

1 **Flower visitation of alien plants is non-linearly related to phylogenetic and floral similarity to native**
2 **plants**

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22 **Conflict of interest**

23 The authors declare that there is no conflict of interest.

24 **Authors' contributions**

25 MR and MvK designed the study, MR, FRJ and PRA collected the data, MR analyzed the data, MR wrote
26 the first draft of the manuscript and all authors contributed to revisions.

27 **Data Availability**

28 Should the manuscript be accepted, the data supporting the results will be archived in a public repository,
29 and the data DOI will be included in the article.

30 **Abstract**

- 31 1. Biological invasions are key to understanding major ecological processes that determine
32 the formation of novel interactions. Flower visitation to alien species may be facilitated
33 by co-flowering natives if they share similar floral traits with the latter. However, if
34 competition for pollinators is important, flower visitation to alien species may be higher if
35 they have traits different from those of native species. We tested whether flower visitation
36 to alien plants depended on phylogenetic relatedness and floral similarity to native plants.
- 37 2. In a field experiment, we simulated invaded communities by adding potted alien plants
38 into co-flowering native communities. We recorded flower visitation to pairs of 34 alien
39 and 20 native species totalling 151 species combinations for 3,068 hours.
- 40 3. Flower visitation to alien species was highest when they had intermediate floral trait
41 distances to native species, and either low or high phylogenetic distances. The alien plants
42 received more similar flower-visitor groups to natives when they had low phylogenetic
43 and either low or high floral trait distances to native plants.
- 44 4. The non-linear patterns between flower visitation and similarity of the alien and native
45 species suggest that an interplay of facilitation and competition simultaneously drives the
46 formation of novel plant-pollinator interactions. The shapes of the relationships of
47 phylogenetic and floral trait distances with flower visitation to alien plants were
48 contrasting, possibly due to different strengths of phylogenetic signal among traits.
- 49 5. We provide experimental evidence for the effects of relatedness and functional similarity
50 to native plants on flower visitation of alien plants. We show that such effects might be
51 non-linear, and that effects of trait dissimilarity and phylogenetic distance on pollinator-
52 mediated interactions can reflect different mechanisms.

53 **Keywords** Darwin's Naturalization Hypothesis, environmental filtering, exotic species, floral
54 traits, invasion ecology, limiting similarity, phylogenetic distance, pollination niche

55

56 **Introduction**

57 Biological invasions are a major characteristic of human-induced global environmental
58 change. Invaded ecosystems and communities in many parts of the world have been affected
59 severely (Fei et al., 2014; Vilà & Hulme, 2017). For this reason, much of the efforts in ecological
60 research has aimed at understanding what determines invasiveness. Furthermore, biological
61 invasions represent natural experiments that offer real-time opportunities to study the assembly of
62 communities (Shea & Chesson, 2002; Tilman, 2004). Specifically, as many alien organisms have
63 integrated into native resident communities, biological invasions are key to understanding the
64 major ecological processes that determine the formation of novel interactions.

65 As related species are likely to be more similar, they should show strong niche overlap
66 and compete for shared resources. Based on this premise, Darwin (1859) posed that relatedness
67 between the alien and the native species could impede the success of alien species (Darwin's
68 Naturalization hypothesis). At the same time, if there are related native species, this indicates that
69 the environment will most likely be suitable for the alien species too (Preadaptation hypothesis).
70 These two hypotheses, with opposing predictions on how relatedness between alien and native
71 species should affect invasion success, are now known as Darwin's Naturalization Conundrum
72 (Diez et al., 2008). Indeed, the results of previous studies testing these hypotheses are largely
73 inconsistent, suggesting that the two mechanisms act at different scales and stages of invasion
74 (Cadotte et al., 2018; Thuiller et al., 2010). Moreover, most of the previous studies were
75 correlative, based on floristic lists and field observations (Cadotte et al., 2018; Gallien &
76 Carboni, 2017; Sheppard et al., 2018), whereas manipulative experiments, in which species are
77 introduced into communities to provide causal insights (e.g. Malecore et al., 2019), are scarce.
78 Furthermore, most previous studies considered direct interactions between alien and native plant
79 species (e.g. competition for space or nutrients), but very few studies have tested indirect
80 interactions such as those mediated by pollinators (but see Bezeng et al., 2015; Burns et al.,
81 2011). However, as about half of all flowering plant species relies on pollinators for at least 80%
82 of their seed production (Rodger et al., 2021), the ability to attract resident pollinators can play a
83 major role in the integration of alien plants in novel communities.

84 To reproduce in the non-native range, alien plants, which are often decoupled from their
85 historical pollinators can use resident pollinators (Razanajatovo et al., 2015; Razanajatovo & van
86 Kleunen, 2016; Traveset & Richardson, 2014), and thereby form novel plant-pollinator

87 interactions. There have been two apparently contradicting major concepts on the roles of plant-
88 pollinator interactions in the assembly of invaded communities (Sargent & Ackerly, 2008). First,
89 in the case of pollinator facilitation, alien plant species that can use the same pollinators as the
90 native plant species (because they have more similar floral traits) should more readily attract
91 pollinators, with similar abundance and composition to native plant species. Second, in the case
92 of pollinator-mediated competition, alien plant species that can use pollinators different from
93 those of native plant species should more readily attract pollinators in the local community. In
94 both cases, the formation of novel plant-pollinator interactions between alien plants and resident
95 pollinators should depend on the plant traits that influence flower visitation.

