CrossMark

The role of plant fidelity and land-use changes on island exotic and indigenous canopy spiders at local and regional scales

Margarita Florencio · François Rigal · Paulo A. V. Borges ·
Pedro Cardoso · Ana M. C. Santos · Jorge M. Lobo

Abstract Understanding the processes that lead to successful invasions is essential for the management of exotic species. We aimed to assess the comparative relevance of habitat (both at local and at regional scale) and plant features on the species richness of local canopy spiders of both indigenous and exotic species. In an oceanic island, Azores archipelago, we collected spiders in 97 transects belonging to four habitat types according to the degree of habitat disturbance, four types of plants with different colonisation origin (indigenous vs. exotic), and four types of plants according to the complexity of the vegetation structure. Generalised linear mixed models and linear regressions were performed separately for indigenous and exotic species at the local and regional landscape scales. At the local scale, habitat and plant origin explained the variation in the species richness of indigenous spiders, whereas exotic spider richness was poorly correlated to habitat and plant structure. The surrounding landscape matrix substantially affected indigenous spiders, but did not affect exotic spiders, with the exception of the negative effect exerted by native forests on the richness of exotic species. Our

M. Florencio · F. Rigal · P. A. V. Borges ·
P. Cardoso · A. M. C. Santos
Azorean Biodiversity Group (CITA-A) and Platform for Enhancing Ecological Research and Sustainability (PEERS), Departamento de Ciências Agrárias, Universidade dos Açores, 9700-042 Angra do Heroísmo, Terceira, Azores, Portugal

M. Florencio (✉) · F. Rigal · P. A. V. Borges ·
P. Cardoso · A. M. C. Santos
CE3C – Centre for Ecology, Evolution and Environmental Changes, Azorean Biodiversity Group,
Azores and Lisbon, Portugal
e-mail: mflorenciodiaz@gmail.com;
margarita@ebd.csic.es

Present Address:
M. Florencio
Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Goiânia, Goiás, Brazil

F. Rigal
Environment and Microbiology Team, Université de Pau et des Pays de l'Adour, IPREM UMR CNRS 5254, BP 1155, 64013 Pau Cedex, France

P. Cardoso
Finnish Museum of Natural History, University of Helsinki, Pohjoinen Rautatiekatu 13, P.O. Box 17, 00014 Helsinki, Finland

A. M. C. Santos · J. M. Lobo
Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales (CSIC), C/José Gutiérrez Abascal 2, 28006 Madrid, Spain

results revealed that the local effect of habitat type, plant origin and plant structure explain variations in the species richness observed at a regional scale. These results shed light on the mechanistic processes behind the role of habitat types in invasions, i.e., plant fidelity and plant structure are revealed as key factors, suggesting that native forests may act as physical barriers to the colonisation of exotic spiders.

Keywords Arthropods · Biotic resistance to invasions · Canopy spiders · Oceanic island · Plant architecture · Species richness

Introduction

Biological invasions are one of the main causes of biodiversity loss on Earth (Vitousek et al. 1996, 1997; Butchart et al. 2010) and have important ecological implications and generate economic losses throughout the world (Lockwood et al. 2007). Exotic species have to overcome several geographical and ecological barriers operating at diverse scales, to succeed in invasions. Firstly, exotic species must overcome large geographical barriers to colonise new territories, which is by definition, mediated by human transport (Diez et al. 2012). Secondly, the successful establishment of species is determined by their reproductive success and dispersal ability, their ability to withstand the new environmental conditions and their interactions with the indigenous species in invaded habitats. Invasion is considered successful only when the species establishes a self-sustaining population, which expands towards new suitable areas (Blackburn et al. 2011). Therefore, managing exotic species requires understanding the factors that lead to success or failure at each step of the invasion process. Nevertheless, the causes of success or failure remain poorly understood and are likely to be complex, multiple and context-dependent (González-Moreno et al. 2014).

The establishment of exotic species is often facilitated by the disruption of native ecosystems through landscape alterations, which might provide new ecological opportunities for invaders (Didham et al. 2007). Additionally, the extinction of those native species that are intolerant to human landscape alterations can vacate ecological niches and enhance the spread of generalist species (McKinney and Lockwood 1999;

Dormann et al. 2007; Ekroos et al. 2010). In contrast with the assumed declining trajectory of native species under human-altered scenarios, the "biotic resistance" (sensu Elton 1958) of well-established and rich native assemblages can resist exotic species introductions (see reviews by Hector et al. 2001; Shea and Chesson 2002). Thus, changes in climatic and structural conditions following landscape alterations can favour the establishment of exotic species in detriment of indigenous species, while natural areas could prevent invasions and thereby maintain high diversity of the native flora and fauna.

Arthropods respond markedly to landscape alterations, and therefore are considered excellent models to analyse the impact of such changes at different scales. Among arthropods, predators are particularly sensitive to external perturbations at a broad spatial scale, promoting changes in local diversity through cascading effects across trophic levels (e.g., Holt 1996). Spiders can be considered ideal models to analyse diversity across spatial scales, because with few exceptions, all are predators that exhibit a high inter- and intraspecific variability in dispersal abilities (Bell et al. 2005; Blandenier 2009; Carvalho and Cardoso 2014). Indeed, spiders have also been recognised as good ecological indicators of ecosystem disturbance in forested landscapes at both short and long time scales (Pearce and Venier 2006). However, spiders appear to be highly conditioned by the structural complexity of the plant species (Jiménez-Valverde and Lobo 2007), which may be independent of their origin (indigenous or exotic species) and habitat characteristics. Thus, a generalist predator group such as spiders might not be excessively influenced by changes in plant species or land-uses, as long as they find appropriate structures to build webs or retreats (Gardner et al. 1995; Bell et al. 2001; Reid and Hochuli 2007). Some previous studies have suggested that plant species can support particular spider species irrespective of the surrounding land-use matrix (Ribeiro et al. 2005; Beals 2006; Goßner et al. 2009). However, other studies have also detected that land-use changes can directly affect local communities irrespective of which plant species are analysed (Fernández-Juricic 2002; Diniz et al. 2012; Florencio et al. 2013). Therefore, the relative importance of land-use changes and plant characteristics for the maintenance of spider communities still remains unclear.

In general, oceanic islands are especially vulnerable to exotic species, as they offer "vacant" niche opportunities in typically non-saturated assemblages, in which competition pressure is usually relaxed (Cornell and Lawton 1992; Simberloff 1995; Sax 2001; Gillespie et al. 2008; Whittaker et al. 2014). This study focuses on canopy spiders from the Azores, one of the most remote oceanic archipelagos on Earth. The Azores has been subjected to strong land-use transformations by human activities and massive species introduction during the last six centuries since human settlement (see Triantis et al. 2010, Borges et al. 2010). These anthropogenic changes have caused rapid, widespread and persistent changes to the flora (Connor et al. 2012) and fauna (Borges et al. 2010), including the possible extinction of numerous spider species (Cardoso et al. 2010). Most disturbed landscapes in the Azores archipelago offer suitable habitats for many exotic species and provide source populations that can migrate into the native habitats, (Borges et al. 2006), exerting disruptive effects on indigenous arthropods (Cardoso et al. 2009; Meijer et al. 2011; Florencio et al. 2013; Cardoso et al. 2013, 2014). Considering a set of exhaustive inventories with a shared survey design, but carried out during successive years, this study aims to assess the comparative relevance of habitat (both at local and at regional scale) and plant features on the richness of both indigenous and exotic local canopy spider species.

