The integration of alien plants in plant-hummingbird pollination networks across the Americas: the importance of species traits and insularity

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ABSTRACT

Aim To investigate the role of alien plants in mutualistic plant-hummingbird networks, assessing the importance of species traits, floral abundances and insularity on alien plant integration.

Location Mainland and insular Americas.

Methods We used species-level network indices to assess the role of alien plants in 21 quantitative plant-hummingbird networks where alien plants occur. We then evaluated whether plant traits, including previous adaptations to bird-pollination, and insularity predict these network indices. Additionally, for a subset of networks for which floral abundance data was available, we tested whether this relate to network indices. Finally, we tested the association between hummingbird traits and the probability of interaction with alien plants across the networks.

Results Within the 21 networks, we identified 32 alien plant species and 352 native plant species. On average, alien plant species attracted more hummingbird species (i.e. aliens had a higher degree) and had a higher proportion of interactions across their hummingbird visitors than native plants (i.e. aliens had a higher species strength). At the same time, an average alien plant was visited more exclusively by certain hummingbird species (i.e. had a higher level of complementary specialization). Large alien plants and those occurring on islands distributed more evenly their interactions, thereby acting as connectors. Other evaluated plant traits and floral abundance were unimportant predictors of species-level indices. Short-billed hummingbirds had higher probability of including alien plants in their interactions than long-billed species.
Main conclusions Alien plants appear strongly integrated once incorporated into plant-hummingbird networks, and thus may have a large influence on network dynamics.

Plant traits and floral abundance were generally poor predictors of how well alien species are integrated. Short-billed hummingbirds, often characterized as functionally generalized pollinators, facilitate the integration of alien plants. Our results show that plant-hummingbird networks are open for invasion.

Key-words

Abundance, exotic plants, generalization, invasion biology, network roles, ornithophily, specialization
Alien species may become invasive and are a major threat to biodiversity and ecosystem functioning, including key ecosystem services such as pollination (Colautti & MacIssac 2004, Gurevitch & Padilla 2004, Pyšek et al. 2004, Morales & Traveset 2009, Simberloff et al. 2013). The successful establishment of alien plant species might be contingent on the acquisition of mutualistic partners, e.g. pollinators, outside their native range (Richardson et al. 2000, Bufford & Daehler 2014, Traveset & Richardson 2014). Under such a scenario, alien plants may compete for pollinators and decrease the fitness of native plants, for instance by offering greater quantities of floral rewards and thereby decreasing the attractiveness of native flowers (Chittka & Schürkens 2001, Morales & Traveset 2009). Conversely, alien plants could also benefit native plants by increasing the overall availability of floral resources, thereby increasing pollinator abundance and activity on native plants (Bjerknes et al. 2007, Lopezaraiza-Mikel et al. 2007, Bartomeus et al. 2008). Thus, alien plants’ ability to establish, and their effect on the pollination of native plants, may depend on their floral traits and the community context (Bjerknes et al. 2007, Morales & Traveset 2009, Gibson et al. 2012, Simberloff et al. 2013).

In order to understand the potential impacts of alien species on ecosystems, it is therefore important to characterize the community-wide roles of these plants (Davis et al. 2011). One approach to doing this is to use ecological interaction network analyses to conduct community-wide studies identifying and describing the interactions between organisms. Several studies have used such an approach to investigate the role of alien plants on plant-pollinator communities (Memmott & Waser 2002, Olesen et al. 2002, Aizen et al. 2008, Vilà et al. 2009, Albrecht et al. 2014, Stouffer et al. 2014, Traveset &
Richardson 2014). However, most of these studies have considered either temperate systems, which predominantly consist of functionally generalized insect pollinators (e.g. Aizen et al. 2008, Bartomeus et al. 2008), or focus on generalized island communities where the impact of invasive species might be most severe (e.g. Olesen et al. 2002, Traveset et al. 2013, Traveset & Richardson 2014, but see Kaiser-Bunbury et al. 2011). As an interaction network's stability may be more sensitive to the integration of alien species in specialized than in generalized systems (Kaiser-Bunbury et al. 2011), studies on specialized systems and over large geographical scales can contribute to our understanding of the general effects of alien species.

