ORIGINAL ARTICLE

Invasibility and species richness of island endemic arthropods: a general model of endemic vs. exotic species

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ABSTRACT

Aim This paper has two objectives. First, we examine how a variety of biotic, abiotic and anthropogenic factors influence the endemic and introduced arthropod richness on an oceanic island. Second, we look at the relationship between the endemic and introduced arthropod richness, to ask whether areas with high levels of endemic species richness deter invasions.

Location The work was carried out on a young volcanic island, Terceira, in the Azores.

Methods We used standard techniques to collect data on arthropod species richness. Environmental data were obtained from the CIELO climatic model and using GIS. The explanatory value of environmental variables on a small-scale gradient of endemic and exotic arthropod species richness was examined with generalized linear models (GLMs). In addition, the impact of both endemic and exotic species richness in the communities was assessed by entering them after the environmental variable(s) to see if they contributed significantly to the final model (the hierarchical method).

Results Abiotic (climatic and geomorphological) variables gave a better explanation of the variation in endemic species richness, whereas anthropogenic variables explained most of the variation in introduced species richness. Furthermore, after accounting for all environmental variables, part of the unexplained variance in the endemic species richness is explained by the introduced species richness and vice-versa. That is, areas with high levels of endemic species richness had many introduced species. There is evidence of a somewhat inverse spatial distribution between a group of oceanic-type, forest-dwelling, endemic, relict arthropods and a group of more generalist endemic arthropods that are able to survive in disturbed marginal sites particularly rich in non-indigenous species.

Main conclusions Richness of endemic species is mainly driven by abiotic factors such as a climatic axis (oceanic-type localities with lower temperatures and summer precipitations) and a binary variable CALD (location of sites in caldeiras or ravines), whereas richness of introduced species depends on disturbance related factors. However, after factoring out these major influences, there is a correlation between endemic and introduced richness, suggesting that – independent of the environmental and geographical factors that affect the distribution of endemic or introduced species – the richest endemic assemblages are more prone to invasion, due probably to a facilitation process. Inconclusive evidence suggests that non-indigenous species are limited to those sites under anthropogenic influence located mainly near forest edges, but the rate of expansion of those species to high-altitude, core pristine sites has still to be tested.

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INTRODUCTION

By their very nature, oceanic island ecosystems offer great opportunities for the study of ecological processes and have for a long time been recognized as natural laboratories (Carlquist, 1974; Williamson, 1981; Whittaker, 1998; Gillespie & Roderick, 2002; Vitousek, 2002). Moreover, as a consequence of their discrete geographical nature and long-term isolation from continental invasion, true oceanic islands are considered hotspots of endemic taxa (Walter, 2004). However, in most human-inhabited islands, the original vegetation is usually highly fragmented and reduced to small areas located in areas characterized by harsh environments that are of no agricultural value. In contrast, habitats altered by humans are characterized by increased species richness and dominance by alien species. Thus, the disturbance of the original environmental conditions creates new opportunities for non-indigenous invasive species through the increase of new and more productive microhabitats; these are usually caused by anthropogenic disturbances which create conditions in which invading species are competitively superior (Suarez *et al.*, 1998; Brooks, 1999; Byers, 2002). Moreover, habitat destruction and fragmentation may be especially detrimental to endemic species and those species occurring at low population densities; such species generally make up a large proportion of native island habitats (Whittaker, 1998; Gillespie & Roderick, 2002; Walter, 2004).

In the Azorean islands, the land-use changes were dramatic following human colonization in the fifteenth century when the native vegetation at low and middle altitudes became gradually extinct or highly modified. In the last century, an increase in pastureland further depleted small fragments at middle altitudes and a large number of exotic plants and animals were accidentally introduced (Silva, 2001; Silva & Smith, 2004). However, no historical data are available to show the invasion of arthropod species into the native vegetation.

Elton (1958) first suggested that more diverse sites should be less prone to non-indigenous species invasion. Since then, there have been numerous studies and discussions about both the influence of species richness and the abundance of dominant species in native assemblages on invasion resistance. Unfortunately, empirical studies of invasibility often provide contradictory results in which species richness and dominance facilitate or impede the invasion success of introduced species (Mack *et al.*, 2000; Kolar & Lodge, 2001; Moore *et al.*, 2001; Rosenzweig, 2001; Kennedy *et al.*, 2002; Bruno *et al.*, 2003; Smith *et al.*, 2004).

Taking into account the fact that island ecosystems are known to be usually non-saturated, they should be considered as highly vulnerable to species invasions (Vitousek *et al.*, 1995; Williamson, 1996). We may ask, then, if those invasions occur by the replacement of extinct native species (maintenance of local diversity) or instead by species addition (increase of local diversity). The 'species replacement hypothesis' illustrated in Wilson's (1961) classic work with ants on islands, provides a good example of changing faunal composition after the introduction of an exotic species (see also Loope *et al.*, 1988). In addition, Sax *et al.* (2002) have shown that the species richness of vascular plants has approximately doubled on oceanic islands as a result of human activities. For instance, in the Azorean islands 70% of current flora consists of exotic species (Dias, 1996; Silva, 2001; Silva & Smith, 2004), and about 58% of the arthropod fauna is also composed of exotic species (Borges *et al.*, 2005a). A large amount of evidence is also available for the extinction of endemic taxa after the spread of exotic species on islands particularly in Hawaii (Howarth & Ramsay, 1991) and other Pacific islands (O'Dowd *et al.*, 2003). However, recent evidence shows that most natural disturbances are non-catastrophic in that some residents survive (Platt & Connell, 2003). Moreover, not all indigenous species respond to fragmentation by declining towards extinction (Didham *et al.*, 1998) and local species richness may also be unaffected (Summerville & Crist, 2004). Accordingly, the question could be formulated in the following way: Which species survive after non-indigenous (exotic) species spread on native island ecosystems? In fact, island agroecosystems are dominated by widely distributed arthropod species (e.g., Borges, 1999; Borges & Brown, 2001), some of them with pest status. However, data on patterns of invasion of pristine habitats on islands by introduced arthropods are scarce (although see Cole *et al.*, 1992; Gaston *et al.*, 2003; O'Dowd *et al.*, 2003) and no work is available on the spatial distribution of endemic and introduced arthropod species richness in native habitats within an island.

Several studies have examined the suite of abiotic factors that influence the native species richness (see Rosenzweig, 1995), while others have focused on the factors that influence invasion by non-native species (see recent reviews by Parker *et al.*, 1999; Sakai *et al.*, 2001). Studies on native arthropods tend to show the relevance of factors such as productivity (Polis *et al.*, 1998), habitat structure (Borges & Brown, 2001, 2004), and area (Rosenzweig, 1995); while studies on non-native taxa tend to show that anthropogenic factors, such as the degree of disturbance, fragmentation and proximity to the edge of a habitat fragment, are frequently the most important predictors (Brooks, 1999; Byers, 2002; With, 2002). Here, we examine how a variety of biotic,

abiotic, and anthropogenic factors influence endemic and introduced arthropod richness on an oceanic island using a set of GIS-based explanatory variables and data on arthropod (endemic and introduced) species richness collected from forty localities on Terceira Island (Azores). We also test to see if, independent of the environmental and geographical correlates of the richness, the richest endemic assemblages are less prone to invasion.

MATERIALS AND METHODS

Area of study

The Azorean archipelago is located in the North Atlantic, roughly between 37° to 40° N latitude and 25° to 31° W longitude. It comprises nine main islands and some small islets aligned in a WNW–ESE direction, that are fully oceanic, that is, they are volcanic islands of recent origin. Terceira Island (Fig. 1c) is a roughly circular island of 402 km^2 area, formed by four main volcanic polygenetic complexes (Cinco Picos, Guilherme Moniz, Pico Alto and Serra de Santa Bárbara) (Nunes, 2000; Montesinos et al., 2003). The highest point (Serra de S. Bárbara, 1023 m a.s.l.) is also the most recent (0.025 Myr BP) of the three major island complexes (Self, 1982).

The climate is temperate oceanic, i.e. strongly influenced by the proximity of the ocean and by its topography, which produces high levels of relative atmospheric humidity that can reach 95% in the native, high altitude, semi-tropical, evergreen laurel forest. The temperate oceanic climate also restricts temperature fluctuations throughout the year. The native forest is characterized by reduced tree stature (usually up to 5 m, rarely reaching 10 m), due to the shallow soil and rugged terrain.

