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

Maruyama, PK

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6 Running header: Alien plants in plant-hummingbird networks

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

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11 **Pietro K. Maruyama<sup>1,2,3</sup>, Jeferson Vizentin-Bugoni<sup>1,2</sup>, Jesper Sonne<sup>2</sup>, Ana M.**  
12 **Martín González<sup>2,4</sup>, Matthias Schleuning<sup>5</sup>, Andréa C. Araujo<sup>6</sup>, Andrea C.**  
13 **Baquero<sup>2</sup>, Juliana Cardona<sup>7</sup>, Paola Cardona<sup>7</sup>, Peter A. Cotton<sup>8</sup>, Glauco Kohler<sup>9</sup>,**  
14 **Carlos Lara<sup>10</sup>, Tiago Malucelli<sup>11</sup>, Oscar Humberto Marín<sup>12,13</sup>, Jeff Ollerton<sup>14</sup>, Ana**  
15 **M. Rui<sup>15</sup>, Allan Timmermann<sup>16</sup>, Isabela G. Varassin<sup>11</sup>, Thais B. Zanata<sup>2,11</sup>, Carsten**  
16 **Rahbek<sup>2,17</sup>, Marlies Sazima<sup>13</sup>, Bo Dalsgaard<sup>2</sup>**

17 1. Programa de Pós-Graduação em Ecologia, Universidade Estadual de Campinas  
18 (Unicamp), Cx. Postal 6109, CEP: 13083-970, Campinas, SP, Brasil

19 2. Center for Macroecology, Evolution and Climate, Natural History Museum of  
20 Denmark, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø,  
21 Denmark

22 3. Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de  
23 Campinas (Unicamp), Cx. Postal 6109, CEP: 13083-970, Campinas, SP, Brasil

24 4. Pacific Ecoinformatics and Computational Ecology Lab, 1604 McGee Ave, 94703  
25 Berkeley, California, USA

- 26 5. Senckenberg Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage  
27 25, 60325 Frankfurt (Main), Germany
- 28 6. Centro de Ciências Biológicas e da Saúde, Universidade Federal de Mato Grosso do  
29 Sul, 79070-900, Campo Grande, Mato Grosso do Sul, Brasil
- 30 7. Grupo de Biodiversidad y Educación Ambiental (BIOEDUQ). Programa de  
31 Licenciatura en Biología y Educación Ambiental. Universidad del Quindío. A.A. 460.  
32 Armenia, Quindío, Colombia
- 33 8. Marine Biology & Ecology Research Centre, Plymouth University, Plymouth PL4  
34 8AA, UK
- 35 9. Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo 2936, Petrópolis,  
36 CEP 69080-971, Manaus, Amazonas, Brasil
- 37 10. Centro de Investigación en Ciencias Biológicas, Universidad Autónoma de  
38 Tlaxcala. Km 10.5 Autopista Tlaxcala-San Martín Texmelucan, San Felipe Ixtacuixtla,  
39 90120, Tlaxcala, México
- 40 11. Laboratório de Ecologia Vegetal, Departamento de Botânica, Universidade Federal  
41 do Paraná, 81531-980 Curitiba, Paraná, Brasil
- 42 12. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Laboratorio de  
43 Ecología en Ambientes Perturbados, Red de Ambiente y Sustentabilidad, Instituto de  
44 Ecología, A.C.
- 45 13. Departamento de Biología Evolutiva, Instituto de Ecología, A.C., Carretera Antigua  
46 a Coatepec 351, El Haya, Xalapa, Veracruz 91070, México
- 47 14. Environmental Research Group, School of Science and Technology, University of  
48 Northampton, Avenue Campus, Northampton, NN2 6JD, UK
- 49 15. Departamento de Ecologia, Zoologia e Genética, Instituto de Biologia, Universidade  
50 Federal de Pelotas, Capão do Leão, Rio Grande do Sul, Brasil
- 51 16. Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus  
52 University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark
- 53 17. Department of Life Sciences, Imperial College London, Silwood Park Campus,  
54 Ascot SL5 7PY, UK  
55

56 **ABSTRACT**

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

60 **Location** Mainland and insular Americas.

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

68 **Results** Within the 21 networks, we identified 32 alien plant species and 352 native  
69 plant species. On average, alien plant species attracted more hummingbird species (i.e.  
70 aliens had a higher degree) and had a higher proportion of interactions across their  
71 hummingbird visitors than native plants (i.e. aliens had a higher species strength). At  
72 the same time, an average alien plant was visited more exclusively by certain  
73 hummingbird species (i.e. had a higher level of complementary specialization). Large  
74 alien plants and those occurring on islands distributed more evenly their interactions,  
75 thereby acting as connectors. Other evaluated plant traits and floral abundance were  
76 unimportant predictors of species-level indices. Short-billed hummingbirds had higher  
77 probability of including alien plants in their interactions than long-billed species.

78 **Main conclusions** Alien plants appear strongly integrated once incorporated into plant-  
79 hummingbird networks, and thus may have a large influence on network dynamics.  
80 Plant traits and floral abundance were generally poor predictors of how well alien  
81 species are integrated. Short-billed hummingbirds, often characterized as functionally  
82 generalized pollinators, facilitate the integration of alien plants. Our results show that  
83 plant-hummingbird networks are open for invasion.

