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PATTERNS OF COLONIZATION AND SPECIES DISTRIBUTION FOR AZOREAN ARTHROPODS: EVOLUTION, DIVERSITY, RARITY AND EXTINCTION

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ABSTRACT

Here we address a list of questions based on long-term ecological and biogeographical studies performed in the Azores, a remote volcanic oceanic archipelago composed by nine islands. The target group are the arthropods, and the main habitat the *Laurisilva*, the Azorean native forest. Diversification of Azorean arthropod species is affected by island age, area and isolation. However, results obtained for over a decade show that distinct groups are differently affected by these factors, which has lead to the extreme diverse distribution patterns currently observed. Spatial distribution of arthropods in each island may be interpreted as caused by a typical "mass effect", with many species following a "source-sink" dynamics. Truly regionally rare species are those that are habitat specialists, many of them being threatened endemic species. Although various endemics persist as sink populations in human-made habitats (*e.g.*, exotic forests), more than half of the original endemic forest arthropods may already have vanished or may eventually be driven to extinction in the future. Those species which have evolved in and are mainly found in native forests, have been dramatically affected by hitherto unrecognized levels of extinction debt, as a result of extensive destruction of native forest. We argue that immediate action to restore and expand native forest habitat is required to avoid a future of disastrous extinctions of a biologically unique fauna with an unique evolutionary history.

RESUMO

Com base em estudos ecológicos e biogeográficos realizados nos Açores (um arquipélago remoto composto por nove ilhas vulcânicas) durante muitos anos de uma forma continuada, apresentamos um conjunto de questões. O grupo alvo são os artrópodes e o principal habitat é a Laurissilva, a floresta nativa dos Açores. A diversificação das espécies de artrópodes dos Açores é afectada pela idade das ilhas, área das ilhas e seu isolamento. No entanto, os estudos que decorreram durante os últimos dez anos mostram que os vários tipos de grupos taxonómicos e ecológicos são afectados de forma diferente por estes factores, tendo como consequência padrões de distribuição espacial únicos. A distribuição espacial dos artrópodes em cada ilha é causada for "efeitos de massa", muitas espécies possuindo dinâmicas "fonte-sumidouro". As espécies verdadeiramente raras à escala regional são aquelas que são especialistas de um particular habitat, muitas delas sendo espécies endémicas ameaçadas. Embora várias espécies endémicas persistam com populações sumidouro em habitats criados pelo Homem (e.g. florestas exóticas), mais de metade das espécies especialistas da floresta nativa já estão extintas ou poderão extinguir-se no futuro. De facto, aquelas espécies que evoluíram e apenas são encontradas nas florestas nativas, foram afectadas de forma dramática como resultado da destruição alargada das florestas nativas dos Açores. Defendemos que a única forma de evitar a extinção de uma fauna única das florestas nativas dos Açores será através de medidas de restauro desta floresta.

INTRODUCTION

Charles Darwin and Alfred R. Wallace were both fascinated by islands and the foundations of their evolutionary theory were mostly based on evidences obtained from isolated oceanic islands like the Galápagos, Hawaii and Madeira. Their initial observations and conclusions were seminal for the formulation of comprehensive theorems and hypotheses on evolutionary mechanisms responsible for the maintenance and increase of biodiversity following island colonization. Since then, islands have been regarded as natural laboratories for the study of evolutionary, ecological and ecosystems processes (Vitousek *et al.*, 1995; Wagner & Funk, 1995; Clarke & Grant, 1996; Thornton, 1996; Whittaker & Fernández-Palacios, 2007), due to their isolated character and their depauperated and disharmonic faunas and floras (Carlquist, 1974; Williamson, 1981; Whittaker & Fernández-Palacios, 2007). Changes in traits related to defences and flight, species radiation and endemism, as well as occupation of vacant niches, are just some examples of important fundamental concepts in Evolutionary Ecology developed as the result of data obtained from island biology studies (Whittaker & Fernández-Palacios, 2007). Not surprisingly, one of the most popular models in ecological literature is the "Theory of Island Biogeography" (MacArthur & Wilson, 1963, 1967), designed to explain patterns of species richness on islands, but with wider applications, namely in biodiversity, conservation and management (Rosenzweig, 2004).

Studies of island species and their natural histories have become fundamental to the understanding of the evolution, biology and ecology of animals and plants. Good examples are the now classic works of Carlquist (1974) and Williamson (1981). Some important works were published about island archipelagos, like the Atlantic Islands (Berry, 1992; Hounsome, 1993; Biscoito, 1995; Ashmole & Ashmole, 2000; Fernández-Palacios & Martin Esquivel, 2002; Fernández-Palacios & Morici, 2004; Serrano *et al.*, 2010), Hawaii (Wagner & Funk, 1995), Krakatau (Thornton & Rosengren, 1988; Thornton, 1996), Pacific Islands (Keast & Miller, 1996) and Pitcairn Islands (Benton & Spencer, 1995). Special publications on evolution on islands (Clarke & Grant, 1996; Emerson, 2002; Gillespie & Roderick, 2002) and one unique on ecological function (Biological Diversity and Ecosystem Function on islands - Vitousek *et al.*, 1995) have been published recently. More than describing unusual body adaptations, such as wingless birds and giant, arborescent herbs, recent studies emphasise how unique and distinct oceanic island ecosystems are. Special attention is given to how fragile these ecosystems are and the need of urgent conservation measures.