Experimental design, arthropod sampling and identification

Small-scale variation in species richness of arthropods in their native habitats in the island of Terceira was obtained by sampling from eight available fragments of native forest (see Fig. 1c). In each of the studied fragments of native forest, several independent transects were established. The sites were chosen in a random manner from among the available forest patches within the studied areas, depending on whether they were accessible or not. In some cases, old paths were used to allow a better penetration to the core of the forest and to avoid border effects. Each transect was 150 m long and 5 m wide, and was established in different years, in the summers of 1999 ($n = 11$), 2001 ($n = 4$), 2002 ($n = 9$) and 2003 ($n = 16$). Whenever possible, a linear direction was followed, but frequently deviations were necessary due to uneven ground and very dense vegetation. In cases where a straight line was impossible, the same direction was kept, thus avoiding a strong bias while setting the transect. A rope was used to mark each transect to facilitate its recognition during the trap recovery. We sampled the epigean arthropod fauna using pitfall traps. At each site ($n = 40$), pitfall traps were in the ground for a 2-week period. All transects consisted of 30 pitfall traps, plastic cups with a top diameter of 42 mm and a dept of 78 mm, dug into the ground so the lip of the cup was flush with the soil surface. Half of the traps ($n = 15$) were filled with c. 60 mL of a non-attractive solution (anti-freeze liquid) with a small proportion of ethylene glycol, and the other half ($n = 15$) with the same volume of a general attractive solution (Turquin), which was made of dark beer and some preservatives (for further details see Turquin, 1973). Into both kinds of traps a few drops of a
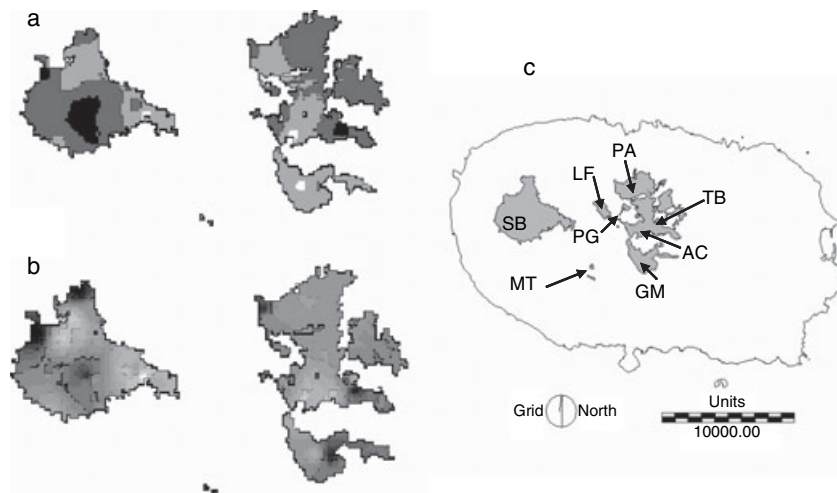
Figure 1 Interpolated maps using a distance-weighted average of the number of endemic species within the natural vegetation of Terceira Island (a), and residuals of the final model built with the chosen explanatory variables (b). Black areas show high species richness and high positive residuals (where observed scores are higher than predicted). The maps are shaded from white to black following the four quartiles of the distribution (i.e. 25%, 50%, 75% and 100%). The map on the right (c) represents the area with natural vegetation within the island with identification of the eight fragments of native forest: AC, Algar do Carvão; GM, Caldeira Guilherme Moniz; LF, Corrente Lava de 1761; MT, Matela; PA, Biscoito da Ferraria/Pico Alto; PG, Pico do Galhardo; SB, St. Bárbara; TB, Terra-Brava.

liquid detergent were added to reduce surface tension. Traps were spaced 5 m apart, starting with a Turquin trap and alternating with the ethylene traps. We used both Turquin traps and ethylene glycol traps not only to survey the relative abundance of each species sampled (with non-attractive traps), but also to capture the maximum number of species (with attractive traps). Traps were protected from the rain by a white plastic plate, at approximately 5 cm above the surface and fixed to the ground by two pieces of wire. Finally, the arthropod samples were taken to the laboratory and transferred into an ethanol (70%) and glycerol (5%) mixture.

All Araneae, Opiliones, Pseudoscorpiones, Diplopoda, Chilopoda and insects (excluding Collembola, Diplura, Diptera and Hymenoptera) were sorted first into morphospecies by students under the supervision of a trained taxonomist (P.B.). The morphospecies approach is common practice in biodiversity studies, which does not compromise scientific accuracy (see Oliver & Beattie, 1996) and has some clear advantages when expertise in all taxonomic groups is not available *in situ*. Later, the morphospecies were identified by one of us (P.B.) using vouchered specimens and all unknown morphospecies were subsequently sent to several taxonomists for species identification. Due to the low levels of diversity and a high percentage of monospecific genera (see Borges *et al.*, 2002) there were relatively few errors in the definition of morphospecies and these could easily be corrected in the data base.

Environmental variables

Geological variables

A digital geological map based on Lloyd & Collis (1981) and digitized by Rodrigues (2002) was used to divide the 40 sampled points into six categorical geological units (peralkaline Pico Alto; peralkaline Santa Bárbara; basalts of 1751; basalts of Santa Bárbara; basalts of Algar Carvão; basalts of Pico da Bagacina) (categorical variable G). Another geological simplified variable (categorical variable G2) was created using only two geological units: basalt ($G2_B$) vs. peralkaline ($G2_P$). In addition, two other categorical variables were created to distinguish samples from volcanic regions (categorical variable VO), and from exposed sites (mountain slopes) vs. those from less exposed sites (caldeiras, fissures, ravines or torrential watercourses) (CALD).

Vegetation variables

All 40 sampled transects were located within native primary and secondary forest or shrub-like formations. Consequently, to assign each site to a vegetation type we used information obtained during a survey of the canopy arthropod fauna (Ribeiro *et al.*, 2005; P.A.V. Borges *et al.*, unpubl. data). A total of 11 vegetation types were created based on the dominance of Azorean endemic and native trees or shrubs (categorical variable V). As the type of trees or shrubs that dominate in a particular transect influence the type of litter, we created another variable to differentiate between litter dominated by broadleaf type trees (*Ilex perado* ssp. *azorica* and *Laurus azorica*) or short-leaf type trees (*Erica azorica* and *Juniperus brevifolia*). This categorical variable (L) in classifying the litter type is potentially a good indicator of litter composition and structure, and indeed of arthropod diversity.

Topographical variables

A land-use map based on CORINE land-use classification was created for the purpose of this work and used to generate three types of land uses: native forest, semi-natural pasture and intensive sown pasture. These three types of land use were gathered based on information from aerial photography and data obtained from Rodrigues (2002) for the central part of the island. This allowed the calculation of the distances between each sampled transect and the minimum distance to: (1) the margin of native vegetation (DNV), (2) semi-natural pasture (DSNP), and (3) intensive sown pasture (DISP).

Based on the altimetry of the island, several continuous or categorical variables were extracted using a GIS (*Idrisi32*; Clark Labs, 2000) for cells of 100×100 m: (1) altitude (ALT), (2) latitude (LAT) and longitude (LONG) in UTM, (3) average slope (SLOPE) of the four 50×50 m squares included in each 100×100 m cell, (4) major aspect of the 100×100 cell (NE, SE, SW and NW; categorical variables), and (5) the impact of the proximity of the main or secondary roads and tracks was obtained by counting the number of 50×50 m pixels of roads within a 1-km radius of the centre of each sampling point (continuous variable R). To do this, the 100×100 m cells were transformed to a resolution of 50×50 m and the roads and tracks were transformed to 50-m pixels using a GIS.

Based on the fact that the sites were located within native vegetation fragments of different areas and shapes, three additional variables were obtained from GIS: (1) area of each forest fragment (AREA), (2) perimeter of the forest fragment (PER), and (3) a circularity index (CIR) obtained by the division of the forest fragment area by its perimeter, giving the fragment shape.

Climatic variables

Climatic variables were investigated because they have been shown to be important correlates of diversity gradients for a variety of taxa (see, for example, Rahbek & Graves, 2001). A total of six variables were obtained from the CIELO interpolated maps (Azevedo, 1996; Azevedo *et al.*, 1999) for all 100×100 m grid cells of Terceira Island. The CIELO model has been developed, calibrated and validated for Terceira Island by Azevedo *et al.* (1999). It was constructed in order to equate the knowledge we have about the processes governing the spatial variation of climatic variables at the local scale, using the smallest number of parameters, with the limited data available from synoptic coastal

meteorological stations. The six variables are of two subtypes and were modelled by one of us (E.B.A., see also Azevedo *et al.*, 1999): 'advective' variables originate from the thermodynamic processes governing the variations of air temperature and humidity, cloudiness of local orographic origin, and precipitation; this includes the so-called Foehn effect, but not occult deposition. The four continuous variables were: precipitation (monthly); maximum daily temperature; mean daily temperature; and minimum daily temperature. Two other variables were of 'radiative' and combined type, and took into account orographic clouds and thermodynamics produced by the advective submodel and the shadow produced by the relief, so generating the dependent variables adjusted to the topography. Those variables are actual evapotranspiration in mm and global radiation.

