

TERRESTRIAL  
ARTHROPODS  
OF MACARONESIA

BIODIVERSITY, ECOLOGY AND EVOLUTION

**Title**

Terrestrial Arthropods of Macaronesia - Biodiversity, Ecology and Evolution

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# Preface

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Long before the Canaries or Madeira became a tourist Mecca, these islands were an object of desire for early European naturalists. The writings of Alexander von Humboldt, extolling the outstanding natural history of the so-called Atlantic Islands, inspired the imagination of eminent researchers, who visited the volcanic archipelagos to explore and describe their peculiar productions, plants and animals unknown to Science at that time. Darwin himself was deeply disappointed when the Beagle anchored facing the harbor of Santa Cruz de Tenerife and was not allowed to disembark due to a local quarantine.

It is known that oceanic islands are special territories for evolution. The biota that arrives to such isolated places is a sample from that of the source areas; not all species have the same dispersal capacity and manage to find their way through. Once they settle, they tend to differentiate from their parents; they evolve. This process of speciation is often explosive on islands, and evolutive radiation has attracted much scientific attention since Darwin got the clues of evolution theory by studying the Galapagos finches. What a pity he did not land in the Canaries!

Many scientists look at islands as laboratories of evolution, as special places where ecosystems are simpler than on continents, where interactions are intense and easier to identify, where the hidden laws of nature should be easier to uncover. Island biology becomes a topic by itself, but almost all advances in this fascinating realm have been carried out by non-islanders.

In the late 80s, the new concept of biodiversity arrives on the scene. Diversity of life forms is seen from a new perspective, more anthropocentric, as a heritage of societies that is needed to support man's welfare, to be preserved, to be better known and understood. If fauna and flora was only a concern for brainy scientists, now biodiversity is a concern for the whole society. Conservation of biodiversity has become a major challenge of today's civilization. With decreasing biodiversity in our planet, our future as a viable species looks grey and greyer.

Just as with many other oceanic islands, the Azores, Madeira s.l., Selvagens, Canaries and Cape Verde, assembled under the geographic term of Macaronesia, support a dense human population. They have a singular biodiversity pregnant with endemisms, and they are ecologically extremely fragile; a combination that poses an additional conservation challenge.

And to support the conceptual framework of conservation, to focus properly our conservation efforts, we need science to register biodiversity in all its extent, and to explain how it works.

If in the past, the advances in knowledge of island biodiversity and ecology relied almost entirely on non-islanders, this situation has now changed. The book in your hands is a good proof of it: a book on islands, written mainly by islanders.

It originated in relation with a research project “*High endemism areas in the archipelago of Madeira –establishing priorities for the conservation of the endemic insect fauna*”, and is supported by the Portuguese Entomological Society and by the Portuguese Foundation for Science and Technology. The scope was promptly opened to include all Macaronesia and other types of habitats. Needless to say, arthropods do not count for all biodiversity but they are the champions of it. Publications on Macaronesian arthropods exist by the thousands and they are widely spread. Consequently, it is not easy to keep updated or to gather a comprehensive overview. One of the purposes of this meritorious compilation is to overcome these drawbacks.

Herein, we will learn about the status of species inventories of all archipelagoes; about the distribution patterns and how land-uses affect arthropods (particularly the endemic ones); about the impact of arthropod exotic species, a conservation “hot potato” on islands that is often relegated in favor of mammals or birds; and about special topics on island ecology with good examples: the role of parthenogenesis, explosive speciation, pollination and other insect-plant interactions.

The pathways of science are never-ending, and there is surprisingly still much to be discovered in Macaronesia, despite being so close to continental Europe. There are also many ecological aspects that deserve to be studied within island environments, for the sake of general theory or for on-the-ground conservation problems. The baton has been passed and we can expect to see more contributions that will be promoted by island scientific institutions, and hopefully supported by island authorities.

Science is universal, but the conservation challenge is ours. The arthropods are indeed the largest -but often overlooked- part of biodiversity. And we should not forget that conservation can only use the best knowledge available.