Here we describe the results of a long-term ecological study on arthropods carried out in the Laurisilva, the native forest of the Azores, a remote volcanic oceanic archipelago. We address a list of questions arising from the results obtained from a number of studies performed in the last ten years.

AZOREAN NATURAL HISTORY AND BIODIVERSITY

Charles Darwin visited the Azores during the expedition of the *Beagle* (September 1836) (Keynes, 1988). Despite a discussion on the mechanisms of dispersal, making reference to the neighbouring archipelago of Madeira, and some mention to arborescence of *Erica azorica* (only studied recently by Ribeiro *et al.*, 2003), he made no significant comments about the arthropods of the Azores. Although the Azores is an isolated archipelago with a diverse geological history and a wide range of elevations, the relatively low endemic richness and the lack of remarkable adaptive radiation compared with other archipelagos (*e.g.*, Canary Islands) resulted in it receiving less attention (but see Wallace, 1876).

Crotch (1867) comments on the almost complete indifference of naturalists towards the Azores, noting, as an example, that while the English entomologist T.V. Wollaston intensively sampled in archipelagoes of Madeira, the Canaries and Cape Verde, he did little in the Azores. The historical lack of interest on Azorean arthropods can, in part, be explained by the lack of knowledge of the faunistic composition of many Azorean taxa until recently (but see Borges *et al.*, 2005a, 2010a), but this trend is changing. Recently there has been an increasingly interest in the Azorean biota that is reflected in the raising number of publications on the biogeography, ecology, applied entomology, biospeleology and systematics of its arthropods (see details below). The present work shows the importance of evidence obtained from the Azores for the understanding of general island processes.

The current estimate of terrestrial species and/or subspecies in the Azores is 6,164 (about 6,112 species), of which 452 (411 species) are endemic (Borges *et al.*, 2010a) (see Table 1). Arthropods are the most diverse taxon with about 2,298 species and subspecies, 266 of which are endemic (Table 1; see also Borges *et al.*, 2010a).

AZOREAN ARTHROPOD BIODIVERSITY: THE MAIN QUESTIONS

Invertebrates are generally relegated to a secondary place in biodiversity conservation programs and there are sociological, educational and scientific reasons for this (Cardoso *et al.*, 2011a, b). One significant factor is the lack of communication between scientists and stakeholders and overcoming this problem is essential for all ongoing arthropod research projects. Conservation of the Azorean natural biodiversity requires the elaboration of a global and integrated strategy based on the knowledge of current species distributions and how of current land-use will impact future distributions (see *e.g.*, Borges *et al.*, 2008; Cardoso *et al.*, 2009b; Meijer *et al.*, 2011). Consequently it is crucial to understand how land overexploitation, increased tourist activities, displacement of native species by exotic ones and climate change, may affect Azorean biodiversity and ecosystem functioning. In the last ten years we have invested considerable effort to raise awareness about the importance of Azorean arthropod biodiversity relative to the total biodiversity of the Azores and of the Atlantic Biogeographic Region (see *e.g.*, Borges *et al.*, 2005a, 2008a, 2010a). Our ultimate goal is to ensure that the highly diverse endemic arthropods island biodiversity conservation areas are protected, in the hopes that this will halt, and hopefully reverse, the general trend of biodiversity decline in the Azores (see Triantis *et al.*, 2010a).

The BALA project (2000-2010; **B**iodiversity of **A**rthropods from the **L**aurisilva of the **A**zores) (see Borges *et al.*, 2000, 2005b; Gaspar *et al.*, 2008), that surveyed arthropods distribution in Azorean native forests, was an important step towards the inclusion of arthropod groups in biodiversity conservation planning in the Azores. The systematically collected data allowed inferences to be made about the biology, ecology, rarity and conservation status of the different arthropod species. Transects

TABLE 1. Total and endemic terrestrial diversity (species and subspecies) of the main groups of the Kingdoms Fungi, Chromista, Protoctista, Plantae and Animalia in the Azores (more details in Borges *et al.*, 2010a).

