



# 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 Trichocereae (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

et al., 2006). This metric can range from zero to one, where one represents a perfect agreement between the observed and the modelled distribution. Generally, values above 0.7 are considered as acceptable (Swets, 1988). A maximum specificity plus sensitivity threshold was used to convert the suitability map into a presence-absence map. This threshold is based on the predictive power of the model according to the presence points initially used for training.

Each model was projected on a specific background area for each cactus species. This area was selected by taking into account the ecoregions (according to Olson and Dinerstein, 2002) in which the presence of the species was recorded, plus a buffer of 100 km around its limits. Thus, the modelling background was restricted to an area that the species can actually occupy, avoiding overprediction of the range as well as artificial AUC values. We were not able to use the same criteria for the models of the pollinator species, since there was not enough information available about their habitat, and the databases were incomplete in some cases. Therefore, this study was carried out using a cactus-centred approach. The modelled area used for pollinator species was the entire extent of continental South America because most species (or genera) had presence records across this area. We considered two possible dispersal scenarios in the future for all species: one assuming full dispersal (i.e., the species were able to occupy any new habitat that the model projected as suitable) and one assuming no dispersal at all (i.e., the species could only inhabit previously occupied habitats, not being able to colonise new ones). We consider that none of these scenarios are fully realistic, but they give an idea of the best and the worst possible cases, which ultimately depends on the dispersal ability of each species.

#### 2.4. Estimate of the impact of climate change on species distributions

Potential climate change impacts on the distributions of the 11 cactus species were estimated using two variables: the change in their range size in future scenarios with respect to their current range (lost or gained habitat), and the direction and magnitude of the displacement of their range centroid position (the centre of an irregular geometric figure, such as the range of a species), measured in kilometres. Additionally, we calculated the difference between the current and future distributions of each cactus species considering only the portion of their range that is shared with their pollinators. Therefore, for each cactus species, we built a map representing the area in which any of their pollinators was also present (Fig. 1). The resulting map represented the spatial match between the range of each cactus species and the range of its pollinators, hereafter, the spatially matched range (SMR). By doing this, we assumed that all pollinators were equally effective and that their mere presence guarantees that the cactus can produce fruits and seeds. The difference between each cactus species range (CR) and its SMR was considered as a measure of the plant-pollinator spatial match. The spatial match was considered high when it surpassed 80% overlap (i.e., more than 80% of the cactus range overlapped with the range of any of their pollinators).

### 3. Results

Maxent showed good predictive performance for the distributions of all modelled species, with relatively high AUC values (see Table A3 in Appendix). The proportion of gained/lost geographic range under the different future climate change scenarios with respect to the current range was variable among the studied cactus species (Tables 1, 2). The distribution models predicted that cacti species would contract  $23.06 \pm 30.62\%$  (mean  $\pm$  SE) of their geographic range by the year 2050 and  $34.55 \pm 35.35\%$  by the year 2070, considering only the CR and a full-dispersal scenario (Table 1). We predicted the biggest CR contraction for *Echinopsis albispinosa* (80% range contraction on average; Fig. 2), followed by *Cleistocactus baumannii* (68.17%) and *E. thelegona* (63.75%). In contrast, the species that showed the lowest CR

contractions were *E. terscheckii* (3.77%) and *E. schickendantzii* (5.81%). Only two species would be favoured, with an expansion of their ranges under the future scenarios: *E. leucantha* (8.13%) and *E. atacamensis* (6%; Table 1; Fig. 2).

Regarding the portion of the geographic range shared with pollinators (SMR), we predicted, on average, a total SMR contraction of  $16.73 \pm 29.78\%$  by the year 2050 and a contraction of  $29.63 \pm 35.88\%$  by 2070 under the full-dispersal scenario (Table 1). We predicted an expansion of the SMR for *E. atacamensis* (20.29%; Fig. 2), *E. leucantha* (10.09%) and *Gymnocalycium saglionis* (7.19%). For the remaining species, we predicted SMR contraction, with *E. albispinosa* (67.19%; Fig. 2), *C. baumannii* (60.51%) and *E. thelegona* (57.99%) being the most negatively affected and *E. terscheckii* (2.64%) and *E. schickendantzii* (0.37%) being the least affected species.

