



# Arthropod assemblage homogenization in oceanic islands: the role of indigenous and exotic species under landscape disturbance

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## ABSTRACT

**Aims** Human landscape disturbance can drive the degradation of natural environments, thereby contributing to indigenous (endemic and native non-endemic) species extinctions, facilitating the establishment of exotic species and ultimately resulting in more similar species compositions over time and space. We assessed whether similarities in epigeal arthropod assemblages differ between indigenous and exotic species in an oceanic archipelago, and we also examined whether such assemblage similarities depend on the most dominant species, the island, the type of habitat, the degree of landscape disturbance or local environmental variables.

**Location** Four oceanic islands in the Azores archipelago, Portugal.

**Methods** We examined the degree of assemblage similarity and the effect of environmental variables and spatial disturbance to explain the epigeal arthropod distributions for indigenous and exotic species.

**Results** Exotic species increased overall assemblage similarity. Distinct arthropod assemblages occurred on the different islands and in the different habitats. Assemblage differences between the habitats depended on the island. This pattern was largely explained by the abundance patterns of the most abundant indigenous and exotic species (ten indigenous and ten exotic species accounted for 75% of total individuals). In comparison with the high explanatory capacity of the habitats and islands per se, local environmental variables and disturbance hardly explained the assemblage composition in both groups of species.

**Main conclusions** We demonstrate that exotic species promote assemblage homogenization on these oceanic islands, and that such process is contingent and independent between islands and habitats. General habitat characteristics seemed to be the main driver of assemblage structure, independently of the different climatic conditions or disturbance levels.

## Keywords

Anthropogenic disturbance, assemblage similarity, biological invasions, epigeal arthropods, land use.

## INTRODUCTION

Human actions have transformed between one-third and one half of the Earth's terrestrial surface, altering the structure and function of ecosystems, and often accelerating natural extinction rates (Vitousek *et al.*, 1997). In particular, the dissemination of exotic species by human actions

and land use change are some of the main drivers of global environmental change and reduction of biodiversity (Vitousek *et al.*, 1996, 1997; Cassey *et al.*, 2005). Thus, although the introduction of exotic species may occasionally increase local biodiversity (Sax *et al.*, 2002), this process typically increases biotic homogenization or regional similarity of local assemblages (Rosenzweig, 2001; Olden & Poff,

2003; Olden & Rooney, 2006) by two different mechanisms: the colonization of non-indigenous species ('winners') and/or the non-random extinction of the most specialized native species ('losers') (McKinney & Lockwood, 1999; Lockwood *et al.*, 2000; Rahel, 2000). Anthropogenic disturbance is one of the main drivers of biotic homogenization associated with changes in the natural colonization and extinction rates, in comparison with non-disturbed environments (Olden & Poff, 2003). Hence, there is evidence of increasing assemblage similarity under landscape transformation and urbanization in different groups of organisms, either vertebrates, for example birds and fishes (Blair, 2001; Hermoso *et al.*, 2012), or invertebrates, for example beetles, spiders and butterflies (Dormann *et al.*, 2007; Ekroos *et al.*, 2010).

The study of biotic homogenization on islands should receive special attention (e.g. Olden *et al.*, 2004; Olden, 2006) because isolated oceanic islands seem to be especially vulnerable to the introduction of exotic species, thanks to the niche opportunities offered by the existence of probable non-saturated assemblages (see Cornell & Lawton, 1992). As a consequence, exotic species that colonize islands may frequently occupy wider environmental ranges than their mainland conspecifics (Sax, 2001), with biotic homogenization expected to be relatively more pronounced on oceanic islands (Blackburn *et al.*, 2008). Whilst a high  $\beta$ -diversity of native elements would be expected between heterogeneous environments of isolated islands, depending on the evolutionary time available for speciation (Cornell & Lawton, 1992; Borges & Hortal, 2009), exotic species introductions should increase the similarity of local assemblages, thus reducing overall biota regional  $\beta$ -diversity.

The Azorean archipelago has suffered from constantly increasing landscape disturbance in the last six centuries since the first human settlements occurred, original native forests remaining only at the highest altitudes in the islands (Borges *et al.*, 2009). Rapid, widespread and persistent vegetation changes have occurred during the last 600 years through intensification of land use management and species introductions, surpassing the effects of past Pleistocene climatic fluctuations (Connor *et al.*, 2012).

In this study, we used a thorough survey of epigeal arthropods on four representative oceanic islands of the Azorean archipelago to examine whether the degree of similarity in local assemblages differs between indigenous (endemic plus native non-endemic) and exotic species and also to determine whether this difference depends on the type of habitat, local environmental conditions, degree of disturbance and/or the idiosyncratic character of the colonization and speciation processes operating on each island. Specifically, we hypothesized (i) that exotic species occurrences should increase the compositional similarity between local assemblages, (ii) that the effect of island and habitat on local assemblages should be significantly lower in the case of exotic species, and (iii) that indigenous and exotic species would preferably occupy minimally and highly disturbed sites,

respectively, being thus distributed according to the degree of landscape disturbance.

