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

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ABSTRACT

1. Land-use change has profoundly impacted pollinator communities throughout the world. However, the processes through which it acts on pollinator diversity and composition are still poorly understood, especially in highly vulnerable island ecosystems.

2. In this study, we investigated the distribution, abundance, richness and composition of flower-visiting insects to assess their response to land-use change in Terceira Island (Azores).

3. Flower-visiting were sampled over two years using a standardized protocol along 50 transects across five different habitats corresponding to a land-use gradient. Insect species were classified as indigenous or exotics. We assessed changes across habitats using multiple diversity indices, species abundance distribution models (SAD) and species composition metrics (β-diversity), along with plant species composition.

4. We observed that indigenous flower-visiting insects were dominant, both in abundance and species richness, across the entire land-use gradient. Species diversity vary only slightly across the gradient. SADs were lognormal in all habitats, with very few truly common and rare flower-visiting insects and a prevalence of species of intermediate abundance. Species replacement was significantly higher mainly between the two most contrasting habitats (i.e. natural forests and intensive pastures) but was significantly correlated with species replacement of host plant species across the gradient.

5. Our results revealed that the Azorean flower-visiting insect communities were highly simplified across the entire gradient with little difference between habitats. In the absence of strong exotic competitors, indigenous flower-visiting insects expand their range and occupy new anthropogenic habitats, also facilitating the expansion of a large number of exotic plant species.

Keywords

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

INTRODUCTION

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

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

Insects are responsible for 78-94% of pollination across all flowering plants, and 75% of global food crops (Klein *et al.*, 2007; Ollerton *et al.*, 2011; Winfree *et al.*, 2011). Guaranteeing a diversity of pollinators, particularly the species with a high degree of specialization (Steffan-Dewenter *et al.*, 2006; Albrecht *et al.*, 2012), is therefore crucial for maintaining gene flow and community stability in plant communities (Ricketts, 2004; Klein *et al.*, 2007; Steffan-Dewenter & Westphal, 2008; Cranmer *et al.*, 2012). Insular ecosystems usually support less complex networks with lower numbers of pollinator species, are mostly comprised of generalist species (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 (38º 37´N - 38º 48´N, 27º 02´W - 27º
134 23´W) with an Area 402 km^2 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) (χ^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 (χ^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 (χ^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

9

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

Insect diversity in the different habitats

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

Habitat similarity

Overall, the analysis of flower-visiting insects β-diversity using Jaccard's index ($β_{total}$) showed significant differences in composition between habitat types (ANOSIM: r = 0.179, P = 0.001, Fig. 3a) with values ranging from 0.835 between NatFor and IntPast to 0.794 between NatFor and ExoFor (Table S7). NatFor was significantly more dissimilar to all anthropogenic habitats (Post-hoc ANOSIM P < 0.05, Table S8) while no significant differences were detected between anthropogenic habitats, except between ExoFor and SemiPast (Post-hoc ANOSIM P = 0.02). $β_{repl}$ was the dominant component of $β_{total}$, with values ranging from 0.602 between ExoFor and both NatFor and NatVeg, to 0.494 between SemiPast and NatFor. $β_{repl}$ had lower but still significant importance (ANOSIM: r = 0.061, P = 0.023, Fig. 3b) in explaining β diversity patterns. Significant differences in $β_{repl}$ were found between NatFor and both ExoFor and IntPast (Post-hoc ANOSIM P < 0.05, Table S8), and between ExoFor and IntPast (Post-hoc ANOSIM P = 0.02). For $β_{rich}$ values ranged from 0.316 between NatFor and SemiPast, to 0.192 between NatFor and ExoFor, but no significant difference between habitat types was found (ANOSIM: r = 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　($\Delta AIC_c = 0$, Table S9), although for the NatFor the PLN had a $\Delta AIC_c < 2$. 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 epigean 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.

Species abundance distributions (SADs) and rarity patterns

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

Conclusions and future directions

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

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

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

Appendix S1. Description of the species abundance distribution models and methodological approach.
Figure S1. Species accumulation curves for several non-parametric estimators and for singletons and doubletons of the different habitat types.
Figure S2. Slopes of species accumulation curves for non-parametric abundance-based estimators Chao 1 and Jackknife 1 of the different habitat types.
Table S1. Habitat descriptions with information on the altitude, main plant species and 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

481   REFERENCES

482   Alarcón, M., Aldasoro, J. J., Roquet, C., & Olesen, J. M. (2014) The Evolution and Pollination of
483   Oceanic Bellflowers (Campanulaceae). *Evolutionary Biology: Genome Evolution, Speciation,*
484   *Coevolution and Origin of Life*, pp. 301-322. Springer International Publishing.

485   Alcover, J. A., Pieper H., Pereira, F. & Rando J. C. (2015) Five new extinct species of rails
486   (Aves: Gruiformes: Rallidae) from the Macaronesian Islands (North Atlantic Ocean). *Zootaxa*,
487   **4057**, 151-190.