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 consists of nine volcanic islands separated into three groups: the western group (Flores and Corvo), the central group (Faial, Pico, S. Jorge, Graciosa and Terceira) and the eastern group (S. Miguel and S. Maria), in addition to small islets aligned in a WNW–ESE direction. The date of origin of the islands ranges from 0.25 Ma for Pico to 8.12 Ma for Santa Maria. The Azores Plateau is characterised by the confluence of the American, Eurasia and African tectonic plates, responsible for active volcanic activity and earthquakes. The climate is temperate oceanic, strongly influenced by the surrounding ocean and the topography of the islands, which together produce high levels of relative atmospheric humidity. This temperate oceanic climate also limits temperature fluctuations throughout the year and a high relative atmospheric humidity in the high-altitude native forests (95 % of the mean annual relative humidity).

The study was performed on the Azorean island of Terceira (400 km^2, Fig. 1), located in the central part of the archipelago, about 1764 km distant from the mainland (Europe) and with the highest altitude at 1023 m in "Serra de Santa Bárbara". Humans settled in Terceira almost 600 years ago. Ca. AD 1700 human activities had already restricted the native forest in most islands to areas above 300 m above sea level, and in ca. AD 1850 had drastically reduced the areas of native forest to those regions located about 500 m above sea level (Triantis et al. 2010). Forestation with the exotic tree *Cryptomeria japonica*, planted for wood production, and the development of an economy dependent on milk production since the 1950s has caused further reduction of native forest area, with the clearing of large fragments at mid- and high-elevations for pastures. Currently, approximately 31 % of the island area has been transformed into intensively managed pasturelands whilst less than 6 % of the area is still occupied by pristine native forests (Fig. 1).

Sampling procedure

Canopy spider assemblages of trees and shrubs were sampled mostly during the summer periods (from June to September) of the different years 1999, 2001–2004, 2006, 2008 and 2011. Species were collected along 97 transects of 100 m in length spread over the whole island (Fig. 1). The mean distance between these transects was 10.5 km ± 6.6 SD (maximum = 31.9 km; minimum = 0.01 km). In each transect, ten replicates of the most abundant and common plants (both trees and shrubs) were sampled (mean = 2.0 plant species per transect ± 1.4 SD). Each plant was sampled every 10 m along each transect (see Ribeiro et al. 2005). Two classical and equivalent sampling procedures for a large range of arboreal arthropods were used: a modified beating tray and an umbrella. The beating tray, which aims at capturing arthropods in general, consisted of an inverted cloth funnel pyramid, 1 m wide and 60 cm deep, in which a plastic bag was placed at the tip where
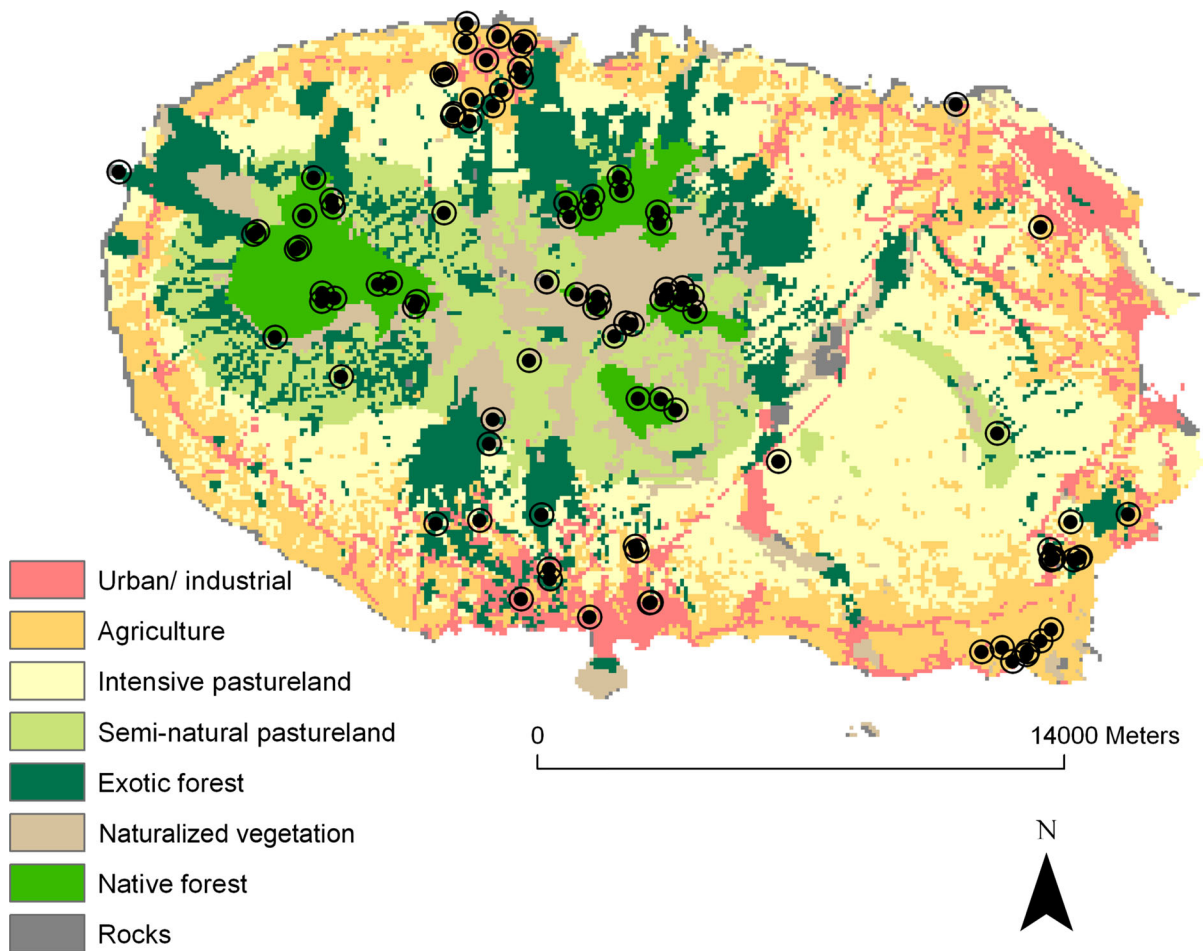
Fig. 1 Land-use map of Terceira Island (the eight considered land-use categories are indicated with different *colours*). The 97 transect locations are represented by *dots*

arthropods, leaves and small branches were collected. For each selected plant, a branch was chosen at random, the beating tray was placed beneath and the branch was hit five times with a beating stick. The sample bags were labelled and frozen until they were sorted. Finally, the sorted specimens were stored in 70 % ethanol with glycerol (see Ribeiro et al. 2005). For the exotic forests and pasturelands, which were sampled during 2011, a "golf umbrella" (1.13 m diameter) was used instead of the described sampling device. The sampling procedure was similar in terms of sampling effort but only focused on spiders; the single difference between these two methods is that the "umbrella" implies the capture in the field of live specimens using a pooter (=entomological aspirator), which considerably reduces the time spent in the

laboratory. Spiders were sorted and identified in the laboratory. Most samples were collected on sunny days, when the vegetation was dry.

We pooled the species richness of the canopy spiders collected from the same plant species per transect (n = 97). However, as some transects were repeatedly surveyed in different years (mean = 1.2 - years per transect ± 0.4 SD) and the data from different plant species were located in the same transect and treated as independent (Table 1), we included the transect identity as a random variable in generalised linear mixed models (see below) to account for the variability generated by the identity of each transect. Therefore, we considered 219 independent sampling units in the following statistical analyses (Table S1, Online Resource 1).