## METHODS

### Study area

The Azorean archipelago is located in the North Atlantic, roughly between 37° and 40° N latitude and between 25° and 31° W longitude. It comprises nine islands, in addition to small islets aligned in a WNW–ESE direction (see Figure S1). The archipelago was created by volcanic activity 8.12–0.3 million years ago, and recurring volcanic activity still regularly generates new small islets or expands existing islands. The climate is temperate and oceanic, being strongly influenced by the proximity of the ocean and by island topography, which together produce high levels of relative atmospheric humidity, with annual averages in forests reaching 95%. This temperate oceanic climate also limits temperature fluctuations throughout the year.

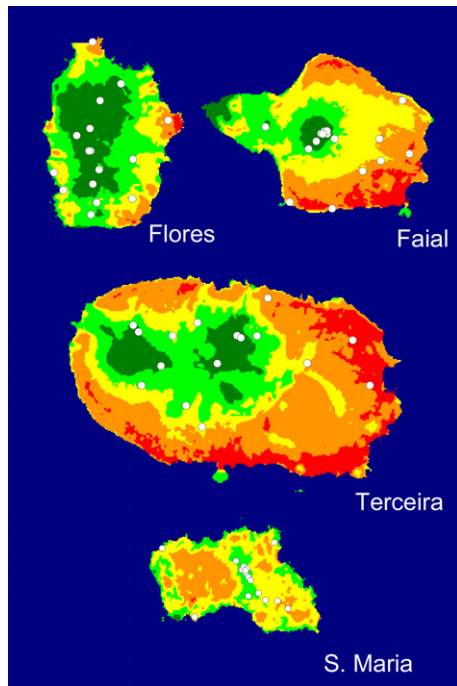
We considered four islands in this study, trying to represent the range of environmental conditions, geographical locations and human disturbance levels found in the Azores. Santa Maria, one of the islands considered, is located in the eastern part of the archipelago being the oldest, smallest and driest island of the four. It has the highest human population density, the lowest percentage of native forests and the highest percentage of intensively managed pastures of the four study islands. Terceira and Faial, two of the other islands considered in this study, are located in the central part of the archipelago, whilst the fourth, Flores, is located in the western part. Terceira has the largest area of the four islands and includes the largest native forests. Faial is characterized by a low population density and a high proportion of seminatural pastures, whilst Flores harbours the highest percentage of native forests (see Figure S1, Table 1).

### Sampling procedure

Four habitat categories, reflecting different habitats and degrees of human alteration, were considered: (i) native forests (*Laurisilva*) located at middle to high altitudes and subject to a null to very low degree of human management, in which *Juniperus brevifolia*, *Laurus azorica*, *Ilex perado* subsp. *azorica* and *Erica azorica* are the most abundant arboreal endemic plant taxa; (ii) exotic forests consisting of mostly monospecific plantations of *Cryptomeria japonica*; (iii) seminatural pastures located at middle to high altitudes that are not intensively managed – low grazing activity is concentrated in summer (Borges & Brown, 1999) – and are mainly composed of native forbs (e.g. *Lotus uliginosus*), exotic and native grasses, rushes, sedges and ferns; and (iv) intensively managed pastures for cattle, managed throughout the year and characterized by poor vascular flora of dominant species, mainly composed of introduced grasses and leguminous forbs (Borges & Brown, 1999).

**Table 1** Area, population density in 2011 (from <http://estatistica.azores.gov.pt>), and extent of the four considered habitats in each one of the four study islands.

Island	Terceira	Santa Maria	Flores	Faial
Area (in km <sup>2</sup> )	400	97	143	173
Population density (hab per km <sup>2</sup> )	140	155	39	22
Native forest, km <sup>2</sup> (%)	23.49 (5.9)	0.13 (0.1)	15.80 (11.2)	2.18 (1.3)
Exotic forest, km <sup>2</sup> (%)	56.95 (14.2)	20.42 (21.3)	31.21 (22.2)	30.31 (17.6)
Seminal pastures, km <sup>2</sup> (%)	44.06 (11.0)	0.63 (0.7)	22.16 (15.7)	37.09 (21.6)
Intensive pastures, km <sup>2</sup> (%)	122.93 (30.8)	42.99 (44.8)	24.52 (17.4)	52.16 (30.3)

**Figure 1** Location of the 64 considered sampling units (transects) in the four study islands. The landscape disturbance gradient in each study island is also represented, from the least impacted areas in dark green, to the most degraded areas in bright red.