One such potential model system is the interaction networks between plants and hummingbirds across the Americas, which range from relatively specialized to generalized networks, and include both mainland and insular environments (Stiles 1981, Dalsgaard et al. 2011, Martín González et al. 2015). Hummingbirds are the most functionally specialized group of nectar-feeding birds and the most important vertebrate pollinators in the Americas (Stiles 1981, Bawa 1990, Cronk & Ojeda 2008). As specific floral phenotypes are often associated with hummingbird pollination (Cronk & Ojeda 2008, Ferreira et al. 2016), it could be expected that alien plants lacking a shared evolutionary history with hummingbirds would not be readily incorporated as important species in those networks (Richardson et al. 2000; Aizen et al. 2008). Conversely, Old World plants with convergent adaptations to bird pollination, notably to sunbirds and honeyeaters in Africa and South-east Asia (Cronk & Ojeda 2008, Fleming & Muchhala 2008, Ollerton et al. 2012, Janeček et al. 2015), could be well-integrated in novel plant-hummingbird communities in the Americas – at least more than alien plant species not previously pollinated by birds (see Johnson & Raguso 2016 for examples between specialized flowers and long tongued hawkmoths).
Given the increasing concerns over the effects of alien species on ecosystems (Davis et al. 2011, Richardson & Ricciardi 2013, Simberloff et al. 2013), community-wide studies on the role of alien plants across large geographic gradients could provide new insights into their potential threats to biodiversity. Here, we characterize the role of alien plants in 21 quantitative plant-hummingbird networks distributed broadly across the Neotropics, including both mainland and island environments (Fig. 1). We asked three questions: 1) whether an average alien plant is topologically more important than a native species, i.e. whether alien plants have a disproportionate large effect on plant-hummingbird networks; 2) whether alien plant traits, such as pre-adaptation to bird pollination in combination to the geographical setting of the network, i.e., insularity, affect the integration of plants into networks; 3) whether hummingbirds with short-bills, often characterized as functionally more generalized, facilitate the integration of alien plant species into networks.

METHODS

Plant-hummingbird networks and alien plants classification

In order to investigate the role of alien plant species in pollination networks, we compiled plant-hummingbird networks in which exotic plant species could be confidently identified (Figure 1). For this, we used an established database on quantitative plant-hummingbird interaction networks (see Dalsgaard et al. 2011 and Martín González et al. 2015 for previous versions of the database, updated details in Table S1-S3). We only considered legitimate interactions here, in which a hummingbird was observed contacting the reproductive structures of the flowers and with potential for pollination. For each network, plants were classified as either native or alien - taking into account the locality of a given network and the plant distribution range according to
openly available databases, notably: Tropicos (http://www.tropicos.org/), GRIN Taxonomy for Plants for North America (http://www.ars-grin.gov/), Flora of the West Indies for the Caribbean (http://botany.si.edu/antilles/WestIndies/query.cfm), Brazilian Flora Checklist for networks from Brazil (http://floradobrasil.jbrj.gov.br/) and The Plant List (http://www.theplantlist.org/). Plant names used here followed The Plant List database. A total of 75 (19%) plant occurrences in the networks were not identified to species level, but to genus or family level only (Table S2); for these we adopted a conservative approach of only attributing "alien" status if the genus/family at the given locality was identified as alien in the databases. We note, however, that excluding these species did not affect the comparison between native and alien plants. Because the geographical origin of some plants is poorly known, the classification of these can be imprecise (Pyšek et al. 2004), and the use of a single general database has been argued for in order to standardize possible bias (Stouffer et al. 2014). However, our dataset is composed primarily of networks from the Neotropical region, which has relatively poor historical species records compared to North America and Europe (Pyšek et al. 2004). Since even for well recorded regions these general databases can fail to successfully classify species (see Stouffer et al. 2014), we preferred to use regional databases, which rely on local plant specialists, e.g. the Brazilian Flora Checklist. Whenever conflicts among databases appeared, or we were unsure of the classification, we contacted experts with working experience on the flora of the specific region (listed in the Acknowledgments). We refer to the plants considered here solely as alien, since to define these as invasive require more than distributional information e.g. ecological and demographic parameters that we currently lack (Colautti & MacIssac 2004). Moreover, all hummingbirds were considered as natives.
Species-level network metrics

