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Insect and spider rarity in an oceanic island (Terceira, Azores): True rare and pseudo-rare species

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Abstract

Until now the mechanisms of how recent historical land-use (hereafter called "habitat") changes in island ecosystems shape the distribution of individual insect species have been poorly understood in the field of conservation biology. In the present study we concentrate on the delicate equilibrium of the contribution of habitat island composition (i.e. habitat

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resource availability) with respect to island insect distribution patterns. In this context we study in detail the distribution patterns of four functional groups (herbivorous sucking insects, herbivorous chewing insects, spiders and other arthropod predators) of endemic, native and exotic arthropod species in a well-studied island of the Azores archipelago (Terceira). Within the bigger context of a standardized sampling program both for epigean and canopy insects and spiders we want to find out which species are truly rare and which are pseudo-rare species in each target habitat. Two dimensions of rarity were measured: abundance and habitat specialization. Two domains of rarity were identified: "among habitats" and "geographic". Some interesting patterns emerged. The high dispersal abilities of many insect and spider species together with the fact that many species from islands tend to be generalists imply that many species tend to be vagrants in several habitats and consequently are locally habitat pseudo-rarities. Two types of local pseudo-rare species were identified: "habitat (or land-use)" and "host plant" pseudo-rarities. Some species are rare in one habitat type whilst they are more common in another, often related habitat, or they are relatively rare in many habitats. This is a consequence of a "mass effect", with many species demonstrating a "source-sink" dynamics. Truly regionally rare species are those that are habitat specialists and many of them are threatened endemic species or recently introduced exotic species. We suggest several hypotheses for the patterns found, based on the former larger distribution and disturbance regimes of the native Laurel forest. Insufficient spatial replication in sampling can lead to the conclusion that numerous species appear to be rare because they were sampled in marginal sites or in the edge of their distribution. Since habitat occurrence is a less reliable predictor of the rarity status, more attention should be given to the standardized sampling of many habitats before extracting conclusions about the threatened status of a particular insect or spider species. Our results provide clear evidence that without adequate spatial data on abundance and habitat requirements, rarity status for insects and spiders on islands and elsewhere cannot be appropriately assessed.

Introduction

Island ecosystems are among some of the most disturbed and endangered of all ecosystems on earth [1-4]. Habitat fragmentation is known to have produced historical impacts on individual species abundance and distribution and on overall community species composition and diversity on islands [5, 6]. Invasive species are also having huge impacts on island indigenous biota and ecosystems [4, 7-9].

It has been estimated that in the past 600 years of human interference in natural ecosystems at least 44 000 insect species have become extinct [10]. However, only about 70 insect extinctions are documented and most of them share some ecological characteristics: i) species with narrow habitat specialization are most prone to extinction; ii) many extinct insects were victim of co-extinction processes (e.g. parasites, pollinators, plant-feeders, mutualists) (see Dunn [10]). This emphasizes the importance to clearly identify not only the patterns of rarity but also the processes involved in species extinctions. Moreover, in the field of conservation biology the mechanisms of how historical and recent land use changes in island ecosystems shape the current distribution of individual insect species have been poorly understood until now (see Howarth and Ramsay [11]).

Rarity includes three main components: i) distribution (or range size); ii) abundance; and iii) habitat specialization [12-15]:

i) range-size (distribution) - one way to examine patterns of distribution is to plot the frequency histogram of species distributions, i.e. a species-range-size distribution [14, 15]. The results of most previous studies suggest that, within a particular taxon or assemblage of species, the untransformed geographic ranges of species are distributed according to a "hollow curve" [13, 16]. Thus, most species have a narrow range while a few are more widespread, distributed evenly throughout the measured range. In some cases, the species-range-size distribution shows a bimodal pattern, in which to the left hand mode is added a right hand mode generated by the widespread group of species that occur in almost all sampled sites.
ii) abundance – this is usually a difficult variable to measure due to the huge effort needed in field work. Abundance of a species is ultimately a result of its birth and death rates, which are functions of its fitness in different environments [17]. Most species have also low densities and a few are abundant throughout their range. However, even the regionally abundant species could have low populations in many places, a pattern known as “the Taylor’s power law”, i.e. there is a positive relationship between the average local abundance of a species across sites and the spatial variance in that abundance (σ^2) [13-15].
iii) habitat specialization – oceanic islands are usually small in area but could have a diverse and patchy habitat distribution. However, few studies have evaluated the impact of habitat fragmentation on island´s native insects (but see Borges et al. [18]), and generally it is considered that most island insect species are generalists [19, 20] and eventually less prone to extinction processes.

As restricted distribution and low abundance are commonly positively correlated [13-15, 21], a great proportion of the species of a particular assemblage are therefore likely to be prone to extinction.

Associated with rarity is the concept of “pseudo-rarity” that was coined by Rabinowitz [12], to classify species that are rare only in part of their range, i.e. for species that may be regarded as rare when they are not [13]. The term “diffusive rarity” [16] was also proposed as a synonym of “pseudo-rarity”. In fact, when a study covers only part of the geographic range of the species (“partial analyses” *sensu* Gaston and Blackburn [22]), there is a great chance that the marginal part of the distribution of many species is being measured. Pseudo-rare species are often referred to as “tourists” or “vagrant”, reflecting their transitory non-resident status in a target habitat. Another possibility is that one has species that may not be regarded as rare when in fact they are, i.e. “non-apparent rarity” [13].

Data availability on the three components of rarity for island insect communities are hard to obtain, but since a recent research project (BALA Project [18, 20, 21, 23, 24]) such type of data is already available for the Azorean islands. The BALA database includes information on the spatial distribution, abundance and habitat specialization in several land-use/habitat types of several groups of arthropods in Terceira Island (Azores). Based on a standardized sampling programme both for epigean and canopy arthropods we want to know which species are truly rare and which ones are pseudo-rare vagrant species.

Two domains of rarity, “within habitat” and “geographic (i.e. island true rare species)”, will be investigated for four functional groups: two groups of herbivore insects (suckers and chewers), spiders and other predatory arthropods. This investigation aims at concentrating on the following: i) describe the anatomy of rarity in a well-sampled oceanic island (Terceira, Azores) ii) identify types of local pseudo-rare species; iii) suggest a protocol to study rarity patterns on islands.

Methods

Study area

The Azores archipelago stretches out over 615 km in the North Atlantic Ocean (37-40 ºN, 25-31 ºW), 1584 km west of southern Europe and 2150 km east of the North American continent (Fig. 1A). It comprises nine main islands of recent volcanic origin, which are distributed in three groups: the occidental group of Corvo and Flores; the central group of Faial, Pico, Graciosa, São Jorge and Terceira; and the oriental group of São Miguel and Santa Maria (Fig. 1B). The largest island is S. Miguel (745 km^2), and the smallest is Corvo (17 km^2). S. Maria is the most southerly island (37° N, 25° W), and Flores is the most westerly one (31° W). The most northerly one is Corvo (39,7° N) (see Fig. 1B).