488   Aizen, M. A., & Feinsinger, P. (1994) Forest fragmentation, pollination, and plant reproduction in
489   a Chaco dry forest, Argentina. *Ecology*, **75**, 330-351.

490   Aranda, S. C., Gabriel, R., Borges, P. A., De Azevedo, E. B., & Lobo, J. M. (2011) Designing a
491   survey protocol to overcome the Wallacean shortfall: a working guide using bryophyte
492   distribution data on Terceira Island (Azores).*The Bryologist*, **114**, 611-624.

493   Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T.,
494   Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J. & Kunin, W. E. (2006)
495   Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands.
496   *Science*, **313,** 351-354.

497   Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: a practical and
498   powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B*, **57**, 289–
499   300.

500   Borges, P. A. (1999) Plant and arthropod species composition of sown and semi-natural pasture
501   communities of three Azorean islands (S. Maria, Terceira and Pico). *Arquipélago*, **17**, 1–21.

502   Borges, P. A. V., Aguiar, C., Amaral, J., Amorim, I. R., André, G., Arraiol, A., Baz, A., Dinis, F.,
503   Enghoff, H., Gaspar, C., Ilharco, F., Mahnert, V., Melo, C., Pereira, F., Quartau, J.A., Ribeiro,
504   S., Ribes, J., Serrano, A. R. M., Sousa, A. B., Strassen, R. Z., Vieira, L., Vieira, V., Vitorino, A. &
505   Wunderlich, J. (2005) Ranking protected areas in the Azores using standardized sampling of
506   soil epigean arthropods. *Biodiversity and Conservation*, **14**, 2029–2060.

507   Borges, P. A. V., Lobo, J. M., Azevedo, E. B., Gaspar, C., Melo, C. & Nunes, L. V.(2006)
508   Invasibility and species richness of island endemic arthropods: a general model of endemic vs.
509   exotic species. *Journal of Biogeography,* **33**, 169-187

510   Borges, P. A., Ugland, K. I., Dinis, F., & Gaspar, C. (2008) Insect and spider rarity in an oceanic
511   island (Terceira, Azores): true rare and pseudo-rare species. In: Fattorini, S. (ed). *Insect*
512   *ecology and conservation.* Research Signpost.

513   Borges, P.A.V., Costa, A., Cunha, R., Gabriel, R., Gonçalves, V., Martins, A.F., Melo, I.,
514   Parente, M., Raposeiro, P., Rodrigues, P., Santos, R.S., Silva, L., Vieira, P. & Vieira, V. (Eds.)
515   (2010) A list of the terrestrial and marine biota from the Azores.Princípia, Oeiras, 432 pp.

516   Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., Rylands, A. B.,
517   Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G. & Hilton-Taylor, C. (2002) Habitat
518   loss and extinction in the hotspots of biodiversity. *Conservation biology*, **16**, 909-923.

519   Burnham, K.P. & Anderson, D.R. (2002) Model selection and multi-model inference: a practical
520   information theoretic approach, 2nd edn. Springer, New-York.

521   Cane, J. H. (2001) Habitat fragmentation and native bees: a premature verdict?. *Conservation*
522   *Ecology*, **5**, 3.

523   Cardoso, P., Aranda, S. C., Lobo, J. M., Dinis, F., Gaspar, C., & Borges, P. A. (2009) A spatial
524   scale assessment of habitat effects on arthropod communities of an oceanic island. *Acta*
525   *Oecologica*, **35**, 590-597.

526 Cardoso, P. Gaspar, C., Dinis, F., & Borges, P. A. (2010a) Patterns of alpha and beta diversity
527 of epigean arthropods at contrasting land-uses of an oceanic island (Terceira, Azores). – In:
528 Serrano, A. R. M. et al. (eds), *Terrestrial arthropods of Macronesia – biodiversity, ecology and*
529 *evolution*. Sociedade Portugesa Entomologia, Lisboa, pp. 73–88.

530 Cardoso, P., Arnedo, M. A., Triantis, K. A., & Borges, P. A. (2010b) Drivers of diversity in
531 Macaronesian spiders and the role of species extinctions. *Journal of Biogeography*, **37**, 1034-
532 1046.

533 Cardoso, P., Rigal, F., Fattorini, S., Terzopoulou, S. & Borges, P. A. (2013) Integrating
534 landscape disturbance and indicator species in conservation studies. *PloS One*, **8**, e63294.

535 Cardoso, P., Rigal, F., Carvalho, J.C., Fortelius,M., Borges, P.A.V., Podani, J. & Schmera, D.
536 (2014) Partitioning taxon, phylogenetic and functional betadiversity into replacement and
537 richness difference components*. Journal of Biogeography*, **41**, 749–761.