For each plant-hummingbird community, interactions were summarized as a bipartite matrix, with each cell filled with the frequency of the pairwise interaction between a plant and a hummingbird species. The role of each plant species within the networks was described by five distinct indices that capture distinct topological properties of a species: 1) the degree of a species ($k_i$) is computed as the number of partners a given species $i$ is linked to in the network; 2) species strength ($s_i$) is the sum of dependencies across all interaction partners of a given species $i$; dependency is calculated as the proportion of interactions performed by species $i$ to a specific partner (Bascompte et al. 2006); 3) complementary specialization, ($d'_i$) quantifies how interaction frequencies of a given species deviate in relation to the availability of interaction partners in the network, defined by their marginal totals; the higher the value of $d'$, the more exclusive are the interactions of the species in relation to the other species in the network (Blüthgen et al. 2006). In addition, we calculated the level of quantitative modularity of each network, i.e. formation of distinct sub-communities within an ecological network characterized by high within-module prevalence over between-module interactions (Dormann & Strauss 2014). For each network, we estimated the module conformation using the QuanBiMo algorithm with the number of Markov Chain Monte Carlo (MCMC) moves to yield no improvement before the algorithm stops set to $10^7$ steps (Dormann & Strauss 2014). From the module conformation with the highest modularity after 20 independent runs for each network (as in Maruyama et al. 2014), we calculated two species-level network indices: 4) between-module connectivity $c$ and 5) within-module connectivity $z$. Whereas $c_i$ describes how evenly the interactions of species $i$ are distributed across modules in the network, $z_i$ quantifies the importance of a given species $i$ within its module (Dormann & Strauss 2014). Species-level network indices showed a positive
correlation in some cases, indicating that species with high values for a given index
tended to also have high values for another index (Table S4). The correlation was
especially high between degree and species strength (Pearson's $r = 0.68$; Table S4), and
between species strength and within module connectivity, i.e. $z$ (Pearson's $r = 0.70$;
Table S4). However, these indices complement each other and we therefore used all five
indices when comparing alien vs. native plants. In order to compare the five species-
level network indices across different networks, we transformed all network indices to
$z$-scores, i.e., indices were standardized within each network by subtracting the mean
value of each group (plants or hummingbirds) and dividing the results by its standard
deviation (as in Vidal et al. 2014). Calculations of species-level network indices were
conducted with the bipartite package (Dormann et al. 2008) in R (R Development Core
Team 2014).

**Question 1:** Are alien plants topologically more important than native plants in the
networks?

To test whether alien plant species differed from native species, we used a null
model to contrast the observed difference of means of the species-level indices between
native and alien plants to the differences of the means calculated from randomizations
shuffling the alien or native status of the plants (the proportion of alien/natives was
fixed; Vidal et al. 2014). The significance ($p$-values) was obtained by dividing the
number of times the absolute differences generated from 10,000 randomizations were
equal or larger than the observed difference of the means by the number of
randomizations (Manly 1997). Whenever a plant species occurred in more than a single
network (74 species, 19.3% of all plants), the average for each of the standardized
indices was calculated and used for the null model analysis. We note that with the
exception of the degree \((k)\) which becomes non-significant, results were qualitatively similar if we consider the instances in which the same species occurred in different networks as distinct samples. Thus, we kept the same approach adopted in Vidal et al. (2014). To quantify the magnitude of the difference between native and alien plant species, we calculated Cohen’s \(d\) effect size as the standardized mean difference between the indices of each group, i.e. the difference between means divided by the standard deviation of the respective index for all plants (Nakagawa & Cuthill 2007, Sullivan & Feinn 2012). For example, an effect size of around 0.5 is considered a medium effect, meaning that an average alien plant species has a higher index value than 69% of the natives (Nakagawa & Cuthill 2007, Sullivan & Feinn 2012).