Located at a mean latitude of 38° and surrounded by the Atlantic Ocean, the Azores enjoy the benefits of a mild and agreeable climate. The warm Gulf Stream is responsible for temperatures that are quite similar at sea level in the south-eastern as well as in the north-western islands. A marked oceanic climate with low thermal amplitude and high precipitation and humidity are characteristic of this archipelago. Given its latitude, it seems probable that the Azores should have suffered the influence of glaciations, but Coope [25] suggests that the Azorean fauna and flora have not been subjected to repeated extermination and recolonization periods as experienced by those more northerly Atlantic islands (e.g. the Shetlands, the Faeroes, Iceland and Greenland) in the wake of the comings and goings of the polar front.

The native forest in the Azores is characterized by an association of native (many endemic) evergreen shrub and tree species. Commonly known as Laurisilva, due to the presence of Laurel species (Lauraceae family), this type of forest also occurs in other islands of Macaronesia region (comprising the Azores, Madeira, Savage, Canaries and Cape Verde archipelagos). It is distinguished from other Laurisilva forests of the Macaronesia by a dense tree and shrub cover of small stature (trees have an average height of 3 m), a closed canopy, high levels of humidity and low understorey light [26].

The Laurisilva occupied large areas of all the islands 550 years ago, when the first human settlements were established on the archipelago. However, clearing for wood, agriculture and pasture, has markedly reduced its area and the native forest is now mostly restricted to high and steep areas. Most of the islands are now covered by the dominant pasture habitat used for milk-cow

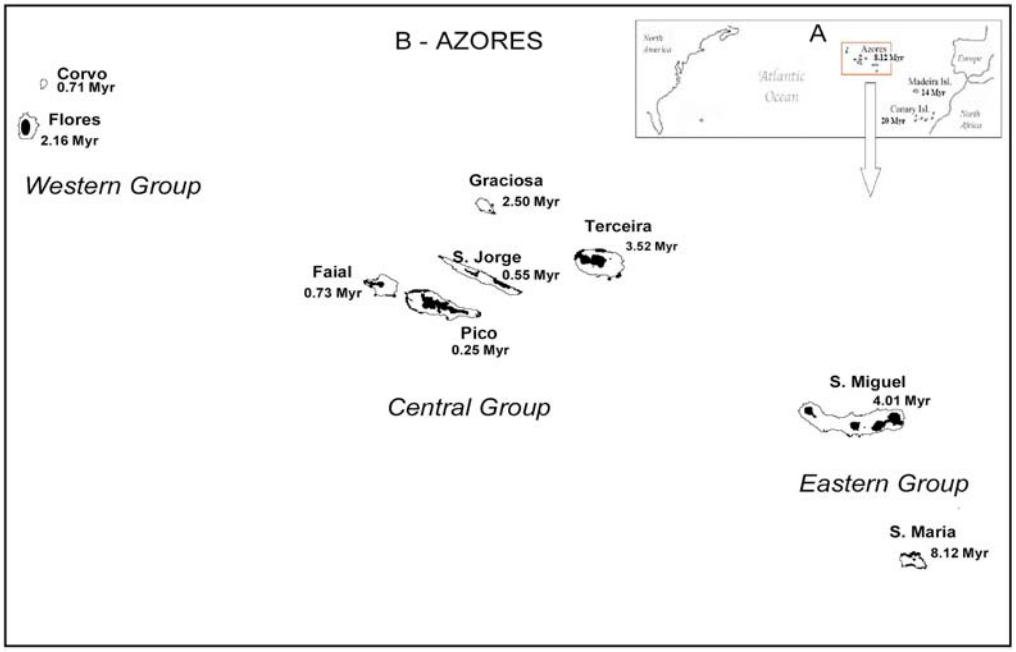

Figure 1. The location of the Azorean archipelago in the North Atlantic (A), and the nine islands of the Azores with estimated geological age (B). Shaded areas correspond to protected island areas based on recent IUCN classification.

industry, semi-natural grassland at high altitudes used mainly in spring and summer for cattle exploitation, exotic plantations of *Cryptomeria japonica* (L. fil.) D. Don and *Eucalyputs* spp., abandoned fields with exotic plants (e.g. *Pittospoum undulatum* Vent.), agriculture fields, coastal habitats (many highly disturbed) and urban areas. Other common habitats are recent lava-flows covered with the endemic early successional tree-shrub *Erica azorica* Hochst. ex Seub. and volcanic lava-tubes and pits.

Habitats in Terceira island

For the current investigation we used a gradient of land-use human alteration in Terceira island based on a recently produced land-use map (F. Dinis, unpublished). Here we are not particularly interested in the way land is managed (land cover or land-use). Our focus is on the resource availability and the ecological niche suitable for each species (see Lindenmayer and Fischer [27]). For simplicity, hereafter we will use "habitat" for the land-uses and/or habitats selected for our study. We selected the following habitats, from the highly pristine native forest canopy to the highly modified orchard canopy: a) native forest canopy; b) native forest soil (a and b are different habitats within the land-use "native forest"); c) natural pasture (soil); d) bog (soil); e) semi-natural pasture (soil); f) intensive pasture (soil); g) exotic plantation (*Eucalyptus* spp. and *Cryptomeria japonica*) (soil); h) orchard canopy (only data from the canopy habitat was available).

With regard to native forest canopy, there is data available on different plant species (see Table 1). We will also investigate patterns of insect and spider occurrence and abundance among plants. Most of the plant species are endemic to the Azores. Three of the host plants are short-leaf species (*Juniperus brevifolia*, *Erica azorica* and *Calluna vulgaris*). With the exception of *Myrsine africana* and *C. vulgaris* most species belong to genera common in Macaronesian Laurisilva.

Table 1. The most common woody plant species (trees and shrubs) present in Terceira native forests, ordered by the number of transects (out of 44) where each species was sampled.

N sites	Code	Species	Family	Structure	Colonization
35	JUN	*Juniperus brevifolia* (Seub.) Antoine	Cupressaceae	Tree	Endemic
30	LAU	*Laurus azorica* (Seub.) Franco	Lauraceae	Tree	Native
20	ERI	*Erica azorica* Hochst. ex Seub.	Ericaceae	Tree/shrub	Endemic
19	VAC	*Vaccinium cylindraceum* Sm.	Ericaceae	Shrub	Endemic
17	ILE	*Ilex perado* Aiton ssp. *azorica* (Loes.)Tutin	Aquifoliaceae	Tree	Endemic
13	MYS	*Myrsine africana* L.	Myrsinaceae	Shrub	Native
3	CAL	*Calluna vulgaris* (L.) Hull	Ericaceae	Shrub	Native
2	FRA	*Frangula azorica* V. Grubov	Rhamnaceae	Tree	Endemic

Datasets: Arthropod sampling and identification

For this investigation we use as a starting point the last published list of Azorean arthropods [28], including data from recent field studies in intensive pasturelands (F. Dinis, unpublished), exotic forests (F. Dinis, unpublished), native forests and natural pasture habitats ([28] and P.A.V. Borges and C. Gaspar, unpublished), and fruit orchards [24]. Details on arthropod sampling and identification are provided elsewhere [18, 20, 23].