538

539 Cardoso, P., Rigal, F. & Carvalho, J. C. (2016) BAT: Biodiversity Assessment Tools. R package
540 version 1.4.0. https://CRAN.R-project.org/package=BAT

541 Cardoso, P., Rigal, F., & Carvalho, J. C. (2015) BAT–Biodiversity Assessment Tools, an R
542 package for the measurement and estimation of alpha and beta taxon, phylogenetic and
543 functional diversity. *Methods in Ecology and Evolution*, **6**, 232-236.

544 Castro-Urgal, R. & Traveset, A. (2014) Differences in flower visitation networks between an
545 oceanic and a continental island. *Botanical Journal of the Linnean Society*, **174**, 478-488.

546 Connor, S. E., van Leeuwen, J. F. N., Rittenour, T. M., van der Knaap, W. O., Ammann, B. and
547 Björck, S. (2012) The ecological impact of oceanic island colonization – a palaeoecological
548 perspective from the Azores.*Journal of Biogeography,* **39**, 1007-1023.

549 Cramer, M. J. & Willig, M. R. (2005) Habitat heterogeneity, species diversity and null models.
550 *Oikos*, **108**, 209-218.

551 Cranmer, L., McCollin, D. & Ollerton, J. (2012) Landscape structure influences pollinator
552 movements and directly affects plant reproductive success. *Oikos*, **121**, 562-568.

553   DROTRH. Direcção Regional do Ordenamento do Território e Recursos Hídricos (2008) *Carta*
554   *de ocupação do solo da Região Autónoma dos Açores.* Secretaria Regional doAmbiente.
555   Direcção Regional do Ordenamento do Território e dos Recursos Hídricos. Ponta Delgada.

556   Elias, R. B., Gil, A., Silva, L., Fernández-Palacios, J. M., Azevedo, E. B. & Reis, F. (2016)
557   Natural zonal vegetation of the Azores Islands: characterization and potential distribution.
558   Phytocoenologia, **46**, 107-123.

559   Fattorini, S., Cardoso, P., Rigal, F., & Borges, P. A. V. (2012) Use of arthropod rarity for area
560   prioritisation: insights from the Azorean Islands. *PLoS One*, **7**, e33995.

561   Fahrig, L. (1997) Relative effects of habitat loss and fragmentation on population extinction. *The*
562   *Journal of Wildlife Management*, 603-610.

563   Fisher, R. A., Corbet, A. S. & Williams, C. B. (1943) The relation between the number of species
564   and the number of individuals in a random sample of an animal population. *Journal of Animal*
565   *Ecology*, **12**, 42–58.

566   Florencio, M., Cardoso, P., Lobo, J. M., Azevedo, E. B. & Borges, P. A. V. (2013) Arthropod
567   assemblage homogenization in oceanic islands: the role of exotic and indigenous species under
568   landscape disturbance. *Diversity and Distributions,* **19**, 1450-1460.

569   Florencio, M., Lobo, J. M., Cardoso, P., Almeida-Neto, M. & Borges, P. A. V. (2015) The
570   colonisation of exotic species does not have to trigger faunal homogenisation: lessons from the
571   assembly patterns of arthropods on oceanic islands. *PLoS One,* **10,** e0128276.

572   Fründ, J., Linsenmair, K. E. & Blüthgen, N. (2010) Pollinator diversity and specialization in
573   relation to flower diversity. *Oikos*, **119**, 1581-1590.

574   Garibaldi, L. A., Steffan-Dewenter, I., Kremen, C., Morales, J. M., Bommarco, R., Cunningham,
575   S. A., Carvalheiro, L. G., Chacoff, N. P., Dudenhöffer, J. H., Greenleaf, S. S., Holzschuh, A.,
576   Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M. M., Morandin, L. A., Potts, S. G., Ricketts,
577   T. H., Szentgyörgyi, H., Viana, B. F., Westphal, C., Winfree, R. & Klein, A. M. (2011) Stability of
578   pollination services decreases with isolation from natural areas despite honey bee visits.
579   *Ecology letters*, **14**, 1062-1072.

580   Gaspar, C. S. (2007) *Arthropod diversity and conservation planning in native forests of the*
581   *Azores archipelago* (Doctoral dissertation, University of Sheffield).

582   Gaspar, C., Gaston, K. J., Borges, P. A., & Cardoso, P. (2011) Selection of priority areas for
583   arthropod conservation in the Azores archipelago.*Journal of Insect Conservation*, **15**, 671-684.

584   Gaston, K. J. (1994) Rarity. London: Chapman and Hall.

585   Gray, J. S., Bjoergesaeter, A. & Ugland, K. I. (2006) On plotting species abundance
586   distributions. *Journal of Animal Ecology*, **75**, 752-756.

587   Groom, S. V., & Schwarz, M. P. (2011) Bees in the Southwest Pacific: Origins, diversity and
588   conservation. *Apidologie*, **42**, 759-770.