In the no-dispersal scenario, where species can only maintain their current occupied range, we predicted a geographic range contraction for all cactus species under all future scenarios. On average, species would contract their CR by  $33.13 \pm 24.32\%$  by the year 2050 and by  $44.79 \pm 27.51\%$  by 2070 (Table 2). Meanwhile, the average percentage of range contraction when the SMR was considered was  $26.18 \pm 24.64\%$  for 2050 and  $38.85 \pm 30.40\%$  for 2070. The most negatively affected species under the no-dispersal scenario were *E. albispinosa*, *C. baumannii* and *E. thelegona* for both the CR alone (80.05, 78.92 and 64.51% range contraction, respectively) and the SMR (67.34, 73.95 and 58.80% range contraction, respectively; Table 2).

A displacement of the geographic range centroid was predicted under the future climate change scenarios for all studied cactus species (Table 3; Fig. 2). This was calculated only for the full-dispersal scenario, considering only the CR, since we aimed to analyse how cacti would move under climatic change. We did not measure the displacement of the range in the no-dispersal scenario, since this scenario assumes that species are not able to move. For most species (73%), the mean range displacement was poleward (southward in this case). The average range centroid displacement for all cactus species was  $54.24 \pm 45.62$  (mean  $\pm$  SE) km for the year 2050 and  $74.89 \pm 72.30$  km for the year 2070. Among the species with the greatest range displacement, we identified *E. leucantha* (114.45 km, on average), *G. saglionis* (113.43 km) and *C. baumannii* (97.47 km), whereas the species with smallest displacement distances were *E. terscheckii* (22.28 km) and *C. smaragdiflorus* (33.47 km).

For six cactus species (*C. smaragdiflorus*, *E. atacamensis*, *E. haematantha*, *E. schickendantzii*, *E. terscheckii* and *E. thelegona*), we found high spatial matching (i.e., the difference between each CR and its SMR was less than 80%) with their pollinators at present (Table 4). Under future climate change scenarios, these species were predicted to increase their spatial match with pollinators, except for *C. smaragdiflorus*, which would still maintain a high spatial match level. The remaining cactus species (*C. baumannii*, *E. albispinosa*, *E. ancistrophora*, *E. leucantha* and *G. saglionis*) showed current spatial matching below 80%. Under future scenarios, three of these species (*C. baumannii*, *E. albispinosa* and *G. saglionis*) would increase their match level above 80% on average, whereas the other two species would maintain their current spatial match level (Table 4).

### 4. Discussion

The importance of the biotic environment in the prediction of the ecological niche of a given species has been indicated in several studies (Araújo and Luoto, 2007; Heikkinen et al., 2007); however, this approach has not been widely used (Schweiger et al., 2010; Giannini et al., 2013; HilleRisLambers et al., 2013; Polce et al., 2014). Our work constitutes the first study that estimates the geographic ranges of cacti using species distribution modelling that includes both abiotic (climatic) variables and biotic interactions.

Cacti establish positive interactions that directly affect their population dynamics, including pollination, seed dispersal and facilitation in

