



Ant-gardens: a specialized ant-epiphyte mutualism capable of facing the effects of climate change

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Received: 9 June 2020 / Revised: 24 January 2021 / Accepted: 11 February 2021
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Abstract

It is suggested that specialized mutualisms are more vulnerable to climate change. Ant-gardens (AGs) are a complex and specialized mutualistic system represented by epiphytic plants that specifically inhabit the arboreal nest built by canopy ants in tropical forests. Different ant-epiphyte ensembles constitute the AGs throughout the Neotropics. However, neither the environmental factors that determine their geographical distribution nor the effects of climate change on this canopy biological system are known. Here, we estimated the ecological niche and elevational distribution of the Neotropical AGs as an entity (regardless of species composition), and individually for six AG ant and 16 AG epiphyte species in order to determine and compare their current and future distributions (vulnerability), using two unrelated Global Circulation Models for the year 2070 under two Representative Concentration Pathways (RCP4.5: optimistic and RCP8.5: pessimistic). The current potential distribution of the AGs is discontinuous from Tamaulipas, Mexico, to Rio Grande do Sul, Brazil, in low elevation areas with high mean annual temperatures ($> 25\text{ }^{\circ}\text{C}$) and precipitation ($> 2400\text{ mm}$). In contrast, the individual distributions of the AG ants and epiphytes tended not to follow to this climatic profile and were segregated by both latitude and elevation. The geographic distribution of most AG ant and epiphyte species diminished under climate change, while that of the AGs increased, even under the pessimistic scenario. This suggests that AGs allow the species that comprise them to broaden their ecological niche and be more resistant to climate change than they would be outside of this system.

Keywords Ecological niche modeling · Elevational distribution · MaxEnt · Neotropics · Niche equivalence · Species distribution models

Communicated by Nigel E. Stork.

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Introduction

Climate change is one of the most serious threats to species conservation, because it has been estimated that it could cause the loss of $\geq 50\%$ of the current distribution of 57% of plant species and 45% of animal species by the year 2080 (Warren et al. 2013). Extinction of species that cannot move to suitable sites has been predicted, as well as those with generation times that preclude them from adapting at a speed matching that of climate change (Colwell et al. 2008; Wiens and Slaton 2012). The impact on the distribution of species will alter (positively or negatively) mutualistic interactions, generating turnover of the associated species, extinction of the mutualism or its transformation into antagonism (Kiers et al. 2010; Van der Putten et al. 2010). It has been hypothesized that mutualistic systems are more vulnerable because the extinction of one of the species could lead to a cascade of extinctions (Dunn et al. 2009; Blois et al. 2013). For this reason, understanding the abiotic and biotic factors that determine the occurrence of mutualistic species (e.g., ants and epiphytes), and thus their potential interactions, represents a key step towards the more accurate prediction of their robustness (alone or associated) in the face of global threats such as climate change.

Mutualistic interactions occur when individuals of different species benefit in a reciprocal manner (Stadler and Dixon 2008), as is the case with the ant-gardens (AGs). The AGs are defined as a community of epiphytic plants established in arboreal nests of canopy ants (Orivel and Leroy 2011). In this mutualistic system, the benefits of ants for epiphytes include the incorporation of their seeds into a nutrient-rich substrate (ant nests) and protection against herbivores and, in return, the epiphytes provide food (e.g., extrafloral nectar), additional nesting sites (domatia in Paleotropical species) and structural support to the ants and their nests, respectively (Kaufmann and Maschwitz 2006; Orivel and Leroy 2011; Chomicki et al. 2017). The co-occurrences between ants and epiphytes that constitute the AGs are obligate since only some ants (AG ant species) can build nests for the establishment of a particular assembly of epiphytic plants (AG epiphyte species; Youngsteadt et al. 2008; Orivel and Leroy 2011). However, it can be observed a few individuals of some AG epiphytes growing outside of AGs (e.g., Davidson 1988; Morales-Linares et al. 2016), but experimental evidence indicates higher growth and survival of them in AGs (Leroy et al. 2017). Furthermore, if one of the mutualistic partners dies or associated ant species abandons the AGs, the AG substrate deteriorates and eventually falls to the ground where both AG ants and AG epiphytes cannot live (e.g., Davidson 1988). Therefore, the AG ant and epiphyte species are considered specialized inhabitants of the AGs (Orivel and Leroy 2011). Also, on a local scale, the AG ant and epiphyte species usually maintain preferential associations between them, but in a large spatial scale (e.g., Southeast Asian) the species-specific associations are rare (Kaufmann and Maschwitz 2006; Chomicki et al. 2017; Morales-Linares, unpublished data). Therefore, the AGs are considered one of the most complex and specialized ant-plant mutualisms (Orivel and Leroy 2011).

With the exception of Africa, AGs have been reported in the Neotropics and Paleotropics (Orivel and Leroy 2011; Chomicki et al. 2017). In the Neotropical region, AGs have been recorded from Mexico to Peru-Brazil (excluding oceanic islands), particularly in tropical rainforests (gaps and forest edges), riparian vegetation and agroecosystems (e.g., Kleinfeldt 1978; Catling 1995; Davidson 1988; Morales-Linares et al. 2016). Around 11 AG ant species and 20 AG epiphyte species constitute the Neotropical AGs (Orivel and Leroy 2011; Morales-Linares et al. 2016), and the ecological network approach has also revealed that the AG ant species tend to share several AG epiphyte species, since unlike

AG ants with a more restricted distribution, more than half of AG epiphyte species have a Neotropical distribution (Morales-Linares, unpublished data). Furthermore, although the occurrence of one AG ant should involve the occurrence of at least one AG epiphyte and the AGs (and vice versa), the distribution/composition of the AG ant and epiphyte species throughout the Neotropics is not homogeneous (Orivel and Leroy 2011). Locally, the associated species in AGs may differ in their preference for sunny or shady areas (e.g., Davidson 1988). However, little is known regarding the abiotic and biotic factors that determine the geographic distribution of AGs and AG ant and epiphyte species individually, both in the current time and under future scenarios of climate change.

The species niche has been defined as the set of environmental factors, including (where applicable) antagonistic interactions (e.g., with competitors), that allow the species to exist (Hutchinson 1957). Actually, the niche can be estimated through ecological niche modeling (ENM) in order to predict the geographic distribution or suitable areas (species distribution model or SDM) for populations of a species (Soberón and Nakamura 2009). ENM basically consists of relating records of occurrence of a species with environmental predictors (e.g., temperature, precipitation, elevation) associated with these records (Pearson and Dawson 2003; Elith and Leathwick 2009), but some recent reviews suggest that using SDMs of associated species (e.g., mutualists) as biotic predictors can improve the performance of focal species models (i.e., biotic *versus* abiotic models; Giannini et al. 2013; Wisz et al. 2013; Anderson 2017). ENM also allows us to test hypotheses regarding the similarity of niches (Warren et al. 2008) and the potential distribution of species under different future scenarios of climate change (Pearson and Dawson 2003; Hijmans and Graham 2006), even considering their ecological interactions (Araújo and Luoto 2007; Wisz et al. 2013). ENM that integrate ecological interactions are generally based on individual estimation of the distribution of the interacting species (e.g., endophyte-plant, pollinator-plant, insect-host plant) to reveal their effects on each other or niche equivalences, and thus potentially estimate their robustness in the face of perturbations such as global climate change (Afkhani et al. 2014; Abrahamczyk et al. 2017; Cunha et al. 2018; Filazzola et al. 2018).