84

85 **Key-words**

86 Abundance, exotic plants, generalization, invasion biology, network roles, ornithophily,  
87 specialization

88

89 **INTRODUCTION**

90 Alien species may become invasive and are a major threat to biodiversity and ecosystem  
91 functioning, including key ecosystem services such as pollination (Colautti & MacIssac  
92 2004, Gurevitch & Padilla 2004, Pyšek et al. 2004, Morales & Traveset 2009,  
93 Simberloff et al. 2013). The successful establishment of alien plant species might be  
94 contingent on the acquisition of mutualistic partners, e.g. pollinators, outside their  
95 native range (Richardson et al. 2000, Bufford & Daehler 2014, Traveset & Richardson  
96 2014). Under such a scenario, alien plants may compete for pollinators and decrease the  
97 fitness of native plants, for instance by offering greater quantities of floral rewards and  
98 thereby decreasing the attractiveness of native flowers (Chittka & Schürkens 2001,  
99 Morales & Traveset 2009). Conversely, alien plants could also benefit native plants by  
100 increasing the overall availability of floral resources, thereby increasing pollinator  
101 abundance and activity on native plants (Bjerknes et al. 2007, Lopezaraiza-Mikel et al.  
102 2007, Bartomeus et al. 2008). Thus, alien plants' ability to establish, and their effect on  
103 the pollination of native plants, may depend on their floral traits and the community  
104 context (Bjerknes et al. 2007, Morales & Traveset 2009, Gibson et al. 2012, Simberloff  
105 et al. 2013).

106 In order to understand the potential impacts of alien species on ecosystems, it is  
107 therefore important to characterize the community-wide roles of these plants (Davis et  
108 al. 2011). One approach to doing this is to use ecological interaction network analyses  
109 to conduct community-wide studies identifying and describing the interactions between  
110 organisms. Several studies have used such an approach to investigate the role of alien  
111 plants on plant-pollinator communities (Memmott & Waser 2002, Olesen et al. 2002,  
112 Aizen et al. 2008, Vilà et al. 2009, Albrecht et al. 2014, Stouffer et al. 2014, Traveset &

113 Richardson 2014). However, most of these studies have considered either temperate  
114 systems, which predominantly consist of functionally generalized insect pollinators (e.g.  
115 Aizen et al. 2008, Bartomeus et al. 2008), or focus on generalized island communities  
116 where the impact of invasive species might be most severe (e.g. Olesen et al. 2002,  
117 Traveset et al. 2013, Traveset & Richardson 2014, but see Kaiser-Bunbury et al. 2011).  
118 As an interaction network's stability may be more sensitive to the integration of alien  
119 species in specialized than in generalized systems (Kaiser-Bunbury et al. 2011), studies  
120 on specialized systems and over large geographical scales can contribute to our  
121 understanding of the general effects of alien species.

122         One such potential model system is the interaction networks between plants and  
123 hummingbirds across the Americas, which range from relatively specialized to  
124 generalized networks, and include both mainland and insular environments (Stiles 1981,  
125 Dalsgaard et al. 2011, Martín González et al. 2015). Hummingbirds are the most  
126 functionally specialized group of nectar-feeding birds and the most important vertebrate  
127 pollinators in the Americas (Stiles 1981, Bawa 1990, Cronk & Ojeda 2008). As specific  
128 floral phenotypes are often associated with hummingbird pollination (Cronk & Ojeda  
129 2008, Ferreira et al. 2016), it could be expected that alien plants lacking a shared  
130 evolutionary history with hummingbirds would not be readily incorporated as important  
131 species in those networks (Richardson et al. 2000; Aizen et al. 2008). Conversely, Old  
132 World plants with convergent adaptations to bird pollination, notably to sunbirds and  
133 honeyeaters in Africa and South-east Asia (Cronk & Ojeda 2008, Fleming & Muchhala  
134 2008, Ollerton et al. 2012, Janeček et al. 2015), could be well-integrated in novel plant-  
135 hummingbird communities in the Americas – at least more than alien plant species not  
136 previously pollinated by birds (see Johnson & Raguso 2016 for examples between  
137 specialized flowers and long tongued hawkmoths).

138           Given the increasing concerns over the effects of alien species on ecosystems  
139 (Davis et al. 2011, Richardson & Ricciardi 2013, Simberloff et al. 2013), community-  
140 wide studies on the role of alien plants across large geographic gradients could provide  
141 new insights into their potential threats to biodiversity. Here, we characterize the role of  
142 alien plants in 21 quantitative plant-hummingbird networks distributed broadly across  
143 the Neotropics, including both mainland and island environments (Fig. 1). We asked  
144 three questions: 1) whether an average alien plant is topologically more important than a  
145 native species, i.e. whether alien plants have a disproportionate large effect on plant-  
146 hummingbird networks; 2) whether alien plant traits, such as pre-adaptation to bird  
147 pollination in combination to the geographical setting of the network, i.e., insularity,  
148 affect the integration of plants into networks; 3) whether hummingbirds with short-bills,  
149 often characterized as functionally more generalized, facilitate the integration of alien  
150 plant species into networks.