589   Grøtan, V. & Engen, S. (2009) poilog: Poisson lognormal and bivariate Poisson lognormal
590   distribution. – R package ver. 0.4.

591   Hatfield, R. G. & LeBuhn, G. (2007) Patch and landscape factors shape community assemblage
592   of bumble bees, Bombus spp.(Hymenoptera: Apidae), in montane meadows. *Biological*
593   *Conservation*, **139**, 150-158.

594   Heneberg, P. & Bogusch, P. (2014) To enrich or not to enrich? Are there any benefits of using
595   multiple colors of pan traps when sampling aculeate Hymenoptera?. *Journal of Insect*
596   *Conservation*, **18**, 1123-1136.

597   Hortal, J., Borges, P. A., & Gaspar, C. (2006) Evaluating the performance of species richness
598   estimators: sensitivity to sample grain size. *Journal of Animal Ecology*, **75**, 274-287.

599   Jiménez-Valverde, A., & Lobo, J. M. (2004) Un método sencillo para seleccionar puntos de
600   muestreo con el objetivo de inventar taxones hiperdiversos: el caso práctivo de las familias
601   Araneidae y Thomisidae (Araneae) en la comunidad de Madrid, España. *Ecología*, **18**, 297-305.

602   Kaiser-Bunbury, C. N., Traveset, A. & Hansen, D. M. (2010) Conservation and restoration of
603   plant–animal mutualisms on oceanic islands. *Perspectives in Plant Ecology, Evolution and*
604   *Systematics*, **12**, 131-143.

605   Kaiser-Bunbury, C. N. & Blüthgen, N. (2015) Integrating network ecology with applied
606   conservation: a synthesis and guide to implementation. *AoB Plants*, **7**, plv076.

607   Klein, A. M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C.,
608   &Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops.
609   *Proceedings of the Royal Society of London B: Biological Sciences*, **274**, 303-313.

610 Kremen, C., Williams, N. M., & Thorp, R. W. (2002). Crop pollination from native bees at risk
611 from agricultural intensification. *Proceedings of the National Academy of Sciences*, **99**, 16812-
612 16816.

613 Kremen, C. (2005) Managing ecosystem services: what do we need to know about their
614 ecology? *Ecology letters*, **8**, 468-479.

615 MacArthur, R., & Wilson, E. (1967) *The Theory of Biogeography*. Princeton University Press,
616 New Jersey.

617 Martins, A. M. F. (1993) The Azores - westernmost Europe: where evolution can be caught red-
618 handed. *Boletim Museu Municipal Funchal*, **2**, 181-198

619 Magurran, A. E. (2004) *Measuring biological diversity*. Oxford: Blackwell Publishing. ISBN 0-
620 632-05633-9

621 Matthews, T. J., Borregaard, M. K., Ugland, K. I., Borges, P. A. V., Rigal, F., Cardoso, P. &
622 Whittaker, R.J. (2014) The gambin model provides a superior fit to species abundance
623 distributions with a single free parameter: evidence, implementation and interpretation.
624 *Ecography*, **37**, 1002 – 1011.

625 Matthews, T. J. & Whittaker, R. J. (2014) Fitting and comparing competing models of the
626 species abundance distribution: assessment and prospect. *Frontiers of Biogeography*, **6**, 67–82.

627 Matthews, T. J. & Whittaker, R. J. (2015) On the species abundance distribution in applied
628 ecology and biodiversity management. *Journal of Applied Ecology,* **52**, 443–454.

629 Meijer, S. S., Whittaker, R. J., & Borges, P. A. (2011) The effects of land-use change on
630 arthropod richness and abundance on Santa Maria Island (Azores): unmanaged plantations
631 favour endemic beetles. *Journal of Insect Conservation*, **15**, 505-522.

632 McGill, B. J., Etienne, R. S., Gray, J. S., Alonso, D., Anderson, M. J., Benecha, H. K., ... &
633 Hurlbert, A. H (2007) Species abundance distributions: moving beyond single prediction
634 theories to integration within an ecological framework. *Ecology Letters*, **10**, 995–1015.

635 Miller, A. E., Brosi, B. J., Magnacca, K., Daily, G. C., & Pejchar, L. (2015) Pollen Carried by
636 Native and Nonnative Bees in the Large-Scale Reforestation of Pastureland in Hawai'i:
637 Implications for Pollination. *Pacific Science*, **69**, 67-79.

638 Nie, N., Hull, C., & Bent, D. (2011) IBM statistical package for the social sciences (SPSS
639 Version 20). *Computer Software.* Chicago, IL: SPSS.

640 Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson
641 G.L., Solymos, P., Henry, M., Stevens, H. & Wagner, H. (2013). Package 'vegan'. Community
642 ecology package, version, 2.