All sucking (Hemiptera and Thysanoptera) and chewing (Orthoptera, Coleoptera and Lepidoptera) herbivorous insect species, spiders and other predatory arthropods (Opiliones, Pseudoscorpiones, Chilopoda and Insecta) were selected from the available databases. The herbivorous species sampled are only the free-living chewing and sucking insect species captured with beating-trays, because efficiently surveying leaf-miners and stem-borers would require other sampling methods. Therefore, four functional groups were considered: suckers, chewers, spiders and other predators.

Voucher specimens and all sorted data are stored in the reference entomological collection at the Department of Agriculture of the University of the Azores (“Arruda Furtado Collection”; curator: ´s e-mail address: P.A.V. Borges).

Data analysis

Species were classified in one of three colonization categories: natives, endemics and introduced. Native species arrived by long-distance dispersal to the Azores and are also known in other archipelagos and on the continental mainland. Endemic species are those that occur only in the Azores, as a result of either speciation events (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 being cosmopolitan species.

To examine distributional patterns we considered the frequency histogram of species distributions, that is, the species-range-size distribution [13]. We evaluate the occurrence frequency distribution of species in the various habitats using the Tokeshi statistical test for bimodality [29] that permits the calculation of the probability under the null hypothesis of the presence of larger numbers of species in the two extreme classes (one habitat only vs. all habitats) [29, 30].

To obtain the regional rarity status of each species we determined for each functional group (suckers, chewers, spiders and other predators) its “species-abundance distribution” (SAD) using the following binning system: bin 1 = number of species with 1 individual per species, bin 2 = number of species with 2–3 individuals per species, bin 3 = 4–7, bin 4 = 8–15, etc., i.e. the interval is on a log scale (see also Gray et al. [31]). Then, we considered as regionally rare all those species that were included in the first three bins (the first quartile of the available bins) following the 25% cut-off rule of Gaston [13], i.e. all species with a maximum of seven specimens in Terceira island.

Ugland and Gray [32] developed a community model assuming that a community is composed of three groups of species each differently adapted to a habitat: i) first a group containing many species which are constantly rare; ii) then an intermediate group occurring regularly in moderate population sizes, iii) finally, a group of common species that occur in large densities. Within each of these groups the species-abundance relation is symmetric and may be modelled by a normal distribution. However, the general pattern of asymmetry commonly found in nature emerges when the three groups are added. This produces a lognormal curve because most of the species are rare.

We here estimate the species abundance distributions of the three groups by the SOLVER algorithm in Excel using ordinary minimization of square difference between the frequencies of the model and observations. In this estimation procedure the parameters fall into two subsets. The first subset includes the three species number in each group under the constraint that their sum is equal to the total number of observed species. The second subset includes the three normal distributions (possibly truncated if they have densities outside the observed range of octaves) for the rare, intermediate and common groups. SOLVER minimizes the sum of the squared deviances by changing the number of species in each group (always keeping their sum equal to the total number of observed species) and the means and standard deviations of the three normal distributions.

Two types of truly rare species were identified: a) “regional”, i.e. having a small population (fewer than 7 individuals sampled in the entire island) in the region considered; b) “habitat”, i.e. those species having small populations in all the habitats surveyed (fewer than seven individuals) but being common in the region. This type of rare species could eventually be also a “pseudo-rare” species generated by the inappropriateness of sampling methods used [13].

Two types of pseudo-rare species were clearly identified: a) “habitat (or land-use)”, species that are regionally abundant and also abundant in at least one or more additional habitats, but which have a small population in the target habitat; and, b) “host plant”, species that are regionally abundant, and abundant on at least one plant in the native forest, but with low population numbers on the target plant. The source of colonists of a “host plant pseudo-rare species” for the canopy of a particular plant could be either a neighbouring large habitat (e.g. soil native forest, natural pasture, semi-natural pasture) or other dominant plants in the canopy.

The regional origin of pseudo-rare species was investigated for each functional group at two different scales: a) the island scale, on which for a particular habitat, the number of species which are abundant but rare elsewhere in other habitats, were counted; b) the native forest canopy scale, on which for a particular plant, the number of species which are abundant and rare elsewhere in other plant canopy, were counted.

All statistics, including χ^2-test were performed using SPSS 14.0 for Windows.

Results

Overall, 71209 individuals corresponding to 375 arthropod species were recorded in all sampled habitats in Terceira island (Table 2). Spiders proved to be the most abundant but not the most diverse group. Altogether, the total of predatory arthropods is almost twice the number of insect herbivores, but herbivores are slightly richer in species.

Table 2. Number of species and individuals found in Terceira island habitats. Data are presented for the overall arthropods collected (all) and separated by functional categories.

	Species		Abundance	
All	**376**		**71209**	
Insect Herbivores	195		25481	
Suckers		97		11433
Chewers		98		14048
Predatory arthropods	181		45728	
Spiders		74		34617
Other predators		107		11111

Species-range-size distributions in habitats

Regarding all the phytophagous and predatory arthropods together, it is seen that most of the species tend to occur in only one habitat or in the canopies of one or two plants (Figs 2 and 3). The Tokeshi test for modality supports this finding showing a strong left unimodal distribution of species for the two spatial scales analysed ($p_l < 0.001$ and p_r n.s.). However there are differences within each of these arthropod subsets depending on their classification as endemic, native or introduced.

In all phytophagous and predatory arthropods most of the introduced and native species had a clear maximum for those belonging to only one habitat (Fig. 2). This unimodal structure was also seen in the endemic suckers (Fig. 2a) and other predators (Fig. 2d), but the pattern was different in endemic spiders (Fig. 2b) and endemic chewing insects (Fig. 2c). For endemic spiders (Fig. 2b) there was an equal frequency of species occupying one to four habitats, while the endemic chewers (Fig. 2c) had similar frequencies for those occupying one and two habitats. Spiders on canopies from indigenous plants (Fig. 3b), showed a slight tendency for a bimodal distribution, which is, however not statistically significant (p_l= 0.0008 and p_r = 0.22). Only the introduced spiders and other predators reveal a maximum for those species occurring in the canopies of only one plant (Figs 3b,d), while the introduced sucking and chewing insects have a similar frequency for the species found in one and two plants (Figs 3a,c). Only the native suckers had a clear dominance for those occupying only one plant (Fig. 3a), while native chewers (Fig. 3c) and other predators (Fig. 3d) had approximately a similar frequency at one or two plants. In sharp contrast, the native spiders (Fig. 3b) had a similar species frequency in the canopies of 1, 6 and 8 plants. However, the endemic species show the largest atypical distributions with regard to canopy occupancies (Fig. 3) since all of the four arthropod subsets show particular patterns. This pattern is revealed by the maximum occurrence for the number of canopies for the endemics (Fig. 3): suckers (2 plants), spiders (6 and 8 plants), chewers (1 plant) and other predators (3 plants). In fact, spiders on canopies have a high proportion of species (47%) which can be found on at least six, seven or eight plants (Fig. 3b). When looking for colonization groups, indigenous spiders (i.e.

