

TERRESTRIAL
ARTHROPODS
OF MACARONESIA

BIODIVERSITY, ECOLOGY AND EVOLUTION

Title

Terrestrial Arthropods of Macaronesia - Biodiversity, Ecology and Evolution

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Preface

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

Canopy habitat area effect on the arthropod species densities in the Azores: pondering the contribution of tourist species and other life histories

Sérvio P. Ribeiro & Paulo A. V. Borges

Introduction

Arthropod population densities and responses to host plant species traits and sizes are well studied in temperate (Southwood & Kennedy, 1983; Kennedy & Southwood, 1984; Brandle & Brandl, 2001; Stork *et al.*, 2001) and tropical continental ecosystems (Marquis, 1984; Ribeiro *et al.*, 1994; Price *et al.*, 1995; Basset *et al.*, 1996; Basset 1999a,b; Kruger & McGavin, 1998; Campos *et al.*, 2006; Ribeiro & Basset, 2007), but rarely on islands (but see Schowalter, 1994; Schowalter & Ganio, 1999; Ribeiro *et al.*, 2005). Ribeiro *et al.* (2005) found that the distribution of insect herbivores in Azorean forests reflected community simplification, i.e., dominance of generalists, strong island effects on species composition, and one key host species (*Erica azorica*, Ericaceae) remarkably influencing most herbivore populations. In addition, predators in Azorean natural ecosystems are mainly spiders, while ants and vertebrates are virtually absent (Borges & Brown, 2001; Borges *et al.*, 2005).

The species-area relationship (SAR) has been frequently used to investigate how host plant abundance influences insect species richness (Southwood & Kennedy, 1983; Kennedy & Southwood, 1984; Brandle & Brandl, 2001). These articles have introduced and developed the concept of the tree species density as a habitat size component and tested whether arthropod species' numbers accumulate in response to the predictability, size, and constancy (both in ecological as well as evolutionary time) of a tree host species. In this respect, Southwood & Kennedy (1983) explicitly develop the concept of trees as islands. However, no previous work has properly incorporated individual tree sizes in its analyses, and conclusions

were drawn based on population densities and the geological time of existence of the tree species.

Likewise, individuals-area relationship studies, reviewed by Connor *et al.* (2000) and further evaluated by Gaston & Matter (2002), contribute for clarifying trends in population maintenance and species co-existence in identifiable habitats. The definition and further dimensioning of specific habitats are necessary steps to proceed in such studies. Since properly described, within-community habitats may be tested as explanatory factors affecting the density and distribution of arthropods guilds, such as herbivores and predators. For instance, the crowns of any tree species populations in a forest represent fragmented habitats within the canopy, distinctly suitable for arthropods from one host species to the other.

Gaston & Matter (2002) distinguished two kinds of individuals-area relationship studies: i) PIARs – “patch individuals-area relationships”, which describe a relationship between species densities and the size of their habitat patches; ii) GIARs – “generalized individuals-area relationships”, which relate species densities to the size of the area from where those densities are measured. Usually, in PIAR studies, animal populations tend to have higher densities in larger patches or islands (Connor *et al.*, 2000), and in GIAR studies the reverse is observed, with a negative individuals-area relationship. According to Gaston & Matter (2002), GIARs are the best choice when habitat patches used by the species are hard to define as the method deals with crude densities. On the contrary, properly delimited tree crowns of different species are conveniently studied using the more precise PIAR methods.

Important ecological hypotheses are related to individual-area relationships. The “resource concentration hypothesis” (Root 1973) states that larger areas have a larger carrying capacity as more resources are available, and is the best fit model to explain the effect of one habitat type (host species) within the forest. Alternatively, the “habitat heterogeneity and encounter-frequency hypothesis” (Strong, Lawton & Southwood 1984) states that larger areas accommodate more habitats and, as a consequence of that, increases the probability of a species matching its niche demands, thus increases species numbers and densities. These hypotheses fit better a whole forest fragment area as habitat. Conversely, the “equilibrium theory hypothesis” (based on the MacArthur & Wilson’s 1967 model) states that the density of individuals remains constant allowing the number of species to vary according to area. Consequently, if the density of arthropods does not vary in relation to area, it implies that in larger habitats with more arthropod species the density of each arthropod species will decline. This model would be applicable to any individuals-area studies.

We performed a PIAR examining how plant cover area and plant crown structure influence the densities of arthropods in the canopies of one specific island, comparing various distinct natural reserves. Species densities were measured for two functional insect herbivore guilds (sap-sucking and leaf-chewing insects) and the most common predatory assembly in this system (spiders) in three different ways: i) the average number of specimens per plant; ii) the average number of specimens per transect, providing both fine and broad scales of species abundance (see Methods); iii) absolute numbers per reserve. Moreover, we investigated common *versus* scarce arthropod species distributions between various plant species.

Two general hypotheses were investigated based on the individuals-area relationship theory: “the host-habitat area hypothesis” (HYP1) and the “a tree is an island hypothesis” (HYP2). We make several testable predictions about the density of arthropods as follows:

Prediction 1 (based on HYP1) - *If there is a positive relationship between density of phytophagous insects or predator arthropods and plant spatial occupancy, the “resource concentration hypothesis” is a likely mechanistic explanation* (Root, 1973).

In the insect-plant relationship, the explanatory variable could be plant cover area measured for several distinct host species (variable: habitat type), at different scales (variable: habitat size).

Prediction 2 (based on HYP1) - *Larger areas accommodate more habitats and, as a consequence, increase the probability of a species matching its niche demands, thus increasing species numbers and overall densities.*

This predicts an output which is equivalent to the “habitat heterogeneity and encounter-frequency hypothesis” (sensu Strong *et al.*, 1984).

Prediction 3 (based on HYP1) - *Insect density accumulates at different scales in response to host species dimensions that could reflect the size of the canopy habitats.*

Hence, we tested the hypothesis that “host-habitat area” affects the following insect density estimates: mean numbers by 1) tree crowns or 2) reserve transects; and 3) total individuals for the studied island. We tested these variables against host-habitat area indices that reflect both individual numbers within certain reserves and individual numbers in relation to the frequency of the hosts in the reserves. The “resource concentration hypothesis” as well as the “habitat heterogeneity and encounter-frequency hypothesis” are non excluding mechanisms possibly related to this prediction. Indeed, resource concentration could be a nested factor within a heterogeneous and suitable habitat.

Prediction 4 (based on HYP2) - *We expect that the greater the number of islands occupied by an ancient host species and the longer it has occupied them, the more predictable is the*

habitat related to its crown, and thus may be identified by archipelago-endemic arthropod species, specialist to this host across islands.

We tested whether the distribution of host species across the islands in the archipelago (as surrogate of time of colonization) could provide a substantial explanation for the insect and spider density (“archipelago wide-ranging effect”).