96 To advance our understanding of the ecological processes that govern the formation of
97 novel plant-pollinator interactions, a trait-based approach (Kraft & Ackerly, 2014; McGill et al.,
98 2006) has been suggested (Aslan et al., 2015). Floral traits, such as flower symmetry, color and
99 size, can act as signals for flower visitors to locate floral rewards, and have therefore been
100 considered as important traits that mediate plant-pollinator interactions (Fornoff et al., 2017;
101 Junker et al., 2015; Ortiz et al., 2021; Reverté et al., 2016). Furthermore, nectar production has
102 been shown to influence the indirect interactions between co-flowering plants with shared
103 pollinators (Carvalho et al., 2014). Nevertheless, the floral traits involved in pollinator
104 attraction are still generally missing from studies in plant-community ecology (E-Vojtkó et al.,
105 2020; Sargent & Ackerly, 2008). A meta-analysis seeking to understand the impacts of alien
106 species on the pollination and reproductive success of native species considered floral traits, and
107 showed that similarities in flower symmetry and color in alien and native plants increased
108 competition for pollinators (Morales & Traveset, 2009). Therefore, similarity in these floral traits
109 may play critical roles in pollinator-mediated alien-native plant interactions.

110 The patterns of novel plant-pollinator interactions may differ with regard to phylogenetic
111 and floral trait distances. While phylogenetic relatedness is frequently assumed to be a proxy for
112 trait similarity, some floral traits may not be evolutionarily conserved (Sargent & Ackerly, 2008).
113 For example, closely related species frequently have different flower colors (Eaton et al., 2012;
114 Shrestha et al., 2014). Alien plant species that are phylogenetically closely related to native
115 species may have either similar or dissimilar traits to native species. Also, alien species that are
116 phylogenetically distantly related to native species may have either similar (convergent
117 evolution) or dissimilar traits to native species. It is therefore important to consider both

118 phylogenetic distance and trait dissimilarity (Cadotte et al., 2013; Lemoine et al., 2015), and to
119 disentangle the effects of both (Marx et al., 2016). Thus, the patterns of novel plant-pollinator
120 interactions might be more complex than those predicted by Darwin's Naturalization Conundrum
121 (Diez et al., 2008). Furthermore, different mechanisms may act simultaneously to drive the
122 success of alien species, as has been shown for direct plant-plant interactions (Malecore et al.,
123 2019; Sheppard et al., 2018). When both pollinator facilitation and competition for pollinators
124 play a role, flower visitation to alien species should be highest or lowest at intermediate
125 phylogenetic and floral trait distances to native species. It is therefore important to consider
126 nonlinear relationships between flower visitation to alien species and phylogenetic and floral trait
127 distances to native species.

128 In a field experiment in which we simulated invaded communities by adding potted alien
129 plants into co-flowering native communities, we tested whether flower visitation to alien plants
130 depended on phylogenetic relatedness and functional similarity to native plants. For pollinator
131 facilitation and competition for flower visitors, respectively, we predicted a negative and a
132 positive relationship between flower visitation to alien species and phylogenetic or floral trait
133 distance to natives. If both mechanisms were operating, we predicted non-linear relationships
134 with either high or low flower visitation at intermediate phylogenetic or floral trait distances (i.e.
135 hump- or U-shaped relationships). Most previous studies on pollinator-mediated alien-native
136 plant interactions investigated the impacts of co-flowering alien plants on the pollination and
137 reproductive success of native species. Our study, in contrast, assessed the outcomes of pollinator
138 facilitation by and competition for flower visitors with native species on alien species to
139 understand how alien plants attract pollinators in the invaded range. More specifically, we asked
140 (1) whether flower visitation to alien plants was related to the phylogenetic and floral trait
141 distances between the alien and native species, and (2) whether the similarity in flower visitor
142 composition was related to the phylogenetic and floral trait distances between the alien and native
143 species.

144 **Materials and Methods**

145 *Study species and sites*

146 To simulate invaded communities in a field experiment in central Europe, we selected 34
147 herbaceous insect-pollinated neophytes (i.e. alien species introduced after the discovery of the

148 Americas in 1492), covering a broad variation in floral traits such as size, symmetry and colors,
149 occurring in semi-natural grasslands and anthropogenic or ruderal habitats, and usually flowering
150 between April and September. The alien species belonged to 14 plant families, 68% were short-
151 lived (annual or biennial), and 24% were self-incompatible (Supporting Information Table S1).
152 The species neophyte status was based on information in the Floraweb
153 (<http://floraweb.de/index.html>) and the Bioflor (Kühn et al., 2004) databases. We precultivated
154 the alien plant species from seeds or seedlings (Table S1) in the research garden of the University
155 of Konstanz in Germany (<http://www.uni-konstanz.de/botanischergarten/>) until they flowered.
156 From May to September 2018, we carried out the field experiment in managed meadows near the
157 city of Konstanz (Table S2).

158 *Experimental set-up and flower-visitation recording*

159 Two to three days before adding alien plants to flowering resident native communities, we
160 prospected grasslands around the city of Konstanz, and identified sites that were visibly
161 dominated by one flowering native species, which served as the host native species. We then
162 recorded the density of flowers as the number of flower units per 1m² for all flowering species
163 recorded in one 25 m² plot at each site. To standardize the number of flower units across different
164 species, we considered a flower unit to correspond to a receptacle area of 1 cm² (Carvalho et
165 al., 2014). We selected a total of 25 sites where the density of flowers for the host native species
166 and for all flowering species ranged from 24 to 4,900 and from 10 to 1,763, respectively (Table
167 S2). To simulate invaded communities, we placed for up to ten alien species (range=4-10,
168 median=5) up to five (range= 2-5, median=4) potted flowering individuals into a site. The exact
169 numbers depended on the availability of flowering alien plants. We paired each added alien plant
170 individual with a host native plant individual. To let the alien plants adjust to the flower-visitor
171 communities, and the insects to the newly added plants, we left the alien plants for two to three
172 days at each site before we recorded flower visitation. We used a total of 20 host native species,
173 i.e. the dominant flowering native species at a site (Table S2), belonging to ten plant families. In
174 total, we had 151 combinations of added alien and host native species, spanning phylogenetic
175 distances between the alien and the native species from 10.64 to 295.60 (median=236.40) million
176 years (for the calculation of phylogenetic distance, see below).