643 Olesen, J. M., Eskildsen, L. I. & Venkatasamy, S. (2002) Invasion of pollination networks on
644 oceanic islands: importance of invader complexes and endemic super generalists. *Diversity and*
645 *Distributions*, **8**, 181–192.

646 Ollerton, J., Winfree, R., & Tarrant, S. (2011) How many flowering plants are pollinated by
647 animals?.*Oikos*, **120**, 321-326.

648 Pinheiro, J. C., & Bates, D. M. (2000) Linear mixed-effects models: basic concepts and
649 examples. *Mixed-Effects Models in S and S-Plus*, pp. 3-56. Springer. ISBN: 978-0-387-98957-0.

650 Pollard, E., & Yates, T. J. (1993) *Monitoring butterflies for ecology and conservation.* Chapman
651 and Hall; London.

652 Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010)
653 Global pollinator declines: trends, impacts and drivers. *Trends in ecology & evolution*, **25**, 345-
654 353.

655 Preston, F. W. (1948) The commonness, and rarity, of species. *Ecology,* **29**, 254–283.

656 Rando, J. C.; Alcover, J. A.; Olson, S. L.; Pieper H. (2013) A new species of extinct scops owl
657 (Aves: Strigiformes: Strigidae: Otus) from São Miguel island (Azores archipelago, north Atlantic
658 ocean). *Zootaxa*, **3647**, 343–357.

659 Régnier, C., Bouchet, P., Hayes, K. A., Yeung, N. W., Christensen, C. C., Chung, D. J. D.,
660 Fontaine, B. and Cowie, R. H. (2015) Extinction in a hyperdiverse endemic Hawaiian land snail
661 family and implications for the underestimation of invertebrate extinction. *Conservation Biology*,
662 **29**, 1715–1723.

663 R Development Core Team (2016) R: a language and environment for statistical computing. R
664 Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org
665 (accessed 24 February 2016).

666   Ribeiro, S. P., Borges, P. A. V., Gaspar, C., Melo, C., Serrano, A. R. M., Amaral, J., Aguiar, C.,
667   André, G., & Quartau, J. A. (2005) Canopy insect herbivores in the Azorean Laurisilva forests:
668   key host plant species in a highly generalist insect community. *Ecography*, **28**, 315-330.

669   Ricketts, T. H. (2004) Tropical forest fragments enhance pollinator activity in nearby coffee
670   crops. *Conservation biology*, **18**, 1262-1271.

671   Sahari, B., Rizali, A., & Buchori, D. (2010) Insect pollinator communities under changing land-
672   use in tropical landscapes: implications for agricultural management in Indonesia. *Tropical*
673   *Rainforests and Agroforests under Global Change,* pp. 97-114. Springer, Berlin, Heidelberg.

674   Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald,
675   E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A.,
676   Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M. & Wall, D. H. (2000) Global
677   biodiversity scenarios for the year 2100. S*cience*, **287**, 1770-1774.

678   Seaby, R., & Henderson, P. (2007) *Species Diversity and Richness IV*. Pisces Conservation
679   Ltd., Lymington, England.

680   Sjögren, E. (1973) Vascular plants new to the Azores and to individual islands in the
681   Archipelago.

682   Solow, A. R. (1993) A simple test for change in community structure. *Journal of Animal Ecology*,
683   **62**: 191-193.

684   Steffan-Dewenter, I. & Westphal, C. (2008) The interplay of pollinator diversity, pollination
685   services and landscape change. *Journal of Applied Ecology*, **45**, 737-741.

686   Steffan-Dewenter, I., Klein, A. M., Gaebele, V., Alfert, T., & Tscharntke, T. (2006) Bee diversity
687   and plant–pollinator interactions in fragmented landscapes. *Specialization and Generalization in*
688   *Plant-Pollinator Interactions*, 387-410.

689   Terzopoulou, S., Rigal, F., Whittaker, R. J., Borges, P. A. V. & Triantis, K. A. (2015) Drivers of
690   extinction: the case of Azorean beetles. *Biology Letters*, **11**, 1-4.

691   Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F.
692   (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of
693   keystone structures. *Journal of biogeography*, **31**, 79-92.

694 Traveset, A. (2002) Consecuencias de la ruptura de mutualismos planta-animal para la
695 distribución de especies vegetales en las Islas Baleares. *Revista chilena de historia natural*, **75**,
696 117-126.

697 Traveset, A., Tur, C., Trøjelsgaard, K., Heleno, R., Castro-Urgal, R. & Olesen, J. M. (2015)
698 Global patterns of mainland and insular pollination networks. *Global Ecology and Biogeography*.
699 doi:10.1111/geb.12362.

700 Triantis, K. A., Borges, P. A. V., Ladle, R. J., Hortal, J., Cardoso, P., Gaspar, C., Dinis, F.,
701 Mendonça, E., Silveira, L. M. A., Gabriel, R., Melo, C., Santos, A. M. C., Amorim, I. R., Ribeiro,
702 S. P., Serrano, A. R. M., Quartau, J. A. & Whittaker, R. J. (2010) Extinction debt on oceanic
703 islands. *Ecography*, **33**, 285-294.

