Exploring palm–insect interactions across geographical and environmental gradients

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To understand the driving factors behind the specificity amongst plant visitors and potential pollinators, we identified *Mystrops* spp. from eight palm species representative of each of the major clades of *Wettinia* (Arecaceae). We collected 31 palm inflorescences of at least three individuals per species from three different regions of across the distribution of the palms (Colombian Andes, Amazon and Choco). Sixty thousand visiting insect individuals were collected, 53% of which correspond to 17 different *Mystrops* morphospecies. The average number of pollinator species was highest in *W. fascicularis* (five species) and lowest in *W. drudei* (one species). We found high specificity between the *Mystrops* assemblages and *Wettinia* spp. and, in general terms, one primary visitor per *Wettinia* sp. These results confirm previous reports of a strong mutualistic relationship between Arecaceae and *Mystrops*. Using inference of environmental niches, we found *Wettinia* spp. to be segregated along their distribution on climatic gradients. Finally, we found that climate has an important role in shaping pollinator species turnover, even after controlling for spatial distance, and that phylogenetic relatedness also has a positive effect on turnover of *Mystrops* spp. © 2016 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2016

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INTRODUCTION

Mutualistic relationships, such as plant-pollinator interactions, have been suggested to drive ecological divergence (Ehrlich & Raven, 1964; Thompson & Cunningham, 2002; Weiblen & Bush, 2002; Thompson, 2005; Whittall & Hodges, 2007). Therefore, it is likely that plant reproductive isolation is closely related to pollination biology and differences in pollinator distribution and plant–pollinator specificity may contribute to population differentiation and coevolution and even drive speciation. Insects are the predominant pollinators across flowering plants and therefore plant–insect interaction is expected to be an important evolutionary factor in most clades across the angiosperm phylogeny (Farrell, Mitter & Futuyma, 1992). Classic examples of plant–insect coevolution are found throughout the plant tree of life and include yucca moths and *Yucca* L. (e.g. Pellmyr, 2003), fig wasps and *Ficus* L. (e.g. Wiebes, 1979) and ants and *Acacia* Mill. (Janzen, 1966). These studies have shown that high pollinator specificity results in high species turnover between host plants (here defined as visited or pollinated plant individuals), although plant–insect coevolution is diffuse when pollinator species use several host plants.

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Further, insect species turnover between plant hosts can be driven by various factors, including environmental and spatial distance, without the influence of host identity (Carstensen *et al.*, 2014). Therefore, the roles of extrinsic and intrinsic mechanisms shaping plant–insect relationship are unclear.

Analysis of species turnover across space (i.e. beta diversity) has been important to disentangling the role of different mechanisms in local species assemblages such as species interactions, environmental heterogeneity and dispersal limitation (Novotny *et al.*, 2007; Bell *et al.*, 2013; Carstensen *et al.*, 2014). A primary hypothesis in plant–insect systems is that species interactions are the strongest driver of insect turnover. This hypothesis suggests that mutualism is strong and species co-vary across their geographical ranges (Thompson, 1999). It also predicts that insect species turnover is low throughout the host plant species range, even across broad environmental or geographical gradients (Godsoe *et al.*, 2009). In contrast, a second hypothesis posits that environmental heterogeneity may increase species turnover within the host plant range. Species distributions are limited by environment (e.g. physiological tolerances), particularly for insects as they are highly affected by climatic conditions (Archibald, Greenwood & Mathewes, 2013). This hypothesis predicts high species turnover across climatic gradients (e.g. along mountain sides). Thirdly, the dispersal limitation hypothesis suggests that dispersal capacity influences insect species turnover, resulting in spatially autocorrelated species composition across landscapes (Novotny *et al.*, 2007). If environmental heterogeneity or dispersal limitation explains insect species variation, the hypothesis of coevolution would be rejected based on plant–insect networks. However, appropriate data to evaluate these hypotheses are limited.