**Question 2: Do plant traits and insularity affect the network roles of alien plants?**

For all alien plants identified in the 21 networks, we classified the species according to traits we hypothesized as relevant for their role in the networks. Trait information was gathered from the original sources of the network data (Table S1), as well as by a follow-up literature search using Google Scholar® with the species name as the search term (a list of the data sources is found in Appendix 1). All alien plants were classified according to (a) the size of the plant, which potentially reflects their floral display (i.e. large or small, the former including trees and large herbs such as bananas, and the latter including shrubs, climbers and small herbs); (b) flower type (tubular, brush or other), (c) the length of the floral corolla or equivalent structures restricting the access to pollinator (mm), and (d) whether or not they are bird-pollinated in their native range (Tables S5-S6). To determine the latter, we used references from the plant-hummingbird network database as well as field based studies on the floral morphology and pollination biology of the plants, including information on the associated floral
visitors and pollinators (Table S5-S6). Additionally, we classified whether an alien plant occurred on an island or on mainland communities. As we were only able to evaluate alien plant traits, and not the traits of the native plants, we asked whether particular characteristics of the aliens influence its integration into the networks.

We evaluated how plant traits and insularity related to plant species-level network indices with linear mixed effects models (LMM) using the *lme4* package (Bates 2014) in R (R Development Core Team. 2014). We used the plant traits (i.e. size, flower type, flower length and previous association to bird pollination) and insularity of the network as fixed factors. Here, we also included the plant family as a fixed factor to, at least partly, account for taxonomic relatedness. Alien plant species identity was included as a random effect to account for non-independence of the observations of the same species in different networks (Bolker et al. 2009, Zuur et al. 2009). We ran models separately for each of the five distinct species-level network indices. The full models included all predictors and were compared to reduced models using the function "dredge" in R package *MuMln* (Barton 2014), according to their Akaike information criteria (AIC) values, corrected for small sample sizes (AICc - Bolker et al. 2009, Zuur et al. 2009). Models with ΔAICc ≤ 2 were considered to be equivalent. We also estimated the proportion of variance explained by the fixed factors in the selected best model as marginal $R^2$, and the proportion of variance explained by fixed and random factors as conditional $R^2$ (Nakagawa & Schielzeth 2013, Barton 2014). For 12 of the networks (57.1% of the dataset), floral abundance data were available and thus we conducted additional analyses evaluating its role on species-level network indices. Following the same procedure to what was done for the entire dataset, we fitted LMMs to evaluate simultaneously the effect of alien plant traits, floral abundance and insularity.
on the species-level indices. Here, as for network indices, the floral abundances were
standardized within each network.

*Question 3: Do hummingbird traits relate to facilitation of alien plant integration?*

Finally, we asked whether hummingbird bill length, a functional bird trait
associated with flower choice (Dalsgaard et al. 2009, Maruyama et al. 2014, Maglianesi et al. 2014), was related to the probability of hummingbirds including alien plants in
their array of interactions. Longer billed-hummingbirds are considered functionally

For this, we compiled information on hummingbird bill lengths (Table S3) and assessed
whether a given hummingbird species interacted with an alien plant across the networks
(a list of the data sources is found in Appendix 1). Then, we fitted a generalized linear
model with binomial error distribution containing hummingbird bill length as predictor
of the probability that a hummingbird species interacted with alien plant species (Zuur et al. 2009). This analysis was conducted at species level, contrasting each species' bill
length to the presence of interaction with alien plants across all the networks in which a
given hummingbird species occurred. We also conducted a similar analysis excluding
hummingbird species occurring on Caribbean islands where networks are small
(Dalsgaard et al. 2009), as well as using the body mass instead of the bill length. As bill
length and body mass in hummingbirds show strong phylogenetic signal (Graham et al.
2012), we also included the hummingbird clades (McGuire et al. 2014) as another fixed
factor in these analysis. The models with and without clade identity were compared by
an analysis of deviance test and their AIC values (Zuur et al. 2009).
The 21 plant-hummingbird networks included a total of 74 hummingbird and 384 plant species, of which 32 plants were classified as being alien to the networks in which they occurred. Individual networks contained between seven and 65 plant species, with a mean of 10.8±8.2% (±sd) and up to 28.6% alien plant species (Figure 1, Table S7). Alien plants belonged to 16 plant families, with Musaceae and Myrtaceae constituting the most frequent families (Table S5-S6). Most alien plant species (~63%) had tubular flowers, and about half of them (~47%) had previous association with bird pollinators (Table S5-S6). Around 50% of alien species originated from Asia, about 19% originated from Africa and 19% from other regions of the Americas (Table S5).

