Biological Conservation 206 (2017) 143–150

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc

Range shifts in response to climate change of *Ophiocordyceps sinensis*, a fungus endemic to the Tibetan Plateau

Yujing Yan [a,1], Yi Li [b,c], Wen-Jing Wang [b], Jin-Sheng He [a], Rui-Heng Yang [b], Hai-Jun Wu [b], Xiao-Liang Wang [b], Lei Jiao [b], Zhiyao Tang [a,*], Yi-Jian Yao [b,*]

[a] Department of Ecology, College of Urban and Environmental Sciences, Key Laboratory of Earth Surface Processes of Ministry of Education, Peking University, Beijing 100871, China
[b] State Key Laboratory of Mycology, Institute of Microbiology, Chinese Academy of Sciences, Beijing 100101, China
[c] Fujian Province Key Laboratory of Plant Virology, Institute of Plant Virology, Fujian Agricultural and Forestry University, Fuzhou 350002, China

ARTICLE INFO

Article history:
Received 21 June 2016
Received in revised form 17 December 2016
Accepted 20 December 2016
Available online xxxx

Keywords:
Climate change
Distribution
Species distribution model
Fungi
Cordyceps sinensis
Tibetan Plateau

ABSTRACT

Recent climate change has been widely recognized to influence the distribution of many plants and animals, while its impacts on the distribution of fungi remain largely unknown. Here, we used *Ophiocordyceps sinensis*, an entomopathogenic fungus and important traditional Chinese medicine whose distribution range was reported as decreased on the Tibetan Plateau in recent decades, as an example to predict the current potential distribution and the possible range shifts in response to climate change of a fungus by using extensive field records and an ensemble species distribution modeling method. It is demonstrated that the distribution range of the fungus wound decrease significantly, shifting upward in altitude and toward the central part of the Plateau. In an unlimited dispersal scenario, net habitat losses of 19% for both years 2050 and 2070 under representative concentration pathways (RCP) 2.6 and of 8% and 4% under RCP8.5 for the years 2050 and 2070, respectively, were predicted. If a non-dispersal scenario was considered, 36–39% of the current habitats would be lost in the future. The results presented here will not only provide useful information for the conservation of *O. sinensis*, but also provide a representative case of evaluating impacts of climate change on fungal distribution using species distribution modeling method.

1. Introduction

Accelerating climate change has been observed over the past 100 years, and further climate warming is predicted to continue through the 21st century (IPCC, 2014). Ample evidence has shown that recent climate change has affected the distribution of species, ecosystems and biodiversity (e.g., Walther et al., 2002; Bellard et al., 2012). For instance, Lenoir et al. (2008) revealed that the optimum elevation of nearly 200 forest plants has shifted upward at an average of 29 m per decade over the 20th century due to climate warming. A recent meta-analysis showed that the recent distributions of species have shifted to higher elevations at a median rate of 11 m and to higher latitudes at a median rate of 17 km per decade (Chen et al., 2011).

As one of the regions that most sensitive to climate change, the Tibetan Plateau has undergone an earlier and faster warming process compared to the global mean (Liu and Chen, 2000; Yao et al., 2000) and may continue at a faster pace in the future (Kirtman et al., 2013). At the same time, the change in precipitation has large inter-annual variability and an inconsistent spatial pattern on the Plateau (Kang et al., 2010; Cuo et al., 2013; Gao et al., 2015). Climate change effects have been documented for plants, e.g., the tree line on the edge of the Plateau was reported to be affected somewhat by the recent warming (Gou et al., 2012; Gaire et al., 2014).

Many studies have reported the response of plants and animals to climate change (e.g., Theurillat and Guisan, 2001; Jump and Peñuelas, 2005; Bradshaw and Holzapfel, 2010). In contrast, the responses of fungi to climate change are less investigated, partly due to the availability of data, even though they may play important roles in ecosystem functioning and stability (Van der Heijden et al., 2008) and some (e.g., truffles and the Chinese caterpillar fungus) have high economic values. Several studies have shown that climate change has altered mushroom fruiting phenology (e.g., Kauserud et al., 2008, 2012), but there are very few studies concerning range shifts of fungi in response to climate change (Shrestha and Bawa, 2014). Whether and how the climate change could affect the spatial distribution of fungi is still unclear. In this study, we used *Ophiocordyceps sinensis* as an example to shed some light on this topic.

Ophiocordyceps sinensis (Berk.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora (synonym: *Cordyceps sinensis* (Berk.) Sacc.) is a highly valued fungus that has been used as a traditional Chinese medicine for centuries (Pegler et al., 1994). The fungus is endemic to the Tibetan Plateau and its surrounding regions, including Tibet, Gansu, Qinghai, Sichuan

* Corresponding authors.
E-mail addresses: zytang@urban.pku.edu.cn (Z. Tang), yaoyj@im.ac.cn (Y.-J. Yao).
[1] These authors contributed equally to this manuscript.

http://dx.doi.org/10.1016/j.biocon.2016.12.023

and Yunnan provinces in China and certain areas of the southern flank of the Himalayas such as Bhutan, India and Nepal (Li et al., 2011). The optimum temperature for hyphal growth ranges from 15 to 18 °C, and the species is usually considered as psychrophilic (Dong and Yao, 2011). *Ophiocordyceps sinensis* parasitizes underground larvae of ghost moth species in the family Hepialidae, especially species of the genus *Thitarodes* (Wang and Yao, 2011). Most of these ghost moth species largely feed on the roots of alpine plants, thereby constituting a complicated system of biotic interactions. Because of its confined distribution and host specificity on moth insects, the natural resource of the fungus is limited and it has been listed as an endangered species under the second class of state protection in China since 1999 (State Forestry Administration and Ministry of Agriculture, 1999). The price of natural *O. sinensis* products has sharply increased over recent years and is now sold at the price of gold and up to four times as much for high quality products (Li et al., 2015). On the other hand, the production and the distribution of the fungus have decreased over recent decades, probably due to over-exploitation, excessive grazing and climate change (Hu et al., 2005). The climate warming and decrease of precipitation on the Plateau were reported to result in reduction of nature habitats, density and the quality of *O. sinensis* (Hu et al., 2005; Li, 2007) and have altered the distribution pattern of the fungus (Yang et al., 2010). However, a contradict report was published recently (Shrestha and Bawa, 2014) indicating that the distribution range of *O. sinensis* might expand under the future climate change in Nepal based on collection records from that country and using the MaxEnt modeling method. Whether the distribution of *O. sinensis* is decreasing or increasing in response to the climate change requires further clarification based on robust data and comprehensive analyses.

In this study, we used a comprehensive collection dataset and an ensemble species distribution modeling method aiming to: 1) investigate whether and how climate change could affect distribution of a fungal species, such as *O. sinensis*., and 2) predict potential range shifts of the fungus in a medium term of about 50–70 years in response to climate change. The results presented here could facilitate the conservation of this precious fungal species and provide a representative case for predicting the impacts of climate change on the distribution of fungal species.