Palms are a well studied plant group that display a wide variety of pollination syndromes and, although they were long thought to be wind pollinated (Faegri & van der Pijl, 1979; Anderson, Overal & Henderson, 1988), they have been shown to maintain strong interactions with insects (Porter-Morgan, 2007; Barfod, Hagen & Borchsenius, 2011). For example, beetles are reported to pollinate 29% of all palms (Barfod *et al.*, 2011). Sap beetles in the genus *Mystrops* are particularly associated with palm flowers, are highly abundant, have been reported to pollinate a large proportion of palm genera and potentially generate coevolutionary relationships with some of these species (e.g. Henderson, 1986; Barfod, Henderson & Balslev, 1987; Anderson *et al.*, 1988; Silberbauer-Gottsberger *et al.*, 2001; Padilha, Couturier & Beserra, 2003; Kirejtshuk & Couturier, 2009, 2010; Barfod *et al.*, 2011; Balhara *et al.*, 2013;

Nuñez, 2014). Visitor insects on flowers have been studied in some palm species (reviewed in Barfod *et al.*, 2011), providing an excellent system to analyse insect species turnover at large geographical scales.

In this study, we sampled *Mystrops* assemblages from eight species of *Wettinia* Poepp. ex. Endl. to determine the degree of plant–insect interaction. Specifically, we aimed to explore the factors that drive plant–insect interaction in the *Wettinia–Mystrops* system. Here, we used three working hypotheses: (1) Specificity of plant–insect interaction is strong and it is maintained across the host plant range, predicting insect turnover to be low within and high between host species. In addition, host species filter pollinators as a mechanism of reproductive isolation, resulting in large pollinator assemblage differences between closely related plant species. Thus, insect species turnover increases with phylogenetic distance between host plants (Kay & Sargent, 2009). (2) Environmental heterogeneity drives insect species turnover. Specifically, climatic tolerance limits species distribution and composition (e.g. Archibald *et al.*, 2013). Thus, species dissimilarity is predicted to increase with climatic differences, irrespective of host identity. (3) Dispersal limitation is an important driver of insect species turnover, assuming low dispersal abilities based on their small body size and short flight distances (Kirejtshuk & Couturier, 2010). Insect species dissimilarity is predicted to increase with spatial distance. To test among these hypotheses, we correlated insect species dissimilarity between host species and across spatial and climatic distance. We also examined phylogenetic distance between host species to explore the effect of relatedness in plant–insect networks.