To our knowledge, the distribution of an ecological interaction *sensu stricto* has not been modeled, such as the AGs, which can be considered an ecologically independent entity because they occur only when the AG ant and epiphyte species co-occur and interact among themselves. Therefore, in this study, we conducted ENM for Neotropical AGs (abiotic and biotic models), and the individual AG ant and epiphyte species (abiotic models) in order to: (1) determine the abiotic (climatic and elevational) and biotic factors associated with their distribution; (2) compare the performance of biotic *versus* abiotic models; (3) test the equivalence of niches in geographic and environmental spaces; and 4) evaluate potential changes on their geographical and altitudinal ranges under two scenarios (RCP4.5: optimistic and RCP8.5: pessimistic) of global climate change. The use of the distribution of partners can improve the prediction of the distribution of focal species (e.g., Giannini et al. 2013), and mutualistic interactions lead to the range overlap of species pairs at both local and broad geographic scales (Araújo and Rozenfeld 2014). Although different ant-epiphyte ensembles occur in AGs throughout the Neotropics, the development of this mutualistic system requires the obligate association between the AG ant and epiphyte species (Orivel and Leroy 2011). Therefore, we hypothesized that the biotic models will perform better than the abiotic models, and the climatic and altitudinal profile that determines the distribution of AGs will be similar for the AG ant and epiphyte species (equivalent niches). In addition, community-level projections of ants and epiphytes suggest a reduction in their geographical ranges and move upslope under climate change (Hsu et al. 2012; Bishop et al. 2019), and specialized species are expected to be the most threatened (Dunn

et al. 2009). Therefore, these range changes are also expected for the AGs (entity) and the AG ant and epiphyte species individually.

Material and methods

Records of occurrence

Records of occurrence of the AGs were obtained from specialized references (e.g., Orivel and Leroy 2011, and references within) in which occurrence of the AGs is explicitly mentioned. Because we modeled AGs as an entity, the ant and epiphyte composition of each AG record was not considered. In the Neotropics, there has been a historic bias towards the knowledge of South American AGs, so the study of the northernmost AGs is recent (Morales-Linares et al. 2016). For this reason, during April and May 2018 and based on herbaria records of AG ant and epiphyte species, fieldwork searches of AGs were conducted in the southeastern Mexico.

We only considered "true" AG ant and AG epiphyte species; the first are those ants able to build AGs, excluding those species that share the nest of AGs (parabiotic ants), such as *Crematogaster levior*; while the latter are epiphytes sown in the nest by AG ants or observed mostly or only in AGs (Orivel and Leroy 2011; Morales-Linares et al. 2018). Occurrence records of the AG ant and epiphyte species were obtained from: (1) the online databases Global Biodiversity Information Facility (GBIF.org 2017), antmaps.org (Janicki et al. 2016), and the World Information Network on Biodiversity (REMIB, by its Spanish acronym), (2) specialized myrmecological and floristic lists (e.g., Fernandes and Souza 2018; Ramos et al. 2019), and (3) field collections in Mexico (AG ants only). All occurrence records were reviewed in order to discard duplicate or dubious information (e.g., coordinates outside of the Neotropics). Only occurrences separated by a distance of > 10 km and filtered through the spThin R package (Aiello-Lammens et al. 2015) were used in order to avoid spatial autocorrelation (Boria et al. 2014). Finally, we only considered AG ant and epiphyte species with ≥ 10 occurrences (Table 1), thus avoiding the generation of imprecise models based on a few records, while seeking to maximize accuracy (van Proosdij et al. 2016).

We consider not using the occurrence records of the AG ant and epiphyte species as AG records, since those species with many records (e.g., *Anthurium gracile*, Table 1) could bias the results of the importance (or similarity) of each one of the associated species concerning the niche/distribution of the AGs (see below). Therefore, we tried to ensure that the AG occurrence records were independent of those of the AG ant and epiphyte species; however, 11 records (24%) were obtained from AG ants (seven belonging to *Azteca gnava*) to increase the number of occurrences in little-explored areas of the Neotropics. All occurrence records are available at: <https://doi.org/10.6084/m9.figshare.13627349.v1>.

Environmental data

Climatic predictors were obtained from Chelsa database version 1.2, which consists of 19 bioclimatic layers related to temperature and precipitation (Karger et al. 2017). The 19 layers were clipped to the area of the continental Neotropics (≈ 18.3 million km²) located between the latitudes 30 °N and 45 °S (Löwenberg-Neto 2014) and resampled at a resolution of 30 arc sec to 2.5 arc min with the raster R package (Hijmans et al. 2016) to identify

Table 1 Records of occurrences and information of the best models of potential distribution of Neotropical Ant-Gardens (AGs) and AG ant and epiphyte species

Biological group, subfamily or family	Models (species)	Occurrences (all/ thinned)	Features classes/RM	AICc (lowest value)	Partial ROC (AUC ratios)*
Ants					
Dolichoderinae	<i>Azteca gnava</i>	37/28	LQ/3.5	706.02	1.68 ± 0.23
	<i>Azteca trillii</i>	10/10	LQ/1.5	265.32	**
Formicinae	<i>Camponotus femoratus</i>	61/58	LQ/0.5	1488.68	1.69 ± 0.16
Myrmicinae	<i>Crematogaster longispina</i>	74/32	LQ/0.5	790.85	1.58 ± 0.33
Ponerinae	<i>Neoponera goeldii</i>	23/18	LQH/2	452.86	1.87 ± 0.12
	<i>Odontomachus mayi</i>	19/17	LQ/4	447.97	1.86 ± 0.12
Epiphytes					
Araceae	<i>Anthurium gracile</i>	972/673	H/1	17388.85	1.69 ± 0.03
	<i>Philodendron deflexum</i>	267/200	LQ/1	4891.11	1.82 ± 0.05
Bromeliaceae	<i>Aechmea longifolia</i>	113/88	LQ/2.5	2146.62	1.79 ± 0.09
	<i>A. mertensii</i>	378/280	LQH/3	7180.34	1.73 ± 0.06
	<i>A. tillandsioides</i>	472/274	LQH/4	6864.09	1.77 ± 0.04
	<i>Neoregelia eleutheropetala</i>	38/31	L/3.5	764.13	1.84 ± 0.15
Cactaceae	<i>Epiphyllum phyllanthus</i>	621/417	LQH/4	11143.15	1.49 ± 0.07
Gesneriaceae	<i>Codonanthe calcarata</i>	197/136	LQ/0.5	3437.86	1.67 ± 0.08
	<i>C. crassifolia</i>	576/388	LQH/3.5	9828.97	1.74 ± 0.03
	<i>C. ulcana</i>	280/191	H/2.5	4841.02	1.73 ± 0.06
Moraceae	<i>Ficus paraisensis</i>	738/453	LQ/0.5	11673.69	1.67 ± 0.04
Orchidaceae	<i>Coryanthes picturata</i>	29/19	LQ/0.5	492.03	1.82 ± 0.21
	<i>C. speciosa</i>	27/20	LQ/3.5	495.24	1.74 ± 0.21
	<i>Epidendrum flexuosum</i>	255/145	LQH/4	3785.21	1.69 ± 0.08
Piperaceae	<i>Peperomia macrostachya</i>	535/368	LQ/0.5	9540.67	1.61 ± 0.05
Solanaceae	<i>Markea utlei</i>	154/105	LQ/0.5	2606.15	1.78 ± 0.08

Table 1 (continued)

Biological group, subfamily or family	Models (species)	Occurrences (all/ thinned)	Features classes/RM	AICc (lowest value)	Partial ROC (AUC ratios)*
Ant-gardens	Abiotic	57/45	LQ/1	1149.33	1.66 ± 0.15
	Biotic-epiphytes		LQ/2.5	1149.25	1.76 ± 0.13
	Biotic-ants		LQH/3.5	1152.36	1.71 ± 0.11
	Biotic (ants + epiphytes)		L/3	1153.95	1.73 ± 0.12
	Abiotic + biotic		LQ/2	1157.43	1.72 ± 0.12

The best model was that with the lowest AICc value (i.e., $\Delta AICc = 0$). The AG Biotic models are ordered from highest to lowest performance. Feature classes: linear (L), quadratic (Q), and hinge (H). Table S1 shows the following five best models ($\Delta AICc > 2$) for the AGs and AG ant and epiphyte species

RM regularization multiplier values (0.5–4), AICc Akaike information criterion corrected for small samples, ROC receiver operating characteristic, AUC area under the curve

*All AUC ratios > 1 (z -tests, $P < 0.05$)

**Jackknife validation = 0.9 (success rate), $P < 0.001$

general climatic patterns according to the scale of the distribution of AGs (Pearson and Dawson 2003).