Table 1 Number of plant species sampled per transect and year

Transect number	1999	2001	2002	2003	2004	2006	2008	2011	Total
1			1^{NaF}					1^{NaF}	2
2			1^{NaF}						1
3								1^{ExF}	1
4				1^{Orc}	1^{Orc}				2
5				1^{Orc}					1
6				1^{Orc}	1^{Orc}				2
7							1^{Orc}		1
8							1^{Orc}		1
9						1^{Orc}			1
10						1^{Orc}			1
11						1^{Orc}			1
12						1^{Orc}			1
13						1^{Orc}			1
14				1^{Orc}	1^{Orc}				2
15				1^{Orc}	1^{Orc}				2
16				1^{Orc}	1^{Orc}				2
17				1^{Orc}	1^{Orc}				2
18				1^{Orc}	1^{Orc}				2
19				1^{Orc}	1^{Orc}				2
20				1^{Orc}	1^{Orc}				2
21								2^{Pas}	2
22								2^{NaF}	2
23								1^{Pas}	1
24								3^{ExF}	3
25								1^{Pas}	1
26								1^{Pas}	1
27	3^{NaF}								3
28	3^{NaF}								3
29				3^{NaF}					3
30				3^{NaF}					3
31				6^{NaF}					6
32				6^{NaF}					6
33				6^{NaF}					6
34				6^{NaF}					6
35				3^{NaF}					3
36				5^{NaF}					5
37			2^{NaF}						2
38				2^{NaF}					2
39				2^{NaF}					2
40			3^{NaF}						3
41				3^{NaF}					3
42				3^{NaF}					3
43				3^{NaF}					3
44	5^{NaF}								5
45	4^{NaF}								4

The number of plant species sampled per transect (numbered) and the different years that each transect was sampled are indicated, as well as the habitat type included in each transect (^{NaF} = native forest, ^{ExF} = exotic forest, ^{Pas} = pastures and ^{Orc} = orchards). Species plants and years of sampling per transect were considered as independent sampling units (total of sampling units = 219)

Table 1 continued

Transect number	1999	2001	2002	2003	2004	2006	2008	2011	Total
46	4[NaF]								4
47	5[NaF]								5
48		3[NaF]							3
49				3[NaF]					3
50				3[NaF]					3
51				3[NaF]					3
52				3[NaF]					3
53				3[NaF]					3
54				3[NaF]					3
55				1[NaF]					1
56				3[NaF]					3
57				2[NaF]					2
58				3[NaF]					3
59				3[NaF]					3
60			1[NaF]						1
61				3[NaF]					3
62				3[NaF]					3
63					3[NaF]				3
64				3[NaF]					3
65				3[NaF]					3
66				4[NaF]					4
67			1[NaF]						1
68								1[Pas]	1
69							1[Orc]		1
70							1[Orc]		1
71							1[Orc]		1
72							1[Orc]		1
73							1[Orc]		1
74							1[Orc]		1
75								2[ExF]	2
76							1[Orc]		1
77							2[Orc]		2
78								1[Pas]	1
79							1[Orc]		1
80							2[Orc]		2
81				1[Orc]	1[Orc]				2
82				1[Orc]	1[Orc]				2
83				1[Orc]	1[Orc]				2
84				1[Orc]	1[Orc]				2
85					1[Orc]				1
86				1[Orc]	1[Orc]				2
87					1[Orc]				1
88				1[Orc]	1[Orc]				2
89					1[Orc]				1
90				1[Orc]	1[Orc]				2

Table 1 continued

Transect number	1999	2001	2002	2003	2004	2006	2008	2011	Total
91				1[Orc]	1[Orc]				2
92				1[Orc]	1[Orc]				2
93				1[Orc]	1[Orc]				2
94				1[Orc]	1[Orc]				2
95				1[Orc]	1[Orc]				2
96							1[Orc]		1
97							1[Orc]		1
Total	24	3	9	119	27	5	16	16	219

Species were classified as indigenous or exotics. Indigenous spiders included endemic (i.e., only occurring in the Azores) and native non-endemic species, which are present both in the Azorean islands and in other nearby archipelagos (Madeira and the Canary Islands) and continental areas, having supposedly arrived in the Azorean archipelago by long-distance dispersal. Exotic spider species are those introduced outside their natural past or present distribution, and known to be in the archipelago as a result of recent human activities and usually through accidental introduction.

We identified the whole spider assemblages to species level; only a non-identified genus (juvenile stage), two species of the genus *Eperigone* and one species of the genus *Theridion* were left unidentified (see Table S2, Online Resource 1). These unidentified species of the genera *Eperigone* and *Theridion* were classified as exotics, since all other species in the same genus, subfamily or family present in the archipelago were exotics (according to Borges et al. 2010). For the unique specimen from an unidentified genus, we assumed it to represent a native species, because exotic species are often cosmopolitan, with good available descriptions and keys. Voucher specimens are housed in the arthropod reference collection "Dalberto Teixeira Pombo" at the University of the Azores.

Data analyses

For statistical analyses, we considered the species richness of indigenous and exotic species as separate response variables. To analyse whether the results were consistent for different life-cycle stages, we also considered adult and juvenile stages of indigenous and exotic species separately (the results are presented in the Electronic Supplementary Material).

To investigate the role of habitat types and plant features at local scales, we assigned three qualitative factors to each sampling unit, which reflected the general habitat type, the origin of the surveyed plants and the plant structure. Each sampling unit was then ascribed to one of the following four habitat types, reflecting different degrees of human alteration: (i) native forests; (ii) exotic forests; (iii) pasturelands, both semi-natural and intensively managed; and (iv) orchards. Concerning the plant origin, we considered four categories: (i) endemic plants, including the Azorean endemics *Erica azorica*, *Ilex perado* spp. *azorica*, *Juniperus brevifolia*, *Laurus azorica, Frangula azorica,* and *Vaccinium cylindraceum*; (ii) native plants, including *Myrsine africana* (also present in Africa and South Asia), *Morella faya*, (also present across the Macaronesian region, Spain and Portugal) and *Calluna vulgaris* (also present in all of Western Europe); (iii) non-edible exotic plants, including *Pittosporum undulatum*, *Metrosideros excelsa*, *Cryptomeria japonica*, *Eucalyptus globulus*, *Banksia integrifolia*, *Ligustrum henryi* and *L. vulgare*, *Acacia melanoxylon*, *Camellia* spp., and exotic species of grasses; and iv) fruit-tree plants. Finally, we considered four categories of plant structure: (i) small trees and shrubs, including *E. azorica*, *M. faya, J. brevifolia, L. azorica, M. africana, C. vulgaris, V. cylindraceum, I. perado* spp. *azorica, Ligustrum* spp.*, Camellia* spp. and vineyards (most of these plants typically occur in high-altitude native forests, where they reach their smallest sizes); (ii) medium-sized trees, which are usually consistent in size, including *F. azorica, P. undulatum, M. excelsa, B. integrifolia*, and fruit-tree plantations; (iii) high trees, including *C. japonica* and

E. globulus; and (iv) ruderal and other non-woody plants (hereafter referred to as "grass" for simplicity), including tall exotic grasses and banana plantations.

Because different sites were sampled in different years, we first tested whether surveys belonging to different years influenced the species richness values. Given the sampling limitation in our data, we examined additional available data collected in 23 transects located in a single native forest surveyed in different years (1999, 2001 and 2003), recording a total of 51 sampling units. We found that species richness differences between years were not statistically significant (see Table S3, Online Resource 2). We thus assumed that between-year differences in the species richness of our study should not be strong enough to mask the results obtained between habitat types.