177 To record flower visitation, we placed a BRINNO TLC200 time-lapse camera
178 (<https://www.brinno.com/time-lapse-camera/TLC200>) at a vertical distance of 25-30 cm above

179 the flowers of the paired flowering alien and native plants (Fig. S1). We set the time-lapse
180 interval at 2 seconds and recorded from 10:30 to 16:30 on a sunny day (except for two set-ups in
181 which we recorded from 9:30 to 14:30 due to logistic constraints). Sampling was done on one day
182 for each setup. By using 40 cameras, we could observe many pairs of plants simultaneously. The
183 alien plants were removed from the experimental plots at the end of the recording day. We
184 collected a total of 3,068 hours of observations, which corresponded to 3 terabytes of video files.
185 We analyzed each video file manually using the Blender software (<https://www.blender.org/>).
186 The video analysis consisted of counting flower visits to the alien and the native plants in each
187 species pair. We considered a flower visit when the flower visitor made contact with reproductive
188 organs (anther and stigma). We attributed each flower visitor to one of the following flower
189 visitor groups: Hymenoptera: honeybees (*Apis* spp.), bumblebees (*Bombus* spp.), other bees and
190 wasps; Coleoptera (beetles); Diptera: hoverflies/syrphids and other flies; Lepidoptera: butterflies
191 and moths; Mecoptera; Neuroptera; other unknown groups (impossible to identify). We recorded
192 flower visitation for each one-hour interval within the whole recording time. We also counted the
193 number of observed alien and native flower units within each frame.

194 ***Measurements of floral traits***

195 Using five plants per added alien and host native species at each site, we measured floral
196 traits that most likely influence flower-visitor attraction. We recorded flower symmetry (radial or
197 bilateral), and measured flower size as the diameter or the largest width of a flower. To measure
198 flower color, we measured floral reflectance spectra using an AvaSpec-2048 fibre optic
199 spectrometer and an Ava Light-XE xenon light source (Avantes, Eerbeek, The Netherlands)
200 relative to a standard white reference tile (WS-2) at an angle of 90°. We measured the reflectance
201 spectra of five corolla samples (each from different plants) per added alien and host native
202 species. We classified the spectra into four binomial categories: blue (wavelength 401-470 nm),
203 green (471-540 nm), yellow (541-610 nm) and red (611-680 nm), based on the presence/absence
204 of local maxima at the respective wavelength interval (Fornoff et al., 2017). As a measure of the
205 presence of floral rewards, we added data on nectar production (yes/no) using database and
206 literature sources (Table S3).

207 ***Calculation of phylogenetic and floral trait distances***

208 To test whether flower visitation to the alien species was influenced by relatedness and
209 floral similarity between the alien and the native species, we calculated phylogenetic and floral

210 trait distances. We constructed a phylogenetic tree for the alien and native species by pruning the
211 dated DaPhnE supertree (Durka & Michalski, 2012). Because *Hypochoeris radiata* was not
212 included in the DaPhnE tree, we added a tip at the root of the Hypochoeris genus using the
213 `add.species.to.genus` function of the `phytools` package (Revell, 2012) in R version R-4.0.4 (R-
214 Core-Team, 2021). For each pair of added alien and host native species, we calculated the
215 phylogenetic distance using the `cophenetic` function of the `ape` package (Paradis & Schliep, 2019)
216 in R. To calculate an overall floral trait distance between each pair of alien and native species, we
217 calculated the Gower dissimilarity (Gower, 1971) based on continuous (flower size) and
218 categorical (flower symmetry, binary floral reflectance components and nectar production) floral
219 traits, using the `gowdis` function of the `FD` package (Laliberté et al., 2014; Laliberté & Legendre,
220 2010) in R. We also calculated single floral trait distances and dissimilarities between the alien
221 and the native species: flower-size distance, flower-symmetry dissimilarity, dissimilarity in each
222 of the four floral reflectance components, and nectar-production-dissimilarity. We calculated
223 absolute and hierarchical floral trait distances (Ferenc & Sheppard, 2020; Kunstler et al., 2012).
224 To assess the association between phylogenetic and floral trait distances, we estimated the
225 strength of the phylogenetic signal, using Pagel's lambda with the `phylosig` function of the
226 `phytools` package for the continuous trait, and the phylogenetic D statistic with the `phylo.d`
227 function of the `caper` package (Orme et al., 2012) for the categorical traits.

228 *Statistical analyses*

229 To test whether flower visitation to alien plant species depended on the phylogenetic and
230 floral trait distances between the alien and the native species, we analyzed the total number of
231 flower visits to the added alien plants, the proportion of flower visits to the alien plant relative to
232 the sum of flower visits to both alien and host native plants, and the similarity between the flower
233 visitor compositions of the alien and the native plants.