The selection of the climatic predictors for the models was carried out in two steps: (1) using the fuzzySim R package (Barbosa 2015), we reduced the multicollinearity among the independent variables, discarding those that presented high correlation values among themselves ($r > 0.7$; Dormann et al. 2013), both for the AGs and for each AG ant and epiphyte species; (2) Due to the close association between the species that constitute the AGs (Orivel and Leroy 2011) and to standardize the predictors for the models and subsequent analyses, we choose only those preselected predictors (step 1) that were common in more than half of the AG ant and epiphyte species, including the AGs. Therefore, the climatic predictors used in the abiotic models were: annual mean temperature (Bio01), annual mean diurnal range (Bio02), isothermality (Bio03), annual precipitation (Bio12), precipitation of driest month (Bio14), precipitation of warmest quarter (Bio18) and precipitation of coldest quarter (Bio19). Furthermore, we obtained the elevation value (in m a.s.l.) for all occurrences of the AGs and the AG ant and epiphyte species from Digital Elevation Model GMTED2010 (Danielson and Gesch 2011).

Ecological niche modeling, niche equivalence and elevational distribution

Recently, the Join SDM approach with Bayesian inference framework has been developed to model multiple species together (presence-absence data) in order to explain and predict the responses of large species assemblages (communities) to environmental factors (e.g., Ovaskainen et al. 2017). However, according to our objectives and the type and amount of data available, we use the algorithm MaxEnt 3.4.1 (Phillips et al. 2017) to generate the ENM of the AGs (abiotic and biotic models) and the AG ant and epiphyte species (abiotic models) and to obtain the species distribution models (SDMs). The MaxEnt method uses the principle of maximum entropy to estimate the niche/distribution of species from spatial information of occurrences and environmental predictors (Phillips et al. 2006); and it is suitable for presence-only data and robust for modeling species with a few occurrence records (Phillips et al. 2006; van Proosdij et al. 2016).

Likewise, we used individual SDM instead of Join SDM because the majority (76 %) of the occurrence records of the studied community (i.e., AGs) were independent of those of the associated species (i.e., AG ants and epiphytes). The latter are a few species with a close degree of association, which is adequate to use them as biotic predictors (Norberg et al. 2019). The abiotic models were generated with the occurrence records (AGs and AG ant and epiphyte species) and the climatic predictors, while the biotic models were performed with the occurrence records of AGs and the biotic predictors, which correspond to the SDMs of the AG ant and epiphyte species obtained with climatic predictors. In particular, we omitted to verify the possible multicollinearity between the biotic predictors (Cunha et al. 2018; Filazzola et al. 2018), since we sought to know the relevance of each of the AG ant and epiphytes species in the models. Four biotic models of the AGs were then generated: AG biotic-ants (SDMs of AG ants), AG biotic-epiphytes (SDMs of AG epiphytes), Biotic (SDMs of AG ant and epiphyte species) and Abiotic + Biotic (climatic predictors and SDMs of AG ant and epiphyte species).

Due to the wide distribution of the AGs, the area of calibration for all models was the continental Neotropics and we assume full dispersal, i.e., the species can occupy all the suitable areas projected for every model (Barve et al. 2011; Löwenberg-Neto 2014). We evaluated the parameterization and complexity (tuning) of the models considering different

feature classes: linear (L), quadratic (Q), and hinge (H), and values of regularization multipliers (RM: 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4) using the ENMeval R package (Muscarella et al. 2014). We used Akaike's information criterion corrected for small sample sizes (AICc), to select the best models; i.e., those with the lowest value of AICc (Muscarella et al. 2014). The corresponding feature classes and RM values of the best models, together with 10,000 background points, were fitted in MaxEnt (Phillips and Dudík 2008). The records of occurrence of each model were divided into two parts: 80% training data and 20% test data. The output format to generate the SDMs or maps was Cloglog, which indicates the probability values, from a totally unsuitable environment (0) to one that is totally suitable (1; Phillips et al. 2017). We also reclassified the SDMs into binary maps (suitable and unsuitable area), using the threshold maximum training sensitivity plus specificity (Max SSS; Liu et al. 2013).

We evaluated the performance of each model using the partial ROC curve test, presenting the value of partial ROC as a ratio between the AUC model (area under the curve) and that expected by chance (Peterson et al. 2008). We obtained the AUC ratios using the ENMGadgets R package (Barve and Barve 2013) through bootstrapping of 50% of the total of the test data available, with 500 iterations and a 5% threshold of error of omission. The AUC ratios have values of between 0 and 2, in which values > 1 represent models with performances greater than would be expected at random (Peterson 2012). Therefore, we conducted a z-test to determine whether the mean value of the AUC ratio was significantly greater than 1 (Peterson et al. 2008). Particularly for the AG ant *Azteca trailii* (only 10 records) we use Jackknife validation (Pearson et al. 2007). The importance of the predictors of each model was calculated in MaxEnt through the percentage of contribution of each predictor in terms of predicting the dependent variable at the time of its entry into each iteration (Phillips et al. 2017).

In order to standardize the tests of niche equivalence among the AGs and the AG ant and epiphyte species, we used their abiotic models only. These were compared in the geographic (two-dimensional map coordinates) and environmental (multi-dimensional space of environmental variables) spaces, since the conditions of particular suitability of a geographic space can amplify the spatial distribution of a species, even when its fundamental niche (environmental space) is narrow (Elith and Leathwick 2009; Warren et al. 2019). We used Schoener's D index (Schoener 1968) to estimate the niche overlap between pairs of models. This index takes values of between 0 (no overlap) and 1 (total overlap; Warren et al. 2008) and its statistical significance was evaluated with an identity test, with 100 pseudo-replicates (randomization) using the R version of the ENMTools software (Warren et al. 2008; Warren et al. 2010). Complementarily, we use the kernel density estimates to visualize the latitudinal distribution of the AGs and the AG ant and epiphyte species considering their occurrence records. Then, we compare the latitudinal distribution among the species using equality permutation tests (1,000 permutations) performed with the *sm* R package (Bowman and Azzalini 2019). In particular, these comparisons were made between the species of each subfamily (AG ants) or family (AG epiphytes) to facilitate the visualization and interpretation of the results.

The elevation can directly influence abiotic factors such as temperature but not directly on the species, and its relationship with these factors may not be maintained in future projections (Anderson 2013). Therefore, we analyzed the elevational distribution of the AGs and the AG ant and epiphyte species using an adaptation of the Kaplan-Meier survival analysis (Kaplan and Meier 1958) to estimate probabilities of occurrence in relation to the elevation. Firstly, we selected the elevation range of 0–900 m a.s.l, since this contains 85–100% of all of the occurrences (see Results), so records ≥ 900 m a.s.l were censored.

Secondly, we calculated the curves of elevational occurrence of the AGs and the AG ant and epiphyte species, and compared these using a log-rank test followed by false discovery rate (FDR) post-hoc tests. Survival analysis and curves were done with the R packages survival (Therneau and Lumley 2018) and survminer (Kassambara and Kosinski 2018).