*Antonio Machado*

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## Patterns of Alpha and Beta Diversity of Epigeal Arthropods at Contrasting Land-Uses of an Oceanic Island (Terceira, Azores)

*Pedro Cardoso, Clara Gaspar, Francisco Dinis & Paulo A. V. Borges*

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### Introduction

Most oceanic archipelagoes ecosystems suffered dramatic changes since human occupation. The level of ecosystem modification varies from low (e.g. Galápagos) to high (e.g. Azores, Madeira, Canary Islands, Hawaii, St. Helena, La Reunión). Thus, islands can be considered as model systems to evaluate the impact of human activities on species diversity (Vitousek, 2002). Contrary to the pristine native ecosystems still prevalent in the Galápagos (Peck, 2005), the Azorean archipelago has suffered drastic land-use changes since the first inhabitants arrived almost 600 years ago (Martins, 1993). These islands, which were mostly forested before human settlement, are now largely occupied by highly modified habitats like intensively managed pastures for cattle industry and large, homogeneous areas forested with exotic species. Currently, the Azorean landscape is completely modified and the original forests are restricted to a few high-altitude fragments (see Martins, 1993; Borges *et al.*, 2000, 2005a, 2006). Even these fragments, varying in size from 4 to 1000 ha, are often disturbed by the invasion of introduced species (Silva & Smith, 2004). It is however among different habitat types that major differences are expected. Intensively managed pastures, for example, are mostly comprised of introduced herbaceous species and exotic forests are dominated by homogeneous plantations of *Cryptomeria japonica* or more diverse *Eucalyptus* woods. As a result of the spread of some invasive species, most woodland is also dominated by *Pittosporum undulatum* and *Acacia melanoxylon*.

Land-use change has influenced all taxonomic groups. However, arthropods are by far the most rich of all taxa in the archipelago and also have the majority of endemic species (Borges *et al.*, 2005b). They are also one of the most significant groups of the recently proposed Top

100 management priority species in Macaronesia (Martín *et al.*, 2008, 2010) and the Azores (Cardoso *et al.*, 2008). Moreover, their distribution is often very restricted, with many species responding in a very fine spatial and temporal scale to habitat change (e.g. Borges *et al.*, 2006; Cardoso *et al.*, 2007, 2010). Being so rich, abundant and yet threatened and sensitive to disturbance, makes arthropods an ideal candidate for studies in human induced land-use change (see e.g. Brown, 1997; Kimberling *et al.*, 2001; Stefanescu *et al.*, 2005; Neville *et al.*, 2008).

To study the effect of land-use change in biological communities it is necessary to understand how are the different components of diversity distributed in space. Diversity has long been separated into different components according to the phenomena that interest ecologists (Whittaker, 1960, 1972): i) local species richness, i.e., alpha (community) diversity that measures the species richness of a local assemblage; ii) beta diversity, the degree of difference between communities (Whittaker *et al.*, 2001), that measures turnover of species between communities and; iii) gamma (regional) diversity, which can be considered an equivalent to alpha diversity on a larger scale, but reflects the allopatric distribution of related taxa.

Alpha diversity, of which species richness is just the most visible measure, is perhaps the most studied aspect of diversity. However, probably more important than knowing how many species live in a site at a given time, it is to know what species are these. In islands, where the introduction of non-indigenous species is one of the major threats to indigenous species (Borges *et al.*, 2006; Martín *et al.*, 2008), especially endemics, this question is even more significant. Even if man-made habitats are species rich, they may be empty of species considered as conservation priority and abundant in exotic species (Cardoso *et al.* 2009a).

The concept of nestedness was coined by Patterson & Atmar (1986; see also Patterson, 1987). Complete nestedness occurs when any site has all the species that are present in all the less rich sites of the same region. Also, every species of that site will be present at all the sites in the region that are richer than itself. Nestedness patterns are usually due to impoverishment caused by selective extinction, for example during fragmentation of large habitats or, in a contrasting process, due to enrichment driven by selective colonization (e.g. Greve *et al.*, 2005). The nestedness concept was also applied in ecological networks, with the reasoning that networks can be nested if generalist species all interact with each other and specialized species only interact with generalist species (Bascompte *et al.*, 2003).

One of the most studied aspects of diversity is the decrease in similarity of communities with an increase in the distance separating them. This phenomenon has been termed distance

