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

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5 Biodiversity Research

6 Running header: Alien plants in plant-hummingbird networks

7

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

10

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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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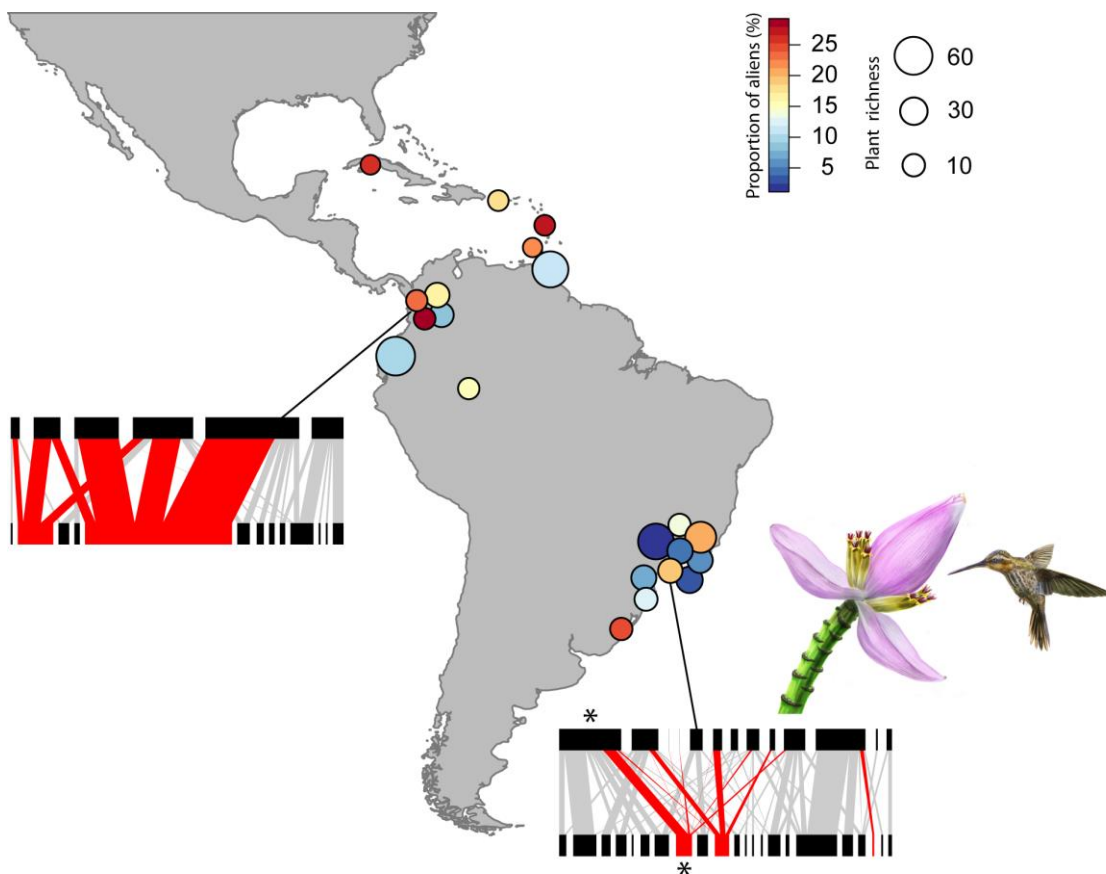
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808 Author contributions: P.K.M., J.V.B., J.S., A.M.M.G, M.Sc. and B.D. contributed with
809 the design for the study. P.K.M., J.V.B., J.S., A.M.M.G., A.C.A., A.C.B., J.C., P.C.,
810 P.A.C., G.K., C.L., T.M., O.H.M., A.M.R., A.T., I.G.V., T.B.Z., M.S. 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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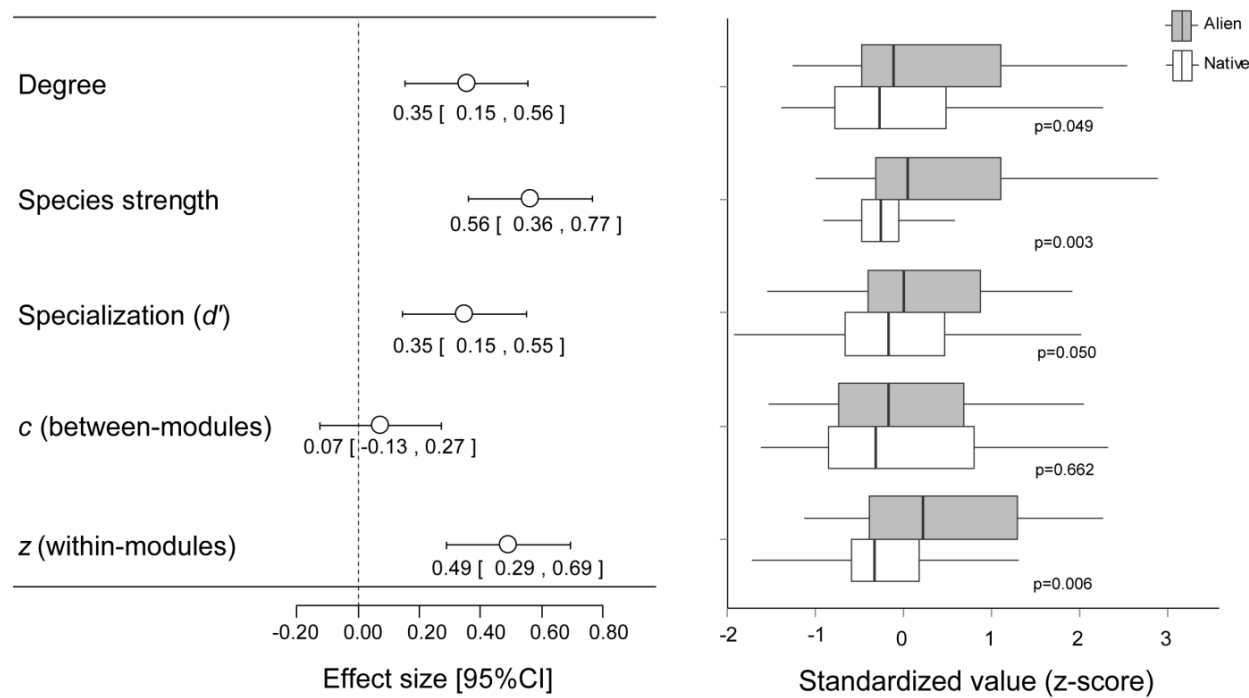
816 **Figure 1** Distribution of 21 Neotropical plant-hummingbird networks containing alien
817 plant species. Circle size represents the total number of plant species in each network;
818 colours indicate the proportion of alien plants in each network. Note that some points
819 have been slightly moved 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).



