans *et al.* 2005; available at <http://www.worldclim.org>). WorldClim is a commonly used, freely accessible global database of temperature and precipitation variables in the form of raster data (Jarvis *et al.* 2005). Of the original 19 bioclimatic layers, four with the lowest Pearson correlation coefficient ($r \leq 0.7$) i.e. mean annual temperature, total annual precipitation, precipitation seasonality (Coefficient of Variation), precipitation of driest quarter (Table 1), were selected for further analyses (Dormann *et al.* 2013).

In this study we aimed to evaluate the impact of climate change on the species’ distribution, consequently only climatic variables were retained for modelling. Topographic predictors (i.e. altitude) were excluded from the analysis even though they are known to affect species distributions, especially in montane ecosystems (Oke & Thompson 2015), because they do not change in climate scenarios and their presence might render the species’ response to climate less sensitive.

Current climate refers to the period from 1960 to 1990 (Hijmans *et al.* 2005). The CCSM4 climate model (Community Climate System Model version 4.0; <http://www.cesm.ucar.edu/models/ccsm4.0/>) with lowest and highest concentration pathways (RCP (Representative Concentration Pathway) 2-6 and 8-5) for the years 2050 and 2070 was used for future climate scenarios. Calculated differences in temperature and precipitation based

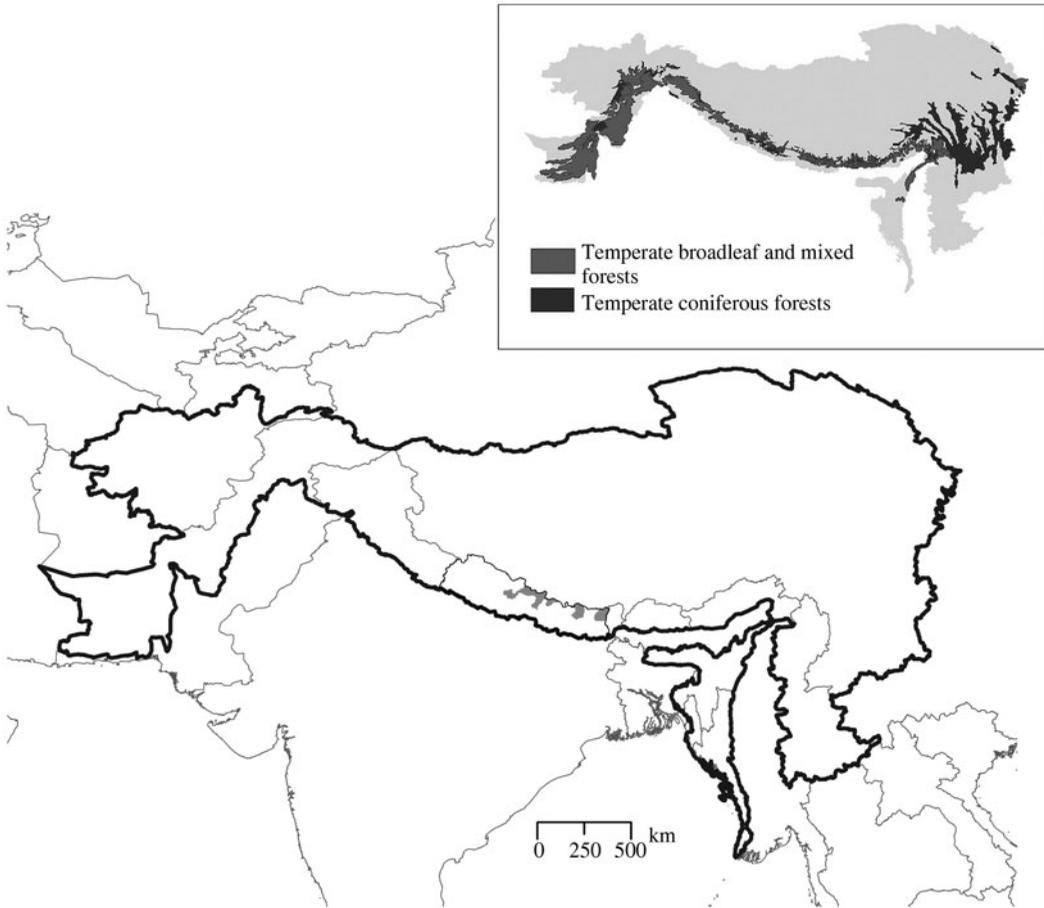


FIG. 1. The Hindu Kush Himalayan (HKH) region (bold boundary) showing the districts of Nepal that were surveyed (shaded). The inset shows the distribution of temperate broad-leaved and mixed forest as well as coniferous forest in the HKH region where phorophytes suitable for *Lobaria pindarensis* colonization are present.

on the reference period revealed that a scenario with emission predictions of 2.6 represents a moderate future climate scenario while a scenario with emission predictions of 8.5 is considered an extreme future climate scenario. Information on habitat types in the HKH region (see insert in Fig. 1) was obtained as a digital polygon data set from the International Centre for Integrated Mountain Development (ICIMOD 2007).

Modelling and projection methods

To model the current and future distribution of *L. pindarensis* and evaluate the relative importance of each predictor variable, we used the Random Forest (RF) algorithm. RF is an advanced machine-learning method that can handle any type of variable (continuous or categorical), automatically considers interactions between

TABLE 1. Climatic variables at localities where *Lobaria pindarensis* has been observed in the Hindu Kush Himalayan region.

Climatic variables	Units	Mean (\pm SD)	Min	Max
Mean annual temperature	$^{\circ}\text{C}$	6.2 ± 2.7	0.4	13.2
Total annual precipitation	mm	991.1 ± 462.2	369	1898
Precipitation seasonality	%	96.1 ± 9.6	70	119
Precipitation of driest quarter	mm	33.5 ± 13.8	17	150

them and produces accurate predictions with a control for overfitting data (Breiman 2001). RF has also been shown to be effective for future estimates of suitable habitat after climate change (Prasad *et al.* 2006). The model was run using the default parameters for RF with a total number of trees grown as implemented in the package ‘biomod2’ ($n = 500$) (Thuiller *et al.* 2013). As the number of true absences was too small (*c.* 30), we randomly selected 1000 background points (pseudo-absences) from the whole HKH region. The selection of the pseudo-absences was repeated five times resulting in five data sets with 1000 pseudo-absence points in each. For classification and machine-learning techniques, randomly selected pseudo-absences and averaging several runs with a small number of pseudo-absences, yields the most reliable distribution models (Barbet-Massin *et al.* 2012). We calibrated the models with a random subset of 70% of the species’ occurrence data and evaluated them with the remaining 30%. Three evaluation metrics were calculated using the repeated cross-validation procedure ($n = 10$) to evaluate the accuracy of the predicted models: the area under the receiver operating characteristic curve (AUC) (Fielding & Bell 1997), Cohen’s kappa statistic (κ) (Cohen 1960), and the true skill statistic (TSS) (Allouche *et al.* 2006).

Variable importance values were estimated based on a randomization procedure as described by Thuiller *et al.* (2009). Variable importance ranges from 0, if the predictor is assumed to have no influence on the model, to 1 if the predictor is very important. The variable importance values were further transformed to the relative scores which add up to 1.

The obtained probabilities of species occurrence were projected in species distributions based on both current and future climates. Finally, we generated the ensemble distribution maps under current and future conditions by averaging the projected probabilities over fitted models (a combination of 10 repetitions and 5 runs for the pseudo-absence selection) for each climate scenario (i.e. the current, 2050 CCSM4 RCP 2.6, 2050 CCSM4 RCP 8.5, 2070 CCSM4 RCP 2.6 and 2070 CCSM4 RCP 8.5). A TSS score > 0.7 was used as a threshold to exclude the low-quality models when building the final ensemble model. To produce binary maps, the ensemble maps for current and future climate scenarios were reclassified into presence/absence values using the threshold at which the sum of sensitivity and specificity calculated on the test data (averaged over the 10 cross-validation replicates) was maximized.