Kingdom and Phylum/ Division	Common name	Total	Endemic
FUNGI		**1328**	**34**
Zygomycota (Fungi)	Zygomycete fungi	2	0
Ascomycota (Fungi)	Sac fungi, Cup fungi	231	20
Ascomycota (Lichen)	Lichen	775	10
Basidiomycota (Fungi)	Basidiomycete fungi	307	4
Basidiomycota (Lichen)	Lichen	6	0
Lichen (Fungi Imperfecti)	Lichen	7	0
CHROMISTA		**4**	**0**
Oomycota	Water molds	4	0
PROTOCTISTA		**575**	**7**
Bacillariophyta	Diatoms	536	7
Amoebozoa	Amoebae	39	0
PLANTAE		**1590**	**80**
Bryophyta	**Bryophytes**	***480***	***7***
Anthocerotophyta	Hornworts	5	0
Marchantiophyta	Liverworts	164	1
Bryophyta	Mosses	311	6
Tracheobionta	**Vascular Plants**	***1110***	***73***
Lycopodiophyta	Quillworts	7	1
Pterydophyta	Ferns	69	6
Pinophyta	Gymnosperms	4	1
Magnoliophyta	Dicots and monocots	1030	65
ANIMALIA		**2667**	**331**
Platyhelminthes	Flatworms	31	0
Nematoda	Roundworms	131	2
Annelida	Earthworms	22	0
Mollusca	Slugs and snails	114	49
Arthropoda	Arthropods	2298	266
Chordata (Vertebrata)	Vertebrates	71	14
TOTAL		**6164**	**452**

(150 m x 5 m) were randomly placed within fragments of protected native forest. The number of transects per forest fragment was set up using a logarithmic scale, assuming a species-area relationship (SAR) with a slope (z) of 0.35 in a log-log scale (*i.e.*, a 10 fold area increase implies a duplication of the number of species): 2 transects were set up for 10 ha forest fragments, 4 transects for 100 ha fragments and 8 transects for 1,000 ha fragments. Consequently, higher sampling effort was applied to larger protected native forest areas (*i.e.* "proportional sampling"), making it possible to capture not only "area *per se* effects" but also unveil patterns that could be prevalent in larger areas, such as, spatial beta diversity.

In this paper we compile and synthesize the results of recent research on the biodiversity and ecology of Azorean arthropods, which were at least partly based on data obtained from long term projects (*e.g.*, BALA, "Biodiversity of cave invertebrates"), and many others of shorter duration (*e.g.*, Interfruta). During the last ten years several general questions were raised and several specific goals (noted below) were pursued:

Inventory of Azorean arthropods and diversity hotspots

- list all arthropod taxa from the Azores (see Borges *et al*., 2005c, 2010b);
- describe new taxa (Blas & Borges, 1999; Ribes & Borges, 2001; Platia & Borges, 2002; Quartau & Borges, 2003; Borges *et al*., 2004, 2007; Borges & Wunderlich, 2008);
- examine the shape and characteristics of discovery curves in order to obtain a provisional picture of the taxonomic completeness of current inventories and an estimation of the amount of work still needed to attain taxonomic completeness (Lobo & Borges, 2010).
- identify hotspots of species diversity in the Azores (*e.g.* Borges *et al*., 2005b; Borges & Gabriel, 2009).

Ecological patterns of species distribution and abundance (i.e. rarity)

- test if the He & Gaston (2003) abundance–variance–occupancy model accurately predicts species distribution across different spatial scales

and whether endemic, native (non-endemic) and introduced species occupy different parts of the abundance–variance–occupancy space (Gaston *et al.*, 2006);
- assess patterns of distribution and species richness of canopy phytophagous insect among islands and host plants (see Ribeiro *et al.*, 2005; Santos *et al.*, 2005);
- describe patterns of rarity in one well-sampled island, i.e., Terceira, identifying types of local pseudo-rare species (Borges *et al.*, 2008);
- explore patterns of diversity, abundance and distribution of different taxonomic, colonization and trophic groups of arthropods in Azorean native forests at different strata and sites (Gaspar *et al.*, 2008);
- test the "resource concentration hypothesis", that predicts there is a positive relationship between the density of phytophagous insects or predator arthropods and the spatial distribution/abundance of host plants (Ribeiro & Borges, 2010);
- test if more abundant and widespread plant species are those that support populations of the rarest regional arthropod species (Ribeiro & Borges, 2010);

Evaluate the role of environmental variables
- examine how a variety of biotic, abiotic and anthropogenic factors influence endemic and introduced arthropod richness on an oceanic island (Terceira) (Santos *et al.*, 2005; Borges *et al.*, 2006);
- evaluate the degree to which environmental suitability assessed with presence/absence models account for abundance estimates (Jimenez-Valverde *et al.*, 2009);

Effects of scale and sampling on species richness, beta diversity and density
- analyze the effect of variation in the size of sampling units on species richness estimations, and evaluate the accuracy of the predictions obtained with various estimators presently available when different strategies are used to group the same dataset into different sized samples (Hortal *et al.*, 2006);
- assess how differently beta diversity measures for incidence data and pairwise comparisons behave with re-

gard to varying degrees of sampling effort, and recommend diversity measures that are relatively robust to undersampling (Cardoso *et al.*, 2009a);
- test the hypothesis that "host-habitat area" affects the following insect density estimates: mean number per tree canopy or reserve transects (Ribeiro & Borges, 2010).