234 We analyzed the total number of flower visits to the alien plants with negative binomial
235 generalized linear mixed models using the `glmer.nb` function in the `lme4` package (Bates et al.,
236 2014) in R. To account for potential variation due to floral characteristics of the observed plants,
237 we included the number of observed flower units of the native plant, the number of observed
238 flower units of the alien plant, the flower size, the flower symmetry (radial=0, bilateral=1), the
239 floral reflectance binary categories Wavelength 401-470 nm, Wavelength 471-540 nm,
240 Wavelength 541-610 nm and Wavelength 611-680 nm of the alien plants, and the nectar

241 production (absent=0, present=1). To account for potential variation of flower-visitor activity
242 during the day, we additionally included the time interval during the day (one-hour intervals as a
243 discrete variable) as an explanatory variable. To test for the effects of either the phylogenetic or
244 the floral trait distance between the alien and the native species, we also included them as
245 explanatory variables. All covariates were centered to means of zero and scaled to standard
246 deviations of one. To test for potential nonlinear effects, we included the quadratic terms for the
247 time interval during the day and phylogenetic or floral trait distance. As the latter were centered
248 and scaled, the non-linear effects test for hump- and U-shaped relationships. We also ran the
249 models with linear terms only, and we present the results of the model with the lowest AIC. To
250 account for non-independence of observations within species, we included identities of the added
251 alien species and the host native species as random factors. Models including site as an additional
252 random factor to account for potential variation due to site characteristics, such as floral
253 abundance, did not converge, as native species and site were largely confounded (Table S1).
254 Similarly, models including date of observation as a random factor to account for potential
255 variation due to change in flower visitor communities along the growing season did not converge.
256 To understand whether the resulting patterns were driven by a particular flower visitor group, we
257 also built similar models in which we used as response variables the number of flower visits to
258 the alien plants by Hymenoptera only and by Diptera only, representing the insect orders that
259 contributed most visits (77.24 % and 10.57 %, respectively). We also built models in which we
260 considered each floral trait distance between the alien and the native species separately, instead of
261 an overall floral trait distance. We considered absolute and hierarchical floral trait distances.
262 Additionally, we built models in which we included both phylogenetic and floral trait distances,
263 instead of separately.

264 To account for the number of flower visits to native plants, we analyzed the logit
265 transformed proportion of flower visits to the alien plant relative to the sum of flower visits to
266 both alien and host native plants (Warton & Hui, 2011) in linear mixed models using the lmer
267 function of the lme4 package in R. We included the same explanatory variables and random
268 factors as in the above models, except for the number of observed flower units of the alien and
269 the native plants, which we replaced with the logit transformed ratio of the number of flower
270 units of the alien plant divided by the sum of the numbers of flower units of the alien and native
271 plants.

272 To analyze the similarity of the flower-visitor compositions between the alien and the
273 native plants, we calculated a Bray-Curtis similarity index (one minus Bray-Curtis dissimilarity
274 index) based on the abundance of each flower-visitor group (excluding the unknown groups). We
275 analyzed the logit transformed Bray-Curtis similarity index in linear mixed models using the lmer
276 function of the lme4 package in R. We included the same explanatory variables and random
277 factors as in the above models. From these models, we excluded the 1,051 observations for which
278 the number of flower visits to the alien or to the native plant was zero, leaving 2,017 observations
279 with flower visits. For all models, we reported the marginal and conditional r^2 (Nakagawa et al.,
280 2017).

281 **Results**

282 *Effects of phylogenetic and floral trait distances on flower visitation*

283 The alien plants received significantly more flower visits in the middle of the day around
284 12:00 (Fig. S2) and the number was higher when more of their flower units were observed
285 (Tables 1 and 2). Moreover, they received more visits when they had larger flowers, when their
286 floral reflectance had local maxima in the yellow wavelength interval 541-610 nm, and when
287 they produced nectar (Tables 1 and 2). The alien plants received significantly fewer flower visits
288 when the number of observed flowers on the paired native plant increased (Tables 1 and 2).
289 Among the floral traits, flower size and symmetry had strong phylogenetic signals (Table 3). We
290 found that the phylogenetic distance between the alien and the native plant had significant
291 nonlinear effects on the total number of flower visits to the alien plant and on the proportion of
292 flower visits to the alien relative to the total number of visits to alien and native plants (Fig. 1a
293 and 1c, Table 1). Flower visitation to aliens was lowest when they had intermediate phylogenetic
294 distances to natives (Fig. 1a and 1c). The floral trait distance between the alien and the native
295 plant also had significant nonlinear effects on the total number of flower visits to the alien plant
296 and on the proportion of flower visits to the alien relative to the total number of visits to alien and
297 native plants (Fig. 1b and 1d, Table 2). The alien plants with intermediate floral trait distances to
298 native plants received the most flower visits (Fig. 1b and 1d). We found qualitatively similar
299 results in the analysis of flower visitation by Hymenoptera only (Table S4), but partly different
300 results in the analysis of flower visitation by Diptera only (Table S5). We also found qualitatively
301 similar results in the analyses including both phylogenetic and floral trait distances (Table S6).

302 When single absolute floral trait distances were considered separately, we found that alien
303 plants received significantly more flower visits when flower symmetry, the presence of local
304 maxima in the green wavelength interval 471-540 nm of the reflectance spectra and nectar
305 production were dissimilar to the native plants (Table S7). Alien plants received significantly
306 fewer flower visits when flower size distance was larger and when the presence of local maxima
307 in the blue wavelength interval 401-470 nm was dissimilar to the native plants (Table S7). When
308 hierarchical floral trait distances were considered, we found that alien plants received
309 significantly more flower visits when native plants had local maxima in the blue wavelength
310 interval 401-470 nm of the flower reflectance spectra and the alien plants not (Table S8). Alien
311 plants received significantly fewer flower visits when native plants produced nectar and the alien
312 plants not (Table S8).