The projected distribution maps (km^2) were used to estimate species distribution shifts under future climate scenarios. The relative exposure (%) of species to climate change was calculated according to Rubio-Salcedo *et al.* (2017) as follows:

$$\frac{\text{future distribution} - \text{current distribution}}{\text{current distribution}} \times 100$$

Finally, a map providing information on habitat types in the HKH region was used as a last step to filter current

predictions in order to remove areas where the presence of *L. pindarensis* is highly improbable (no suitable substrata available). Under a future climate, two possible scenarios of species distributions were considered: 1) without migration of species to new (previously unoccupied) locations; 2) assuming species migration (by dispersal) to new climatically suitable habitats. Since information on habitat types in the HKH region under a future climate was not available, we could not evaluate the real impact of future changes in forest areas on predicted species distribution and, therefore, our assessment of future *L. pindarensis* habitat loss must be accepted with caution.

Results

Occurrence of *Lobaria pindarensis* in HKH region

We collected a total of 1397 records of *Lobaria pindarensis*, comprising 1391 from Nepal and three records each from India and Bhutan. The taxonomic status of records from China (mainly Yunnan Province) in an ongoing project needs confirmation and those records were excluded in this study. The Nepal Himalayas is the stronghold for *L. pindarensis*, where it occurs in a wide range of locations in semi-humid to humid areas from the central to the eastern part of Nepal. The Olangchung Gola and Ghunsa Valleys of Taplejung District and the Dudh-kunda Valley of Solukhumbu District in Nepal harboured the maximum number of species records, 307, 273 and 255 individuals, respectively. Very low numbers were recorded from the Myagdi District of Nepal (Fig. 2).

The highest number of individuals (922 or 66% of the total number) was observed between 3200 m and 3800 m (Fig. 3). The lower limit of distribution (2036 m) was recorded in Kyanjin Valley, Rasuwa, Nepal (28°09′458″N, 85°25′19″E, 21 Apr 2009), while the upper limit (4000 m) was found near Dinga Samba, Olangchung Gola Valley, Taplejung, Nepal (27°43′010″N, 87°43′998″E, 20 May 2011). The highest and lowest altitudinal limits reported for India and Bhutan were 2700–3048 m and 2400–3000 m, respectively.

Our study showed that *L. pindarensis* occurs mainly in coniferous (silver fir), birch-*Rhododendron* and varying shrub forests from temperate to subalpine zones (more than

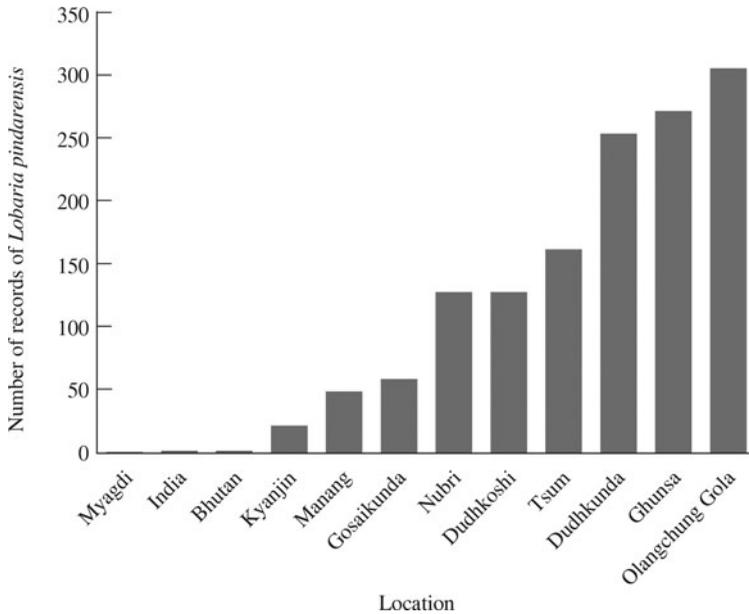


Fig. 2. Number of records of *Lobaria pindarensis* in India, Bhutan and ten valleys in Nepal.

90% of the total occurrences). Only 7% of records were documented in temperate broad-leaved and mixed forests.

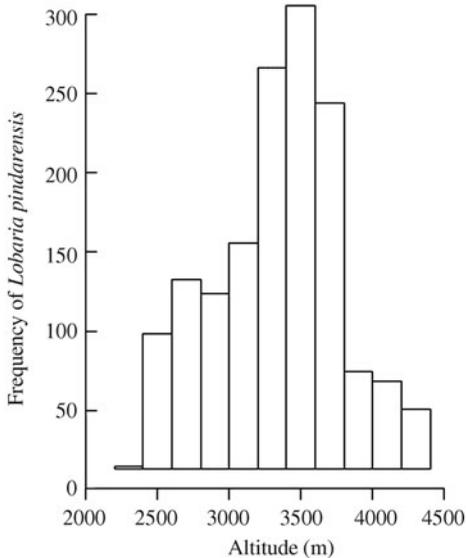


Fig. 3. The change in frequency of *Lobaria pindarensis* with altitude in Nepal.

Model accuracy and predicted current distribution

All fitted models showed high values of model accuracy regardless of the evaluation metric (Table 2). The AUC score of the final ensemble model (averaged over the repetitions and all pseudo-absence data sets) was 0.998 ± 0.005 , indicating a highly predictive model performance. Among the climatic variables tested, precipitation of the driest quarter (42%) and mean annual temperature (36%) contributed most to the predicted species distribution. The mean annual temperature of current suitable habitat (obtained from the observed species localities) ranged from 0.4°C to 13.2°C , while the total annual precipitation ranged from 369 mm to 1898 mm (Table 1).

The total area of current suitable habitat (\approx climate space) for *L. pindarensis* in the HKH region is $74\,552\text{ km}^2$, 28% of which is located in Nepal (Fig. 4, Supplementary Material Fig. S1, available online). The model predicted three fragmented areas where *L. pindarensis* might potentially occur under the current climate. When ensemble

TABLE 2. Model accuracy values (AUC, Kappa and TSS) for each of 10 cross-validation repetitions (runs) and each of five random pseudo-absence data sets (PA). Model accuracy (mean ± SD) is given for the final ensemble model used for the projection of species distribution to current and future climate scenarios.

Run	AUC					Kappa					TSS				
	PA1	PA2	PA3	PA4	PA5	PA1	PA2	PA3	PA4	PA5	PA1	PA2	PA3	PA4	PA5
	1	0.992	0.985	0.998	0.992	0.986	0.861	0.791	0.936	0.856	0.827	0.920	0.943	0.960	0.970
2	0.989	0.986	0.998	0.991	0.989	0.805	0.779	0.922	0.887	0.805	0.920	0.930	0.983	0.946	0.923
3	1.000	0.989	0.992	0.994	0.994	0.979	0.809	0.861	0.875	0.839	0.990	0.930	0.943	0.967	0.950
4	0.992	0.978	0.990	0.992	0.985	0.839	0.712	0.795	0.870	0.798	0.930	0.920	0.950	0.920	0.933
5	0.991	0.994	0.999	0.992	0.993	0.883	0.870	0.960	0.861	0.879	0.917	0.967	0.980	0.957	0.943
6	0.991	0.988	0.995	0.991	0.989	0.897	0.811	0.942	0.839	0.844	0.893	0.960	0.990	0.937	0.910
7	0.998	0.988	0.989	0.992	0.994	0.940	0.815	0.870	0.866	0.853	0.956	0.920	0.910	0.933	0.960
8	0.995	0.992	0.995	0.988	0.994	0.879	0.839	0.870	0.833	0.870	0.947	0.923	0.967	0.947	0.953
9	0.993	0.979	0.998	0.995	0.994	0.901	0.724	0.922	0.919	0.897	0.923	0.890	0.953	0.943	0.970
10	0.983	0.987	0.986	0.996	0.980	0.798	0.787	0.805	0.940	0.766	0.876	0.876	0.913	0.956	0.873
Mean ± SD			0.998 ± 0.005					0.851 ± 0.058					0.985 ± 0.027		

modelling uncertainty is mapped, the predicted values are highly consistent within these three potential areas (SD < 0.05; Fig. 5), with higher values of standard deviations indicating locations where the predictions of *L. pindarensis* distribution are uncertain. The area predicted in the middle ranges from central to the eastern Nepal corresponding to the known distribution of *L. pindarensis* based on observed records. In addition, new localities for this species were predicted in the Sichuan and Yunnan Provinces of China and along the northern part of the Afghanistan-Pakistan border.