Effect of disturbance in ecological communities
- understand how several taxonomic and ecological attributes of arthropod communities vary with respect to different levels of disturbance as well as assessing to what extent potential disturbance factors are influencing site integrity (Santos *et al.*, 2005; Cardoso *et al.*, 2007);

Biogeography of Azorean arthropods
- investigate some biodiversity patterns relating to spider distribution between islands, habitats, colonization status and biogeographical origin (Borges & Wunderlich, 2008);
- study the factors promoting diversification of several Azorean arthropod groups (Borges & Hortal 2009) and extending this to the rest of Macaronesia (Cardoso *et al.*, 2010a; Triantis *et al.*, 2010b);
- identify the biogeographical factors underlying spider species richness in the Macaronesian region and assessing the importance of species extinctions in shaping current diversity (Cardoso *et al.*, 2010a);
- investigate whether there is a significant gain in information if one uses non-parametric richness estimators to build SAR models with standardized surveys data, rather than using the observed number of species (S_{obs}) (Borges *et al.*, 2009);
- investigate if species-area relationships from entire archipelagos are congruent with those of their constituent islands (Santos *et al.*, 2010).

Surrogacy patterns in arthropods
- evaluate the effectiveness of arthropods as predictors of diversity for a wide range of taxonomic and non-taxonomic groups, for multiple measures of biodiversity and for different spatial scales (Gaspar *et al.*, 2010);
- evaluate the effectiveness of cave-adapted arthropods as

predictors of diversity of rare bryophytes in cave entrances and the diversity of bacteria in cave mats.

Conservation of Azorean arthropods

- examine the relative value of 19 forest fragments in seven of the Azorean islands to improve the conservation of Azorean soil epigean arthropod biodiversity (Borges *et al.*, 2005b; Gaspar *et al.*, 2011);
- investigate the relationships between endemic and introduced arthropod richness, to assess whether areas with high levels of endemic species richness deter invasions (Borges *et al.*, 2006);
- investigate the relevance of current human-made habitats (*e.g.* exotic forest; agroecosystems) for the protection of rare species (see Cardoso *et al.*, 2009b, 2010b; Meijer *et al.*, 2011);
- test nestedness patterns of endemic, native and introduced species (Cardoso *et al.*, 2010b);
- quantify the magnitude and taxonomic distribution of extinction debt in the Azores as an important step for effective conservation planning (Triantis *et al.*, 2010a);
- list the 100 highest management priority taxa in Macaronesia and in the Azores, the so-called Top 100 (Cardoso *et al.*, 2008; Martín *et al.*, 2010).
- genetic characterization of populations of endemic species to investigate their uniqueness and examine how this information could help in the prioritization of conservation efforts.

WHAT HAVE WE LEARNED SO FAR?

Inventory of Azorean arthropods and diversity hotspots

The knowledge base of Azorean arthropod biodiversity is not uniform, and many groups have not been adequately sampled. Furthermore, many groups have not received appropriate taxonomic revision, due to little traditional taxonomic research being carried out in the last decade, and the lack of taxonomists familiar with the Azorean fauna (Amorim, 2005; Borges *et al.*, 2005a; Lobo & Borges, 2010). As with any other biome, solving this problem is not simple since, for example, traditional taxonomic work has been neglected in the last decades in Europe (see Boero, 2010). The most relevant effort to rectify the lack of taxonomic expertise preventing advance in biodiversity research was the establishment of the "Azorean Biodiversity Group" (http://cita.angra.uac.pt/biodiversidade/), that, among other things, is supporting research on classical (as well as molecular) taxonomy and ecology of arthropods of the Azores. Moreover, the web site "Azorean Biodiversity Portal" (http://www.azoresbioportal.angra.uac.pt/) (see Borges *et al.*, 2010c) allows everyone to access updated information on Azorean biodiversity. As a direct outcome of this online database many national and international taxonomists have shown a growing interest in Azorean biodiversity and many new collaborations have been established, including taxonomic revisions (see Borges *et al.*, 2010b) and additional field work to collect specimens.

The results obtained during the BALA project (see above) showed that some forest reserves are clearly more diverse than others, both in terms of alpha and gamma diversities. The effect of forest fragmentation has not been studied in detail (see future work below), but the data obtained suggests that small fragments play a much more important role than previously thought (see Borges *et al.*, 2005b; Borges & Gabriel, 2009). For instance, based both on the presence of unique species and high species richness, the Pico Alto region in the archipelago´s oldest island, Santa Maria, is a hotspot of biodiversity (Borges *et al.*, 2005b; Borges & Gabriel, 2009). Over 57 endemic arthropod species are known from Pico Alto (Santa Maria Isl.), *i.e.* 21% of the Azorean endemic arthropods occurring in an area representing <0.25% of Azorean native forests. Other relevant areas occur on the islands of São Miguel (Pico da Vara), Terceira (Terra Brava, Caldeira da Serra de Santa Bárbara), São Jorge (Topo), Pico (Caveiro, Mistério da Prainha) and Flores (Morro Alto and Pico da Sé) (see Borges & Gabriel, 2009; online at http://www.azoresbioportal.angra.uac.pt/files/publicacoes_Brochura BIODIVERSIDADE AORES vFINAL.pdf).