Both indigenous and exotic spider species richness per sampling unit were regressed against the three considered factors (habitat, plant origin and plant structure) using generalised linear mixed models (GLMMs) with a Poisson error distribution and a log-link function. Due to the lack of sufficient transects for the combination of the 64 considered categories (four habitat types × four plant origin categories × four plant structure categories), interactions were not considered in our analysis (see Table S1, Online Resource 1). The GLMMs were implemented using the 'glmer' function in the 'lme4' package (Douglas et al. 2013) in R software (R Development Core Team 2013). Habitat, plant origin and plant structure were considered as fixed effects in a *full model*, whereas transect identity was included as a random factor. Subsequently, the full model was simplified (reduced model) using backward elimination based on likelihood ratio tests (LRT) until only significant predictors remained (Pinheiro and Bates 2000). We checked for overdispersion in our GLMMs using the dispersion scale factor, which was <1 in all the models examined; hence, it was unnecessary to use quasipoisson errors to correct for overdispersion (see Table S4 in Online Resource 3 and Zuur et al. 2009). We performed Tukey's post hoc tests using GLMMs, and only included each significant fixed factor, to identify the categories that were significantly different from each other using the function 'glht' of the R package 'multcopm' (Hothorn et al. 2008). To quantify the variability explained by the significant fixed factors, we calculated the proportion of variability (R^2) explained solely by those significant fixed factors,

following the method recently developed by Nakagawa and Schielzeth (2013). This method allows to quantify the part of the variability explained by both fixed and random factors together (called conditional R^2, hereafter referee to as R^2_c), as well as the fraction of the variability explained solely by the fixed factor(s) (called marginal R^2, hereafter referred to as R^2_m). Both R^2_c and R^2_m were calculated using the R code available in the Supporting Information of Nakagawa and Schielzeth (2013). In order to assess the independent contribution of each factor to the full model, we implemented a simple decomposition of R^2_m following the theorem of hierarchy (Chevan and Sutherland 1991). This allowed us to quantify the pure independent effect of each explanatory factor, as well as the joint effect that cannot be unambiguously assigned to any factor (Chevan and Sutherland 1991; Mac Nally 2000; see Online Resource 4). Finally, to assess the ability of our models to account for spatial structure in species richness, we finally examined the spatial autocorrelation in both raw species richness values and in the residuals of the reduced models by performing correlograms (see Fig. S2, Online Resource 5).

To quantify the role of habitat scale on species richness, we calculated the percentage area occupied by the different land-uses at increasing buffer distances from each of the 97 transects, that were then used as richness predictors. Buffers were constructed using different radius distances to the central point of each transect as centroid. Distances were selected to cover local (100 m transect) to regional scales (i.e. 100, 200, 500, 1000 and 5000 m, see Fig. 1). The species richness of the 219 sampling units were then averaged for each transect across the different sampled plants or years and were considered as the response variable to assess the effect of the different spatial scales in our analyses. To construct the land-use map, Terceira Island was divided into eight regional land-use areas according to their vegetation and degree of anthropization, using a digital map at 100 × 100 m resolution (DROTRH 2008). The occupied percentages by the eight considered land-uses included in the five buffer distances (8 × 5 = 45 explanatory variables) were calculated using GIS-based software (ArcGIS 10 ArcMap v. 10.1). The eight land-use types were: (1) urban/industrial areas, including cities and industrial zones; (2) agricultural areas, consisting of mainly wheat, corn, barley and other cereal

plantations, and banana, apple, orange, vineyard, olive and peach as fruit-tree plantations; (3) intensive pasturelands managed for cattle throughout the whole year and characterised by mainly introduced grasses and leguminous forbs (Borges and Brown 1999); (4) semi-natural pasturelands managed with low cattle-grazing activity (Borges and Brown 1999), composed of native forbs and exotic and native grasses, rushes, sedges and ferns; (5) exotic forests dominated by monospecific tree plantations of *C. japonica* and *Eucalyptus* spp.; (6) naturalized vegetation composed of endemic, native or exotic plant species colonising abandoned anthropized landscapes; (7) native forests mainly dominated by endemic plants; and (8) rocky areas without vegetation. Urban, agriculture and rocky areas are located close to the coast, followed in altitude by intensive pasturelands. In contrast, native forests, exotic forests, semi-natural pasturelands and naturalised vegetation are located at mid- and high altitudes in the centre of the island (Fig. 1).

To measure the relationship between species richness and relative habitat area across the local–regional gradient, we performed linear regressions between the mean species richness per transect and the percentage area occupied by each land-use type across the five buffers. We examined whether the local species richness of each transect was associated with the local land-use conditions prevailing in the sampling locality, or whether regional conditions have a higher explanatory capacity. To do this, we used the 'glm' function in R software (R Development Core Team 2013). The explained variability (in %) of each land-use type was estimated through the reduction in deviance from a null model in which no predictor was considered.

Results

We recorded 61 species of arboreal canopy spiders (38 exotic and 23 indigenous species; Table S2, Online Resource 2).

Likelihood ratio tests revealed that habitat best explained species richness for both indigenous and exotic species. Moreover, plant origin had a significant effect only for indigenous species and plant structure only for exotic species (Table 2). Both plant origin and plant structure had no significant effects when adult and juvenile stages were analysed separately, with the

Table 2 Generalised linear mixed models (GLMMs) performed on the species richness of the indigenous and exotic species, separately

	Indigenous species		Exotic species	
	χ^2	P	χ^2	P
Habitat	15.91	<0.01	20.17	<0.001
Plant origin	8.95	<0.05	1.84	0.61
Plant structure	5.79	0.12	11.83	<0.01

Habitats, plant origin and plant structure were considered as fixed factors (*full model*), and transect identity as random factors. *Habitat*, *plant origin* and *plant structure* refer the *full model* excluding these fixed factors. Significance of effects was assessed by means of likelihood ratio tests (LRT) of reduced models lacking the factor being tested against the full model. χ^2 distributions were used to estimate the significance (see Online Resource 3, Table S5 for results considering separately adult and juvenile stages)

exception of the significant effect of plant structure on adults of exotic species (Table S5, Online Resource 3). The decomposition of explained variability shows that both habitat and plant origin are the variables with a higher contribution to explaining the total variability in indigenous species richness (24 % for each one), although plant structure also explained 20 % of the variation (Fig. 2a). For exotic species, the pure independent effect of habitat was 11 % and that of plant structure was 7 %, whereas plant origin only explained 2 % of species richness variability (Fig. 2b). Although the random effect of the transect identity hardly explained variability for indigenous species, it accounted for a high proportion of the explained variability for exotic species (Table S6, Online Resource 3). Tukey's post hoc tests for habitat categories revealed that indigenous species formed the maximum species richness in native forest and pastures, and the lowest in orchards (Fig. 3a). Contrary to this pattern, exotic species formed the lowest number of species in native forests but also presenting a low species richness in orchards (Fig. 3b). The patterns were consistent for adult and juvenile stages (Fig. S1, Online Resource 3). For indigenous species, Tukey's post hoc test for plant origin revealed higher species richness for endemic and native plants, and lower species richness in fruit trees (Fig. 4a). For exotic species, Tukey's post hoc test for plant structure revealed higher species richness for the high trees and grass categories (Fig. 4b). For both indigenous and exotic species, the residuals of the reduced models did