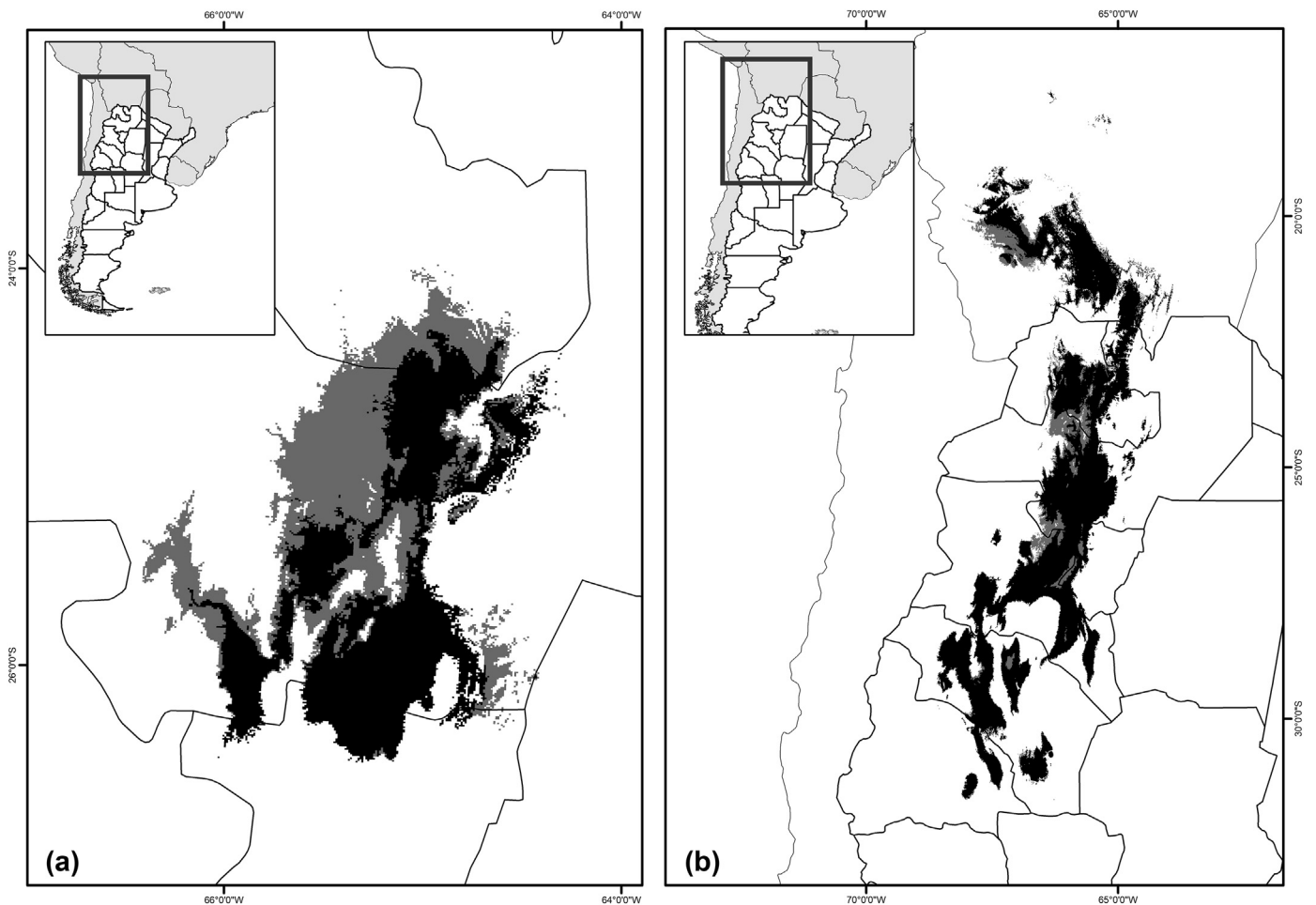


Fig. 1. Current geographic range of *Echinopsis albispinosa* (a) and *E. atacamensis* (b). Black areas represent the spatially matched range (where both the cactus and any of its pollinators are present), whereas grey areas represent climatically viable habitat for the cactus species where no pollinators are present.

early establishment (Gibson and Nobel, 1986; Godínez-Alvarez et al., 2003). Here, we incorporated a biotic agent to better estimate the ecological niche of these plants: the plant-pollinator interaction. This constitutes a necessary interaction for many cactus species (Fleming et al., 2001; Gorostiague and Ortega-Baes, 2016), especially for the group of species included in this study, since all of them are self-incompatible (i.e., they need a pollen vector to set fruits and seeds). Thus, information about the identity of the pollinators, as well as their specificity and degree of dependency, is needed to understand how these

interactions can limit the distribution of a species.