Results obtained from other studies, such as the survey of subterranean invertebrates (1999-2005) revealed the poor stage of knowledge on the Azorean cave invertebrates. For instance, the number of cave

Trechus listed for the islands increased from 4 to 7, plus an epigean species in the same genus (Borges *et al*., 2004; Amorim, 2005; Borges *et al*., 2007).

Ecological patterns of species distribution and abundance (i.e. rarity)

The data for diverse species assemblages at different spatial scales, regardless of species status, can be well described by an abundance-variance-occupancy model (Gaston *et al*., 2006). Most importantly, we observed that outliers include restricted specialized forest endemic species (*e.g. Trechus terrabravensis* and *Cedrorum azoricus azoricus*) that only occupy pristine native forest sites where they are quite abundant (Gaston *et al*., 2006).

We have found that free-living herbivores insect in the canopies of Azorean native forests are mainly generalists, as expected for a relatively young and isolated volcanic archipelago (Ribeiro *et al*., 2005). Interestingly, the proportion of rare species is higher for herbivores insects than for predatory arthropods (Borges *et al*., 2008). Ribeiro & Borges (2010) also showed that there is a clear dominance of generalist species in canopies of Azorean trees and shrubs, which holds also true for the overall spider and chewing insect communities in Terceira island (Borges *et al*., 2008). The observation of a widespread distribution of spiders on tree canopies in the native forest could be explained by their high dispersal ability and generalist feeding habits (Borges & Wunderlich, 2008). Consequently, the abundance of herbivorous insects seems to be strongly affected by the occurrence and population densities of spider species. One particular plant species, *Erica azorica*, has greater than expected herbivore densities per crown, possibly as it represents enemy free/predictable space (Ribeiro & Borges, 2010). In the case of agricultural habitats, we found that both abundance and species richness of predatory groups inhabiting the canopy of different fruit trees (apple, orange, and peach trees) are negatively correlated with canopy volume, and positively correlated with tree density. On the other hand, herbivore species, especially sucking insect species, show the opposite trend (Santos *et al*., 2005).

In terms of rarity, four important types were detected in the Azores (see Borges *et al.*, 2008; Ribeiro & Borges, 2010): 1) dense and intermediately dense species; 2) truly rare species, which are rare on any host species and with very low population densities regionally; 3) pseudo-rare species found in small numbers on a specific host tree, which are dense on neighbouring tree species, *i.e.* host-tourists; 4) pseudo-rare species found in small numbers on any tree species that are common in other habitats on the island, i.e., habitat-tourists.

Truly rare and specialist species should also be favoured by the presence of large quantities of resources, and although large tree species have similar numbers of rare species, most of these species are truly rare on *Juniperus brevifolia*, *Laurus azorica* and *Erica azorica* (see Ribeiro & Borges, 2010). Therefore, the high frequency of *E. azorica* and *J. brevifolia* populations throughout the Azorean native forest fragments creates the opportunity for the survival of rare insect and spider species populations on these hosts (Ribeiro & Borges, 2010).

Other surveys focused on arthropods from very specific habitats typical of volcanic islands such as the Azores - lava tubes and volcanic pits - revealed that cave adapted species rarity vary as a function of cave abundance and the number that have actually been sampled (see Amorim, 2005). For the most studied Azorean cave beetle species, (in the genus *Trechus*) some are found at high densities at many sites (*e.g.*, *T. picoensis* from Pico Isl. occurs in 9 caves and 134 specimens have been collected so far from the Torres lava tube), while others are only found at one site and despite the amount of sampling efforts involved only a few specimens have been collected (*e.g.*, only 2 individuals of *T. jorgensis* are known from Bocas do Fogo pit in São Jorge Isl.).

Evaluate the role of environmental variables

We have shown for the soil arthropod fauna of native forest in Terceira Island that abiotic (climatic and geomorphological) variables provided a better explanation for the variation in endemic species richness than anthropogenic ones, whereas the inverse was observed with respect to introduced species richness (see Borges *et al.*, 2006). Concerning the abundance of species, Jimenez-Valverde *et al.*, (2009) observed that Azorean arthropod species are highly influenced by land-use variables, in such a way that the climate factors lose relevance and the climatic suitability may be diluted in predicting local abundance of species. However, in their analysis of the arthropod communities associated with fruit orchards, Santos *et al.*, (2005) found a strong influence of both climatic and anthropogenic variables on the abundance and diversity of different functional guilds.