Fig. 2 Hierarchical variation partitioning based on the decomposition of R_m^2 only attributable to the independent and joint effects of the three fixed factors, habitat, plant origin and plant structure, for **a** indigenous species and **b** exotic species after generalised linear mixed models (explanatory variability range 0–1)
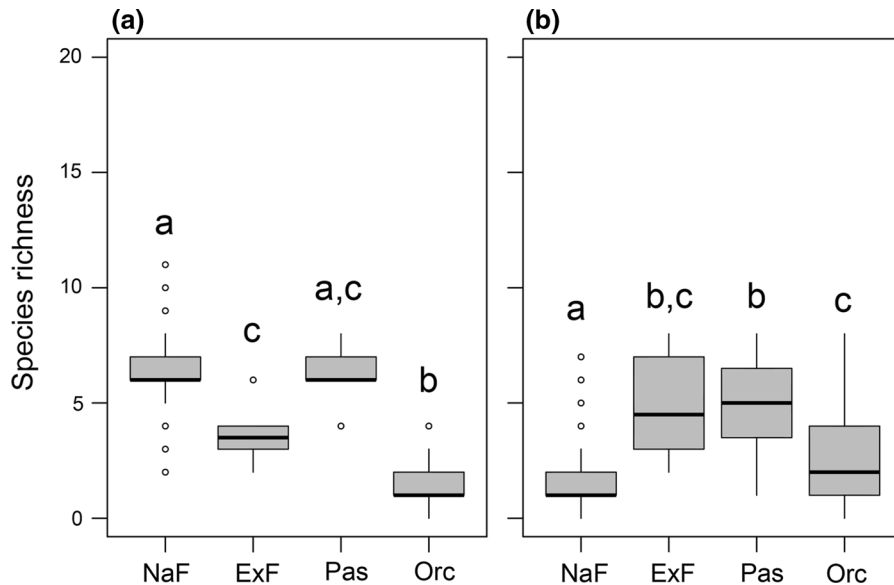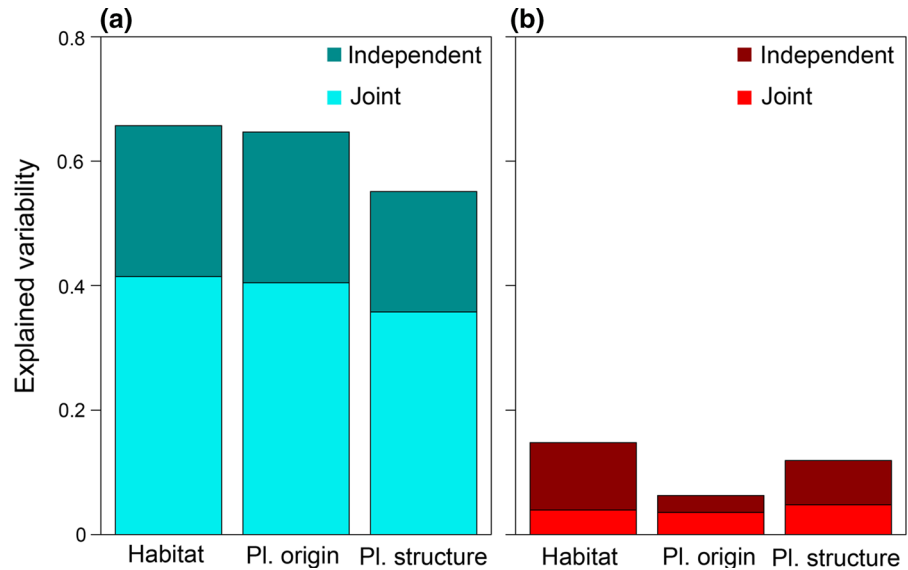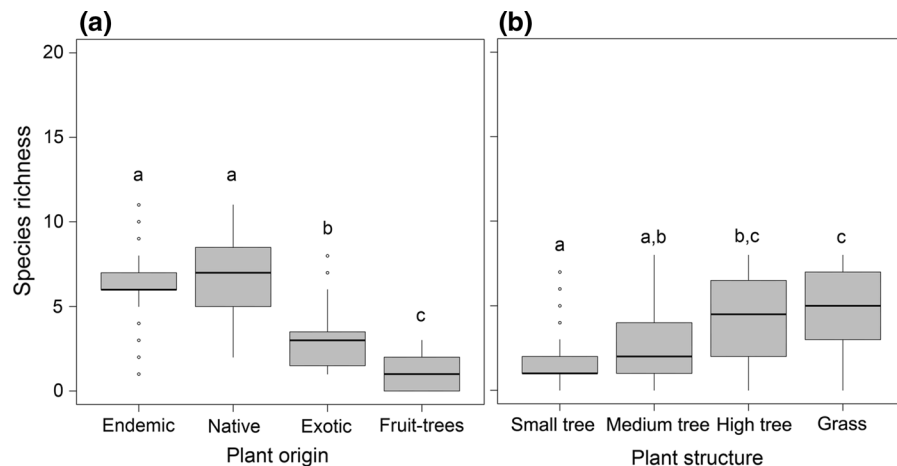

Fig. 3 *Box plot* indicating the median, maximum, minimum, and upper and lower quartiles of species richness represented by habitat categories (NaF = native forest, ExF = exotic forest, Pas = pastures and Orc = orchards) for **a** indigenous and **b** exotic species. *Different letters* indicate significance differences after Tukey's post hoc tests (see Fig. S1 in Online Resource 3 for additional results that consider adult and juvenile stages separately, and Table S7 in Online Resource 3 for detailed *P* values)

not show statistically significant spatial autocorrelation values, except for the first two kilometres in the case of the juvenile stages of indigenous species (Fig. S2, Online Resource 5). The drastic reduction in the spatial structure of these residuals compared to the raw values of species richness indicates that the considered variables properly captured the variability in species richness.

For indigenous species, the proportion of the different habitat variables measured at increasing distances had a high capacity in explaining the variation in local species richness (Fig. 5a). We

Fig. 4 *Box plot* indicating the median, maximum, minimum, and upper and lower quartiles of the species richness of **a** indigenous and **b** exotic spiders, represented by the categories of the plant origin (endemic, native, exotic plants and fruit trees) and of the plant structure (small, medium and high trees, and grass), respectively. Different letters indicate significance differences after Tukey's post hoc tests (see Table S7 in Online Resource 3 for detailed *P* values)

detected that mainly agricultural, but also urban and intensive pastureland areas, had the highest negative effects and explanatory capacity (ca. 60 % of the variability in the case of agriculture). These negative effects in local richness seemed to be independent of the considered distances (Fig. 5a). Naturalised vegetation, exotic forest and semi-natural pastures appear to favour the species richness of indigenous assemblages when located at larger distances (Fig. 5a), whereas native forests had a consistent, high and positive effect on species richness at all the considered distances (ca. 50 % of the variability, Fig. 5a). Habitat variables did not appear to be relevant at any of the considered distances in the case of exotic species
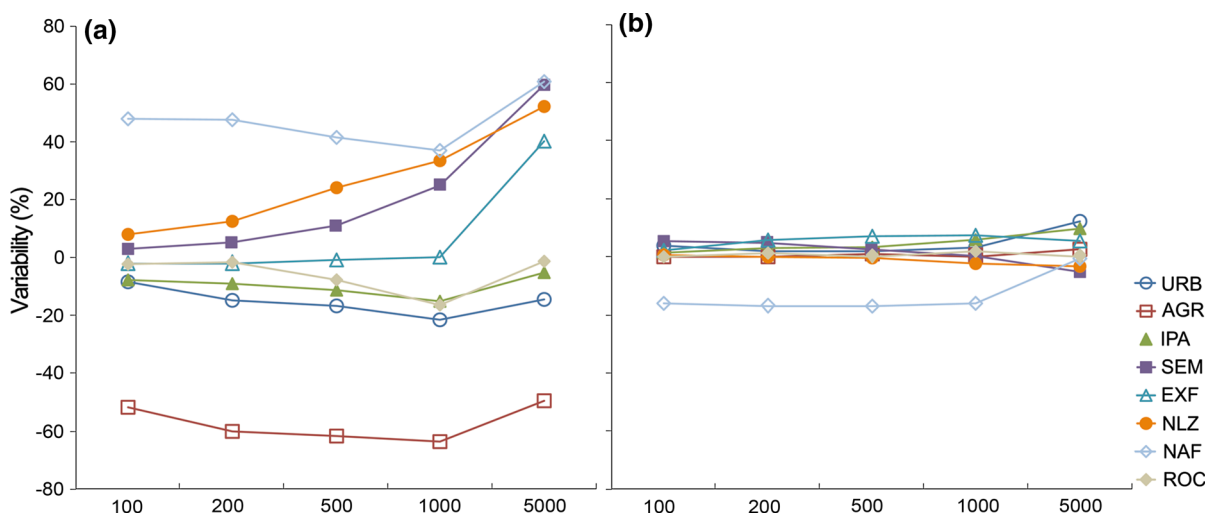
Fig. 5 Explained variability of the species richness by the proportion of the eight land-uses at the 100, 200, 500, 1000 and 5000 m buffer distances using linear regressions. The positive (+) and negative (−) values indicate the sign of the effects using the estimated coefficient of each linear regression. Results are shown for the **a** indigenous and **b** exotic species. Land-uses are indicated: *URB* urban/industrial areas, *ARG* agriculture areas, *IPA* intensively managed pasturelands, *SEM* semi-natural pasturelands, *EXF* exotic forests, *NLZ* naturalised vegetation, *NAF* native forests and *ROC* rocky areas (see Methods for a detailed description of the considered land uses; see Fig. S3 in Online Resource 6 for results that consider adult and juvenile stages separately; see Table S8 in Online Resource 6 for detailed *P* values)