Four transects (sampling units) were randomly selected per each combination of habitat and island ( $n = 4^3 = 64$ ; Fig. 1). Native forests were sampled between 1997 and 2004, always during summer (Borges *et al.*, 2005a). Data were collected in the other three habitats on Santa Maria, Faial and Flores during the summer of 2009 (see also Meijer *et al.*, 2011) and on Terceira during the summer of 2008 (see Cardoso *et al.*, 2009). Because different habitats were sampled at different years in different islands due to resource limitations, we used additional transects sampled in one locality of the Terceira Island at different years (i.e. 16 transects in native forest in ‘Serra de Santa Bárbara’ surveyed during 1999, 2001 and 2003) to discard a possible effect of the sampling year on the assemblage compositions. We have built triangular similarity matrices using the inverse of the Bray–Curtis index of dissimilarity, performing an one-way analysis of similarity (ANOSIM) using

the year as grouping factor (the ANOSIM statistic  $R$ , range from 0 to 1, being 1 when the dissimilarity between the factor levels is maximum, Clarke & Warwick, 2001). Using these additional data, we did not detect a statistically significant effect of the sampling year on the composition of epigeal arthropod assemblages ( $R = 0.06$ ,  $P = 0.287$ ), and thus, we continued with the analyses.

Each 150 m transect consisted of 30 pitfall traps spaced 5 m apart. The pitfall traps were plastic cups with diameters of 42 mm and depths of 78 mm; they were buried in the ground so that the rims of the cups were level with the surface. Half of the traps in each transect were filled with approximately 60 ml of an antifreeze liquid (diluted ethylene glycol), and the other half were filled with the same volume of an attractive Turquin solution. The ethylene and Turquin traps were alternated in each transect. Traps were left in the field for 2 weeks. The obtained arthropods were preserved in a mixture that included 70% ethanol and 5% glycerol for identification in the laboratory at the species level (Araneae, Opiliones, Pseudoscorpiones, Diplopoda, Chilopoda and insects, excluding Collembola, Diplura, Diptera and Hymenoptera; see Borges *et al.*, 2005a for a detailed description). Because approximately only 16% of taxa were left unidentified, we use the term ‘species’ throughout the text for simplicity.

### Environmental variables

The altitudes of transects were calculated using a digital elevation model with a  $100 \times 100$ -m resolution. The slope was calculated based on the altitude difference between the altitude of the focal cell and the four adjacent cells. The climatic variables considered were the annual cumulative precipitation (in mm) and the average annual temperature ( $^{\circ}\text{C}$ ), obtained at the same resolution, from interpolations of CIELO maps (Azevedo, 1996; Azevedo *et al.*, 1999), which were conducted by one of the authors of this study (Azevedo, 2010). Based on an index of disturbance ranging from 0 to 100 (Cardoso *et al.*, 2013), we developed a map reflecting the anthropogenic landscape disturbance of each cell in the four study islands, extracting the value corresponding to the cell at the middle of each transect. This index is intended to represent both the local disturbance of each cell and those of the surrounding cells. For all of the islands considered, the

values of the disturbance index increased from the central high-altitude and inaccessible zones towards the coast, with the exception of Santa Maria, for which the central zones were most affected by disturbance (Fig. 1).

### Preliminary analysis

Arthropods were grouped into two colonization categories: indigenous and exotic species. Indigenous species may be endemic (i.e. occurring only in the Azores) or native (present both in the Azorean Islands and in other nearby Macaronesian archipelagos, Madeira and the Canary Islands). We considered as exotic species those whose original distribution range did not include the Azores archipelago and believed to have been introduced in the Macaronesian region after human settlement in the 15th century. This was usually inferred either from historical records of detected species introductions or from their current distribution being closely associated with human activity. For unidentified species, if other species in the same genus, subfamily or family were present in the archipelago and all belonged to the same colonization category (according to Borges *et al.*, 2010), the unknown species would be classified similarly. Otherwise, we assumed the species to be native.

We constructed an abundance matrix using total abundance values for each species obtained in the 30 pitfall traps of each transect (the sampling unit). As the survey effort required to obtain reliable inventories for each sampling unit differed depending on the habitat (see Appendix S1, Fig. S2), we built comparable assemblage matrices, selecting at random in each sampling unit a number of individuals equal to the minimum number obtained in any sampling unit (62 individuals). These rarefied inventories were subsequently used to estimate compositional differences and select the most relevant explanatory variables. Because between-habitat or between-island differences can be influenced by the rarefied assemblages, we repeated the process 15 times, examining whether compositional differences were related to the two main factors considered (habitats and islands).

### Assemblage similarity changes: the effects of habitats and islands

We analysed the compositional similarity of all pairwise rarefied sampling units using the Bray–Curtis index of similarity (the inverse of the Bray–Curtis index of dissimilarity), thus obtaining a triangular similarity matrix. These matrices were constructed for the whole epigeal arthropod data set and separately for indigenous and exotic species. The values of all the pairwise comparisons between sampling units ( $n = 2016$ ) were compared by nonparametric Wilcoxon matched pair tests to estimate whether the addition of exotic species significantly increased the similarity of initial assemblages with indigenous species only. A similar analysis was also performed separately for pairwise comparisons between sampling units ( $n = 120$ ) belonging to each one of the four habitat categories.

