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1 **Impact of land use change on flower-visiting insect communities on an oceanic island**

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18

19 **ABSTRACT**

- 20 1. Land-use change has profoundly impacted pollinator communities throughout the
21 world. However, the processes through which it acts on pollinator diversity and
22 composition are still poorly understood, especially in highly vulnerable island
23 ecosystems.
- 24 2. In this study, we investigated the distribution, abundance, richness and composition
25 of flower-visiting insects to assess their response to land-use change in Terceira
26 Island (Azores).
- 27 3. Flower-visiting were sampled over two years using a standardized protocol along 50
28 transects across five different habitats corresponding to a land-use gradient. Insect
29 species were classified as indigenous or exotics. We assessed changes across
30 habitats using multiple diversity indices, species abundance distribution models
31 (SAD) and species composition metrics (β -diversity), along with plant species
32 composition.
- 33 4. We observed that indigenous flower-visiting insects were dominant, both in
34 abundance and species richness, across the entire land-use gradient. Species
35 diversity vary only slightly across the gradient. SADs were lognormal in all habitats,
36 with very few truly common and rare flower-visiting insects and a prevalence of
37 species of intermediate abundance. Species replacement was significantly higher
38 mainly between the two most contrasting habitats (i.e. natural forests and intensive
39 pastures) but was significantly correlated with species replacement of host plant
40 species across the gradient.
- 41 5. Our results revealed that the Azorean flower-visiting insect communities were highly
42 simplified across the entire gradient with little difference between habitats. In the
43 absence of strong exotic competitors, indigenous flower-visiting insects expand their
44 range and occupy new anthropogenic habitats, also facilitating the expansion of a
45 large number of exotic plant species.

46
47 **Keywords**

48 Community assembly, beta diversity, exotic species, flower-visiting insects, land-use change,
49 oceanic islands, native species, pollinator networks, species abundance distribution.

50 **Manuscript running title:** Flower-visiting insects across land-uses

51 INTRODUCTION

52 Land-use change is leading to the loss and degradation of natural habitats, resulting in the
53 severe disruption of biodiversity processes and patterns throughout the world (Sala *et al.*, 2000).
54 In particular, land-use change has profoundly impacted species ranges and abundances and is
55 now recognized as a major driver of the current extinction crisis (Fahrig, 1997; Brooks *et al.*,
56 2002). As a consequence, key ecosystem processes such as pollination interaction networks
57 have been severely affected, with dramatic consequences for ecosystem functioning and the
58 provision of goods and services for humans (Cane, 2001; Kearns, 2001; Warren *et al.*, 2001;
59 Williams *et al.*, 2001; Kremen *et al.*, 2002; Biesmeijer *et al.*, 2006; Klein *et al.*, 2007; Steffan-
60 Dewenter & Westphal, 2008; Winfree *et al.*, 2009; Potts *et al.*, 2010; Groom & Schwarz, 2011;
61 Rader *et al.*, 2014). The implementation of appropriate management actions to mitigate the
62 impact of human disturbance on pollination interaction networks requires, therefore, a better
63 understanding of how species diversity, distribution and abundance patterns of pollinators are
64 altered in response to land-use change.

65 Over the last century, island ecosystems have been disproportionately affected by
66 anthropogenic alterations and a large proportion of recorded extinctions have taken place on
67 islands (e.g. Cardoso *et al.*, 2010b; Rando *et al.*, 2013; Alcover *et al.*, 2015; Régnier *et al.*,
68 2015; Terzopoulou *et al.*, 2015). Land conversion of native forest to agricultural and exotic forest
69 is now recognized as one of the major causes of island biodiversity decline, with many extant
70 species predicted to be committed to future extinction as a result of land use change ('the
71 extinction debt'; Triantis *et al.*, 2010). These profound changes are known to have impacted
72 several components of island ecosystems (see Connor *et al.*, 2012), but very little is known
73 about the impact of land-use change on island ecological networks, and in particular, on
74 pollinating insects.

75 Insects are responsible for 78-94% of pollination across all flowering plants, and 75% of global
76 food crops (Klein *et al.*, 2007; Ollerton *et al.*, 2011; Winfree *et al.*, 2011). Guaranteeing a
77 diversity of pollinators, particularly the species with a high degree of specialization (Steffan-
78 Dewenter *et al.*, 2006; Albrecht *et al.*, 2012), is therefore crucial for maintaining gene flow and
79 community stability in plant communities (Ricketts, 2004; Klein *et al.*, 2007; Steffan-Dewenter &
80 Westphal, 2008; Cranmer *et al.*, 2012). Insular ecosystems usually support less complex
81 networks with lower numbers of pollinator species, are mostly comprised of generalist species
82 (Olesen *et al.*, 2002; Whittaker & Fernández-Palacios, 2007) and have less redundancy

83 between species in comparison with continental areas (Olesen *et al.*, 2002). Thus, pollinator
84 networks on oceanic islands are potentially highly vulnerable to any kind of disturbance
85 (Traveset, 2002), and can be considered ideal model systems to evaluate the impact of land-
86 use change on the diversity, distribution and abundance of pollinator species (Alarcón *et al.*,
87 2014; Castro-Urgal & Traveset, 2014; Traveset *et al.*, 2015; Kaiser-Bunbury & Blüthgen, 2015).

88 Over the last decade, a large range of negative impacts that can be attributed to land-use
89 change have already been documented for pollinator communities. For instance, previous
90 studies have identified a negative correlation between land-use intensity and the provision of
91 functions sustained by pollinator species (Garibaldi *et al.*, 2011, Winfree *et al.*, 2011, Rader *et*
92 *al.*, 2014). With increasing land-use intensity, a clear increase of the dominance of common
93 species has also been identified (Tylianakis *et al.*, 2005), especially in small island populations
94 that are more susceptible to the disruption of interaction networks (Kaiser-Bunbury *et al.*, 2010).
95 In response to intermediate disturbances, studies have also underlined the presence of an initial
96 increase in local pollinator richness, but with some degree of regional homogenization, as the
97 few specialists are replaced by abundant, often invasive, generalists (Kremen *et al.*, 2005;
98 Rader *et al.*, 2014).

