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Will climate change cause spatial mismatch between plants and their pollinators? A test using Andean cactus species

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ABSTRACT

Climate change can disrupt mutualisms by causing temporal or spatial mismatch between interacting species. However, the effects of climate change forecasts on biotic interactions remain poorly studied. In cactus species, pollination constitutes a fundamental process in the production of fruits and seeds. Thus, we aimed to analyse the impact of future climate change on the geographical distributions of 11 cactus species from the southern Central Andes and their spatial match with their pollinators. We used species distribution modelling to forecast the geographic range shifts of these cactus species and their pollinators under two future scenarios (RCP 4.5 and RCP 8.5) for the years 2050 and 2070. We predicted geographic range contractions under future scenarios that reached almost 80% for some cactus species. Our results indicate that the geographical distributions of cacti would be constrained by the presence of the pollinator species on which they depend in the present; however, climate change would not cause spatial mismatch between cacti and their animal pollinators in the future. For most cactus species, we predicted an increase in the spatial match with their mutualists under future scenarios. This is the first study that estimates the geographic range of cacti using both abiotic and biotic factors. Given the importance that positive interactions have on the life cycle of many plant species, our approach could be used to better understand the potential effects of climate change, particularly on species that are of special interest for conservation actions.

1. Introduction

Biodiversity currently faces serious threats due to environmental changes caused by human activities (Primack, 2008; Sodhi and Ehrlich, 2010; Barnosky et al., 2011). These threats can be classified into five groups, which were pollution, biological invasions, overexploitation, land-use change and climate change (Sala et al., 2000; Tylianakis et al., 2008; Sodhi and Ehrlich, 2010). In particular, climate change constitutes a potential threat that would have more severe consequences in the future; however, numerous studies have shown that this phenomenon is already causing shifts in the distribution and abundance of living organisms (Parmesan and Yohe, 2003; Parmesan, 2006; Kerr et al., 2015). The extant evidence suggests that climate change would have negative impacts on most species (Hughes, 2000; Parmesan, 2006; Barnosky et al., 2011; IPCC, 2014). Reductions in population size, the local extinction of populations, and even the global extinction of some species have been predicted under climate change scenarios (Bellard et al., 2012; Tilman et al., 2017). In addition, it has been indicated that climate change can disrupt ecological interactions by causing a temporal (i.e., altering phenology; Memmott et al., 2007; Parmesan, 2007) or spatial mismatch (i.e., range contraction, expansion or shift; Schweiger et al., 2010, 2012; Settele et al., 2016) between interacting species. Disruptions would be especially important for mutualistic interactions in which one species depends on the other to fulfil one of the stages of its life cycle; for example, self-incompatible plants that depend on their pollinators to produce fruits and seeds. For these species, estimates of the effects of climate change should also consider whether a mismatch with the interacting species is expected.

Traditionally, it has been considered that abiotic factors determine the geographic range of a species at the global scale, and numerous studies have used climatic variables to estimate their current and future ranges via species distribution models (SDMs). However, it has been suggested that biotic interactions can determine the geographical limits of species, not only at a local scale but also at regional or global scales (Araújo and Luoto, 2007; Hof et al., 2012; Wisz et al., 2013; Anderson, 2017). Thus, the distribution of a given species would be determined both by environmental variables, such as climate, and its biotic interactions (e.g., competition and mutualisms; Soberón, 2007; Soberón and Nakamura, 2009), which should also be taken into account as a component of their niche, especially if they are strongly necessary

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interactions (Anderson, 2017). Despite this, the role of biotic interactions in climate change forecasts remains poorly studied (Araújo and Luoto, 2007; HilleRisLambers et al., 2013), which has been pointed out as a conceptual weakness of SDMs (Soberón and Peterson, 2005). Along with environmental variables and biotic interactions, a third dimension should also be taken into account: the geographic space that the species can actually reach and occupy (for example, because of geographic barriers). Thus, the realised niche of a given species would be determined by the intersection of these three dimensions (also known as the BAM diagram; Soberón and Peterson, 2005). Although there are still limitations on interpreting the result of SDMs, this approach gives us guidelines to improve them and make more realistic forecasts.

Cacti are a conspicuous group of plants that are distributed in the Western Hemisphere and typically inhabit arid and semi-arid environments. This family constitutes a priority group for conservation actions, given that a high proportion of its species are threatened by extinction, mainly because of land-use change and overexploitation as a result of illegal collection (Ortega-Baes et al., 2010; Goettsch et al., 2015). Like for all biodiversity, anthropogenic climate change is a potential threat to this family of plants; however, there are no assessments of its effects at present. The evolutionary diversification of this family has been associated with the process of aridisation of the American continents, which occurred as a consequence of orographic rise (e.g., the Andes mountain range in South America; Hershkovitz and Zimmer, 1997; Hernández-Hernández et al., 2014). Under a global warming scenario, in which many environments would become more arid (IPCC, 2014), cacti species could occupy new areas that were not suitable before, and climate change could therefore actually cause an expansion of the geographic range of these species in the future. However, the chances of this group of plants colonising new environments will depend on the possibility that the species on which they depend can also expand their range margins (i.e., the spatial match with their mutualists).