METHODS

STUDY SYSTEM: *WETTINIA* SPECIES AND *MYSTROPS* SPECIES

Wettinia comprises 21 species distributed from central Panama and Venezuela south to Bolivia (Henderson, Galeano & Bernal, 1995). Most of the species are found in Colombia and Ecuador and the Choco region is especially diverse with ten endemic species. *Wettinia* spp. are widely represented in the Andes, in contrast with lowland Amazonia, where only three species are found (Henderson *et al.*, 1995; Galeano & Bernal, 2010). We sampled eight species representing sister lineages from each of the major clades of *Wettinia* from a robust molecular phylogenetic tree of tribe Iriarteeae (Fig. 1; Bacon *et al.*, 2016, this issue; for voucher information, see that paper). Selected sister taxa were chosen based on accessibility of field sites: three endemics from the Choco
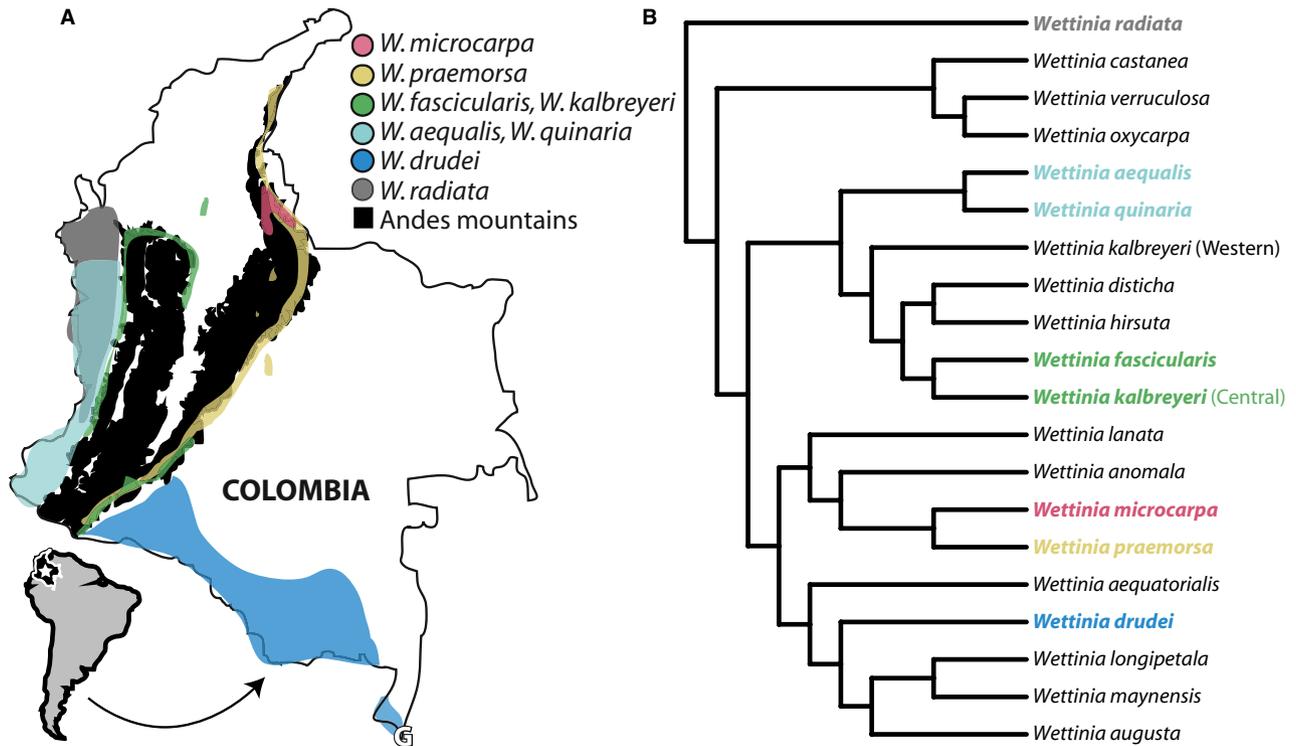
Figure 1. Geographical distribution and phylogenetic position of *Wettinia* spp. A. Distribution of eight study palm species along the Andes of Colombia. B. Phylogenetic tree for *Wettinia* (Bacon *et al.*, 2016) showing sister species pairs from this study.

region, *Wettinia aequalis* (O.F.Cook & Doyle) R.Bernal, *W. quinaria* (O.F.Cook & Doyle) Burret and *W. radiata* (O.F.Cook & Doyle) R.Bernal; *W. fascicularis* (Burret) H.E.Moore & J.Dransf. and *W. kalbreyeri* (Burret) R.Bernal from the Central Cordillera of Colombia and Ecuador; *W. microcarpa* (Burret) R.Bernal and *W. praemorsa* (Willd.) Wess.Boer from the Eastern Cordillera of Colombia; and the Amazonian species *W. drudei* (O.F.Cook & Doyle) A.J.Hend. (Supporting Information, Table S1).

We collected insect visitors from 31 staminate inflorescences from at least three individuals of each of the eight palm species. Whole inflorescence were collected and placed in a plastic bag containing 70% ethanol to preserve insects, which were subsequently sorted and counted and morphological and anatomical characters were compared between all samples. We used dorsal pubescence, body coloration and pronotum shape diagnostic characters to define morphospecies, as widely used in this insect group (Kirejtshuk & Couturier, 2010).

DETERMINANTS OF INSECT ASSEMBLAGES

We assessed insect species turnover in relation to spatial, climatic and phylogenetic distance between palm species. We applied three metrics of species turnover that measure different assemblage properties. The Bray-Curtis metric is focused on shared species and includes the variation present in insect abundance. We also used Manhattan and Euclidean distances (log-transformed), which incorporate species absence and therefore facilitate comparison with results from Bray-Curtis. We used the 'cophenetic' function to estimate divergence between palm species based on the most recent *Wettinia* molecular phylogenetic tree (Bacon *et al.*, 2016) and the 'pointDistance' function to measure the spatial distance between points on a sphere based on geographical coordinates, both in the R package raster (Hijmans & Etten, 2012). Climatic data were obtained for each locality from the Worldclim database (Hijmans *et al.*, 2005). We found high correlation between bioclimatic variables (Pearson $R > 0.7$), so we reduced the dataset to include only minimum annual temperature and precipitation of the driest quarter, considered the major limiting factors of insect distribution (Deutsch *et al.*, 2008). Finally, we estimated the Euclidean distance of each these variables between localities.

