

Distribution and abundance of arthropod species in pasture communities of three Azorean islands (Santa Maria, Terceira and Pico)

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This work provides evidence that the "hollow curve" is a consistent pattern in the range size distribution of taxonomic and ecological groups of arthropod pasture dwelling species. Many of the inconsistent results relating range size to herbivores diet breadth are probably due to historical constraints in the colonization of the islands and particular characteristics of the habitats studied (e.g. types of resources available). The positive relationship between range size and abundance may be explained by the "resource usage model". However, the slope of the regression line relating distribution to abundance was similar for different groups which suggests there is no difference in the way that the species' local abundance scales with distribution in the four assemblages of species studied and that there is a close relationship between the trophic groups studied. This suggests that the "resource availability model" could be the explanation for the distribution and abundance of pasture spider and insect species. More work needs to be conducted in order to evaluate the relationship between diet breadth, habitat specialization and range size in the islands.

Key words: range size, functional groups, herbivore, predator, resource availability model

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INTRODUCTION

Since the classic work of Andrewartha & Birch (1954) on the distribution and abundance of animals, the study of distribution has become one of the key issues in ecological studies, and is intrinsic to the concept of "Ecology" (Krebs 1994).

One way to examine patterns of distribution is to plot the frequency histogram of species distributions, that is, a species-range-size distribution (Gaston 1994a; Brown 1995). 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" (Schoener 1987; Gaston 1994b). Thus,

most species have a narrow range while a few are more widespread, distributed throughout all the measured range (Gaston & Blackburn 2000).

In some cases, the species-range-size distribution shows a bimodal pattern (Hanski 1982; Gaston 1994a; Brown 1984, 1995), 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. The "hollow curve" pattern has important implications in terms of conservation biology, since a large set of the species in any community that shows it, can be regarded as rare in terms of the extent of their distribution (Gaston & Blackburn 2000). As restricted distribution and low abundance are commonly positively correlated (see also below) (Hanski 1982; Brown 1984, 1995; Gaston 1994a,

1996; Gaston & Blackburn 2000), a great proportion of the species of a particular assemblage are therefore likely to be prone to extinction (Lawton 1993; Gaston 1996; Gaston & Blackburn 2000).

Range size is commonly correlated with several other variables. Gaston et al. (1997) list and discuss eight mechanisms that have been proposed to, or might possibly, generate positive relationships between the local abundance and regional distribution of species. In the "sampling artefact" model the relationship arises as a consequence of a systematic under-estimation of the range sizes of species with lower local abundances. The "phylogenetic non-independence" model, also considers that the positive relationship between abundance and distribution of species might be artefactual and results from non-independence of species as data points for statistical analysis (i.e. phylogenetic relatedness) (Harvey 1996). The "core and satellite species hypothesis" (Hanski 1982) and the "resource usage model" (Brown 1984, 1995) were proposed to explain the finding that a few species are regionally common (widespread) and locally abundant (the "core" species in Hanski's model; the generalists or broad-niched species in Brown's model), while most species can be regarded as having low ranges and low local abundances (the "satellite" species in Hanski's model; the specialists or narrow-niched species in Brown's model). In Brown's model ("breadth of resource usage" *sensu* Gaston et al. 1997) there is an attainment of higher local abundances and wider distributions by species with greater resource breadths. A positive abundance - range size relationship is an assumption of the "core and satellite species hypothesis" (Hanski 1982; Hanski et al. 1993), but other metapopulation models also predict this pattern (Gaston et al. 1997).

Other explanations for the positive abundance - range size relationship are: the "habitat availability model" (Venier & Fahrig 1996), in which the positive relationship between abundance and distribution arises on a patchy landscape if individual species have differences in habitat use and consequently different amounts of habitat are available to them on the same landscape ("habitat selection" model *sensu*

Gaston et al. 1997); the "population model" (Holt et al. 1997) (= "vital rates" *sensu* Gaston et al. 1997) in which, assuming that all species are similar in their response to density-dependent factors but differ to their response to density-independent factors affecting birth and death rates, then a positive relationship between distribution and abundance is obtained using a simple demographic model. To the six models already listed, two other are also summarized in Gaston et al. (1997) (see also Lawton 2000; Gaston 2003): "range position", i.e. species closer to the edges of their geographic ranges have lower abundances in, and occupy a smaller proportion of, study areas; "resource availability", i.e. attainment of higher local abundances and wider distributions by species with greater resource availability (see also Gaston 1994a).

We demonstrated elsewhere that in the Azores natives, endemics and exotics are part of the same plot in testing the non independence between abundance and range size for arthropods (see Gaston et al. 2006), that is, they all lie on the same bivariate abundance - occupancy relationship. Therefore, here we will analyse the community without separating species into their colonization status. Here we go further and study patterns of distribution and abundance of different functional arthropod groups in human altered grassland habitats, i.e. old semi-natural pastures and recent intensive pastures. The aims of the current paper are: i) to give an integrated picture of distribution patterns in several ecological functional arthropod groups; ii) test the non independence between abundance and range size in human-modified habitats and clarify the mechanisms generating it.