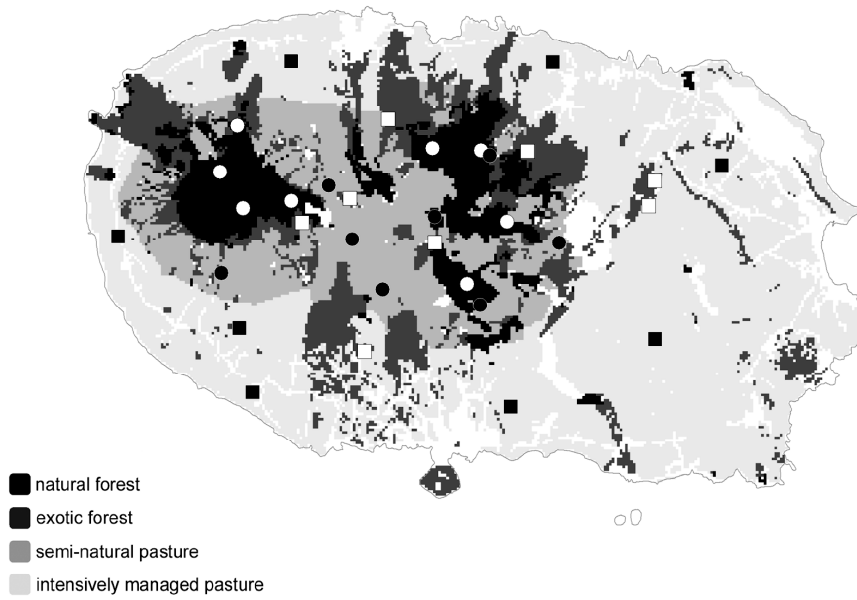
decay of similarity. It was first put into a framework by Nekola & White (1999) with North American floras. They have noticed that there was a significant decrease of similarity values as distance between pairs of sites increased. Either related with a similar decrease in environmental similarity, dispersal limitation of species or spatial autocorrelation, this pattern was later found for a number of taxonomic groups, e.g. plants (Condit *et al.*, 2002; Kluth & Bruelheide, 2004; Qian *et al.*, 2005; Davidar *et al.*, 2007; Qian, 2008), stream invertebrates (Lloyd *et al.*, 2005; Thompson & Townsend, 2006), fish parasites (Poulin, 2003; Oliva & González, 2005) and microbes (Green *et al.*, 2004). It is often hard to separate geographic distance and climatic distance influence on the distance decay of similarity, as both factors are usually correlated (but see Qian *et al.*, 2005; Qian, 2008). It is mainly historical factors that determine decay in similarity with distance, even when there is no climate difference. Species evolve and spread in time, and when geographical distance is determining decay in similarity it is a consequence of the history of regions (Qian *et al.*, 2005).

This work is an overview of diversity patterns in different land-use types in Terceira Island, Azores and had the objectives of: 1) knowing which species, endemic, native or introduced, occur at each habitat type and in what abundance; 2) compare the different habitat types in their species composition; 3) test for nestedness patterns of endemic, native and introduced species; and 4) study the distance decay of similarity between the different habitat types. We hypothesize a predictable and nested loss of endemic and native species from more natural to more humanized habitats due to selective extinction. On the contrary, we expect a loss of introduced species in the opposite direction of habitat naturalness due to selective colonization. We also hypothesize that in oceanic islands, habitats with more introduced species, probably with higher dispersal capacity, would not show a distance decay pattern. On the contrary, we expect that habitats with more native species, especially endemics, with narrower ecological limits, will show significant distance decay of similarity.

### Study sites

For the current investigation, we used a gradient of human induced land-use change in Terceira (Fig. 1). We discriminated the following four habitat types, which comprise around 87% of the total island area: natural forest dominated by evergreen trees and shrubs (includes *Laurus-Ilex*, *Juniperus* and *Erica* type forests), exotic forest (*Eucalyptus* spp. and *Cryptomeria japonica*), semi-natural pasture (located above 400 m and with the grazing

concentrated in the Summer months) and intensively managed pasture (grazed usually all year in three-week intervals). We sampled eight sites of each habitat type (Fig. 1).



**Figure 1.** Distribution of the four studied habitat types in Terceira Island. Open circles – natural forests; open squares – exotic forests; filled circles – semi-natural pastures; filled squares – intensively managed pastures.

The sites were scattered in the landscape, covering all the fragments or regions that each habitat occupied. Due to the concentration of native forests in central high altitude areas, and of intensively managed pastures in peripheral low-altitude areas, the habitats tended to be present in well delimited regions in the island, with clear geographical separation.

### Sampling procedures

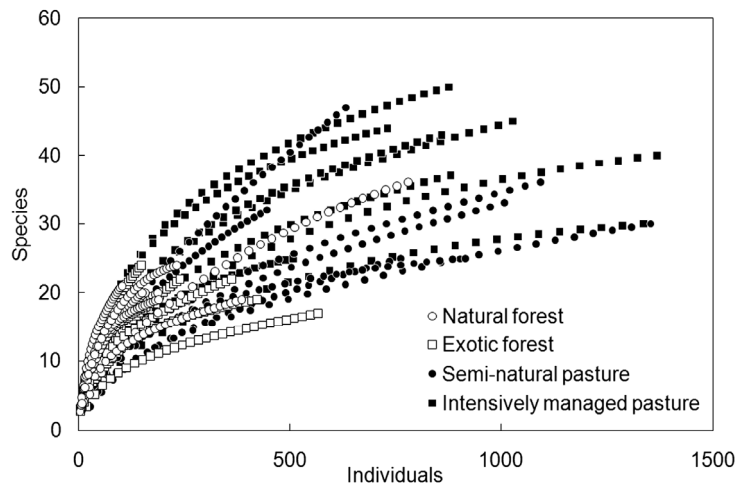
At each site, a 150 m long transect was used to capture epigaeic fauna. Thirty pitfall traps, plastic cups with a top diameter of 42 mm and 78 mm deep, were dug into the ground so that the rim of the cup was flush with the soil surface. Half of the traps were filled with approximately 60 ml of anti-freeze liquid with a small proportion of ethylene glycol, and the other half with the same volume of a general attractive solution (Turquin), made of dark beer