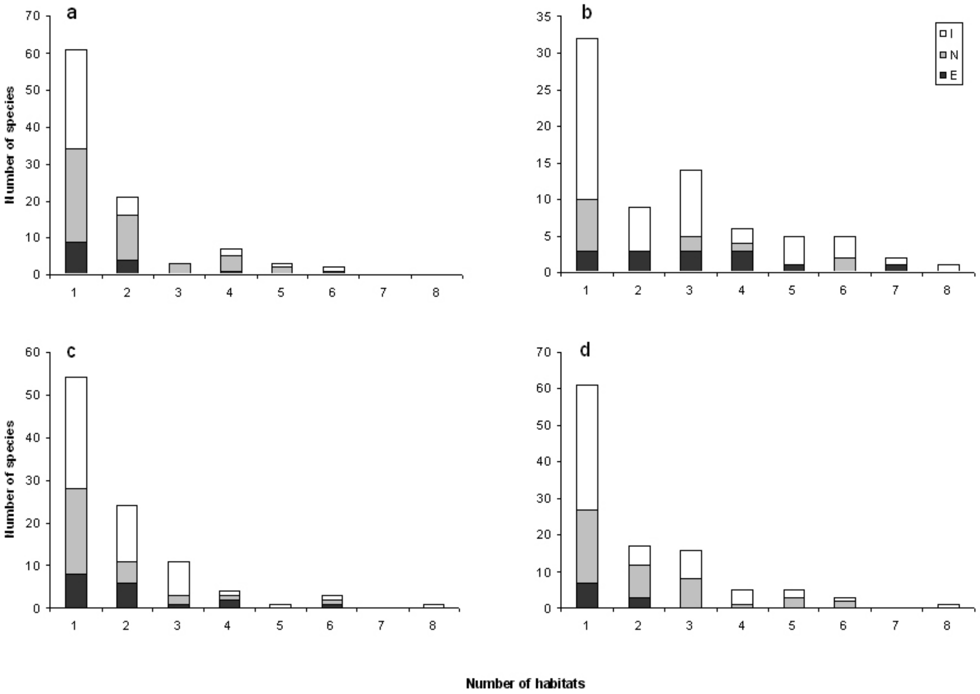

Figure 2. Frequency histogram showing the number of species of sucking insects (a), spiders (b), chewing insects (c) and other predators (d) occupying the eight studied habitats. E = endemic from the Azores; N = native from the Azores; I = introduced in the Azores.

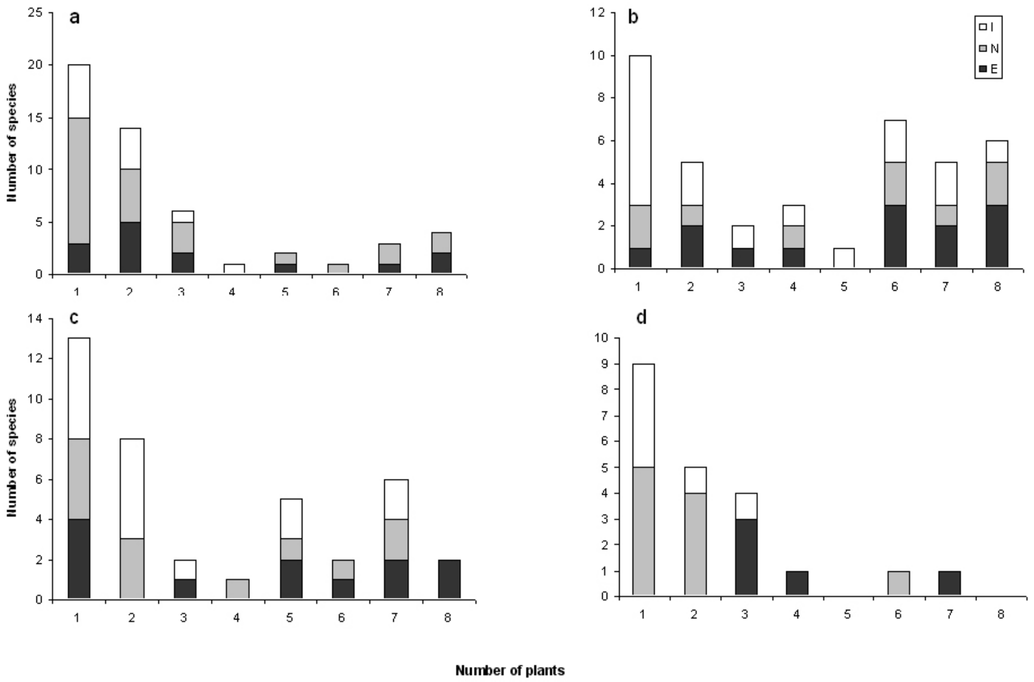

Figure 3. Frequency histogram showing the number of species of sucking insects (a), spiders (b), chewing insects (c) and other predators (d) occupying the canopies of the eight studied plants from native forest. E = endemic from the Azores; N = native from the Azores; I = introduced in the Azores.

endemic plus native) are slightly right unimodal ($p_l = 0.29$ and $p_r = 0.04$), due to the fact that 5 out of 22 indigenous species occur in the eight studied plants. Those generalist predatory spider species are widespread in the native Laurisilva forest (see Fig. 4).

Species-abundance distributions (SAD)

Species-abundance distribution plots (Fig. 5) allowed the selection of the rare regional species when based on abundance information only, selecting those included in the three first bins (i.e. all species with 7 or fewer individuals sampled). The proportion of rare species is higher in herbivores insects (Chewers: 57%, Fig. 5c; Suckers: 47%, Fig. 5a) than in predatory arthropods (Spiders: 30 %, Fig. 5b; other predators: 45%, Fig. 5d) ($\chi^2 = 6.78$; $p = 0.009$). With the exception of spiders, the mode of octave-based relative abundance plots (Fig. 5a,c,d) was clearly the first octave. In the case of spiders (Fig. 5b) the mode was in the sixth octave.

The species abundance distributions plots (Fig. 5) clearly reveal a bimodal pattern, so the lognormal distribution may only be regarded as a rough first approximation. In fact, the pattern of the four arthropod groups strongly resembles the pattern generally observed in macrobenthic communities [33].