Prediction 5 (based on HYP2) – *We predict that the more abundant and widespread plant species are those that are able to recruit the rarest regional arthropod species, thereby increasing insect density on their crowns.*

This prediction follows MacArthur & Wilson’s classical 1967 hypothesis, and a nested distribution pattern is expected, in which the arthropod species composition of the less abundant plant species is a proper subset of the species found in more abundant and widespread plant species.

The Azorean islands offer unique conditions for such an investigation, as their geological origins and the ecological communities of all terrestrial ecosystems are well known (Borges & Brown, 1999, 2001; Borges *et al.*, 2000, 2005, 2006). Aspects of adaptative syndromes and emergent life-history properties are discussed, as well as implications of present data for canopy insect communities in continental ecosystems, namely in the tropics.

Site description

The study was undertaken on Terceira Island, one of the nine islands of the archipelago of the Azores (North Atlantic; 37-40° N, 25-31° W). Terceira Island, the third largest island in the archipelago, is a roughly circular island of 402 km² in area, formed by four main volcanic polygenetic complexes (Cinco Picos, Guilherme Moniz, Pico Alto and Serra de Santa Bárbara) (Montesinos *et al.*, 2003). The highest point (Serra de S. Bárbara, 1023 m) is also the most recently formed (0.025 Myr B.P.) of the four major island complexes (Self, 1982), and the presence of trachytic and basaltic flows suggests that Santa Bárbara is an actively growing volcano (Calvert *et al.*, 2006).

The climate is temperate oceanic, with relative atmospheric humidity that can reach 95% in the native, evergreen forest at high altitude, and small temperature fluctuations throughout the year. The predominant vegetation form is “Laurisilva”, or laurel forest, a humid evergreen broadleaf and microphyllous (hereafter short-leaf) laurel type of forest that originally covered

most of Western Europe during the Tertiary (Dias, 1996). For more details on the native vegetation of these islands, see Fernández-Palacios & Dias (2002) and Ribeiro *et al.* (2005).

Experimental design and host plants

The study was undertaken in eight fragments of laurisilva within protected areas in Terceira Island. The forest fragments sampled include one of the largest and best preserved Laurisilva forests of the Azores (“Serra de Santa Bárbara and Mistérios Negros”) (see Borges *et al.*, 2006), part of the NATURA 2000 European Community Conservation scheme. A total of 44 transects of 150x5 m were established randomly to quantify arthropod diversity, and distributed proportionally to the size of the fragments (Table I). The analyses developed here deal with the adjustment of different sampling sizes, which was necessary to detect insect species variation related to increasing habitats and resources in large reserves (see further discussion on the sampling design in Borges *et al.*, 2005, 2006; Ribeiro *et al.*, 2005). For each transect, the three most abundant and common woody plant species (trees and large shrubs) were sampled (Table I). The sampling followed a block design based on 10 replicates that grouped together one of each tree species, separated by 15m intervals along the transect. Arthropods were sampled from one branch per tree. In most cases, three plant species were clearly dominant, and the choice of sampled host was quite obvious. However in some transects, fewer than three dominant woody plant species were present, so the survey was restricted to these (see Ribeiro *et al.*, 2005), while in some other transects, more than three plants were sampled to reflect their high frequency (Table I).

In total, seven species were sampled (see Table I). Most of the species are Azorean endemics. With the exception of *Myrsine africana* and *Calluna vulgaris*, most species are exclusive to the Macaronesian Laurisilva. Three of the host plants are short-leaf species (*Juniperus brevifolia*, *Erica azorica* and *C. vulgaris*). The Azorean Laurisilva forest is characterized by reduced tree height (usually up to 5 m, rarely reaching 10 m), shaped by the volcanic, shallow soil and sinuous terrain, which rises to tree top level in some areas, and falls five to six meters below in other areas. A high crown foliage density, and thus low canopy openness is typical of these forests, which also display a particularly dense cover of moss and liverwort epiphytes (see Gabriel & Bates, 2005).

Table I. List of the host plants sampled for arthropods and distribution per fragment and transects. The colonization status of the species is given (END – endemic to the Azores; NAT – native of the islands, but not endemic).

Plant species	Family	Status	Transects (Total =44)
<i>Juniperus brevifolia</i> (Seub.) Antoine	Cupressaceae	END	35
<i>Laurus azorica</i> (Seub.) Franco	Lauraceae	END	30
<i>Erica azorica</i> Hochst. ex Seub.	Ericaceae	END	20
<i>Vaccinium cylindraceum</i> Sm.	Ericaceae	END	19
<i>Ilex perado</i> Aiton ssp. <i>azorica</i> (Loes.) Tutin	Aquifoliaceae	END	17
<i>Myrsine africana</i> L.	Myrsinaceae	NAT	13
<i>Calluna vulgaris</i> (L.) Hull	Ericaceae	NAT	3

Species in the fragment sample	Fragment	Total number of transects in the fragment
<i>Erica azorica</i>	Algar do Carvão	2
ALL	Biscoito da Ferraria	8
<i>Laurus azorica</i> , <i>Erica azorica</i> , <i>Vaccinium cylindraceum</i>	Caldeira Guilherme Moniz	4
<i>Erica azorica</i>	Corrente Lava	1
<i>Juniperus brevifolia</i> , <i>Laurus azorica</i> , <i>Erica azorica</i> , <i>Vaccinium cylindraceum</i>	Matela	2
<i>Juniperus brevifolia</i> , <i>Ilex perado</i> Aiton ssp. <i>azorica</i> , <i>Laurus azorica</i> , <i>Vaccinium cylindraceum</i>	Pico Galhardo	4
ALL	Serra Santa Bárbara	16
ALL	Terra Brava	7

Arthropod sampling and identification

For the canopy arthropod sampling, a modified beating tray was used, that consisted of a cloth-inverted cone of 1 m in diameter and 60 cm deep (after Basset, 1999a; Ribeiro *et al.*, 2005). A 1-litre plastic bag was placed at the bottom, where arthropods, leaves and small branches were collected. For each selected plant, a branch was chosen at random, the beating tray was placed beneath and the branch was hit five times with a beating stick. Whenever possible, sampling was performed on warm, sunny days, and always when the vegetation was

dry. Samples were labelled and frozen until they were sorted. The sorted specimens were stored in 70 % ethanol with glycerol.

Arthropod identification was performed by trained parataxonomists who sorted samples into morphospecies (or RTUs = recognizable taxonomic units, *sensu* Oliver & Beattie, 1996) using a non-complete reference collection. A senior taxonomist (P.A.V. Borges) then performed a detailed correction in identification of each sample, adding new species or morphospecies to the reference collection. In many cases, morphospecies were sent to expert taxonomists for identification to the species level (see Borges *et al.*, 2005). Immature stages were also considered in the identification process. For the current manuscript, all sap-sucking (Hemiptera and Thysanoptera) and leaf-chewing (Orthoptera, Coleoptera and Lepidoptera) herbivorous insect species, and predatory spiders are considered. The herbivorous species include only the free-living sucking and chewing insect species captured with beating-trays, as surveying canopy leaf-miners and stem-borers would require other sampling methods (see Ribeiro & Basset, 2007). Voucher specimens and all sorted data are stored in the reference insect collection in the Department of Agriculture of the University of the Azores (“Arruda Furtado Collection”; curator’s e-mail address: pborges@uac.pt).