Effects of scale and sampling in species richness, beta diversity and density

Arthropod data from BALA´s standardized sampling protocol was used to evaluate the effects of scale (across sites, forest fragments and islands) and sampling in species richness, beta diversity and density (see Hortal *et al.*, 2006; Cardoso *et al.*, 2009a; Ribeiro & Borges, 2010). Several estimators (ACE, Chao1, Jackknife1 and 2 and Bootstrap) provided consistent estimations of species richness, regardless of sample grain size. In addition several nonparametric estimators presented certain insensitivity to how samples are aggregated (Hortal *et al.*, 2006).

Cardoso *et al.*, (2009a) demonstrated that beta diversity values are close to the real values, when communities being compared approach sampling completeness. However, the β_{-2} index from Harrison *et al.*, (1992) should be used as the most consistent measure in cases in which the sampling completeness degree of a dataset is unknown.

In general, the three structurally most complex and abundant plant "host islands", *i.e.*, *E. azorica*, *J. brevifolia* and *L. azorica*, accumulated the highest proportion of regionally rare arthropod species, corroborating the "host as an island hypothesis" (Ribeiro & Borges, 2010).

Effect of disturbance in ecological communities

In broad terms current fragments of Azorean native forest are not uniform in their conservation status. In fact, Cardoso *et al.* (2007) clearly demonstrated that when using an Index of Biotic Integrity (IBI) adapted to the epigean arthropods of the Azorean native forests, many fragments of native forest would be considered highly disturbed. More importantly, these authors showed that most species thrived in highly disturbed sites are of limited importance for conservation efforts, and that the percentage of endemic species is significantly higher in pristine than in degraded sites.

Biogeography of Azorean arthropods

Borges & Brown (1999) showed that island geological age was an important variable explaining Azorean endemic arthropods species richness. Recently, there has been increased interest in the determining the importance of geological age and other geographical variables to explain patterns of island diversity in Macaronesia (*e.g.* Whittaker *et al.*, 2008, 2009; Borges & Hortal, 2009; Borges *et al.*, 2009; Cardoso *et al.*, 2010a; Triantis *et al.*, 2010b).

In most of these studies the main observation was that a combination of islands' area and geological age are enough to provide a basic explanation for the diversity of endemic arthropods in the Azores, in spite of some differences between taxonomic or ecological groups and the additional role of island relative isolation (Borges & Hortal, 2009; but see Cardoso *et al.*, 2010a). The main conclusion was that due to the recent age of the archipelago (see Borges & Hortal, 2009; Triantis *et al.*, 2010b) a simple area-age model (AT) is adequate for the Azorean fauna, and not the more complex area-age-age^2 (ATT^2) firstly proposed by Whittaker *et al.* (2008, 2009) within the context of The General Dynamic Model of Oceanic Island Biogeography (GDM). In fact, when testing the GDM, Borges & Hortal (2009) showed that: i) cave species appear to have evolved quite quickly, producing a number of species during the initial stages of island development, when cave systems formed by lava tubes and volcanic pits were abundant and pristine prior to natural collapsing of structures; ii) taxa with low dispersal ability, particularly beetles, showed strong negative relationships with the distance to Santa Maria, the oldest island and reservoir of lineages either coming from the mainland or remaining from the older archipelago composed of Santa Maria and the Northeast part of São Miguel; iii) the diversity of evolutionary responses in different organisms is so varied that no general model, like the one proposed by Whittaker and colleagues (Whittaker *et al*., 2008, 2009) is able to predict the patterns and processes of diversification.

Spiders apparently follow a different pattern from the one observed for most arthropod groups. Analyzing the biogeographical factors underlying spider species richness in the Macaronesian region Cardoso *et al*. (2010a) showed that for the Azores, island area and the proportion of remaining natural forest were the best predictors of species richness. The effect of island age on species richness, if important in diversification processes, has nowadays been masked by the effect of native habitat destruction. Triantis *et al.* (2010b) found that the AT model was the most parsimonious for explaining diversity patterns of indigenous, endemic, single island endemic and proportion of single island endemic beetles and arthropods in the Azores, corroborating the results of Borges & Hortal (2009).

Santos *et al*. (2010) observed that archipelagos follow the same island species–area relationships (ISAR) as their constituent islands, which means that the Macaronesian archipelagos could be studied as four data points when testing the relationship between species richness and area. Borges *et al*. (2009) found that if data comes from standardized surveys (as is the case of BALA data), the slope and goodness of fit for species area relationships obtained with estimated values (using non-parametric estimators; see also Hortal *et al*., 2006) were not significantly different from those obtained from observed species richness.

Molecular data generated for a few Azorean endemic arthropods groups (the beetles *Trechus* and *Tarphius*, and the butterfly *Hipparchia*) and their neighboring insular and continental congeneric species reveal that the Azorean taxa form monophyletic clades (Fujaco *et al*., 2003; Amorim, 2005). This supports single colonization events of the Azores, as expected for such remote oceanic island. If true, then the diversification currently observed within these groups would be the result of intra archipelago speciation from single ancestors, as opposed of multiple arrivals of distinct lineages (Amorim *et al*., subm.). Nevertheless, the possibility that multiple colonization events occurred but have gone extinct cannot be completely dismissed.