99 In the present study, we investigate the flower-visiting insect species communities of the Azores
100 archipelago. Located in the North Atlantic Ocean, the archipelago is composed of nine main
101 island, all volcanic and of recent origin (the oldest island being 8.12 Myr BP). The Azorean
102 climate is temperate oceanic, characterized by high levels of relative humidity and small
103 temperature fluctuations. Since the 15th century and the arrival of humans to the Azores, the
104 native semi-tropical evergreen laurel forest (Laurisilva), originally covering most of the surface
105 area across the islands, has been gradually replaced by agricultural land uses (i.e. intensively
106 managed pastures for cattle and semi-natural pastures) and exotic forest (plantations of
107 introduced wood species). Most of the native forest is nowadays confined to *Juniperus-Ilex*
108 montane forests, characterized by reduced tree stature (usually up to 5 m, rarely reaching 10 m)
109 on shallow soil and rugged terrain at high altitude, mostly between 800 and 1000 m.a.s.l
110 (Martins, 1993; Borges *et al.*, 2005; Cardoso *et al.*, 2009, 2010a, Elias *et al.*, 2016). Recent
111 investigation of the impact of land-use changes in the Azores has shown that native forests and
112 intensively managed pastures are the most important habitats influencing arthropods species
113 composition and diversity, playing a fundamental role as source habitats for endemic and exotic
114 species, respectively (Borges *et al.*, 2008; Cardoso *et al.*, 2009, 2010a). Intermediate-disturbed
115 habitats, such as semi-natural pastures and exotic forests, also perform important functional

116 roles, acting as corridors connecting native forest fragments for many indigenous arthropod
117 species (Borges *et al.*, 2008; Cardoso *et al.*, 2009). However, despite the persistence of some
118 Azorean native species in anthropogenic habitats (Fattorini *et al.*, 2012), the large spread of
119 exotic species throughout the landscape matrix tends to promote biotic homogenization of
120 arthropod species at both local and island scales (Florencio *et al.*, 2013).

121 In this contribution, we examine the impact of land-use change on flower-visiting insect species
122 community structure in an Azorean island. Based on previous work on Azorean arthropod
123 communities (Borges *et al.*, 2008; Cardoso *et al.*, 2009, 2010a; Florencio *et al.*, 2013, 2015), we
124 predict that: 1) native habitats such as natural forest should support a higher abundance and
125 richness of indigenous flower-visiting insects in comparison to non-native land-uses; 2) species
126 composition of flower-visiting insect communities should change from native habitats to non-
127 native land-uses and 3) the dominance of a few common and many rare flower-visiting insect
128 species should increase as disturbance increases.

129

130 METHODS

131 Study area, sampling and species identification

132 Our study was conducted on Terceira Island. Terceira is an island from the central group of the
133 Azores archipelago, located in the North Atlantic Ocean (38° 37'N - 38° 48'N, 27° 02'W - 27°
134 23'W) with an Area 402 km² and maximum elevation of 1023 m. Field work was conducted from
135 June to September 2013 and from July to October 2014, due to favourable weather conditions
136 and relatively high number of plant species in the flowering period. For the current study, we
137 selected five distinct habitat types covering a large percentage of the total island area with, from
138 the least to the most disturbed, natural forests (NatFor), naturalized vegetation areas (NatVeg),
139 exotic forests (ExoFor), semi-natural pastures (SemiPast) and intensively managed pastures
140 (IntPast) (Cardoso *et al.*, 2013). Compared with previous ecological studies undertaken in the
141 Azores (Borges *et al.*, 2008; Cardoso *et al.*, 2009, 2010a; Florencio *et al.*, 2013, 2015) we
142 added naturalized vegetation areas, dominated by *Erica azorica*, *Pittosporum undulatum* and
143 *Rubus hochstetterorum*, as an important habitat for flower visiting insects, because of its recent
144 growing extent due to pasture abandonment and combination of native and exotic flora. Detailed
145 features regarding each habitat type are outlined in Table S1.

146 In each habitat type we chose 10 sites in which 10m long line-transects (1m width) were set up
147 (Pollard & Yates, 1993), making a total of 50 transects located across the entire island (Fig. 1,
148 see Table S2 for details). To select the 10 sites per habitat type we tried to maximize the
149 covered environmental diversity following Jiménez-Valverde & Lobo (2004) and Aranda *et al.*
150 (2011). First, an environmental matrix for Terceira Island (see Borges *et al.*, 2006) was compiled
151 using climatic, topographic and geological variables with a resolution of 100x100m. Using the k-
152 means non-hierarchical clustering algorithm we grouped all cells of each habitat type in 10
153 clusters, making a total 50 clusters (5 habitats x 10 groups). For each cluster, we ordered the
154 cells according to their distance to the group's multidimensional centroid using Euclidean
155 distance. The first cell in this ranking, deemed to be the most representative of the cluster, was
156 chosen for sampling. If it was impossible to reach the selected cell in the field due to
157 inaccessibility or lack of authorization from land owners, the second cell was chosen and so
158 forth.

159 Transect surveys were carried out once per year and repeated in the following year, in a
160 randomised order, under sunlight (from 9 a.m. to 6 p.m) and only in sunny weather, with a
161 duration of 180 minutes per transect. Transect location was selected to encompass spots of
162 dense flowering. Each flower along every 10 m transect was surveyed for 4 minutes to
163 guarantee effective contact of the insect, therefore only insects probing for nectar or
164 eating/collecting pollen (foraging) were recorded. Flower-visiting insects were observed and
165 collected with a pooter when it was not possible to identify them in the field. The specimens
166 collected were sorted first into morphospecies and later identified to species-level under the
167 supervision of PAVB, following the taxonomic nomenclature in Borges *et al.* (2010). When
168 species-level identification could not be resolved, individuals were identified to the lowest
169 taxonomic unit possible and classified as morphospecies (see Acknowledgements). Voucher
170 specimens and a reference collection were deposited in EDTP – Entomoteca Dalberto Teixeira
171 Pombo, University of Azores, Angra do Heroísmo, Portugal. All species were classified as
172 indigenous or exotic species. Indigenous species may be endemic (i.e. found only in the
173 Azores) or native non-endemic (i.e. species that colonised the Azores by natural long-distance
174 dispersal mechanisms). Exotic species are those whose original distribution range did not
175 include the Azores and are believed to have arrived as a consequence of human activities;
176 these species often have a cosmopolitan distribution (see Borges *et al.*, 2010).