704 Ugland, K. I., Lambshead, P. J. D., McGill, B., Gray, J. S., O'Dea, N., Ladle, R. & Whittaker, R.
705 (2007) Modelling dimensionality in species abundance distributions: description and evaluation
706 of the Gambin model. *Evolutionary Ecology Research*, **9**, 313 – 324.

707 Warren, M. S., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., Roy, D. B., Telfer, M.
708 G., Jeffcoate, G., Willis, S. G.,Greatorex-Davies, J. N., Moss, D.& Thomas, C. D. (2001) Rapid
709 responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**,
710 65-69.

711 Whittaker, R. J. & Fernández-Palacios, J. M. (2007) *Island biogeography: ecology, evolution,*
712 *and conservation.* Oxford University Press.

713 Winfree, R., Aguilar, R., Vázquez, D. P., LeBuhn, G. & Aizen, M. A. (2009) A meta-analysis of
714 bees' responses to anthropogenic disturbance. *Ecology*, **90**, 2068-2076.

715 Winfree, R., Bartomeus, I. & Cariveau, D. P. (2011) Native pollinators in anthropogenic habitats.
716 *Annual Review of Ecology, Evolution, and Systematics*, **42**, 1.

717 Winfree, R. & Kremen, C. (2009) Are ecosystem services stabilized by differences among
718 species? A test using crop pollination. *Proceedings of the Royal Society of London B: Biological*
719 *Sciences*, **276**, 229-237.

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

Habitats	Insect Species			Plant Species		
	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

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

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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)).
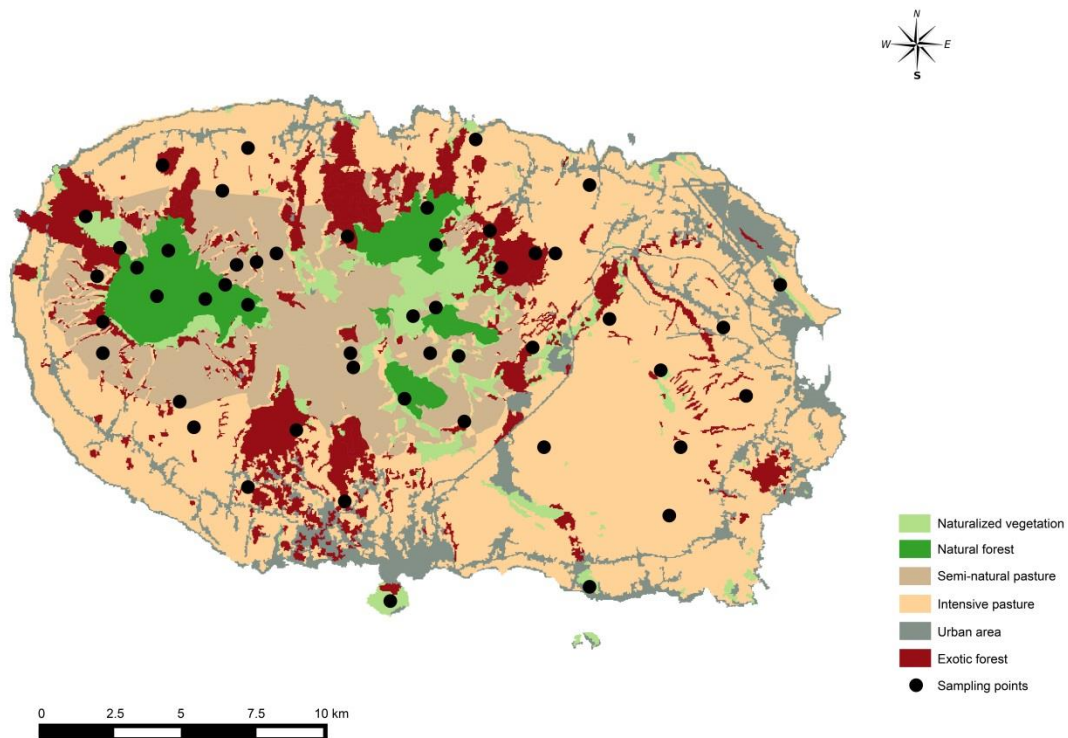742