Biotic interactions can be incorporated into geographic range estimates using different procedures, depending, for example, on the specificity or strength of the interaction (Giannini et al., 2013; Anderson, 2017). Here, we assumed that the portion of the climatically viable habitat of a given cactus species where pollinators are not present would not actually represent viable habitat for the plant. This means that although at these sites the abiotic dimension of their niche would be suitable for the development of viable populations, they would lack

Table 1

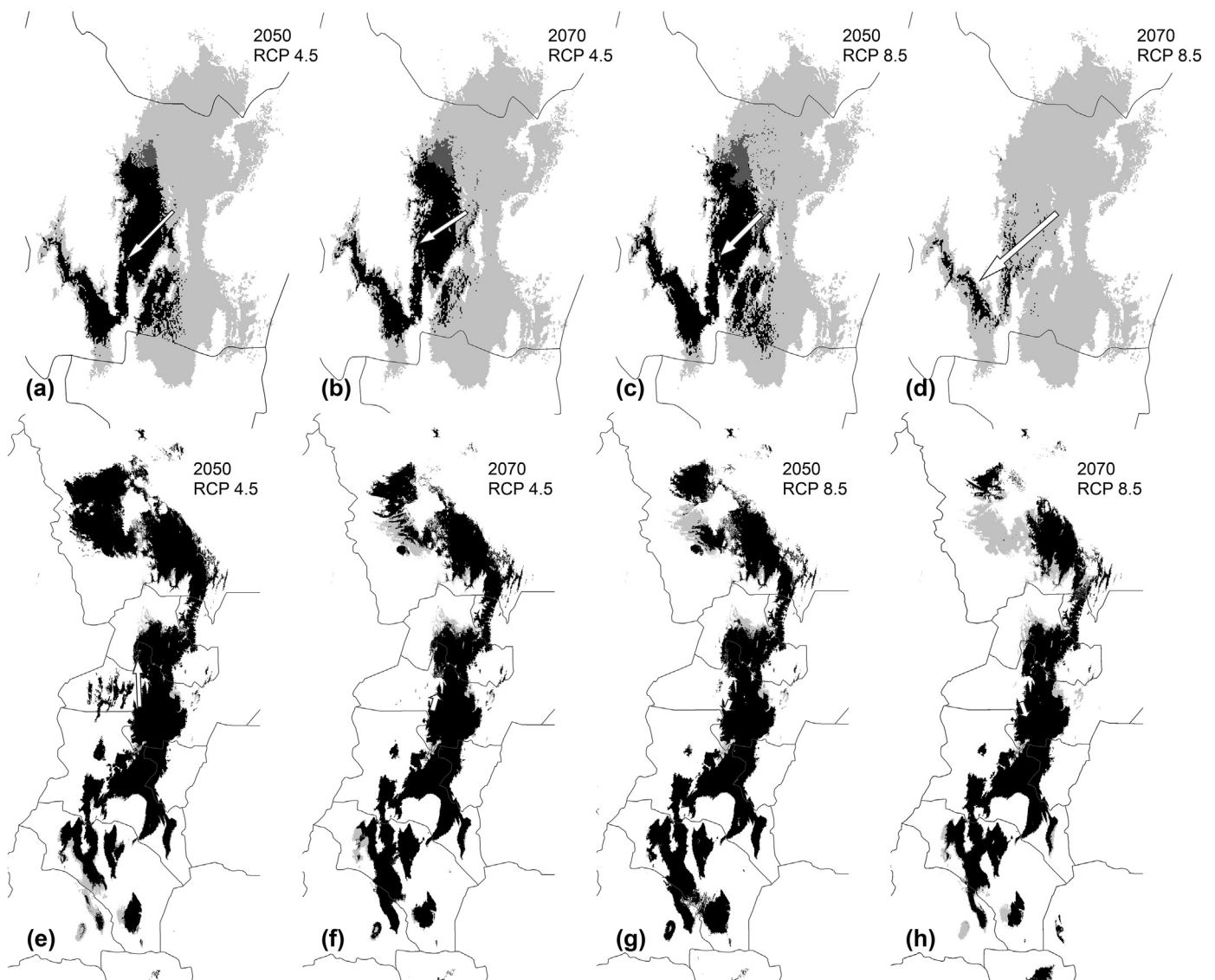
Relative range contraction or expansion (percentage) for 11 cactus species under future climate change scenarios with respect to their present ranges, under a full-dispersal scenario.