Range shifts under future climate scenarios

Our results showed that, depending on different climate scenarios, the existing area suitable for *L. pindarensis* in the HKH region will decline overall by 30–70% (Table 3, Fig. 6). The extreme future climate scenario predicted a considerably higher habitat loss (53–68%) compared to the moderate future climate scenario (34–38%). However, assuming dispersal of *L. pindarensis* to previously unoccupied areas which become climatically suitable for colonization, predicted habitat loss is less extreme (c. 1–9%). The extreme future climate scenario even predicted an 11% increase in distribution, based on suitable habitat and assuming successful migration of the species, though achieving this seems rather unlikely considering limited substratum availability.

The main reason for the predicted habitat loss of *L. pindarensis* in the HKH region is the expected increase in temperature and precipitation. Based on the predicted changes in climate, the mean annual temperature in the predicted current *L. pindarensis* habitats will increase by 1.5 °C (2050) and 1.4 °C (2070) under the moderate future climate scenario; and more dramatically, by 2.7 °C (2050) and 3.7 °C (2070), under the extreme future climate scenario (Fig. 7). The mean annual precipitation in the species' current habitats will increase by 56 mm (2050) and 64 mm (2070) under the moderate future climate scenario and by 79 mm (2050) and

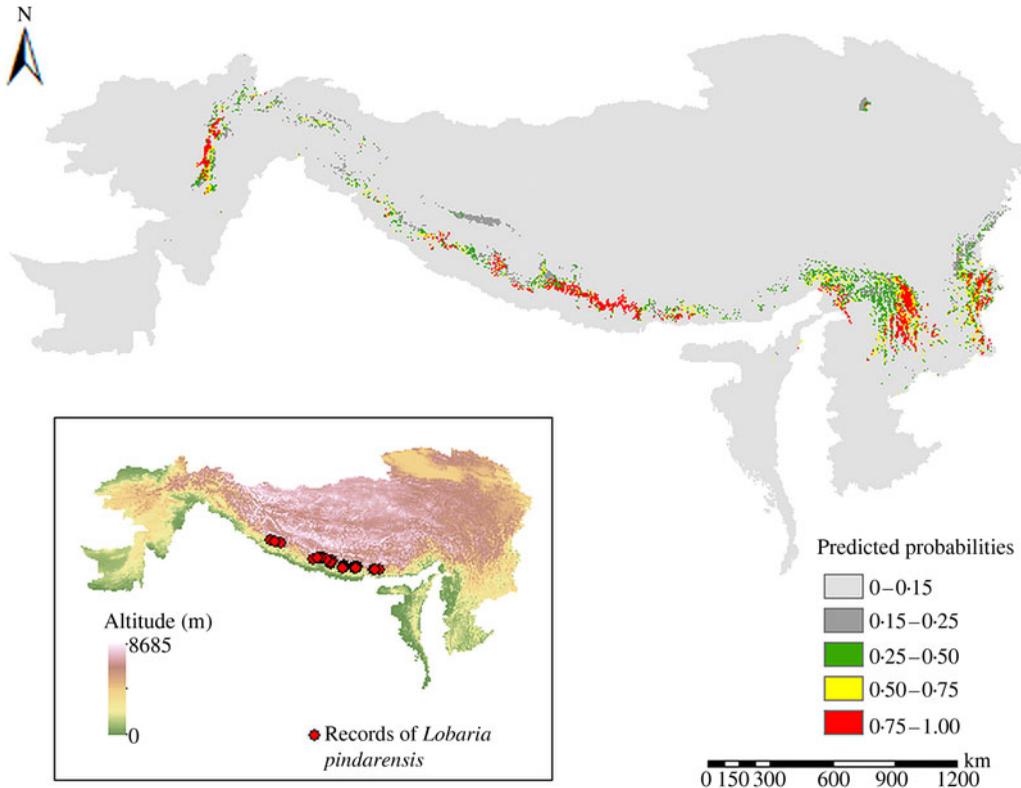


FIG. 4. Potential habitat areas of *Lobaria pindarensis* in the Hindu Kush Himalayan region predicted using the ensemble model. This model represents a mean of projected probabilities using all fitted models calibrated with climatic variables determined from the current climate. The inset shows current records of *L. pindarensis* in India, Nepal and Bhutan.

125 mm (2070) under the extreme future climate scenario (Fig. 7).

The distribution of *L. pindarensis* is also predicted to shift to higher elevations (Fig. 8) with a more pronounced loss of habitat under an extreme future climate scenario. In general, the southern central range of current suitable habitat is predicted to move further north by 90–100 km and then expand to the east by *c.* 500 km (Supplementary Material Fig. S2, available online). The potential range shift would be considerably less under a moderate climate scenario. The current habitat area in Nepal is also predicted to shift towards the north-east (Supplementary Material Fig. S2, available online), while a dramatic habitat loss is shown under future climates if species dispersal is limited by natural

or human-related factors (Supplementary Material Fig. S2, available online). Furthermore, a geographical shift in species distribution is predicted to an area where the model is highly uncertain (Fig. 5).

Discussion

Potential distribution of *Lobaria pindarensis* in the Hindu Kush Himalayan region

Our extensive field study in Nepal revealed an altitudinal range for *L. pindarensis* of 2036–4000 m. The highest frequency of occurrence was found at 3200–3600 m. This altitudinal optimum of the species coincides with the mid-elevational maximum of lichen species

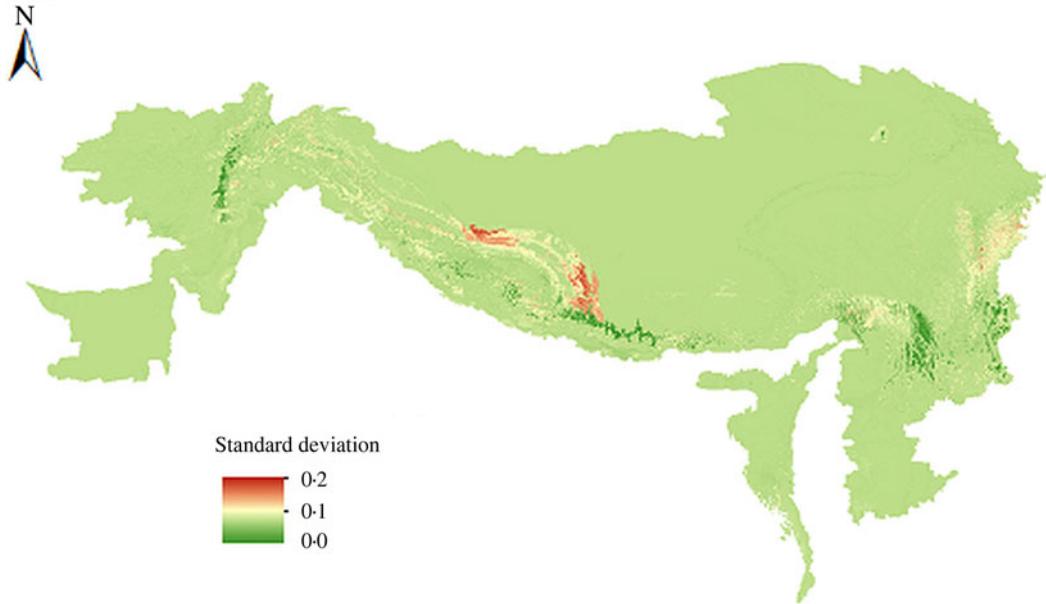


FIG. 5. A map of the ensemble modelling uncertainty in the Hindu Kush Himalayan region. A high standard deviation indicates locations where the predicted values for the distribution of *Lobaria pindarensis* are highly uncertain.