Assemblage similarity differences between island and habitat categories, as well as the possible interaction between these two factors, were analysed using a two-way crossed permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001). This nonparametric procedure allows us to analyse differences between two or more groups or factors based on any distance or similarity measure. PERMANOVA analyses were performed for the whole epigeal arthropod data set and separately for indigenous and exotic species. Statistically significant differences were tested by permutation of group membership with 9999 replicates using the software PRIMER v.6 (Anderson *et al.*, 2008).

To examine the contribution of the dominant species to the homogenization of indigenous and exotic assemblages, we first used the original data to identify the most abundant species as those cumulatively representing at least 75% of total collected abundance. Subsequently, two-way crossed PERMANOVA analyses were carried out, again using islands and habitats as factors. Mann–Whitney  $U$ -tests were also used to compare the coefficient of variation (the ratio of the standard deviation to the mean) of the species abundances between islands and between habitats for both species groups (indigenous and exotic). To perform these tests, we considered the total species abundance captured per island and per habitat. We also used the number of individuals of the most abundant species to estimate abundance differences between islands and habitats by simple chi-square tests (the expected values corresponded to the equitable probability of species abundance in the different islands and habitats).

### Environmental variables and landscape disturbance

We examined the comparative role of the environmental variables and the disturbance index in explaining differences in the assemblages' composition. To do that, we performed multiple regressions of distance matrices (MRM), an extension of partial Mantel analysis (Legendre *et al.*, 1994) involving in our case a multiple regression of a response matrix on two different explanatory matrices. Spearman rank correlation coefficients ( $r_s$ ) as measure of between matrix congruence. The statistical significance of MRM models was assessed using 1000 Monte Carlo permutations (Mantel, 1967). Three different triangular matrices were used for this purpose: (i) a compositional dissimilarity response matrix derived from the use of the Bray–Curtis index of dissimilarity of raw abundances; (ii) an environmental matrix using Euclidean distances on the selected environmental variables ( $\log x + 1$  values of altitude, slope, temperature and precipitation) and (iii) a disturbance matrix using Euclidean distances on the formerly mentioned disturbance index. We repeated these calculations both for indigenous and exotic species. Thus, we constructed three different models: (i) the *environmental model*, only including the environmental matrix; (ii) the *disturbance model*, only including the disturbance matrix; and (iii) the *full model*, which includes the environmental matrix plus the disturbance matrix, to

discriminate partial effects for both indigenous and exotic species. All these calculations were performed using R software 2.14.2 (R Development Core Team, 2012; 'ecodist' version 1.2.7. package, Goslee & Urban, 2007).

## RESULTS

In total, 289 species of epigeal arthropod species were collected on the four studied islands: 129 indigenous (39 endemic and 90 native non-endemic) and 160 exotic species. Among the islands, Santa Maria had the highest number of endemic and exotic species and the highest proportion of exclusive species (i.e. species only occurring on one of the islands considered). Among the habitats, the highest number and proportion of exclusive native non-endemic and exotic species occurred in intensive pastures, whilst the highest values for endemic species occurred in native forests (Table 2).

### Assemblage similarity changes

The Bray–Curtis index of similarity values between sampling units were significantly higher for the epigeal arthropod assemblages as a whole than when only indigenous species were considered (Table 3). This was true for each one of the habitat categories considered, except for the seminatural pastures, where there were no significant differences in two of the fifteen rarefied matrices (see Table S1). In general, incorporating exotic species changes the values of the Bray–Curtis index of similarity in a 48%, being these percentages lower in the case of native forests (21%) and seminatural pastures (19%) than for exotic forest (74%) or intensive pastures (55%).

### The effects of habitats and islands on similarity patterns

We detected consistent and statistically significant effects of both habitat and island factors on compositional similarities,

as well as a significant effect of the interaction between habitat and island factors. This result appears in all ( $n = 15$ ) the rarefied matrices considered ( $P < 0.001$  in all cases; see Table S2), for both the epigeal arthropod assemblage as a whole and also separately for indigenous and exotic species. Habitats seemed to influence the resemblance of the assemblages to a greater extent than did the islands (Table 4). Approximately 30% of the compositional variability in sampling units was related to habitat differences, this effect being stronger for exotic species than for indigenous ones (Table 4). The effect of islands explains approximately 10% of the compositional variability, and this effect was similar for the two groups of species. The statistically significant role played by the habitat  $\times$  island interaction suggests that between-habitat differences in the faunistic composition of sampling units may also depend on the considered island.