313 *Effects of phylogenetic and floral trait distances on similarity in composition of flower visitors to*
314 *alien and native species*

315 The alien plants received significantly more similar flower visitors to those on native
316 plants when the floral reflectance of the alien plant had local maxima in the yellow wavelength
317 interval 541-610 nm, and marginally significantly when the alien plant produced nectar (Table 4).
318 The alien plants received significantly fewer flower visitors that were similar to those on native
319 plants when the number of observed flowers on the native plants increased (Table 4). We found
320 that the phylogenetic distance between the alien and the native plant had a significant negative
321 effect on the similarity between the flower visitor compositions of the alien and the native plants
322 (Fig. 1e, Table 4). The alien plants with high phylogenetic distances to native plants had the least
323 similar flower visitor composition to native plants. The floral trait distance between the alien and
324 the native plant had a significant nonlinear effect on the similarity between the flower visitor
325 compositions of the alien and the native plants (Fig. 1f, Table 4). The alien plants with
326 intermediate floral trait distances to native plants had the least similar flower visitor composition
327 to native plants (Fig. 1f).

328 **Discussion**

329 In a field experiment simulating invaded co-flowering communities, we found that flower
330 visitation to alien species was highest when they had intermediate floral trait distances to native
331 species, but either low or high phylogenetic distances. This apparent discrepancy may be due to

332 different strengths of phylogenetic signal among traits. The alien plants also received more
333 similar flower visitor groups to natives when they had low phylogenetic and either low or high
334 floral trait distances. The non-linear patterns could be the combined result of facilitation for
335 flower visitation (causing a negative relationship between phylogenetic or floral trait distance and
336 flower visitation to alien species) and competition for flower visitors (causing a positive
337 relationship) (Gallien & Carboni, 2017).

338 *Non-linear effects of phylogenetic and floral trait distances*

339 Environmental filtering would benefit alien plants that are similar to the native ones, and
340 pollination could be one of the environmental filters. Novel pollinator-mediated alien-native plant
341 interactions can be characterized by a positive influence of co-flowering native plants on the
342 pollination of alien plants (facilitation). Pollinator facilitation operates through different trait-
343 based-effect mechanisms including mimic and magnet effects (Braun & Lortie, 2019). Dominant
344 co-flowering native plants can act as mimic or magnet species that attract pollinators to serve the
345 aliens plants, which have usually left their historical pollinators behind. Pollinator facilitation has
346 been documented in different invaded and non-invaded flowering communities (Bergamo et al.,
347 2020; Ha et al., 2021; Molina-Montenegro et al., 2008; Tur et al., 2016). Some previous studies
348 also provided evidence for pollinator facilitation by alien species to co-flowering natives through
349 the magnet species effect (Groulx & Sargent, 2018; Masters & Emery, 2015; Montero-Castaño &
350 Vilà, 2015; Stiers et al., 2014). The non-linear patterns between flower visitation and similarity of
351 the alien and native species in our study suggest flower visitor facilitation by native species to
352 alien species, at least partially. Nevertheless, more detailed assessments on its effects on plant
353 reproduction should be required to understand the exact processes operating.

354 The observed patterns of novel pollinator-mediated alien-native plant interactions can also
355 be the outcome of a negative influence of co-flowering native plants on the flower visitation to
356 alien plants (competition). Such competitive interactions are expected to be strongest between
357 plant species that are very similar. The mechanisms of competition for pollinators are complex,
358 including effects of the number of visits on quantity and quality of conspecific pollen received
359 (Mitchell et al., 2009). Alien plants co-occurring and sharing pollinators with one or more
360 dominant flowering natives can compete for pollinator attention, leading to a reduction in flower
361 visitation to the aliens. Pollinator facilitation and competition for pollinators can also act

362 simultaneously in pollinator-mediated alien-native plant interactions (e.g. Bergamo et al., 2018).
363 As we did not quantify visitation to aliens in the absence of natives, we could not quantify
364 facilitation and competition directly. However, as the strength of facilitative and competitive
365 interactions is likely to depend on the dissimilarity of the species, the non-linear patterns we
366 found suggest an interplay of facilitation and competition (Gallien & Carboni, 2017).

367 *A discrepancy between the effects of phylogenetic and floral trait distances*

368 Most studies on Darwin's Naturalization Conundrum use phylogenetic distance because it
369 should reflect how functionally dissimilar the species are. This is based on the idea that most
370 traits are phylogenetically conserved. While we found strong phylogenetic signals for flower size
371 and symmetry, the signals were much weaker for spectral reflectance and nectar production,
372 suggesting that phylogenetic distance might not entirely capture functional trait distance. Other
373 studies have also found that flower color is not strongly conserved (Rausher, 2008; Shrestha et
374 al., 2014). On the other hand, in contrast with our results, (Ornelas et al., 2007) found a strong
375 phylogenetic signal in nectar volume and sugar production in their study using 289 species.
376 Remarkably, in our study, while flower visitation was highest at intermediate floral trait distances
377 it was lowest at intermediate phylogenetic distances. This shows that patterns for phylogenetic
378 and trait dissimilarity do not need to be consistent, and may reflect different mechanisms.

379 Whether co-flowering alien and native plants interact via pollinator facilitation and
380 competition for pollinators depends on the degree of pollinator sharing. In an analysis of 29
381 plant-pollinator networks, (Vamosi et al., 2014) found that pollinators were more likely to visit
382 closely related species. By analyzing the phylogenetic relatedness among both plants and animals
383 in 36 plant-pollinator and 23 plant-frugivore networks, (Rezende et al., 2007) found that
384 phylogenetically closely related species interacted with a similar set of species. In our study, alien
385 plants with high phylogenetic and intermediate floral trait distances to native plants had the least
386 similar flower-visitor composition to natives (Fig. 1). This suggests that floral trait distances may
387 influence pollinator sharing. Also, the higher visitation of alien plants with intermediate floral
388 trait distances may be largely due to visitation by insects that do not visit the native plants.
389 Nevertheless, future studies should identify flower visitors to more resolved taxonomic levels to
390 more accurately assess the relationships of phylogenetic and floral trait distances with pollinator
391 sharing.