TABLE 3. Predicted loss, gain and relative exposure of *Lobaria pindarensis* habitats in the Hindu Kush Himalayan region in 2050 and 2070, under moderate (RCP 2.6) and extreme (RCP 8.5) future climate scenarios.

Future climate scenarios	Year	Loss		Gain		Predicted future distribution area, (km ²)		Relative exposure, (%)	
		km ²	%	km ²	%	No migration	With migration	No migration	With migration
RCP 2.6	2050	25418	34.2	25017	33.6	48946	73963	-34.2	-0.5
	2070	28589	38.4	21618	29.1	45775	67393	-38.4	-9.4
RCP 8.5	2050	39639	53.3	37018	49.8	34725	71743	-53.3	-3.5
	2070	50883	68.4	59231	79.7	23481	82712	-68.4	11.2

richness in Nepal (Baniya *et al.* 2010), which was reported at 3100–3400 m. Mid-elevation peaks in species richness of higher plants (Vetaas & Grytnes 2002; Bhattacharai & Vetaas 2003; Rokaya *et al.* 2012; Subedi *et al.* 2015), orchids (Acharya *et al.* 2011), bryophytes (Grau *et al.* 2007), birds (Poudel & Sipoš 2014; Katuwal *et al.* 2016) as well as lichens (Wolf 1993; Negi 2000; Pinokiyo *et al.* 2008; Baniya *et al.* 2010; Rai *et al.* 2012) have previously been observed in the

Himalayas. Similarly, Wolf (1993) showed that lichen species richness tends to peak at intermediate altitudes in the northern Andes.

The evergreen cloud forest zone at high altitudes is composed of deciduous (*Quercus semecarpifolia* or *Betula utilis* forests) and pure or mixed coniferous forests with *Abies spectabilis* and *Tsuga dumosa* dominant (Miehe 1989, 2015). The high rainfall (c. 4000 mm on southern slopes) and cool summer temperatures (c. 14–17 °C) of this zone favour luxuriant forests

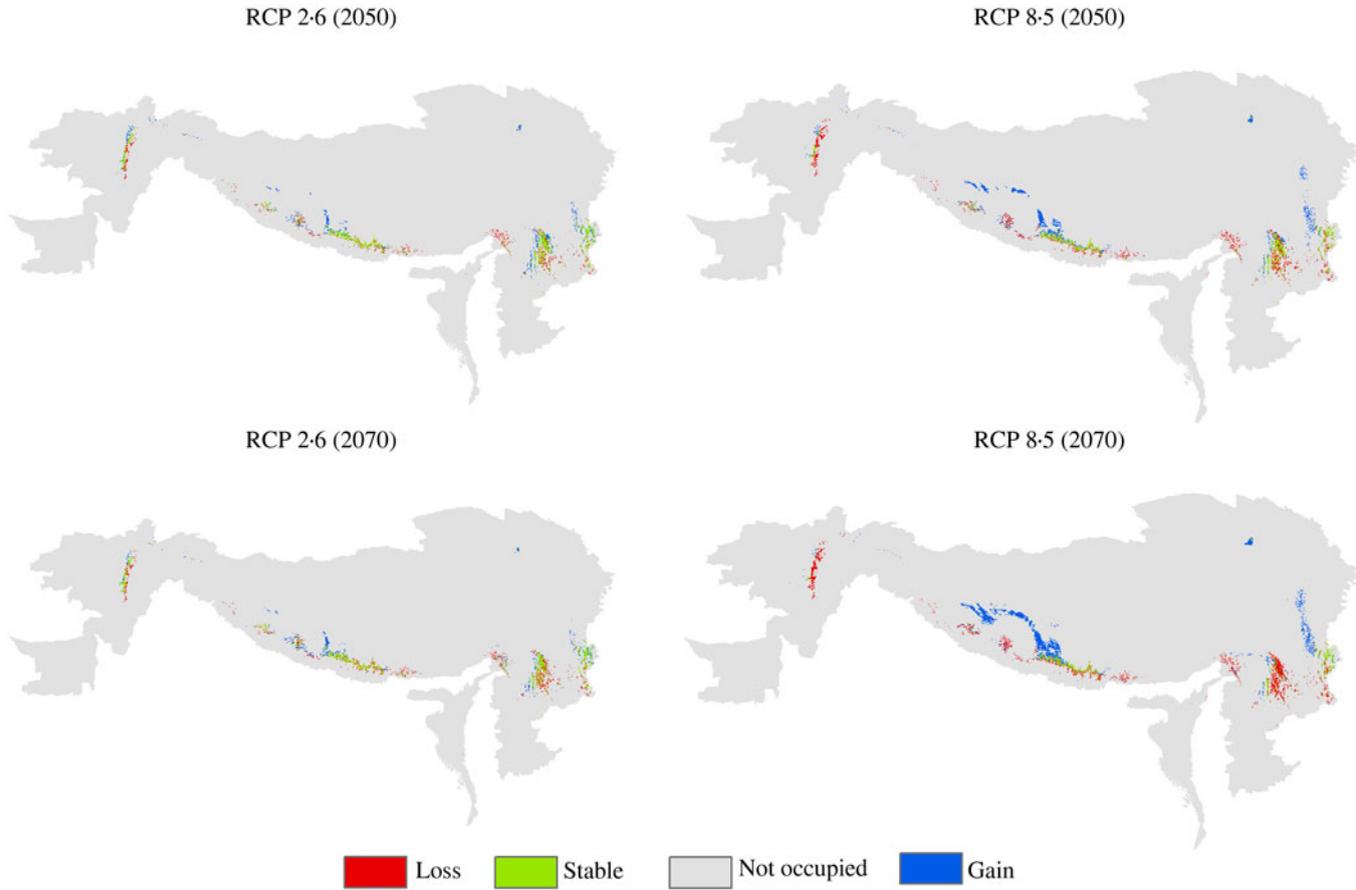


FIG. 6. Predicted change in habitat availability for *Lobaria pindarensis* in the Hindu Kush Himalayan region under moderate (RCP 2·6) and extreme (RCP 8·5) future climate scenarios in 2050 and 2070. Loss = predicted to be a loss of habitat; stable = stable habitat; not occupied = habitat unoccupied and will remain so in the future; gain = habitat previously unoccupied but is predicted to be occupied in the future.

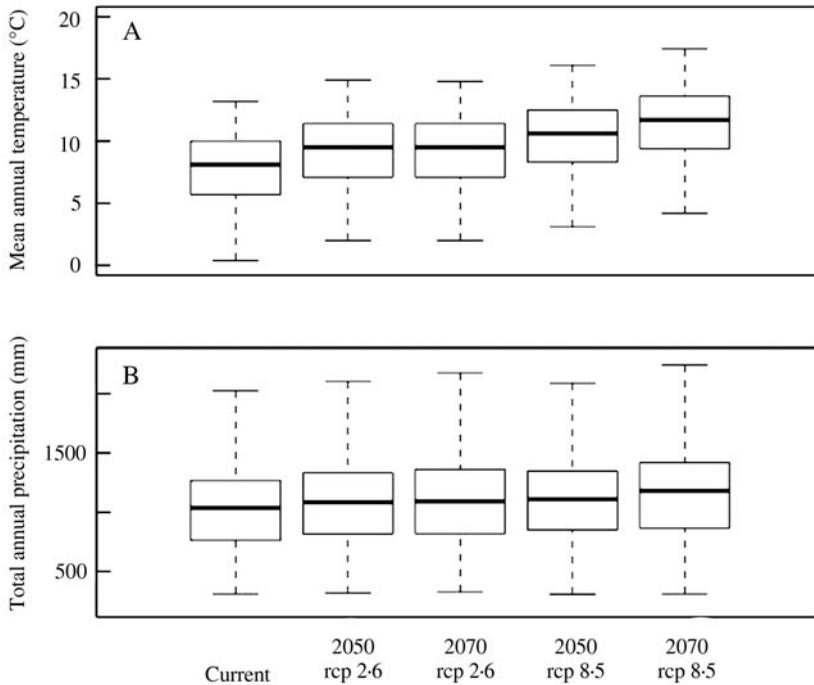


Fig. 7. Changes in mean annual temperature (A) and total annual precipitation (B) in the predicted habitats of *Lobaria pindarensis* in the Hindu Kush Himalayan region under moderate (RCP 2·6) and extreme (RCP 8·5) future climate scenarios in the 2050s and 2070s. 'Current' refers to the range of temperature and precipitation found under the current climate in the predicted localities shown in Fig. 4.