### The role of abundant species

Ten indigenous and ten exotic species accounted for 75% of all obtained individuals (see Fig. 2). PERMANOVA analyses considering only these species also revealed statistically significant effects of both habitat and island factors ( $P < 0.001$  in all cases, see Table S3). Habitat was found to explain approximately 37% of compositional similarities for indigenous species and approximately 44% for exotic species. The effect of islands on compositional similarities was found to be approximately 16% for indigenous species and only 11% for exotic ones. The interaction between habitats and islands was also statistically significant for the two groups of species (Table 5).

Most of the abundant indigenous and exotic species did not differ in their coefficients of variation between the different islands (Mann–Whitney  $U$ -test = 45,  $P = 0.71$ ) or between the different habitats (Mann–Whitney  $U$ -test = 47,  $P = 0.82$ , see Table S4). Chi-square tests showed that both indigenous and exotic abundant species presented similar figures for collected individuals across the four islands

**Table 2** Total number of species and number of exclusive species only occurring in one of the islands and habitats for the four considered islands, indicating the corresponding number of indigenous, separated in endemic and native (non-endemic) species, and of exotic species.

	All species				Exclusive species			
	Endemic	Native	Exotic	Total	Endemic	Native	Exotic	Total
<b>Islands</b>								
Faial	8	46	79	133	0	9	12	21
Flores	14	37	61	112	5	4	4	13
Santa Maria	22	44	111	177	14	15	37	66
Terceira	17	55	85	157	8	14	15	37
<b>Habitats</b>								
Native forest	31	37	67	135	14	11	12	37
Exotic forest	19	35	58	112	4	12	9	25
Seminatural pastures	14	38	86	138	2	5	15	22
Intensively managed pastures	5	46	108	159	0	20	40	60

**Table 3** Bray–Curtis index of similarity values calculated using the whole epigeal arthropod assemblages and only considering indigenous species. The values were calculated using all the considered habitats and also separately for each habitat: native forests (Natf), exotic forest (Exf), seminatural pastures (Seminpast) and intensive pastures (Intpast). Averaged Wilcoxon *Z* values for the 15 rarefied matrices and number of cases (*Nc*) in which these similarity values are statistically different ( $P < 0.01$ , SD is indicated for the similarity values and the *Z* values, see Table S1 in supplementary material for the *Z* values of the fifteen rarefied matrices).

	All habitats	SD	Natf	SD	Exf	SD	Seminpast	SD	Intpast	SD
All species	19.43	0.27	32.03	0.66	32.99	1.39	31.10	1.19	26.69	1.01
Only indigenous species	13.10	0.63	26.38	1.48	18.92	1.52	26.06	2.36	17.21	1.62
Wilcoxon <i>Z</i> values	22.76	1.66	6.04	0.96	7.28	0.56	3.05	1.05	5.81	0.75
<i>Nc</i>	15		15		15		13		15	

**Table 4** Percentage of mean explanatory capacity (EC) of the two considered factors (habitats and islands) on the differences in assemblage similarity of sampling units, for the whole epigeal arthropod assemblages and separately for the exotic and indigenous species. The explanatory capacity of the interaction between habitats and islands is also included. Mean and 95% confidence interval (CI 95%) values were calculated considering 15 rarefied matrices in which the influence of these factors on assemblage similarities were examined by a two-way crossed permutational multivariate analysis of variance (PERMANOVA, see Methods). All tests were statistically significant with  $P < 0.001$ .

	EC	CI 95%
Habitats		
Whole assemblage	29.2	28.5–30.7
Exotic species	30.9	30.1–32.6
Indigenous species	21.4	20.4–23.6
Islands		
Whole assemblage	11.2	10.5–12.8
Exotic species	9.2	8.8–10.3
Indigenous species	10.1	9.3–11.9
Habitat x islands		
Whole assemblage	15.0	13.9–17.3
Exotic species	14.2	12.9–17.2
Indigenous species	14.2	12.9–17.2

( $P > 0.12$  in all cases), except for one single-island indigenous species. In contrast, six species significantly differed in their abundances between the considered habitats. Four of these species were indigenous and two were exotic species that were the most specialized for their particular habitats (Fig. 2).

