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

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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

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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.