Each of the six climatic variables data were available for all months, but only winter and summer months were used as independent variables both individually and collated in 'winter' and 'summer' variables. When selecting only winter and summer months we reduced the impact of collinearity of variables and had two contrasting sets of variables representing the harsh and pleasant climate. Therefore, a total of 48 climatic variables were available (6 variables × 6 months; plus 6 winter variables and 6 summer variables). To simplify these data a principal components analysis (PCA) was undertaken using the standardized scores of these climatic variables, resulting in the selection of three components with eigenvalues higher than 1 (3.3, 8.0 and 2.0, respectively) which explain 95.9% of the total variance in the climatic data (72.1, 19.0 and 4.7, respectively). The first component (CA1) is positively correlated with high temperatures and low summer precipitation (Mediterranean vs. oceanic gradient); while the second component (CA2) is positively correlated with the evapotranspiration and radiation scores; the third component (CA3) is negatively correlated with the winter rainfall (factor loadings higher than 0.8). The scores of these three PCA components were used as independent variables in the regression analysis.

Other variables

Each transect was located within a forest fragment and a categorical variable was created to assign each transect to one of eight possible native vegetation fragments (categorical variable F).

The occurrence of water runoff is supposed to be an important factor in the Azorean, native, semi-tropical, evergreen, laurel forest. Therefore, all sites with watercourses (dry or seasonally wet streambeds) crossed by a transect or with torrential watercourses were classified as 'presence of water runoff'(1), in contrast to no evidence of water runoff (0) (categorical variable W). Water runoff generation proved to be of potential use in predicting soil properties that control plant distribution (Dirnbock *et al.*, 2003).

A variable usually positively associated with plant diversity and productivity is pH (Roem & Berendse, 2000; Dzwonko,

2001; Perelman *et al.*, 2001; Roem *et al.*, 2002). In each transect, five cores were taken. In the laboratory, all samples were homogenized and mixed to obtain a 'composite sample'. The samples were assayed for organic matter (continuous variable OM) and soil pH (continuous variable pH). The organic matter was obtained through 'loss of weight by calcination'.

Data analysis

Arthropods were grouped into three colonization categories: native, endemic and introduced species. All unclassified species were assumed to be native. Native species arrived by long-distance dispersal to the Azores and are also present in other nearby archipelagos (Madeira and the Canary Islands) and on the continents. Endemic species are those that occur only in the Azores, as a result of either speciation event (neo-endemics) or extinction of the mainland populations (palaeo-endemics). Introduced species are those believed to be in the archipelago as a result of human activities; some of them are cosmopolitan species. For the current study only endemic and introduced species will be considered. Feeding *habitus* for each species was obtained from taxonomists and general faunal literature.

To detect the spatial structure in the distribution of the number of species, a Trend Surface Analysis (TSA) was conducted (Legendre & Legendre, 1998), submitting the nine terms of a third degree polynomial of central latitude and central longitude of sites, as explanatory variables in a backward regression procedure in order to remove the non-significant spatial terms. Moreover, to examine if the spatial structures are caused by the autocorrelation in the response variable, the Moran's *I* autocorrelation coefficient with a Bonferroni-corrected significance level (Sawada, 1999) was calculated against several distance classes. After submitting the dependent variable to a regression analysis with the explanatory variables, the regression residuals were checked for autocorrelation. If regression analysis residuals are spatially autocorrelated, one or several important spatially structured explanatory variables can be left out (Cliff & Ord, 1984; Legendre & Legendre, 1998; Keitt *et al.*, 2002) and mapping these residuals can help to recognize these neglected factors.

Generalized Linear Models (GLM) (McCullagh & Nelder, 1989; Dobson, 1990) have been used to summarize the relationship between number of species and explanatory variables. GLMs are an extension of linear models that allow for non-linearity in the data and also a wide range of model specification distributions other than the normal distribution of the random component. In our case the assumed relationship between the number of species and the explanatory variables is logarithmic (the link function), while a Poisson error distribution for the number of species was assumed (see Crawley, 1993). The explanatory capacity of each explanatory variable was first tested individually, and then we calculated a complete predictive model by a stepwise backward procedure in order to account for a model able to explain the maximum variation in the dependent variable. Curvilinear relationships

between dependent variables and explanatory continuous variables were examined by selecting the linear, quadratic or cubic function of each explanatory variable; this significantly increases the predictive capacity of the model.

The percentage of dissimilarity between localities was computed using the number of individuals of each species in each locality. The subsequent triangular matrix was subjected to a cluster analysis with the Ward method as the linkage rule to describe the main groups of localities according to the faunal composition. The environmental and biological differences among these faunal groups of localities were analysed by the nonparametric Mann Whitney *U*-test and the Pearson chi-square coefficient (Legendre & Legendre, 1998).

Ultimately, as the residuals of the regression analysis using the selected explanatory variables can be considered as the variation in species richness not attributable to environmental or geographical factors, these residuals were regressed against one another as an estimate of the possible interaction between the two groups of species (Shenbrot & Krasnov, 2002). These residuals are also included as an explanatory variable in the final models (obtained with the environmental and geographical variables) in order to check if the richness variation in endemic species not attributable to environmental or geographical factors can influence the predictive capacity of the obtained model for introduced species, and vice versa.

RESULTS

Species composition

From a total of 20,085 specimens, we recorded 150 species of arthropods in the 40 localities (transects). From those species, 37 (25%) are endemic to the Azores (Araneae = 12; Microcoryphia = 1; Trichoptera = 1; Hemiptera = 3; Lepidoptera = 9; Plannipenia = 1; Coleoptera = 10), 64 are native and 49 introduced (= exotic) (see Appendix 1).

The feeding guilds were structured as follows: 68 species were predators (18 endemic and 25 introduced), 59 species were herbivorous (16 endemic and 15 introduced), 21 species were saprophagous (2 endemics and 9 introduced) and 2 species were fungivorous (1 endemic). The richest taxonomic groups were Coleoptera (48 spp.; 20% endemic and 45% introduced), Araneae (31 spp.; 39% endemic and 42% introduced), Hemiptera (22 spp.; 14% endemic and 23% introduced), Lepidoptera (21 spp.; 43% endemic and 19% introduced) and Diplopoda (7 spp.; 43% introduced).

Endemic species richness

Although none of the nine spatial terms of a third degree polynomial of latitude and longitude are significant in a stepwise backward regression, the number of endemic species seems to show a structured spatial pattern (Fig. 1a) summarized by the significant positive autocorrelation score of Moran's *I* (0.39) at the first lag distance, and a negative autocorrelation score (−0.31) at the fourth lag distance
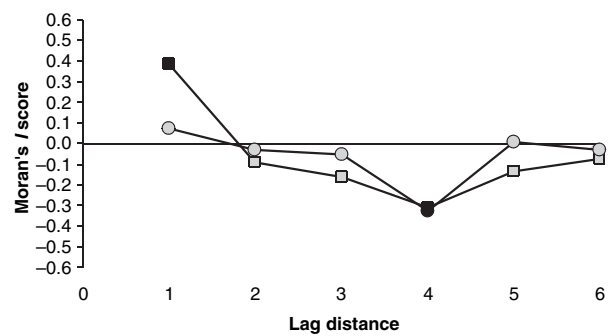
Figure 2 Moran's *I* autocorrelation scores for the number of endemic species (squares) and for the residuals of the final model (circles) of richness variation of endemic species (49.86% of total deviance). The lag distance is 500 m, a similar figure to the mean distance between localities (483 m). In black the significant autocorrelation scores at *P* < 0.05.

(Fig. 2). Thus, nearby localities separated by 500 m have similar scores of species richness but sites located at approximately 2000-m distance generally differ in their scores of endemic species richness.

Only nine of the analysed variables (three quantitative and six categorical binary variables) were correlated with endemic species (Table 1). The most important quantitative variable is the first PCA climatic axis (CA1), which explains almost 29% of the total deviance, showing that the number of endemic species is higher in oceanic-type localities with lower temperatures and lower summer precipitation. Greater endemic species richness was found in sites in caldeiras or ravines (CALD) and these constituted the binary variable. More species also occur in localities with acidic soils (pH), with watercourses (W), with litter from broadleaf trees (L), with canopy vegetation dominated by *Laurus azorica* and *Ilex perado* ssp. *azorica* species (VAL), with peralkaline lava composition (G2P), and with fewer roads (R).