### The role of environmental variables and landscape disturbance

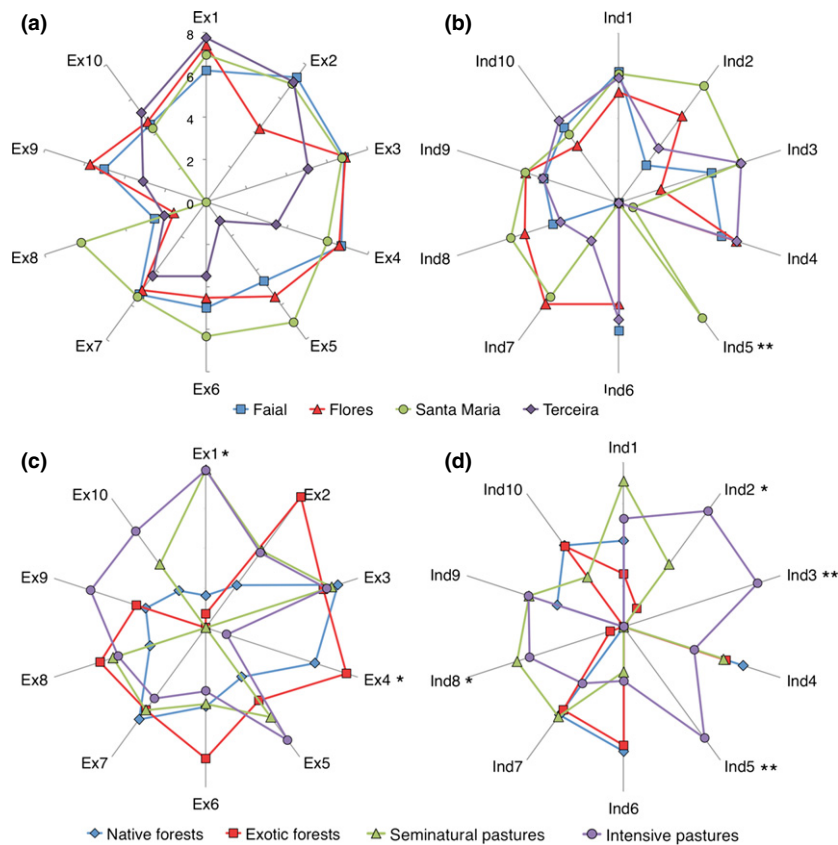
A small but statistically significant amount of the total compositional variation in indigenous and exotic assemblages was explained by the environmental model (4% and 6% of total variability, respectively) and by the disturbance model (2% and 4% respectively). Although the full model was also statistically significant for the two groups of species, the inclusion of the disturbance index in the environmental

model only slightly improved the explained variance in the case of exotic species ( $\approx 7\%$ , Table 6).

## DISCUSSION

Human-induced landscape changes can drive important biodiversity changes associated with the introduction of exotic species and the extinction of indigenous ones (Vitousek *et al.*, 1997), ultimately increasing the regional similarity between assemblages around the world (Dormann *et al.*, 2007). The results of this study show that the addition of exotic species increases the similarity of local assemblages and that this assemblage homogenization occurs in most islands and habitats (both natural and human-made habitats). Moreover, the assemblage homogenization process due to the incorporation of exotic species is contingent, that is, the homogenization process going on in each habitat is different on each island. Although the effects of habitat change in Azorean epigeal arthropod assemblages have been studied for single islands (e.g. Borges *et al.*, 2008; Cardoso *et al.*, 2009, 2010b; Meijer *et al.*, 2011), the novelty of our results resides in the habitat effect having been found to be dependent on the island. Different islands suffered different land use change processes at different times and with different intensity (e.g. the degree of deforestation; Cardoso *et al.*, 2010a; Triantis *et al.*, 2010), and this may be responsible for the observed island effect. For example, those islands with highest native forest destruction and fragmentation may present favourable conditions for the introduction of a greater number of exotic species and extirpation of indigenous species (McKinney & Lockwood, 1999). Nevertheless, this result implies the unpredictability of future compositional assemblages with the colonization of exotic species.

The homogenization pattern was also observed when only the ten most abundant species of each group, indigenous or exotic, were considered. Moreover, the most abundant indigenous and exotic species were similarly distributed across the different islands and habitats. Exotic species in particular were generally widespread on the four islands, and only one indigenous species, *Loboptera decipiens* (Germar), was found on a single island, Santa Maria. However, indigenous species seemed to be more habitat-specialized, with four of the ten species (*Heteroderes azoricus* (Tarnier),



**Figure 2** Log ( $X + 1$ )-transformed abundance of the ten most abundant species representing 75% of the total abundance in the four islands for (a) exotic (Ex) and (b) indigenous species (Ind) and abundances of the same species in the four considered habitats for (c) exotic and (d) indigenous species. Significant differences between islands and between habitats in the species abundances are shown ( $\chi^2$ ,  $df = 3$ , \* is  $P < 0.05$ , \*\* is  $P < 0.01$ ). The exotic species are as follows: Ex1 is *Oedothorax fuscus* (Blackwall), Ex2 is *Stelidota geminata* (Say), Ex3 is *Ommatoiuulus moreletii* (Lucas), Ex4 is *Blaniulus guttulatus* (Fabricius), Ex5 is *Euborellia annulipes* (Lucas), Ex6 is *Polydesmus coriaceus* Porat, Ex7 is *Tenuiphantes tenuis* (Blackwall), Ex8 is *Paranachus albipes* (Fabricius), Ex9 is *Anotylus nitidifrons* (Wollaston), Ex10 is *Erigone autumnalis* Emerton; the endemic species are as follows: Ind1 is *Pardosa acorensis* Simon and Ind2 is *Heteroderes azoricus* (Tarnier); the native non-endemic species are as follows: Ind3 is *Hirticollis quadriguttatus* (Rossi), Ind4 is *Lithobius pilicornis* (Newport), Ind5 is *Loboptera decipiens* (Germar), Ind6 is *Leiobunum blackwalli* Meade, Ind7 is *Homalenotus coriaceus* (Simon), Ind8 is *Rugilus orbiculatus orbiculatus* (Paykull), Ind9 is *Anoscopus albifrons* (Linnaeus), Ind10 is *Tenuiphantes miguelensis* Wunderlich.