We regressed insect turnover as a response variable with climate, spatial distance and phylogenetic

Table 1. *Mystrops* morphospecies diversity metrics on *Wettinia* species

Host species	Elevation min	Elevation max	Morphospecies richness (number of shared species)	Total abundance	Abundance (%)	*Mystrops* abundance	Main visitor (%)
Wettinia microcarpa	1800	2300	5 (3)	2819 ± 1427	39.95	1126 ± 464	29.49
Wettinia fascicularis	1200	2000	5 (3)	2426 ± 1122	56.55	1372 ± 570	40.12
Wettinia kalbreyeri	400	2200	4 (2)	5426 ± 3752	41.67	2259 ± 727	77.74
Wettinia radiata	0	1000	3 (2)	2120 ± 340	67.08	1422 ± 231	73.89
Wettinia praemorsa	400	2400	3 (2)	1320 ± 534	67.73	894 ± 500	62.34
Wettinia aequalis	0	800	3 (1)	1800 ± 650	52.78	950 ± 274	85.07
Wettinia quinaria	0	1100	2 (1)	4123 ± 2011	57.36	2365 ± 1148	96.29
Wettinia drudei	75	700	1 (1)	515 ± 211	41.94	216 ± 87	100

distance as independent variables using a multiple regression matrix (Lichstein, 2007). We ran this analysis for each combination of variables to estimate the individual effect on the total explained variance. These analyses were run using the 'MRM' function implemented in R package ecodist (Goslee & Urban, 2007). We chose this method to analyse beta diversity over others because our sampling is geographically biased and the behaviour of other methods under these conditions is unclear (Legendre, Borcard & Peres-Neto, 2005). Finally, we assessed the degree of pollinator specificity using an analysis of similarity (ANOSIM; Clarke, 1993) to compare insect species assemblages within and between palm species. ANOSIM estimates the proportion of differences within and between categories, in our case host palm species. We used the 'plotweb' function implemented in the R package bipartite (Dormann, Gruber & Fründ, 2008) to visualize the degree of specificity between insects and palms.

PALM SPECIES DISTRIBUTION MODELING

Insect species dissimilarity may be related to climatic differences because each *Wettinia* sp. occupies a different climatic profile. Thus, the effect of climate and host identity could be mixed. To disentangle these effects, we obtained occurrence data for the eight *Wettinia* spp. derived from the Missouri Botanical Garden (Tropicos), Instituto Sinchi (Colombian Amazon herbarium), Universidad de Antioquia herbarium, Universidad Nacional de Colombia herbarium and the Flora de Antioquia databases. All georeferences were carefully reviewed to avoid geographical biases. We used the MaxEnt algorithm (Phillips, Dudik & Schapire, 2004) in the R package dismo version 0.9–3 (Hijmans *et al.*, 2011) to model palm species distributions. Because our purpose was compare amongst palm species, rather than understand their relationship with bioclimatic variables, we included all 19 climatic layers from the

WorldClim database (Hijmans *et al.*, 2005). We used 10 000 background points from which 90% were randomly selected to characterize the surrounding environment of each palm species and 75% of the randomly sampled points from the presence data used as input for MaxEnt. The remaining background and presence data points were used to evaluate the fit of the models.

RESULTS

We found 21 insect species belonging to the genus *Mystrops* associated with the eight *Wettinia* spp. ($N = 31$ inflorescences). Of all insects collected in each palm inflorescence, 40–68% belong to *Mystrops*, the most abundant visitor. Lowland palm species tend to host lower *Mystrops* abundance and species richness than highland palms (Table 1). The sister species *W. fascicularis* and *W. kalbreyeri* share their principal visitor species. Choco *Wettinia* spp. share one *Mystrops* sp., although the morphospecies was present in low abundances. Despite being sampled in different cordilleras, *W. kalbreyeri* and *W. microcarpa* share their principal visitors. In addition, *W. microcarpa* shares one pollinator species with *W. praemorsa*, although it was rarely collected and had low abundance. The Amazonian species, *W. drudei*, does not share any pollinator with other of the host species analysed (Fig. 2). We found a general pattern of high differentiation in the pollinator species assemblage between species based on ANOSIM results (R: 0.98, $P < 0.001$; Fig. 2).