2. Materials and methods

2.1. Occurrence data

Occurrence data of *O. sinensis* were mainly based on field collections made on the Tibetan Plateau beginning in 2000. The latitude, longitude and elevation were recorded for each specimen during fieldwork. Additional records with reliable evidence in the literature were also included in the analyses. A total of 206 records from 84 counties of China and 12 different localities in Nepal were established (Suppl. Table A.1), covering nearly the whole distribution area and representing all types of known natural habitats of *O. sinensis* (Fig. 3).

2.2. Climate data

Available climate data were collected from 21 National Weather Stations located in the distribution area of *O. sinensis* (Suppl. Table A.2) in Tibet, Sichuan and Qinghai provinces.

2.3. Environmental variables

Given that the distribution of *O. sinensis* is influenced by climate, vegetation and soil properties (Yang et al., 2010), a dataset with a total of 29 environmental layers representing climate, soil physical and chemical properties and vegetation was compiled. The environmental data were grouped (correlation coefficient > |0.85|) using a spearman correlation analysis (Suppl. Table A.3). To eliminate the effects of collinearity, factors were selected from each group based on previous reports of the factors potentially affecting *O. sinensis* (e.g., Xu, 2007; Jin et al., 2010). Finally, 17 environmental variables, including seven climatic variables, i.e., isothermality (ISO), mean diurnal range (MDR), mean temperature of the wettest quarter (MTWQ), precipitation of the driest quarter (PDQ), precipitation seasonality (PS), precipitation of the wettest quarter (PWEQ) and precipitation of the warmest quarter (PWAQ); eight soil properties, i.e., bulk density of the fine earth fraction (BLD), cation exchange capacity (CEC), coarse fragments volumetric (CFRVOL), clay content mass fraction (CLYPPT), soil organic carbon (ORCDRC), soil pH in H2O (PHIHOX), silt content mass fraction (SLTPPT) and sand content mass fraction (SNDPPT); and two vegetation cover categories including shrub (SV) and herbaceous vegetation (HV), were compiled at 30-second (approximately 1-km) resolution to model the habitat of *O. sinensis*.

The current climatic variables (mean of 1950–2000) were downloaded from the WorldClim dataset (Hijmans et al., 2005, http://www.worldclim.org/). Soil properties were obtained from ISRIC SoilGrids 2014 (Hengl et al., 2014). A standard depth of 10 cm was chosen for the predicted mean soil properties as the larva of host insects are often observed in soil at depths of 0–25 cm during the growing season (Liu et al., 2005). Vegetation cover was obtained from a global consensus land-cover product using generalized land-cover classes (Tuanmu and Jetz, 2014). The soil properties and the vegetation cover type were assumed to be stable in the Tibetan Plateau (Li et al., 2013; Gao et al., 2016); there is a time lag of decades to centuries for soil and vegetation to catch up with sudden climate change (Adams, 2010).

Future climate can be projected with general circulation models (GCMs). A number of GCMs have been used and their outcomes varied a lot in different regions (Flato et al., 2013). To eliminate the bias of such difference, five GCMs from Coupled Model Intercomparison Project Phase 5 (CMIP5) including BCC-CSM1.1 (Beijing Climate Center, China Meteorological Administration, China), HadGEM2-ES (Met Office Hadley Centre, UK), IPSL-CM5A-MR (Institute Pierre-Simon Laplace, France), MRI-CGCM3 (Meteorological Research Institute, Japan) and NorESM1-M (Norwegian Climate Centre, Norway) were chosen for climate prediction for the years 2050 (mean of 2030–2060) and 2070 (mean of 2060–2080). These models were selected because of their acceptable performance at simulating the current climate of the Tibetan Plateau (Su et al., 2013) and the online data availability (http://www.worldclim.org/). In addition to the five GCMs, their mean values were also calculated and used as the future climate datasets in this study. Four different Representative Concentration Pathways (RCPs), i.e., a stringent mitigation scenario (RCP2.6), two intermediate scenarios (RCP4.5 and RCP6.0) and one scenario with very high GHG emissions (RCP8.5), were included in the IPCC Fifth Assessment Report (IPCC AR5, Kirtman et al., 2013). The RCP2.6 and RCP8.5 were used in this study to represent two extreme scenarios with the lowest and the highest greenhouse gas emissions, respectively. Annual mean temperature will rise approximately 2 °C under the RCP2.6 scenario, whereas it will rise approximately 5 °C under the RCP8.5 scenario in the study area by 2070. The future climate data at 30-second resolution were also collected from the WorldClim dataset. All environmental layers were cropped to the Tibetan Plateau and its surrounding regions (N 22° − 42°, E 71° − 108°). Information regarding the distribution of current climate and projected climate change in study areas is provided in Suppl. Figs. A.1, A.2 and A.3.

2.4. Species distribution modeling

Biomod2, a comprehensive modeling package for R, was employed to conduct the modeling process (Thuiller et al., 2009). Six modeling methods, including classification tree analysis (CTA), generalized additive models (GAM), generalized linear models (GLM), multivariate adaptive regression (MARS), maximum entropy (MaxEnt) and random forest (RF), were adopted.

As all modeling methods other than MaxEnt are presence-absence models, two sets of pseudo-absence data (Wisz and Guisan, 2009; Barbet-Massin et al., 2012), each comprising 2180 records, were randomly generated for the absence data of *O. sinensis*. The occurrence data were combined with each pseudo-absence dataset separately and then randomly split into 75% (used for training) and 25% (used for calibrating). The random split was repeated five times. In addition to these five split datasets, another dataset using all data as training and calibrating was also applied to the six modeling methods. Finally, 12 runs (six for each set of pseudo-absence data) were performed for each model, and a total of 72 species distribution models were generated.

The variable importance for all 17 environmental variables was computed using Biomod2, and the computation was repeated three times. Variables with mean importance >0.05 across all models were used to build the final predictive models. To evaluate the performance of different models, two common measures of accuracy, i.e., area under the receiver operating characteristic curve (AUC, Hanley and McNeil, 1982) and true skill statistic (TSS, Allouche et al., 2006) were applied. AUC is independent of prevalence and ranges from 0.5 to 1 with values higher than 0.7 indicating good performance of the model (Swets, 1988). TSS ranges from −1 to +1, with scores higher than zero indicating non-randomness (Allouche et al., 2006). To distinguish the major trends of predicted patterns, models with an AUC higher than 0.95 were assembled using the committee averaging algorithm (Araújo and New, 2007). Projected probabilities of occurrences were converted to a binary presence/absence map based on the receiver operating characteristic (ROC) threshold (Nenzén and Araújo, 2011).

2.5. Data analysis

Two possible dispersal scenarios, i.e., the universal dispersal and the non-dispersal scenarios, were considered for the future distribution in 2050 and 2070. Habitat changes were plotted if more than three GCMs reached an agreement. Range shifts of different elevations were also calculated for the years 2050 and 2070 using altitude data obtained from the Shuttle Radar Topography Mission (http://srtm.usgs.gov/). Response curves were plotted for the four most important variables based on the mean occurrence probability at each value by modeling the species distribution using each variable separately using GAM, GLM, MARS and MaxEnt. All of the analyses in this study were performed in R3.2.0 (R Core Team, 2015) and ArcGIS 10.2 (ArcGIS, 2013).