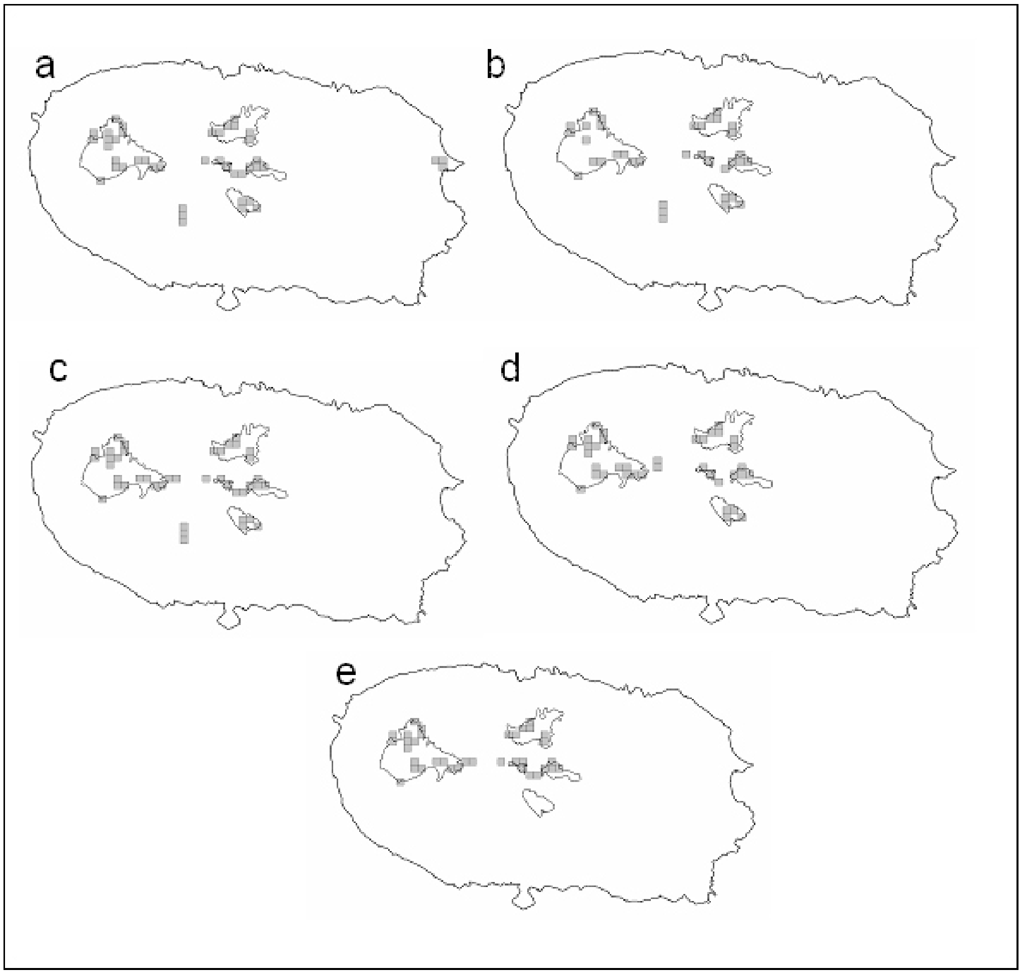

Figure 4. Distribution of the indigenous spiders *Lathys dentichelis* (Simon) (a), *Macaroeris cata* (Blackwall) (b), *Savigniorrhipis acoreensis* Wunderlich (c), *Rugathodes acoreensis* Wunderlich (d) and *Sancus acoreensis* (Wunderlich) (e) in native forest fragments of Terceira island.

According to the SAD model developed by Ugland and Gray [32], this typical bimodality is due to the integration of three different subgroups (rare, intermediate and abundant) in the community. By varying the relative species richness in each of these three groups it is possible to derive histograms with bimodality. Rather than fitting a lognormal curve to the observed histograms we therefore estimate the decomposition of the community into three abundance groups.

Figure 6 shows the application to the Azorean arthropods of the Ugland and Gray SAD model [32]. It is seen that the four functional groups differ substantially. The 97 sucking insects (Fig. 6a) have the classical pattern with a steady decline in group numbers: 44 rare, 40 intermediate and 13 abundant. In contrast the 73 spiders have a pattern that is rarely observed since the group of abundant species dominates (Fig. 6b): 27 rare, 16 intermediate and 30 abundant. Also the 98 chewing insects have a very aberrant pattern with a highly dominating intermediate group (Fig. 6c): 24 rare, 72 intermediate and only 2 common. In practice this means that the chewers only have two groups where there are three times as many intermediate species as rare ones. Finally, the 107 other predators have a characteristic three groups pattern (Fig. 3d), but while the intermediate dominates (59), there are approximately equal many rare (27) as abundant species (21). If we aggregate all the four subclasses we obtain 375 species following the classical pattern: 177 rare, 159 intermediate and 39 abundant species (Fig. 6e).

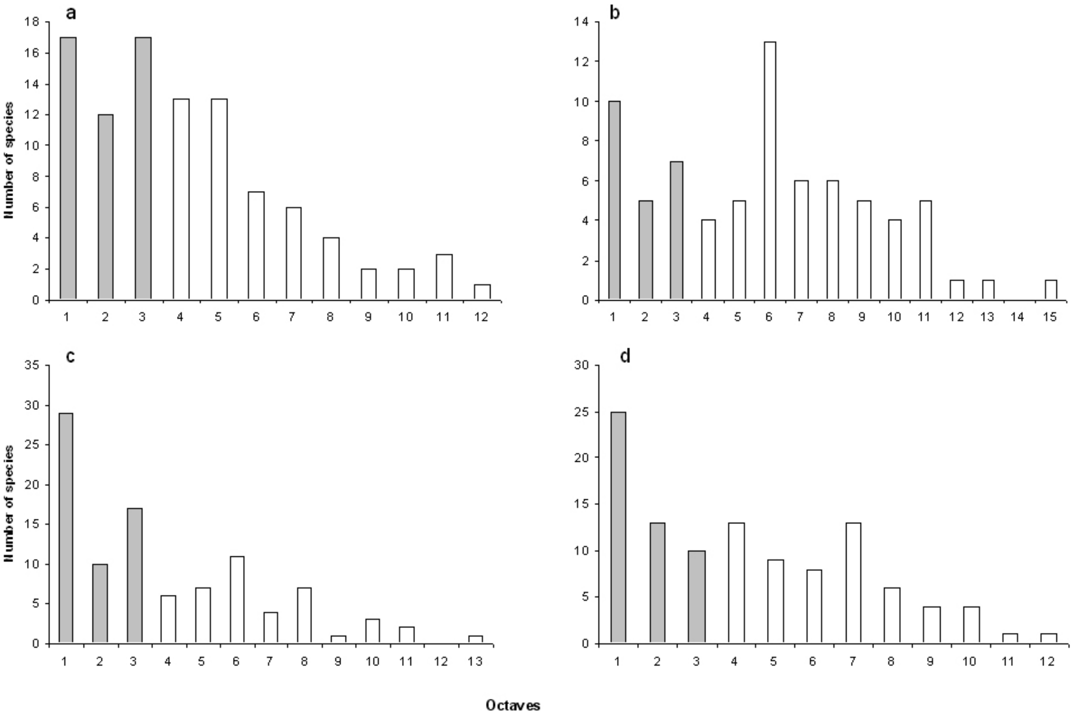

Figure 5. Species abundance distribution histograms for sucking insects (a), spiders (b), chewing insects (c) and other predators (d) from Terceira island. The grey bars are the rare species (see text).