Geographic and elevational distribution under future scenarios of climate change

We made future projections of the distribution of the AGs and AG ant and epiphyte species using only abiotic models and considering two unrelated Global Circulation Models (GCMs): ACCESS1.0 and MIROC5 (Sanderson et al. 2015), based on the CMIP5 project and obtained from Chelsa database version 1.2 (Karger et al. 2017). For each GCM, we selected the period of time 2070 (2061–2080) and two Representative Concentration Pathways (RCPs): 4.5 and 8.5. The RCP4.5 (optimistic scenario) considers a CO₂ concentration of 650 ppm and an increase of 1.0–2.6 °C in global mean temperature by 2100, while RCP8.5 (pessimistic scenario), is one without mitigation and with a CO₂ concentration of 1350 ppm and an increase of 2.6–4.8 °C (Harris et al. 2014). All of the models were projected in MaxEnt (Phillips et al. 2017) using the same climatic predictors as used for the current time, and the resulting future SDMs were reclassified into binary maps. Subsequently, the current binary maps (Max SSS threshold) were subtracted from the future binary maps in order to account for the unsuitable, lost, maintained and gained areas through the raster R package (Hijmans et al. 2016). Finally, we obtained the elevation values for the pixels of occurrence of the current and future binary predictions from Digital Elevation Model GMTED2010 (Danielson and Gesch 2011). With the exception of the MaxEnt program, all analyses were conducted in R version 3.5.1 (R Core Team 2018).

Results

The ecological niche and its equivalence among the AGs and the AG ant and epiphyte species

We obtained a total of 3996 records of occurrence, of which 163 corresponded to six AG ants, 3788 to 16 AG epiphytes and 45 to AGs (Table 1; Figs. 1, S1, S2). The best model (lowest AICc) of potential geographic distribution was found for all AG ant and epiphyte species and for the AGs (one abiotic model and four biotic models; Tables 1, S1; Figs. 1, S1, S2), which also presented better performance than that expected by chance (partial-ROC tests and jackknife validation; Table 1). Only the AG abiotic and AG biotic-epiphytes models were equally probable (AICc = 1149.33 and 1149.25, respectively) and significantly better than the other AG models ($\Delta\text{AICc} > 2$), but the AG abiotic model predicted the largest suitable area (4.84 million km²; Table 1, Fig. 1).

In general, the climatic predictors with the greatest contribution differed among the abiotic models (Table S2; Fig. S3). However, mean diurnal range tended to be the most important predictor for most of the AG ant and epiphyte species (Table S2), with an optimum temperature fluctuation value of 15 °C (Fig. S3). For the AGs, mean diurnal range was not important and the abiotic model showed that the greatest probability of occurrence is from 2,400 mm of precipitation and a temperature of 25 °C, also considering an optimum of 500 mm of precipitation during the coldest quarter (Table S3, Fig. S3). Some AG ant and epiphyte species presented similar relationships with the climatic predictors of greatest

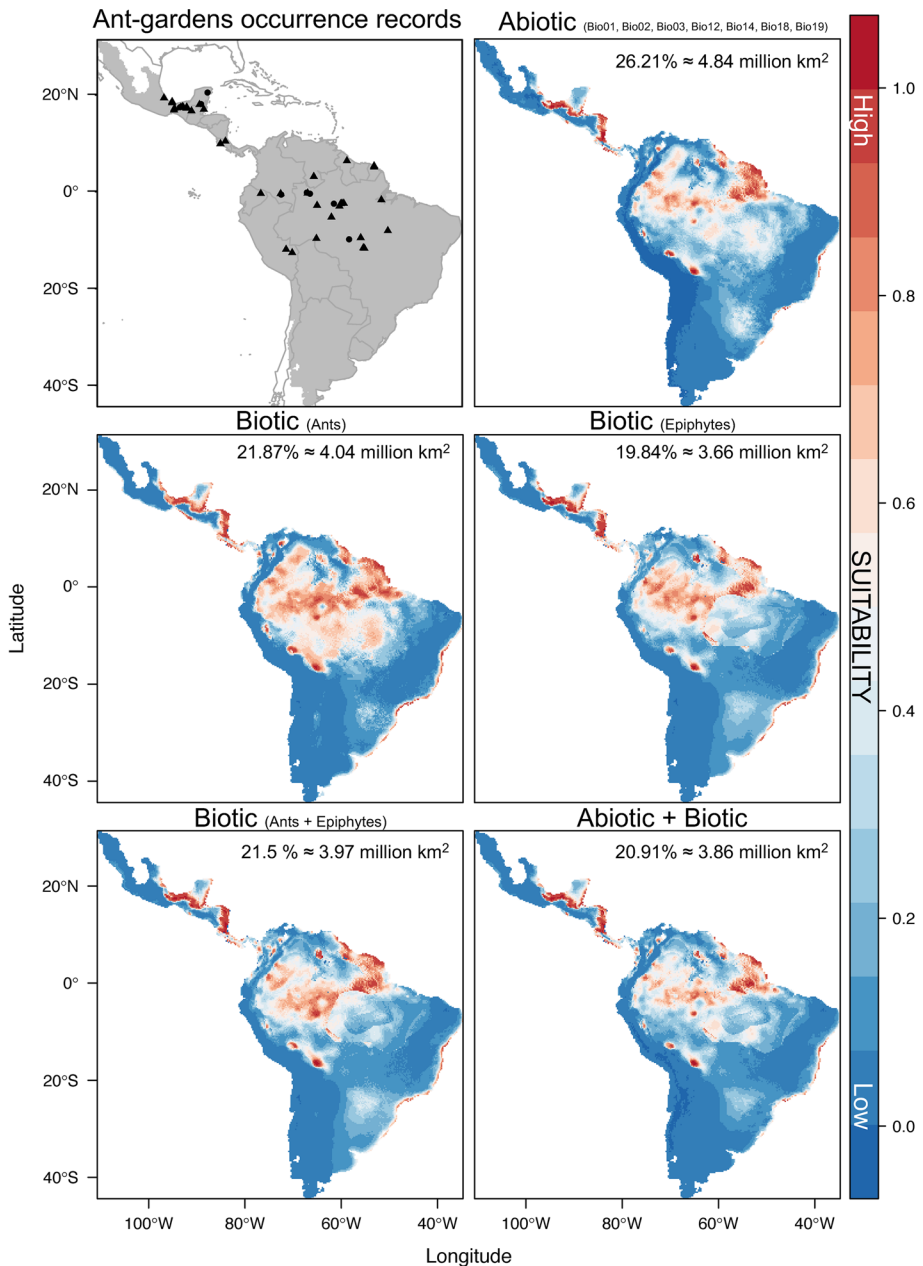


Fig. 1 Potential geographic distribution (Cloglog outputs) of the Ant-gardens (AGs) in the Neotropics considering abiotic and biotic models. The abiotic models use climatic predictors related to temperature (Bio01, Bio02, and Bio03) and precipitation (Bio12, Bio14, Bio18, and Bio19), while the biotic models use as predictors the species distribution models (SDMs) of the AG ant and epiphyte species. In the upper left panel, triangles = training data and circles = test data. Each panel shows the suitable area (% and million km²), which was estimated by applying the maximum training sensitivity plus specificity threshold

importance to the AGs, such as the AG ants *Azteca gnava* and *Crematogaster longispina* and the AG epiphytes *Coryanthes picturata*, *Peperomia macrostachya* and *Aechmea tillandsioides* with precipitation, and the AG ant *Camponotus femoratus* with temperature (Fig. S3). In the AG biotic models, the AG ant *Azteca gnava* was the most important predictor in the model which incorporated ants only, while the AG epiphytes *Coryanthes picturata*, *Peperomia macrostachya* and *Epidendrum flexuosum* were the most important predictors in the models which incorporated epiphytes (Table S3, Fig. S3).