Question 1: Are alien plants topologically more important than native plants in the networks?

Overall, alien plant species had higher values of species strength than native species (effect size, \( k \): Cohen's \( d = 0.56; 95\% \) Confidence Interval = 0.36-0.77; null model \( p = 0.003; \) Figure 2). Likewise, alien plants also had higher values of within module connectivity (\( z \): Cohen's \( d = 0.49; 95\% \) CI = 0.29-0.69; \( p = 0.006; \) Figure 2). For degree (\( k \)) and complementary specialization (\( d' \)), 95% CI of effect sizes did also not overlap zero and null models were significant (\( k \): Cohen's \( d = 0.35; 95\% \) CI = 0.15-0.56; \( p = 0.049; \) \( d' \): Cohen's \( d = 0.35, 95\% \) CI = 0.15-0.55; \( p = 0.050; \) Figure 2). However, alien plants did not differ from native species in connecting distinct modules (\( c \): Cohen's \( d = 0.07; 95\% \) CI = -0.12-0.27; \( p = 0.662 \)). Hence, an average alien plant is more important for hummingbirds than an average native plant in terms of relative interaction frequency. There is also a tendency for alien plant species to have more partners and for some hummingbird species to interact more exclusively with alien plants than natives.
Question 2: Do plant traits and insularity affect the network roles of alien plants?

Alien plant traits did not relate to species-level network indices, except for between-module connectivity ($c$), since the model containing only the intercept was always included within the best models (Table S8). For $c$, the best two models included insularity and size of the alien plants; the model containing both terms had $R^2$ marginal $= 0.22$ and $R^2$ conditional $= 0.33$. Specifically, aliens on islands (estimate $= 0.35$, SE $= 0.30$) and larger alien plants (estimate $= 0.75$, SE $= 0.27$) had higher values for connectivity, i.e. were more important for interconnecting modules. Plant family was not included in any of the best models. Considering the subset of networks for which we had floral abundance data, this did not relate to species topological roles in any of the LMMs, as in all cases the intercept only model was as good as models including floral abundance (Table S9). Importantly, the results of LMMs for this reduced dataset were fairly consistent and we again have that insularity (estimate $= 0.68$, SE $= 0.18$) and plant size (estimate $= 1.18$, SE $= 0.36$) relate to $c$ ($R^2$ marginal $= 0.42$ and $R^2$ conditional $= 0.97$).

Question 3: Do hummingbird traits relate to facilitation of alien plant integration?

We found that short-billed hummingbirds were more likely to interact with alien plants than were long-billed hummingbirds (slope: -0.10; $p < 0.01$; Figure 3). The model including the hummingbird clades did not differ from the one without (Deviance $= 6.68$, $p > 0.46$) and had higher value of AIC ($\Delta$AIC $= 9.32$). Excluding the hummingbird species occurring in the Caribbean islands did not change our results (slope: -0.08; $p = 0.036$; Figure S1) and body mass was found unrelated to the probability of using alien plants ($p = 0.091$).
DISCUSSION

We have shown that alien plants are strongly integrated into plant-hummingbird networks, playing key roles in the networks where they occur. Alien plants have more partners (higher degree) and hummingbirds show higher dependency on them than on an average native plant, both across the entire network and within their modules. Although we note that the networks contained many more native than alien plant species (352 versus 32 species, range 2.0% to 28.6% of the species), these results suggest that alien plants are important and act as core generalists in these networks (Aizen et al. 2008, Bartomeus et al. 2008, Vilà et al. 2009, Stouffer et al. 2014, Traveset & Richardson 2014). Moreover, some alien plants may function as private or somewhat exclusive floral resources for some hummingbird species, as revealed by their high degree of complementary specialization (Blüthgen et al. 2006, Stouffer et al. 2014).