Using all the former significant explanatory variables, a complete model was obtained by a stepwise backward procedure. This model is only composed of two variables (CALD and CA1) accounting for *c.* 50% of the total variation in endemic species richness. The residuals of this model were normally distributed and the plot of residuals versus predicted values formed a homogeneous cloud around the centre. However, a significant and negative autocorrelation score remained at the fourth lag distance (Moran's *I* = 0.33; *P* < 0.05; see Fig. 2), probably due to the effect of a neglected variable. Examining the spatial distribution of this variable (Fig. 1b), the model partially underestimates the observed species richness in some areas with intermediate or high species richness scores and overestimates in some areas with poor scores. The negative autocorrelation score at the distance of 2 km of these residuals may be a result of the mean separation between species in rich and poor areas.

As total abundance and species richness are correlated (Spearman rank correlation coefficient; *r*~s~ = 0.57; *P* < 0.001),

Table 1 Significant relationship between the number of endemic species and the used explanatory variables when the influence of these variables is tested individually by Generalized Linear Models. We assume that the relationship between the number of species and the explanatory variables is logarithmic and that errors follow a Poisson distribution. CALD, exposed sites (mountain slopes) vs. less exposed sites (caldeiras, fissures, ravines or torrential watercourses); CA1, the first axis of a principal component analysis (PCA); ALT, altitude; W, presence of water courses; L, litter type; VAL, vegetation type dominated by *Ilex perado* ssp. *azorica* and *Laurus azorica*; G2$_P$, categorical geological type Peralkaline; R, distance to roads

Explanatory variable	d.f.	Deviance	Stat/d.f.	Change in deviance	F	Explained deviance (%)	Sign
Null model	39	239.78	6.15				
CALD	38	153.89	4.05	85.88	21.21***	35.82	+
CA1	38	170.77	4.49	69.01	15.36***	28.78	−
pH	38	188.89	4.97	50.89	10.24***	21.22	−
ALT	38	190.13	5.00	49.64	9.92***	20.70	+
W	38	202.77	5.34	37.00	6.93***	15.43	+
L	38	204.37	5.38	35.41	6.58**	14.77	+
VAL	38	208.77	5.49	31.00	5.64**	12.93	+
G2$_P$	38	210.29	5.53	29.48	5.33*	12.30	+
R	38	215.69	5.67	24.09	4.24*	10.05	−

***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$

we assume that a similar group of variables influences the spatial variation of endemic species abundance. However, two main groups of localities (A and B) are derived from the cluster analysis of species abundance scores (Fig. 3). Both groups of localities do not significantly differ in the number of endemic species (Mann Whitney *U*-test, $Z = 1.30$, n.s.; $n_1 = 25$, $n_2 = 15$), but they differ in the number of introduced species ($Z = 1.98$, $P = 0.05$; $n_1 = 25$, $n_2 = 15$), which is higher in group B localities (median = 7, mean = 6.3) than in group A localities (median = 5, mean = 4.9). Moreover, both groups

of localities could be distinguished by the scores of three quantitative variables and five categorical binary variables (Table 2). Group B localities are characterized by a higher perimeter of natural vegetation fragments, a shorter distance to intensive pasturelands and a greater amount of nearby roads. Thus, these quantitative variables are related to the existence of fragmented patches of natural vegetation and also to anthropogenic disturbance of the landscape. Among the categorical variables, most of the localities of group B are found in arid and exposed basaltic soils dominated by *Erica azorica* vegetation.
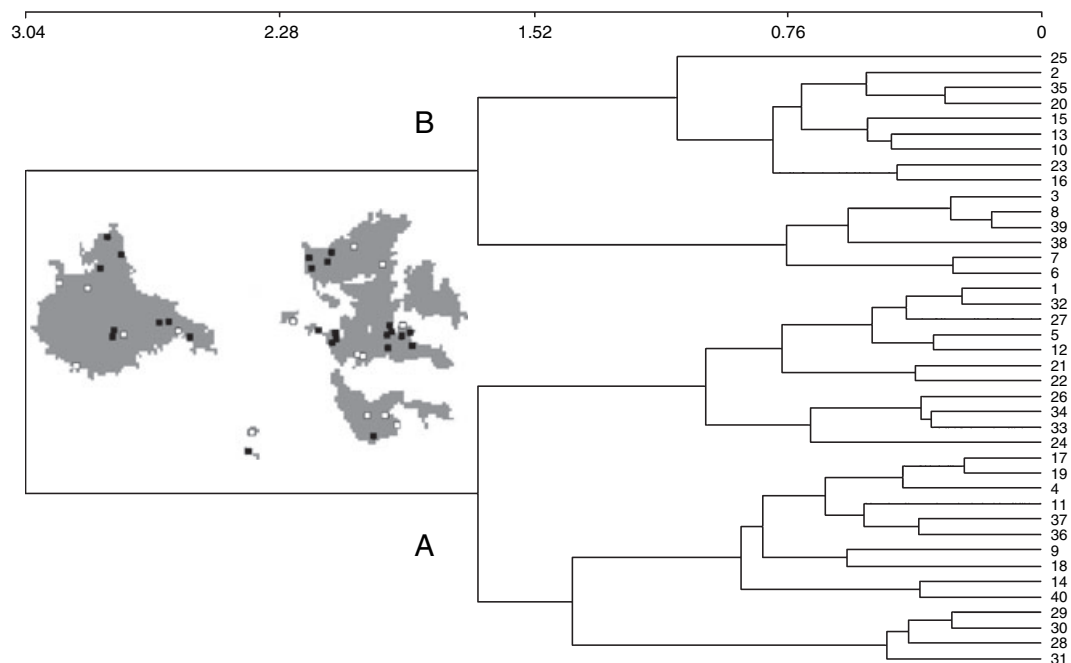
Figure 3 Two main groups of localities represented by numbers (A = filled squares, B = open squares) derived from the cluster analysis of endemic species abundance scores. The percent of dissimilarity was used as the measure of resemblance and the Ward method as the linkage rule.

Table 2 Z scores of the Mann–Whitney U-test comparing the values of the quantitative variables between the two groups of localities previously defined by a cluster analysis performed taking into account the abundance of endemic species in each locality (Fig. 3). χ^2 is the Pearson chi-square value measuring the association between explanatory binary variables (d.f. = 1) for the same groups of localities. The variables considered have higher scores or are associated with the localities of group B (see Fig. 3). Negative values indicate a negative association or relation with the group B localities

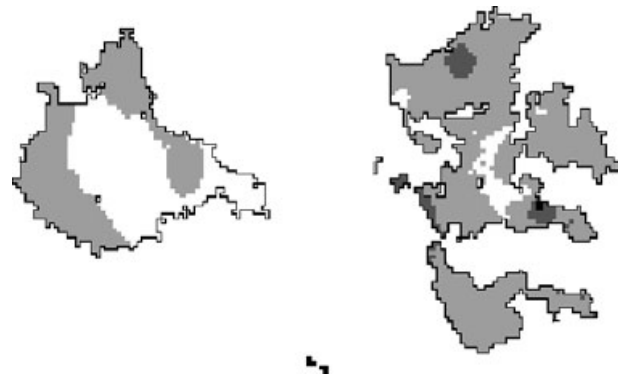| Explanatory variable	Z	P	χ^2
Perimeter	2.14	0.02	
Distance to anthropic pasturelands	−1.98	0.05	
Roads	2.60	0.009	
Basaltic lava composition		0.0003	13.49
Exposed sites		0.002	9.74
Canopy vegetation dominated by *Erica*		0.006	7.41
Absence of watercourses		0.0003	13.15
North orientation		0.03	4.75

Introduced species richness

The spatial distribution in the number of introduced species is very different from that of endemic species richness (Fig. 4), showing a clearly structured pattern in which the greatest richness is located on the periphery of natural vegetation areas and in small fragments of vegetation. When the species richness of introduced species is regressed with the third degree polynomial of latitude and longitude, only the linear term of latitude shows a significant explanatory capacity ($F_{(1,38)} = 6.65$; $P = 0.01$), showing that more species occur at lower latitudes (south to north gradient). The autocorrelation analyses do not show significant Moran's I scores at any lag distance, although a marginal positive autocorrelation score occurs at the first lag distance (from 0 to 500 m; $I = 0.29$, $P = 0.09$).

Figure 4 Interpolated map to represent the variation in the mean number of introduced arthropod species within the natural vegetation of Terceira Island. Black areas represent high scores of species richness. The maps are shaded from white to black following the four quartiles of the distribution (i.e. 25%, 50%, 75% and 100%).