3. Results

3.1. Model performance

All six modeling methods performed well, with AUC values ranging from 0.84 to 0.99 and TSS values ranging from 0.67 to 0.99 (Fig. 1, Suppl. Table A.4). Among the 72 tested models, four models with AUC > 0.95, including one MaxEnt and three RF, were used to make the consensus model. The AUC, sensitivity and specificity values of the consensus model are 0.99, 95.55 and 95.43, respectively.

3.2. Environmental variables

Among the 17 environmental variables tested, four of them, i.e., PWAQ, MTWQ, PWEQ and HV, were recognized as the most predominant factors that could affect the distribution of *O. sinensis*, with mean importance values of 0.48, 0.42, 0.38 and 0.18, respectively (Table 1). Different models showed quite similar patterns. The response curves illustrated the characteristics of the most suitable habitats (Fig. 2). The species preferred approximately 5–17 °C of MTWQ, with the highest probability of occurrence at approximately 10 °C (Fig. 2b). Along the precipitation gradient, the species preferred approximately 200–600 mm (best at 400 mm) of both PWAQ and PWEQ (Fig. 2a and c).

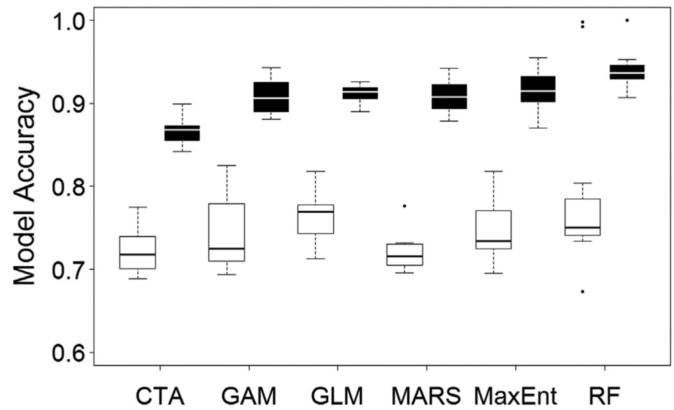

Fig. 1. Performance comparison of six modeling methods using AUC and TSS. CTA, classification tree analysis; GAM, generalized additive models; GLM, generalized linear models; MARS, multivariate adaptive regression; MaxEnt, maximum entropy; RF, random forest. Black bars depict quantiles of AUC values, and a value higher than 0.7 indicates good performance of the model. White bars depict quantiles of TSS values, and a value higher than zero indicates non-randomness.

Vegetation cover was less constrained compared to PWAQ, MTWQ and PWEQ. Suitable herbaceous coverage was approximately 50% to 90% with 70% as the highest (Fig. 2d), indicating a preference for grassland with a sparse shrub layer. The main vegetation types of the distribution areas were alpine meadow (approximately 45%) and subalpine shrub (approximately 30%), and the soil types are leptosols (approximately 46%) and cryosols (approximately 28%).

3.3. Field observations of PWAQ, PWEQ and MTWQ

According to the recorded climate data from 21 national weather stations, the warmest and wettest season is from June to August in most cases except in Aba and Zayü (Suppl. Table A.2). The PWAQ and the PWEQ are thus nearly identical, ranging from 226 to 398 mm with averages of 329 and 326 mm, respectively (Suppl. Table A.2). The MTWQ varies from 7.8 to 13.8 °C with an average of 10.9 °C.

Table 1
Mean importance of 17 environmental variables.

Environmental categories	Environmental variables	Mean importance
Climatic variables	PWAQ	0.48
	MTWQ	0.42
	PWEQ	0.38
	ISO	0.05
	MDR	0.05
	PDQ	0.05
	PS	0.04
Soil properties	BLD	0.05
	CLYPPT	0.05
	ORCDRC	0.05
	SNDPPT	0.05
	CRFVOL	0.03
	PHIHOX	0.03
	SLTPPT	0.03
	CEC	0.02
Vegetation cover	HV	0.18
	SV	0.02

PWAQ = precipitation of the warmest quarter; MTWQ = mean temperature of the wettest quarter; PWEQ = precipitation of the wettest quarter; ISO = isothermality; MDR = mean diurnal range; PDQ = precipitation of the driest quarter; PS = precipitation seasonality; BLD = bulk density; CLYPPT = soil texture fraction clay; ORCDRC = soil organic carbon content; SNDPPT = soil texture fraction sand; CRFVOL = coarse fragments volumetric; PHIHOX = soil pH in H2O; SLTPPT = soil texture fraction silt; CEC = cation exchange capacity; HV = coverage of herbaceous plants; SV = coverage of shrubs.

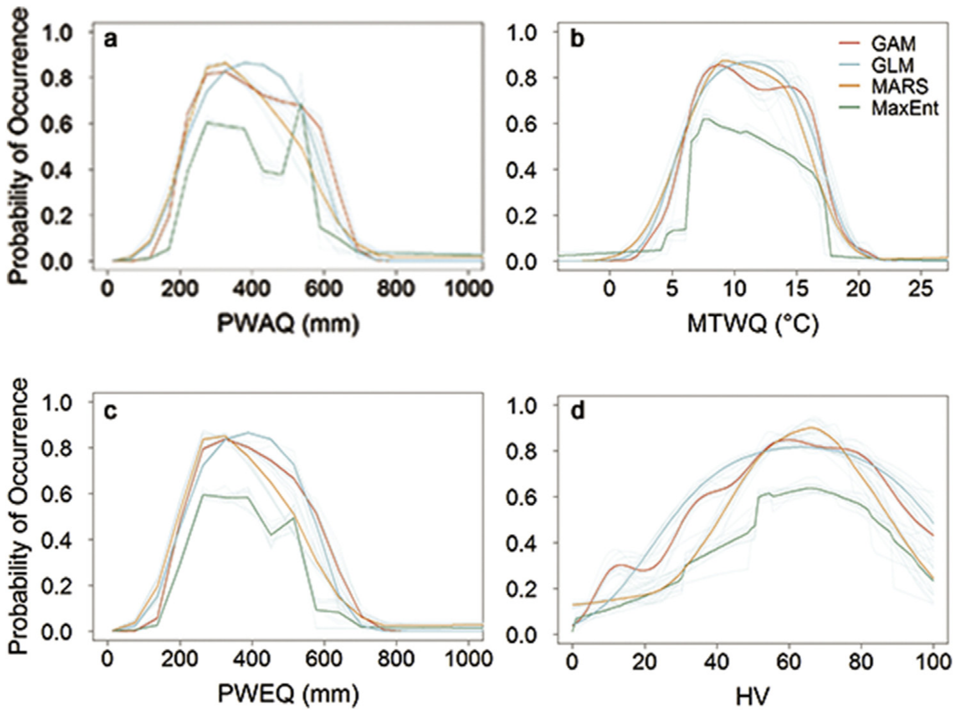

Fig. 2. Response curves for the four most important environment variables. (a) Precipitation of the warmest quarter (PWAQ); (b) Mean temperature of the wettest quarter (MTWQ); (c) Precipitation of the wettest quarter (PWEQ); (d) Coverage of herbaceous vegetation (HV).