and some preservatives. Traps were spaced 5 m from one another, starting with a Turquin trap and alternating with the ethylene traps and were left in the field for 2 weeks, once per site, usually during the months of June, July or September of different years (Borges *et al.*, 2005a).

The majority of arthropods (excluding Crustacea, Acari, Collembola, Hymenoptera and Diptera) were identified to species level or, when not possible, morphospecies. All species were classified as: **endemic** - those that occur only in the Azores as a result of either speciation events (neo-endemics) or extinction of the mainland populations (palaeo-endemics); **native** - species whose occurrence on Azores cannot be associated with human activities (intentional or accidental human introduction) and that are also known from other regions; or **introduced** - those believed to have arrived to Azores as a result of human activities and generally have a wide, often cosmopolitan, distribution.

### Statistical analysis

The species accumulation curves for the different habitats (Fig. 2) revealed that pastures were apparently much better sampled than forest habitats with the same sampling effort. We have therefore compared different habitats with the percentages of endemic, native and introduced species and individuals instead of their absolute values.



**Figure 2.** Randomized accumulation curves for the 32 sampled sites.

A Multidimensional scaling (MDS) analysis using the Bray-Curtis measure was made for a previous examination of differences between sites and habitat types. We used the Community Analysis Package (Seaby & Henderson, 2007) for calculations. With the same software, we made an Analysis of Similarity (ANOSIM) with  $\log(x+1)$  transformed data and 1000 randomizations to identify if differences between habitat compositions were statistically significant. Similarity Percentages (SIMPER) statistics were used to find which species were more strongly causing the differences found between habitats.

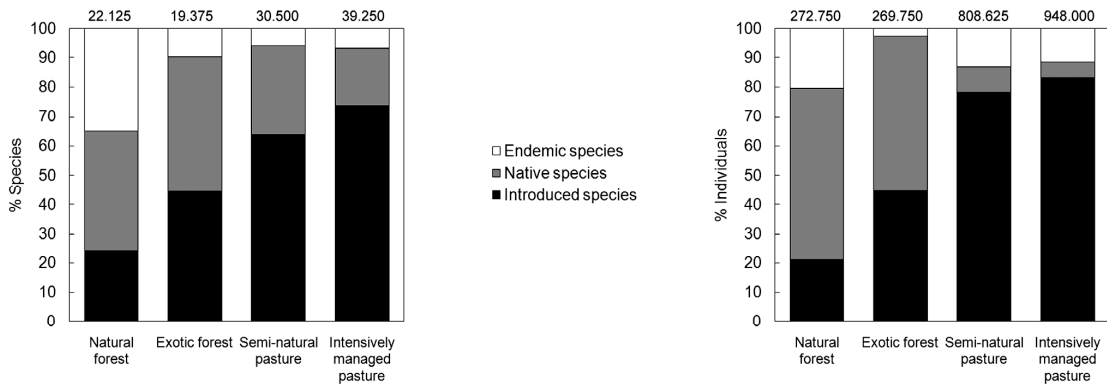
Atmar & Patterson (1993) have created the matrix temperature,  $T$ , as a measure of nestedness in a parallel with the entropy concept in thermodynamics theory (but see Almeida-Neto *et al.*, 2007). Although  $T$  is still much used, we have opted to calculate the NODF measure (Almeida-Neto *et al.*, 2008) implemented in the software ANINHADO (Guimarães & Guimarães, 2006), due its theoretical properties and statistical behavior, being more conservative in finding nestedness patterns than  $T$  (Almeida-Neto *et al.*, 2008). The NODF values of observed matrices of endemic, native and introduced species were calculated and compared with the NODF values of 1000 random matrices so that significance could be attributed. The most appropriate null models with which to compare the observed datasets have been much debated (e.g. Moore & Swihart, 2007). We have compared our datasets with matrices where presences were randomly assigned to any cell within the matrix.