Data Analysis

The host habitat area hypothesis

Host plant spatial indices - In order to define the habitat size at the level of the tree species crown within a forest canopy, we found it appropriate to determine an estimate of the volumes of such habitats relative to other adjacent habitats (other host species crowns), and to consider such dimension rather than a simple bi-dimensional area measurement. At the individual plant scale, each crown size was defined from one single crown dimension, the branch length, which represented the actual dimension of a micro-habitat from where insects were sampled. Branch length has previously shown a strong correlation with other tree architecture dimensions (Ribeiro *et al.*, 2003). In addition, the average tree species height was used to complete the measure of plant size, and the number of trees per 10 m² was used to scale up the individual volume from a local habitat scale to the forest scale (data from Alves, 2005). Such volumes were used to calculate two habitat-dimension indices.

The “area-habitat index” (AHI):

$$\mathbf{AHI (HOST } i) = \text{Br (HOST } i) * \text{H (HOST } i) * \text{D (HOST } i)$$

Where (Br) is the average length of the sampled branches in Terceira (taken from a sub-set of 20 individuals of each species sampled in both continuous, well-preserved reserve and fragmented, more vulnerable forests - see Cardoso *et al.*, 2007); (H) is the average height of the species (described for the islands in previous works – see Ribeiro *et al.*, 2005); and (D) is Alves (2005) measurements of host plant density per 10 m² along transects in Terceira. The index provides an estimate of the habitat volumetric measure for each host species at a local scale (Table II).

The “regional-occupancy index” (ROI),

$$\mathbf{ROI (HOST } i) = \text{AHI (HOST } i) * \Sigma (T)$$

is the product of AHI and the sum of the (T) transects where the host species was found (see Table I). This index gives a volumetric measure of the habitat of the host species adjusted to a larger scale, which represents the host frequency in different reserves/locations.

Table II. Area-habitat (AHI) and regional-occupancy indexes (ROI) (values are log-transformed).

Species	area-habitat index	Regional-occupancy index
<i>Juniperus brevifolia</i>	2.195325705	3.739394
<i>Laurus azorica</i>	1.882312062	3.359433
<i>Erica azorica</i>	1.626367515	2.927398
<i>Ilex perado azorica</i>	1.457784431	2.085233
<i>Myrsine africana</i>	1.344675788	2.688233
<i>Vaccinium cylindraceum</i>	0.806479756	2.458619
<i>Calluna vulgaris</i>	0.524216245	1.001337

Because our calculation deals with both population density (in the ROI equation) and frequency per reserve, we were able to draw stronger conclusions compared with Strong’s work (1974a,b), which calculated habitat area without testing the differences between sparsely, yet widely, distributed species from those locally abundant and regionally dominant species. Finally, the concept of a habitat area-volume (hereafter habitat size) as defined by the distribution and size of such host species was applied in a way that seems more effective than

that employed by Southwood (1961), Strong (1974a) or Claridge & Wilson (1978), based on fossil records. Whereas Claridge & Wilson (1978) themselves criticized the geological data base used for the analyses of UK flora area effect, we chose to consider the distribution range of a species in the archipelago (see the “Archipelago wide-ranging effect” analysis below), along with life history traits, to evaluate its evolutionary importance when interpreting the results.

Arthropod density measures and spatial scale - Both indices were tested for all arthropods/feeding guilds in separate, and accordingly to the scale of interest: forest, host population, or island scale. By considering the number of arthropods at each of these scales, we controlled variances and dealt with the blocking design, ultimately avoiding the undesirable effects of spatial autocorrelations. First,

Mean arthropod (FOREST SCALE) =

$$\log_{10} (\Sigma (\text{individuals on HOST}_i \text{ crowns}) / \text{no of sampled (HOST } i \text{) crowns})$$

Thus, the number of herbivore insects/spiders actually obtained from each sample was used to give the mean number of insects/spiders per tree crown per host species. This value was used to investigate the effect of habitat area-volume on “alpha density”, or, local packing of populations at the forest scale. Second,

Mean arthropod (HOST POPULATION SCALE) =

$$\log_{10} (\Sigma (\text{individuals on HOST}_i \text{ crowns}) / \text{no of sampled Transects})$$

i.e., the total number of herbivore insects/spiders sampled on each host species was averaged by the number of transects in which that host species occurred across reserves. This value reflects regional density adjusted by sampling size, and should represent host population scale. Finally,

Total arthropod (ISLAND SCALE) =

$$\log_{10} (\Sigma (\text{individuals on HOST}_i \text{ crowns}))$$

i.e., the total number of herbivore insects/spiders in the sampling universe was tested comparing hosts across transect/reserves, thus the island scale (or “gamma” density).

“Archipelago wide-ranging effect” – Furthermore, a stepwise multiple regression analysis testing the effect of ROI along with the effect of the host species frequency in other islands in the Azores was undertaken to determine the importance the host colonization history for inter-island insect density maintenance (tested for the log distribution of the total number of arthropods).

The tree as an island hypothesis: rarity status and life histories

In order to test whether the accumulation of rare species could affect overall insect/spider density, we determined the number of rare insect/spider species associated with each of the plant species. This enabled further test of the HYP2 (the hypothesis that “a tree is an island”), by considering patterns of rarity at different scales (see Southwood & Kennedy, 1983; Kennedy & Southwood, 1984; Brandle & Brandl, 2001).

First, we determined for each plant the associated arthropod “species abundance distributions” (SAD) using the following binning system (modified \log_2 classes): 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., thus the interval is on a log scale (see also Gray *et al.*, 2006). We considered as rare all species included in the first three bins (the first quartile of the 12 available bins), i.e., all species with a maximum of seven specimens on a particular host plant. Regionally rare species are those with a maximum of seven specimens sampled from all plants on Terceira Island. Pseudo-rarity status was investigated for species that were rare at both the forest and host population scales. Therefore, species rare in one host species and abundant in others were defined as “host-tourists” when found in the former. Further, previous knowledge on the fauna of natural, semi-natural and intensive pastures (Borges & Brown, 2001; Borges *et al.*, 2008) allowed us to coin the definition of “habitat-tourists”, i.e., species that are rare in the whole canopy but are abundant pasture specialists.

Additional analysis

We used ordinary linear least-squares (OLS) regression analyses to test the impact of tree architectural simplification (calculated as $1/AHI$) on number of arthropod individuals. For this purpose, we calculated, for each functional group (sap-sucking, leaf-chewing and spiders), the percentage of “tourist species” and used these percentages as response variables in regressions against $1/AHI$. We performed an arcsine transformation [$y' = \arcsin(\sqrt{y})$] of the proportions of “tourist species” and then performed regressions on the arcsine-transformed

proportions against 1/AHI. This analysis allowed us to investigate the accumulation of pseudo-rare species common elsewhere in the canopy (i.e. on other trees).