Cactus species typically establish mutualistic interactions with other organisms, associated with pollination, seed dispersal, and early establishment (Gibson and Nobel, 1986; Godínez-Alvarez et al., 2003). In particular, pollination constitutes a fundamental process for the reproduction of a large proportion of this group of plants because they depend exclusively on their pollinators to set fruits and seeds (i.e., many are self-incompatible species; Fleming et al., 2001; Ortega-Baes et al., 2011; Ortega-Baes and Gorostiague, 2013; Gorostiague and Ortega-Baes, 2016, 2017). Thus, the presence or absence of pollinating animals in a given area could be a determinant of the occurrence of the cactus species that depend on them. Based on the above information, it is important to evaluate whether climatic change could cause spatial mismatch in cactus-pollinator interactions. Since most studies predict that climate change will cause spatial mismatch in plant-pollinator interactions (Giannini et al., 2013; HilleRisLambers et al., 2013; Polce et al., 2014; Settele et al., 2016), we aimed to test the generality of this idea using cacti and their pollinators.

In this context, we analysed the impact of climate change on the geographical distribution of 11 cactus species that occur in the southern Central Andes, a hotspot of cactus diversity, evaluating the spatial match with their pollinators. The ideas presented here were tested using species for which data on their reproductive systems and pollinating agents were available. Specifically, we addressed the following questions: 1) What is the current level of spatial match between the geographical distribution of cactus species and that of their pollinators? 2) How will the distribution of these cactus species change under climate change scenarios predicted for 2050 and 2070? and 3) What level of spatial mismatch between cacti and their pollinators will be caused by future climate change? As far as we know, this will constitute the first study that evaluates the effects of climate change on the distribution of South American cactus species.

2. Material and methods

2.1. Study species

For this study, we included cactus species of tribe Trichocereeae (subfamily Cactoideae) from north-western Argentina for which we had data about their reproductive system and their pollinators. The species were *Cleistocactus baumannii* (Lem.) Lem., *C. smaragdiflorus* (F.A.C. Weber) Britton & Rose, *Echinopsis albispinosa* (= *E. tubiflora*) K. Schum., *E. ancistrophora* Speg., *E. atacamensis* (Phil.) H. Friedrich & G.D. Rowley, *E. haematantha* (Speg.) D.R. Hunt, *E. leucantha* Schum., *E. schickendantzii* F.A.C. Weber, *E. terscheckii* (J. Parm. ex Pfeiff.) H. Friedrich & G.D. Rowley, *E. thelegona* (F.A.C. Weber) H. Friedrich & G.D. Rowley and *Gymnocalycium saglionis* (F. Cels) Britton & Rose. Presence records for these species were obtained from herbarium data and field records (Ortega-Baes, unpublished data), summing to 341 georeferenced records for all species.

Information about the identity of the pollinators of each cactus species was obtained from previously published studies (Schlumpberger and Badano, 2005; Schlumpberger et al., 2009; Ortega-Baes et al., 2011; Alonso-Pedano and Ortega-Baes, 2012; Ortega-Baes and Gorostiague, 2013; Gorostiague and Ortega-Baes, 2016, 2017) and from unpublished data based on field records (Gorostiague and Ortega-Baes, unpublished data). All species were self-incompatible and thus dependent on their flower visitors to set fruits and seeds. We included a total of 18 species and 11 genera of animals that pollinate the cactus species mentioned above, including birds, bees, wasps and moths (see Table A1 in Appendix). The presence records of these animals were obtained from the Global Biodiversity Information Facility (http://data.gbif.org) and were later checked regarding their taxonomic reliability (according to Scheldeman and van Zonneveld, 2010). Dubious or unreliable records were deleted since they can introduce errors to model results. The geographical coordinates were manually checked using GIS software (QGIS Development Team, 2011). In some cases, when the records of the pollinator species were not available, presence records of the genus were used. The genus was considered as a surrogate of the pollinator species in these cases.

2.2. Climate data

Environmental data were obtained from the WorldClim database (Hijmans et al., 2005). We used 19 bioclimatic variables based on combinations of temperature and precipitation, as well as altitude (Rabus et al., 2003; see Table A2 in Appendix). For future projections, we used two potential future global change scenarios from the Intergovernmental Panel on Climate Change: an intermediate scenario (RCP 4.5) and a severe scenario (RCP 8.5; IPCC, 2014). Future climate change scenarios were evaluated for the years 2050 and 2070 using the ACCESS1 global circulation model.

2.3. Species distribution modelling

The current and future geographical distributions of each of the species included in the analyses were determined using Maxent version 3.3.3 (Phillips et al., 2006). This algorithm was chosen because of its good performance compared with other modelling techniques, especially when a low number of occurrences is available (Elith et al., 2006; Hernandez et al., 2006; Wisz et al., 2008; Aguirre-Gutiérrez et al., 2013). A regularization multiplier of 1 and a default prevalence of 50% were used for all species, and the model was allowed to extrapolate and do clamping (for future projections outside the original range of the species). Cross-validation was used to validate the models, and ten replicates were performed for each species (setting aside 10% of the presence points in each run for validation), from which an average map was used in the analyses. To test the accuracy of the predictions of each model, we used the area under the curve (AUC) of a ROC plot (Phillips