3.4. Predicted current distribution and range shifts

The collection data used in this study were plotted on a map of the Tibetan Plateau (Fig. 3, shown as dots), and the predicted current distribution of *O. sinensis* was shaded in green (Fig. 3). The fungus was shown to distribute mainly in the Qinghai, Tibet, Sichuan, Yunnan and Gansu provinces in China and in certain areas of the southern Himalayas, including Bhutan, India, Nepal and probably Myanmar (Fig. 3). The predicted suitable area was 3.54×10^5 km^2 in total worldwide, of which China, Nepal, India, Bhutan and Myanmar accounted for 94.6%, 2.8%, 1.4%, 0.9% and 0.3%, respectively (Suppl. Table A.5). Within China, Qinghai, Tibet, Sichuan, Gansu and Yunnan accounted for 29.9%, 28.7%, 24.6%, 9.9% and 1.3%, respectively (Suppl. Table A.5). The fungus is predicted to occur in a total of 214 counties in the five provinces (Suppl. Table A.6). According to the prediction, >90% of the suitable areas were located at elevations of 3000–5000 m, with only 7.3% and 0.2% located at elevations <3000 m and >5000, respectively. Predicted suitable areas were 14.9%, 26.1%, 31.8% and 19.6% for the elevation bands of 3000–3500 m, 3500–4000 m, 4000–4500 m and 4500–5000 m, respectively (Suppl. Table A.7).

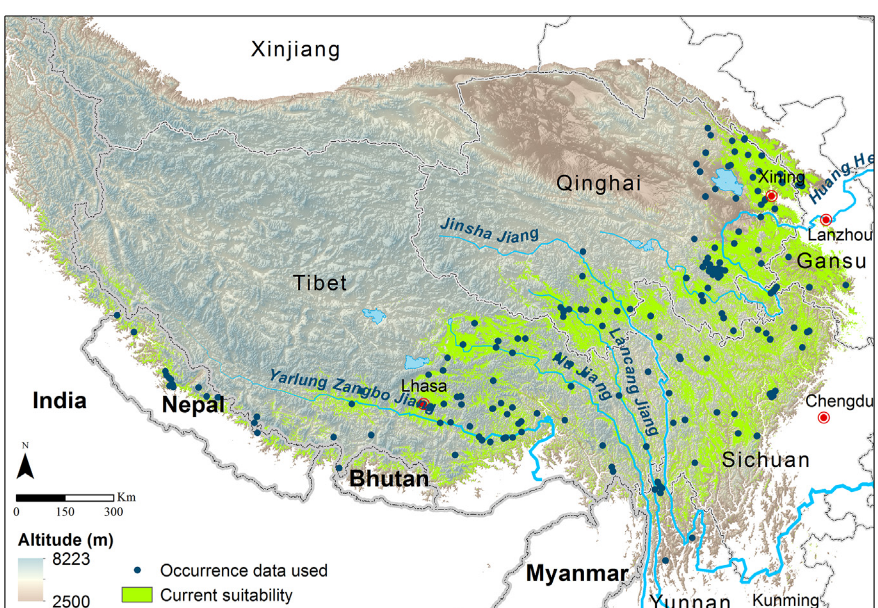

Fig. 3. Location of occurrence data used for species distribution modeling and the predicted current distribution of *Ophiocordyceps sinensis*. The colored map shows the areas with elevations higher than 2500 m.

Distribution ranges of *O. sinensis* shifted inconsistently in specific areas across six GCMs in different time periods (2050 and 2070) and two RCPs (RCP2.6 and RCP8.5). Both gain and loss events would occur in response to climate change under the unlimited dispersal scenario. Gained habitats were mainly located in the Qinghai Province and in certain parts of Sichuan and Tibet, usually within areas with relatively high elevations (Fig. 4). Habitat loss predictions were located on the edge of the Plateau or at relatively low elevations (Fig. 4). The amount of gained habitat was usually less than the amount of lost habitat, except in the case of the year 2070 if the highest anthropogenic greenhouse gas emission (RCP8.5) was considered. The net loss of habitat would be 19% for both years 2050 and 2070 under RCP2.6, while the reduction would be 8% and 4% under RCP8.5 for the years 2050 and 2070, respectively (Table 2). China, Nepal, Bhutan, India and Myanmar will lose 17%, 41%, 31%, 71%, and 55% of the habitats in 2050 and 17%, 36%, 26%, 69%, and 46% in 2070 under the RCP2.6 scenario and will lose 6%, 34%, 11%, 74%, and 44% in 2050 under RCP8.5. While there will be a slight gain (12%) for Bhutan under RCP8.5 in 2070, China, Nepal, India and Myanmar will lose 2%, 26%, 69% and 42% of the habitats under this scenario (Suppl. Table A.5).

If a non-dispersal scenario was considered, i.e., the species would not effectively colonize habitats that become suitable, the total habitat loss will reach as much as 37% (RCP2.6) and 36% (RCP8.5) for the year 2050, and 37% (RCP2.6) and 39% (RCP8.5) for the year 2070 (Table 2). The habitat loss for China, Nepal, Bhutan, India and Myanmar would be 36%, 49%, 35%, 73%, and 55% in 2050 and 37%, 48%, 28%, 72%, and 48% in 2070 under the RCP2.6 and would be 35%, 49%, 23%, 78%, and 47% in 2050 and 38%, 52%, 18%, 76%, and 46% in 2070 under the RCP8.5. Of the five main provinces in China, Yunnan was expected to face the largest decrease in suitable habitat percentage (50–60%) under all pathways, while Tibet will lose the largest suitable acreage except in the case of the year 2050 under RCP2.6 (Suppl. Table A.5).

Range shifts varied greatly at different elevation bands. Most habitats lower than 3000 m would be lost, especially under the RCP8.5 scenario (Fig. 5). The lost distribution (6–8%) at elevations of 3000–3500 m was far more than that gained (1–2%) (Fig. 5, Suppl. Table A.7). For the elevations of 3500–4000 m and 4000–4500 m, potential gained habitats were less than the lost in the years 2050 and 2070 regardless of which RCPs were used, while in the regions above 4500 m, potential gained distribution was more than that lost, especially under the RCP8.5 scenario (Fig. 5).