The niche identity tests among the AGs and the AG ant and epiphyte species showed generally higher percentages of equivalent niches in the environmental space (49–83%) than in the geographical space (28–73%; Table 2). The percentages of equivalent niches considering both geographical and environmental spaces were 60% for combinations among AG ants (e.g., *Azteca gnava* and *Crematogaster longispina*), 33% for AG ants and AG epiphytes (e.g., *Crematogaster longispina* and *Aechmea tillandsioides*), and 19% for AG epiphytes (e.g., *Epidendrum flexuosum* and *Coryanthes* spp.; Tables 2, S4). Only 31% of the AG epiphytes (e.g., *Aechmea tillandsioides*) and 50% of the AG ants (e.g., *Azteca gnava*) presented niches equivalent to those of the AGs, in both geographic and environmental spaces (Tables 2, S4). On the other hand, the species of each subfamily (AG ants) or family (AG epiphytes) showed differences in their latitudinal distribution, except for the AG ants *Neoponera goeldii* and *Odontomachus mayi* (Ponerinae) registered only in South America (Figs. S4, S5). Among the AG ants, 66% of the species were recorded exclusively in South America (e.g., *Camponotus femoratus*), and only *Azteca gnava* showed a Neotropical distribution, being the only species recorded in the northern part of the Neotropics (Figs. S1, S4). Among the AG epiphytes, 56% of the species showed a Neotropical distribution (e.g., *Epidendrum flexuosum*), and 37.5% occurred exclusively in South America (e.g., *Aechmea mertensii* and *Codonanthe calcarata*), while *Coryanthes picturata* occurred only from southern Mexico to Central America (Figs. S2 and S5).

Elevational distribution

The curves of elevational occurrence of the AGs and the AG ant and epiphyte species differed significantly (log-rank $\chi^2 = 316$, $df = 22$, $P < 0.001$) and these presented a probability of $\geq 50\%$ of occurrence at between 39 (i.e., *Neoponera goeldii*) and 286 m a.s.l. (i.e., *Philodendron deflexum*; Fig. 2, Table S5). The AGs had a greater probability of occurrence below 112 m a.s.l., but the most extreme values were recorded in the north of the Neotropics (Mexico), where they occur from 21 to 646 m a.s.l. (Fig. 2, Table S5). Only

Table 2 Percentage of equivalent niches among the Neotropical Ant-gardens (AGs), AG ants and AG epiphytes in both geographic and environmental spaces

Niche equivalence	Ants	Epiphytes	Ants and epiphytes	AGs and ants	AGs and epiphytes
Number of combinations	15	120	96	6	16
Non-equivalence (%)	20	41.67	34.38	16.67	31.25
Equivalence (%): geographic space (GEO)	73.33	28.33	42.71	50	31.25
Equivalence (%): environmental space (ENV)	66.67	49.17	56.25	83.33	68.75
Equivalence (%): GEO and ENV	60	19.16	33.33	50	31.25

Details of niche identity tests are shown in Table S4

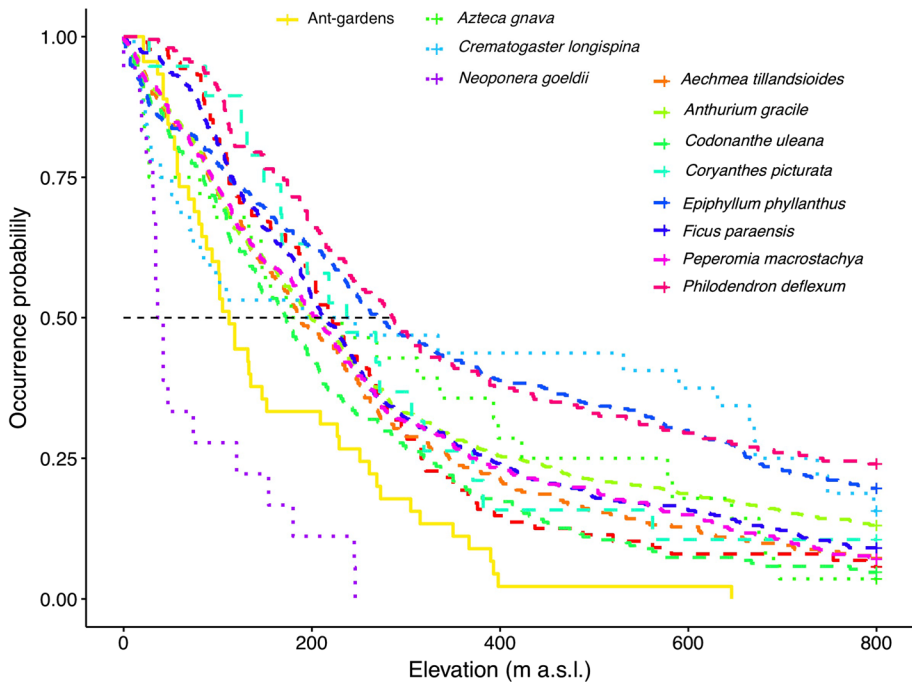


Fig. 2 Altitudinal distribution of the Neotropical Ant-gardens (AGs) and the AG ant and epiphyte species. Only the AG ants (dotted lines) and AG epiphytes (dashed lines) that had significant differences (FDR post-hoc tests, $P < 0.05$) with respect to the AGs (solid line) are shown. The black dashed line represents the median probability of occurrence. Elevation details and all FDR post-hoc tests of the species are shown in Tables S5 and S6, respectively

three (50%) AG ants (e.g., *Camponotus femoratus*) and seven (44%) AG epiphytes (e.g., *Aechmea mertensii*) presented curves of elevational occurrence that were statistically similar to those of the AGs (Fig. 2). The curves of the AG ants *Crematogaster longispina* and *Azteca gnava* were similar to each other, but different from those of *Neoponera goeldii*, *Camponotus femoratus*, *Odontomachus mayi* (except *Azteca trailii*), occurring at high and low elevations, respectively (Fig. 2, Table S6). Only the AG ant *Azteca gnava* presented a curve similar to that of all AG epiphytes except *Philodendron deflexum* (Fig. 2, Table S6). Among AG epiphytes, the curves of *Aechmea mertensii*, *Anthurium gracile* and *Philodendron deflexum* were the most dissimilar, and tended to occur at low, medium and high elevations, respectively (Fig. 2, Tables S5, S6).

Geographic and elevational distribution under climate change

Among the current SDMs, the AGs presented an intermediate potential distribution of 4.84 million km² (26% of the Neotropics) and the AG epiphytes *Peperomia macrostachya* and *Coryanthes picturata* presented the greatest (7.2 million km², 39%) and lowest (1.34 million km², 7%) potential distribution, respectively, while the AG ants also showed a wide (*Odontomachus mayi* = 6.89 million km², 37%) or narrow (*Azteca gnava* = 1.48 million km², 8%) potential distribution (Table S7, Figs. 3, S6, S7). The suitable area of the Neotropical AGs is distributed in a discontinuous manner from Tamaulipas, Mexico (in the