compared to the mid-hills and lowlands of Nepal (Miehe 1989; Bhattarai *et al.* 2004). Similarly, in the western dry areas of Nepal (Miehe *et al.* 2001), lower abundance of foliose lichens including *L. pindarensis* would be expected than in the central and eastern parts of the country. Indeed, we did not observe *L. pindarensis* in the Dadelhdhura, Baitadi, Jajarkot and Rolpa districts in western Nepal.

The potential distribution of species predicted by the SDM approach could be useful for finding suitable sites for the reintroduction and re-colonization of species or for discovering unknown populations (Pearce & Lindenmayer 1998; Ferial & Peterson 2002; Raxworthy *et al.* 2003; Araújo & Peterson 2012). However, for the realistic forecasting of distribution patterns for epiphytic lichens, the characteristics of their host trees should also be taken into consideration (Dymytrova *et al.* 2016; Eaton *et al.* 2018). In our study

we filtered current predictions to remove areas outside of the coniferous and broad-leaved mixed forests where the substrata suitable for *L. pindarensis* colonization occurs. Hence, three fragmented areas were predicted where *L. pindarensis* might potentially occur under the current climate. In addition to locations in Nepal that correspond to current records, new localities outside its known distribution were predicted in the Sichuan and Yunnan Provinces of China and along the northern part of the Afghanistan-Pakistan border. The Yunnan and Sichuan Provinces of China are situated in the eastern part of the Himalayas and south-western part of China. These provinces represent fragile mountain ecosystems harbouring diverse climatic zones and vegetation (Zomer *et al.* 2015). Similar to Nepal, the climate of this region is also influenced by the monsoon, with dry (November–May) and

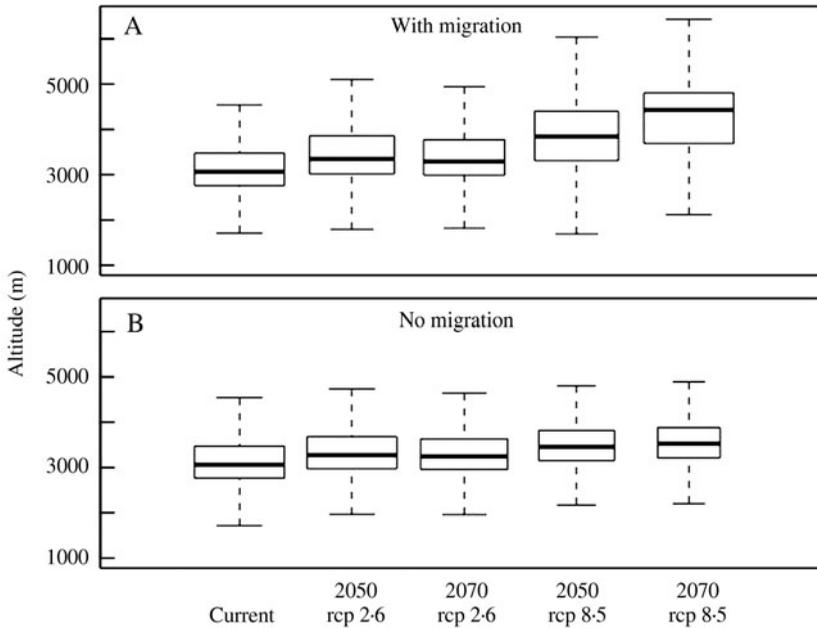


FIG. 8. Changes in the altitudinal range of *Lobaria pindarensis* in the Hindu Kush Himalayan region under moderate (RCP 2-6) and extreme (RCP 8-5) future climate scenarios in the 2050s and 2070s. A, with migration = assumption of migration to new (previously unoccupied) habitats; B, without such migration. 'Current' represents altitudinal range of *L. pindarensis* in the HKH region derived from predicted localities (shown in Fig. 4) under current climate conditions.

wet (June–October) seasons (Yang *et al.* 2006). Thus, we postulate that *L. pindarensis* might also occur in China. On the other hand, 11 species of *Lobaria* (i.e. *L. adscripturians*, *L. dentata*, *L. isidiophora*, *L. isidiosa*, *L. kurokawae*, *L. meridionalis*, *L. orientalis*, *L. pseudopulmonaria*, *L. retigera*, *L. yoshimurae* and *L. yunnanensis*) that need further taxonomic revision have been previously reported from these provinces (Yoshimura 1969; Wang *et al.* 2001; Cornejo *et al.* 2009; Wang & Qian 2013). It is well known that SDM is an effective approach for predicting and discovering previously unknown populations of various taxa, in particular genetically and ecologically related species (Raxworthy *et al.* 2003; Fordham *et al.* 2014; Morales-Castilla *et al.* 2017). Taking this into consideration, we believe that our distribution model might also be representative for other *Lobaria* species that have similar climatic and substratum preferences and, therefore, are ecologically related to *L. pindarensis*. In future, an

intensive field survey will be necessary in these potential new areas to check for *Lobaria* species.

Range shifts under future climate change

Previous studies have revealed significant habitat loss for many lichen species in different geographical regions caused by climate change (Ellis *et al.* 2007b; Hauck 2009; Lang *et al.* 2012; Ellis 2013; Rubio-Salcedo *et al.* 2017). Allen & Lendemer (2016) have recently shown that climate change poses a significant threat to montane lichens, especially narrowly endemic species of high altitudes. Our models also predicted a loss of habitat (30–70%) in the Hindu Kush Himalayan region for the endemic lichen *L. pindarensis* under future climate change. These losses were generally more pronounced for the extreme future climate scenario (with emission predictions of 8-5) than

for the moderate climate scenario (with emission predictions of 2·6). We found that under future climate change the distribution area of *L. pindarensis* might be shifted to high altitudes and expand further to the north-east where temperature and precipitation values will remain within the optimal range for this species. Northward and uphill migration as a response to climate change has been shown for other taxa (Parmesan & Yohe 2003; Pauli *et al.* 2012). However, accounting for the geographical pattern of forests where the substrata suitable for colonization by *L. pindarensis* occur had a significant impact on the distribution pattern of this epiphytic lichen. Information on habitat types in the HKH region is not available under future climate scenarios and, therefore, we were unable to adequately evaluate whether the predicted future distributional and altitudinal shifts in *L. pindarensis* habitat would be realistic. Nevertheless, we postulate that shifts to high altitudes is highly probable within the observed range of this species (up to 4000 m), while further altitudinal expansion of *L. pindarensis* would be limited by the timberline of coniferous and shrub forests. The Himalayas have the highest timberlines in the world (Shi & Ning 2013; Gaire *et al.* 2014) but at the same time are one of the areas most severely affected by anthropogenic and climatic impacts (Myers *et al.* 2000). Therefore, protection of high altitude forests is very important to ensure that epiphytic species can disperse upwards as the climate warms. This will mainly require fencing of some pastures to facilitate establishment of tree and shrub species at uphill sites. Furthermore, scientific evidence-based forest management at the timberline would help to balance pressure caused by the overharvesting of forests by hoteliers and the local population.