4. Discussion

This study presents an example of predicting the potential range shifts of a fungal species in response to climate change. As one of the most medicinally, economically and ecologically important fungi (Cannon, 2010; Zhang et al., 2012), the distribution of *O. sinensis* has been well-documented (Li et al., 2011). Based on mainly field collection records covering almost the entire distribution area, the distribution of *O. sinensis* was generally predicted to decrease by using an ensemble modeling approach considering different modeling algorithms, climate models and greenhouse gas emission scenarios. The net habitat loss would be 19% for both years 2050 and 2070 under RCP2.6, and would

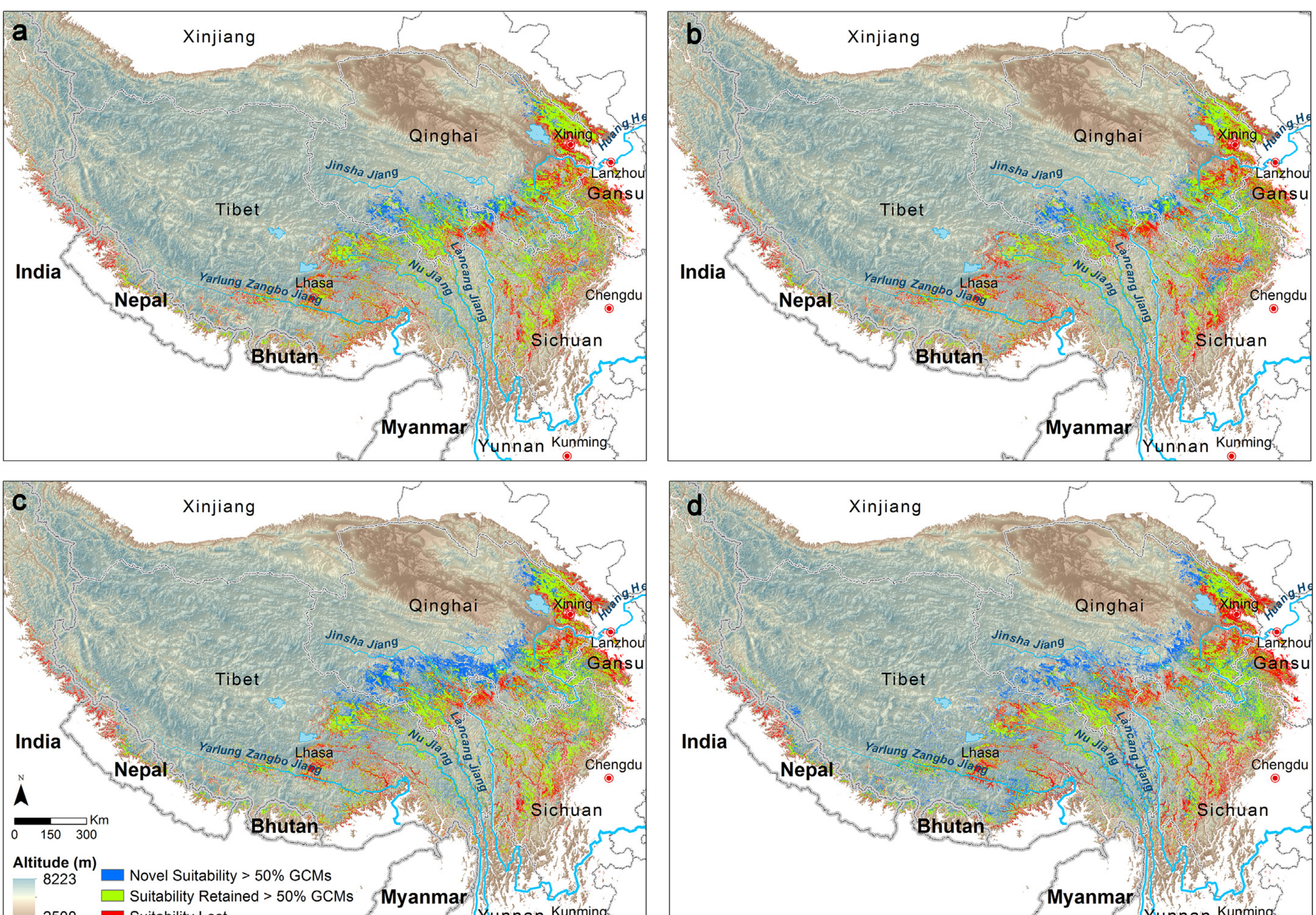

Fig. 4. Predicted range shifts of *Ophiocordyceps sinensis* under future climate change. (a), RCP2.6 in 2050; (b), RCP2.6 in 2070; (c), RCP8.5 in 2050; (d), RCP8.5 in 2070. The colored map shows the areas with elevations higher than 2500 m.

Table 2
Predicted range shifts of *Ophiocordyceps sinensis* under the two dispersal scenarios.

Years	Scenarios	Gain (%)*	Loss (%)	Net loss of habitats (%)	
				Universal dispersal	Non-dispersal
2050	RCP2.6	18.1 (17.8–38.7)	36.6 (39.6–42.2)	18.5 (1.3–24.4)	36.6 (39.6–42.2)
	RCP8.5	28.0 (13.8–38.6)	35.7 (39.7–45.0)	17.7 (1.2–31.2)	35.7 (39.7–45.0)
2070	RCP2.6	18.7 (29.1–60.5)	37.4 (39.4–44.6)	18.7 (16.8–15.5)	37.4 (39.4–44.6)
	RCP8.5	35.1 (49.1–69.7)	38.7 (40.8–51.3)	3.6 (−18.4–−6.4)	38.7 (40.8–51.3)

* Values before the parentheses indicate the proportion of range shifts that were supported by >50% global climate models (GCMs), and values in parentheses indicate minimum and maximum values of five different GCMs.

be 8% and 4% under RCP8.5 for the years 2050 and 2070, respectively, in the unlimited dispersal scenario. The potential habitat expansion predicted by Shrestha and Bawa (2014) contradicts to the results presented here. It is likely due to different occurrence data and modeling strategies. The opposite prediction by Shrestha and Bawa (2014) may be resulted from the limited collection records from only about 2.8% of the total distribution area of the species and a single modeling method of MaxEnt. Beside the habitat loss, the fungus was found to move uphill and toward the central part of the Plateau. Climate change has impacts on species distribution range and pattern has been reported in animals and plants. About 30–50% of distribution areas were predicted to lose for 22 ungulates on the Tibetan Plateau (Luo et al., 2015a). A range reduction of almost 30% by 2020, 70% by 2050 and over 80% by 2080 was predicted for snub-nosed monkey, with a trend of migrating to higher elevations (Luo et al., 2015b). A recent study suggested that forests and shrub lands on the Plateau might expand in response to the future climate change, while alpine steppes and meadows would not change that much (Gao et al., 2016). As *O. sinensis* is an entomopathogenic fungus requiring insect larvae to complete its life cycle, it is sensible that the fungus shows a pattern that much more similar to animals than to plants.

Ophiocordyceps sinensis is strictly associated with larvae of Hepialidae. The host insects are unlikely to inhabit those predicted new habitats because they usually have low migration rates (Cheng et al., 2007; Quan et al., 2014). Without considering the intrinsic dispersal ability, the changeability of vegetation could also affect the dispersal rate of host insects since they are largely fed on certain alpine plants. Several plot-based studies of vegetation suggested that the species composition may change, but vegetation type (especially at class level) barely changed on the Tibetan Plateau in a few decades (Li et al., 2013). A more recent study also suggested that forests and shrub lands might expand, while alpine steppes and meadows would not change that much in response to the future climate change (Gao et al., 2016). Since most plants in the distribution area of *O. sinensis* are perennial species with low migration abilities, the assumption that the vegetation is stable to year 2070 is reasonable. Thus, it is more reasonable to use the non-dispersal scenario rather than the unlimited dispersal scenario for this species. In the non-dispersal scenario, the potential net habitat loss will then reach 37% (RCP2.6) and 36% (RCP8.5) for the year 2050 and 37% (RCP2.6) and 39% (RCP8.5) for the year 2070, respectively.