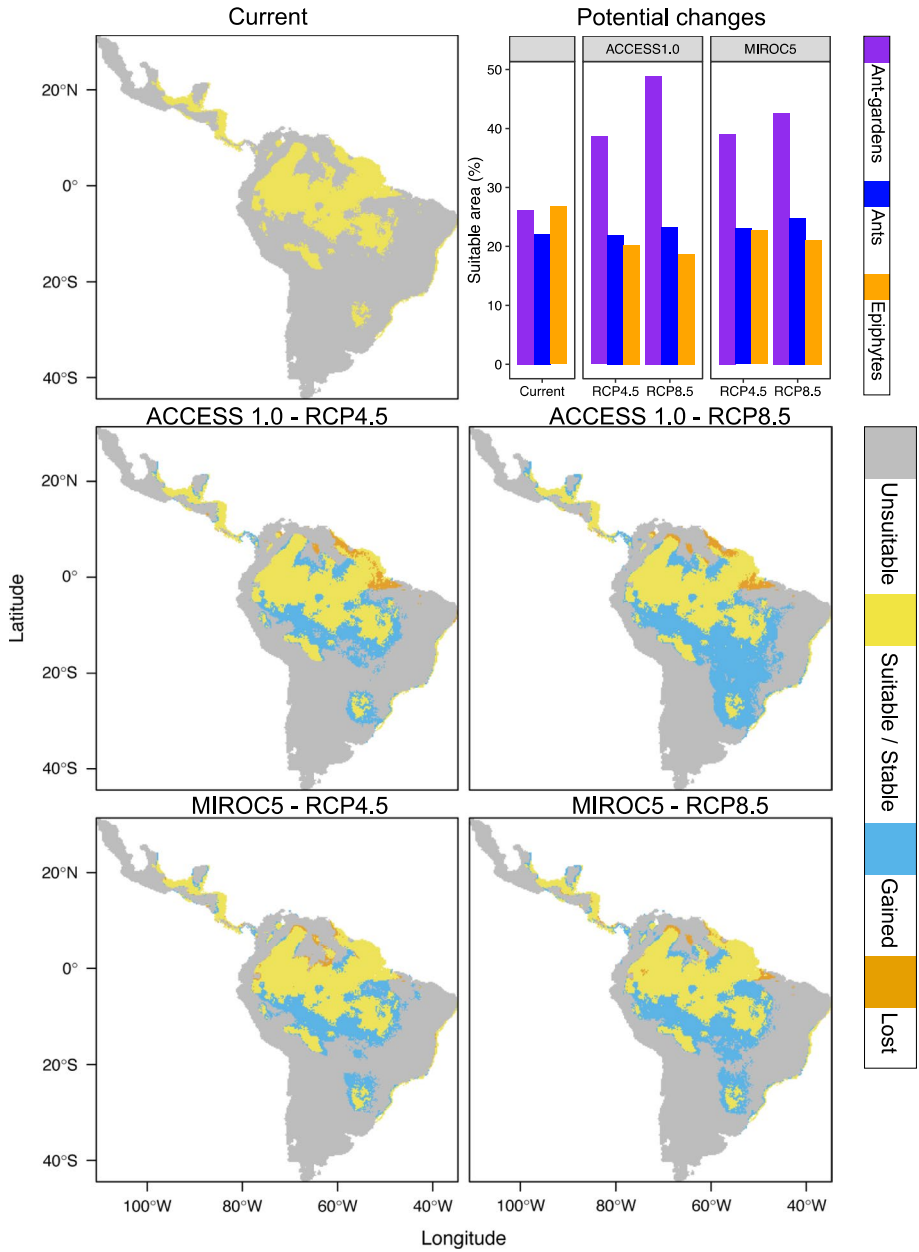


Fig. 3 Potential changes in the suitable area of the Neotropical Ant-gardens (AGs) and the AG ant and epiphyte species (mean values) by the year 2070 under two global circulation models (ACCESS 1.0 and MIROC5) of climate change and considering two representative concentration pathways of carbon dioxide (low, RCP4.5 and high, RCP8.5). Suitable area (future scenarios) = maintained + gained areas. Values and maps per species are presented in Table S7 and Figs. S6, S7

north) to Rio Grande do Sul, Brazil (in the south), and is divided into three main zones: the south east of Mexico-Central America, the Amazon basin and the Atlantic forest (Fig. 3).

The suitable area (maintained + gained areas) of the AGs and the AG ant and epiphyte species showed important changes by the year 2070 under the scenarios of climate change (RCP4.5 and RCP8.5), and these patterns of change tended to be similar across the GCMs (ACCESS 1.0 and MIROC5; Table S7, Figs. 3, S6, S7). The suitable area increased for the AGs in both RCPs with values of up to +86% in the ACCESS-RCP8.5, relative to the current time. On the other hand, the suitable area for AG ants (mean values) also increased slightly (except ACCESS-RCP4.5) with values of up to 12% in the MIROC5-RCP8.5, while for the AG epiphytes (mean values), it diminished in both RCPs with values of up to -30% in the ACCESS-RCP8.5 (Fig. 3). The greatest expansion of suitable area for the AGs occurred towards the south of the Amazon basin, connecting it with the southernmost portion of the Atlantic forest, while little reduction occurred to the northeast of the Amazon basin (Fig. 3).

Individually, 54% of the total species of AG ants and epiphytes would reduce their suitable area in both RCPs, with the AG ant *Crematogaster longispina* and AG epiphyte *Epiphyllum phyllanthus* being the species most affected with reductions of their suitable area of between -76% and -90% (Table S7, Figs. S6, S7). In contrast, the AG ant *Camponotus femoratus* could have an increase in its suitable area of from +79% (MIROC5-RCP4.5) to +112% (ACCESS-RCP8.5), while the AG epiphyte *Aechmea longifolia* showed increases with values of +43% (ACCESS-RCP4.5) and +70% (MIROC5-RCP8.5) relative to the current time (Table S7, Figs. S6, S7).

The potential elevational distribution for the year 2070 (RCP4.5 and RCP8.5) showed an upward shift for both the AGs and the AG ant and epiphyte species (mean values), with maximum increases in the RCP8.5 of +52% (83 m, ACCESS), +36% (80 m, MIROC5) and +34% (90 m, ACCESS), respectively, relative to the current time (Fig. 4). Individually, the greatest upward shifts among the AG ant and epiphyte species were for the AG ant *Crematogaster longispina* with +88% (327 m, MIROC5-RCP8.5) and the AG epiphyte *Epiphyllum phyllanthus* with +163% (690 m, ACCESS-RCP8.5; Table S8). Only the AG epiphytes of the genus *Coryanthes* showed a downward shift from -11 to -48% (-24 to -79 m) in all of the GCMs and RCPs (Table S8).

Discussion

Ecological niche and elevational distribution

In this study, we analyze for the first time the climatic and biotic factors that determine the current and future distribution of a specialized ant-plant mutualism. Modeling the AGs as an entity can be considered a baseline to better understand the geographic distribution of this mutualism in relation to environmental factors since the AG ant and epiphyte species that constitute them are not uniformly distributed. Also, we evaluate the hypothesis that suggests that species that depend on specialized mutualistic systems could disappear if their mutualistic partners are extinct by climate change (Dunn et al. 2009). Our findings highlight that most of the associated species in AGs will be negatively affected by climate change, but not AGs when they are considered as an entity, which can be explained by the differences in their responses to environmental factors and the non-specific ant-epiphyte associations in large geographical scale. This could be