151

## 152 **METHODS**

### 153 *Plant-hummingbird networks and alien plants classification*

154 In order to investigate the role of alien plant species in pollination networks, we  
155 compiled plant-hummingbird networks in which exotic plant species could be  
156 confidently identified (Figure 1). For this, we used an established database on  
157 quantitative plant-hummingbird interaction networks (see Dalsgaard et al. 2011 and  
158 Martín González et al. 2015 for previous versions of the database, updated details in  
159 Table S1-S3). We only considered legitimate interactions here, in which a hummingbird  
160 was observed contacting the reproductive structures of the flowers and with potential for  
161 pollination. For each network, plants were classified as either native or alien - taking  
162 into account the locality of a given network and the plant distribution range according to

163 openly available databases, notably: Tropicos (<http://www.tropicos.org/>), GRIN  
164 Taxonomy for Plants for North America (<http://www.ars-grin.gov/>), Flora of the West  
165 Indies for the Caribbean (<http://botany.si.edu/antilles/WestIndies/query.cfm>), Brazilian  
166 Flora Checklist for networks from Brazil (<http://floradobrasil.jbrj.gov.br/>) and The Plant  
167 List (<http://www.theplantlist.org/>). Plant names used here followed The Plant List  
168 database. A total of 75 (19%) plant occurrences in the networks were not identified to  
169 species level, but to genus or family level only (Table S2); for these we adopted a  
170 conservative approach of only attributing "alien" status if the genus/family at the given  
171 locality was identified as alien in the databases. We note, however, that excluding these  
172 species did not affect the comparison between native and alien plants. Because the  
173 geographical origin of some plants is poorly known, the classification of these can be  
174 imprecise (Pyšek et al. 2004), and the use of a single general database has been argued  
175 for in order to standardize possible bias (Stouffer et al. 2014). However, our dataset is  
176 composed primarily of networks from the Neotropical region, which has relatively poor  
177 historical species records compared to North America and Europe (Pyšek et al. 2004).  
178 Since even for well recorded regions these general databases can fail to successfully  
179 classify species (see Stouffer et al. 2014), we preferred to use regional databases, which  
180 rely on local plant specialists, e.g. the Brazilian Flora Checklist. Whenever conflicts  
181 among databases appeared, or we were unsure of the classification, we contacted  
182 experts with working experience on the flora of the specific region (listed in the  
183 Acknowledgments). We refer to the plants considered here solely as alien, since to  
184 define these as invasive require more than distributional information e.g. ecological and  
185 demographic parameters that we currently lack (Colautti & MacIssac 2004). Moreover,  
186 all hummingbirds were considered as natives.

187

188 *Species-level network metrics*

189 For each plant-hummingbird community, interactions were summarized as a bipartite  
190 matrix, with each cell filled with the frequency of the pairwise interaction between a  
191 plant and a hummingbird species. The role of each plant species within the networks  
192 was described by five distinct indices that capture distinct topological properties of a  
193 species: 1) the degree of a species ( $k_i$ ) is computed as the number of partners a given  
194 species  $i$  is linked to in the network; 2) species strength ( $s_i$ ) is the sum of dependencies  
195 across all interaction partners of a given species  $i$ ; dependency is calculated as the  
196 proportion of interactions performed by species  $i$  to a specific partner (Bascompte et al.  
197 2006); 3) complementary specialization, ( $d'_i$ ) quantifies how interaction frequencies of a  
198 given species deviate in relation to the availability of interaction partners in the network,  
199 defined by their marginal totals; the higher the value of  $d'$ , the more exclusive are the  
200 interactions of the species in relation to the other species in the network (Blüthgen et al.  
201 2006). In addition, we calculated the level of quantitative modularity of each network,  
202 i.e. formation of distinct sub-communities within an ecological network characterized  
203 by high within-module prevalence over between-module interactions (Dormann &  
204 Strauss 2014). For each network, we estimated the module conformation using the  
205 QuanBiMo algorithm with the number of Markov Chain Monte Carlo (MCMC) moves  
206 to yield no improvement before the algorithm stops set to  $10^7$  steps (Dormann & Strauss  
207 2014). From the module conformation with the highest modularity after 20 independent  
208 runs for each network (as in Maruyama et al. 2014), we calculated two species-level  
209 network indices: 4) between-module connectivity  $c$  and 5) within-module connectivity  
210  $z$ . Whereas  $c_i$  describes how evenly the interactions of species  $i$  are distributed across  
211 modules in the network,  $z_i$  quantifies the importance of a given species  $i$  within its  
212 module (Dormann & Strauss 2014). Species-level network indices showed a positive

213 correlation in some cases, indicating that species with high values for a given index  
214 tended to also have high values for another index (Table S4). The correlation was  
215 especially high between degree and species strength (Pearson's  $r = 0.68$ ; Table S4), and  
216 between species strength and within module connectivity, i.e.  $z$  (Pearson's  $r = 0.70$ ;  
217 Table S4). However, these indices complement each other and we therefore used all five  
218 indices when comparing alien vs. native plants. In order to compare the five species-  
219 level network indices across different networks, we transformed all network indices to  
220 z-scores, i.e., indices were standardized within each network by subtracting the mean  
221 value of each group (plants or hummingbirds) and dividing the results by its standard  
222 deviation (as in Vidal et al. 2014). Calculations of species-level network indices were  
223 conducted with the *bipartite* package (Dormann et al. 2008) in R (R Development Core  
224 Team 2014).