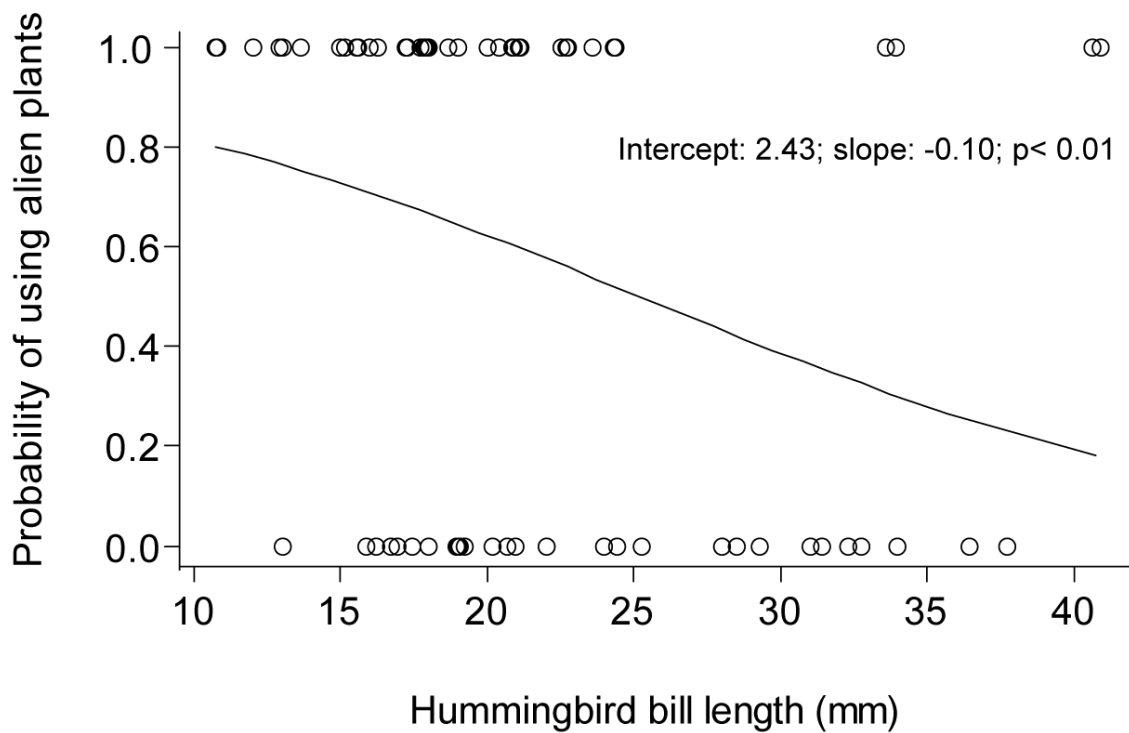
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828 **Figure 2** Species-level network indices for 352 native and 32 alien plant species across 21 plant-hummingbird networks. On the left, we show
 829 the effect sizes (Cohen's *d*) comparing alien and native plant species for various network indices; 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.



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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