392 In line with previous findings on pollinator-mediated interactions between alien and
393 native plants (Morales & Traveset, 2009), we found that dissimilarity in floral symmetry was
394 associated with competition for pollinators, as indicated by a positive relationship between floral
395 symmetry dissimilarity and flower visitation to alien plants (Table S7). However, our result on
396 dissimilarity in flower color was partly different from previous studies, as dissimilarity in
397 different components of floral reflectance was associated with either competition or facilitation.
398 For example, we found a negative relationship between dissimilarity in the blue wavelength
399 patterns of petals and flower visitation to alien plants (Table S7). This may be driven by the most
400 abundant flower visitors in our study, the bees (Hymenoptera), which frequently prefer the blue
401 wavelengths (Hsu & Yang, 2012; Razanajatovo et al., 2015). Our findings could thus indicate
402 that similarity in blue wavelength patterns in the petals may increase pollinator facilitation by
403 bees. While previous studies on pollinator-mediated community assembly processes were based
404 on patterns of floral trait distributions within communities (de Jager et al., 2011; Fornoff et al.,
405 2017), by using a manipulative experiment and focusing on pairs of alien and native plants, our
406 results suggest an important role of floral trait similarity in the formation of novel interactions.

407 In our study, the shapes of the relationships of phylogenetic and floral trait distances with
408 flower visitation to alien plants were contrasting (Fig. 1). The reason for this apparent
409 discrepancy could lay in the floral traits considered in the study and that we may not have
410 measured all relevant traits. If the floral traits are evolutionarily conserved, patterns of trait
411 similarity can be reflected by phylogenetic relatedness (Sargent & Ackerly, 2008). Out of the
412 seven traits included in our study, only flower size and symmetry had strong phylogenetic signals
413 (Table 3). Furthermore, single floral trait distances had different directions of effects, suggesting
414 facilitative, neutral or competitive effects (Table S7). While for the number of visits to aliens, our
415 phylogenetic distance model had the best fit (lowest AIC), interestingly, for the proportional
416 visits and the visitor community similarity, the floral trait distance models had the best fit. Thus,
417 our findings suggest that both phylogenetic and floral trait distances influence pollinator
418 mediated alien-native plant interactions.

419 *Flower visitation as a proxy for reproductive success*

420 As flower visitors vary in their pollination effectiveness and can even be antagonists, by
421 considering only flower visitation, we cannot be completely certain about which visitors are

422 effective pollinators. Charlebois & Sargent (2017) found a significant relationship between
423 change in flower visitation and change in reproductive success, with a large variability in
424 reproductive success unexplained by change in visitation. They suggested that although flower
425 visitation is not the ideal proxy for reproductive success, it is still very useful (Charlebois &
426 Sargent, 2017). Because seed production and its effect on population growth and invasion should
427 be most important for short-lived self-incompatible alien plants, the ability to attract pollinators
428 in the invaded range might be crucial for such species. Our study included both short- and long-
429 lived species, and self-compatible and self-incompatible species (Table S1), but these life-history
430 characteristics were not related to flower visitation (Tables S9 and S10). Future experiments
431 should assess whether the magnitude of pollen limitation of seed production, and subsequent
432 population dynamics of the alien plants is related to phylogenetic and floral trait distances to co-
433 flowering natives.

434 **Conclusions**

435 By showing nonlinear effects of phylogenetic and floral trait distances to native species
436 on flower visitation to alien species, this study advances our understanding of how alien plants
437 receive pollination services in the invaded range. Multiple mechanisms and processes including
438 an interplay of pollinator facilitation and competition for pollinators can simultaneously act to
439 engage the formation of novel pollination interactions. We illustrate the importance of
440 considering floral traits in plant community ecology studies to understand major ecological
441 processes such as the formation of novel interactions.