177

178 Data analysis

179 Initially, we performed several statistical comparison tests (Chi-square, paired *t* test, analysis of
180 variance (ANOVA) followed by Tukey HSD *post-hoc* tests) to identify potential differences
181 between the 2 years of sampling (2013-2014), regarding habitat types, taxonomic orders,
182 colonization status, abundance and richness. A statistically significant increase in species
183 richness was observed between the two years ($t = -4.4$; $p = 0.006$; Table S5), which was
184 primarily a result of the addition of rare species between years, although in absolute terms the
185 increase was small. The difference in total abundance of individuals per species between years
186 was found to be non-significant ($t = 1.43$; $p = 0.22$; Table S5). Therefore, in the following
187 analyses we combined data from the same transects of both years to obtain a better sampling
188 completeness.

189 Using equivalent sampling effort in combination with the same standardized method in different
190 habitat types may still result in differences in inventory completeness due to differences in the
191 abundance of plant species in different transects. To analyse the variation in flower-visiting
192 insect species accumulation between habitats and rule out possible biases in the sampling
193 effort, we constructed species accumulation curves for the observed number of species, species
194 richness estimates, singletons, and doubletons using the non-parametric estimators Chao 1 and
195 Jackknife 1 (Jack1, both abundance-based). Species accumulation curves were constructed
196 randomly selecting the order of transect addition at each iteration. We repeated this process
197 1000 times, and used the mean of the 1000 random runs. To analyse the estimators'
198 performance across all habitats, slopes were calculated along the entire curve. Sampling
199 completeness was calculated in two ways: first, we calculated the ratio of observed richness to
200 estimated richness ratio with Chao1, due to its higher precision (Hortal *et al.*, 2006) and second,
201 we recorded the final slope of species richness accumulation curves built with both observed
202 and estimated richness as the inverse of the number of individuals needed to add the final
203 single species to the accumulation curve (see Cardoso *et al.*, 2009 for more details).

204 To investigate differences in flower-visiting insects' diversity between habitats, we calculated the
205 mean number of individuals, species richness and two commonly used diversity indices namely
206 Shannon-Wiener (H') and Pielou's evenness (J'). In addition, we calculated the Berger-Parker
207 dominance index (D), which expresses the proportional abundance of the most abundant
208 species, presented in the inverse format ($1/D$), so that an increase in the value of the index
209 accompanies an increase in diversity and a decrease in dominance (Magurran, 2004). To test
210 for statistically significant differences in diversity between habitats, we applied one-way
211 ANOVAs followed by Tukey HSD *post-hoc* tests. ANOVAs were performed using generalized

212 least square models (GLS; Pinheiro & Bates, 2000) to account for potential heteroscedasticity.
213 Additionally, we also tested the ability of the GLS models to account for potential spatial
214 structures by estimating the Moran's I spatial autocorrelation index for GLS residuals using the
215 latitude and longitude of each transect site. When the overall GLS was statistically significant,
216 the Tukey's post hoc test was used to identify statistically significant pairwise differences
217 between habitats.

218 We studied the dissimilarity in flower-visiting species composition between sites of all habitat
219 types using Jaccard's index as an overall beta diversity measure (β_{total}), and decomposing it into
220 its replacement (β_{repl}) and richness difference (β_{rich}) components (Carvalho *et al.*, 2012; Cardoso
221 *et al.*, 2014). β diversity indices were computed using presence/absence data. We also
222 computed β diversity with log-transformed abundance data (results not shown), but the results
223 were similar (Cardoso *et al.*, 2015). Dissimilarity distances were visualized using non-metric
224 multidimensional scaling ordinations (NMDS). To examine between-habitat differences in
225 species composition, we used an analysis of similarities (ANOSIM) using the three beta
226 diversity components as dissimilarity measures, followed by *post-hoc* tests with p-values
227 adjusted using the Benjamini & Hochberg (1995) correction for multiple testing. We also
228 computed β_{total} , β_{repl} and β_{rich} for plant species composition and correlated each β component of
229 flower-visiting insects with its respective component for plants communities using Mantel tests
230 with Spearman correlation.

231 In addition to examining patterns in flower-visiting species diversity and composition, we also
232 explored variations in the species abundance distributions (SADs) of flower-visiting species
233 (Matthews & Whittaker, 2015) across the five habitat types. To determine the shape of the SAD
234 in each sample, we fitted logseries, lognormal and gambin SAD models to the observed
235 abundance data, using both binned and un-binned data with the logseries and lognormal
236 models, and only binned data with the gambin model (Matthews *et al.*, 2014). The theoretical
237 description of these SAD models and the complete methodological approach, including how the
238 models were fitted and compared, and classification types of rare species is provided in
239 Appendix S1.

240 All analyses were performed with Microsoft Excel, IBM SPSS 20.0 (Nie *et al.*, 2011) and the R
241 statistical environment (R Core Team, 2016) using the R packages *BAT* (Cardoso *et al.*, 2015,
242 2016), *vegan* (Oksanen *et al.*, 2013), *poilog* (Grøtan & Engen, 2009) and *gambin* (Matthews *et*
243 *al.*, 2014).

244 RESULTS

245 Species composition

246 Insects visited 2134 flowers (49% of the 4354 sampled flowers) belonging to 48 plant species
247 from 21 families. The number of plant species surveyed per habitat type was distributed as
248 follows: 17 plant species (1134 flowers) were identified in NatFor, 27 plant species (815 flowers)
249 in NatVeg, 26 plant species (820 flowers) in ExoFor , 15 plant species (828 flowers) in SemiPast
250 and 14 plant species (757 flowers) in IntPast (see Table S4).

251 The sampled flower-visiting insects belonged to 54 species and morphospecies from four orders
252 namely Coleoptera, Diptera, Hymenoptera and Lepidoptera (Table S3). The most representative
253 group was Diptera, with 51% of the individuals, followed by Hymenoptera with 25%, Coleoptera
254 with 18% and finally the Lepidoptera with 6%. The most common species were *Sepsis*
255 *neocynepsia* (Diptera) (17% of the individuals) and *Anaspis proteus* (Coleoptera) (16.5%),
256 followed by *Bombus ruderatus* (6.3%), *Apis mellifera* (5%), *Lasioglossum villosulum* (all
257 Hymenoptera) (4.5%) and *Stomorhina lunata* (Diptera) (4.6%) (Table S3). Flies (Diptera) were
258 the most represented group in all habitats, invariably followed by bees (Hymenoptera) ($\chi^2= 4.81$,
259 $df = 12$, $p=0.96$). *Sepsis neocynepsia* (Diptera) had the highest number of individuals in three
260 habitat types: NatVeg, SemiPast and IntPast, whereas *Anaspis proteus* (Coleoptera) was
261 dominant in NatFor and *Bombus ruderatus* (Hymenoptera) in ExoFor.