In addition to the climate change, human activities can also affect the distribution of the fungus. Excessive grazing would destroy alpine meadows that may harbor the fungus, causing habitat loss. Over-exploitation, especially the activity of collecting mature specimens, would inhibit the spore dissemination and cause decrease of mycelial biomass in soil, which may also result in habitat loss. Therefore, the actual habitat loss could be more than that predicted. The fungus is endangered by both human activity and climate change. Due to data deficiency, it is difficult to estimate the relative impacts of climate change and human activities. However, our analysis stressed the high risk of potential habitat loss caused by climate change alone for *O. sinensis*.

The reliability of the modeling strategy was tested in several ways. Firstly, the predicted current distribution of *O. sinensis*, as a part of the

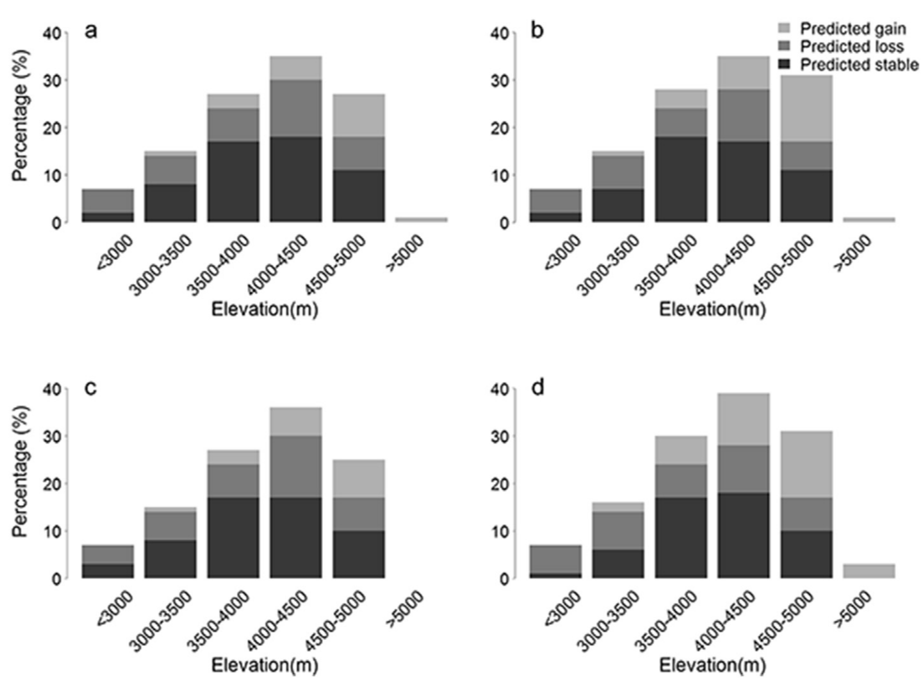

Fig. 5. Predicted range shifts of different elevation pixels. (a), RCP2.6 in 2050; (b), RCP2.6 in 2070; (c), RCP8.5 in 2050; (d), RCP8.5 in 2070.

results, was compared to the reported distribution (Li et al., 2011). The modeling approach correctly predicted the 106 confirmed and 29 excluded distribution counties recorded by Li et al. (2011). For the 65 possible and three suspicious distribution counties (Li et al., 2011), 60 of the former and two of the latter were included in the current prediction. The two suspicious distribution counties, i.e., Madoi and Dulan, were located on the Plateau and predicted to have a limited potential distribution area of 1260 km^2 and 112 km^2, respectively. These two counties lie in the area adjacent to occurring counties with more limited distribution than most of those predicted counties in the surrounding area. The remaining suspicious site that was located on the very edge of the Plateau, Mt. Emei in Sichuan Province, was completely out of the predicted range distribution. The well concordance between the prediction and collection records supported the accuracy of the modeling strategy. Secondly, the predicted ranges of the four most predominant environmental factors were also compared to the field observations or to those reported previously. The predicted ranges of precipitation of the wettest (PWEQ) and the warmest (PWAQ) quarter (both are 200–600 mm, best at 400 mm) are comparable to the observed data from 21 weather stations on the Tibetan Plateau, which is 226 to 398 mm (average at 329 and 326 mm respectively). The predicted mean temperature of the wettest quarter (MTWQ) of 5–17 °C with the highest occurrence probability at approximately 10 °C is also accordant with the records of weather stations (7.8 to 13.8 °C, average at 10.9 °C). The predicted herbaceous coverage of the suitable habitats (50–90% with 70% as the highest) is similar to field observations (60–90%) reported from different regions (Xu, 2007; Jin et al., 2010; Yang et al., 2013). Further, the species distribution modeling predicted that the precipitation of the wettest and the warmest quarter and the mean temperature of the wettest quarter are critically important. It is quite reasonable as the warmest and wettest season, June to August in most parts of the Tibetan Plateau, is the time for growth and reproduction of the fungus, host insects and vegetation.

Species distribution modeling methods based on bioclimatic variables may overestimate the actual extent of the ranges, as biotic factors and dispersal of the species are not taken into account (Pineda and Lobo, 2009). Indeed, besides the formerly reported sites (Li et al., 2011), 64 additional counties, including those far from the Tibetan Plateau, were also predicted. The unusually high proportion of distribution areas in a number of counties, especially those in Gansu and Qinghai provinces, coupled with distribution of areas with altitudes lower than 3000 m where *O. sinensis* has never been recorded, all indicate an overestimation. Those predicted sites may have potential suitable habitats, but the fungus or its host insects have not yet colonized there. It is also worth mentioning that a current distribution area of 4900 km^2 was predicted in Myanmar, a country with some mountainous areas in the northern part but without any report of the species occurrence. It cannot be judged whether that is an overestimation or a real distribution until a thorough investigation to that country is carried out.

It was predicted that the current distribution areas of *O. sinensis* at low elevations and on the edge of the Tibetan Plateau have high risks to be lost. As an important and valued traditional Chinese medicine, the species should be protected to some extent. Although impacts of human activities to the distribution of the species are not fully understood, protection actions to reduce such impacts should take into account since the impacts of climate change are irreversible and hard to eliminate. Restricting the harvest intensity and maintaining a portion of mature individuals could benefit the conservation of the fungus. Setting up nature preservation zones is also helpful to the species conservation. Identification of representative areas that harbor more diversity and face more risks could make the conservation plan more effective.

5. Conclusions

The present study indicates a net loss of habitats of *O. sinensis* in most distribution areas as a result of future climate change. These predictions provide analytical evidence, rather than experiences, to support that the natural resource of *O. sinensis* is endangered by climate change in addition to human activities. It provides basic information for the development of conservation strategies for this valuable fungus and shows that more attention and the priority should be given to the areas at lower elevations and on the edge of the Tibetan Plateau.