Surrogacy patterns in arthropods

Gaspar *et al*. (2010) evaluated the effectiveness of taxonomic, colonization and trophic groups of arthropods from native forests of the Azores archipelago as surrogates of the diversity of other arthropod groups. The results indicated that spiders (Araneae) and true bugs (Hemiptera) may be more promising surrogates of arthropod diversity for the Azorean native forests at the transect, fragment and island scales (Gaspar *et al*., 2010). As spiders are easy to identify, abundant in both terrestrially and within tree canopies (Borges & Wunderlich, 2008; Borges *et al*., 2008; Gaspar *et al*., 2008) and probably good indicators of futures trends for other taxa (Cardoso *et al*., 2010a), we suggest the use of this group for future rapid monitoring studies in Azorean forests.

Conservation of Azorean arthropods

Human activities and invasive species are among the most important factors impacting Azorean arthropod communities (Godman, 1870; Borges *et al*., 2006, 2008). The number of described species known from the Azores is continuously rising (Borges *et al*., 2010a), but a great proportion are recently introduced ones, that tend to exhibit lower densities, less spatial density variance, and occupy fewer sites than native and endemic species (Gaston *et al*., 2006). On Terceira island, non-indigenous species are mainly limited to those sites under anthropogenic influence located mainly on low to medium altitude areas or, when in high-altitude forests, in marginal areas of the few forest remnants (Borges *et al*., 2006). For example, the protection of forest specialists, like the ground-beetles *Trechus terrabravensis* and *Cedrorum azoricus azoricus* (see Gaston *et al*., 2006) requires the management of invasive species, to avoid them entering the pristine native forest sites, such as those found in Serra de Santa Bárbara (see also Borges *et al*., 2006; Cardoso *et al*., 2007).

The impacts of land use changes are severe (Borges *et al*., 2008; Cardoso *et al*., 2009) and many Azorean endemic forest dependent species are on the edge of extinction (Triantis *et al*., 2010a). Despite the fact that unmanaged exotic forests are providing alternative habitat suitable for some endemic species (forest specialist arthropods, particularly saproxylic beetles from S. Maria Island; Meijer *et al.*, 2011), most endemic forest specialist arthropods are restricted to native forests and only have sink populations in semi-natural grasslands or exotic forests (Borges *et al.*, 2008; Cardoso *et al.*, 2009; Triantis *et al.*, 2010a).

Endemic and introduced species were all found to be highly nested in habitats of Terceira Island. Indeed, native forests and intensively managed pastures seem to be the main drivers of species composition at any site, having mostly endemic and introduced species, respectively (Cardoso *et al.*, 2010b). This result implies that 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 analysis (Cardoso *et al.*, 2009b; 2010b). The roles of selective extinction (see also Triantis *et al.*, 2010a), as is exemplified by a gradient of disturbance (Cardoso *et al.*, 2007), and habitat change could explain the nested pattern for endemics.

Interestingly, hardly any exotic insect or spider were able to colonize the native forest canopy habitat (Borges *et al.*, 2008; Borges & Wunderlich, 2008), so are not widespread in all the Azorean habitats. For instance, the Azorean *Laurisilva* seems that has not yet been colonized by any of the invasive ant species found adjacently to human constructions. Spiders are the most abundant terrestrial predators in the Azores (Borges & Wunderlich, 2008; see also Gaspar *et al.*, 2008), particularly in forests, and may serve as early indicators for future disappearance patterns of other insular taxa (Cardoso *et al.*, 2010a).

The most disturbed study sites in the Azores were found on the islands of Faial (Cabeço do Fogo), Flores (Caldeiras Funda, Rasa), Pico (Lagoa do Caiado), São Jorge (Pico Pinheiro), São Miguel (Atalhada, Graminhais, Pico da Vara), Santa Maria (Pico Alto) and Terceira (Algar do Carvão, Matela, Pico do Galhardo), while the pristine areas were on Terceira (Terra Brava, Biscoito da Ferraria, Caldeira da Serra de Santa Bárbara), Pico (Caveiro, Mistério da Prainha) and Flores

(Morro Alto, Pico da Sé) islands (Cardoso *et al.*, 2007; Gaspar *et al.*, 2011).

