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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

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

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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

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

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

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

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

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

METHODS

Study area, sampling and species identification

Our study was conducted on Terceira Island. Terceira is an island from the central group of the Azores archipelago, located in the North Atlantic Ocean (38º 37´N - 38º 48´N, 27º 02´W - 27º 23´W) with an Area 402 km^2 and maximum elevation of 1023 m. Field work was conducted from June to September 2013 and from July to October 2014, due to favourable weather conditions and relatively high number of plant species in the flowering period. For the current study, we selected five distinct habitat types covering a large percentage of the total island area with, from the least to the most disturbed, natural forests (NatFor), naturalized vegetation areas (NatVeg), exotic forests (ExoFor), semi-natural pastures (SemiPast) and intensively managed pastures (IntPast) (Cardoso *et al*., 2013). Compared with previous ecological studies undertaken in the Azores (Borges *et al.*, 2008; Cardoso *et al.*, 2009, 2010a; Florencio *et al.*, 2013, 2015) we added naturalized vegetation areas, dominated by *Erica azorica*, *Pittosporum undulatum* and *Rubus hochstetterorum*, as an important habitat for flower visiting insects, because of its recent growing extent due to pasture abandonment and combination of native and exotic flora. Detailed features regarding each habitat type are outlined in Table S1.

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

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

Data analysis

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

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

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

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

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

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

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

RESULTS

Species composition

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

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

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

Sampling completeness

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

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).

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

Species abundance distributions (SADs) and rarity patterns

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

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

DISCUSSION

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

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

Insect diversity in the different habitats

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

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

Habitat similarity

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

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.

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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.

Table S2. Geographical coordinates for all sites in Terceira Island for each habitat type.

Table S3. Abundance and number of individuals per insect species/morphospecies in each habitat type.

Table S4. Number of flowers per plant species in each habitat type.

Table S5. Number of species/morphospecies studied in 2013 and 2014 years per each habitat type.

Table S6. Number of individuals, species/morphospecies, singletons and doubletons studied in each habitat type. **Table S7.** Comparison of total beta diversity (β_{total}), replacement beta diversity (β_{repl}) and richness beta diversity (β_{rich}) values along a gradient of increasing dissimilarity for all transects considered together of each habitat.

Table S8. P-values of the post hoc pairwise Analysis of similarities (ANOSIM) corrected for multiple tests.

Table S9. AIC_c values for the SAD model selection. The three SAD models (logseries, PLN and gambin were fitted to flower-visiting insect data from five land use types.

REFERENCES

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

	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

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

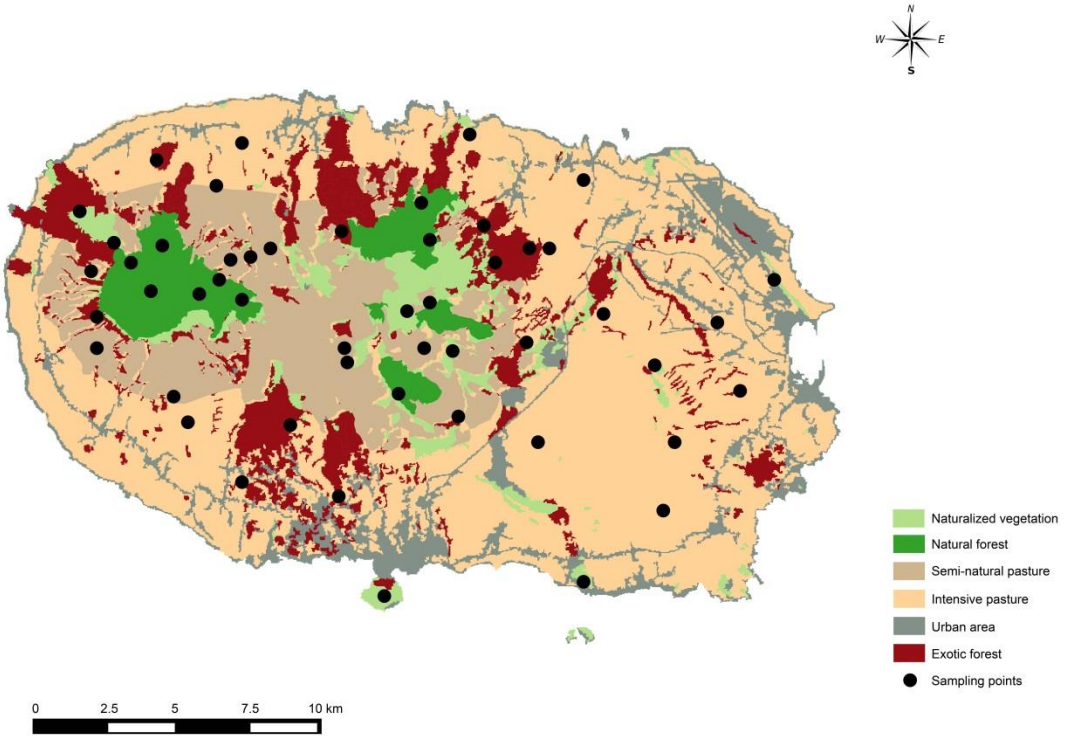
Figure 1. Land use distribution map of Terceira Island with the selected sampling sites as black dots: NatFor (natural forests), SemiPast (semi-natural pastures), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), IntPast (intensively managed pastures) (cartographic information from DROTRH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