On the other hand, a distributional shift of *L. pindarensis* as a result of climate change is likely to be limited, as together with other species of *Lobaria*, it is mainly associated with undisturbed old-growth forests, which allows time for effective dispersal given the low dispersal capacity of such species (Silllett *et al.* 2000; Werth *et al.* 2006; Devkota *et al.*

2017). Moreover, natural barriers such as mountain peaks and valleys, are expected to limit the predicted species expansion to the north-east. These factors (i.e. low dispersal capacity and natural barriers) are likely to counteract the range gain (11%) predicted by the extreme future scenario (2070) because this increase in *L. pindarensis* distribution is predicated on the long-distance (>100 km) migration of this species.

Finally, it should be emphasised that the predicted habitat loss of *L. pindarensis* in the HKH region should be interpreted with caution due to limitations of the SDM approach (Pearson & Dawson 2003; Araújo & Peterson 2012; Ellis *et al.* 2017). For instance, the geographical shift in species distribution resulting from climate change includes a shift into an area for which model predictions are highly uncertain. In addition, our future models do not incorporate data on forest patterns, or species migration rates that are crucial for realistic projections of species distribution in any future climate (Engler *et al.* 2009; Meier *et al.* 2012).

Our study contributes further evidence of the high sensitivity to climate change of tripartite macrolichens in mountain areas. The predicted habitat loss for *L. pindarensis* in the Himalayas caused by future climate change and weak dispersal capacity emphasizes the vulnerability of this endemic species and necessitates precautionary strategies for sustainable management of the region and consequently effective species conservation.

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We are grateful to Krishna K. Shrestha for his cooperation in implementing a collaborative research project between the Central Department of Botany, Tribhuvan University and the Swiss Federal Research Institute WSL. The Department of National Parks and Wildlife Conservation (DNPWC), Ministry of Forests and Environment (previously Ministry of Forests and Soil Conservation), the Government of Nepal and the National Trust for Nature Conservation (NTNC) are thanked for providing research permissions. Sanjeev K. Rai, Jyoti P. Gajurel, Laxmi Sankhi, Til B. Chongbang and Hem B. Katuwal are acknowledged for their valuable assistance during field trips. This research was supported by the Swiss National Science Foundation (grant JRP IZ70Z0_131338/1 to CS).

SUPPLEMENTARY MATERIAL

For supplementary material accompanying this paper visit <https://doi.org/10.1017/S002428291900001X>.

REFERENCES

- Acharya, K. P., Vetaas, O. R. & Birks, H. J. B. (2011) Orchid species richness along Himalayan elevational gradients. *Journal of Biogeography* **38**: 1821–1833.
- Allen, J. L. & Lendemer, J. C. (2016) Climate change impacts on endemic, high-elevation lichens in a biodiversity hotspot. *Biodiversity and Conservation* **25**: 555–568.
- 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**: 1223–1232.
- Anderson, J. T., Panetta, A. M. & Mitchell-Olds, T. (2012) Evolutionary and ecological responses to anthropogenic climate change. *Plant Physiology* **160**: 1728–1740.
- Aptroot, A. & Feijen, F. J. (2002) Annotated checklist of the lichens and lichenicolous fungi of Bhutan. *Fungal Diversity* **11**: 21–48.
- Aptroot, A. & van Herk, C. M. (2007) Further evidence of the effects of global warming on lichens, particularly those with *Trentepohlia* phycobionts. *Environmental Pollution* **146**: 293–298.
- Araújo, M. B. & Peterson, T. A. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology* **97**: 1527–1539.
- Baniya, C. B., Solhøy, T., Gauslaa, Y. & Palmer, M. W. (2010) The elevation gradient of lichen species richness in Nepal. *Lichenologist* **42**: 83–96.
- Barbet-Massin, M., Jiguet, F., Albert, C. H. & Thuiller, W. (2012) Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution* **3**: 327–338.
- Bergamini, A., Ungricht, S. & Hofmann, H. (2009) An elevational shift of cryophilous bryophytes in the last century – an effect of climate warming? *Diversity and Distributions* **15**: 871–879.
- Bhattarai, K. R. & Vetaas, O. R. (2003) Variation in plant species richness of different life forms along a subtropical elevation gradient in the Himalayas, east Nepal. *Global Ecology and Biogeography* **12**: 327–340.
- Bhattarai, K. R., Vetaas, O. R. & Grytnes, J. A. (2004) Relationship between plant species richness and biomass in an arid sub-alpine grassland of the central Himalayas, Nepal. *Folia Geobotanica* **39**: 57–71.
- Bolliger, J., Bergamini, A., Stofer, S., Kienast, F. & Scheidegger, C. (2007) Predicting the potential spatial distributions of epiphytic lichen species at the landscape scale. *Lichenologist* **39**: 279–291.
- Braidwood, D. & Ellis, C. J. (2012) Bioclimatic equilibrium for lichen distributions on disjunct continental landmasses. *Botany* **90**: 1316–1325.
- Breiman, L. (2001) Random forests. *Machine Learning* **45**: 5–32.
- Chaudhary, R. P. (1998) *Biodiversity in Nepal: Status and Conservation*. Bangkok and Saharanpur: S. Devi & Teeprass Books.
- Chettri, N., Shakya, B., Thapa, R. & Sharma, E. (2010) Status of a protected area system in the Hindu Kush-Himalayas: an analysis of PA coverage. *International Journal of Biodiversity Science and Management* **4**: 164–178.
- Cohen, J. (1960) A coefficient of agreement for nominal scales. *Educational and Psychological Measurement* **20**: 37–46.
- Cornejo, C., Chabanenko, S. & Scheidegger, C. (2009) Phylogenetic analysis indicates transitions from vegetative to sexual reproduction in the *Lobaria retigera* group (Lecanoromycetidae, Ascomycota). *Lichenologist* **41**: 275–284.
- D’Andrea, L., Broennimann, O., Kozłowski, G., Guisan, A., Morin, X., Keller-Senften, J. & Felber, F. (2009) Climate change, anthropogenic disturbance and the northward range expansion of *Lactuca serriola* (Asteraceae). *Journal of Biogeography* **36**: 1573–1587.
- Devkota, S., Cornejo, C., Werth, S., Chaudhary, R. P. & Scheidegger, C. (2014) Characterization of microsatellite loci in the Himalayan lichen fungus *Lobaria pindarensis* (Lobariaceae). *Applications in Plant Sciences* **2**: 1300101.
- Devkota, S., Keller, C., Olley, L., Werth, S., Chaudhary, R. P. & Scheidegger, C. (2017) Distribution and national conservation status of the lichen family Lobariaceae (Peltigerales): from subtropical luxuriant forests to the alpine scrub of Nepal Himalaya. *Mycosphere* **8**: 630–647.
- Dimri, A. & Dash, S. (2012) Wintertime climatic trends in the western Himalayas. *Climate Change* **111**: 775–800.
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., García Marquéz, J. R., Gruber, B., Lafourcade, B., Leitão, P. J., et al. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**: 27–46.
- Dullinger, S., Gatringer, A., Thuiller, W., Moser, D., Zimmermann, N. E., Guisan, A., Willner, W., Plutzer, C., Leitner, M., Mang, T., et al. (2012) Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Climate Change* **2**: 619–622.
- Dymytrova, L., Stofer, S., Ginzler, C., Breiner, F. T. & Scheidegger, C. (2016) Forest-structure data improve distribution models of threatened habitat specialists: implications for conservation of epiphytic lichens in forest landscapes. *Biological Conservation* **196**: 31–38.
- Eaton, S., Ellis, C., Genney, D., Thompson, R., Yahr, R. & Haydon, D. T. (2018) Adding small species to the big picture: species distribution modelling in an age of landscape scale conservation. *Biological Conservation* **217**: 251–258.
- Elith, J. & Graham, C. H. (2009) Do they? How do they? WHY do they differ? On finding reasons for differing