225

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

228 To test whether alien plant species differed from native species, we used a null  
229 model to contrast the observed difference of means of the species-level indices between  
230 native and alien plants to the differences of the means calculated from randomizations  
231 shuffling the alien or native status of the plants (the proportion of alien/natives was  
232 fixed; Vidal et al. 2014). The significance ( $p$ -values) was obtained by dividing the  
233 number of times the absolute differences generated from 10,000 randomizations were  
234 equal or larger than the observed difference of the means by the number of  
235 randomizations (Manly 1997). Whenever a plant species occurred in more than a single  
236 network (74 species, 19.3% of all plants), the average for each of the standardized  
237 indices was calculated and used for the null model analysis. We note that with the

238 exception of the degree ( $k$ ) which becomes non-significant, results were qualitatively  
239 similar if we consider the instances in which the same species occurred in different  
240 networks as distinct samples. Thus, we kept the same approach adopted in Vidal et al.  
241 (2014). To quantify the magnitude of the difference between native and alien plant  
242 species, we calculated Cohen's  $d$  effect size as the standardized mean difference  
243 between the indices of each group, i.e. the difference between means divided by the  
244 standard deviation of the respective index for all plants (Nakagawa & Cuthill 2007,  
245 Sullivan & Feinn 2012). For example, an effect size of around 0.5 is considered a  
246 medium effect, meaning that an average alien plant species has a higher index value  
247 than 69% of the natives (Nakagawa & Cuthill 2007, Sullivan & Feinn 2012).

248

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

250 For all alien plants identified in the 21 networks, we classified the species according to  
251 traits we hypothesized as relevant for their role in the networks. Trait information was  
252 gathered from the original sources of the network data (Table S1), as well as by a  
253 follow-up literature search using Google Scholar® with the species name as the search  
254 term (a list of the data sources is found in Appendix 1). All alien plants were classified  
255 according to (a) the size of the plant, which potentially reflects their floral display (i.e.  
256 large or small, the former including trees and large herbs such as bananas, and the latter  
257 including shrubs, climbers and small herbs); (b) flower type (tubular, brush or other),  
258 (c) the length of the floral corolla or equivalent structures restricting the access to  
259 pollinator (mm), and (d) whether or not they are bird-pollinated in their native range  
260 (Tables S5-S6). To determine the latter, we used references from the plant-  
261 hummingbird network database as well as field based studies on the floral morphology  
262 and pollination biology of the plants, including information on the associated floral

263 visitors and pollinators (Table S5-S6). Additionally, we classified whether an alien plant  
264 occurred on an island or on mainland communities. As we were only able to evaluate  
265 alien plant traits, and not the traits of the native plants, we asked whether particular  
266 characteristics of the aliens influence its integration into the networks.

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

287 on the species-level indices. Here, as for network indices, the floral abundances were  
288 standardized within each network.

289

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

291 Finally, we asked whether hummingbird bill length, a functional bird trait  
292 associated with flower choice (Dalsgaard et al. 2009, Maruyama et al. 2014, Maglianesi  
293 et al. 2014), was related to the probability of hummingbirds including alien plants in  
294 their array of interactions. Longer billed-hummingbirds are considered functionally  
295 more specialized (Dalsgaard et al. 2009, Maruyama et al. 2014, Maglianesi et al. 2014).  
296 For this, we compiled information on hummingbird bill lengths (Table S3) and assessed  
297 whether a given hummingbird species interacted with an alien plant across the networks  
298 (a list of the data sources is found in Appendix 1). Then, we fitted a generalized linear  
299 model with binomial error distribution containing hummingbird bill length as predictor  
300 of the probability that a hummingbird species interacted with alien plant species (Zuur  
301 et al. 2009). This analysis was conducted at species level, contrasting each species' bill  
302 length to the presence of interaction with alien plants across all the networks in which a  
303 given hummingbird species occurred. We also conducted a similar analysis excluding  
304 hummingbird species occurring on Caribbean islands where networks are small  
305 (Dalsgaard et al. 2009), as well as using the body mass instead of the bill length. As bill  
306 length and body mass in hummingbirds show strong phylogenetic signal (Graham et al.  
307 2012), we also included the hummingbird clades (McGuire et al. 2014) as another fixed  
308 factor in these analysis. The models with and without clade identity were compared by  
309 an analysis of deviance test and their AIC values (Zuur et al. 2009).