Beta diversity metrics affect the interpretation of our results. Bray–Curtis and Euclidean log-transformed based analyses show similar results and large proportions of explained variance. In contrast, Manhattan distance is poorly related to predictor variables (Table 2). We interpret our results based on log-transformed Euclidian metric because

Figure 2. Plot of the interaction web between *Wettinia* and *Mystrops* visitor insect species from the ANOSIM analysis. Overall, high specificity is found between visiting insect species and particular plant species, although *W. praemorsa*, *W. microcarpa*, *W. kalbreyeri* and *W. radiata* share *Mystrops* visitors with other congeners, as shown by the crossing green lines and darker grey boxes.
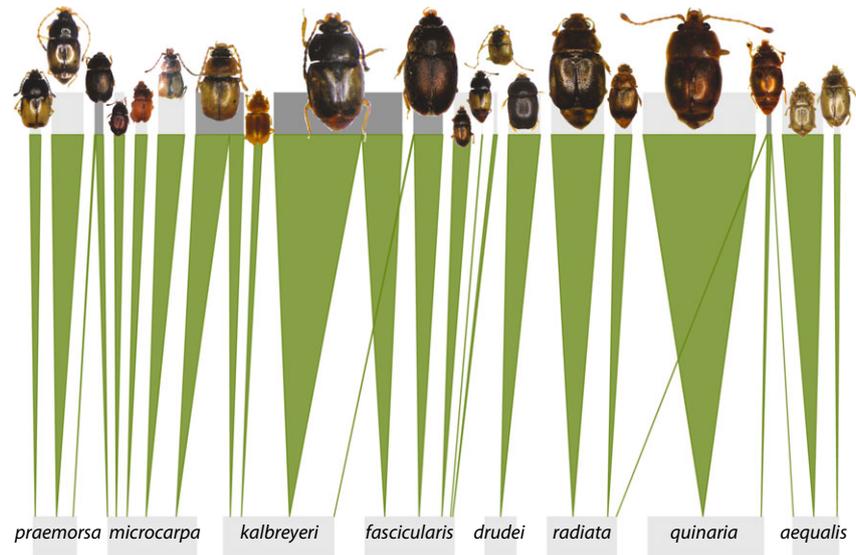
pollination interactions are influenced by pollinator abundance. We found that phylogenetic distance between palms is positively related with turnover of *Mystrops* spp. and explains the largest proportion of variance (Table 2), implying that closely related species share a larger proportion of pollinators (Fig. 2). In addition, climatic divergence between sites in conjunction with phylogenetic relatedness between hosts explains 57% of the variance. Finally, our results show that spatial distance has a minor role driving species turnover (Table 2; Fig. 2).

The environmental niche models for *Wettinia* highlight the variation in species distributions, which could be the result of adaptations to different climatic regimes, producing different distributional patterns. The spatial distribution models inferred using MaxEnt show some species are widespread (*W. drudei* and *W. praemorsa*), some are restricted to high elevations in the Andes (1500–2500 m; *W. fascicularis* and *W. kalbreyeri*) and others that are restricted to the lowland regions of Choco (*W. aequalis*, *W. quinaria* and *W. radiata*; Fig. 3). Some palm species have overlapping ranges, and thus they could share pollinator species where they occur in sympatry, as is the case for the species in the lowlands in Choco (sharing one *Mystrops* sp.) and for two palm species distributed along the Andes (sharing two *Mystrops* spp.).