Ten variables (six quantitative and four categorical binary variables) were statistically significant for the number of introduced species (Table 3). The most important variable is the circularity (CIR) of the fragment of natural vegetation to which each locality belongs, explaining 36% of the total deviance. Other significant variables are: the Matela fragment of natural vegetation found at lower altitudes (FMT); a third PCA climatic axis (CA3); the amount of roads (R); altitude (ALT); the distance to semi-natural pasturelands (DSNP); the area of the fragment (AREA); the Santa Barbara volcano or forest fragment (VOSB, FSB); and the south-west orientation (OSW). Thus, the number of introduced species is, higher at: low altitude and dry sites located near pastures; in the south-west oriented sites; in sites located in small fragments of natural vegetation with lower circularity, crossed by routes, similar to the Matela fragment; and in sites other than the large

Table 3 Individually significantly relationships between the number of introduced species and the explanatory variables using generalized linear models. We assume that the relationship between the number of species and the explanatory variables is logarithmic and that errors follow a Poisson distribution. CIR, circularity index; FMT, forest fragment of Matela; CA3, the third axis of a principal components analysis (PCA); R, distance to roads; ALT, altitude; DSNP, minimum distance to semi-natural pastures; AREA, area of forest fragment; VOSB, Volcan of St. Bárbara; FSB, forest fragment of St. Bárbara; OSW, aspect of the 100×100 cell south-west

Explanatory variable	d.f.	Deviance	Stat/d.f.	Change in deviance	F	Explained deviance (%)	Sign
Null model	39	241.78	6.20				
CIR	38	154.71	4.07	87.07	21.39	36.01	−
FMT	38	176.34	4.64	65.44	14.10	27.06	+
CA3	38	178.45	4.696	63.33	13.48	26.19	−
R	38	182.54	4.80	59.23	12.33	24.50	+
ALT	38	182.87	4.81	58.90	12.24	24.36	−
DSNP	38	188.00	4.95	53.77	10.87	22.24	−
AREA	38	192.80	5.07	48.98	9.65	20.26	−
VOSB	38	198.33	5.22	43.45	8.32	17.97	−
FSB	38	198.33	5.22	43.45	8.32	17.97	−
OSW	38	204.37	5.38	37.41	6.95	15.47	+

***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$

Figure 5 Three main groups of localities represented by numbers (A = filled squares, B1 open squares and B2 = crosses) derived from the cluster analysis of introduced species abundance scores. The percent of dissimilarity was used as the measure of resemblance and the Ward method as the linkage rule.

Table 4 Z scores of the Mann-Whitney U-test used to compare the values of the quantitative variables between the two groups of localities, previously defined by a cluster analysis performed taking into account of the abundance of introduced species in each locality (Fig. 5). χ^2 is the Pearson chi-square value measuring the association between explanatory binary variables (d.f. = 1) for the same groups of localities. The variables considered have higher scores or are associated with the localities of group B (see Fig. 3). Negative values indicate a negative association or relation with the group B localities

Explanatory variable	Z	P	χ^2
Roads	2.98	0.003	
Circularity	−2.39	0.02	
Basaltic lava composition		0.0006	11.88
Volcan Pico Alto		0.02	−5.10
Exposed sites		0.002	9.72
Fragment Guilherme Moniz		0.02	5.43
Canopy vegetation dominated by *Erica*		0.02	5.43
Canopy vegetation dominated by *Erica* and *Laurus*		0.008	6.98
Canopy vegetation dominated by *Juniperus* and *Laurus*		0.004	−8.18
Absence of watercourses		0.00004	16.83
South-east orientation		0.05	3.96

Santa Barbara fragments. When all the formerly significant variables are considered together, a stepwise backward procedure selects a final model with CIR and OSW as significant variables accounting for 41.6% of the total deviance. The residuals of this model are also normally distributed and no aberrant features can be distinguished, nor does any autocorrelation occur at any lag distance.

Cluster analysis of species abundance scores shows two main groups of localities (Fig. 5) that significantly differ in the number of endemic species (Mann Whitney U-test, $Z = 2.43$, $P = 0.01$; $n_1 = 22$, $n_2 = 18$) but not in the number of introduced species ($Z = 0.35$, n.s.). In both groups of localities a similar number of introduced species can be found, but group B localities contain a lower number of endemic species than group A localities. Group B localities could be further subdivided into two groups, the abundance of most introduced species being higher in group B2 (see Appendix 1). Both groups of localities can be distinguished by the scores of two quantitative variables and nine categorical binary variables (Table 4). Thus, group B localities are also characterized by variables related to the existence of fragmented and anthropogenic patches of natural vegetation under dry conditions; lower circularity of the fragments of natural vegetation; more roads; exposed and basaltic soils; vegetation dominated by *Erica* and *Laurus*; the absence of watercourses; and a south-east
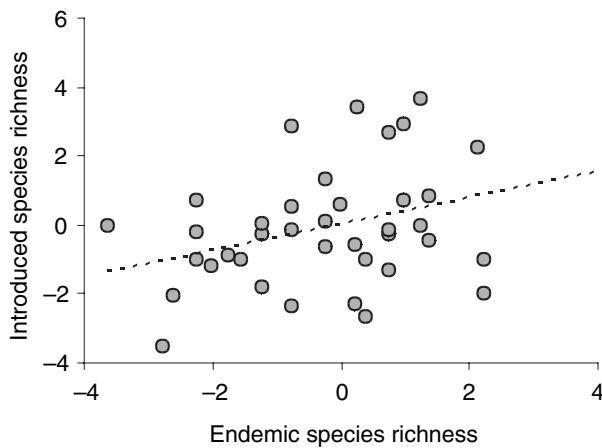
Figure 6 Relationship between the residuals of the final models for endemic and introduced species taking into account the considered environmental and geographical explanatory variables. The broken line represents the linear regression between both residual scores.

orientation. Only six out of the 40 transects changed between these two cluster groups when using the introduced data set instead of the endemic data set.

Endemic vs. introduced patterns of species richness distribution

When the number of introduced species was added as an explanatory variable to the final model, built for the endemic species, we obtained a significant increase in the explained deviance ($F = 4.94$; $P < 0.05$; a change in total explained deviance from 49.86% to 55.81%) in which a significant and positive coefficient occurred for the number of introduced species. The addition of the abundance of introduced species also increases the total explained deviance (53.46%), but the change in deviance is not significant ($F = 2.93$; n.s.). Moreover, when the number of endemic species was added to the final model of the introduced species we also obtained a significant increase in the explained deviance ($F = 8.31$; $P < 0.01$), but the change in deviance was higher (from 41.57% to 52.73%). The addition of the abundance of endemic species increases the explained deviance even more (to 56.44%; $F = 8.31$; $P = 0.001$).

Although the numbers of introduced and endemic species are not significantly correlated ($r_s = 0.08$, n.s.), removing the variation in species richness that is attributable to environmental and geographical variables makes the residuals of both final models significantly and positively correlated ($r_s = 0.36$, $P = 0.02$). A simple linear regression of the residuals of the introduced species richness as a dependent variable against residuals of endemic species richness as an independent variable (Fig. 6) shows a statistically significant positive value of the regression slope ($B = 0.45 \pm 0.16$; $t_{(38)} = 2.82$; $P = 0.008$)

DISCUSSION

Environmental variables related to species richness

The estimation of the influence of explanatory variables on species richness variation is a difficult task because of the frequent lack of relationship between multivariate environmental and spatial correlations and the underlying true causal relationships (Levin, 1992; Legendre & Legendre, 1998; Shipley, 1999). Thus, factors correlated with the number of species are frequently the only possible starting point when we try to identify the factors that might explain patterns of geographical species richness. In the present study we aimed to obtain correlates of species richness in sampled sites, and the variables worked well. Hence, the relationships identified in our paper, as in all correlative studies, may not necessarily identify causal factors, and so must always be considered preliminary hypotheses. Moreover, the spatial resolution of sampled data is of major importance (Lee *et al.*, 2002). Much of the recent work on environmental surrogacy of species richness is based on a very coarse resolution, frequently impractical for immediate real-world application. Consequently, the present work is a valuable study that aims to relate environmental variables to the variation in arthropod species richness at fine spatial scales (e.g. 100 m × 100 m).