310

311 **RESULTS**

312 The 21 plant-hummingbird networks included a total of 74 hummingbird and 384 plant  
313 species, of which 32 plants were classified as being alien to the networks in which they  
314 occurred. Individual networks contained between seven and 65 plant species, with a  
315 mean of  $10.8 \pm 8.2\%$  ( $\pm$ sd) and up to 28.6% alien plant species (Figure 1, Table S7).  
316 Alien plants belonged to 16 plant families, with Musaceae and Myrtaceae constituting  
317 the most frequent families (Table S5-S6). Most alien plant species (~63%) had tubular  
318 flowers, and about half of them (~47%) had previous association with bird pollinators  
319 (Table S5-S6). Around 50% of alien species originated from Asia, about 19% originated  
320 from Africa and 19% from other regions of the Americas (Table S5).

321

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

324 Overall, alien plant species had higher values of species strength than native species  
325 (effect size,  $k$ : Cohen's  $d = 0.56$ ; 95% Confidence Interval = 0.36-0.77; null model  $p =$   
326 0.003; Figure 2). Likewise, alien plants also had higher values of within module  
327 connectivity ( $z$ : Cohen's  $d = 0.49$ ; 95% CI = 0.29-0.69;  $p = 0.006$ ; Figure 2). For degree  
328 ( $k$ ) and complementary specialization ( $d'$ ), 95% CI of effect sizes did also not overlap  
329 zero and null models were significant ( $k$ : Cohen's  $d = 0.35$ ; 95% CI = 0.15-0.56;  $p =$   
330 0.049;  $d'$ : Cohen's  $d = 0.35$ , 95% CI = 0.15-0.55;  $p = 0.050$ ; Figure 2). However, alien  
331 plants did not differ from native species in connecting distinct modules ( $c$ : Cohen's  $d =$   
332 0.07; 95% CI = -0.12-0.27;  $p = 0.662$ ). Hence, an average alien plant is more important  
333 for hummingbirds than an average native plant in terms of relative interaction  
334 frequency. There is also a tendency for alien plant species to have more partners and for  
335 some hummingbird species to interact more exclusively with alien plants than natives.

336

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

338 Alien plant traits did not relate to species-level network indices, except for  
339 between-module connectivity ( $c$ ), since the model containing only the intercept was  
340 always included within the best models (Table S8). For  $c$ , the best two models included  
341 insularity and size of the alien plants; the model containing both terms had  $R^2$  marginal  
342 = 0.22 and  $R^2$  conditional = 0.33. Specifically, aliens on islands (estimate = 0.35, SE =  
343 0.30) and larger alien plants (estimate = 0.75, SE = 0.27) had higher values for  
344 connectivity, i.e. were more important for interconnecting modules. Plant family was  
345 not included in any of the best models. Considering the subset of networks for which we  
346 had floral abundance data, this did not relate to species topological roles in any of the  
347 LMMs, as in all cases the intercept only model was as good as models including floral  
348 abundance (Table S9). Importantly, the results of LMMs for this reduced dataset were  
349 fairly consistent and we again have that insularity (estimate = 0.68, SE = 0.18) and plant  
350 size (estimate = 1.18, SE = 0.36) relate to  $c$  ( $R^2$  marginal = 0.42 and  $R^2$  conditional =  
351 0.97).

352

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

354 We found that short-billed hummingbirds were more likely to interact with alien plants  
355 than were long-billed hummingbirds (slope: -0.10;  $p < 0.01$ ; Figure 3). The model  
356 including the hummingbird clades did not differ from the one without (Deviance = 6.68,  
357  $p > 0.46$ ) and had higher value of AIC ( $\Delta AIC = 9.32$ ). Excluding the hummingbird  
358 species occurring in the Caribbean islands did not change our results (slope: -0.08;  $p =$   
359 0.036; Figure S1) and body mass was found unrelated to the probability of using alien  
360 plants ( $p = 0.091$ ).

361

362 **DISCUSSION**

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

374 The traits we hypothesized *a priori* to determine how alien plants would  
375 integrate into the networks showed little importance. For instance, convergent evolution  
376 to bird pollination has been suggested as an example of previous adaptation to specific  
377 pollinator types aiding the incorporation of aliens to novel plant-pollinator networks  
378 (Richardson et al. 2000, Ollerton et al. 2012). However, this pre-adaptation did not  
379 apply to network roles of alien plants in plant-hummingbird networks. Hummingbirds  
380 may favour specific floral traits (Cronk & Ojeda 2008, Ferreira et al. 2016), but they  
381 may also show opportunism in flower use by legitimately visiting plants that do not  
382 obviously conform to the bird pollination syndrome of ornithophily (e.g. Dalsgaard et  
383 al. 2009, Maruyama et al. 2013). Due to this opportunism, specialized floral traits may  
384 not relate to plant species roles in plant-hummingbird networks (Maruyama et al. 2013).  
385 Nevertheless, one possible limitation is the fact that we only considered plant species  
386 recorded as visited by hummingbirds, i.e., participating in the web of interactions. It is

387 possible that other alien plants were present in the studied communities and that these  
388 were not visited by hummingbirds. If such non-participating alien species had been  
389 considered, plant traits, including the previous adaptation to bird-pollination, could have  
390 emerged as important for alien integration into the plant-hummingbird web. Likewise  
391 we did not include non-hummingbird pollinators and insects may overlap with  
392 hummingbirds on the phenotypically more generalised plant species (e.g. Dalsgaard et  
393 al. 2009, Maruyama et al. 2013); thus other pollinators may also influence alien plant  
394 integration.