DISCUSSION

Taken together, our results indicate that *Mystrops* spp. are common visitors to *Wettinia* spp. and probably play a strong role in pollination biology. Furthermore, we found low compositional similarities

between host palm insect communities and that insect turnover is affected by climate rather than spatial distance. Similar patterns have been reported in other pollination studies (Henderson, 1986; Barfod *et al.*, 1987; Anderson *et al.*, 1988; Silberbauer-Gottsberger *et al.*, 2003; Padilha, *et al.*, 2003; Nuñez, Bernal & Knudsen, 2005). For example, the oil palm *Elaeis guineensis* Jacq. is highly dependent on a single insect species and the pollinator assemblage of

Table 2. Multiple regression matrix using three methods and their respective statistical support values

MODEL A vegdist(samp)	Method = 'euclidean'	R^2	P
Geog	−0.0008	0.0534	0.01
Climate	1.2788	0.5271	0.01
Phy	0.1393	0.4732	0.01
Total		0.6749	0.01
MODEL B vegdist(samp)	Method = 'manhattan'	R^2	P
Geog	−0.9619	0.0223	0.07
Climate	255.2996	0.1872	0.01
Phy	37.7329	0.1674	0.01
Total		0.3737	0.01
MODEL C vegdist(samp)	Method = 'bray'	R^2	P
Geog	0.0001	0.2571	0.01
Climate	0.0606	0.4652	0.01
Phy2	0.0078	0.5344	0.01
Total		0.7062	0.01

Attalea phalerata Mart. ex Spreng. is dominated by *Mystrops mexicana*, even in individuals separated by 600 km (Barfod *et al.*, 1987).

Our data show that climatic differences and host identity together influence insect species turnover. Also, we found that spatial distance is a weak predictor of species turnover, rejecting the hypothesis of dispersal limitation as a possible driver of turnover of *Mystrops* spp. (Fig. 2, Table 2; e.g. Novotny *et al.*, 2007). A lack of spatial signal may be due to the scale of measurement, although *Mystrops* spp. are shared between individuals located in different mountain ranges from Colombia, suggesting that strong geographical barriers have a weak effect on *Mystrops* dispersion. Therefore, insect presence is limited by palm ranges, which suggests that insect composition is strongly affected by host palm presence (Godsoe *et al.*, 2009). Moreover, we found that climate has an important role in shaping insect species turnover, even after controlling for spatial distance. In this way, species turnover is probably related to the climatic affinities of host species (Archibald *et al.*, 2013), but it is unclear whether this influence is over insect species, palm species or both. *Wettinia* spp. are distributed across different climatic conditions, as shown in the distribution models (Fig. 4). Further, palm flowers control the temperature and microclimate conditions that provide refuge for insect species (e.g. Nuñez, 2014). Thus, the effects of climate on insect species turnover could be indirect and may be related to palm distribution across climatic space. Taken together, we suggest that host identity and species interaction are the strongest drivers of insect turnover although explicit, fine-scale hypotheses and further experiments are needed.