Species	Cactus species range				Spatially matched range (cactus + pollinators)			
	RCP 4.5 scenario		RCP 8.5 scenario		RCP 4.5 scenario		RCP 8.5 scenario	
	Year 2050	Year 2070	Year 2050	Year 2070	Year 2050	Year 2070	Year 2050	Year 2070
<i>Cleistocactus baumannii</i>	-62.04	-68.06	-66.64	-75.94	-54.45	-58.40	-58.82	-70.37
<i>C. smaragdiflorus</i>	-23.29	-32.11	2.65	-39.07	-39.25	-39.51	-29.49	-43.94
<i>Echinopsis albispinosa</i>	-75.21	-77.30	-71.34	-96.16	-57.62	-63.23	-54.72	-93.18
<i>E. ancistrophora</i>	-40.56	-52.57	-44.44	-72.43	-28.90	-50.53	-36.70	-77.78
<i>E. atacamensis</i>	21.29	4.82	7.27	-9.37	37.63	18.95	21.73	2.85
<i>E. haematantha</i>	-0.95	-22.84	-10.95	-39.35	-0.04	-21.52	-9.43	-38.31
<i>E. leucantha</i>	-10.49	-15.94	20.65	38.28	-1.94	12.83	26.01	3.45
<i>E. schickendanzii</i>	1.71	-6.50	-9.96	-8.49	7.99	-1.63	-5.42	-2.43
<i>E. terscheckii</i>	-2.01	2.70	8.55	-24.33	-8.52	7.30	7.69	-17.00
<i>E. thelegona</i>	-52.82	-66.26	-52.37	-83.55	-48.20	-60.84	-42.66	-80.27
<i>Gymnocalycium saglionis</i>	-12.49	-18.20	-33.89	2.55	17.61	11.46	-10.63	10.31



**Table 2**  
Relative range contraction or expansion (percentage) for 11 cactus species under future climate change scenarios with respect to their present ranges, under a no-dispersal scenario.

Species	Cactus species range				Spatially matched range (cacti + pollinators)			
	RCP 4.5 scenario		RCP 8.5 scenario		RCP 4.5 scenario		RCP 8.5 scenario	
	Year 2050	Year 2070	Year 2050	Year 2070	Year 2050	Year 2070	Year 2050	Year 2070
<i>Cleistocactus baumannii</i>	-72.18	-78.74	-77.24	-87.51	-67.54	-72.38	-71.97	-83.89
<i>C. smaragdiflorus</i>	-27.62	-34.08	-15.09	-41.24	-41.63	-41.58	-36.50	-46.14
<i>Echinopsis albispinosa</i>	-75.21	-77.35	-71.45	-96.17	-57.72	-63.33	-54.98	-93.33
<i>E. ancistrophora</i>	-43.20	-54.01	-47.09	-72.85	-33.66	-51.82	-37.69	-78.08
<i>E. atacamensis</i>	-12.30	-14.04	-13.43	-25.23	-0.60	-2.58	-1.81	-15.28
<i>E. haematantha</i>	-15.46	-27.29	-18.38	-41.95	-14.37	-26.04	-16.89	-40.89
<i>E. leucantha</i>	-14.83	-23.87	-9.28	-11.81	-7.30	5.37	11.20	-26.21
<i>E. schickendantzii</i>	-8.41	-15.60	-18.03	-20.73	-2.61	-10.85	-13.25	-15.42
<i>E. terscheckii</i>	-18.66	-11.47	-7.75	-32.98	-21.01	-7.79	-8.67	-26.59
<i>E. thelegona</i>	-53.37	-67.06	-53.90	-83.73	-48.85	-61.54	-44.37	-80.42
<i>Gymnocalycium saglionis</i>	-17.67	-26.19	-38.40	-41.57	10.61	1.09	-16.24	-17.06



**Fig. 2.** Future geographic range of *Echinopsis albispinosa* (a–d) and *E. atacamensis* (e–h) under different climate change scenarios. Black areas represent the spatially matched range, dark grey areas represent climatically viable habitat for the cactus species where no pollinators are present, and the current range of each cactus species is represented in light grey. Arrows represent the displacement of the geographic range centroid.

**Table 3** Displacement of the geographic range centroid of 11 cactus species under different future climate change scenarios. Estimates of range displacement were calculated only for the full-dispersal scenario using the cactus range alone (without pollinators). The angle of displacement is represented in degrees with respect to the cardinal directions (90° = north). Direction of displacement: NE (northeast), NW (northwest), SE (southeast), SW (southwest).