395         It has been suggested that invasive plants, i.e. widespread and abundant alien  
396 plants, may become core components of plant-insect pollinator networks due to their  
397 high abundance in invaded communities (Lopezaraiza-Mikel et al. 2007, Aizen et al.  
398 2008, Albrecht et al. 2014). However, recent studies have shown that abundance has  
399 minor importance in structuring interactions among plants and hummingbirds, in  
400 contrast to more generalized insect pollination systems (Maruyama et al. 2014,  
401 Vizentin-Bugoni et al. 2014, 2016). In accordance, analyses conducted with the subset  
402 of the networks for which we have floral abundance data show that there is no  
403 association between floral abundance and their species-level indices. Thus, for plant-  
404 hummingbird networks, floral abundance is a poor predictor of alien topological  
405 importance. Instead, we suggest that other plant traits that we lack in our dataset, such  
406 as the temporal availability of alien flowers in relation to native plants (i.e. phenology),  
407 or higher nectar secretion rates, could be important for explaining the integration of  
408 alien species in these networks (see Chittka & Schürkens 2001, Godoy et al. 2009).

409         Although most plant traits evaluated here did not relate to the role of alien plants  
410 in the networks, we found that larger alien plants had higher values of between module  
411 connectivity than smaller alien plants. Thus, presumably those alien plants that have

412 bigger floral display distribute their interactions more widely among modules in  
413 networks, acting as connectors in these networks. This is important since connectors are  
414 suggested to blur the boundaries between modules affecting the network dynamics  
415 (Albrecht et al. 2014). Alien plants occurring in depauperate island networks were also  
416 better connectors than alien plants on the mainland, which indicates that they may have  
417 greater potential to affect insular than mainland communities (e.g. Traveset et al. 2013,  
418 but see Kaiser-Bunbury et al. 2011).

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

432

## 433 **CONCLUSION**

434 Invasive plants are regarded as one of the major current threats to biodiversity. One of  
435 the key components for alien plants to establish in novel ecosystems is their successful  
436 integration into mutualistic networks (Richardson et al. 2000, Traveset & Richardson

437 2014). Although examples of successful integration of alien species in temperate and  
438 insular insect-plant systems are common (e.g. Olesen et al. 2002, Aizen et al. 2008,  
439 Bartomeus et al. 2008, Vilà et al. 2009, Stouffer et al. 2014), here we show that alien  
440 plants are strongly integrated into the web of interactions even for more specialized  
441 tropical pollination systems, such as hummingbird pollination. Further research  
442 incorporating complementary data, such as interspecific pollen deposition or the  
443 contribution of hummingbirds to alien plant reproduction, are essential next steps to  
444 fully assess the impact and integration of alien plants in this system (Richardson et al.  
445 2000, Lopezaraiza-Mikel et al. 2007, Bufford & Daehler 2014, Traveset & Richardson  
446 2014). By acting as core generalist species in the networks, these plants may impact the  
447 entire plant-pollinator network (Traveset et al. 2013) and even modify their eco-  
448 evolutionary dynamics (Guimarães et al. 2011). In sum, our results here show that  
449 plant-hummingbird networks are dynamic and open for invasion, emulating what  
450 happens in other plant-pollinator systems.

451

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467

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644

645 **Appendix 1 – Data sources**

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786 **SUPPORTING INFORMATION:**