262 At the island scale we observed that the majority of flower-visiting insects were native non-
263 endemic species (82.1%) while only a small percentage was endemic (5.4%) or exotic (12.5%).
264 These proportions were similar throughout all habitats ($\chi^2 = 0.89$, $df = 8$, $P = 1$), showing that
265 indigenous species dominated flower-visiting insect's communities across the entire gradient
266 (Table 1). On the other hand, at the island scale the majority of host plants were exotic species
267 (75%), and a small percentage was native non-endemic (14.6%) or endemic (10.4%). These
268 proportions slightly differed between habitats ($\chi^2 = 17.5$, $df = 8$, $P = 0.025$), although the
269 introduced plant species were dominant in all habitats with the exception of NatFor (Table 1).

270 Sampling completeness

271 The average numbers of flower-visiting insect species per habitat estimated by the Chao1 and
272 Jack1 estimators were found to be close to the observed richness values (Table S6).
273 Considering the estimates obtained with Chao 1, the sampling completeness values for each
274 habitat varied between 98% for NatFor and 63% for SemiPast, with 90% for ExoFor, 87% for

275 IntPast and 86% for NatVeg, all representing a good level of sampling completeness (Cardoso
276 *et al.*, 2009). The species accumulation curves (Fig. S1) approached an asymptote (with slope
277 values between 0.002 and 0.08 by the end of the accumulation process) and the final slope
278 values of estimators' curves were close to 0 for all habitats, which shows that the inventory was
279 relatively complete in all habitats (Fig. S2).

280 Insect diversity in the different habitats

281 Mean number of individuals, species evenness (J') and dominance ($1/D$) for flower-visiting
282 insects did not show any significant differences between habitats ($F_{1,4} = 1.185$, $P = 0.330$; $F_{1,4} =$
283 1.682 , $P = 0.171$ and $F_{1,4} = 2.513$ $P = 0.055$ respectively, Fig2a, d, e). However, species
284 richness differed significantly between habitats ($F_{1,4} = 4.231$, $P = 0.005$) with NatFor being the
285 richest habitat and NatVeg and SemiPast being the poorest (Fig. 2b). Shannon-Wiener H' index
286 differed marginally between habitats ($F_{1,4} = 2.711$, $P = 0.042$) with ExoFor being significantly
287 more diverse than SemiPast (Fig. 2c). No spatial autocorrelation was detected in the residuals
288 of the GLS models ($I = 0.007$, $P = 0.214$; $I = -0.006$, $P = 0.534$; $I = -0.020$, $P = 0.297$; $I = -0.011$,
289 $P = 0.661$ and $I = -0.020$, $P = 0.872$ for mean number of individuals, species richness, Shannon-
290 Wiener, evenness and dominance respectively).

291 Habitat similarity

292 Overall, the analysis of flower-visiting insects β -diversity using Jaccard's index (β_{total}) showed
293 significant differences in composition between habitat types (ANOSIM: $r = 0.179$, $P = 0.001$, Fig.
294 3a) with values ranging from 0.835 between NatFor and IntPast to 0.794 between NatFor and
295 ExoFor (Table S7). NatFor was significantly more dissimilar to all anthropogenic habitats (Post-
296 hoc ANOSIM $P < 0.05$, Table S8) while no significant differences were detected between
297 anthropogenic habitats, except between ExoFor and SemiPast (Post-hoc ANOSIM $P = 0.02$).
298 β_{repl} was the dominant component of β_{total} , with values ranging from 0.602 between ExoFor and
299 both NatFor and NatVeg, to 0.494 between SemiPast and NatFor. β_{repl} had lower but still
300 significant importance (ANOSIM: $r = 0.061$, $P = 0.023$, Fig. 3b) in explaining β diversity patterns.
301 Significant differences in β_{repl} were found between NatFor and both ExoFor and IntPast (Post-
302 hoc ANOSIM $P < 0.05$, Table S8), and between ExoFor and IntPast (Post-hoc ANOSIM $P =$
303 0.02). For β_{rich} values ranged from 0.316 between NatFor and SemiPast, to 0.192 between
304 NatFor and ExoFor, but no significant difference between habitat types was found (ANOSIM: $r =$
305 0.019 , $P = 0.233$).

306 Significant correlations were found between the flower-visiting insects and plant species of the
307 three β measurements (Fig. 4a, b, c) with the pattern of β_{total} being mostly driven by the β_{rich}
308 component.

309 Species abundance distributions (SADs) and rarity patterns

310 Considering the binned data, the gambin model provided the best fit to all five habitat types
311 ($\Delta\text{AIC}_c = 0$, Table S9), although for the NatFor the PLN had a $\Delta\text{AIC}_c < 2$. The PLN always
312 provided a better fit to the binned data than the logseries. However, when the logseries and
313 PLN were fitted to the unbinned data, the logseries provided a better fit to all five habitat types,
314 indicating a greater number of rare species than predicted by the PLN (Table S9). The gambin
315 model provided a good fit to the data in all habitat types according to the Pearson's chi-square
316 (χ^2) goodness of fit test for NatFor: $\chi^2 = 6.376$, $P = 0.605$; NatVeg: $\chi^2 = 5.963$, $P = 0.31$; ExoFor:
317 $\chi^2 = 1.568$, $P = 0.905$; SemiPast: $\chi^2 = 11.303$, $P = 0.079$ and IntPast: $\chi^2 = 2.656$, $P=0.753$. The
318 α parameter of the gambin model did not show substantial variations between habitats with
319 values of 2.364 for NatFor, 2.348 for SemiPast, 3.244 for NatVeg, 4.502 for ExoFor and 3.965
320 IntPast. Alpha values in this range indicate positively skewed lognormal-like (i.e. more rare
321 species than predicted by a standard lognormal model) to standard lognormal SAD shapes (Fig.
322 5), with the lower values of α in NatFor and SemiPast denoting a relatively higher proportion of
323 rarer species in these two habitat types.