Using GLM we were able to obtain sets of geographical and environmental variables (e.g. spatial, topographical, geological, climatic and anthropogenic) that are able to explain a reasonably high proportion of the variability of the endemic and introduced arthropod species richness (*c.* 50%) within an oceanic island (Terceira, Azores), and which significantly reduces or eliminates the spatial structure present in the data. The climatic variables were highly collinear, but we were successful in combining them in only three PCA components showing that climatic gradients correlated well with endemic (axis 1) and introduced (axis 3) species richness. However, a climatic axis was retained only in the final model that explains the endemic species richness. Moreover, the binary variable CALD, also retained in the endemic final model, means that local hotspots of endemic species richness are associated with sites located within caldeiras, fissures, ravines or torrential watercourses within which a microclimate characterized by constant high humidity and stable temperatures is present. Therefore, there is a strong direct or indirect link between climatic variables and endemic spatial patterns of species richness, reflecting that endemics are more diverse in non-exposed sites with a temperate oceanic climate and summer precipitation. At these sites (see Fig. 1a) a special type of forest predominates, the so-called *Laurisilva* with a dominance of broadleaf trees and *Juniperus brevifolia*. We may conclude that CALD areas are synonymous with sites with stable climates that allowed the survival of endemic species, despite their limited geographic range. In fact, the endemic arthropod community showed a clear contrast between strictly forest and mixed grassland-forest species (see Appendix 1), with specialized forest species contributing to a few hotspots of endemic

species richness in isolated pristine areas (see Figs 1a & 3; Appendix 1), and generalist grassland-forest species contributing to marginal fragmented patches of native vegetation (Appendix 1).

Since the set of Azorean endemic arthropod forest species studied is composed of both predatory and phytophagous functional groups, it is not surprising that other variables, which are not accounted for and are associated with productivity, could be strongly associated with herbivore richness. However, only a few species of herbivores were available for testing as a functional group, and data on canopy arthropods are being collated for that purpose (P. A. V. Borges et al., unpubl. data).

The negative impact of anthropogenic activities (e.g. fragmentation and habitat loss) on species richness or community composition is well known (Floren et al., 2001; Tole, 2002). Here we showed that hotspots of introduced species richness are mainly positively correlated with anthropogenic surrogate environmental variables (e.g. distance to man-made habitats, edge effects and roads; see Malcolm, 1994; Fagan et al., 1999; Bolger et al., 2000; Haskell, 2000; Helms & Vinson, 2002; Holway et al., 2002; or With, 2002). Therefore, the most important variables for endemic taxa are environmental ones, and for the introduced taxa the most important are anthropogenic, which conforms well to the expected ecological features of these two groups of species.

Endemic vs. introduced species

The apparent effects of invasive species on native communities depends largely on the scale of study; in some cases biological invaders can contribute to species gain, and invasive meltdown (sensu Simberloff & Von Holle, 1999), in which the presence of invasive species helps the invasion of more non-indigenous species. In contrast to that, introduced species could contribute to endemic species extinctions even beyond those caused by habitat loss (Brooks et al., 2002). At first, the pattern that we observed does not seem to support the hypothesis of the extinction of endemic species due to the introduction of foreign species. However, only a group of grassland or generalist forest endemic species, well adapted to the type of disturbance and prevailing in some of the sites located near disturbed human-made habitats, are living side by side with introduced species. Because of the restricted distribution of more specialized forest endemic taxa (found only in more pristine areas) we can argue that an increase in the disturbance level would intensify the impact of introduced species on endemic species (Byers, 2002).

In our case, after the inclusion of the most important environmental and geographical determinants, we showed that a higher number of endemic species can inhabit localities with more introduced species, and the number of endemic species and, principally, their abundance greatly and positively influences the species richness of introduced species. Moreover, the residuals of species richness of both groups of species were positively correlated when the influence of the environmental and geographical variables was removed; two groups of localities seem to be clearly delimited according to the faunal composition of endemic or introduced species, with both groups differing in the type of variables that discriminate against them (anthropic vs. environmental) and also in the richness of introduced or endemic species. In our opinion these results suggest the existence of a facilitation process that partially explains the richness of the introduced species in this Azorean island. This is an interesting proposal which is supported by the results obtained and the rigorous approach used to avoid spurious correlations. The correlation between endemic and introduced species number is estimated only after considering the influence of significant environmental variables (Shenbrot & Krasnov, 2002). It may be possible that some neglected environmental variable may increase the explanatory capacity of the obtained models, so diminishing the significance of the number of endemic species in explaining the richness of introduced species. However, we have used a large number of environmental variables, and it is very probable that any newly selected environmental variable will be correlated to any of those formerly used. We have as yet not considered many of the key mechanisms that enable the success of exotic species and their interaction with native communities (Hierro et al., 2005). Positive correlation between exotic and native species, after controlling the effect of energy availability, has recently also been found in birds in Great Britain (Evans et al., 2005). Some studies demonstrate that such facilitation processes can be the rule on some occasions because introduced species may be a particularly abundant resource for generalist native species, increasing both their populations and their geographical distribution (Wormington & Leach, 1992; Pearson et al., 2000; Maerz et al., 2005). In the case of the Azorean islands, some results suggest that native pollinators together with some exotic insects are assisting invasive plants (Olesen et al., 2002), a situation that is explained by the super-generalization of native pollinators in the Azores and by low interspecific competition. However, as shown in Fig. 5, the sites were grouped following a gradient of richness and abundance of introduced species: with a group of pristine sites poor in exotic arthropods located far away from roads and human activities and found within caldeiras and ravines (Group A; Fig. 5); another group of sites located at the margins of native forest with some exotic species but with a low number of introduced species (Group B1; Fig. 5; Appendix 1); and finally a group of sites in small fragments near man-made habitats and with a high number of introduced arthropods (Group B2; Fig. 5; Appendix 1). In fact, there is evidence of a somewhat inverse spatial distribution between a group of oceanic-type, forest-dwelling, endemic relict arthropods and a group of more generalist endemic arthropods (Figs 1 & 4; Appendix 1), some of them grassland species common in semi-natural pastures from the Azores. These patterns are in agreement with results obtained in other island systems, in which the net increase in species richness through the addition of exotic
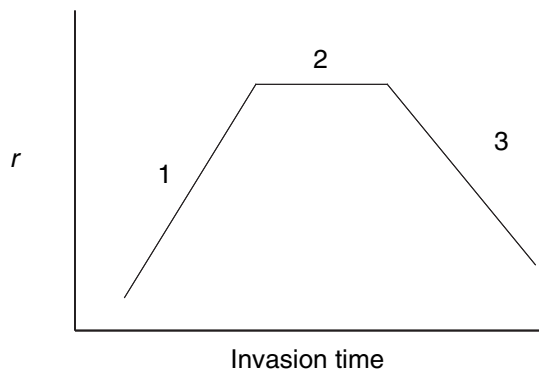
Figure 7 Model showing a hump-shaped relationship between correlation coefficients (r) relating exotic and native (and or endemic) species richness and invasion time.

species has usually resulted in the extinction or range reduction of rare endemic species (Gillespie & Roderick, 2002; Hulme, 2003). Therefore, the impact of non-indigenous arthropod species in the studied oceanic island is likely to be severe because of their range expansion. However, it remains to be seen if these non-indigenous species are able to occupy dense high-altitude *Laurisilva* forest, now the last refuge of some restricted endemic taxa.

A general model of native vs. exotic species richness dynamics

Our data suggest a facilitation process in which the diversity of endemic species is favoured by the diversity of introduced species, probably because many of these (endemic) species are predators. In this process the diversity of introduced species is favoured by the richness and abundance of generalist endemic species. If this mutual influence is asymmetric, as our results suggest, the most diverse assemblages of autochthonous fauna could help the colonization of biological invaders. This begs the question how this pattern could have arisen on shorter ecological time-scales.

Despite the available empirical and theoretical data on invasion processes, there is no study testing the relationship between non-indigenous (i.e. exotic) and endemic species richness in ecological time in true islands while taking into account a spatial variability of both colonization type groups and environmental variables.

Based on what is known in the literature relating to native versus exotic patterns of species richness (see Rosenzweig, 2001; see also Olden & Poff, 2003), and comparing local with regional species richness (see a recent revision by Srivastava, 1999), the data reported here suggest that there is a hump-shaped relationship between correlation coefficients linking exotic and native species richness and invasion time (Fig. 7). The model could be explained in the following way.

1. In an isolated and recent volcanic oceanic island, such as that studied here, the endemic fauna is poor and disharmonic (Borges & Brown, 1999; Ribeiro *et al.*, 2005). The local native

communities are not saturated, and consequently, there are plenty of opportunities for exotic species, available in the regional pool, to invade and colonize disturbed and marginal fragments of native vegetation. In this way, local or alpha species richness may increase through regional enrichment at fine-local scales (see Cornell & Lawton, 1992; Srivastava, 1999; Borges & Brown, 2004). In this ecological phase, the correlation coefficients relating exotic with native species richness should be positive, simulating an invasive meltdown (*sensu* Simberloff & Von Holle, 1999), but with the presence of non-indigenous species helping the dispersal of wide-ranged, generalist, endemic predatory species between fragments. This happens because the productivity of the overall system increases with more species and this also simulates the first part of the hump-shaped curve of the productivity–diversity relationship (see Waide *et al.*, 1999; Mouquet *et al.*, 2002). This is the first part (1) of the curve in Fig. 7.