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

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

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

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

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

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

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

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

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

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

801 **BIOSKETCH**

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

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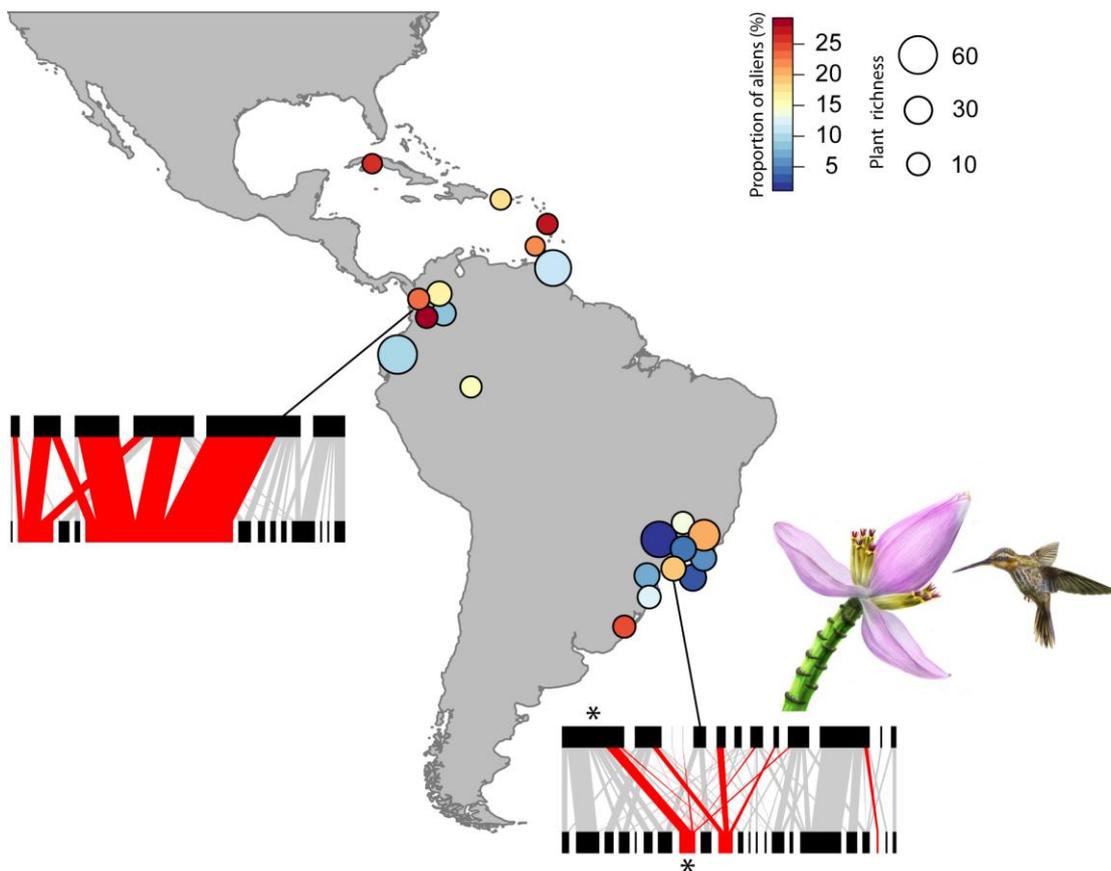
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808 Author contributions: P.K.M., J.V.B., J.S., A.M.M.G, M.Sc. and B.D. contributed with  
809 the design for the study. P.K.M., J.V.B., J.S., A.M.M.G., A.C.A., A.C.B., J.C., P.C.,  
810 P.A.C., G.K., C.L., T.M., O.H.M., A.M.R., A.T., I.G.V., T.B.Z., M.S. and B.D.  
811 provided and/or assembled the data used. P.K.M. analysed the data with advises from  
812 M.Sc. and B.D., and led the writing. All authors contributed by critically reading the  
813 subsequent versions of manuscript.

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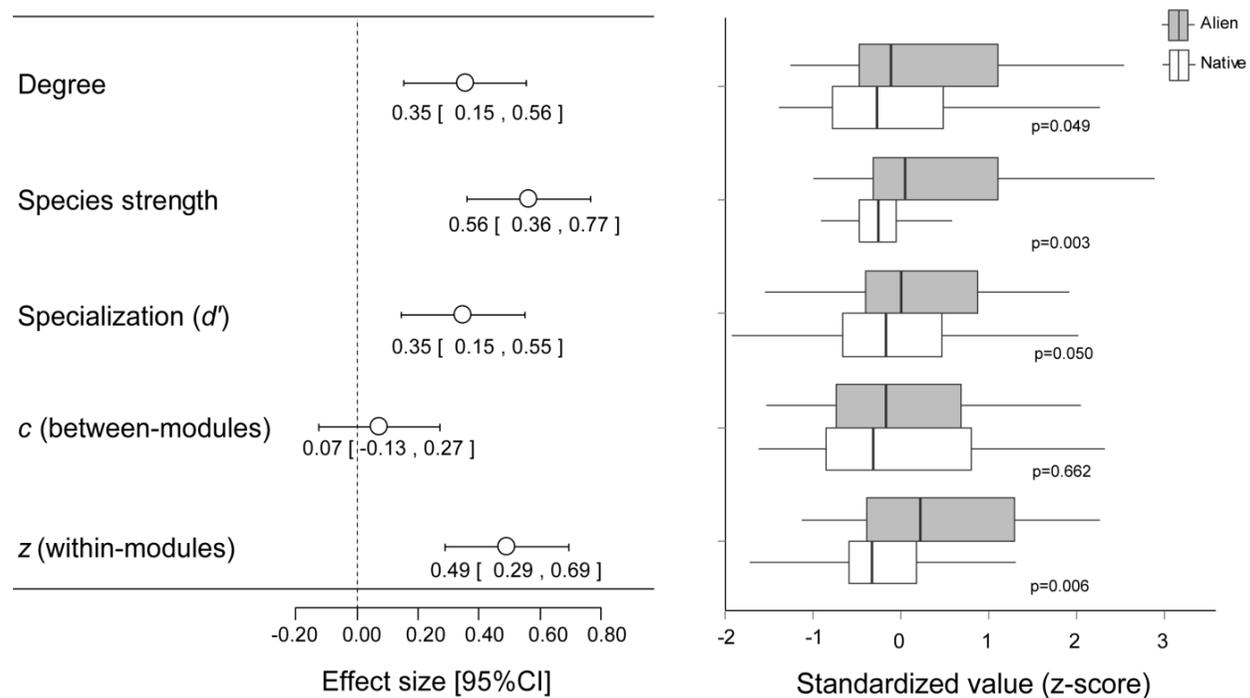
816 **Figure 1** Distribution of 21 Neotropical plant-hummingbird networks containing alien  
817 plant species. Circle size represents the total number of plant species in each network;  
818 colours indicate the proportion of alien plants in each network. Note that some points  
819 have been slightly moved to avoid overlap. Two network representations illustrate how  
820 alien plants are integrated into the networks (top network, Colombian Andes, Snow &  
821 Snow 1980; bottom network, Brazilian Atlantic Rainforest, Maruyama et al. 2015). Top  
822 and bottom rectangles denote hummingbirds and plants, respectively. Alien plants and  
823 their interactions are marked in red. The illustration depicts one such interaction from  
824 the bottom network, between the Saw-billed hermit *Ramphodon naevius* and the  
825 Flowering banana *Musa ornata* originally from Southeast Asia (credit: Pedro Lorenzo).