Types of rarity

When one concentrates only on the rare species in each habitat, both aerial habitats (native forest canopy and orchard canopy) have the highest proportion of herbivorous regionally rare species (Figs 7a,c). For spiders and other predatory arthropods, the intensive pasture and orchard canopy are the habitats which have the highest proportion of regionally rare species (Figs 7b,d). Interestingly, the proportion of pseudo-rare species is consistently high (> 50% of the rare species in the target habitat) for all functional groups in the exotic

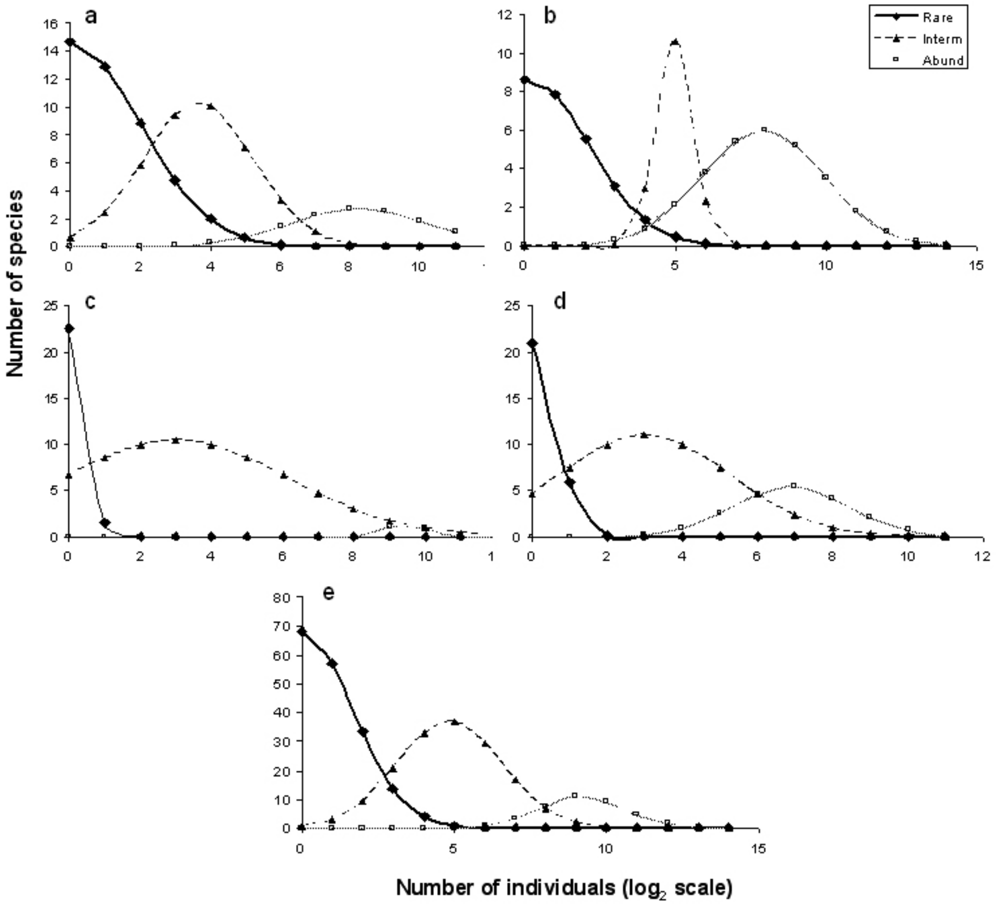

Figure 6. Decomposing species-abundance distributions into three distinct abundance groups (rare, intermediate and abundant) for: sucking insects (a), spiders (b), chewing insects (c), other predators (d), and overall arthropods (e) from Terceira Island.

plantations, bogs and natural pastures (Fig. 7). A high proportion of pseudo-rare species was also found for “other predators” in native forest canopies (Fig. 7d) and for spiders in semi-natural pastures and native forest soil (Fig. 7b). Consequently, the only functional group with a consistently high proportion of pseudo-rare species in most habitats is the spider group (Fig. 7b).

Habitat rarities (i.e. species which are regionally abundant, but rare in all habitats) are only prevalent in relation to other types of rarity in semi-natural pasture habitats for suckers (Fig. 7a) and in intensive pastures for chewers (Fig. 7c).

At island scale, the source habitats for colonists are clearly the native forest, the semi-natural and the intensive pasture for spiders and other predators (Figs 8b,d), and mainly the native forest for insect herbivores (Figs 8a,c). Most of the source species (species common in a given habitat and rare in the remaining habitats) in the native forest are indigenous to the archipelago

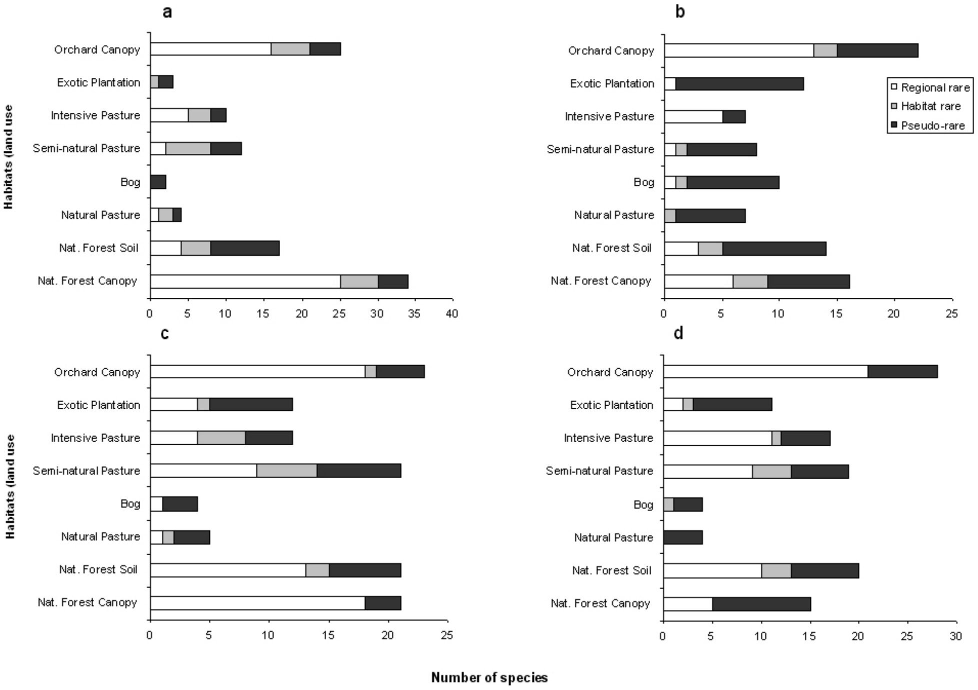

Figure 7. Number of regional, habitat and pseudo-rare species of sucking insects (a), spiders (b), chewing insects (c) and other predators (d) in different habitats from Terceira island.