*Hirticollis quadriguttatus* (Rossi), *L. decipiens* and *Rugilus orbiculatus orbiculatus* (Paykull)) occurring in highest abundance in pastures, whilst only two exotic species were found to be more abundant in particular habitats: *Oedothorax fuscus* (Blackwall) in pastures and *Blaniulus guttulatus* (Fabricius) in forests. Abundance differences of indigenous populations among islands may be due to major differences in native forest area, meaning that available space for many of the more specialized species is much different. Exotic species, mostly bound to exotic habitats, do not have area constraints, therefore not showing such marked differences in abundance. For exotic species, species abundances may be more related to processes mediating exotic species colonization across the islands. Exotic species were more widespread in the different habitats and more abundant than indigenous species, which may be explained by their greater tolerance to biotic and abiotic changes (Sax, 2001).

The results of our study reveal a generalist character of many of the most abundant indigenous and exotic species,

which occur with similar abundances on almost all the islands and habitats studied. The current general distribution of these species seems to suggest that exotic species introductions and indigenous species extinctions could have started probably around the time of the first human settlements six centuries ago, generating the assemblage homogenization analysed in the present study. Habitat loss and landscape disturbance may increase arthropod assemblage similarities in favour of widespread, generalist and readily dispersed species, but to the detriment of the most specialized rare species with weak dispersal abilities that are less tolerant of human perturbations (McKinney & Lockwood, 1999; Dormann *et al.*, 2007; Ekroos *et al.*, 2010). Assemblages composed of dominant generalist species favour the introduction of exotic species in a wide range of environments and the loss of the main specialists (McKinney, 2004). It would be the case for the intensively managed pastures considered in our study, which presented the highest number of exotic species and no exclusive endemic species. In contrast, assemblages composed

**Table 5** Percentage of explanatory capacity (EC) of the two considered factors (habitats and islands) on the differences in assemblage similarity of sampling units, separately for the ten most abundant species of exotic and indigenous species, considering thus the non-rarefied original data. The explanatory capacity of the interaction between habitats and islands is also included. The influence of these factors on such differences was examined by a two-way crossed permutational multivariate analysis of variance (PERMANOVA, see Methods). All habitat and island effects as well as the habitat x island interaction were statistically significant ( $P < 0.001$ ).

Effects	EC
<b>Habitats</b>	
Exotic species	44.2
Indigenous species	36.6
<b>Islands</b>	
Exotic species	11.3
Indigenous species	16
<b>Habitat x islands</b>	
Exotic species	12.4
Indigenous species	11.1

**Table 6** Mean and 95% confidence interval (CI 95%) of the coefficients of determination ( $R^2$ ), after multiple regressions of distance matrices (1000 permutations) performed on the 15 rarefied matrices. We associated the Bray–Curtis index of dissimilarity of the indigenous and the exotic assemblages, with the environmental variables (*environmental model*) and the disturbance index (*disturbance model*) alone, and with both together (*full model*). The mean of the  $P$  values is also indicated. All environmental, disturbance and full models were statistically significant at  $P < 0.01$  (see Table S5).

	$R^2$	CI 95%	$P$
<b>Indigenous species</b>			
Environmental model	0.04	0.03–0.05	0.001
Disturbance model	0.02	0.02–0.03	0.001
Full model	0.04	0.04–0.06	0.001
<b>Exotic species</b>			
Environmental model	0.06	0.04–0.09	0.001
Disturbance model	0.04	0.03–0.05	0.001
Full model	0.07	0.05–0.09	0.001

of native specialists usually hinder the establishment of introduced species (Dormann *et al.*, 2007; Sax *et al.*, 2007). However, although the native forests considered in our study presented the highest number of exclusive endemic species, they also harboured an important proportion of exotic species.

Environmental variables and the disturbance index significantly influenced the distribution of indigenous and exotic assemblages in our study. However, these local variables had a low explanatory capacity in comparison with coarse factors as the habitat type or the islands. In other words, the assemblage composition of the two groups of species seem to be mainly

determined by the general habitat structural characteristics, independently of the different climatic conditions or the disturbance existing in these habitats. This highlights the fact that human-induced landscape changes summarized in the habitats may have more significant effects on species distributions and abundances than natural events, such as climate (e.g. Kerbiriou *et al.*, 2009; Connor *et al.*, 2012).