Species	RCP 4.5 scenario						RCP 8.5 scenario						Average		
	Year 2050			Year 2070			Year 2050			Year 2070			Year 2070		
	Magnitude (km)	Angle	Direction	Magnitude (km)	Angle	Direction	Magnitude (km)	Angle	Direction	Magnitude (km)	Angle	Direction	Magnitude (km)	Angle	Direction
<i>Cleistoactis baumannii</i>	96.11	-165.56	SW	79.36	-163.52	SW	103.40	-158.93	SW	110.99	-159.94	SW	97.47	-161.99	SW
<i>C. smaragdiformis</i>	32.50	-104.51	SW	21.04	-110.38	SW	44.73	-92.11	SW	35.61	-117.83	SW	33.47	-106.21	SW
<i>Echinopsis albispinosa</i>	43.47	-135.48	SW	39.51	-149.18	SW	43.29	-136.99	SW	72.13	-138.44	SW	49.60	-140.02	SW
<i>E. ancistrophora</i>	17.23	166.43	NW	42.13	-117.73	SW	75.16	-96.94	SW	86.52	-103.48	SW	55.26	-37.93	SE
<i>E. atacamensis</i>	132.94	94.40	NW	25.28	86.14	NE	12.28	-104.54	SW	34.01	-69.09	SE	51.13	1.73	NE
<i>E. haematantha</i>	64.99	86.49	NE	41.47	-81.07	SE	29.05	-97.11	SW	109.56	-89.63	SE	61.27	-45.33	SE
<i>E. leucantha</i>	38.34	86.55	NE	64.27	64.62	NE	203.36	-80.14	SE	151.85	-78.78	SE	114.45	-1.94	SE
<i>E. schickendantzii</i>	29.89	99.71	NW	43.34	87.75	NE	53.75	86.41	NE	79.64	97.28	NW	51.65	92.79	NW
<i>E. terscheckii</i>	9.40	53.16	NE	25.29	82.60	NE	22.32	-108.54	SW	32.13	106.92	NW	22.28	33.54	NE
<i>E. thelegona</i>	36.57	-133.52	SW	64.82	-141.79	SW	53.04	-142.20	SW	86.21	-145.11	SW	60.16	-140.66	SW
<i>Gymnocalyxium saglionis</i>	16.43	-150.64	SW	40.53	-131.56	SW	34.94	157.94	NW	361.83	-101.36	SW	113.43	-56.41	SE

the biotic dimension (sensu the BAM diagram, Soberón and Peterson, 2005). Thus, the plants would not count on the mutualistic interactions necessary for their reproduction (Soberón, 2007; Schweiger et al., 2012). According to the results obtained for the current geographic ranges, six cactus species showed a high level of spatial match with their pollinators (i.e., more than 80% of their geographic range was shared). For the other five cactus species, we found a lower percentage of matched range, reaching 50% for some species. This suggests that the current geographic ranges of cacti are limited, to a greater or lesser extent, by the presence of the pollinator species on which they depend. Therefore, the ranges of these species would be constrained by biotic interactions, as has been suggested in previous studies with other organisms (Hof et al., 2012). Even when abiotic variables would determine the range of a given species at a higher hierarchic level (Holland and Molina-Freaner, 2013), our results highlight the importance of the incorporation of biotic interactions to improve estimates of its range under a more realistic ecological environment (Soberón, 2007; Giannini et al., 2013; Anderson, 2017).