Log₁₀ transformed habitat indices and arthropod variables were used for several reasons: a) to overcome the non-constant variance and non-linearity of the data; b) because higher r^2 values were consistently obtained when using the log-log model; and c) because the residuals appeared to show no pronounced patterns or structure in the log-log model.

The OLS regression and correlation statistics were performed using SPSS version 14.0.

The host-habitat area hypothesis: chosen hosts at local scale do not affect the positive effect of habitat size at island scale

Arthropod density at a local/forest scale

Whatever index was used, the total number of arthropods did not vary significantly with increasing habitat area (Appendix 1), although regression models using AHI showed a better fitted slope (0.28) than models using ROI (0.18). Such lack of significance was due to the herbivorous insects, which did not vary with habitat size when averaged by tree crown (Figure 1a; Appendix 1). Still, a strong positive outlier appeared due the larger than expected insect herbivore numbers on the crown of *E. azorica* (Figure 1a). On the other hand, spiders responded positively to habitat area at this scale, showing a 0.3 increase in individuals per area, in a model that explained 55% of the data variance ($\text{Log } N = 0.3064 \cdot \text{Log AHI} + 0.516$; $F_{1,6} = 6.25$, $p < 0.05$; Fig 1b). For spiders, *E. azorica* was not an outlier, suggesting that this host species accumulates only a greater number of herbivores than other plants.

Arthropod density at a regional/host population scale

When testing the total arthropod density at the host population scale, a significant pattern was masked by the contrasting responses of herbivores and spiders. However, at this scale, total herbivores, as well as separated sap-sucking and leaf-chewing guilds responded positively to increasing host habitat area (Fig. 2), while spiders did not (Appendix 1). Sap-sucking insect density increased at a rate of 0.49 per increase in host area (Fig. 2a) and leaf chewing insects increased by 0.59 (Fig. 2b), while both models explained similar levels of data variance. The data adjusted better to the AHI index at this scale. Nevertheless, the spider

density distribution actually showed larger variance unrelated to host-habitat areas at this scale.

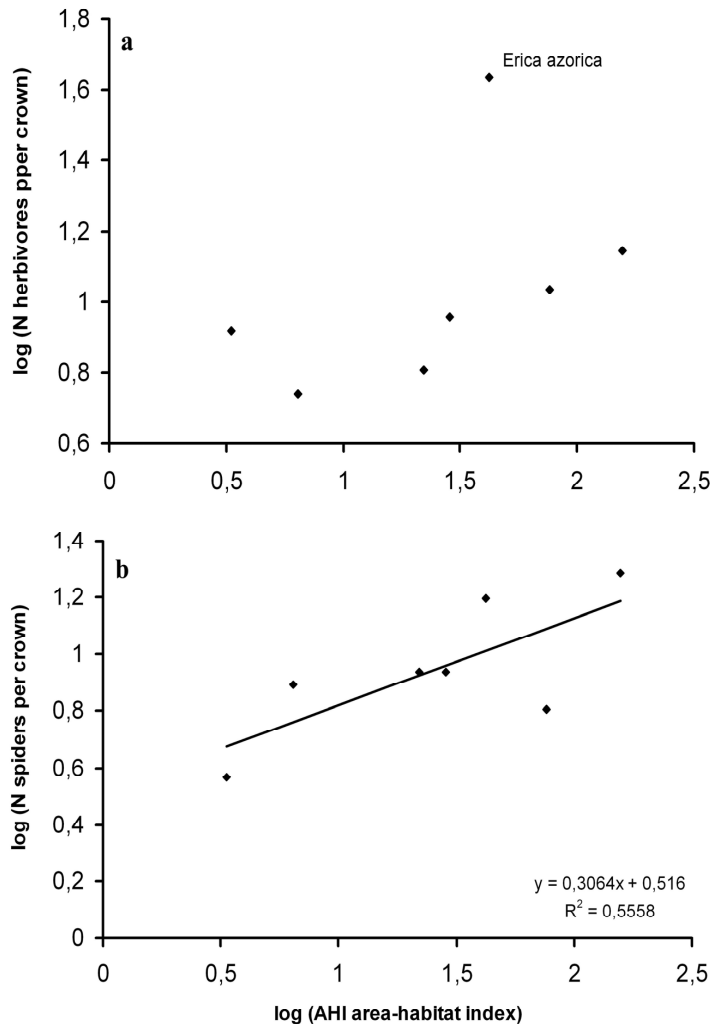


Figure 1. Log mean number of herbivores (a) and spiders (b) per crown as a function of the logarithm of the “area habitat index” (AHI). *Erica azorica* is an outlier only for herbivores.

Arthropod density at a gamma/island scale

Overall arthropod density at this scale resulted in significant models, although the data adjusted better to the ROI than to AHI index (Fig. 3). Sap-suckers and spiders showed increases in abundance of 0.59 and 0.83, respectively, per unit of increasing habitat, and the ROI models explained 83% and 86% of the data variance of both guilds. Leaf-chewers’ models were not significant mainly due to the much greater than expected number of chewers on *E. azorica* (Appendix 1, Fig. 3).