Despite the role of climate, insect assemblages are largely divergent between palm species. However, closely related species share more species, contrary to expectations related to pollinator divergence increasing reproductive isolation (Kay & Sargent, 2009). In this way, major *Wettinia* clades demonstrate divergence in pollinators, implying clear reproductive isolation between them and possibilities for hybridization between closely related species. Accordingly, phylogenetic reconstruction of *Wettinia* relationships showed evidence of hybridization between closely related species, specifically in the two distinct clades of *W. kalbreyeri* resolved in Bacon *et al.* (2016: Fig. 1). This leads to the question: can pollinators
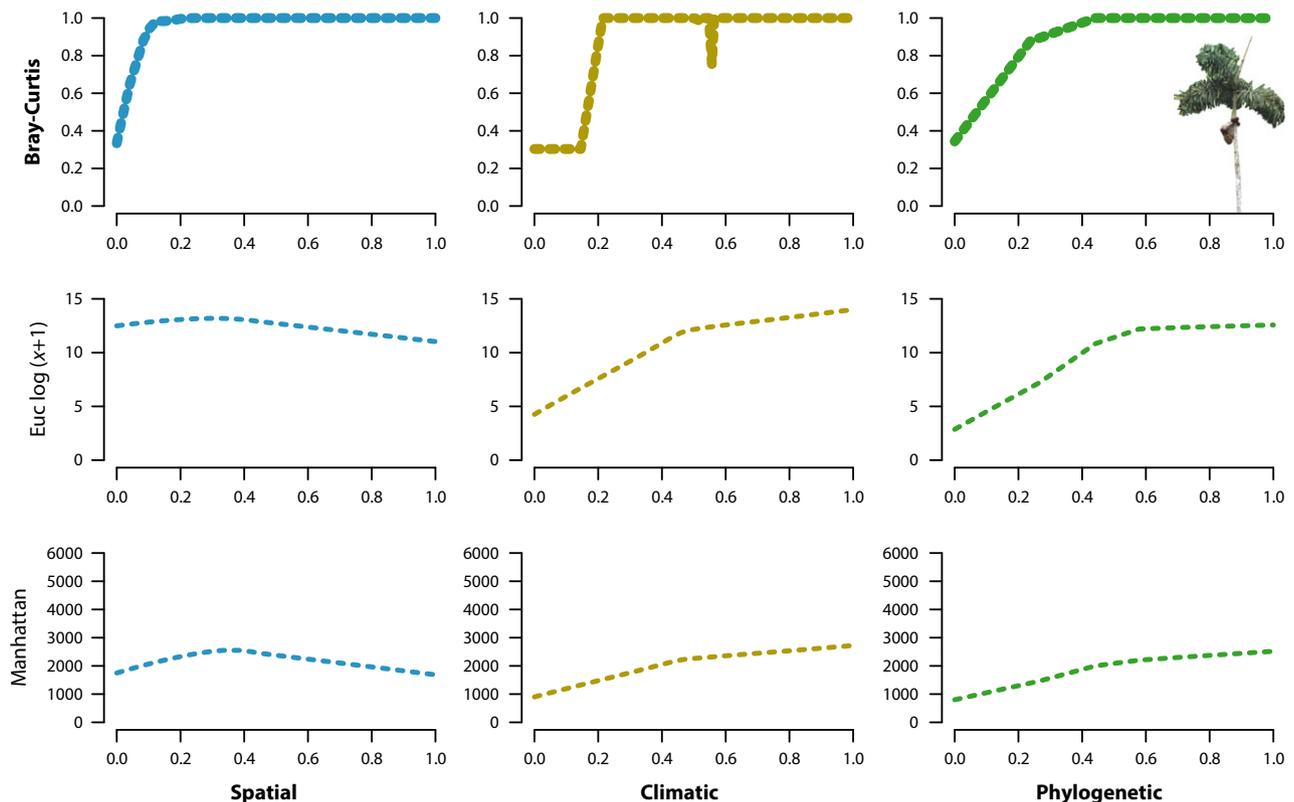