324 In regards to the species classified as common species (i.e. the 25% most abundant), there is
325 only one habitat type with one species having more than 128 specimens: NatFor with *Anaspis*
326 *proteus* (264 specimens). However, when considering regional abundance in the island, there
327 are three true common species (*Sepsis neocynepsia* with 362 specimens, *Anaspis proteus* with
328 352 specimens and *Bombus ruderatus* with 134 specimens) (Fig. 5). The proportions of rare
329 flower-visiting insect species represented in the first two bins of the SADs histograms in Figure
330 5 were decomposed into pseudo-rare and regionally rare species. The pseudo-rare species are
331 relatively high in numbers when data from all habitats are aggregated, but are rare in some
332 particular habitats and are the species primarily responsible for the differences in proportions of
333 rare species between habitat types. The regionally rare species i.e. the number of species with
334 less than four individuals (Fig. 5 Island; i.e. the first quartile of available bins) only comprise 5
335 species. These are the truly rare species. All habitats revealed a high number of intermediate
336 abundance species (Fig. 5), as is to be expected in lognormal shaped SADs (Table 2).

337

338 DISCUSSION

339 In this study, we documented the influence of different levels of disturbance on the distribution,
340 composition, richness and abundance of flower-visiting insect species on an Azorean island.
341 First, we revealed that the island flower-visiting insect community is dominated by widespread
342 generalist native species of intermediate abundance, despite the high representation of exotic
343 plant species. Second, we showed that the species diversity, species abundance distribution
344 (SAD) and species composition of flower-visiting insect species vary only slightly across the
345 land-use gradients. Species replacement was significantly higher mainly between the two most
346 contrasting habitats (i.e. natural forests and intensive pastures). Finally, species composition of
347 flower-visiting insects was influenced by the distribution of host plant species regardless of the
348 landscape matrix.

349 With the exception of the study of Olesen *et al.* (2002), to our knowledge there is no other study
350 investigating flower-visiting insect communities in the Azores. In fact, although there are many
351 studies investigating the impacts of land-use change on the community structure of pollinator
352 insects on continental regions, such studies are scarce on oceanic islands. In one of the few
353 examples, Sahari *et al.* (2010), in contrast to our results, showed that landscape change in Java
354 Island (Indonesia) strongly affects insect pollinating species composition and richness with
355 increasing rainforest isolation and land-use intensity, indicating significant changes in species
356 composition between habitat types in the tropics, with emphasis on case-studies of wild and
357 crop plants from Indonesia.

358 Insect diversity in the different habitats

359 Our results demonstrated a surprising uniformity of several community metrics across the
360 different habitats, suggesting that similar mechanisms may control flower-visiting species
361 diversity across our land-use gradient. In most of the habitats, native non-endemic flies were the
362 group with the largest number of species, a pattern already documented for island pollination
363 networks (Castro-Urgal & Traveset, 2014). Concerning our original aims and hypotheses, as
364 expected, natural forest was found to be a favourable habitat for indigenous flower-visiting
365 insects, although we did not observe statistical differences between habitat types in terms of
366 abundance (Fig.2a, S1 and Table S5). This could be explained by adaptation or cross-scale
367 resilience and response diversity of the native flower-visiting insect species to non-native
368 habitats (see also Winfree & Kremen, 2009 and Cardoso *et al.*, 2010a), a possible consequence
369 of the island small area relative to the flower-visiting species foraging area (Miller *et al.*, 2015)

370 and loss of native habitats. Hence these differences in insect flower-visiting community could
371 have been also influenced by the variation of altitude through the different habitat types; native
372 forest being always at higher altitude than intensively managed pastures (Table S1). In
373 conclusion, and even considering that exotic plants dominate all habitats with the exception of
374 native forest, indigenous flower-visiting insects' diversity did not greatly vary, both in terms of
375 abundance and species diversity, across the entire gradient.

376 Habitat similarity

377 As in previous studies focusing on the impact of land use change in Azorean arthropod
378 communities (e.g. Borges *et al.*, 2008; Cardoso *et al.*, 2009, 2010a; Meijer *et al.*, 2011), native
379 forest and intensively managed pasture showed the most contrasting flower-visiting species
380 composition. This difference was mostly a consequence of replacement differences (species
381 substitution), with only a minor contribution of species richness variation (Fig. 3). This result
382 differs from a previous work conducted with epigeal arthropods in Terceira (see Cardoso *et al.*,
383 2009), where strong differences in species composition were reported between all types of
384 habitats. Our finding illustrates the need for further investigation concerning the role of
385 landscape dynamics on Azorean insect pollinator species. The few differences in community
386 composition reported across habitats could also be explained by the 'habitat heterogeneity
387 hypothesis' (e.g. MacArthur & Wilson, 1967), where the flower-visiting species, due to low
388 interspecific competition, predation and parasitic pressures (Olesen *et al.*, 2002; Ribeiro *et al.*,
389 2005) subdivide the landscape into suitable habitats (i.e. niche partitioning), based on plant
390 communities (Tews *et al.*, 2004; Cramer & Willig, 2005). In fact, flower-visiting species
391 composition was found to be mostly influenced by host plant species composition across all
392 habitats (Fig. 4). The fact that differences in flower-visiting insects' composition correlated with
393 differences in host plant species composition across habitat types (Fig. 4) implies that any
394 changes in vegetation composition (i.e. replacement of native by exotic or invasive plants) might
395 have a profound impact on pollinating insect community structure in the Azores. Interestingly,
396 the high correlation between similarity values of plant and arthropod community structure was
397 also observed by Borges (1999) for phytophagous insects and predatory arthropods from sown
398 and semi-natural pastures in the Azores. In an additional study, Fründ *et al.* (2010) reported
399 positive diversity correlation between 1764 individuals of 131 pollinator species with 77 plant
400 species (n = 27 networks) across sites at a regional scale, even though only parts of the
401 variation of bees and hoverfly diversity was explained by the diversity of flower species.