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/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.
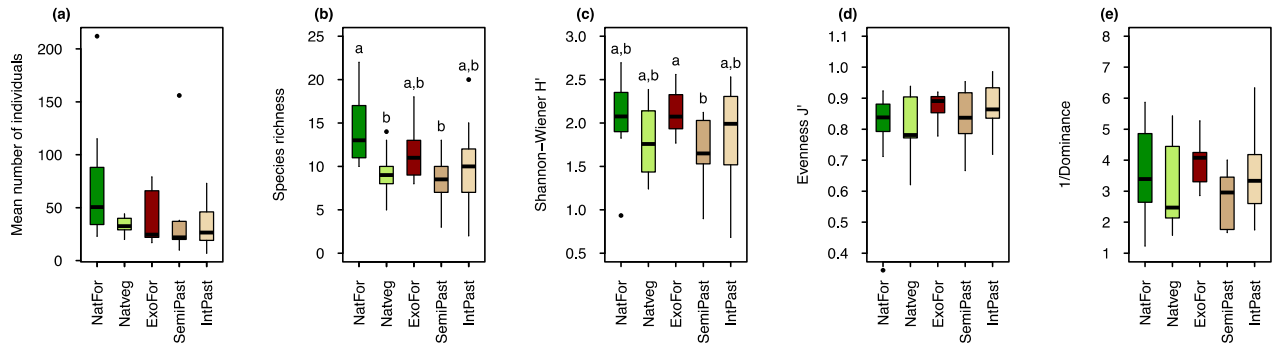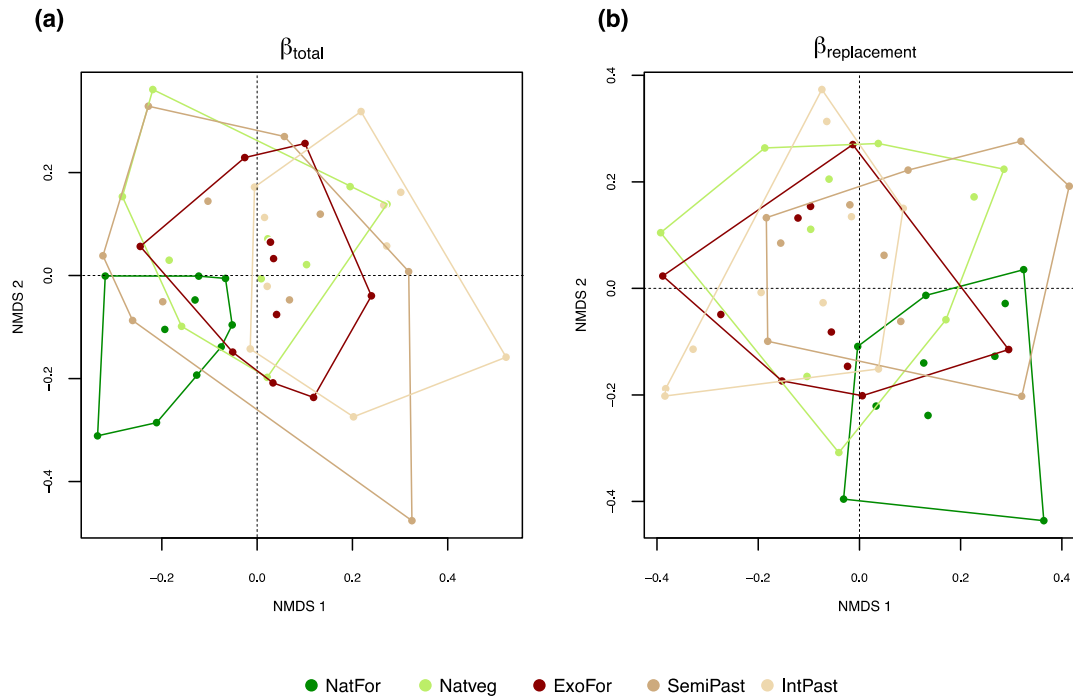766   (see Gray *et al.*, 2006 and Matthews *et al.*, 2014).

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Figure 1. Land use distribution map of Terceira Island with the selected sampling sites as black dots: NatFor (natural forests), SemiPast (semi-natural pastures), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), IntPast (intensively managed pastures) (cartographic information from DROTRH (2008) and Gaspar (2007), see also Gaspar *et al.* (2011)).