For distance decay we used the Sørensen index of similarity for presence-absence data, the Sørensen estimator for abundance data developed by Chao *et al.* (2005) and implemented in EstimateS software (Colwell, 2006) and the Bray-Curtis index of similarity. The Sørensen index was chosen because it is widely used in distance decay statistics (e.g. Morlon *et al.*, 2008). The Sørensen estimator was also used as it presents two advantages over the first: uses quantitative data and estimates the final value of the index for undersampled communities (see Cardoso *et al.* 2009b). The Bray-Curtis index was chosen because it was also used in MDS, ANOSIM and SIMPER analyses. Distance decay curves were calculated with both raw and log-transformed values for similarity and distance between sites (four possible combinations) but only the best fits with a least squares regression were considered. With eight sites sampled, 28 paired comparisons were made per habitat. As these pairwise values were not independent, significance of the adjusted curves was subjected to Mantel tests, randomizing 1000 times the similarity values. The number of random curves with higher  $r^2$  than the observed curve was used to calculate the latter's significance value.

### Patterns of alpha and beta diversity

A total 18,393 arthropod specimens were identified to species, or in some cases, to morphospecies level. Of the 202 epigeic arthropod taxa identified, 29 were considered to be Azorean endemics, 65 native to the islands (excluding endemics) and 108 introduced.

We found a clear gradient of all species groups from natural forests to intensively managed pastures (Fig. 3). The percentage of endemic species was higher in natural forests, followed by exotic forests and finally the two pasture habitat types (Fig. 3). The percentage of native species followed a similar trend. The percentage of introduced species, as expected, followed the precise opposite pattern, with higher values in intensively managed pastures (Fig. 3). All abundance values had a similar pattern to species richness for all groups, except for a very low abundance of endemics in exotic forests (Fig. 3).

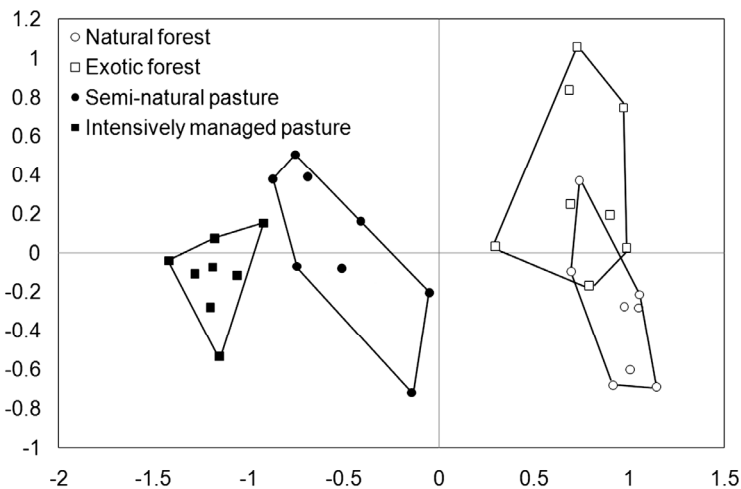


**Figure 3.** Average proportions of endemic, native and introduced species and individuals for the eight sites sampled per habitat type. The average number of species or individuals per site is indicated above each column.

The MDS revealed that the different habitats had very characteristic communities, with all sites in segregated clusters (Fig. 4). Only natural and exotic forests had some sites mixed together, but as an exception. The ANOSIM confirmed that habitats were statistically different in species composition ( $R = 0.801$ ;  $p = 0.001$ ). All pairwise comparisons between habitats were significant ( $R > 0.634$ ;  $p = 0.001$  in all cases) even between natural and exotic forests ( $R = 0.345$ ;  $p = 0.002$ ). The SIMPER analysis revealed that forests are better differentiated from pastures by the high abundance of three native and one introduced species, while pastures present two introduced spiders in much higher abundances than forests (Table I).