Invasive plant species are the most important drivers in terms of ecological and ecosystem change in the Azores (Borges *et al.*, 2010d) and the spread of species like *Hedychium gardneranum*, *Hydrangea macrophylla*, *Rubus ulmifolius*, *Pittosporum undulatum*, *Clethra arborea* (see Silva & Smith, 2006; Hortal *et al.*, 2010) is of great concern. Areas of high conservation value due to the presence of single island endemics, such as Pico Alto on Santa Maria and Pico da Vara on São Miguel, are now heavily disturbed by invasive plants. Human driven ecosystem disturbances have to be minimized and special measures by the Azorean Government are already being applied for the control of invasive plants in several islands. The ongoing projects in Pico da Vara (S. Miguel) to manage areas of special importance for birds are good examples of active conservation in the Azores (*e.g.* Ceia *et al.*, 2009; Heleno *et al.*, 2009).

A list of Azorean threatened taxa, based on both protection priority and management feasibility, has been drawn up (Cardoso *et al.*, 2008; Martín *et al.*, 2010). Arthropods represent 17 species of the 100 most important Macaronesian taxa (Martín *et al.*, 2010) and 24 of the 100 most important in the Azores (Cardoso *et al.*, 2008). This list will be used to determine those new species to be included in the revision of the NATURA 2000 list of Azorean priority species for conservation (Paulino Costa, pers. comm.). This will be an important step towards the inclusion of arthropods in conservation initiatives for the Azorean archipelago, including several new areas based on the occurrence of unique arthropod species (e.g. Atalhada in São Miguel; Pico Alto in Santa Maria; Fontinhas in Terceira) (see Gaspar *et al.*, 2011).

Future work in the conservation of Azorean biodiversity

The study of arthropod ecology in the Azores has proven to be a valuable tool for designing biodiversity conservation plans in the archipelago. However, any hope for a successful management and conservation program of endemic fauna and flora must meet local economic interests. Local people, with direct interest in the use of land for agriculture have a higher impact on the sustainability of the Azorean habitats than policy makers, managers and conservationists altogether. Several initiatives, resulting from outcomes of the BALA project, have been undertaken through organized seminars and meetings as well as brochures and books (Borges & Gabriel, 2009; Cardoso *et al*., 2009c) in recent years increasing public understanding of why value arthropod biodiversity and thus to protect their habitats. The information on arthropod diversity and distribution provided by the BALA project and parallel studies is being used by the regional government to define and give legal status to the designated areas for protection. The next steps would be to establish management plans for the areas, including the establishment of periodic diversity monitoring plans for these zones to determine the effectiveness of the conservation strategies adopted to date. The management and monitoring plans should include: i) the identification of specific threats to the protected areas, ii) the definition of practical measures to minimize these threats, and iii) the selection of specific groups of organisms and sampling methods that can be used to periodically monitor the overall diversity of the areas.

FUTURE RESEARCH AND CONCLUDING REMARKS

The islands of the Azores have undergone dramatic changes in land-use and their biodiversity is now under serious threat (see Borges *et al*., 2008). With the current knowledge on Azorean arthropod biodiversity it is now possible to address more complex issues, such as being able to:

1) predict species extinctions using the available information of species abundance on Azorean islands (see also Triantis *et al*., 2010a) and compare data obtained in 1999-2000 with new data that was collected in 2010 (FCT Project PTDC/BIA-BEC/100182/2008 – "Predicting extinctions on islands: a multi-scale assessment);
2) evaluate the extent and the mechanisms through which fragmentation of natural habitats affects species communities. To do this, we will build a relevant framework to evaluate and compare habitat size effects on the species richness of native versus ex-

otic free-living herbivore insects and predatory spiders. We anticipate that these results will advance in species–area relationship modelling techniques, that are crucial for both theoretical and conservation applications in the Azores (see a recent application in Guilhaumon *et al*., 2008);

3) the study of species-environment relationships, as islands are especially good places to address these questions;
4) identify evolutionary significant units for conservation by generating mitochondrial and nuclear molecular datasets of several arthropod endemic species (e.g., FCT - PTDC/BIA-BEC/104571/2008 project – "What can the Macaronesian islands teach us about speciation? A case study of *Tarphius* beetles and *Hipparchia* butterflies").

Further studies, using different sampling techniques, should be carried out to improve our knowledge of the diversity and distribution of less known groups of arthropods, such as Hymenoptera, Diptera, Collembola and Acari, these less known groups of arthropods are diverse and abundant and should play important functional roles in native communities.

Time scale, whether it is hours, days, months or years, has seldom been explored in the previous projects, despite the fact it will also influence the way diversity and distribution of arthropods is perceived, and hence, may provide additional information that is important for conservation planning. A study is currently exploring spider diversity in a native forest fragment at different hours of the day (Cardoso, unpublished data). Furthermore, a comparison of data from 2000 with those from 2010 (FCT Project PTDC/BIA-BEC/100182/2008 – "Predicting extinctions on islands: a multi-scale assessment; Triantis *et al*., 2010a) will also offer valuable insights on the effect of time scale on the diversity and distribution of arthropods in the Azores.

The patterns and causes of arthropod rarity in Azorean native forests should continue to be explored in detail to distinguish between arthropod species that are truly rare from those that are rare at a given time, as this has major implications for the definition of the most effective conservation strategies.

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