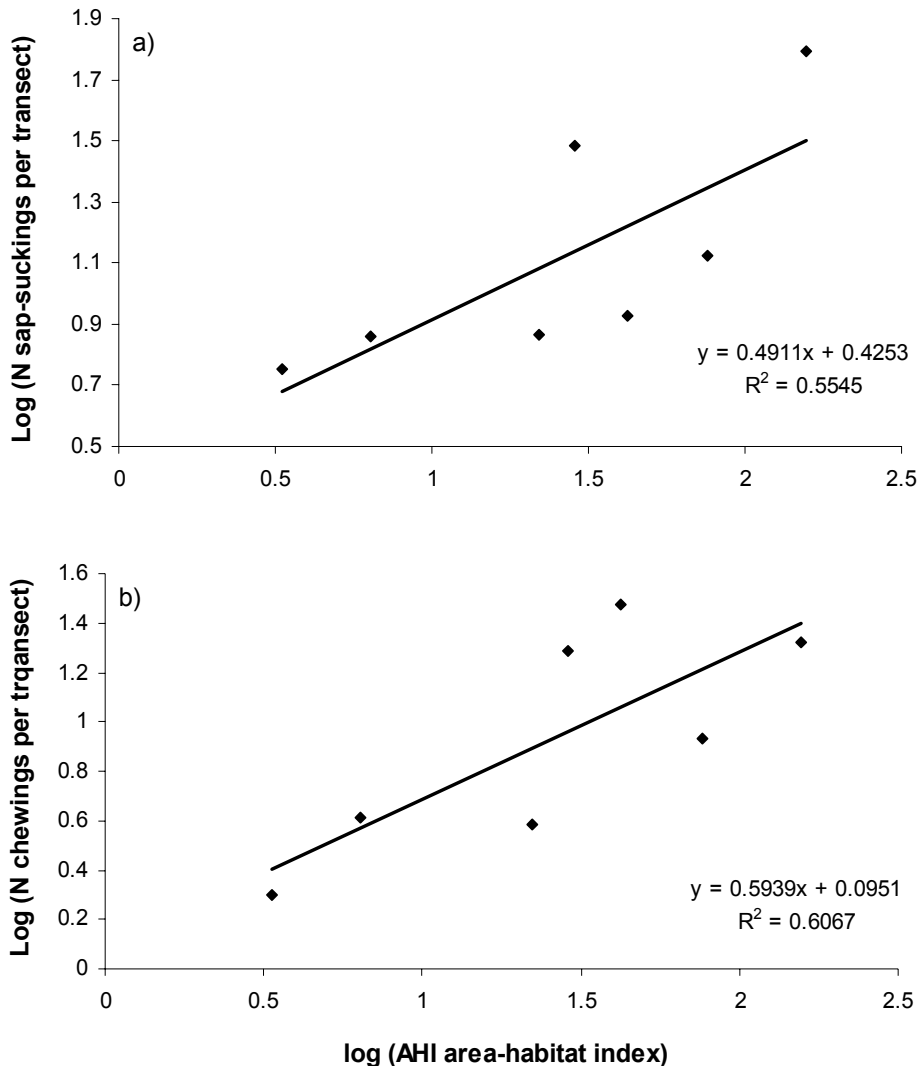


Figure 2. Log mean number of herbivore per transect (sap-sucking – a; leaf-chewing – b) as a function of the logarithm of the “area habitat index” (AHI).

Arthropod density at the gamma/island scale and the archipelago wide-ranging effect

The best suited model for testing the island effect on number of arthropods included the ROI index plus the host frequency in the different islands of the Azores. This model explained 98.5 % of the data variation versus 86.2 % when including only the ROI index [Log N = 0.36*(Log ROI) + 0.17*(Frequency in archipelago) + 1.8; ANOVA $F_{2,6} = 130.18$, $p < 0.0001$; t-test for ROI = 6.6, $p < 0.003$; t-test for Frequency in the Archipelago = 5.7, $p < 0.005$].

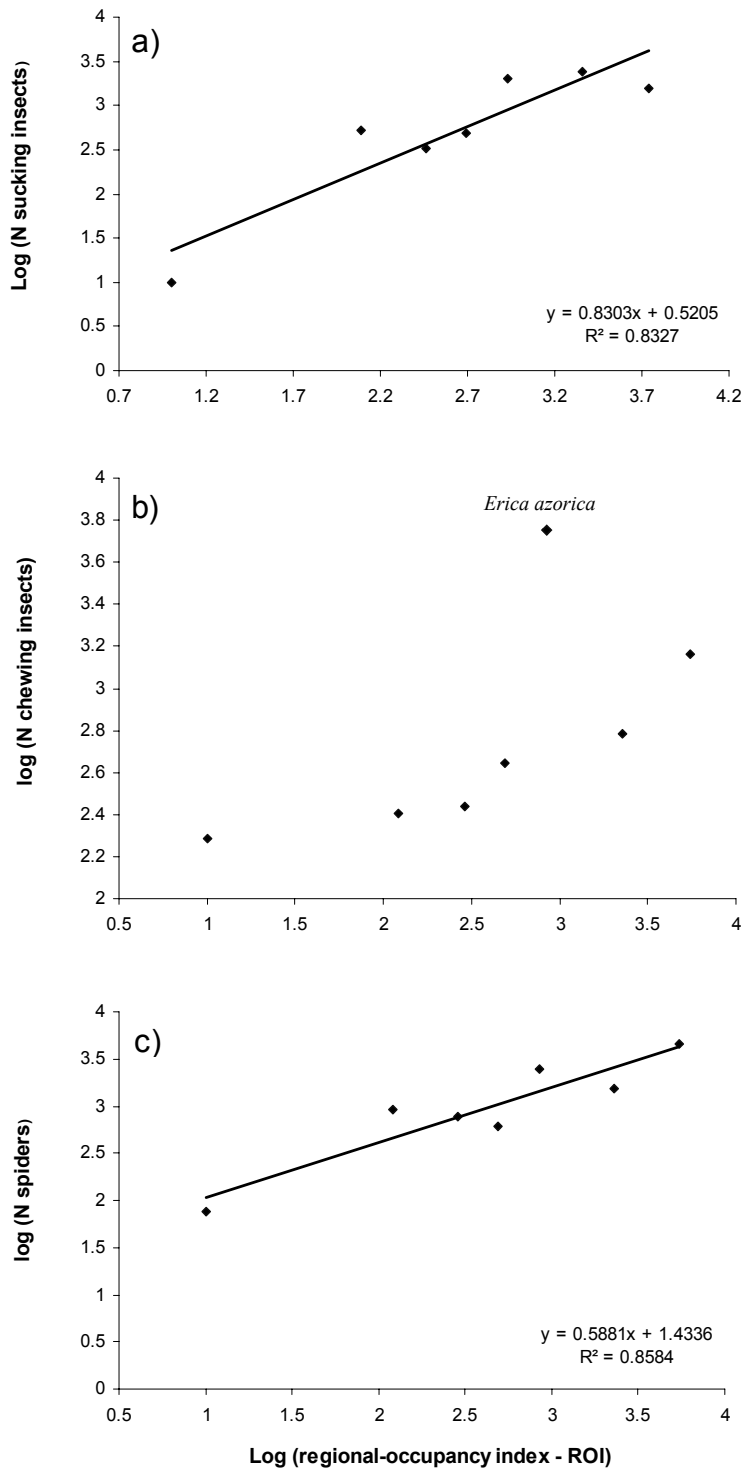


Figure 3. Log mean number of herbivore per reserve (sap-sucking – a; leaf-chewing - b), and spider (c) individuals as a function of the logarithm of the “regional-occupancy index” (ROI).

The tree as an island hypothesis: how many arthropods are accidentally captured and how many evolved to choose large, and evolutionarily predictable habitat?

The three structurally most complex and abundant “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”. Particularly for spiders, half of the density found on these three hosts was related to the sum of individuals of rare species in the ecosystem, including a substantial number of pasture specialist species (i.e. “habitat-tourists”) (Table III).

Both individual plant size and population wide range, thus the predictability of the host habitat in time and space, affected positively the arthropod species’ density and distribution. Although these tree species capture regional rare species as expected, we also found that both *E. azorica* and *J. brevifolia* have many real rare insect species feeding exclusively on them (Table III). Thus, the most complex and abundant tree species accumulate more habitat and feeding specialist herbivores, as a consequence. Nevertheless, the observed rarity pattern clearly showed that *J. brevifolia* and *E. azorica* hardly presented host-tourists (Figs. 4a, e), conversely to smaller host habitats. For sap-sucking insects, the tree species with lower proportions of rare “host-tourists” were *E. azorica* and *L. azorica* (Fig. 4c), both large habitats. On the contrary, other host tree species do had high proportions of the low-density leaf chewing insect and spider species which were abundant on *J. brevifolia* and *E. azorica* (Figs. 4a, e).