**Table I.** SIMPER results of species contributing more than 10% to the observed similarity within habitats.

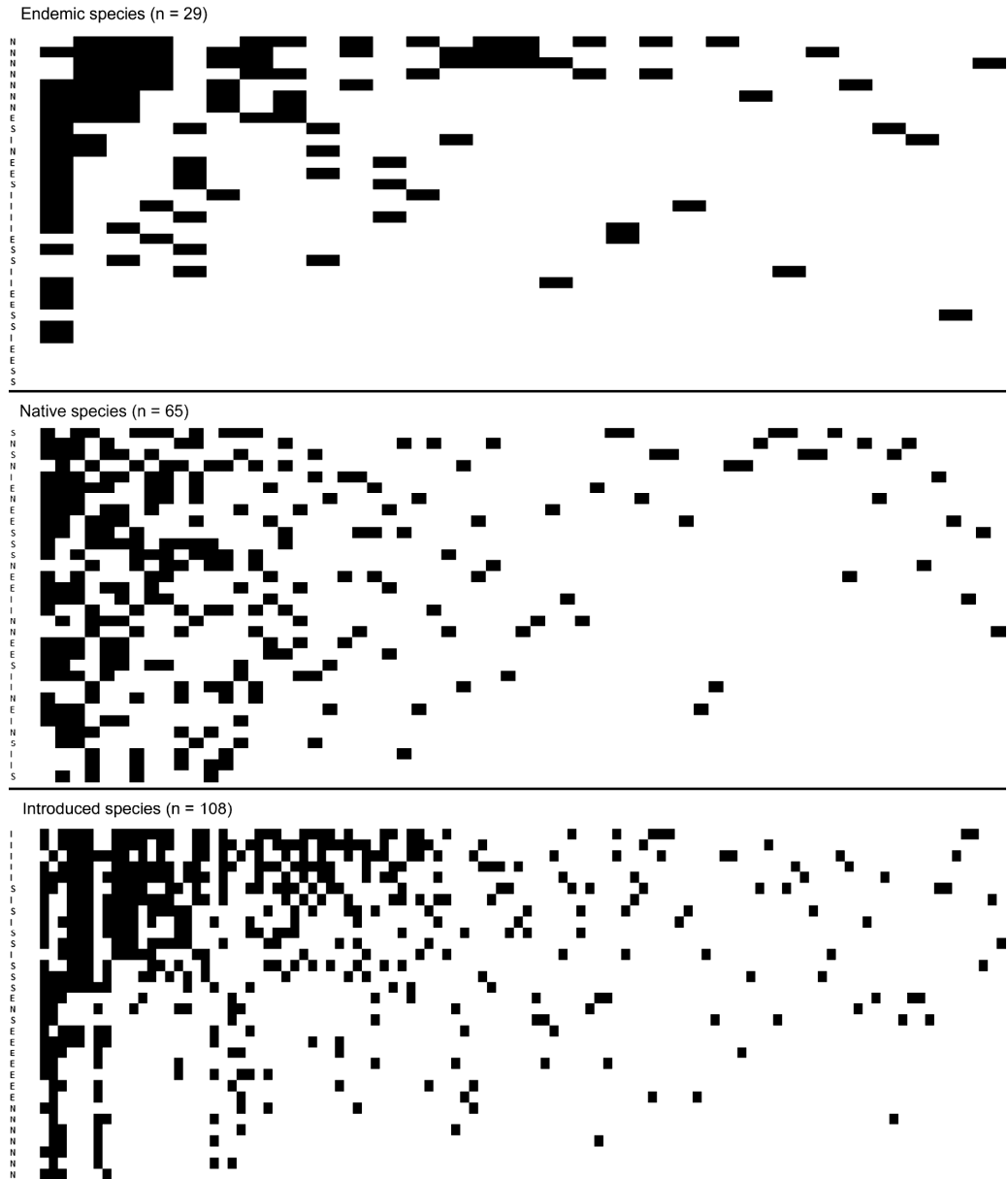
Species	Taxon	Distribution	Native forests	Exotic forests	Semi-natural pastures	Intensively managed pastures
<i>Lithobius pilicornis pilicornis</i> Newport	Chilopoda	Native	17.624%	11.809%	3.604%	-
<i>Tenuiphantes miguelensis</i> Wunderlich	Araneae	Native	15.045%	7.351%	0.942%	-
<i>Leiobunum blackwalli</i> Meade	Opiliones	Native	7.314%	26.545%	2.331%	-
<i>Ommatoiulus moreletii</i> (Lucas)	Diplopoda	Introduced	8.948%	17.329%	-	-
<i>Oedothorax fuscus</i> (Blackwall)	Araneae	Introduced	-	-	25.467%	13.301%
<i>Erigone autumnalis</i> Emerton	Araneae	Introduced	-	-	10.176%	7.853%



**Figure 4.** Multidimensional scaling (MDS) for the 32 sampled sites.

The assemblages of endemic (NODF = 29.33), native (NODF = 23.64) and introduced (NODF = 30) species were all found to be highly nested ( $p < 0.001$  in all cases). Natural forests and intensively managed pastures accumulated most endemic and introduced species respectively (Fig. 5).

None of the distance decay similarity regressions made with the Sørensen indices, qualitative or quantitative, were significant (Table II). The only significant slopes were found for exotic forests using the Bray-Curtis similarity, although the slope for native forests with the same index was close to significance (Table II; Fig. 6). Slopes for raw distance and similarity presented higher correlations than slopes of log-transformed values, so only raw values were considered.



**Figure 5.** Nestedness matrices for endemic, native and introduced species. Sites are in rows and species are in columns: N – natural forests; E – exotic forests; S – semi-natural pastures; I – intensively managed pastures.