Here, we considered that the areas within the climatic niche of a cactus species that lack pollinators would not be viable for the plant, assuming that this interaction is constant across time and space (Anderson, 2017). This assumption must be considered cautiously because the identity and effectiveness of pollinators could be variable across the distribution of the plant species (Waser et al., 1996; Fleming et al., 2001), making it difficult to estimate the biotic dimension of their niche (Soberón and Peterson, 2005). For example, in the areas where no pollinators were predicted to occur (i.e., plant-pollinator spatial mismatch), other pollen vectors that were not previously recorded could visit the flowers. Many cacti have proven to present generalised pollination systems (Ortega-Baes et al., 2011; Gorostiague and Ortega-Baes, 2016), and it is therefore reasonable to expect this to occur. Additionally, the geographic ranges of all species were estimated from a probabilistic suitability map that was later transformed into an absence-presence map using a threshold. The selected threshold could underestimate the presence of a pollinator species, eliminating areas it actually inhabits. Thus, a series of questions that should be approached in future studies arises from the results obtained here. First, the sites where a given cactus species was predicted to occur but where no pollinators would be available should be evaluated. If the cactus is present at these sites, the animals that pollinate their flowers should be identified. Finally, the accuracy of distribution models in predicting the presence of a given organism should also be evaluated, which highlights the need to perform ground validation for species distribution models. Ground validation has been very important for the identification of previously unknown populations of species of conservation priority (e.g., rare or endemic species, Rebelo and Jones, 2010; Rinnohofer et al., 2012), such as cacti.

In the presence of change in the climatic conditions of its environment, a population of a given species has three possible fates: adaptation to the new conditions (e.g., by short-term natural selection), local extinction, or migration to new environments that allow its persistence (Parmesan, 2006). However, it has been suggested that local adaptation would be difficult to achieve over a short time, and many studies assume that this is not a viable option (Parmesan, 2006; Corlett and Westcott, 2013; Kerr et al., 2015). Since our approach focused on cacti, we initially estimated potential range shifts (encompassing local extinction and migration) caused by climate change. For most cactus species, we predicted a contraction of the geographic range, reaching almost 80% for some species. However, two species (*Echinopsis leucantha* and *E. atacamensis*) were predicted to expand their ranges under future climate change scenarios. Therefore, climate change would have different effects on different species, being positive for some and negative for others. Our results do not support our initial hypothesis, that climate change-induced aridisation could cause range expansion in all the species of this family, as has occurred during the historic radiation process of the group (Hershkovitz and Zimmer, 1997; Hernández-

**Table 4**

Spatial mismatch between cacti and their pollinators in the present and under future climate change scenarios. Values indicate the percentage of the range of each cactus species that is not shared with any of its pollinator species.

Species	Full dispersal					No dispersal			
	RCP 4.5 scenario			RCP 8.5 scenario		RCP 4.5 scenario		RCP 8.5 scenario	
	Present	Year 2050	Year 2070	Year 2050	Year 2070	Year 2050	Year 2070	Year 2050	Year 2070
<i>Cleistocactus baumannii</i>	-26.67	-12.01	-4.48	-9.48	-9.68	-14.46	-4.71	-9.68	-5.40
<i>C. smaragdiflorus</i>	-1.92	-22.32	-12.60	-32.63	-9.76	-20.91	-13.08	-26.65	-10.09
<i>Echinopsis albispinosa</i>	-43.99	-4.23	-9.28	-11.52	-0.38	-4.45	-9.33	-11.66	-2.46
<i>E. ancistrophora</i>	-46.34	-35.82	-44.03	-38.86	-56.75	-37.33	-43.78	-36.81	-56.67
<i>E. atacamensis</i>	-11.88	-0.01	0	0	0	-0.13	-0.13	-0.05	-0.15
<i>E. haematantha</i>	-1.68	-0.78	0	0	0	-0.42	0	0	0
<i>E. leucantha</i>	-49.91	-45.12	-32.76	-47.68	-62.53	-45.48	-30.67	-38.60	-58.09
<i>E. schickendantzii</i>	-6.30	-0.51	-1.42	-1.57	-0.09	-0.36	-1.03	-0.83	-0.02
<i>E. terscheckii</i>	-9.15	-15.19	-5.09	-9.87	-0.35	-11.78	-5.38	-10.06	-0.49
<i>E. thelegona</i>	-18.08	-10.07	-4.90	-1.38	-1.71	-10.13	-4.35	-1.15	-1.42
<i>Gymnocalycium saglionis</i>	-30.83	-7.03	-5.75	-6.49	-25.59	-7.06	-5.26	-5.94	-1.80

Hernández et al., 2014). However, further studies with a larger number of species from different regions across the Americas should confirm the generality of the results obtained here.