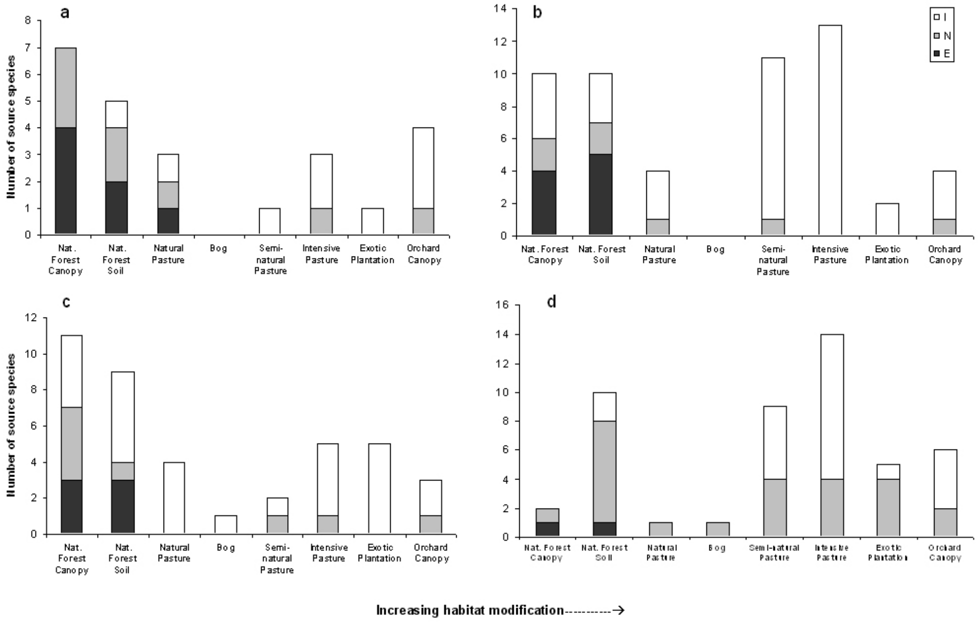

Figure 8. Number of species from source habitats, "source species" (species common in the habitat and rare in other(s) habitats) of sucking insects (a), spiders (b), chewing insects (c) and other predators (d) in different habitats from Terceira island. E = endemic from the Azores; N = native from the Azores; I = introduced in the Azores.

(endemic or native), while in the other habitats most of the species from source habitats are exotic (Fig. 8).

At canopy scale, for spiders (Fig. 9b) and herbivorous chewing insects (Fig. 9c) three plants have a clear source role, *Juniperus brevifolia*, *Erica azorica* and *Laurus azorica*. For sucking insects (Fig. 9a), several plants have a "source role", with *E. azorica* revealing a clear dominance over *J. brevifolia*. Most of the species enrolled in these dispersal movements between plants are indigenous to the archipelago (Fig. 9).

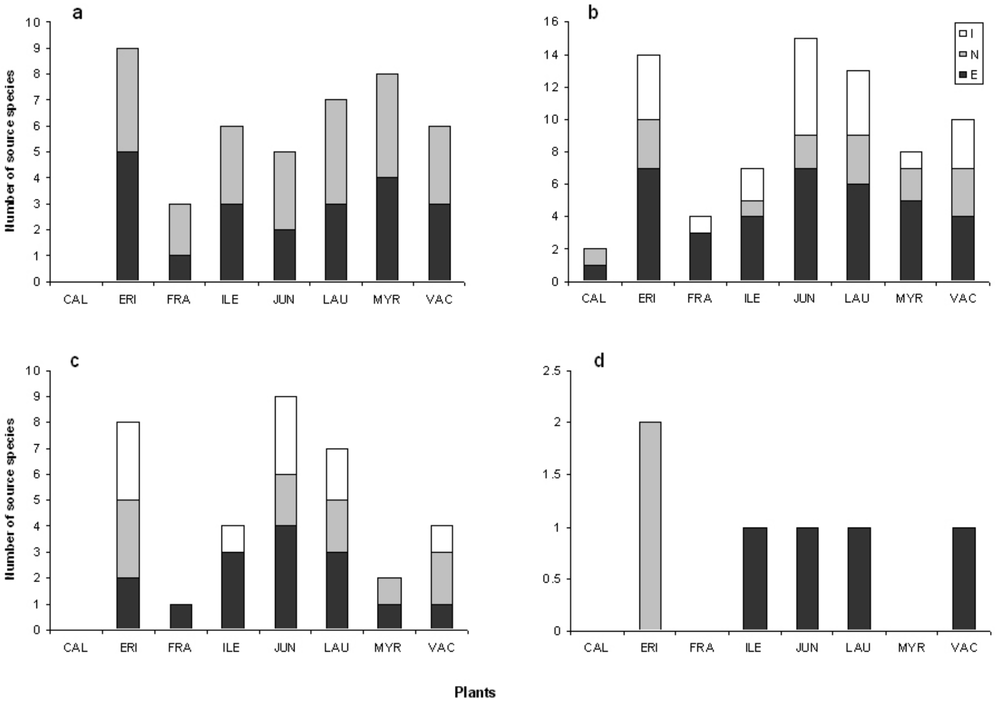

Figure 9. Number of "source species" (species common in the habitat and rare in other(s) habitats) of sucking insects (a), spiders (b), chewing insects (c) and other predators (d) in different canopies of the eight studied plants from native forest. E = endemic from the Azores; N = native from the Azores; I = introduced in the Azores. Acronyms of plant species as in Table 1.

Discussion

Nomenclature on rarity and methodological caveats

The nomenclature concerning rarity is full of specific denominations: rare vs. common (for distribution and abundance data); small population vs. large population (for abundance data); restricted vs. wide (for distribution data); unique and duplicate rare species (for restricted species – distribution data), singleton and doubleton rare species (for small populations – abundance data). Associated with this, in close connection there is the nomenclature related with pseudo-rarity: “pseudo-rare”, “tourist”, “vagrant”, “edge-species” (for both distribution and abundance data).

For the present study we used mainly abundance data to qualify the rarity status of species. However, estimates of rarity based solely on abundance may be problematic for invertebrates, since abundance data suffers from many intrinsic problems due to problems on temporal variability, disturbance regimes, local environmental variations, and biotic factors (e.g. predation, competition) [34]. However, this study is based on well replicated and properly-designed hierarchical sampling programme that encompasses several habitats and a wide range of environmental conditions in the Terceira island. Consequently we expect that our sampling programme sampled adequately not only the common species but also the rare ones, at least for taxa that are adequately sampled with the used sampling methods.

Patterns and mechanisms

The overall arthropod community here analysed is approximately log-normal (Figs 5 and 6e), a common pattern in natural communities [35, 36], which means that to the right hand tail of abundant species commonly found in all samples and habitats, a large group of rare species is added. However, the observed SADs are all bimodal (Fig 5), so more than one log-normal distribution underlies the data (Figs 6 a-d). In fact, there are striking differences in patterns of commonness and rarity between the four investigated functional groups, with only sucking insects showing the classical pattern of many rare species, a large group of intermediate abundant species and a small number of common species. The most interesting pattern is shown by spiders and chewing insects in which there is respectively a dominance of the abundant and intermediate groups. We showed elsewhere ([20] and Ribeiro and Borges, unpublished] that there is a clear dominance of generalist species in canopies of Azorean trees and shrubs. Based on our results, this holds also true for the overall spider and chewing insect communities in Terceira island. The fact that many arthropod species have a wide distribution in the island (Fig. 4) and are common or intermediately common means that there is abundant resources and low competition. The landscape is organized in a mosaic dominated by pasture, semi-natural pastures, exotic forest and native forest with high structural heterogeneity of vegetation. Thus, it seems that environmental requirements in terms of habitat structure are available throughout most of Terceira for many species of chewing insects and spiders.