Figure 3. Plot of beta diversity of *Mystrops* palm-visitor insect as a function of spatial, climate and phylogenetic distance using three different statistical metrics, of which the Bray-Curtis was the most supported from our data.
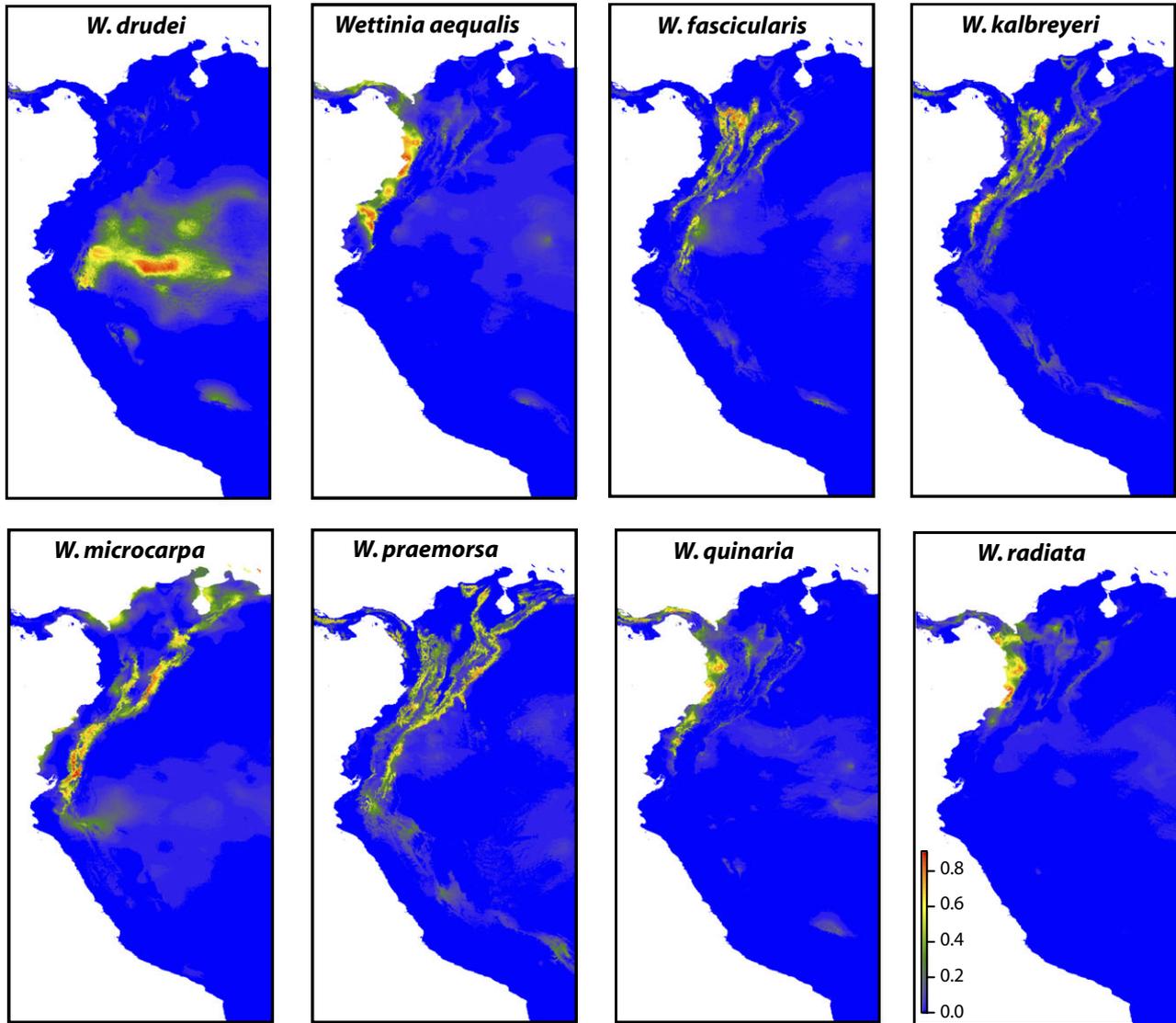
Figure 4. Ecological niche models for the studied *Wettinia* spp. All niche models recovered a betamultiplier of 1 and all AUC scores were > 0.94. Probability of occurrence increases with the heat of the colour; cold blue and hot red hues represent low and high probability, respectively.

influence population isolation and potential diversification in palms? If species are co-distributed and maintain long-term interactions, co-evolutionary relationship may emerge (Thompson, 2005). Population reproductive isolation at large scales can also be an important mechanism of species diversification, but explicit tests of this hypothesis require well-resolved phylogenetic trees for both taxa (e.g. Ramírez *et al.*, 2011).

It is important to bear in mind that insect speciation rates must be higher than speciation rates in palms based on differences in generation time (i.e. affecting mutational rate; Kay & Sargent, 2009). With this, palm population isolation may have produced rapid insect speciation rates, resulting in species-specific relationships, in accordance with our observations (Fig. 2). Insect adaptability to specific phenology or phytochemical signals to each palm species could be determined by the effectiveness of coevolutionary relationships in this system. However, the physical signals, resource gains and physiological advantages for insects in *Wettinia* flowers are unknown and need further study (Bawa, 1990; Armbruster, 2014). We suggest future studies include broad geographical sampling and ecological, morphological and physiological traits to understand the mutualistic relationship in this system across geographical ranges as possible mechanism of palm

speciation. Also, these analyses provide evidence that plant–insect networks maybe affected indirectly by climate change (Hegland *et al.*, 2009).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Localities of collection points in this study in which staminate inflorescences were collected from at least three individuals of each host palm species.