In addition, it is also important to highlight that the range expansion of *E. leucantha* and *E. atacamensis* was predicted under a full-dispersal scenario (i.e., species have the capacity to occupy all the newly available environments). It is difficult to estimate the speed at which species can reach these environments, and some previous studies indicate that many plant species could not keep pace with the rate of future climate change (Corlett and Westcott, 2013). This is particularly important for cactus species, since the recruitment of new individuals is a rare phenomenon in this family (Godínez-Alvarez et al., 2003). For many cactus species, seed establishment is an unusual process, since large quantities of seeds are produced annually, but only a few germinate, and seedlings are likely to die within their first year (Godínez-Alvarez et al., 2003). Additionally, we must take into account the seed dispersal system of the species studied because little is known about this process for the family. For southern South America, in particular, there are no studies on cactus seed dispersal at all. Field observations suggest that there are differences among species in relation to the animals that can act as seed vectors. Thus, in columnar cacti (e.g., *E. atacamensis* and *E. terscheckii*), seeds would be dispersed by animals with relatively high vagility, such as birds, while in globose cacti (e.g., *E. albispinosa*, *E. ancistrophora* and *E. haematantha*), seeds would be dispersed by animals with relatively low vagility, such as ants (Ortega-Baes and Gorostiague, unpublished data). In this context, we consider it important to contemplate the no-dispersal scenario, where species would only maintain the portion of their geographic range that they currently occupy. Under this scenario, our results indicated that all cactus species will be negatively affected by reductions in their ranges under future climate change.

Our results suggest that, in general, climate change would not cause spatial mismatch between cacti and their pollinators. In contrast to what we expected, most species would actually increase the spatial match with their mutualists under future climate change scenarios. This does not correspond with the results obtained in other studies, where a spatial disruption of plant-pollinator interactions is predicted to occur (Giannini et al., 2013; Polce et al., 2014). Those cactus species that showed a high spatial match level in the present were projected to maintain it under future scenarios, whereas the group of species with a low spatial match in the present (less than 80% of their ranges overlapped with those of pollinators) showed a better spatial match under future scenarios. A possible explanation for this is that the increase in spatial matching would actually be a consequence of the contraction of the geographic ranges of the cactus species. Thus, a more restricted cactus range would be more likely to overlap with the ranges of any of its pollinators, especially when pollinating animals would be affected in the same way as cacti. Our results highlight the need to evaluate other

biotic interactions, since not all of them will respond in the same way to climate change.

Furthermore, it has been proposed that more specialised mutualisms are at greater risk of mismatch between the interacting species, being therefore more vulnerable to the negative effects of climate change (Memmott et al., 2007; Schweiger et al., 2012; Rafferty et al., 2015). Regarding this idea, no clear support was found for the species studied here. For example, *Cleistocactus baumannii*, a functionally specialist species (pollinated exclusively by hummingbirds; Gorostiague and Ortega-Baes, 2016), had relatively low spatial matching in the present that would increase under future scenarios, while its congener *C. smaragdiflorus*, a functionally generalist species (pollinated by hummingbirds and bees; Gorostiague and Ortega-Baes, 2016), had good current spatial matching that would decrease under future scenarios. It is possible that the vulnerability of these plants in terms of maintaining their mutualists depends not only on the number of pollinating species or groups but also on their geographic rarity (e.g., geographic range size; Schweiger et al., 2012).

## 5. Conclusions

Our study emphasizes the importance of incorporating biotic interactions into forecasts that evaluate the effects of climate change on species distributions. For this, basic information about the interactions that the focal group establish is required (e.g., their degree of dependence on the interaction; Giannini et al., 2013; Settele et al., 2016). This information is fragmentary and usually restricted to a single interaction which was evaluated in a single locality. Thus, further studies that evaluate the role of other biotic interactions beyond pollination are needed. Particularly for cacti, animal-mediated seed dispersal and facilitation by nurse plants for seed establishment are also essential for their life cycles and should therefore be taken into account. Finally, the climate change-induced disruption of biotic interactions was evaluated here only at a spatial scale, by estimating the overlap between the geographic ranges of mutualists. Progress should be made in studies focused on the temporal or phenological mismatch that climate change can cause in biotic interactions. For this, information based on long-term studies is needed.

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interest.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2018.07.003>.

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