All species belonging to the first three bins/categories of the species abundance distributions (SAD) are rare (Fig. 5), that is, have low populations in the island of Terceira. However, those regionally rare species are not obligatorily truly rare, since methodological bias could occur and the two methods employed to sample them (pitfall traps and canopy beating) do not sample adequately all species. In addition we emphasize that for all the four arthropod groups the estimated governing species abundance distribution for the intermediate group has density in the first three octaves. Thus, some of the species found in densities below eight individuals may at another time be found in a much larger density since these species are not truly rare, but belong to the intermediate group.

The results obtained differed clearly between herbivores insects and predatory arthropods (spiders and remaining predators). In fact, the proportion of rare species is higher among herbivores insects than among predators, which may be a consequence of more specialized niches in the herbivores. Spiders in particular showed more abundant populations (see also Fig. 6b). Moreover, the only functional group with a consistently high proportion of pseudo-rare species in most habitats is the spider group, a consequence of being able to use many types of resources and disperse easily.

When looking at the habitats, the results showed two main patterns:

i) regardless of the functional group, native forest and intensive pasture are the main source habitats. The “resource concentration hypothesis” [37], explains mainly the distribution of abundant species, and since native forest and intensive pasture are the main habitats in the island, it comes as no surprise that both work as source of colonists for the other habitats.

ii) the proportion of pseudo-rare species is consistently high for all functional groups in the exotic plantations, bogs and natural pastures. The “habitat heterogeneity hypothesis” [38] partially explains all the life histories, but it is particularly adequate for tourists (i.e. pseudo-rare species). The Terceira landscape consists of a mosaic of exotic plantations, bogs and natural pastures surrounded by a matrix of native forest and intensive pasture. In response to the landscape heterogeneity common species exploit these small habitats that are exposed to an extra fauna best adapted to the main habitats on the island.

When looking at the canopy scale (i.e. canopy of native forest plants), the results showed two main patterns:

iii) three plants have a clear source role, *Juniperus brevifolia*, *Erica azorica* and *Laurus azorica*. These are the common and more complex plants in the native forest ([20] and Ribeiro and Borges, unpublished) and consequently constitute a permanent source of colonists for the remaining plants.

iv) most of the species enrolled in colonization movements between plants are indigenous from the archipelago. In fact, few exotic insects and spiders were able to colonize the canopy habitat (see also Borges and Wunderlich [39]).

Rare species usually differ from common species in their patterns of resource usage [13, 14]. For instance, many true rare species could use resources that are themselves scarce in nature or instead use a narrower range of resources than common species. As referred above, clearly many of the pseudo-rarities are due to the fact that island species are able to use a wide range of resources and consequently can be found in many habitats, but in low numbers in those less adequate.

The observed differences between insect herbivores functional groups and spiders are somewhat intriguing, since usually we should expect that rare species in terms of abundance have a greater probability of belonging to higher levels of the trophic hierarchy. The bimodal distribution of spiders on the tree canopies in the native forest is easily explained by: i) their high dispersal ability and wide resource use; ii) taxonomic disharmony, i.e. the absence of native ants in Azorean native canopies allows the dominance of spiders in the predatory trophic guild. However, as spiders showed also a great proportion of pseudo-rarities, this means that in many of the habitats (e.g. plant canopies) few individuals are able to maintain stable populations without the help of continuous recolonization.

As referred above, the large native forest and intensive pasture habitats provide resources for two main types of organisms, indigenous and exotic species respectively. Those habitats support species that are locally common but rare elsewhere (see also below).

Conservation implications

The knowledge of the movements of introduced arthropod species from intensive pastures, where they are common, to the surrounded habitat matrix has some important conservation implications. Borges et al. [18] showed that fragments of native forest are being invaded by exotic species, and our results bring new evidence on how this is happening. Many of those species have small populations being pseudo-rare, but could dramatically affect the native habitats in the near future.

A small island like Terceira have a set of habitats that work as source for some species and sink for many species. If most human-altered habitats are poor-quality habitats (i.e. sink) for most indigenous species, then indigenous fauna could be under threat due to the fragmentation of the landscape. Our results show that there are two main types of arthropod dispersal movements in the Terceira island: i) endemic and native species are dispersing from native habitats to human-altered habitats; and ii) many exotic species are dispersing to the native forest. Moreover, within the forest, there are movements between canopy and soil and between the canopies of trees and shrubs. These complex dynamics imply that there is a continuous rain of propagules in the landscape. The wide occupancy of endemics in the canopies of indigenous trees and shrubs (Fig. 3) implies that canopy native arthropod community is largely dominated by generalist species well adapted to this specialized habitat (see also Ribeiro et al. [20]). Concentrating on common regional species, our results showed clearly that there are source-sink dynamics within Terceira island. The source-sink dynamics concept (*sensu* Shmida and Wilson [40]) explains how a species can occur in unsuitable places, maintaining populations due to immigration [40-42]. Then, the rarity patterns at a particular habitat could be caused by the so-called "mass-effects" [40].

It should be taken into account that, when inventorying diversity in only one habitat we are sampling: i) the common species well adapted to the habitat; ii) true rare species that maintain a low density population due to intrinsic factors (regional and habitat rarities); iii) ecological pseudo-rare species, those adequately sampled by the sampling methods here employed and that are maintained in the community only by the influx of immigrants from the surrounded habitats; iv) methodological and temporal pseudo-rare species, that are in fact common in the habitat but are methodological edge species not adequately sampled by the combination of techniques used in this study.

In this study we clearly identified a high proportion of pseudo-rarities in most human-altered habitats. We are aware that many of the rare chewing insects are probably methodological pseudo-rarities, since, for instance, pitfall and beating samples are not adequate techniques to sample Lepidoptera larvae and adults.

Conclusions and implications for future work

The main conclusion of this study is that many species rare in one particular habitat often are regional common species well adapted to other habitats in the landscape. On the other hand, there is also another scale to be considered, that is the island of Terceira in the context of the planet: many endemic species in Terceira island are common in native forest (see Fig. 4), but their endemic status make them world restricted rare species. The fragmentation of native forest, the spread of invasive species and the human continuous disturbance in the margins of native habitats are factors that make island regional common endemic arthropods potentially rare species in the near future.

Our results contribute substantially to the understanding of arthropod rarity patterns and mechanisms involved in pseudo-rarity in a well studied oceanic island. Since habitat occurrence is a less reliable predictor of the regional rarity status, more attention should be given to the standardized sampling of many habitats before extracting conclusions about the rarity status of a particular insect or spider species. Our results provide clear evidence that without adequate spatial data on abundance and habitat requirements, rarity status for insects and spiders on islands and elsewhere cannot be appropriately assessed. Thus, an improved understanding of the spatial extent of arthropod distribution among habitats in islands is critical to document the rarity status of species.

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