## CONCLUSIONS

The Azores Islands have the highest proportion of exotic species in Macaronesia, with approximately 58% of the arthropods having been introduced as part of past native habitat destruction related to the introduction of plants and goods from different Portuguese colonies (Borges *et al.*, 2005b). In our study, exotic species were found to drive the biotic homogenization of the islands, but our results also suggest that this homogenization is contingent and island-dependent, so it may have a specific trajectory depending on the habitat and island conditions. These results cast some doubt on the direction of future faunistic compositions when arthropod exotic species colonize island assemblages. We also address the most important drivers of the homogenization pattern, which is more important than simply describing the process itself (Rooney *et al.*, 2007): (i) we confirm that exotic species increased the compositional similarity of the local assemblages; (ii) the effects of the islands and habitats on the assemblages' composition were similar for both groups of species, indigenous and exotic, rejecting the initial hypothesis that it would be lower for exotic species; and (iii) habitats per se importantly influenced assemblage composition, in comparison with minor effects of local environmental and disturbance variables, rejecting the hypothesis that assemblage composition would be strongly correlated with the degree of environmental change or landscape disturbance. Our results also indicate that restoration programmes should focus on restoring the original habitats, irrespectively of climate conditions, because both exotic forest and intensive pastures seem to experience higher rates of homogenization with the colonization of exotic species. In addition to the positive and negative roles of the native forests and intensively managed pastures, respectively, for indigenous species (see also Borges *et al.*, 2006), the roles of exotic forests and seminatural pastures seem to be fundamental for connectivity (Cardoso *et al.*, 2009, 2010b). Our results cannot reveal the degree to which assemblage compositions have changed with respect to past assemblages, because the identity and quantity of extinct species are unknown, and we can neither predict the extent and the direction of future changes. A monitoring programme should be established to measure further changes in epigeal arthropod assemblages in the Azores. Further studies should be focused on the persistence of indigenous species in these habitats to preserve the original arthropod assemblages, which is a current priority for conservation (Olden & Poff, 2003; Olden, 2006; Naeem *et al.*, 2012).



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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** We calculated species accumulation curves for each sampling unit (transect;  $n = 64$ ), using the inventories obtained in their corresponding 30 pitfall traps.

**Figure S1** Location of the nine islands in the Azorean archipelago, aligned in a WNW ESE direction. The study islands are highlighted (Flores, Faial, Terceira and Santa Maria), where a detail of the surface area occupied by native forests is also indicated in grey.

**Figure S2** Boxplot indicating the median, maximum, minimum, and upper and lower quartiles of the slope values reflecting completeness in the sampling units for exotic forest (Exf), intensive pastures (Intpast), native forest (Natf) and seminatural pastures (Seminpast).

**Table S1** Bray–Curtis index of similarity values of the whole epigeal arthropod assemblages and only considering the indigenous species performed on 15 rarefied matrices (from 1 to 15; see Methods), for all habitats, and separately within each habitat: native forests (Natf), exotic forest (Exf), seminatural pastures (Seminpast) and intensive pastures (Intpast). Significant differences between the whole assemblage and the indigenous species similarities are also indicated after Wilcoxon matched pair tests.

**Table S2** Pseudo-F values of two-way crossed PERMANOVA analyses performed on 15 rarefied matrices (from 1 to 15; see methods), indicating the pseudo-F values for the differences in assemblage similarity in the composition of sampling units according to the two considered factors (habitats and islands) as well as their interaction.

**Table S3** Pseudo-F values of two-way crossed PERMANOVA analyses performed separately on the ten most abundant

species of the indigenous and exotic species using the non-rarefied original data, indicating the pseudo-F values for the differences in assemblage similarity in the composition of sampling units according to the two considered factors (habitats and islands) as well as their interaction (habitat  $\times$  island).

**Table S4** Coefficients of variation of the 20 most abundant indigenous and exotic species captured per island and per considered habitat.

**Table S5** Coefficients of determination ( $R^2$ ) and Spearman's correlation coefficients  $r_s$  (ranged 0–1) after multiple regression models (1000 Monte Carlo permutations,  $P$  values are also indicated) performed on 15 rarefied matrices (from 1 to 15; see methods).

## BIOSKETCH

**Margarita Florencio** is a postdoctoral researcher of the Azorean Biodiversity group (<http://www.gba.uac.pt>). Her current research is the study of human disturbance and exotic species leading to changes in arthropod community ecology, using as model epigeal and canopy invertebrates in the Azores archipelago. Margarita Florencio's research line includes the study of community ecology and conservation related to aquatic invertebrate assemblages in temporary ponds. Her main focus is on biodiversity patterns at spatial and temporal scales, and on the biotic and abiotic variables determining changes in assemblage compositions.

Author contributions: P.A.V.B. and P.C. collected the data, M.F., P.C. and J.M.L. performed statistical analyses, E.B.A. extracted the environmental variables, M.F. leads the writing and all the authors partially contributed to all phases of the manuscript writing.

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