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).

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).

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).

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).



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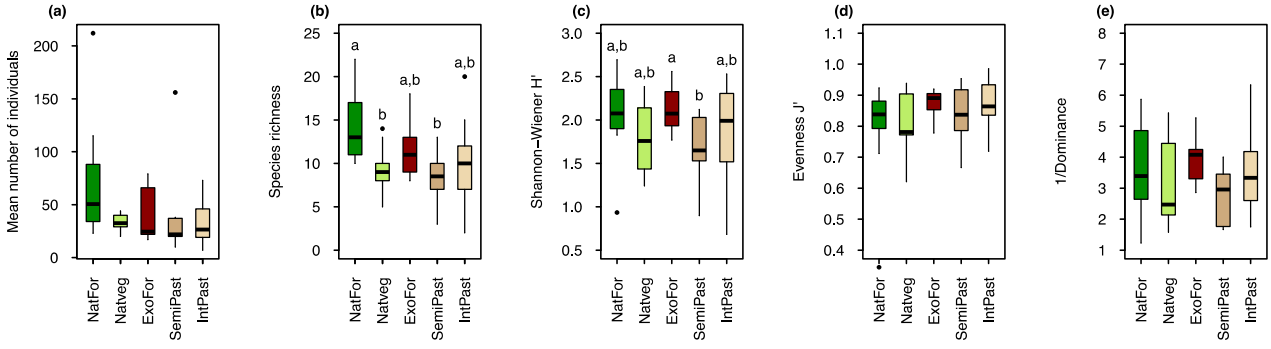

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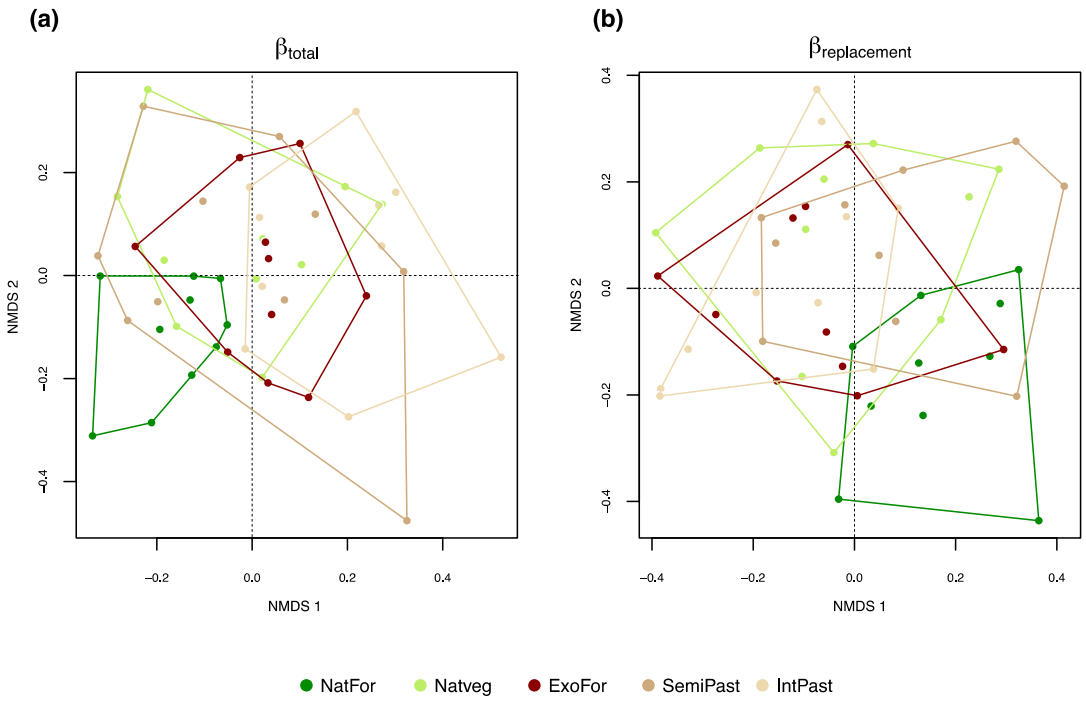