- performances of species distribution models. *Ecography* **32**: 66–67.
- Ellis, C. J. (2013) A risk-based model of climate change threat: hazard, exposure, and vulnerability in the ecology of lichen epiphytes. *Botany* **91**: 1–11.
- Ellis, C. J., Coppins, B. J. & Dawson, T. P. (2007a) Predicted response of the lichen epiphyte *Lecanora populicola* to climate change scenarios in a clean-air region of northern Britain. *Biological Conservation* **135**: 396–404.
- Ellis, C. J., Coppins, B. J., Dawson, T. P. & Seaward, M. R. D. (2007b) Response of British lichens to climate change scenarios: trends and uncertainties in the projected impact for contrasting biogeographic groups. *Biological Conservation* **140**: 217–235.
- Ellis, C. J., Geddes, H., McCheyne, N. & Stansfield, A. (2017) Lichen epiphyte response to non-analogue monthly climates: a critique of bioclimatic models. *Perspectives in Plant Ecology, Evolution and Systematics* **25**: 45–58.
- Engler, R., Guisan, A. & Rechsteiner, L. (2004) An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology* **41**: 263–274.
- Engler, R., Randin, C. F., Vittoz, P., Czaka, T., Beniston, M., Zimmermann, N. E. & Guisan, A. (2009) Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? *Ecography* **32**: 34–45.
- Feria, P. A. & Peterson, T. A. (2002) Prediction of bird community composition based on point-occurrence data and inferential algorithms: a valuable tool in biodiversity assessments. *Diversity and Distributions* **8**: 49–56.
- Fielding, A. H. & Bell, J. F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24**: 38–49.
- Fordham, D. A., Brook, B. W., Moritz, C. & Nogues-Bravo, D. (2014) Better forecasts of range dynamics using genetic data. *Trends in Ecology and Evolution* **29**: 436–443.
- Gaire, N. P., Koirala, M., Bhujju, D. R. & Borgaonkar, H. P. (2014) Treeline dynamics with climate change at the central Nepal Himalaya. *Climate of the Past* **10**: 1277–1290.
- Grau, O., Grytnes, J.-A. & Birks, H. J. B. (2007) A comparison of altitudinal species richness patterns of bryophytes with other plant groups in Nepal, Central Himalaya. *Journal of Biogeography* **34**: 1907–1915.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**: 993–1009.
- Hauck, M. (2009) Global warming and alternative causes of decline in arctic-alpine and boreal-montane lichens in north-western Central Europe. *Global Change Biology* **15**: 2653–2661.
- Hernandez, P. A., Franke, I., Herzog, S. K., Pacheco, V., Paniagua, L., Quintana, H. L., Soto, A., Swenson, J. J., Tovar, C., Valqui, T. H., et al. (2008) Predicting species distributions in poorly-studied landscapes. *Biodiversity and Conservation* **17**: 1353–1366.
- 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**: 1965–1978.
- ICIMOD (2007) *Ecological Regions of Hindu Kush Himalayan (HKH) Region*. Digital polygon dataset. ICIMOD, Kathmandu, Nepal.
- IPCC (2007) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor & H. L. Miller, eds). Cambridge and New York: Cambridge University Press.
- Jarvis, A., Yeaman, S., Guarino, L. & Tohme, J. (2005) The role of geographic analysis in locating, understanding, and using plant genetic diversity. *Methods in Enzymology* **395**: 279–298.
- Joshi, M. & Awasthi, D. D. (1982) The lichen family *Stictaceae* in India and Nepal. *Biological Memoirs* **7**: 165–190.
- Katuwal, H. B., Basnet, K., Khanal, B., Devkota, S., Rai, S. K., Gajurel, J. P., Scheidegger, C. & Nobis, M. P. (2016) Seasonal changes in bird species and feeding guilds along elevational gradients of the Central Himalayas, Nepal. *PLoS ONE* **11**: 1–17.
- Lang, S. I., Cornelissen, J. H. C., Shaver, G. R., Ahrens, M., Callaghan, T. V., Molau, U., Ter Braak, C. J. F., Holzer, A. & Aerts, R. (2012) Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. *Global Change Biology* **18**: 1096–1107.
- Lenoir, J. & Svenning, J. C. (2015) Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography* **38**: 15–28.
- Meier, E. S., Lischke, H., Schmatz, D. R. & Zimmermann, N. E. (2012) Climate, competition and connectivity affect future migration and ranges of European trees. *Global Ecology and Biogeography* **21**: 164–178.
- Merow, C., Smith, M. J. & Silander, J. A. (2013) A practical guide to MaxEnt for modeling species’ distributions: what it does, and why inputs and settings matter. *Ecography* **36**: 1058–1069.
- Miehe, G. (1989) Vegetation patterns on Mount Everest as influenced by monsoon and fohn. *Vegetatio* **79**: 21–32.
- Miehe, G. (2015) Glacial foreland successions. In *Nepal: An Introduction to the Natural History, Ecology and Human Environment of the Himalayas* (G. Miehe, C. Pendry & R. P. Chaudhary, eds): 80–90. Edinburgh: Royal Botanic Garden Edinburgh.
- Miehe, G., Winniger, M., Boehner, J. & Zhang, Y. (2001) Climatic diagrams of high Asia. *Erdkunde* **55**: 94–97.
- Morales-Castilla, I., Davies, T. J., Pearse, W. D. & Peres-Neto, P. (2017) Combining phylogeny and