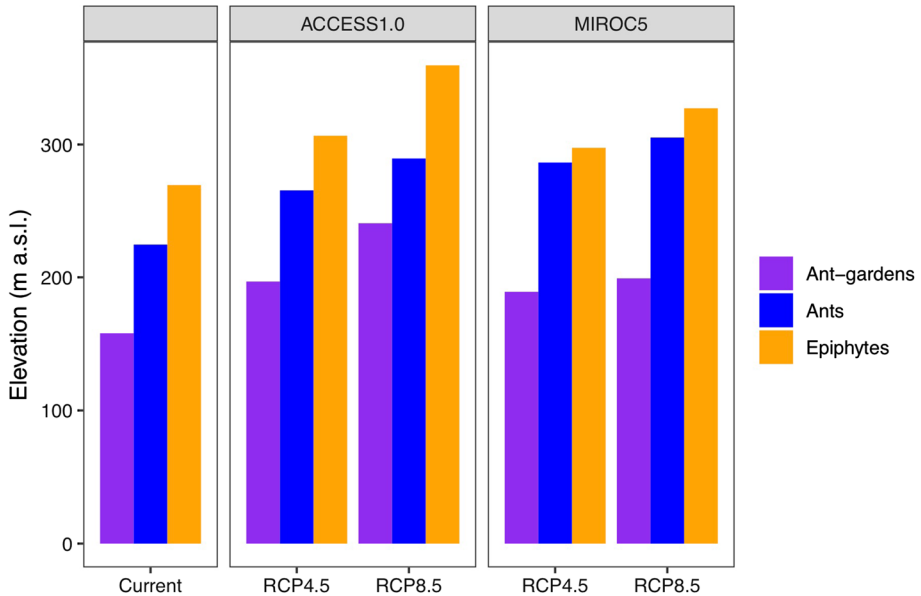


Fig. 4 Current mean elevation and potential changes in the altitudinal distribution of the Neotropical Ant-gardens (AGs) and AG ant and epiphyte species (mean values) by the year 2070 under two global circulation models (ACCESS 1.0 and MIROC5) of climate change and considering two representative concentration pathways of carbon dioxide (low, RCP4.5 and high, RCP8.5). Values per species are presented in Table S8

similar to generalist mutualisms observed between epiphytic ferns and their ant inhabitants along a disturbance gradient of a rainforest, where the benefits of mutualism are maintained despite species turnover (Fayle et al. 2015).

Even when we take into account all the available ecological knowledge about AGs and AG ant and epiphyte species, the interpretation of some of our results should be taken with caution, since we obtained a low number of occurrences for some species and do not consider their dispersal capacities (Barve et al. 2011). In general, ants may not have dispersal restrictions because winged reproductive individuals can fly up to kilometers to establish new colonies (Helms 2018; Bishop et al. 2019), which is similar for most of the wind-dispersed seeds of epiphytes (including AG epiphytes, Zotz and Bader 2009; Hsu et al. 2012) and to a lesser extent for epiphyte species dispersed by vertebrates and/or ants (e.g., AG epiphytes; Orivel and Leroy 2011). Therefore, both canopy ants and epiphytes (including AG ants and epiphytes) may be limited by establishment sites (host trees) rather than their dispersal capacity (Diamond et al. 2012; Hsu et al. 2012).

Our results support the idea of complexity of the AGs (Orivel and Leroy 2011), since the occurrence of AGs as an entity is related to a climatic and altitudinal profile that was not shared by all of the AG ant and epiphyte species. The AGs presence is favored by high values (annual means) of precipitation (> 2400 mm) and temperature (> 25 °C), and low elevation (< 112 m a.s.l.), indicating that this mutualism follows the climatic and altitudinal profile of the lowland tropical rainforest (Burnham and Johnson 2004; Jaramillo and Cárdenas 2013), as has been suggested in ecological studies (e.g.,

Davidson 1988). On the other hand, the relatively low fluctuation of the temperature (mean diurnal range, ≥ 15 °C) was an important predictor for most of the AG ant and epiphyte species, and could be related to the narrow thermal ranges that characterize tropical species (Colwell et al. 2008; Diamond et al. 2012). The ENM of insect-host plant interactions has suggested that the distribution of host plants (biotic models) are a good or even better predictor for insects than climatic variables (abiotic models; Araújo and Luoto 2007; Cunha et al. 2018). Our findings are partially in line with previous studies, since none of the AG biotic models showed better performance than the AG abiotic model, only the AG biotic-epiphytes model was similar to the AG abiotic model. This could be due to the multispecies nature of the AGs (Orivel and Leroy 2011), since although AG ant and epiphyte species must co-occur to form the AGs, both their niches (geographic and environmental spaces) and altitude curves tended to differ. Considering the AG biotic models, the occurrences of the AG epiphytes *Coryanthes picturata*, *Peperomia macrostachya*, *Epidendrum flexuosum*, and the AG ant *Azteca gnava* suggests the highest probability of occurrence of the Neotropical AGs, probably because they are locally abundant (Catling 1995; Davidson 1988; Morales-Linares et al. 2016) and widely distributed (except *Coryanthes picturata*).

Therefore, although more than half of the AG ant and epiphyte species have similar climatic requirements, their distribution in the Neotropics is segregated, in terms of both latitude and elevation, which could in principle be due to historic processes of dispersion and radiation (e.g., Givnish et al. 2011; Pérez-Escobar et al. 2017), partly explained by orographic events such as the Andean uplift (Luebert and Weigend 2014). Thus, considering the latitudinal distribution of the most representative AG ant and epiphyte species, the AGs can be classified into two sections: Mexico-Central America (*Azteca gnava* and *Coryanthes picturata*) and South America (*Camponotus femoratus* or *Odontomachus mayi*, and *Aechmea mertensii* or *Codonanthe calcarata*). However, the AG ant *Azteca gnava* and several AG epiphytes (e.g., *Epidendrum flexuosum*) show a Neotropical distribution, but little is known about their co-occurrences and interactions throughout their entire distribution range (Morales-Linares, unpublished data). On the other hand, if the altitudinal curves are considered, the AGs can be classified into three different elevations: low (e.g., *Neoponera goeldii* and *Neoregelia eleutheropetala*), middle (e.g., *Azteca gnava* and *Codonanthe uleana*) and high (e.g., *Crematogaster longispina* and *Epiphyllum phyllanthus*).

A phylogenetic study in Paleotropical AGs has suggested that expansion of the AG epiphytes selected by the AG ants promotes the specialization of new AG epiphyte lineages (Chomicki et al. 2017). In this context, our results show non-equivalent niches between the AG ants of Mexico-Central America and South America, while the AG epiphytes of the genera *Aechmea*, *Codonanthe* and *Coryanthes* tended to show equivalent niches in the environmental space, but not in the geographic space. These AG epiphytes even tend to present a preferential association with some of the AG ants at the local scale, mediated by the creation of particular microhabitats (Leroy et al. 2017) and/or preferential myrmecochory (Orivel and Dejean 1999). For this reason, these patterns of niche/distribution and ensembles of species show that a few AG ants can interact with various AG epiphytes, but also suggest that congeneric AG epiphytes have segregated themselves among the AG ants, probably as a result of particular co-evolutionary processes (specialization; Chomicki et al. 2017).

The niches (geographic and/or environmental space) and altitudinal curves coincide with some of the preferential associations among the AG ant and epiphyte species mediated by myrmecochory, such as *Neoponera goeldii* and *Aechmea mertensii* in French Guiana (Orivel and Dejean 1999), *Crematogaster longispina* and *Codonanthe crassifolia* in Costa

Rica (Kleinfeldt 1986) and *Azteca gnava* and *Coryanthes picturata* in Mexico (Morales-Linares et al. 2018). In contrast, although *Camponotus femoratus* and *Peperomia macros-tachya* maintain a close co-occurrence in AGs of Peru (Davidson 1988; Youngsteadt et al. 2008), their niches and altitudinal curves are dissimilar, probably due to the fact that AG epiphyte showed the greatest area of potential distribution (7.2 million km²) and higher occurrence at intermediate altitudes (median = 207 m a.s.l), representing an area 1.7 times greater and 2.7 times higher the altitude of the AG ant. In general, AGs have a potential distribution larger than that of their AG ants, but smaller than most of the AG epiphytes, suggesting that the latter have greater plasticity (e.g., Leroy et al. 2017). This is because several AG epiphytes are autogamous (Madison 1979; Davidson 1988), and some of them do not show germination restrictions (Kleinfeldt 1978; Leroy et al. 2017), which could also explain why some individuals have been observed outside AGs in some localities (e.g., Morales-Linares et al. 2016). However, plant performance of the AG epiphytes is considerably greater when growing in the AGs (Leroy et al. 2017), so regardless of climatically suitable areas, the AGs represent the niche space in which their occurrence is maximized.