2. However, with time the communities could eventually be saturated and there would be no relationship between exotic and native species richness – the levelling (part 2) of the curve in Fig. 7. Here we may argue that local saturation will be difficult to attain due to the poverty of the Azorean regional fauna, but as shown by Borges & Brown (2004) some functional groups like spiders are saturated at a local scale due to habitat structure limitations.

3. As a consequence of community saturation, biotic interactions between species should be more important and limit the number of species that can coexist in a local community (Cornell & Lawton, 1992; see also Borges & Brown, 2004). If non-indigenous species are more adaptable to the new habitats, then the extinction of endemic taxa should occur locally with a strong impact on the regional endemic species pool. In this final phase, the correlation coefficients between exotic and native species richness should be negative, native species-poor communities being less resistant to exotic invasion (part 3 of the curve in Fig. 7).

Many studies have reported negative correlations between native and introduced species, from which it is interpreted that species-rich communities are more resistant to invasion. At the same time other studies reported positive relationships, which would indicate a facilitation process or suggest that the same abiotic factors, and consequently sites ideal for native fauna are also ideal for exotic fauna. These patterns are probably scale-dependent (Olden & Poff, 2003), which makes it even more difficult to test these hypotheses. A negative relationship between native and exotic species richness usually appears when smaller study unit areas are analysed, while a positive relationship seems to occur at larger scales. However, neutral models show that it is not necessary to assume biotic interactions between exotic and native species to obtain relationships like these (Fridley *et al.*, 2004), and that a strong and negative relationship is inevitable if the number of individuals in the community is fixed and sufficiently small (Herben *et al.*, 2004). Hence, if we want to understand how the biological assemblages are structured after the arrival of foreign organisms, we need to develop new and more efficient

approaches to examine the relationship between introduced and native or endemic species, in order to be able to distinguish the unavoidable mathematical and scale effects of the consequences resulting from genuine biotic interactions.

Conservation aspects

The area selected for this study represents one of the most important *Laurisilva* vegetation systems of the Azores, most of which is under NATURA 2000 management. Natural areas are established to preserve indigenous (endemic *plus* native) species. Thus, the evidence of the occurrence of highly diverse local communities of endemic and introduced arthropod species, with endemics apparently being well adapted within such communities, does not mean that we should be less worried about invasive species and the conservation of endemic taxa in the Azores. Invasions by alien arthropod species are an actual and future environmental threat (Vitousek *et al.*, 1996; Williamson, 1996). It may happen that this 'endemic-introduced' community of highly generalist species could increase its distribution towards the centre of large fragments of *Laurisilva* using corridors made by edge effects and land-use activities at the margins of pristine native vegetation areas where novel interactions can occur. If environmental factors (e.g. climate) are not a limitation for that dispersal movement, then what we are observing is the process already in movement, as Figs 1a and 4 forecast.

Predicting changes in these communities is difficult with current data, but the replacement of restricted, specialized arthropod forest-dwelling endemics by endemic generalist grassland arthropods could cause a homogenization of endemic fauna in the future. This 'species replacement' pattern has been observed for several taxa (see Cowie, 2001; Gaston *et al.*, 2003; Summerville & Crist, 2003) and suggests a decrease of regional diversity in spite of the ongoing maintenance of local species diversity. This will lead to a spatially similar, endemic arthropod faunal composition in the island. In fact, this pattern of biotic homogenization is of great contemporary concern (Vitousek *et al.*, 1996; Williamson, 1996; Gaston *et al.*, 2003; Olden & Poff, 2003). The species replacement may occur as a consequence of low habitat quality due to edge effects and replacement of plant vegetation cover by a set of grassland type species. In some marginal places the native forest cover was once replaced by grassland and later abandoned, the forest taking over again as secondary forest. Although our level of understanding of the processes causing the spatial autocorrelation in species richness in the studied area is as yet insufficient, the evidence presented here suggests that pristine communities are still protected from non-indigenous taxa only because of their isolation in inaccessible places and physiological adaptations to a moist environment with low temperatures and precipitation in summer months. The ecological demands of the strictly forest-dwelling species are probably not easily achievable for extant non-indigenous species currently found in Terceira, but this only makes careful management of those sites a major priority. Because endemic restricted species are absent even in relatively undisturbed

secondary forests the protection of mature core forests should remain a high conservation priority in the Azores (see also Borges *et al.*, 2000; Borges *et al.*, 2005b). The fragmentation of these native habitats may help the invasion by introduced species in a positive feedback way (With, 2002). In fact, the areas with more diverse and abundant assemblages of native arthropods are those that are likely to experience the greater impact by the more diverse communities of introduced species, possibly because these places can harbour a bigger variety and quantity of resources. Thus, if there is a group of anthropogenic-related variables clearly associated with the increase in diversity of introduced species assemblages, it is obviously necessary to encourage those management techniques which will reduce or at least not encourage these factors, taking special care in places with a great diversity of endemic species.

CONCLUSIONS

This study shows clearly that two different sets of environmental variables explain the spatial distribution of endemic and introduced arthropod species richness within the native forest of an oceanic island (in this case, Terceira). Abiotic (climatic and geomorphological) variables explained most of the variation in endemic species richness, whereas anthropogenic variables explained most of the variation in introduced species richness. Moreover, there is evidence of a somewhat inverse spatial distribution between a group of endemic, forest-dwelling relict arthropods and a group of more generalist endemic arthropods that are able to survive in disturbed marginal sites particularly rich in non-indigenous species. All these results lead to the idea that non-stochastic processes are involved in structuring arthropod communities in the studied native habitats of Terceira Island. The mechanisms of species assemblage are not yet known in these systems, but competition could be important in structuring spider communities (Borges & Brown, 2004).

The data also show that the richest endemic assemblages are prone to invasion as a consequence of facilitation processes, but probably the group of endemics involved are of low conservation value due to their wide distribution. This means that taking into account only raw values of endemic species richness could be misleading, as the contribution of rare endemics could be underestimated.

A drawback of the approach taken here is that the spatial patterns of endemic species composition should be addressed when counting species at any scale of biodiversity study.

Inconclusive evidence suggests that non-indigenous species are limited to those sites under anthropogenic influence located mainly in marginal places, but the rate of expansion of those species to high-altitude, core pristine sites remains to be tested. At present the effect of fragmentation on the survival of rare arthropod endemics in Terceira Island is unknown. If the fragmentation continues, we do not know the threshold at which environmental factors alone could limit the expansion of generalist arthropod species.

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Appendix 1 Biological differences between faunistic groups of localities (A vs. B) analyzed by the non-parametric Mann Whitney U test for (a) endemic and (b) introduced arthropod species with information on the habitats of each species (F = forest specialist; G = grassland specialist) and their ecology (P = predator; H = herbivore; S = saprophagous; F = fungivorous).