The traits we hypothesized a priori to determine how alien plants would integrate into the networks showed little importance. For instance, convergent evolution to bird pollination has been suggested as an example of previous adaptation to specific pollinator types aiding the incorporation of aliens to novel plant-pollinator networks (Richardson et al. 2000, Ollerton et al. 2012). However, this pre-adaptation did not apply to network roles of alien plants in plant-hummingbird networks. Hummingbirds may favour specific floral traits (Cronk & Ojeda 2008, Ferreira et al. 2016), but they may also show opportunism in flower use by legitimately visiting plants that do not obviously conform to the bird pollination syndrome of ornithophily (e.g. Dalsgaard et al. 2009, Maruyama et al. 2013). Due to this opportunism, specialized floral traits may not relate to plant species roles in plant-hummingbird networks (Maruyama et al. 2013). Nevertheless, one possible limitation is the fact that we only considered plant species recorded as visited by hummingbirds, i.e., participating in the web of interactions. It is
possible that other alien plants were present in the studied communities and that these were not visited by hummingbirds. If such non-participating alien species had been considered, plant traits, including the previous adaptation to bird-pollination, could have emerged as important for alien integration into the plant-hummingbird web. Likewise we did not include non-hummingbird pollinators and insects may overlap with hummingbirds on the phenotypically more generalised plant species (e.g. Dalsgaard et al. 2009, Maruyama et al. 2013); thus other pollinators may also influence alien plant integration.

It has been suggested that invasive plants, i.e. widespread and abundant alien plants, may become core components of plant-insect pollinator networks due to their high abundance in invaded communities (Lopezaraiza-Mikel et al. 2007, Aizen et al. 2008, Albrecht et al. 2014). However, recent studies have shown that abundance has minor importance in structuring interactions among plants and hummingbirds, in contrast to more generalized insect pollination systems (Maruyama et al. 2014, Vizentin-Bugoni et al. 2014, 2016). In accordance, analyses conducted with the subset of the networks for which we have floral abundance data show that there is no association between floral abundance and their species-level indices. Thus, for plant-hummingbird networks, floral abundance is a poor predictor of alien topological importance. Instead, we suggest that other plant traits that we lack in our dataset, such as the temporal availability of alien flowers in relation to native plants (i.e. phenology), or higher nectar secretion rates, could be important for explaining the integration of alien species in these networks (see Chittka & Schürkens 2001, Godoy et al. 2009).

Although most plant traits evaluated here did not relate to the role of alien plants in the networks, we found that larger alien plants had higher values of between module connectivity than smaller alien plants. Thus, presumably those alien plants that have
bigger floral display distribute their interactions more widely among modules in networks, acting as connectors in these networks. This is important since connectors are suggested to blur the boundaries between modules affecting the network dynamics (Albrecht et al. 2014). Alien plants occurring in depauperate island networks were also better connectors than alien plants on the mainland, which indicates that they may have greater potential to affect insular than mainland communities (e.g. Traveset et al. 2013, but see Kaiser-Bunbury et al. 2011).

From the hummingbird perspective, we show that shorter billed hummingbirds have higher probabilities of incorporating alien plant species in their web of interactions. Although there is variation in this trend, since some longer-billed hummingbirds used alien plants (Figure 3), this result is consistent to the setting in which longer-billed hummingbirds avoid interacting with more generalised flowers due competition with shorter-billed hummingbirds (Maglianesi et al. 2015). Studies have suggested that generalist insect pollinators facilitate alien plant establishment, since these often include alien plants in their interactions (Richardson et al. 2000, Memmott & Waser 2002, Olesen et al. 2002, Lopezaraiza-Mikel et al. 2007, Aizen et al. 2008, Bartomeus et al. 2008, Traveset et al. 2013, Stouffer et al. 2014). In previous studies, however, "generalists" were defined based in their roles in networks, e.g., number of partners. Here, we show a link between integration of alien plants and a functional trait of the pollinators, i.e. bill length of hummingbirds.