## Discussion

The Azorean islands were mostly covered by forests before human settlement. After the

arrival of the first populations, deforestation started at a fast pace (Frutuoso, 1963; Martins, 1993; Silveira, 2007), as did the introduction of species, which was mostly involuntary for arthropods. Endemic species, often with narrow environmental and habitat requirements, are now mostly confined to the natural forest patches that subsisted, nowadays occupying only 2% of the archipelago area (Gaspar, 2007). The *Laurisilva* of the Azores is unique, both in the forest structure, with trees up to 5 meters high, in extremely rugged terrain and abundant moss cover and in plant species composition dominated by few endemic trees and shrubs. Endemics are therefore adapted to this particular habitat type. Due to a relative microclimatic (although not habitat) similarity, some species have been able to occupy exotic forests, however, in much lower abundances than in natural forests. The low abundance of endemics in exotic forests despite the relatively high richness reveals the existence of non-sustainable populations mostly as a consequence of mass effects and a source-sink dynamics between natural and exotic forests (Shmida & Wilson, 1985). On the other hand, the abundance of endemics in pastures is relatively high. This is explained by the high abundance of only a few endemic species that were able to adapt to open habitats, like the spider *Pardosa acorensis* and the beetle *Heteroderes azoricus*.

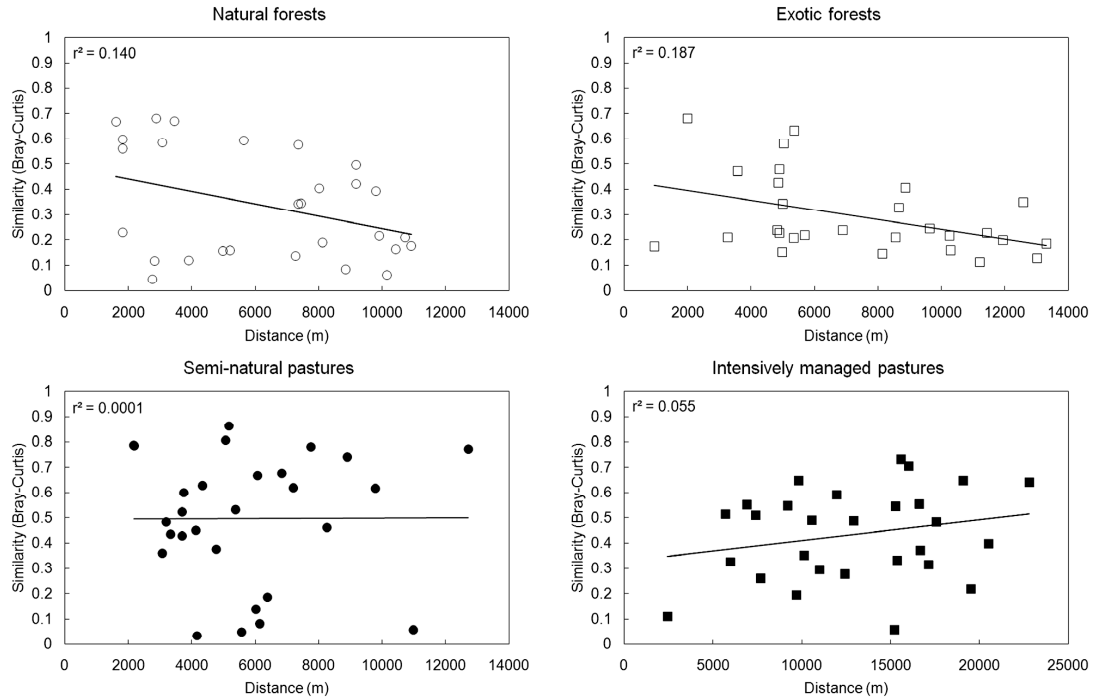
Native species should have looser habitat requirements than endemic species. However, if a species was able to naturally colonize the Azores it was probably a forest adapted species because forests were occupying most of the islands area before human influence. Even if in other regions they occur in forest types other than the ones of the Azores, they still remained as forest specialists. As a consequence, they are as rich and abundant in exotic as in natural forests but much less abundant in pastures, a habitat which, if existing, would be mostly residual in the islands before human influence.

**Table II.** Pearson  $r^2$  of the distance decay similarity curves for the different habitat types (n = 28 per habitat). Numbers in parenthesis are the p-values of regressions as given by Mantel tests with 1000 randomizations.