richness (Fig. 5b). Only the area with native forest exercised a significantly negative effect on the species richness of exotic species across almost all the considered distances (ca. 16 % of the variability); however, this effect disappeared at 5-km distance (Fig. 5b). Both adult and juvenile stages showed highly similar patterns (Fig. S3, Online Resource 6).

Discussion

We have recorded 63 % of the spider species ever recorded in Terceira Island, including 80 % of all indigenous and 56 % of all exotic species (Borges et al. 2010). To our knowledge, this is the first study to assess the independent effects of land-use (habitat), plant structure and plant origin on a particular predator group (arboreal canopy spiders), addressing the comparative role of these variables according to the colonisation origin of the species (indigenous vs. exotic), and also examining the distance effects of different land-uses across a disturbance gradient.

Our results firstly indicate that habitat and plant variables are better predictors of the variation in local richness of indigenous rather than of exotic species; the selected predictors accounted for about 60 % of the total variability in the case of indigenous species and approximately 15 % for the exotics. Thus, the local richness of indigenous species has a high degree of environmental determinism, whereas the local richness of exotic species might depend on other non-considered or contingent factors, which in turn, are much less predictable. Interestingly, transect identity accounted for a certain proportion of variability in the case of exotic species, which could be associated somehow with the unequal and non-synchronized sampling of habitats across the different years. However, we consider that a more probable explanation is the unpredictable nature in the colonization of exotic species. Exotic species would be much more prone than natives to the occurrence of vagrants as well as to rapid demographic fluctuations and contingent spatial factors; the relevance of transect identity would be related with these non-considered factors.

According to our results, indigenous species richness would be highly sensitive to land-use changes, whereas exotic species richness would be homogeneously distributed across all non-native habitat types. The vast majority of species captured in this study, both indigenous or exotics, are excellent dispersers by means of ballooning. Yet, while almost all indigenous species are exclusively adapted to forest habitats (with few exceptions, e.g. *Pardosa acorensis*), exotic species would be capable of colonising a wider range of environmental conditions as consequence of their probable higher tolerances. Fidelity for endemic/native plants in indigenous species and plant structure in exotic spiders appears to play a key role in the processes that comprise local richness, corroborating the importance of native forests as refuge areas for indigenous arboreal canopy spiders (e.g., Borges et al. 2008), but also suggesting that these habitats may act as physical barriers to the colonisation of exotic spiders.

Although it was not possible to examine the interactions between the three factors considered herein (habitat, plant origin and plant structure), our results clearly suggest that plant origin and structure appear to be determinants in predicting the local species richness of canopy spiders. However, the impossibility of measuring the interactions of these factors did not allow exploring possible patterns of source-sink dynamics in exotic plants located in native habitats and vice versa. The fidelity to plant origin observed in indigenous spiders might be related to the abundance of specialist herbivorous insects, which regulate prey availability and thus, modulate the spider species richness as a predator group (e.g., Markó et al. 2009, 2010). However, studies that address the role of prey diversity on predator occurrences in arthropods have reported contradictory results. Beals (2006) highlighted that spiders' plant fidelity is mainly determined by the plant requirements of their prey (i.e., bottom-up effect). However, Ribeiro et al. (2005) detected low plant fidelity of herbivorous canopy arthropods in the Azores, suggesting in turn, that the arthropod fauna in the Azorean native forest is composed mostly of generalist species. On the other hand, a higher diversity of herbivorous canopy arthropods was recorded in one of the most complex structured plants, *Erica azorica*, suggesting a positive linkage between species richness and the complexity of plant structure (Ribeiro et al. 2005; Ribeiro and Borges 2010). This last example highlights that the species richness of spiders might be also driven by

plant structure (e.g., ramification complexity, leaf area). Although we could not address this issue due to a lack of data, we detected that exotic species are favoured by the plant structure of non-native vegetation.

The study of landscape matrix effects on indigenous and exotic species richness revealed a consistent response across all the considered spatial distances. Indigenous species were negatively affected by the occurrence of disturbed habitats at any distance but were positively affected by the occurrence of native forest, whereas the species richness of exotic species was negatively affected by the presence of native forest. For indigenous species, the negative effects of the more disturbed land-uses (particularly agricultural areas) on species richness diminished at a 5-km buffer distance, the same distance at which positive effects of less-disturbed land-uses were observed. These results suggest (i) that altered landscapes should be located at 5 km as minor distance to reduce the negative effect on indigenous species richness, and (ii) that less-disturbed land-uses might act as corridors to connect the small patches of native forest across the landscape matrix (see Cardoso et al. 2009; Meijer et al. 2011). Notably, none of the land-uses, except natural forests, affected the species richness of exotic spiders either positively or negatively independently of the considered distance, probably again showing the unpredictable and eclectic nature of the colonisation process of these species; only the existence of native forest appears to hinder the occurrence of a rich assemblage of exotic species. However, we cannot completely reject the possibility that our sampling limitations in the anthropogenic habitats exotic forests and pasturelands could have influenced the observed pattern. In the case of indigenous assemblages, both historical contingency (e.g., the native habitat represents the original habitat where speciation occurred) and the recent human impact of landscape degradation (detrimental land-use effects could be more evident for endemic species which theoretically are not pre-adapted to anthropogenic disturbance, see e.g. Cardoso et al. 2009), have influenced the current distribution of these species. In contrast, the exotic species that successfully invade are usually opportunistic generalists with a high environmental tolerance, and occupy large ecological niches (Sax 2001; Blackburn et al. 2004). Additionally, the apparent random spread

of exotic species in the Azores might also be driven by an absence of resource limitations, which relaxes species competition (see Hubbell 2006). Therefore, this finding suggests an apparent biotic resistance of the indigenous assemblages to exotic species introductions in native forests. Bear in mind that biotic resistance has been largely defined in terms of biotic interactions, i.e., a more efficient use of resources in saturated indigenous assemblages would predict that less available niche space is occupied by exotic species (Elton 1958; Tilman 1997; Shurin 2000). However, native forests on the study island appear to exhibit a non-saturated arthropod fauna (Borges et al. 2006; Whittaker et al. 2014), which might lead to little biotic resistance that could be attributable to biotic interactions. We thus suggest three alternative processes operating in native forests that might drive the low species richness of exotic species: (i) native forests might present unfavourable harsh environmental conditions (e.g., constant high relative humidity and altitude and little light and low temperature) for most exotic species, which often experience drier continental conditions in their original native distributions (e.g., *Clubiona terrestris*, *Neriene clathrata*, *Nigma puella*); (ii) high-altitude native forests remain as isolated areas reducing the possibility of human-mediated transports for exotic species; or (iii) other physical processes might be operating to repel invasions, e.g., habitat characteristics associated with plant physiognomy and architecture might also mediate biotic resistance to invaders in native assemblages (Byers 2002; Levine et al. 2004). The use of local habitat is revealed as a determinant to explain the variability in the species richness of both indigenous and exotic species of canopy spiders. However, habitat effects at regional scales were not evident for exotic species. In this regard, we also documented the importance of plant origin and structure on canopy spider richness, for indigenous but mainly for exotic species. In this study, habitat and plant categories were inevitably related. Native forests are mainly composed of endemic and native plants, whereas more disturbed areas, such as exotic forests or orchards, include mainly exotic plants. As a consequence, indigenous canopy spiders decreased in species richness when habitat disturbance increased, with maximum richness being detected in endemic/native plant species occurring in native forests. In contrast, the richness of exotic