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Figure 2. Species diversity metrics of flower-visiting insects across the different habitat types**.** (a)Mean abundance, (b) mean species richness, (c) Shannon-Wiener H´, (d) Pielou's Evenness J´ and (e) Inverse Berger-Parker 1/Dominance. For species richness (b), habitat types accompanied by a different letter are significantly different from each other (post hoc tests; $P < 0.05$). NatFor (natural forests), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), SemiPast (semi-natural pastures), and IntPast (intensively managed pastures).
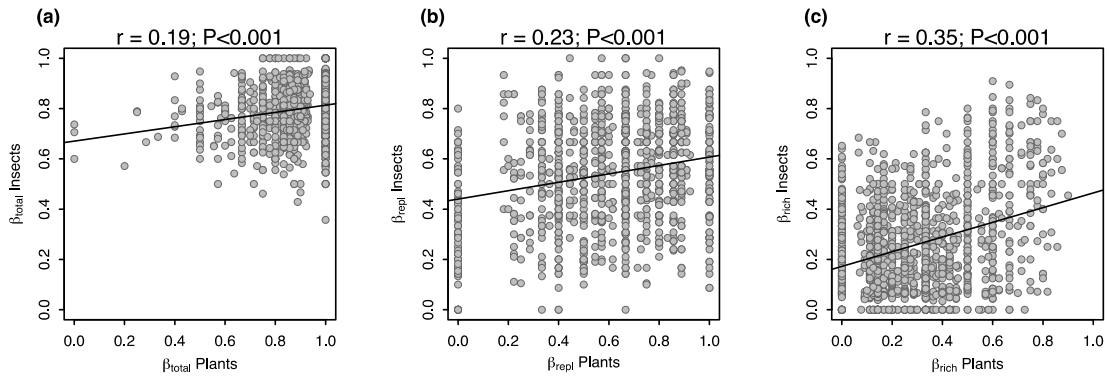
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Figure 3. Two-dimensional ordination solution using non-metric multidimensional scaling (NMDS) with the β diversity measures β_{total} (a) and β_{repl} (b) for flower-visiting insects. Dots indicate transects while lines delimit the smallest polygon that encloses all transects for a given habitat. The stress value of NMDS was 0.17 and 0.18 for β_{total} and β_{repl} respectively. NatFor (natural forest), NatVeg (naturalized vegetation areas), ExoFor (exotic forest), SemiPast (semi-natural pasture), and IntPast (intensively managed pasture).
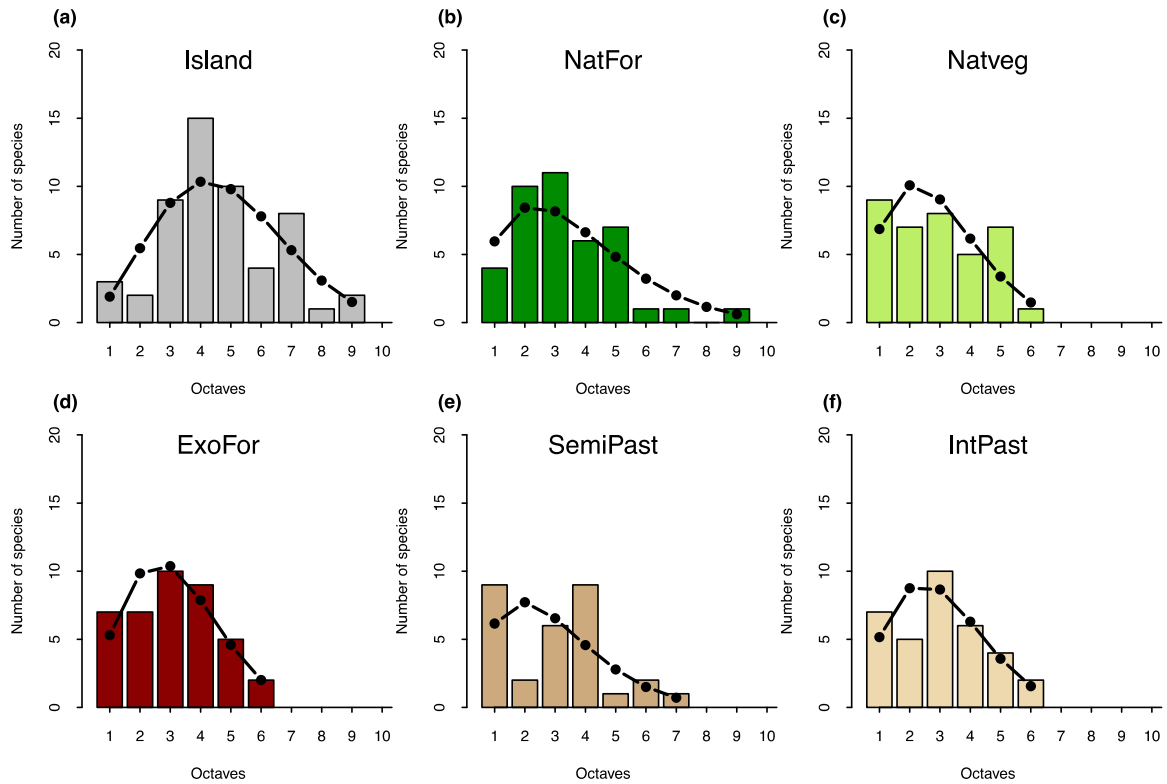
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Figure 4. Correlations between species composition (β diversity) of flower-visiting insects and plants across the 50 transects. Correlations were performed with β_{total} (a) β_{repl} (b) and β_{rich} (c). Spearman correlation coefficient and its associated p-values of the Mantel test are given on the top of each panel. NatFor (natural forest), NatVeg (naturalized vegetation areas), ExoFor (exotic forest), SemiPast (semi-natural pasture) and IntPast (intensively managed pasture).

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