					Relative abundance			
Hab.	Species	Ecol.	Order	Family	A	B	Z	P-level
a) Endemic species								
F	*Lepthyphantes acoreensis* Wunderlich	P	Araneae	Linyphiidae	**5.00**	2.63	0.45	0.650
F	*Porrhomma borgesi* Wunderlich	P	Araneae	Linyphiidae	**0.50**	0.13	1.82	0.069
F	Agyneta n. sp.	P	Araneae	Linyphiidae	**0.38**			
G	*Walckenaeria grandis* (Wunderlich)	P	Araneae	Linyphiidae	0.17	**0.25**		
F	Gen. sp. (n. sp.)	P	Araneae	Linyphiidae	**0.17**	0.13		
G	*Minicia floresensis* Wunderlich	P	Araneae	Linyphiidae		**0.19**		
G	*Acorigone acoreensis* (Wunderlich)	P	Araneae	Linyphiidae		**0.13**		
G	*Pardosa acoreensis* Simon	P	Araneae	Lycosidae	0.54	**19.19**	3.36	**0.001**
G	*Pisaura acoreensis* Wunderlich	P	Araneae	Pisauridae	0.13	**0.38**	0.59	0.554
G	*Neon acoreensis* Wunderlich	P	Araneae	Salticidae		**0.06**		
F	*Sancus acoreensis* (Wunderlich)	P	Araneae	Tetragnathidae	**0.33**			
F	*Rugathodes acoreensis* Wunderlich	P	Araneae	Theridiidae	**3.25**	0.81	2.49	**0.013**
F	*Trechus terrabravensis* Borges, Serrano & Amorim	P	Coleoptera	Carabidae	**10.25**			
F	*Cedrorum azoricus azoricus* Borges & Serrano	P	Coleoptera	Carabidae	**2.33**	0.19	1.07	0.285
F	*Atlantocis gillerforsi* Israelson	F	Coleoptera	Cisidae	**0.04**			
F	*Laparocerus azoricus* (Drouet)	H	Coleoptera	Curculionidae	**2.67**			
F	*Pseudechinosoma nodosum* Hustache	H	Coleoptera	Curculionidae	**0.13**	0.06		
F	*Alestrus dolosus* (Crotch)	H	Coleoptera	Elateridae	0.50	**2.50**	0.42	0.675
F	*Athous azoricus* Platia & Gudenzi	H	Coleoptera	Elateridae		**0.06**		
F	Gen. sp. 2	S	Coleoptera	Lathridiidae	**0.04**			
F	*Phloeonomus azoricus* Fauvel	P	Coleoptera	Staphylinidae		**0.06**		
F	*Atheta* sp.	P	Coleoptera	Staphylinidae	**0.04**			
F	*Pinalitus oromii* Ribes	H	Heteroptera	Miridae	0.04	**0.13**	0.53	0.593
F	*Aphrodes hamiltoni* Quartau & Borges	H	Homoptera	Cicadellidae	**5.25**	1.94	1.11	0.268
F	*Cixius azoterceirae* Remane & Asche	H	Homoptera	Cixiidae	1.04	**1.38**	0.08	0.937
F	*Cyclophora azorensis* (Prout)	H	Lepidoptera	Geometridae	**0.25**	0.19	0.73	0.463
F	*Cleora fortunata azorica* Pinker	H	Lepidoptera	Geometridae	0.04	**0.25**	1.83	0.068
F	Gen. sp. 1	H	Lepidoptera	Geometridae	0.04	0.06		
F	*Xanthorhoe inaequata* (Warren)	H	Lepidoptera	Geometridae	0.04	**0.06**		
F	*Eudonia melanographa* (Hampson)	H	Lepidoptera	Pyralidae	**0.42**			
F	*Scoparia coecimaculalis* Warren	H	Lepidoptera	Pyralidae	0.04	**0.19**		
F	*Scoparia semiamplalis* Warren	H	Lepidoptera	Pyralidae	**0.04**			
F	Gen. sp. 3	H	Lepidoptera	Pyralidae	**0.04**			
F	*Argyresthia atlanticella* Rebel	H	Lepidoptera	Yponomeutidae	**9.58**	2.81	2.71	**0.007**
F	*Trigoniophthalmus borgesi* Mendes *et al.*	S	Microcoryphia	Machilidae	**0.42**	0.19	1.10	0.272
F	*Hemerobius azoricus* Tjeder	P	Neuroptera	Hemerobiidae	0.04	**0.06**		
F	*Limnephilus atlanticus* Nybom	P	Trichoptera	Limnephilidae	**0.04**			

					Relative abundance				
					A	B1	B2	Z (A vs. B)	P-level
b) Introduced species									
G	*Lycosoides coarctata* (Dufour)	P	Araneae	Agelenidae			**0.10**		
F	*Clubiona terrestris* Westring	P	Araneae	Clubionidae			**0.20**		
G	*Clubiona decora* (Blackwall)	P	Araneae	Clubionidae			**0.10**		
G/F	*Dysdera crocata* C. L. Koch	P	Araneae	Dysderidae	1.36	1.13	**6.60**	2.20	**0.02771**
G	*Drassodes lapidosus* (Walckenaer)	P	Araneae	Gnaphosidae			**0.10**		
G	*Tenuiphantes tenuis* (Blackwall)	P	Araneae	Linyphiidae	0.50	1.00	**13.20**	0.53	0.59298
G	*Erigone atra* (Blackwall)	P	Araneae	Linyphiidae	0.05	**0.13**			
G	*Oedothorax fuscus* (Blackwall)	P	Araneae	Linyphiidae	**0.09**				
G	*Eperigone bryantae* Ivie & Barrows	P	Araneae	Linyphiidae	0.05		**0.10**		
G	*Eperigone* sp.	P	Araneae	Linyphiidae		**0.13**			

Appendix 1 *continued*

Hab.	Species	Ecol.	Order	Family	Relative abundance A	B1	B2	Z (A vs. B)	P-level
G/F	*Ero furcata* (Villers)	P	Araneae	Mimetidae	0.50	0.63	**1.10**		
F	*Metellina merianae* (Scopoli)	P	Araneae	Tetragnathidae	**0.05**				
G	*Achaearanea acoreensis* (Berland)	P	Araneae	Theriididae			0.10		
G	Gen. sp. 8	S	Coleoptera	Anthicidae	**0.05**				
G/F	*Paranchus albipes* (Fabricius)	P	Coleoptera	Carabidae	**18.50**				
F	*Pterostichus* (*Argutor*) *vernalis* (Panzer)	P	Coleoptera	Carabidae	**0.09**				
G	*Anisodactylus binotatus* (Fabricius)	P	Coleoptera	Carabidae			0.10		
G/F	*Amara aenea* (De Geer)	P	Coleoptera	Carabidae	**0.05**				
G	*Cryptophagus* sp.	S	Coleoptera	Cryptophagidae	**0.05**				
F	*Xyleborus saxesenii* Ratzeburg	H	Coleoptera	Curculionidae			0.30		
G	Gen. sp. 7	H	Coleoptera	Curculionidae			0.20		
G	*Sphenophorus abbreviatus* (Fabricius)	H	Coleoptera	Dryophthoridae	**0.05**				
G	*Cercyon haemorhoidalis* (Fabricius)	S	Coleoptera	Hydrophilidae	**0.14**		0.00		
F/G	*Stelidota geminata* (Say)	S	Coleoptera	Nitidulidae	0.36		**0.90**		
G/F	*Epuraea biguttata* (Thunberg)	H	Coleoptera	Nitidulidae			**1.20**		
G	*Carpophilus* sp.	S	Coleoptera	Nitidulidae	**0.05**				
G	*Onthophagus taurus* (Schreber)	S	Coleoptera	Scarabaeidae		0.13			
F	*Coccotrypes carpophagus* (Hornung)	H	Coleoptera	Scolytidae	0.09		**2.20**		
G	*Anotylus nitidifrons* (Wollaston)	P	Coleoptera	Staphylinidae			2.30		
G	*Amisha analis* (Gravenhorst)	P	Coleoptera	Staphylinidae	0.05		**0.10**		
G	*Cordalia obscura* (Gravenhorst)	P	Coleoptera	Staphylinidae			0.10		
G	*Atheta atramentaria* (Gyllenhal)	P	Coleoptera	Staphylinidae	**0.05**				
G	*Aleochara bipustulata* (Linnaeus)	P	Coleoptera	Staphylinidae			0.10		
G	*Xantholinus longiventris* Heer	P	Coleoptera	Staphylinidae	**0.05**				
G/F	Gen. sp. 6	P	Dermaptera	?			0.20		
F	*Blanuilus guttullatus* (Fabricius)	S	Diplopoda	Blaniulidae			10.00		
F	*Choneiulus palmatus* (Nemec) (??)	S	Diplopoda	Blaniulidae	**0.09**				
G/F	*Ommatoiulus moreleti* (Lucas)	H	Diplopoda	Julidae	7.45	11.50	**58.40**	3.15	**0.00161**
F	*Brachysteles parvicornis* (Costa)	P	Heteroptera	Anthocoridae	**0.05**				
G	*Pseudacaudella rubida* (Borner)	H	Homoptera	Aphididae	**0.09**				
G	*Rhopalosiphum insertum* (Walker)	H	Homoptera	Aphididae	0.05		**0.10**		
G	*Neomyzus circumflexus* (Buckton)	H	Homoptera	Aphididae	**0.05**				
G	*Anoscopus albifrons* (Linnaeus)	H	Homoptera	Cicadellidae	0.36	0.13	**4.90**		
F	Gen. sp. 9	H	Lepidoptera	Noctuidae	**0.05**				
F	Gen. sp. 4	H	Lepidoptera	Tortricidae	**18.27**	1.88	0.40	2.67	**0.00769**
F	Gen. sp. 5	H	Lepidoptera	Tortricidae	**0.77**				
F	*Rhopobota naevana* Huebner	H	Lepidoptera	Tortricidae	**0.05**				
G	*Nesothrips propinquis* (Bagnall)	H	Thysanoptera	Phlaeothripidae	**0.05**				
G	*Hercinothrips bicinctus* (Bagnall)	H	Thysanoptera	Thripidae			**0.30**		