Changes in geographic and altitudinal distribution due to climate change

Tropical ants and vascular epiphytes are guilds considered vulnerable to climate change (Zotz and Bader 2009; Diamond et al. 2012), however, analysis of their geographic and altitudinal distribution under scenarios of climate change is scarce (e.g., Hsu et al. 2012; Bishop et al. 2019). Our study reveals, for the first time, the potential responses to climate change of one of the most complex ant-plant mutualisms. First, we determined that the current suitable area for the Neotropical AGs has a discontinuous distribution from Mexico to the Atlantic forest in Brazil (≈ 4.84 million km²). Second, in the face of climate change, the predictions of the models suggest that the suitable area for the AGs (high temperatures and precipitation) will not diminish but in fact increase, with the greatest expansion predicted from the Amazon basin to the Atlantic forest under the pessimistic climate change scenario (2070-RCP8.5), which coincides with the predicted increases of temperature and precipitation for southeastern South America (Magrin et al. 2014).

Among AG ants, only *Camponotus femoratus* and *Neoponera goeldii* showed an expansion in future suitable area, probably due to the fact that its distribution was positively influenced by temperature. In contrast, the reduced precipitation from southeastern Mexico to northern South America (Magrin et al. 2014) could explain the losses for the other AG ants. It has been estimated that, by the year 2100, there will be a reduction of ca. 50% in the suitable areas for vascular epiphytes in Taiwan (Hsu et al. 2012), which is similar to the loss estimated for some of the AG epiphytes (except *Epiphyllum phyllanthus*, - 90%). This is probably because the mean diurnal range is an important predictor for AG epiphytes, and will show more variation in the future (Magrin et al. 2014). However, the AG bromeliads tended to show increases in suitable area under climate change, which could eventually be favored by their tolerance to high temperatures (Müller et al. 2018) and light conditions in the habitats (Leroy et al. 2017) compared to other non-AG bromeliad species.

Therefore, all AG ants and epiphytes will conserve at least a part of suitable area under climate change; however, the range expansion of the AGs in the future could be represented by a lower diversity of associated species since almost only the AG ant *Camponotus femoratus* and the AG bromeliad *Aechmea longifolia* showed a similar pattern to that of the AGs concerning the increase in the suitable area. In general, these results suggest adverse effects on the conservation of the Neotropical AGs, since this mutualistic system as an

entity would show a taxonomic and functional simplification (i.e., biotic homogenization; Olden and Rooney 2006). However, it has been suggested that mutualistic species that are vulnerable to climate change could survive by maintaining their association with stronger partners (Afkhani et al. 2014; Filazzola et al. 2018) and/or by incorporating novel partners (Kiers et al. 2010). In this sense, some of the natural mechanisms that would promote the conservation of the AGs in the future are the occurrence of species that facilitate the establishment of the other species (Catling 1995; Morales-Linares, unpublished data), and even the eventual association of novel species to mutualism (Chomicki et al. 2017). On the other hand, the AG ants show a preference for habitat and host trees; thus, the negative effects of climate change for the AGs must be counteracted by the conservation of forest cover, including mature rainforests (e.g., *Camponotus femoratus*) and agroecosystems (e.g., *Azteca gnava*), which harbor different AG host trees that offer food resources for the AG ants, either directly (e.g., extrafloral nectar) and/or indirectly through other associated species (homopterans; Davidson 1988; Kaufmann and Maschwitz 2006; Orivel and Leroy 2011; Morales-Linares et al. 2016).

An upward shift of species from lowland tropical rainforest is expected in the future, due mainly to the increase in temperatures and deforestation (Colwell et al. 2008; Guo et al. 2018). In general, upward shifts of the AGs and AG ant and epiphyte species was manifested in two patterns: an increase in suitable area (e.g., AGs) or because the remaining suitable areas were found at higher elevations (AG epiphytes). However, the maximum shift upward of the AGs was 240 m (+ 83 m) relative to the current time, for which reason they remain within the range of the lowland tropical rainforest (< 700 m a.s.l.; Burnham and Johnson, 2004). Most AG ant and epiphyte species were also maintained at < 700 m a.s.l. (except *Epiphyllum phyllanthus* and *Anthurium gracile*). However, the maximum upward shift (mean values) of the AG ants was 1.7 times lower than the 145 m (optimistic scenario) or 13 times lower than the 1,050 m (pessimistic scenario) estimated for montane ant assemblages located in subtropical zones of Argentina, Australia, and South Africa (Bishop et al. 2019), while for AG epiphytes it was 4.5 times lower than the \approx 400 m reported for vascular epiphytes in the subtropical island of Taiwan (Hsu et al. 2012). In contrast, the AG orchids of the genus *Coryanthes* showed downward elevation shifts, probably due to their restricted and/or patchy geographic distribution in the Neotropics. However, unlike other AG epiphytes, the latitudinal and altitudinal distribution of these orchids could also be influenced by their pollinators (Pérez-Escobar et al. 2017). Therefore, our results suggest that the AGs and AG ant and epiphyte species will not show a significant upward shift under climate change.

The canopy is a stressful environment for the epiphytes (greater exposure to wind and limited access to water and nutrients), but the association with ants (i.e., AGs) and termites (Flores-Palacios and Ortiz-Pulido 2005) provides them with suitable substrates containing key resources (e.g., N, P, K; Blüthgen et al. 2001). In addition, a mutualistic species associated with several species (generalist) can expand its niche and increase its tolerance to different abiotic and biotic factors (Batstone et al. 2018), which has led to the evolution and specialization of the AGs (Chomicki et al. 2017). The main contribution and novelty of this study was to determine that the Neotropical AGs are restricted to low altitude areas with high temperatures and precipitation, but that the AG ant and epiphyte species are not individually coupled to this climatic and altitudinal profile. The AGs therefore do not represent the sum of the AG ant and epiphyte species, but can be considered an entity that maximizes the distribution and permanence in the future ("environmental micro-buffer") of the AG ant and epiphyte species, even under the most pessimistic scenario of climate change. However, habitat loss and land use change continue to be considered the main threats to

vascular epiphytes and ants (Zotz and Bader 2009; Sánchez-Bayo and Wyckhuys 2019) and, in the context of climate change, the loss of ecological interactions could be even more rapid than the loss of species (Valiente-Banuet et al. 2015). Therefore, although the suitable area for AGs may expand in the future, the functionality and associated diversity of this mutualism could be affected.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-021-02138-2>.

Acknowledgements We thank Michelle I. Ramos-Robles for assistance in the field and comments regarding the ecological niche modeling, and Miguel Vásquez Bolaños for identification of the AG ants of southeastern Mexico. The comments and criticism of K. MacMillan and three anonymous reviewers improved the manuscript.

Author contributions JML conceived and designed the research. JML analyzed the data. JML, VHHT, AMCL and AFP wrote the manuscript.

Funding The first author received the support of the Programa para el Desarrollo Profesional Docente en Educación Superior (PRODEP Grant 511-6/17-8702) and the fieldwork was funded by the Cuerpo Académico Biología del Dosel.

Data availability Occurrence records of the Ant-gardens (AGs) and the AG ant and epiphyte species are available at: <https://doi.org/10.6084/m9.figshare.13627349.v1>.

Code availability The R codes are available from the corresponding author on request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Informed consent We agree with the potential publication.

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