Acknowledgments

This research was supported by the Ministry of Science and Technology of China (2012FY111600), the Chinese Academy of Sciences (KSCX2-YW-G-076 and the scheme of Introduction of Overseas Outstanding Talents) and the National Natural Science Foundation of China (31170017 and 31170499). We also thank the Sino-German Centre for the research promotion of participation in a summer school in Jingdezhen (GZ 1146).

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.12.023.

References

Adams, J., 2010. Vegetation–Climate Interaction. How Vegetation Makes the Global Environment. Springer, New York.

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43: 1223–1232. http://dx.doi.org/10.1111/j.1365-2664.2006.01214.x.

Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22:42–47. http://dx.doi.org/10.1016/j.tree.2006.09.010.

ArcGIS, 2013. ArcMap version 10.2. ESRI Inc, Redlands. http://www.esri.com.

Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol. Evol. 3: 327–338. http://dx.doi.org/10.1111/j.2041-210X.2011.00172.x.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. Ecol. Lett. 15:365–377. http://dx.doi.org/10.1111/j.1461-0248.2011.01736.x.

Bradshaw, W.E., Holzapfel, C.M., 2010. Light, time, and the physiology of biotic response to rapid climate change in animals. Annu. Rev. Physiol. 72:147–166. http://dx.doi.org/10.1146/annurev-physiol-021909-135837.

Cannon, P.F., 2010. The caterpillar fungus, a flagship species for conservation of fungi. Fungal Conserv. 1, 35–39.

Chen, I., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026. http://dx.doi.org/10.1126/science.1206432.

Cheng, Z., Geng, Y., Liang, H., Yang, X., Li, S., Zhu, Y., Guo, G., Zhou, T., Chen, J., 2007. Phylogenetic relationships of host insects of *Cordyceps sinensis* inferred from mitochondrial cytochrome *b* sequences. Prog. Nat. Sci. 17:789–797. http://dx.doi.org/10.1080/10002007088537474.

Cuo, L., Zhang, Y., Wang, Q., Zhang, L., Zhou, B., Hao, Z., Su, F., 2013. Climate change on the northern Tibetan Plateau during 1957–2009: spatial patterns and possible mechanisms. J. Clim. 26:85. http://dx.doi.org/10.1175/JCLI-D-11-00738.1.

Dong, C.H., Yao, Y.J., 2011. On the reliability of fungal materials used in studies on *Ophiocordyceps sinensis*. J. Ind. Microbiol. Biotechnol. 38:1027–1035. http://dx.doi.org/10.1007/s10295-010-0877-4.

Flato, G., Marotzke, J., Abiodun, B., Braconnot, P., Chou, S.C., Collins, W., Cox, P., Driouech, F., Emori, S., Eyring, V., Forest, C., Gleckler, P., Guilyardi, E., Jakob, C., Kattsov, V., Reason, C., Rummukainen, M., 2013. Evaluation of climate models. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Climate Change 2013: the Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Gaire, N.P., Koirala, M., Bhuju, D.R., Borgaonkar, H.P., 2014. Treeline dynamics with climate change at the central Nepal Himalaya. Clim. Past 10:1277–1290. http://dx.doi.org/10.5194/cp-10-1277-2014.

Gao, Y., Li, X., Leung, L.R., Chen, D., Xu, J., 2015. Aridity changes in the Tibetan Plateau in a warming climate. Environ. Res. Lett. 10, 34013.

Gao, Q., Guo, Y., Xu, H., Ganjurjav, H., Li, Y., Wan, Y., Qin, X., Ma, X., Liu, S., 2016. Climate change and its impacts on vegetation distribution and net primary productivity of the alpine ecosystem in the Qinghai-Tibetan Plateau. Sci. Total Environ. 554–555: 34–41. http://dx.doi.org/10.1016/j.scitotenv.2016.02.131.

Gou, X., Zhang, F., Deng, Y., Ettl, G.J., Yang, M., Gao, L., Fang, K., 2012. Patterns and dynamics of tree-line response to climate change in the eastern Qilian Mountains, northwestern China. Dendrochronologia 30:121–126. http://dx.doi.org/10.1016/j.dendro.2011.05.002.

Hanley, J.A., McNeil, B.J., 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143:29–36. http://dx.doi.org/10.1148/radiology.143.1.7063747.

Hengl, T., de Jesus, J.M., MacMillan, R.A., Batjes, N.H., Heuvelink, G.B.M., Ribeiro, E., Samuel-Rosa, A., Kempen, B., Leenaars, J.G.B., Walsh, M.G., Gonzalez, M.R., 2014. SoilGrids1km — global soil information based on automated mapping. PLoS One 9, e105992. http://dx.doi.org/10.1371/journal.pone.0105992.

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. Int. J. Climatol. 25:1965–1978. http://dx.doi.org/10.1002/joc.1276.

Hu, Q., Liao, C., Wang, X., 2005. Countermeasures for protecting, developing and utilizing Chinese caterpillar fungus and their resources in China. Chin. J. Agric. Resour. Reg. Plan. 26, 43–47.

IPCC, 2014. Climate Change: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland, p. 151.

Jin, Y.X., Xu, B., Yang, X.C., Qin, Z.H., Gao, M.F., Lu, H.Y., Zhu, L.B., 2010. The spatial distribution of *Cordyceps sinensis* in Nakchu Prefecture of Tibetan Plateau. Acta Ecol. Sin. 30, 1532–1538.

Jump, A.S., Peñuelas, J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change. Ecol. Lett. 8:1010–1020. http://dx.doi.org/10.1111/j.1461-0248.2005.00796.x.

Kang, S., Xu, Y., You, Q., Flügel, W.-A., Pepin, N., Yao, T., 2010. Review of climate and cryospheric change in the Tibetan Plateau. Environ. Res. Lett. 5:15101. http://dx.doi.org/10.1088/1748-9326/5/1/015101.

Kauserud, H., Stige, L.C., Vik, J.O., Okland, R.H., Hoiland, K., Stenseth, N.C., 2008. Mushroom fruiting and climate change. Proc. Natl. Acad. Sci. 105:3811–3814. http://dx.doi.org/10.1073/pnas.0709037105.

Kauserud, H., Heegaard, E., Buntgen, U., Halvorsen, R., Egli, S., Senn-Irlet, B., Krisai-Greilhuber, I., Damon, W., Sparks, T., Norden, J., Hoiland, K., Kirk, P., Semenov, M., Boddy, L., Stenseth, N.C., 2012. Warming-induced shift in European mushroom fruiting phenology. Proc. Natl. Acad. Sci. 109:14488–14493. http://dx.doi.org/10.1073/pnas.1200789109.

Kirtman, B., Power, S.B., Adedoyin, J.A., Boer, G.J., Bojariu, R., Camilloni, I., Doblas-Reyes, F.J., Fiore, A.M., Kimoto, M., Meehl, G.A., Prather, M., Sarr, A., Schär, C., Sutton, R., van Oldenborgh, G.J., Vecchi, G., Wang, H.J., 2013. Near-term climate change: projections and predictability. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Climate Change 2013: the Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 953–1028.