- co-occurrence to improve single species distribution models. *Global Ecology and Biogeography* **26**: 740–752.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.
- Nascimbene, J., Gabriele, C., Benesperi, R., Catalano, I., Cataldo, D., Grillo, M., Isocrono, D., Matteucci, E., Ongaro, S., Potenza, G., *et al.* (2016) Climate change fosters the decline of epiphytic *Lobaria* species in Italy. *Biological Conservation* **201**: 377–384.
- Negi, H. R. (2000) On the patterns of abundance and diversity of macrolichens of Chopta-Tungnath in Garhwal Himalaya. *Journal of Bioscience* **25**: 367–378.
- Ohsawa, M., Shakya, P. R. & Numata, M. (1986) Distribution and succession of West Himalayan forest types in the eastern part of the Nepal Himalaya. *Mountain Research and Development* **6**: 143–157.
- Oke, O. A. & Thompson, K. A. (2015) Distribution models for mountain plant species: the value of elevation. *Ecological Modelling* **301**: 72–77.
- Parnesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* **37**: 637–669.
- Parnesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.
- Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J. L. B., Coldea, G., Dick, J., Erschbamer, B., Calzado, R. F., *et al.* (2012) Recent plant diversity changes on Europe's mountain summits. *Science* **336**: 353–355.
- Pearce, J. & Lindenmayer, D. (1998) Bioclimatic analysis to enhance reintroduction biology of the endangered helmeted honeyeater (*Lichenostomus melanops cassidix*) in southeastern Australia. *Natural Area Journal* **6**: 238–243.
- 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**: 361–371.
- Pinokiy, A., Singh, K. P. & Singh, J. S. (2008) Diversity and distribution of lichens in relation to altitude within a protected biodiversity hot spot, north-east India. *Lichenologist* **40**: 47–62.
- Poudel, P. K. & Sipos, J. (2014) Conservation status affects elevational gradient in bird diversity in the Himalaya: a new perspective. *Global Ecology and Conservation* **2**: 338–348.
- Prasad, A. M., Iverson, L. R. & Liaw, A. (2006) Newer classification and regression tree techniques: bagging and random forests for ecological prediction. *Ecosystems* **9**: 181–199.
- Rai, H., Upreti, D. K. & Gupta, R. K. (2012) Diversity and distribution of terricolous lichens as indicator of habitat heterogeneity and grazing induced trampling in a temperate-alpine shrub and meadow. *Biodiversity and Conservation* **21**: 97–113.
- Rai, S. K., Sharma, S., Shrestha, K. K., Gajurel, J. P., Devkota, S., Nobis, M. P. & Scheidegger, C. (2016) Effects of the environment on species richness and composition of vascular plants in Manaslu Conservation Area and Sagarmatha region of Nepalese Himalaya. *Banko Janakari* **26**: 3–16.
- Raxworthy, C. J., Martinez-Meyer, E., Horning, N., Nussbaum, R. A., Schneider, G. E., Ortega-Huerta, M. A. & Peterson, T. A. (2003) Predicting distributions of known and unknown reptile species in Madagascar. *Nature* **426**: 837–841.
- Raxworthy, C. J., Pearson, R. G., Rabibisoa, N., Rakotondrazafy, A. M., Ramanamanjato, J. P., Raselimanana, A. P., Wu, S., Nussbaum, R. A. & Stone, D. A. (2008) Extinction vulnerability of tropical montane endemism from warming and upslope displacement: a preliminary appraisal for the highest massif in Madagascar. *Global Change Biology* **14**: 1703–1720.
- Rokaya, M. B., Münzbergová, Z., Shrestha, M. R. & Timsina, B. (2012) Distribution patterns of medicinal plants along an elevational gradient in central Himalaya, Nepal. *Journal of Mountain Science* **9**: 201–213.
- Rubio-Salcedo, M., Psomas, A., Prieto, M., Zimmermann, E. & Martinez, I. (2017) Case study of the implications of climate change for lichen diversity and distributions. *Biodiversity and Conservation* **26**: 1121–1141.
- Scheidegger, C., Nobis, M. P. & Shrestha, K. K. (2010) Biodiversity and livelihood in land-use gradients in an era of climate change – outline of a Nepal-Swiss research project. *Botanica Orientalis: Journal of Plant Science* **7**: 7–17.
- Sharma, E. (2012) Climate change and its impacts in the Hindu Kush-Himalayas: an introduction. In *Climate Change Modeling for Local Adaptation in the Hindu Kush-Himalayan Region (Community, Environment and Disaster Risk Management, Vol. 11)* (A. Lamadrid & K. Ilan, eds): 17–32. Bingley, West Yorkshire: Emerald Group Publishing Limited.
- Sharma, E. & Tsering, K. (2009) Climate change in the Himalayas: the vulnerability of biodiversity. *Sustainable Mountain Development* **55**: 10–12.
- Shi, P. & Ning, W. (2013) The timberline ecotone in the Himalayan region: an ecological review. In *High-Altitude Rangelands and their Interfaces in the Hindu Kush Himalayas* (W. Ning, G. S. Rawat, S. Joshi, M. Ismail & E. Sharma, eds): 108–116. Kathmandu, Nepal: ICIMOD.
- Shrestha, A., Wake, C., Dibb, J. & Mayewski, P. (2000) Precipitation fluctuations in the Nepal Himalaya and its vicinity and relationship with some large scale climatological parameters. *International Journal of Climatology* **20**: 317–327.
- Sillett, S. C., McCune, B., Peck, J. E., Rambo, T. R. & Ruchty, A. (2000) Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecological Applications* **10**: 789–799.
- Singh, S., Bassignana-Khadka, I., Karky, B. & Sharma, E. (2011) *Climate Change in the Hindu Kush-Himalayas: The State of Current Knowledge*. Kathmandu, Nepal: ICIMOD.
- Škaloud, P., Friedl, T., Hallmann, C., Beck, A. & Dal Grande, F. (2016) Taxonomic revision and species

- delimitation of coccoid green algae currently assigned to the genus *Dictyochloropsis* (*Trebouxiophyceae*, Chlorophyta). *Journal of Phycology* **52**: 599–617.
- Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchhalter, M., Barni, E., et al. (2018) Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature* **556**: 231–234.
- Subedi, S. C., Bhattarai, K. R. & Chaudhary, R. P. (2015) Distribution pattern of vascular plant species of mountains in Nepal and their fate against global warming. *Journal of Mountain Science* **12**: 1345–1354.
- Szczepańska, K., Pruchniewicz, D. & Kossowska, M. (2015) Modeling the potential distribution of three lichens of the *Xanthoparmelia pulla* group (*Parmeliaceae*, Ascomycota) in Central Europe. *Acta Societatis Botanicorum Poloniae* **84**: 431–438.
- Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M. B. (2009) BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography* **32**: 369–373.
- Thuiller, W., Georges, D. & Engler, R. (2013) *Biomod2: Ensemble Platform for Species Distribution Modeling*. R package version 3. URL: <https://cran.r-project.org/package=biomod2>
- Tse-ring, K., Sharma, E., Chettri, N. & Shrestha, A. (2010) *Climate Change Impact and Vulnerability in the Eastern Himalayas – Synthesis Report. Climate Change Vulnerability of Mountain Ecosystems in the Eastern Himalayas*. Kathmandu, Nepal: ICIMOD.
- Upreti, D. K. & Negi, H. R. (1996) Folk use of *Thamnoelia vermicularis* (Swartz) Ach. in Lata Village of Nanda Devi Biosphere Reserve. *Ethnobotany* **8**: 83–86.
- Upreti, D. K. & Ranjan, M. (1988) A note on some macrolichens from Thimphu District, Bhutan. *Journal of Recent Advances in Applied Sciences* **3**: 426–432.
- van Herk, C. M., Aptroot, A. & van Dobben, H. F. (2002) Long-term monitoring in the Netherlands suggests that lichens respond to global warming. *Lichenologist* **34**: 141–154.
- Vetaas, O. R. & Grytnes, J. (2002) Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecology and Biogeography* **11**: 291–301.
- Walker, W. S., Kellndorfer, J. M. & Pierce, L. E. (2007) Quality assessment of SRTM C- and X-band interferometric data: implications for the retrieval of vegetation canopy height. *Remote Sensing of Environment* **106**: 428–448.
- Wang, L. S. & Qian, Z. G. (2013) *Illustrated Medicinal Lichens of China*. Kunming: Yunnan Keji Chubanshe. [In Chinese]
- Wang, L. S., Narui, T., Harada, H., Culberson, C. F. & Culberson, W. L. (2001) Ethnic uses of lichens in Yunnan, China. *Bryologist* **104**: 345–349.
- Waser, L. T., Kuechler, M., Schwarz, M., Ivits, E., Stofer, S. & Scheidegger, C. (2007) Prediction of lichen diversity in an UNESCO biosphere reserve – correlation of high resolution remote sensing data with field samples. *Environmental Modeling and Assessment* **12**: 315–328.
- Werth, S., Wagner, H. H., Gugerli, F., Holderegger, R., Csencsics, D., Kalwij, J. M., Scheidegger, C. & Jesse, M. (2006) Quantifying dispersal and establishment limitation in a population of an epiphytic lichen. *Ecology* **87**: 2037–2046.
- Wiersma, Y. F. & Skinner, R. (2011) Predictive distribution model for the boreal felt lichen *Erioderma pedicellatum* in Newfoundland, Canada. *Endangered Species Research* **15**: 115–127.
- Wolf, J. H. D. (1993) Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Annals of the Missouri Botanical Garden* **80**: 928–960.
- Yang, X., Skidmore, A. K., Melick, D. R., Zhou, Z. & Xu, J. (2006) Mapping non-wood forest product (matsutake mushrooms) using logistic regression and a GIS expert system. *Ecological Modelling* **198**: 208–218.
- Yoshimura, I. (1969) Lichenological notes 2–6. *Journal of the Hattori Botanical Laboratory* **32**: 67–78.
- Zomer, R. J., Xu, J., Wang, M., Trabucco, A. & Li, Z. (2015) Projected impact of climate change on the effectiveness of the existing protected area network for biodiversity conservation within Yunnan Province, China. *Biological Conservation* **184**: 335–345.