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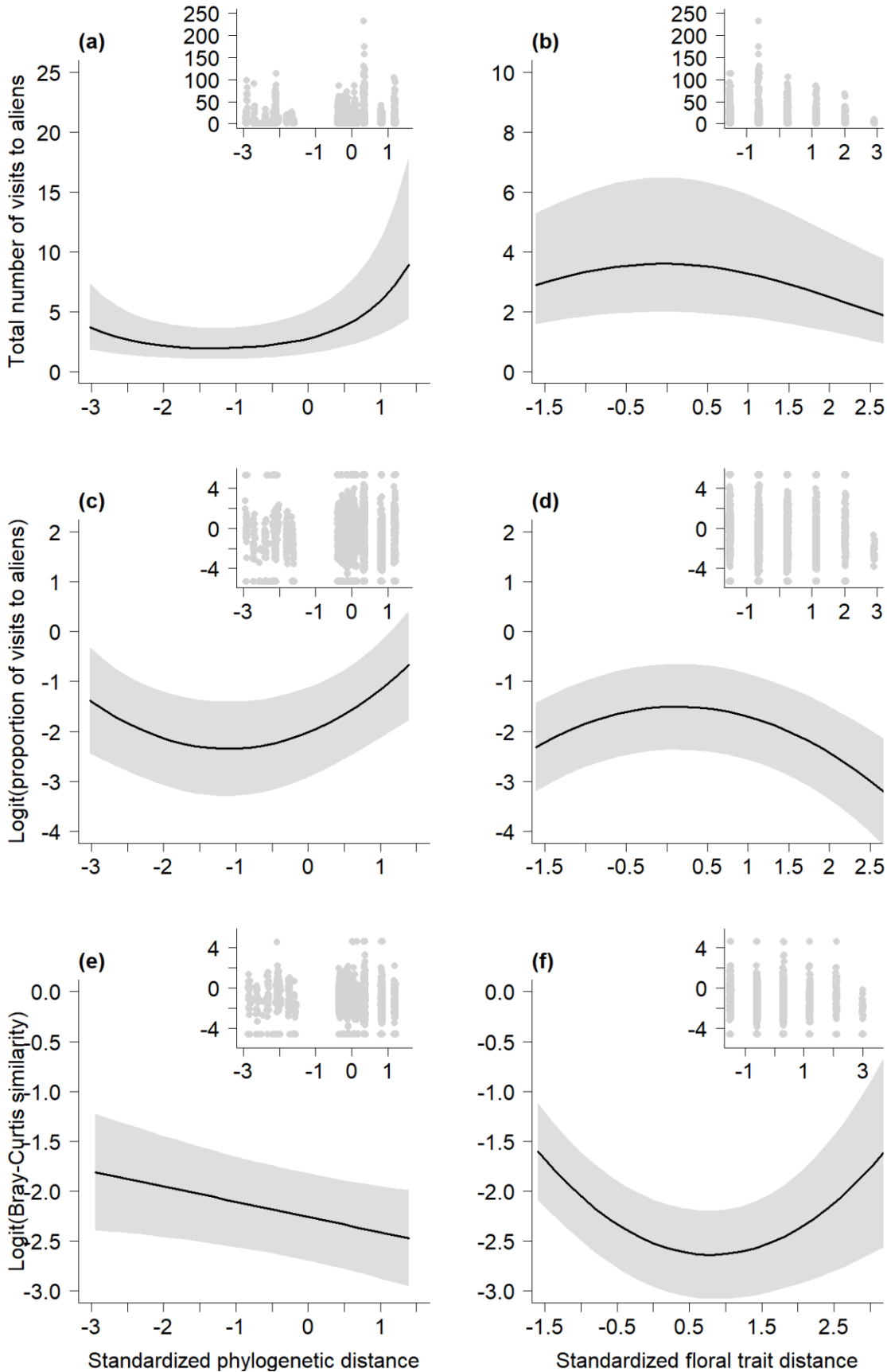
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644

645

646 **Figure**

647 **Fig. 1** Effects of phylogenetic and floral trait distances on flower visitation to alien plants and on
648 similarity in composition of flower visitors to alien and native plants. (a) Effects of phylogenetic
649 distance on the total number of flower visits to alien plants. (b) Effects of floral trait distance on
650 the total number of flower visits to alien plants. (c) Effects of phylogenetic distance on the
651 proportion of flower visits to alien plants. (d) Effects of floral trait distance on the proportion of
652 flower visits to alien plants. (e) Effects of phylogenetic distance on the similarity in composition
653 of flower visitors to alien and native plants. (f). Effects of floral trait distance on the similarity in
654 composition of flower visitors to alien and native plants. Continuous and dashed curves indicate
655 significant and non-significant effects, respectively. Polygons delimit 95 % confidence intervals.
656 Insets at the right upper corner of each graph show the raw data.



658 **Tables**

659 **Table 1** Results of a negative binomial generalized linear mixed model and a linear mixed model testing how the phylogenetic
 660 distance between the alien and the native plants influence the total number of flower visits to the alien plant and the proportion of
 661 flower visits to the alien relative to the total number of flower visits to the alien and the native plants (n=3068).

| Response variables | Total number of flower visits to the alien plant | Proportion of flower visits to the alien relative to the sum of flower visits to the alien and native plants |
|---|--|--|
| Fixed terms | Estimate (Standard error) | Estimate (Standard error) |
| Intercept | 1.014 (0.302) | -2.018 (0.449) |
| Number of flower units of the native plant | -0.133 (0.032) | |
| Number of flower units of the alien plant | 0.381 (0.045) | |
| Number of flower units of the alien divided by the sum of the number of flower units of the alien and the native plants | | 1.178 (0.073) |
| Flower size of the alien plant | 0.482 (0.173) | 1.016 (0.267) |
| Flower symmetry of the alien plant | 0.145 (0.322) | 0.509 (0.522) |
| Floral reflectance Wavelength 401-470 nm of the alien plant | -0.554 (0.792) | -0.146 (1.087) |
| Floral reflectance Wavelength 471-540 nm of the alien plant | 2.172 (1.646) | 4.225 (2.258) |
| Floral reflectance Wavelength 541-610 nm of the alien plant | 2.116 (1.017) | 2.875 (1.414) |
| Floral reflectance Wavelength 611-680 nm of the alien plant | 0.787 (0.648) | 0.822 (0.902) |
| Nectar production of the alien plant | 2.220 (1.227) | 1.150 (1.642) |

| | | |
|---|-----------------------|-----------------------|
| Time during the day | -0.067 (0.023) | -0.101 (0.041) |
| Time during the day squared | -0.059 (0.025) | -0.121 (0.047) |
| Phylogenetic distance between the alien and the native plants | 0.545 (0.097) | 0.593 (0.173) |
| Phylogenetic distance between the alien and the native plants squared | 0.212 (0.046) | 0.266 (0.082) |
| Random terms | SD | SD |
| Alien species | 1.564 | 2.136 |
| Native species | 0.468 | 1.002 |
| Residuals | | 2.220 |
| AIC | 16600.400 | 13829.740 |
| Marginal r^2 | 0.263 | 0.233 |
| Conditional r^2 | 0.832 | 0.640 |

662 Significant model parameters are highlighted in bold ($p < 0.05$), and marginally significant model parameters are italicized ($p < 0.1$).