species was higher in exotic forests and lower in ruderal plants mainly associated with disturbed habitats. In orchards, we cannot exclude that the low diversity of spiders might also be attributable to the harmful effect of pesticides on canopy species, which might restrict the set of species that can survive in this habitat, irrespective of their colonisation origin (Santos et al. 2005; Markó et al. 2009, 2010).

In this study, exotic spiders contributed importantly to the total species richness (62 %), in contrast to native non-endemic (15 %) and endemic spider species (23 %). Given this high proportion of exotic species at the regional scale and the persistent and dramatic effects of agriculture at the local and regional scales, we suggest some guidelines for landscape management, particularly, (i) the location of agricultural areas as far apart from native forests as possible, (ii) a high proportion of semi-natural pastures, naturalised vegetation and exotic forest instead of other land-uses, to favour the connectivity across small patches of native forests, and (iii) the restoration of native forest as an essential practice to guarantee the conservation of native spiders (see also Cardoso et al. 2009, Meijer et al. 2011).

References

Beals ML (2006) Understanding community structure: a data-driven multivariate approach. Oecologia 150:484–495. doi:10.1007/s00442-006-0551-8

Bell JR, Wheater CP, Cullen WR (2001) The implication of grassland and heathland management for the conservation of spider communities: a review. J Zool 225:377–387. doi:10.1017/S0952836901001479

Bell JR, Bohan DA, Shaw EM, Weyman GS (2005) Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. Bull Entomol Res 95:69–114. doi:10.1079/BER2004350

Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston KJ (2004) Avian extinction and mammalian introductions on oceanic islands. Science 305:1955–1958. doi:10.1126/science.1101617

Blackburn TM, Pysek P, Bacher S, Carlton JT, Duncan RP, Jarosík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26:333–339. doi:10.1016/j.tree.2011.03.023

Blandenier G (2009) Ballooning of spiders (Araneae) in Switzerland: general results from an eleven-year survey. Bull Br Arachnol Soc 14:308–316. doi:10.13156/arac.2009.14.7.308

Borges PAV, Brown VK (1999) Effect of island geological age on the arthropod species richness of Azorean pastures. Biol J Linn Soc 66:373–410. doi:10.1111/j.1095-8312.1999.tb01897.x

Borges PAV, Lobo JM, Azevedo EB, Gaspar CS, Melo C, Nunes LV (2006) Invasibility and species richness of island endemic arthropods: a general model of endemic vs. exotic species. J Biogeogr 33:169–187. doi:10.1111/j.1365-2699.2005.01324.x

Borges PAV, Ugland KI, Dinis FO, 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, Kerala, pp 47–70

Borges PAV, Vieira V, Amorim IR, Bicudo N, Fritzén N, Gaspar C, Heleno R, Hortal J, Lissner J, Logunov D, Machado A, Marcelino J, Meijer SS, Melo C, Mendonça EP, Moniz J, Pereira F, Santos AS, Simões AM, Torrão E (2010) List of arthropods (Arthropoda). In: Borges PAV, Costa A, Cunha R, Gabriel R, Gonçalves VA, Martins F, Melo I, Parente M, Raposeiro P, Rodrigues P, Santos RS, Silva L, Vieira P, Vieira V (eds) A list of the terrestrial and marine biota from the Azores. Princípia, Cascais, pp 179–246

Butchart SHM, Walpole M, Collen B, Van Strien A, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque J-F, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Hernández Morcillo M, Oldfield TEE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vié J-C, Watson R (2010) Global biodiversity: indicators of recent declines. Science 328:1164–1168. doi:10.1126/science.1187512

Byers JE (2002) Physical habitat attribute mediates biotic resistance to non-indigenous species invasion. Oecologia 130:146–156. doi:10.1007/s004420100777

Cardoso P, Aranda SC, Lobo JM, Dinis F, Gaspar C, Borges PAV (2009) A spatial scale assessment of habitat effects on arthropod communities of an oceanic island. Acta Oecol 35:590–597. doi:10.1016/j.actao.2009.05.005

Cardoso P, Arnedo MA, Triantis KA, Borges PA (2010) Drivers of diversity in Macaronesian spiders and the role of species extinctions. J Biogeogr 37:1034–1046. doi:10.1111/j.1365-2699.2009.02264.x

Cardoso P, Rigal F, Fattorini S, Terzopoulou S, Borges PAV (2013) Integrating landscape disturbance and indicator species in conservation studies. PLoS One 8:e63294. doi:10.1371/journal.pone.0063294

Cardoso P, Rigal F, Carvalho JC, Fortelius M, Borges PAV, Podani J, Schmera D (2014) Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. J Biogeogr 41:749–761. doi:10.1111/jbi.12239

Carvalho JC, Cardoso P (2014) Drivers of beta diversity in Macaronesian spiders in relation to dispersal ability. J Biogeogr 41:1859–1870. doi:10.1111/jbi.12348

Chevan A, Sutherland M (1991) Hierarchical partitioning. Am Stat 45:90–96. doi:10.1080/00031305.1991.10475776

Connor SE, van Leeuwen JFN, Rittenour TM, van der Knaap WO, Ammann B, Björck S (2012) The ecological impact of oceanic island colonization—a palaeoecological perspective from the Azores. J Biogeogr 39:1007–1023. doi:10.1111/j.1365-2699.2011.02671.x

Cornell HV, Lawton JH (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: a theorical perspective. J Anim Ecol 61:1–2

Didham RK, Tylianakis JM, Gemmell NJ, Rand TA, Ewers RM (2007) Interactive effects of habitat modification and species invasion on native species decline. Trends Ecol Evol 22:489–496. doi:10.1016/j.tree.2007.07.001

Diez JM, D'Antonio CM, Dukes JS, Grosholz ED, Olden JD, Sorte CJ, Blumenthal DM, Bradley BA, Early R, Ibáñez I, Jones SJ, Lawler JJ, Miller LP (2012) Will extreme climatic events facilitate biological invasions? Front Ecol Environ 10:249–257. doi:10.1890/110137

Diniz S, Lewinsohn TM, Prado PI (2012) Comparing assemblages of Asteraceae and their insect herbivores under different land-use regimens. Austral Ecol 37:419–428. doi:10.1111/j.1442-9993.2011.02294.x

Dormann CF, Schweiger O, Augenstein I, Bailey D, Billeter R, de Blust G, DeFilippi R, Frenzel M, Hendrickx F, Herzog F, Klotz S, Liira J, Maelfait J-P, Schmidt T, Speelmans M, van Wingerden WKRE, Zobel M (2007) Effects of landscape structure and land-use intensity on similarity of plant and animal communities. Global Ecol Biogeogr 16:774–787. doi:10.1111/j.1466-8238.2007.00344.x

Douglas B, Maechler M, Bolker B (2013) lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-2. http://CRAN.R-project.org/package=lm4. Accessed 21 May 2015