In addition, there was found a strong correlation between the index of tree architecture simplification ($1/AHI$) and proportion of “host tourists”. Therefore, the proportion of rare species that are common on other plants increases in simpler plant species for leaf chewing insects ($r = 0.76$; $y = 0.38x + 0.40$; $F_{1,5} = 6.76$, $p = 0.04$; $r^2 = 0.58$) (Fig. 4b); sap-sucking insects ($r = 0.69$; $y = 0.26x + 0.34$; $F_{1,5} = 4.59$, but only marginally significant, $p = 0.08$, $r^2 = 0.48$) (Fig. 4d) and spiders ($r = 0.84$; $y = 0.48x + 0.30$; $F_{1,5} = 11.74$, $p = 0.018$; $r^2 = 0.70$) (Figure 4f). Hence, *J. brevifolia*, *E. azorica* and *L. azorica* appear to define the arthropod community in such a powerful way that their abundant specialists species are frequently recruited as tourists by other hosts, where these insects occur in lower densities.

Table III. Number and percentage of regionally rare species, total number of species, total number of rare species and total number and percentage of abundant species, in each host plant for sap-sucking insects, leaf chewing insects and spiders.

Plant host species	Total number of species	Total number of rare species (*)	Number of regional rare species	% Regional rare species	Number of abundant species	% abundant species
Sap-sucking herbivores						
<i>Juniperus brevifolia</i>	24	18	11	61	6	25
<i>Erica azorica</i>	29	19	13	68	10	34
<i>Laurus azorica</i>	21	13	9	69	8	38
<i>Ilex perado azorica</i>	18	12	5	42	6	33
<i>Vaccinium cylindraceum</i>	12	4	2	50	8	67
<i>Myrsine africana</i>	21	12	8	67	9	43
<i>Calluna vulgaris</i>	9	8	3	38	1	11
Leaf chewing herbivores						
<i>Juniperus brevifolia</i>	30	16	13	80	14	47
<i>Erica azorica</i>	21	11	5	45	10	48
<i>Laurus azorica</i>	26	16	8	50	10	30
<i>Ilex perado azorica</i>	23	16	7	44	7	34
<i>Vaccinium cylindraceum</i>	18	11	5	46	7	39
<i>Myrsine africana</i>	14	10	2	20	4	29
<i>Calluna vulgaris</i>	5	4	0	0	1	20
Spiders						
<i>Juniperus brevifolia</i>	30	12 (4 pasture specialist tourists)	7	58	18	60
<i>Erica azorica</i>	32	17 (6 pasture specialist tourists)	9	53	15	47
<i>Laurus azorica</i>	25	11 (5 pasture specialist tourists)	4	36	14	56
<i>Ilex perado azorica</i>	26	17	5	29	9	35
<i>Vaccinium cylindraceum</i>	27	16	3	19	11	41
<i>Myrsine africana</i>	25	16	2	13	9	36
<i>Calluna vulgaris</i>	12	9	0	0	3	25

(*) Actual regional rare species + habitat tourists + host tourists.

The evolutionary role of long lived and large host-habitats

Population density is a life history component, and for canopy arthropod species it reflects fitness or survival chances in different tree species. In other words, insect densities reflect enemy-free space, nutritional harshness and other unmeasured environmental conditions (Price, 1994; Price *et al.*, 1998; Ribeiro *et al.*, 2005).

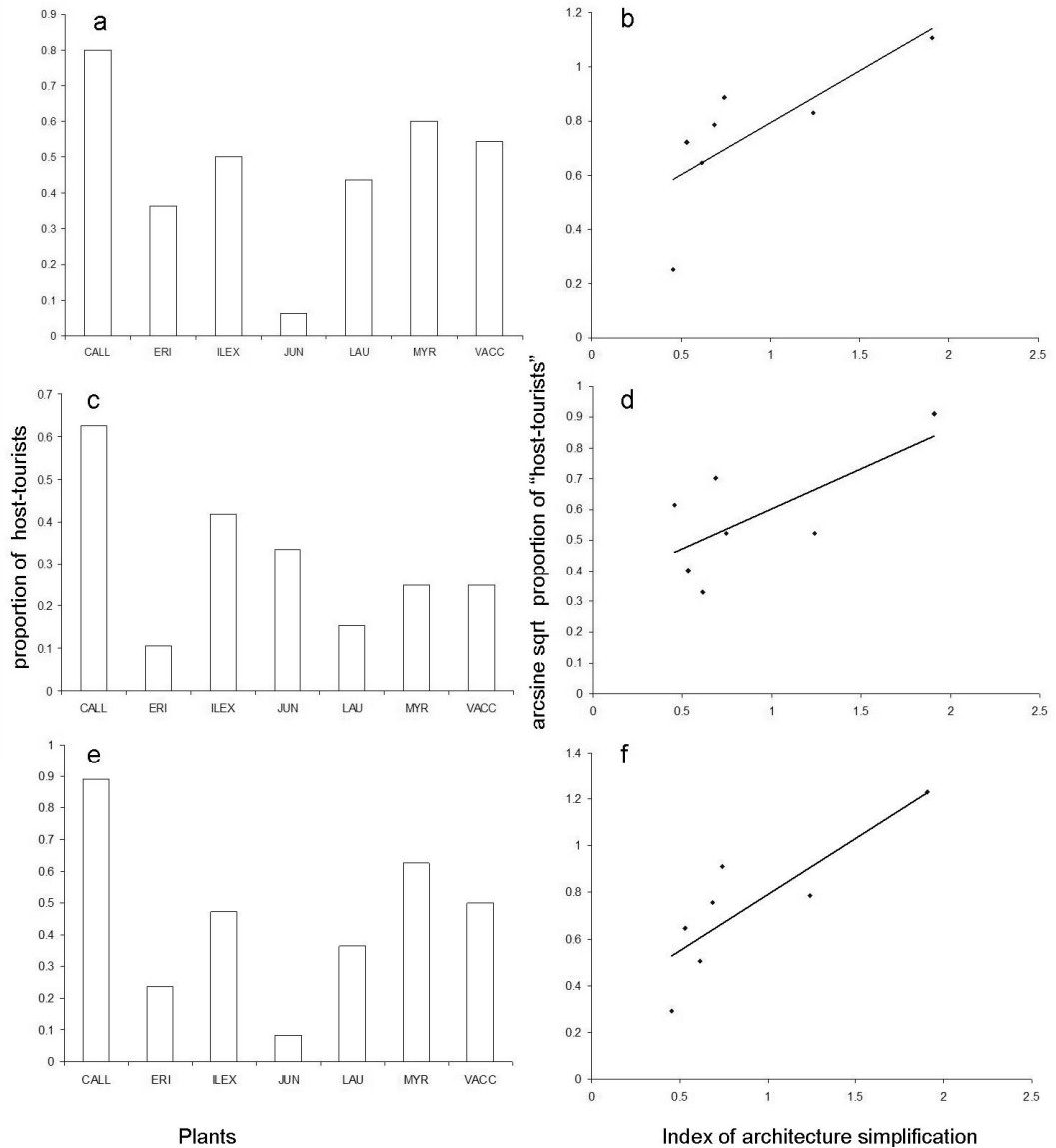


Figure 4. Proportion of rare species of leaf chewing insects (a), sap-sucking insects (c) and spiders (e) common on other plants (i.e. “host-tourists”) for the studied trees and shrubs, and the relationship between the arcsine sqrt proportion of “host-tourists” and the index of architectural simplification (1/AHI) for leaf chewing insects (b), sap-sucking insects (d) and spiders (f) (see text for further explanations). CALL - *Calluna vulgaris*; ERI - *Erica azorica*; ILEX - *Ilex perado azorica*; JUN - *Juniperus brevifolia*; LAU - *Laurus azorica*; MYR - *Myrsine africana*; VACC - *Vaccinium cylindraceum*.