CONCLUSION

Invasive plants are regarded as one of the major current threats to biodiversity. One of the key components for alien plants to establish in novel ecosystems is their successful integration into mutualistic networks (Richardson et al. 2000, Traveset & Richardson
Although examples of successful integration of alien species in temperate and insular insect-plant systems are common (e.g. Olesen et al. 2002, Aizen et al. 2008, Bartomeus et al. 2008, Vilà et al. 2009, Stouffer et al. 2014), here we show that alien plants are strongly integrated into the web of interactions even for more specialized tropical pollination systems, such as hummingbird pollination. Further research incorporating complementary data, such as interspecific pollen deposition or the contribution of hummingbirds to alien plant reproduction, are essential next steps to fully assess the impact and integration of alien plants in this system (Richardson et al. 2000, Lopezaraiza-Mikel et al. 2007, Bufford & Daehler 2014, Traveset & Richardson 2014). By acting as core generalist species in the networks, these plants may impact the entire plant-pollinator network (Traveset et al. 2013) and even modify their eco-evolutionary dynamics (Guimarães et al. 2011). In sum, our results here show that plant-hummingbird networks are dynamic and open for invasion, emulating what happens in other plant-pollinator systems.

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with species richness, contemporary precipitation and Quaternary climate-change velocity. *PLoS ONE* 6, e25891.


Appendix 1 – Data sources


Cardona, J., & Cardona P.A. (2011) Uso de recursos florales por el ensamble de aves nectarívoras en el campus de la Universidad del Quindio. BSc Thesis. Universidad del Quindio, Colombia.


Crome F.H.J. & Irvine A. K. (1986) "Two Bob each way": the pollination and breeding system of the Australian rain forest tree Syzygium corniflorum (Myrtaceae). Biotropica, 18, 115-125.


SUPPORTING INFORMATION:

Figure S1 Probability of hummingbirds incorporating alien plants into their interactions in relation to their bill length, excluding island networks.

Table S1 Coordinates, description, location and data references for each studied plant-hummingbird network.

Table S2 List of plant species found across plant-hummingbird networks.

Table S3 List of hummingbird species found across plant-hummingbird networks.

Table S4 Pearson correlation $r$ among distinct species-level network indices.

Table S5 List of the alien plant species found across plant-hummingbird networks.

Table S6 Details on the assessment of alien plants' pollination system.

Table S7 Proportion of alien plant species and their interactions across networks.

Table S8 Model selection results for linear mixed effect models explaining network indices of the alien plant species.

Table S9 Model selection results for the subset of 12 networks with floral abundance data.

BIOSKETCH

Pietro K. Maruyama is an ecologist, especially interested in natural history and plant-animal mutualistic interactions in megadiverse tropical ecosystems, such as the Cerrado and Atlantic Rainforest. This study is part of an ongoing research collaboration on plant-hummingbird networks across the Americas, involving numerous researchers.

Figure 1 Distribution of 21 Neotropical plant-hummingbird networks containing alien plant species. Circle size represents the total number of plant species in each network; colours indicate the proportion of alien plants in each network. Note that some points have been slightly moved to avoid overlap. Two network representations illustrate how alien plants are integrated into the networks (top network, Colombian Andes, Snow & Snow 1980; bottom network, Brazilian Atlantic Rainforest, Maruyama et al. 2015). Top and bottom rectangles denote hummingbirds and plants, respectively. Alien plants and their interactions are marked in red. The illustration depicts one such interaction from the bottom network, between the Saw-billed hermit Ramphodon naevius and the Flowering banana Musa ornata originally from Southeast Asia (credit: Pedro Lorenzo).
Figure 2 Species-level network indices for 352 native and 32 alien plant species across 21 plant-hummingbird networks. On the left, we show the effect sizes (Cohen’s d) comparing alien and native plant species for various network indices; an effect size is considered significant if the 95% CI of the mean differences do not overlap zero (Nakagawa & Cuthill 2007). On the right, box-plots illustrate the distribution of standardized index values along with their significance, as obtained from null model analysis. With the exception of c, both approaches found that an average alien plant have higher network index values than an average native plant.
Figure 3 Probability of hummingbird species incorporating alien plant species into their interactions in relation to their bill length. Each circle illustrates whether a given hummingbird species incorporates alien plants (1), or not (0). The fitted line reflects the modelled probability of hummingbird species feeding on alien plants; showing that short-billed hummingbirds have a higher probability of feeding on alien plants than do long-billed hummingbird species. We used Generalized Linear Models with binomial error distribution to assess the significance of the relationships. A Mann-Whitney test likewise shows significant difference between the bill length of those hummingbirds incorporating and those not incorporating alien plants in their interactions ($p = 0.004$).