DROTRH (2008) Carta de ocupação do solo da região Autónoma dos Açores—Projecto SUEMAC. Secretaria Regional do Ambiente, Direcção Regional do Ordenamento do território e dos Recursos Hídricos, Ponta Delgada

Ekroos J, Heliölä J, Kuussaari M (2010) Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. J Appl Ecol 47:459–467. doi:10.1111/j.1365-2664.2009.01767.x

Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London

Fernández-Juricic E (2002) Can human disturbance promote nestedness? A case study with breeding birds in urban habitat fragments. Oecologia 131:269–278. doi:10.1007/s00442-002-0883-y

Florencio M, Cardoso C, Lobo JM, de Azevedo EB, Borges PAV (2013) Arthropod assemblage homogenisation in oceanic islands: the role of indigenous and exotic species under landscape disturbance. Divers Distrib 19:1450–1460. doi:10.1111/ddi.12121

Gardner SM, Cabido MR, Valladares GR, Diaz S (1995) The influence of habitat structure on arthropod diversity in Argentine semi-arid Chaco forest. J Veg Sci 6:349–356. doi:10.2307/3236234

Gillespie RG, Claridge EM, Roderick GK (2008) Biodiversity dynamics in isolated island communities: interaction between natural and human-mediated processes. Mol Ecol 17:45–57. doi:10.1111/j.1365-294X.2007.03466.x

González-Moreno P, Diez JM, Ibáñez I, Font X, Vilà M (2014) Plant invasions are context-dependent: multiscale effects of climate, human activity and habitat. Divers Distrib 20:720–731. doi:10.1111/ddi.12206

Goßner MM, Chao A, Bailey RI, Prinzing A, Goßner MM (2009) Native fauna on exotic trees: phylogenetic conservatism and geographic contingency in two lineages of phytophages on two lineages of trees. Am Nat 173:599–614. doi:10.1086/597603

Hector A, Dobson K, Minns A, Bazeley-White E, Lawton JH (2001) Community diversity and invasion resistance: an experimental test in a grassland ecosystem and a review of comparable studies. Ecol Res 16:819–831. doi:10.1046/j.1440-1703.2001.00443.x

Holt RD (1996) Food webs in space: an island biogeographic perspective. In: Polis G, Winemiller K (eds) Food Webs: contemporary perspectives. Chapman and Hall, New York, pp 313–323

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biometrical J 50:346–363

Hubbell SP (2006) Neutral theory and the evolution of ecological equivalence. Ecology 87:1387–1398. doi:10.1890/0012-9658(2006)87[1387:NTATEO]2.0.CO;2

Jiménez-Valverde A, Lobo JM (2007) Determinants of local spider (Araneidae and Thomisidae) species richness on a regional scale: climate and altitude vs. habitat structure. Ecol Entomol 32:113–122. doi:10.1111/j.1365-2311.2006.00848.x

Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecol Lett 7:975–989. doi:10.1111/j.1461-0248.2004.00657.x

Lockwood JL, Hoopes MF, Marchetti MP (2007) Invasion ecology. Blackwell Publishing, Oxford

Mac Nally R (2000) Regression and model-building in conservation biology, biogeography and ecology: the distinction between—and reconciliation of—'predictive' and 'explanatory' models. Biodivers Conserv 9:655–671. doi:10.1023/A:1008985925162

Markó V, Keresztes B, Fountain MT, Cross JV (2009) Prey availability, pesticides and the abundance of orchard spider communities. Biol Control 48:115–124. doi:10.1016/j.biocontrol.2008.10.002

Markó V, Bogya S, Kondorosy E, Blommers LHM (2010) Side effects of kaolin particle films on apple orchard bug, beetle and spider communities. Int J Pest Manag 56:189–199. doi:10.1080/09670870903324206

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–453. doi:10.1016/S0169-5347(99)01679-1

Meijer SS, Whittaker RJ, Borges PAV (2011) The effects of land-use change on arthropod richness and abundance on Santa Maria Island (Azores): unmanaged plantations favour endemic beetles. J Insect Conserv 15:505–522. doi:10.1007/s10841-010-9330-2

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142. doi:10.1111/j.2041-210x.2012.00261.x

Pearce JL, Venier LA (2006) The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: a review. Ecol Indic 6:780–793. doi:10.1016/j.ecolind.2005.03.005

Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Springer-Verlag, New York

R Development Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/. Accessed 21 May 2015

Reid AM, Hochuli DF (2007) Grassland invertebrate assemblages in managed landscapes: effect of host plant and microhabitat architecture. Austral Ecol 32:708–718. doi:10.1111/j.1442-9993.2007.01767.x

Ribeiro SP, Borges PAV (2010) Canopy habitat area effect on the arthropod species densities in the Azores: pondering the contribution of tourist species and other life histories. In: Serrano ARM, Borges PAV, Boieiro M, Oromí P (eds) Terrestrial arthropods of Macaronesia—Biodiversity, ecology and evolution. Sociedade Portuguesa de Entomologia, Lisboa, pp 89–114

Ribeiro SP, Borges PAV, Gaspar C, Melo C, Serrano ARM, Amaral J, Aguiar C, André G, Quartau JA (2005) Canopy insect herbivores in Azorean Laurisilva forests: key host plant species in a highly generalist insect community. Ecography 28:315–330. doi:10.1111/j.0906-7590.2005.04104.x

Santos AMC, Borges PAV, Hortal J, Rodrigues AC, Medeiros C, Azevedo EB, Melo C, Lopes DJH (2005) Diversidade da fauna de insectos fitófagos e de inimigos naturais em culturas frutícolas da ilha Terceira (Açores): a importância do maneio e da heterogeneidade ambiental. In: Lopes D, Pereira A, Mexia A, Mumford J, Cabrera R (eds) A Fruticultura na Macaronésia—O Contributo do projecto INTERFRUTA para o seu desenvolvimento. Universidade dos Açores, Angra do Heroísmo, pp 115–134

Sax DF (2001) Latitudinal gradients and geographic ranges of exotic species. J Biogeogr 28:139–150. doi:10.1046/j.1365-2699.2001.00536.x

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends Ecol Evol 17:170–176. doi:10.1016/S0169-5347(02)02495-3

Shurin JB (2000) Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. Ecology 81:3074–3086. doi:10.1890/0012-9658(2000)081[3074:DLIRAT]2.0.CO;2

Simberloff D (1995) Why do introduced species appear to devastate islands more than Maitland areas? Pac Sci 49:87–97

Tilman D (1997) Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78:81–92. doi:10.1890/0012-9658(1997)078[0081:CIRLAG]2.0.CO;2

Triantis KA, Borges PAV, Ladle RJ, Hortal J, Cardoso P, Gaspar C, Dinis F, Mendonça E, Silveira LMA, Gabriel R, Melo C, Santos AMC, Amorim IR, Ribeiro SP, Serrano ARM, Quartau JA, Whittaker RJ (2010) Extinction debt on oceanic islands. Ecography 33:285–294. doi:10.1111/j.1600-0587.2010.06203.x

Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R (1996) Biological invasions as global environmental change. Am Sci 84:468–478

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. Science 277:494–499. doi:10.1126/science.277.5325.494

Whittaker RJ, Rigal F, Borges PAV, Cardoso P, Terzopoulou S, Casanoves F, Pla L, Guilhaumon F, Ladle R, Triantis KA (2014) Functional biogeography of oceanic islands and the scaling of functional diversity in the Azores. P Nat Acad Sci USA 11:13709–13714. doi:10.1073/pnas.1218036111

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) GLM and GAM for count data. Overdispersion. In: Gail M, Krickeberg K, Samet JM, Tsiatis A, Wong W (eds) Mixed effects models and extensions in ecology with R. Statistics for Biology and Health, Springer, New York, pp 224–227