402 Species abundance distributions (SADs) and rarity patterns

403 The structure of flower-visiting insect species relative abundances did not differ substantially
404 between habitats (Fig. 2a and Fig. 5), in spite of the clear land-use gradient present in Terceira,
405 and the fact that previous studies have reported a clear effect of land-use change on SAD form
406 for epigeal arthropods on the same island (see Matthews *et al.*, 2014). In fact, we found only
407 slight variation in the form of the SAD between habitat types as highlighted by the small
408 differences in gambin's α values calculated using binned data, and the fact that the logseries
409 model provided the best fit to the non-binned data from all five habitat types. The SAD form in
410 the different habitat types was accurately assessed by the gambin model for which the range of
411 α values were characteristic of lognormal-like SADs (Ugland *et al.*, 2007; Matthews *et al.*, 2014),
412 albeit with a relatively higher than expected proportion of rare species in native forest and semi-
413 natural pasture (Table 2; Fig. 5). These results reveal therefore that most flower-visiting species,
414 across all habitats, were of intermediate abundance. This could be explained by the fact that
415 Azorean communities are largely unsaturated with ample resources, both features associated
416 with low competition for food (Preston, 1948; Borges *et al.*, 2008; Miller *et al.*, 2015) (Table S9;
417 Fig. 5). However, we also documented the presence of rare species although these were mostly
418 considered to be pseudo-rare species (i.e. these species are rare in a given habitat but more
419 frequent in others) that were likely present due to source-sink dynamics across habitat types.
420 Our work supports the view that Azorean arthropod communities are highly simplified,
421 characterized by a dominance of generalist species (see also Olesen *et al.*, 2002; Ribeiro *et al.*,
422 2005; Whittaker & Fernández-Palacios, 2007; Traveset *et al.*, 2015), the presence of multiple
423 local habitat pseudo-rarities, and few regionally rare species (see also Borges *et al.*, 2008).
424 Borges *et al.* (2008) also reported another example of a functional group in the Azorean
425 arthropod community with a high proportion of pseudo-rare species, in that case spiders which,
426 similarly to pollinator insects, have many species able to use diverse resources, not limited to
427 one specific habitat.

428 Conclusions and future directions

429 Our finding supports the observations of Olesen *et al.* (2002) reported for a different Azorean
430 island (Flores), where indigenous super-generalist species tend to include exotic plants in their
431 set of pollinated plants without any clear evidence for a facilitation between exotic plant and
432 pollinator species. Therefore, our findings emphasize the need for further studies on pollination
433 networks on islands to investigate the spread of exotic and invasive plants by indigenous

434 pollinating insects that could in turn threaten the endemic flora. Finally, also further work is
435 needed to clarify whether the Azorean indigenous pollinating insect species are behaving as
436 “jacks of all trades, masters of none”, i.e., what is the efficacy of these species in pollen
437 transport and plant reproduction in the Azores? Given that we documented only a slight
438 variation in pollinator community according to a land-use gradient, we suggest this is a starting
439 point for assessing the insects’ pollinators’ behaviour along a disturbance gradient in the other
440 islands of the Azores archipelago, and compare it at island-level with Terceira flower-visiting
441 insect communities. In conclusion, our study offers one of the first exhaustive assessments of
442 the impact of land-use change on an Azorean island flower-visiting insect community, revealing
443 (1) the influence of plant species composition on flower-visiting insect species composition, and
444 (2) providing evidence for potential occupation of native flower-visiting insects in new
445 anthropogenic habitats.

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454 SUPPORTING INFORMATION

455 Additional Supporting Information may be found in the online version of this article under the
456 DOI reference:

457

458 **Appendix S1.** Description of the species abundance distribution models and methodological
459 approach.

460 **Figure S1.** Species accumulation curves for several non-parametric estimators and for
461 singletons and doubletons of the different habitat types.

462 **Figure S2.** Slopes of species accumulation curves for non-parametric abundance-based
463 estimators Chao 1 and Jackknife 1 of the different habitat types.

464 **Table S1.** Habitat descriptions with information on the altitude, main plant species and
465 disturbance index.

466 **Table S2.** Geographical coordinates for all sites in Terceira Island for each habitat type.
467 **Table S3.** Abundance and number of individuals per insect species/morphospecies in each
468 habitat type.
469 **Table S4.** Number of flowers per plant species in each habitat type.
470 **Table S5.** Number of species/morphospecies studied in 2013 and 2014 years per each habitat
471 type.
472 **Table S6.** Number of individuals, species/morphospecies, singletons and doubletons studied in
473 each habitat type. **Table S7.** Comparison of total beta diversity (β_{total}), replacement beta
474 diversity (β_{repl}) and richness beta diversity (β_{rich}) values along a gradient of increasing
475 dissimilarity for all transects considered together of each habitat.
476 **Table S8.** P-values of the post hoc pairwise Analysis of similarities (ANOSIM) corrected for
477 multiple tests.
478 **Table S9.** AIC_c values for the SAD model selection. The three SAD models (logseries, PLN and
479 gambin were fitted to flower-visiting insect data from five land use types.

480

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720 **Table 1.** Number of endemic, native non-endemic and introduced flower-visiting insects and
 721 plant species per each habitat type: NatFor (natural forests), SemiPast (semi-natural pastures),
 722 NatVeg (naturalized vegetation areas), ExoFor (exotic forests), IntPast (intensively managed
 723 pastures).

	Insect Species			Plant Species		
Habitats	Endemics	Natives	Introduced	Endemics	Natives	Introduced
NatFor	2	34	5	5	6	6
NatVeg	1	31	5	5	7	16
ExoFor	2	32	6	2	3	22
SemiPast	1	24	5	0	2	14
IntPast	2	27	5	0	2	13

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732

733 **Table 2.** Number of regionally rare, habitat rare, pseudo-rare intermediate and common species
 734 of flower-visiting insects for NatFor (natural forests), SemiPast (semi-natural pastures), NatVeg
 735 (naturalized vegetation areas), ExoFor (exotic forests), and IntPast (intensively managed
 736 pastures) and island (region).

Habitats	Regionally Rare	Pseudo-rare	Intermediate	Common
Island	5	--	46	3
NatFor	1	13	26	1
NatVeg	2	14	21	0
ExoFor	2	12	26	0
SemiPast	0	11	19	0
IntPast	1	11	22	0