In terms of population density, four important spider and insect life histories were detected in this study: 1) dense and intermediately dense species; 2) truly rare species, which are rare on any host species and then 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 - habitat-tourists - (see also Borges *et al.*, 2008). Those life histories can then be studied grouped by guilds or separately in order to test habitat area effects. Some classical habitat area-related explanatory hypotheses are supported by the present data, and show similarities with the two hypotheses currently developed here. Figure 5 summarizes the hypotheses, predictions and findings of this work. “The resource concentration hypothesis” (Root, 1973) explains mainly the distribution of abundant species/life histories. In the present study, most abundant arthropods occur preferentially on *J. brevifolia* and *E. azorica*, or *L. azorica*, which have the largest crowns and the densest and most widespread populations. This hypothesis is equivalent to our “host-habitat area” hypothesis, which thus corroborates particularly prediction 1, but is also compatible with predictions 2 and 3 (Fig. 5).

As posed initially, the effect of resource concentration could be a nested factor within any heterogeneous and frequent suitable habitat, and thus act as the ultimate factor explaining arthropod’s choices of host crowns for feeding, hiding or reproduction. Therefore, it could be considered a background mechanism for all life history densities distribution.

The “habitat heterogeneity hypothesis” (Strong *et al.*, 1984, our prediction 2) partially explains the increase in densities with habitat area for all of the life histories, but is particularly relevant to abundant generalist as well as host tourist species, which cross over variable habitat types (host species).

At the ecological time scale, as predicted, the results also match the classical island biogeography hypothesis (MacArthur & Wilson, 1967). Thus, plants with simpler architecture accumulated a higher proportion of host-tourists, i.e., rare phytophagous and spider species that are common on *E. azorica* and *J. brevifolia* canopies. Therefore, a nested species composition of insect and spider fauna in forest tree crowns is expected, with the species occurring in less complex host plant species being subsets of the species community occurring on richer and more complex host plants (prediction 5).

The “encounter-frequency hypothesis” (Southwood, 1961; Strong *et al.*, 1984) partially explains all of the life histories but, it is particularly good for habitat tourists. The presence of habitat tourists can be caused by mass effects (Shmida & Wilson, 1985), i.e. species arriving at a host plant by dispersal from the nearby source habitats where they are more abundant. Indeed, habitat tourists contributed to the global density on *J. brevifolia* and *E. azorica* (prediction 2), as the chance of falling onto the crowns of these species will always be greater

than onto other species. Although with respect to herbivores it is harder to say how many are truly rare or are habitat tourists, 38 % of spider species on the three most abundant host trees were habitat tourists (with dense populations in natural grasslands and pastures elsewhere; Borges & Wunderlich, 2008, see below). For example, *Oedothorax fuscus* (Blackwall) which has an extremely high abundance in pastures (Borges & Brown, 2001; Borges *et al.*, 2008) is a moderately abundant species on *E. azorica* and *J. brevifolia* and rare on the other host species.

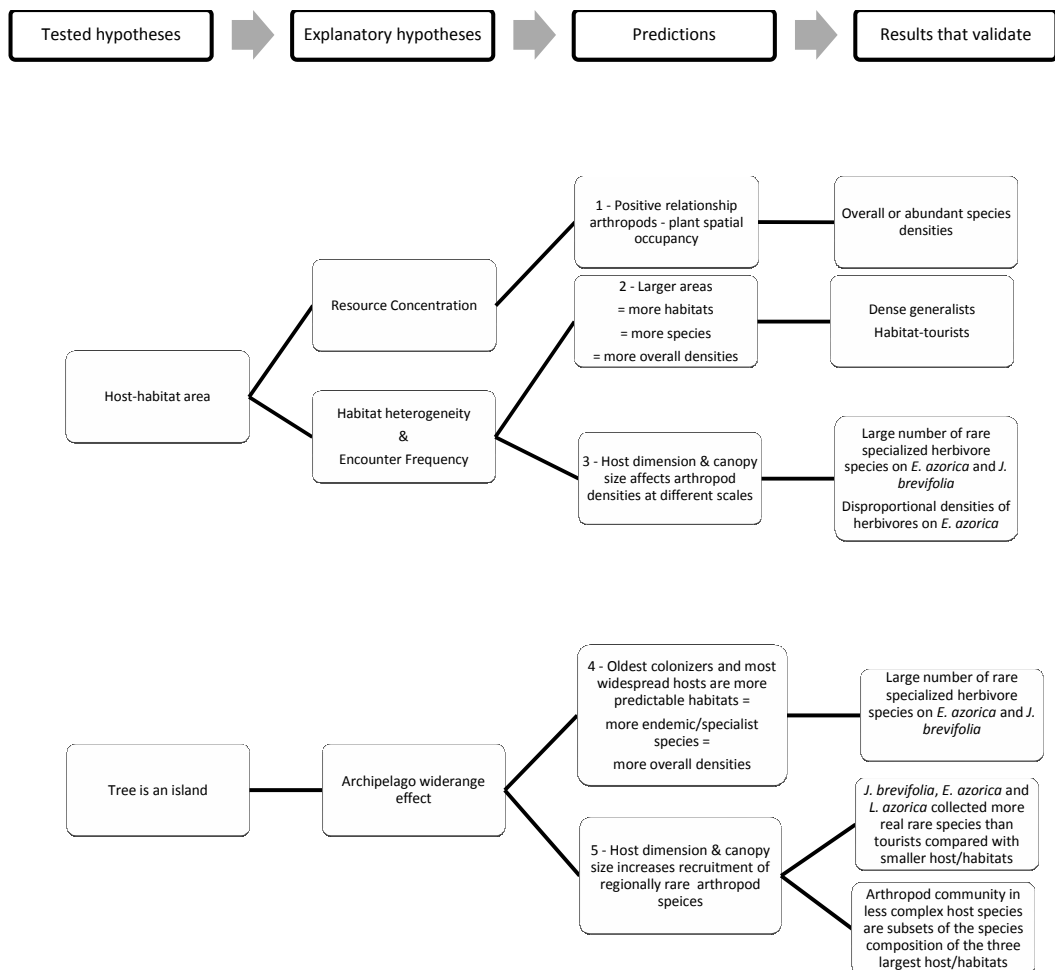


Figure 5. Flow-chart of the relation between hypotheses, predictions and results.