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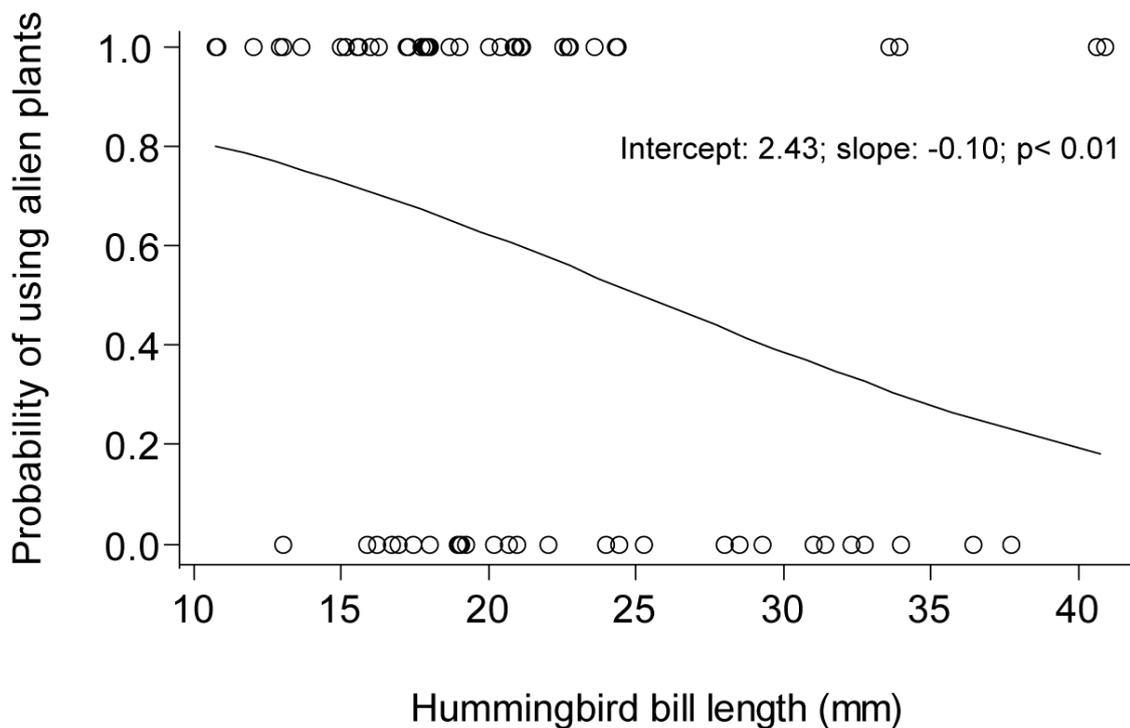
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828 **Figure 2** Species-level network indices for 352 native and 32 alien plant species across 21 plant-hummingbird networks. On the left, we show  
 829 the effect sizes (Cohen's *d*) comparing alien and native plant species for various network indices; an effect size is considered significant if the  
 830 95% CI of the mean differences do not overlap zero (Nakagawa & Cuthill 2007). On the right, box-plots illustrate the distribution of standardized  
 831 index values along with their significance, as obtained from null model analysis. With the exception of *c*, both approaches found that an average  
 832 alien plant have higher network index values than an average native plant.



833

834 **Figure 3** Probability of hummingbird species incorporating alien plant species into their  
835 interactions in relation to their bill length. Each circle illustrates whether a given  
836 hummingbird species incorporates alien plants (1), or not (0). The fitted line reflects the  
837 modelled probability of hummingbird species feeding on alien plants; showing that  
838 short-billed hummingbirds have a higher probability of feeding on alien plants than do  
839 long-billed hummingbird species. We used Generalized Linear Models with binomial  
840 error distribution to assess the significance of the relationships. A Mann-Whitney test  
841 likewise shows significant difference between the bill length of those hummingbirds  
842 incorporating and those not incorporating alien plants in their interactions ( $p = 0.004$ ).



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