	Sørensen presence-absence	Sørensen abundance estimator	Bray-Curtis
Natural forests	0.021 (0.479)	0.004 (0.759)	0.140 (0.061)
Exotic forests	0.055 (0.22)	0.078 (0.133)	0.187 ( <b>0.017</b> )
Semi-natural pastures	0.005 (0.696)	0.041 (0.306)	0.000 (0.985)
Intensively managed pastures	0.046 (0.297)	0.000 (0.970)	0.055 (0.222)

Introduced species are naturally associated with introduced habitats, especially pastures and marginal abandoned fields. With their high dispersal capacity many have however spread

even to natural forests which, being small and fragmented, are prone to colonization from neighboring habitats. The decreasing proportion of introduced species and individuals from intensively managed pastures to natural forests is very clear.



**Figure 6.** Distance decay similarity analyses with the Bray-Curtis index for each habitat type. Twenty-eight pairwise comparisons were made per habitat. Curves were fitted by least squares regression.

All habitat types have characteristic communities, as confirmed by MDS and ANOSIM analyses. However, differences are larger between forest and pasture habitats. Navarrete & Halffter (2008) found a similar pattern, with canopy cover being the main driver of richness and composition of dung beetle communities. Pastures were indeed much different from both forest types they studied, with these much similar in many respects. In Azores, these differences seem strongly driven by the abundances of a few native and introduced species (SIMPER results). Forest and pasture specialist species are causing the large differences between these two habitat types, and the different abundances of each determine the differences between the two forest types and the two pasture types. As an example, *Lithobius pilicornis* and *Tenuiphantes miguelensis* are always present in very high abundances in native forests, lower abundances in exotic forests and are almost non-existent in pastures. *Leiobunum blackwalli* and *Ommatoiulus moreletii* are very abundant in exotic forests, less so

in natural forests and almost non-existent in pastures. *Oedothorax fuscus* and *Erigone autumnalis* are very abundant in both pasture habitat types. All these species are either arachnids or myriapods. The results suggest that these species have two characteristics in common. First, they are habitat specialists, although as generalist predators (or herbivore in the case of the diplopod) they mostly depend on the habitat structure. Second, if in the right habitat they have a large dispersal capacity and the ability to sustain large populations. This combination of habitat specialization but high abundance probably makes them ideal candidates for indicator species.

Natural forests and intensively managed pastures seem to be the main drivers of species composition of any site. Exotic forests and semi-natural pastures are mainly recipients of species from the other habitat types. There is a predictable pattern of species loss and gain from natural forests to exotic forests, semi-natural pastures and finally intensively managed pastures, as suggested by the nestedness patterns. As hypothesized, endemic species are lost and introduced species gained along this gradient. As forests occupied the entire island before human settlement, the nested pattern for endemics should be caused by selective extinction, along a species gradient of tolerance to disturbance and habitat change. The nested pattern for introduced species should be caused by selective colonization from a highly disturbed source (see Patterson & Atmar, 1986; Patterson, 1987; Greve *et al.*, 2005). Although native species were also nested, they did not show an obvious trend between habitat types. This was caused by the large richness of natives in exotic forests and even semi-natural pastures.

The causes that may potentially lead to differences in distance decay between different habitats are numerous. These include (see also Nekola & White, 1999; Soininen *et al.*, 2007; Morlon *et al.*, 2008): i) the balance between common, intermediate and rare species at each site; ii) different dominant families or genera; iii) different dispersal capacities of species and; iv) habitat fragmentation. Any of these factors may increase or decrease the slope in distance decay curves. For Terceira Island, the patterns found for distance decay of the Bray-Curtis similarity index suggest that, as hypothesized, habitats with more endemic and native species showed a significant or close to significant distance decay of similarity. The decay occurred even at distances as small as the ones possible in a relatively small island. A rapid decline in similarity at short distances was previously attributed to aggregation of species populations (Condit *et al.*, 2002). This aggregated pattern could be caused by three factors: i) microhabitat, topography or microclimate variation, which would apparently be more marked in forests, natural or exotic; ii) endemic and native species, which dominate forest habitats, have more restricted distributions than introduced species, more common in pastures. In fact,

it is expected that introduced species have higher environmental tolerance and therefore should be able to spread rapidly once they reach the islands. The distance decay pattern is attenuated if most species are widespread (Morlon *et al.*, 2008); iii) forests are fragmented, while pastures constitute continuous areas (Fig. 1). Fragmentation with consequent dispersal barriers to many species leads to higher isolation and a higher distance decay slope.

As a conclusion, all patterns studied show the same trend. That natural forests and intensively managed pastures are the main sources of species for all other habitats, with the first being the most important habitat for endemic species. Exotic forests are however important areas for non-endemic native species. Both forest types present a finer grain in the distribution of species than pastures, which are much more uniform along their extent.

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