663 **Table 2** Results of a negative binomial generalized linear mixed model and a linear mixed model testing how the floral trait distance
 664 based on floral traits between the alien and the native plants influence the total number of flower visits to the alien plant and the
 665 proportion of flower visits to the alien relative to the sum of flower visits to the alien and the native plants (n=3068).

| Response variables | Total number of flower visits to the alien plant | Proportion of flower visits to the alien relative to the sum of flower visits to the alien and native plants |
|---|--|--|
| Fixed terms | Estimate (Standard error) | Estimate (Standard error) |
| Intercept | 1.280 (0.295) | -1.507 (0.423) |
| Number of flower units of the native plant | -0.156 (0.032) | |
| Number of flower units of the alien plant | 0.369 (0.046) | |
| Number of flower units of the alien divided by the sum of the number of flower units of the alien and the native plants | | 1.330 (0.073) |
| Flower size of the alien plant | 0.563 (0.174) | 0.986 (0.256) |
| Flower symmetry of the alien plant | 0.233 (0.328) | 0.538 (0.513) |
| Floral reflectance Wavelength 401-470 nm of the alien plant | -0.480 (0.769) | -0.055 (1.015) |
| Floral reflectance Wavelength 471-540 nm of the alien plant | 1.431 (1.597) | 2.587 (2.133) |
| Floral reflectance Wavelength 541-610 nm of the alien plant | <i>1.838 (0.992)</i> | 2.507 (1.333) |
| Floral reflectance Wavelength 611-680 nm of the alien plant | 0.804 (0.632) | 0.872 (0.847) |
| Nectar production of the alien plant | 2.240 (1.191) | 1.335 (1.538) |
| Time during the day | -0.068 (0.023) | -0.099 (0.041) |
| Time during the day squared | -0.059 (0.026) | -0.122 (0.047) |

| | | |
|---|-----------------------|-----------------------|
| Floral trait distance between the alien and the native plants | -0.008 (0.036) | 0.070 (0.065) |
| Floral trait distance between the alien and the native plants squared | -0.088 (0.025) | -0.266 (0.045) |
| Random terms | SD | SD |
| Alien species | 1.521 | 1.991 |
| Native species | 0.479 | 1.041 |
| Residuals | | 2.212 |
| AIC | 16620.000 | 13807.730 |
| Marginal r^2 | 0.240 | 0.226 |
| Conditional r^2 | 0.818 | 0.619 |

666 Significant model parameters are highlighted in bold ($p < 0.05$), and marginally significant model parameters are italicized ($p < 0.1$).

667 **Table 3** Strength of the phylogenetic signals for the floral traits of the alien and native species
668 using Pagel's lambda (continuous trait) and phylogenetic D values (categorical traits).

| Floral traits | Phylogenetic signal |
|--|---------------------|
| Flower size | 0.956 ^a |
| Flower symmetry | 0.968 ^b |
| Floral reflectance Wavelength 401-470 nm | 0.041 ^b |
| Floral reflectance Wavelength 471-540 nm | 0.337 ^b |
| Floral reflectance Wavelength 541-610 nm | 0.434 ^b |
| Floral reflectance Wavelength 611-680 nm | 0.013 ^b |
| Nectar production | 0.198 ^b |

669 ^aA value of 1 indicates that the trait follows a pure Brownian motion model of evolution, ^bthe
670 probabilities of phylogenetic D values resulting from Brownian phylogenetic structure are shown.

671 **Table 4** Results of two linear mixed models testing how the phylogenetic or the floral trait distance based on floral traits between the
672 alien and the native plants influence the similarity between the flower visitor composition of the alien and the native plants (logit Bray-
673 Curtis similarity index, n=2017).

| | Analysis with phylogenetic distance Estimate (Standard error) | Analysis with floral trait distance Estimate (Standard error) |
|---|--|--|
| Fixed terms | | |
| Intercept | -2.258 (0.219) | -2.521 (0.218) |
| Number of flower units of the native plant | -0.114 (0.053) | -0.102 (0.050) |
| Number of flower units of the alien plant | 0.002 (0.065) | 0.022 (0.058) |
| Flower size of the alien plant | 0.024 (0.146) | 0.028 (0.172) |
| Flower symmetry of the alien plant | -0.161 (0.344) | 0.016 (0.346) |
| Floral reflectance Wavelength 401-470 nm of the alien plant | 0.242 (0.455) | 0.007 (0.459) |
| Floral reflectance Wavelength 471-540 nm of the alien plant | -0.222 (1.089) | -0.770 (1.110) |
| Floral reflectance Wavelength 541-610 nm of the alien plant | 1.693 (0.650) | 1.499 (0.655) |
| Floral reflectance Wavelength 611-680 nm of the alien plant | 0.662 (0.419) | 0.519 (0.419) |
| Nectar production of the alien plant | 1.369 (0.820) | 0.965 (0.826) |
| Time during the day | -0.047 (0.039) | -0.049 (0.040) |
| Time during the day squared | -0.033 (0.043) | -0.030 (0.045) |
| Phylogenetic or floral trait distance between the alien and the native plants | -0.153 (0.068) | -0.290 (0.059) |

| | | |
|---|----------|----------------------|
| Phylogenetic or floral trait distance between the alien and the native plants squared | | 0.180 (0.041) |
| Random terms | SD | SD |
| Alien species | 0.846 | 0.853 |
| Native species | 0.611 | 0.575 |
| Residuals | 1.704 | 1.689 |
| AIC | 8039.000 | 8008.542 |
| Marginal r^2 | 0.045 | 0.062 |
| Conditional r^2 | 0.305 | 0.316 |

674 Significant model parameters are highlighted in bold ($p < 0.05$), and marginally significant model parameters are italicized ($p < 0.1$).