737

738 **Figure 1.** Land use distribution map of Terceira Island with the selected sampling sites as black
739 dots: NatFor (natural forests), SemiPast (semi-natural pastures), NatVeg (naturalized vegetation
740 areas), ExoFor (exotic forests), IntPast (intensively managed pastures) (cartographic
741 information from DROTRH (2008) and Gaspar (2007), see also Gaspar *et al.* (2011)).
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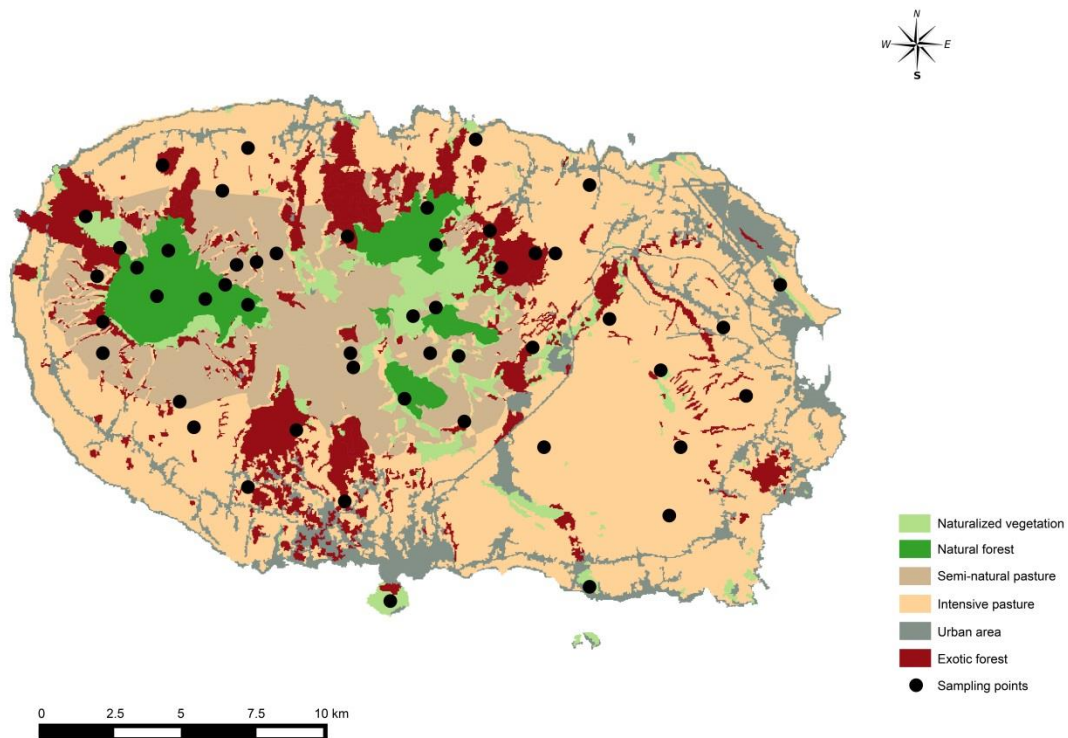
743 **Figure 2.** Species diversity metrics of flower-visiting insects across the different habitat types.
744 (a) Mean abundance, (b) mean species richness, (c) Shannon-Wiener H' , (d) Pielou's Evenness
745 J' and (e) Inverse Berger-Parker $1/\text{Dominance}$. For species richness (b), habitat types
746 accompanied by a different letter are significantly different from each other (post hoc tests; $P <$
747 0.05). NatFor (natural forests), NatVeg (naturalized vegetation areas), ExoFor (exotic forests),
748 SemiPast (semi-natural pastures), and IntPast (intensively managed pastures).

749 **Figure 3.** Two-dimensional ordination solution using non-metric multidimensional scaling
750 (NMDS) with the β diversity measures β_{total} (a) and β_{repl} (b) for flower-visiting insects. Dots
751 indicate transects while lines delimit the smallest polygon that encloses all transects for a given
752 habitat. The stress value of NMDS was 0.17 and 0.18 for β_{total} and β_{repl} respectively. NatFor
753 (natural forest), NatVeg (naturalized vegetation areas), ExoFor (exotic forest), SemiPast (semi-
754 natural pasture), and IntPast (intensively managed pasture).

755 **Figure 4.** Correlations between species composition (β diversity) of flower-visiting insects and
756 plants across the 50 transects. Correlations were performed with β_{total} (a) β_{repl} (b) and β_{rich} (c).
757 Spearman correlation coefficient and its associated p-values of the Mantel test are given on the
758 top of each panel. NatFor (natural forest), NatVeg (naturalized vegetation areas), ExoFor (exotic
759 forest), SemiPast (semi-natural pasture) and IntPast (intensively managed pasture).

760 **Figure 5.** Species abundance distribution (SADs) histograms for flower-visiting insects, with
761 predicted values of the gambin model (black dots), for all habitats, (a), natural forest (b),
762 naturalized vegetation (c), exotic forest (d) semi-natural pasture (e), and intensively managed
763 pasture (f). The following binning system was used: bin 1 corresponds to the number of species
764 with 1 individual per species, bin 2 corresponds to the number of species with 2-3 individuals
765 per species, bin 3 corresponds to the number of species with 4-7 individuals per species, etc.
766 (see Gray *et al.*, 2006 and Matthews *et al.*, 2014).