Truly rare and specialist species should also be favoured by the presence of large amounts of resources. Table III shows that, although large tree species populations have similar numbers of rare species, most of these species are truly rare on *J. brevifolia*, *L. azorica* and *E. azorica*. For instance, while *I. perado azorica* (the fourth largest host habitat) only collects host tourists, *J. brevifolia* and *E. azorica* host the truly rare species. Indeed, about 87 % of the rare spider species are truly rare species on *J. brevifolia*, 82 % on *E. azorica*, and 67% on *L. azorica*, thus fully agreeing with predictions 4 and 5, concerning the “tree as an island” hypothesis. In other words, the high frequency of *E. azorica* and *J. brevifolia* populations throughout the native forest fragments expose these hosts to the evolution of rare insect species populations. On an evolutionary time scale, this may have resulted in fixing a favourable insect species’ choice for the large host/habitats, which increases speciality, and may relates to the evolution of endemism.

Beyond rarity, the proportion of generalist herbivore species is still an issue of great relevance for insect-plant and tropical ecology (Basset *et al.*, 1996; Basset, 1999b; Novotny *et al.*, 2002). Many of the tropical singletons may be, in fact, host tourists (see Novotny *et al.*, 2002). In the laurisilva canopy, only a few host species were omitted from the study, while in the tropics, even when covering the most important trees (see Basset *et al.*, 2007; Ribeiro & Basset, 2007), there will always be a large number of unstudied host trees that could be a source of ‘false’ rare species, i.e. host tourists.

Interaction mechanisms and unpredicted patterns: the evolution of host fidelity and enemy-free space

An important aspect to point out is the relatively lower insect densities found in *L. azorica* than in *E. azorica*. The former was actually denser and created more habitat than the latter in the studied reserves (Table II), but *E. azorica* supported more insect herbivore individuals (as well as more truly rare forest species) than the model prediction. Ribeiro *et al.* (2005) suggested that the presence of a greater number of herbivorous insects on the crowns of *E. Azorica* could be explained by a combination of habitat fidelity (an evolutionary by-product of the antiqueness and frequency of the species in the archipelago’s early successional habitats) and enemy-free space.

Still, as concerns prediction 3, the arthropod densities showed different responses depending on scale. Models explained larger data variance at the highest, island/gamma scale than at other scales. At local scale, deviance from the model's expected values could represent interaction responses to the guild characteristic. For instance, at crown level, the chance to meet a rare tourist spider on *L. azorica* doubled compared to *E. azorica*. This could result in an advantage for insect herbivores (preys) to be in the latter host. The indirect effect of the lower probability of encounter with unknown predators and the higher numbers of herbivores per *E. azorica* crown are likely correlated phenomena, although further experimental studies are needed to confirm this hypothesis.

Some of the rare canopy spider species are actually abundant species in natural grasslands or pastures on the island of Terceira (Borges & Wunderlich, 2008; Borges *et al.*, 2008), which are likely to be collected within the forest due to their widespread net balloon type of dispersion. However, from the functional point of view, at the host species level, any rare spider causes similar effects on herbivore populations, namely on their habitat choice. For instance, the number of spider nests on the crowns of *J. brevifolia* appeared to be very variable, sometimes reaching high densities. Therefore, this habitat may result in particular great risk for insects, when compared with crowns of *E. azorica*, where the frequency of rare spiders was slightly smaller. Indeed, not only the number of rare spiders, but also the absolute number of spiders on *J. brevifolia* should result in a risky, unpredictable environment relative to *E. azorica*, for at least two reasons: 1) the absolute number of spiders on the former tree species was 6.5 times greater than on the latter; 2) the raw data followed a Poisson distribution (with variance increasing with mean), and thus some tree crowns of *J. brevifolia* had a much greater than expected number of spiders while others had as few as any other tree species. This particular situation increases the unpredictability of risk, which does not occur so severely among *E. azorica* crowns.

Hence, the probability of having a detectable enemy-free space within an *E. azorica* crown is highest among the largest host-habitat environments. Such a pattern may strongly contribute to the greater local diversity of herbivorous species (numbers per tree crown) on *E. azorica* compared with those on *J. brevifolia*, although the latter supports greater gamma diversity, as found by Ribeiro *et al.* (2005).

Conclusions

The present work distinguishes the components of arthropod density and evaluates habitat size effects on the population distributions of free-living herbivores and spiders. We conclude that abundant and evolutionarily predictable habitats define a large proportion of the arthropod density variation in the laurel canopy forest. Such habitats appear favourable to the evolution of abundant as well as rare specialized species, but are also extremely important to abundant generalists. Truly rare species in the ecosystem comprise about 60% of all species, with sample values varying from zero in small unpredictable habitats (leaf chewing herbivores and spiders on the crowns of the shrub *C. vulgaris*) to 80% (leaf chewing herbivores on the crowns of *J. brevifolia*). The pattern of distribution of truly rare species of arthropods suggests that habitat specialization, followed by species packing on resources, may be a crucial mechanism for evolution of the canopy biodiversity.

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Appendix 1 – Table for regression models.

	Equation	r ²	p
A) FOREST SCALE			
AHI Index			
All arthropods	log N = 0.95 + 0.28 log AHI	0.40	n.s.
Herbivores	log N = 0.68 + 0.25 log AHI	0.24	n.s.
Spiders	log N = 0.51 + 0.30 log AHI	0.55	0.05
ROI Index			
All arthropods	log N = 0.88 + 0.18 log ROI	0.37	n.s.
Herbivores	log N = 0.66 + 0.14 log ROI	0.18	n.s.
Spiders	log N = 0.40 + 0.20 log ROI	0.60	0.04
B) HOST POPULATION SCALE			
AHI Index			
Herbivores	log N = 0.59 + 0.55 log AHI	0.69	0.02
Sap-sucking herbivores	log N = 0.42 + 0.49 log AHI	0.55	0.05
Leaf-chewing herbivores	log N = 0.09 + 0.59 log AHI	0.61	0.04
Spiders	log N = 0.84 + 0.42 log AHI	0.46	n.s.
C) ISLAND SCALE			
AHI Index			
Sap-sucking herbivores	log N = 1.07 + 1.14 log AHI	0.67	0.02
Leaf-chewing herbivores	log N = 1.97 + 0.58 log AHI	0.43	0.11
Spiders	log N = 1.79 + 0.83 log AHI	0.73	0.02
ROI Index			
Sap-sucking herbivores	log N = 0.52 + 0.83 log ROI	0.83	0.004
Leaf-chewing herbivores	log N = 1.82 + 0.36 log ROI	0.40	0.12
Spiders	log N = 1.43 + 0.59 log ROI	0.86	0.003