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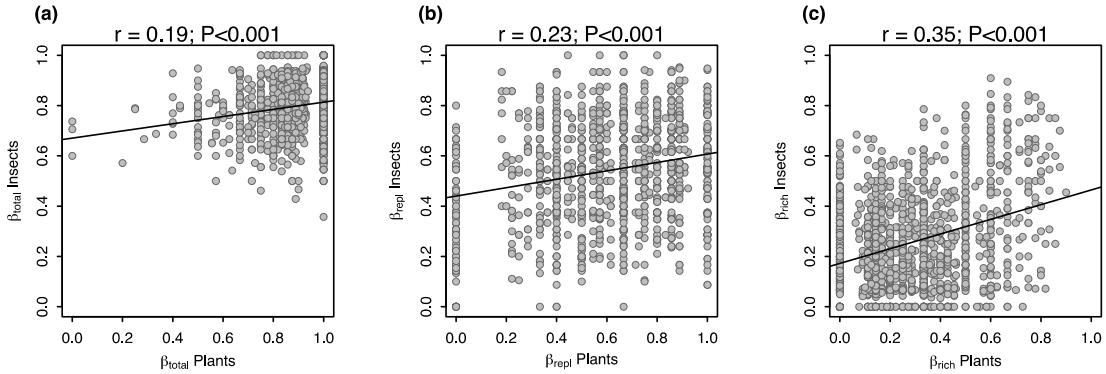

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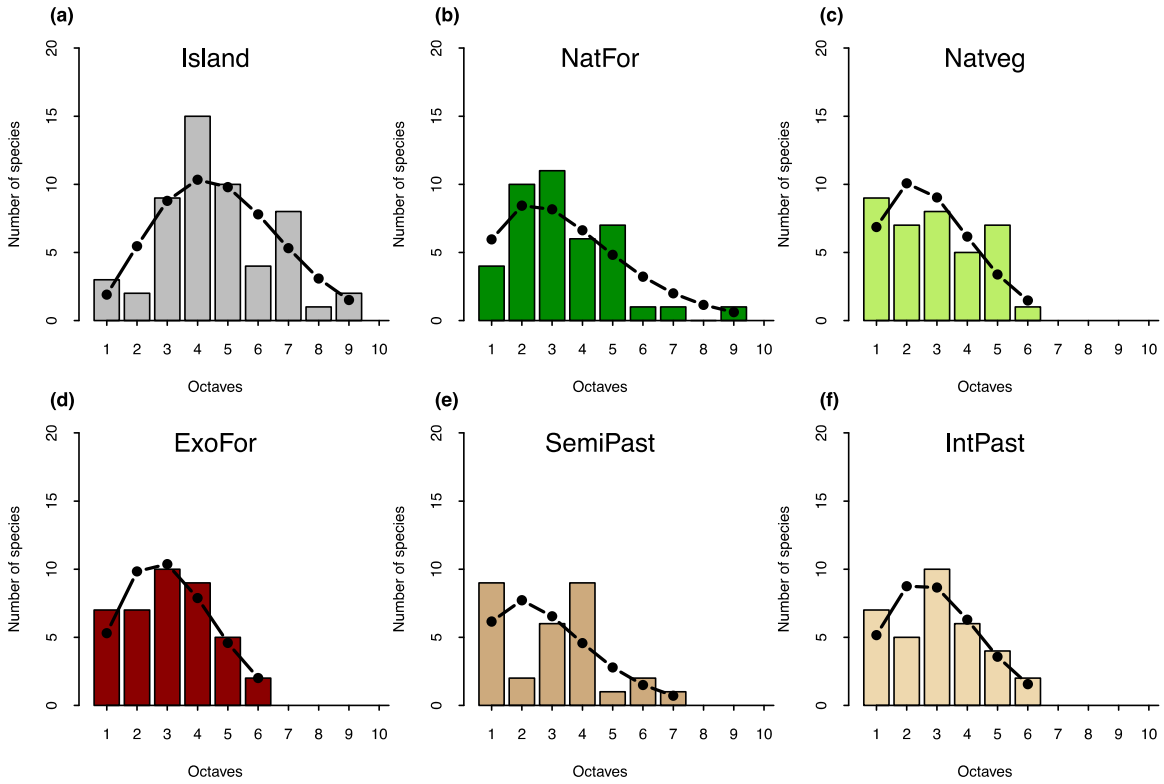

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