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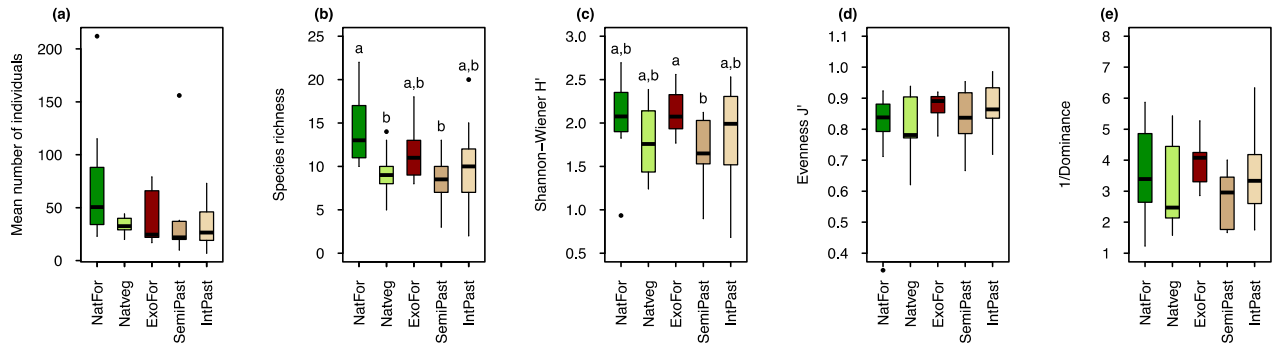
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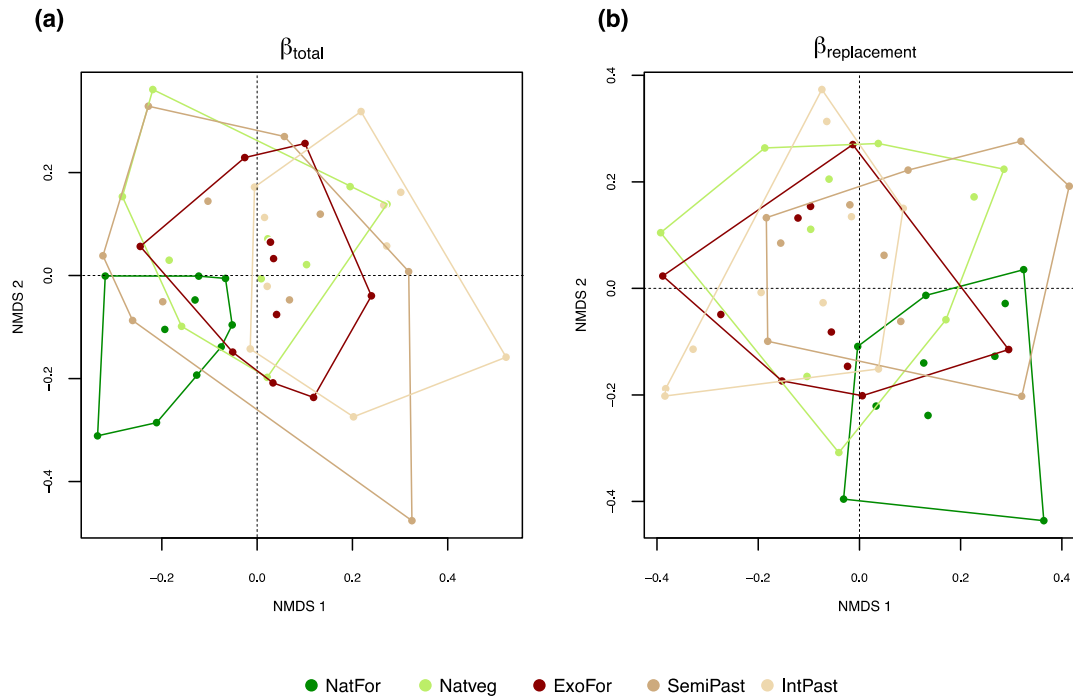
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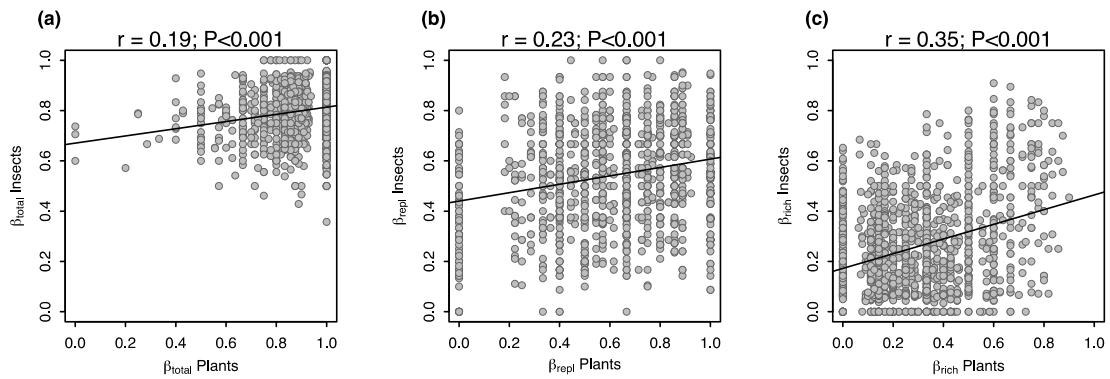


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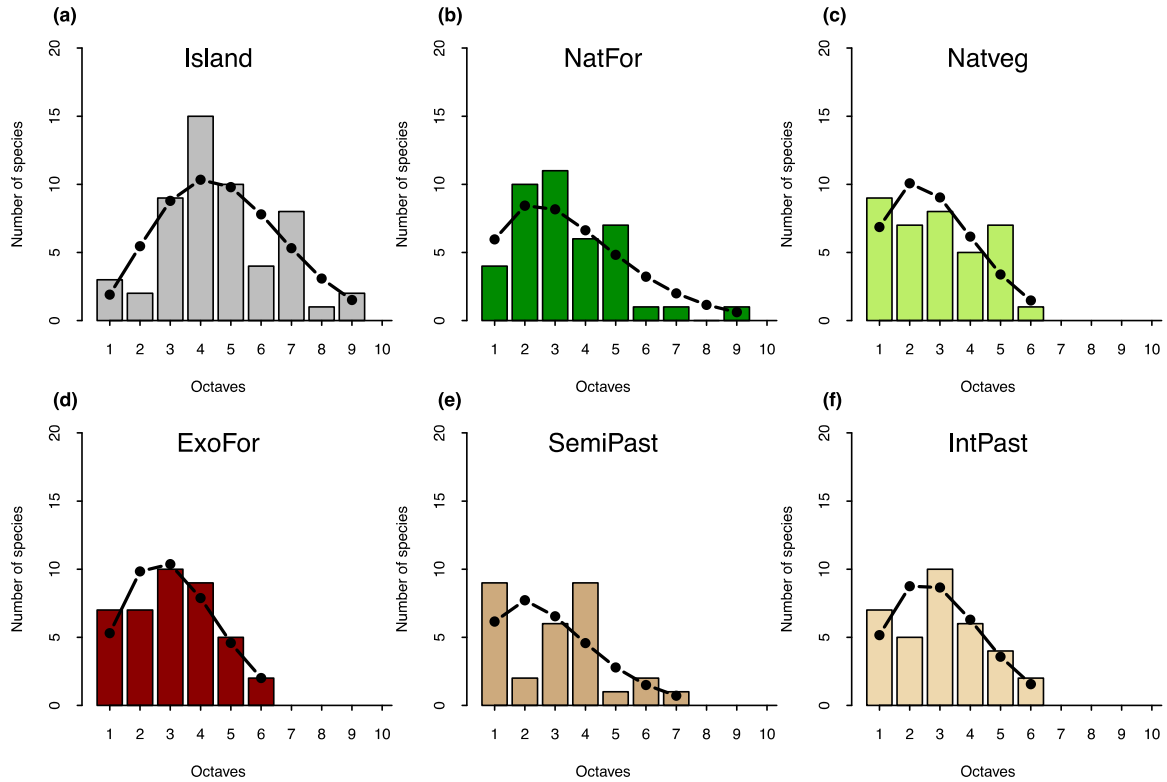
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