Lenoir, J., Gégout, J.C., Marquet, P.a., de Ruffray, P.A., Brisse, H., 2008. A significant upward shift in plant species optimum elevation during the 20th century. Science 320: 1768–1771. http://dx.doi.org/10.1126/science.1156831.

Li, Y.L., 2007. Analysis of Cordyceps sinensis (Berk.) Sacc. about protecting and using in Qinghai Province. Spec. Wild Econ. Anim. Plant Res. 29, 61–64.

Li, Y., Wang, X.-L., Jiao, L., Jiang, Y., Li, H., Jiang, S.-P., Lhosumtseiring, N., Fu, S.-Z., Dong, C.-H., Zhan, Y., Yao, Y.-J., 2011. A survey of the geographic distribution of *Ophiocordyceps sinensis*. J. Microbiol. 49:913–919. http://dx.doi.org/10.1007/s12275-011-1193-z.

Li, F., Xu, Z., Feng, Y., Liu, M., Liu, W., 2013. Changes of land cover in the Yarlung Tsangpo River basin from 1985 to 2005. Environ. Earth Sci. 68:181–188. http://dx.doi.org/10.1007/s12665-012-1730-z.

Li, Y., Hu, X.D., Yang, R.H., Hsiang, T., Wang, K., Liang, D.Q., Liang, F., Cao, D.M., Zhou, F., Wen, G., Yao, Y.J., 2015. Complete mitochondrial genome of the medicinal fungus *Ophiocordyceps sinensis*. Sci. Rep. 5:13892. http://dx.doi.org/10.1038/srep13892.

Liu, X., Chen, B., 2000. Climatic warming in the Tibetan Plateau during recent decades. Int. J. Climatol. 20:1729–1742. http://dx.doi.org/10.1002/1097-0088(20001130)20:14<1729::AID-JOC556>3.0.CO;2-Y.

Liu, F., Wu, X.L., Yin, D.H., Chen, S.J., Zeng, W., 2005. Progress in biological studies on the host insects of *Cordyceps sinensis*. Chongqing J. Res. Chin. Drugs Herbs 1, 45–52.

Luo, Z.H., Jiang, Z.G., Tang, S.H., 2015a. Impacts of climate change on distributions and diversity of ungulates on the Tibetan Plateau. Ecol. Appl. 25:24–38. http://dx.doi.org/10.1890/13-1499.1.

Luo, Z.H., Zhou, S.R., Yu, W.D., Yu, H.L., Yang, J.Y., Tian, Y.H., Zhao, M., Wu, H., 2015b. Impacts of climate change on the distribution of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in Shennongjia area. China. Am. J. Primatol. 77:135–151. http://dx.doi.org/10.1002/ajp.22317.

Nenzén, H.K., Araújo, M.B., 2011. Choice of threshold alters projections of species range shifts under climate change. Ecol. Model. 222:3346–3354. http://dx.doi.org/10.1016/j.ecolmodel.2011.07.011.

Pegler, D.N., Yao, Y.J., Li, Y., 1994. The Chinese 'caterpillar fungus'. Mycologist 8, 3–5.

Pineda, E., Lobo, J.M., 2009. Assessing the accuracy of species distribution models to predict amphibian species richness patterns. J. Anim. Ecol. 78:182–190. http://dx.doi.org/10.1111/j.1365-2656.2008.01471.x.

Quan, Q.M., Chen, L.L., Wang, X., Li, S., Yang, X.L., Zhu, Y.G., Wang, M., Cheng, Z., 2014. Genetic diversity and distribution patterns of host insects of caterpillar fungus *Ophiocordyceps sinensis* in the Qinghai-Tibet Plateau. PLoS One 9, e92293. http://dx.doi.org/10.1371/journal.pone.0092293.

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org.

Shrestha, U.B., Bawa, K.S., 2014. Impact of climate change on potential distribution of Chinese caterpillar fungus (*Ophiocordyceps sinensis*) in Nepal Himalaya. PLoS One 9, e106405. http://dx.doi.org/10.1371/journal.pone.0106405.

State Forestry Administration and Ministry of Agriculture, 1999,. The List of the Wild Plants Under the State Emphasized Protection. (http://www.gov.cn/gongbao/content/2000/content_60072.htm/ (accessed 2015.04.15)).

Su, F., Duan, X., Chen, D., Hao, Z., Cuo, L., 2013. Evaluation of the global climate models in the CMIP5 over the Tibetan Plateau. J. Clim. 26:3187–3208. http://dx.doi.org/10.1175/JCLI-D-12-00321.1.

Swets, J., 1988. Measuring the accuracy of diagnostic systems. Science 240:1285–1293. http://dx.doi.org/10.1126/science.3287615.

Theurillat, J., Guisan, A., 2001. Potential impact of climate change on vegetation in the European Alps: a review. Clim. Chang. 50:77–109. http://dx.doi.org/10.1023/A:1010632015572.

Thuiller, W., Lafourcade, B., Engler, R., Araújo, M.B., 2009. BIOMOD – a platform for ensemble forecasting of species distributions. Ecography 32:369–373. http://dx.doi.org/10.1111/j.1600-0587.2008.05742.x.

Tuanmu, M.-N., Jetz, W., 2014. A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. Glob. Ecol. Biogeogr. 23:1031–1045. http://dx.doi.org/10.1111/geb.12182.

Van der Heijden, M.G., Bardgett, R.D., Van Straalen, N.M., 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol. Lett. 11:296–310. http://dx.doi.org/10.1111/j.1461-0248.2007.01139.x.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416:389–395. http://dx.doi.org/10.1038/416389a.

Wang, X., Yao, Y., 2011. Host insect species of *Ophiocordyceps sinensis*: A review. Zookeys: 43–59 http://dx.doi.org/10.3897/zookeys.127.802.

Wisz, M., Guisan, A., 2009. Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. BMC Ecol. 9:1–13. http://dx.doi.org/10.1186/1472-6785-9-8.

Xu, H.F., 2007. Ecological investigation of *Cordycepes sinensis* in Zaduo of Qinghai Province. Pratacult. Anim. Husb. 2, 30–34.

Yang, D., Peng, Y., Chen, J., Cao, Y., Yang, P., 2010. The distribution pattern of *Cordyceps sinensis* in China and the response to environmental changes. Chinese J. Grassl. 32, 22–27.

Yang, L., Si, S.B., He, J.S., 2013. Analysis of plant community and soil physicochemical properties in *Ophiocordyceps sinensis* adaptive area in Maqin County of Qinghai Province. Acta Agrest. Sin. 21, 467–473.

Yao, T., Liu, X., Wang, N., Shi, Y., 2000. Amplitude of climatic changes in Qinghai-Tibetan Plateau. Chin. Sci. Bull. 45:1236–1243. http://dx.doi.org/10.1007/BF02886087.

Zhang, Y., Li, E., Wang, C., Li, Y., Liu, X., 2012. *Ophiocordyceps sinensis*, the flagship fungus of China: terminology, life strategy and ecology. Mycology 3:2–10. http://dx.doi.org/10.1080/21501203.2011.654354.