MATERIAL AND METHODS

SITES AND EXPERIMENTAL DESIGN

Two replicates ("cerrados") of recently sown pastures (SP) and old semi-natural pastures (SNP) were selected in three Azorean islands (Santa Maria, Terceira and Pico) at a high-altitude level (see Borges 1999; Borges & Brown 1999, 2001, 2004). The present study includes one habitat subject to high grazing pressure (sown pastures) and another with lower grazing management

(semi-natural pastures); it also includes drier pastures (sown sites of Santa Maria and Terceira) and highly moist soils of low pH (natural sites from the three islands. Having taken into account that the islands have different maximum altitude, Santa Maria being the lowest altitude island and Pico the highest Azorean island, the range of altitudes of the 12 field sites lays between 290 and 800 m (see Appendix I in Borges 1999 for a detailed description). In all the 12 pastures (3 islands x 2 pasture types x 2 replicates) an area of at least 900 m² was fenced during January and February 1994 with posts and barbed wire. A preliminary study indicated that rabbit grazing was unequal in the studied system. Consequently, rabbit fences to avoid differential rabbit grazing pressure were erected in April 1994. After the field sites were fenced, in each of them 20 3x3 (9 m²) plots were marked with coloured small wood posts. All field sites were grazed regularly by dairy and beef cattle, thereby maintaining the traditional management of the sites (see Appendix I in Borges 1999). Sampling occurred always three weeks after a grazing event.

ARTHROPOD DATA SET

The main data set with the arthropod distributions in the 12 studied field sites used in Borges (1999) was also used here. For each of the 237 arthropod species (128 herbivores and 117 predators; note that some species were listed as both herbivores and predators), information was gathered on diet breadth for the herbivores. As stated before (Borges 1999; Borges & Brown 2001, 2004), the sources of information were independent for each taxonomic group, being mainly given by the taxonomists that identified the morphospecies who are experts in the Macaronesian faunas (see a detailed list of contributions in Borges & Brown 1999).

SPECIES ABUNDANCE DATA SETS

For the study of the relationship between abundance and range size, summer samples were selected because the vegetation is at its maximum productivity at this time. The summer of 1994 was chosen in preference to that of 1995 because the latter was an atypical year (one of the rainiest years in the Azores of the last 10 years). The

arthropod abundance was assessed with the Vortis suction apparatus and is given as the number of specimens per square meter. The range size obtained for each species is that obtained from presence/absence data matrices generated from the Summer 1994 samples, using the Vortis suction machine for the arthropods, and is given as the number of occupied sites from a maximum of 12. Therefore, for the range size - abundance relationship, the range sizes do not include the pitfall data used elsewhere (see Borges & Brown 1999).

DATA ANALYSIS

Species range sizes of arthropods were measured in terms of number of sites occupied with a maximum occupancy of 12. To have a measure of the shape of the frequency distribution of species, its skewness and kurtosis were calculated. As numbers of species differ between groups of species, in figures the proportion of species was used instead of number of species occurring in each range size category. Moreover, we also evaluate the occurrence frequency distribution of species in the various sites using the Tokeshi statistical test for bimodality (Tokeshi 1992; Barreto et al. 2003), that allows the calculation of the probability under the null hypothesis of the presence of larger numbers of species in the two extreme classes (one site only vs. all sites).

The range size - diet breadth relationship is investigated separately for sucking and chewing herbivores. Each species of herbivore was allocated to one of four diet categories, species or genus monophages, family monophages, oligophages and polyphages. In the cases where information was not available, the species was not used in the analysis. For the 2x2 contingency table analysis, the diet categories were simplified in order to avoid overdispersion of the data. Without such modification, some cells would have had expected frequencies less than five. For such smaller samples, the recommended statistical test is the Fisher's exact test. However, as in most cases the expected frequencies were so small that they could easily be a result of chance, a more robust test was used. The *G*-test was chosen since is the most reliable means of analysing frequency data (Crawley 1993). The

new categories were for diet breadth: the four categories mentioned above were reduced to only two by grouping the species/genus and family monophages as "specialists" and the oligophages and polyphages as "generalists".

For the arthropods, abundance was measured as the logarithm of the mean number of individuals per square meter in each field site. As the frequency distribution of abundance within each species was shown to be right skewed, the geometric mean was chosen instead the arithmetic mean, since it provides a much more accurate representation of the central tendency (Zar 1984). The sites used to calculate the regressions were only those where a species occurred. I examined the relationship between abundance and range size for all arthropod species, herbivores, predators and spiders with ordinary least-squares (OLS) regression and compared the fits using range size with both untransformed and logarithmic transformed values. The best fit was considered to be that resulting in the higher r^2 value. Finally, data was plotted from the best model.

All statistics, including G -test, Spearman's rank correlation and OLS regression analyses were performed using the STATVIEW 512+ *Macintosh* statistical package. The graphs were created using a *Macintosh* package (Cricket Graph III).

RESULTS

SPECIES-RANGE-SIZE DISTRIBUTIONS

The Tokeshi test for modality shows a strong left unimodal distribution of species for the several groups of arthropods analysed ($p_l < 0.001$ and

p_r n.s.; Fig. 1). However there are differences within each of these arthropod subsets. Spiders, chewers and predatory insects showed particularly interesting range size distributions. Almost half of the 50 species of Araneae occurred at only one site, giving the highest skew and kurtosis values in comparison with the other groups of species studied. This is due to the presence of very rare endemic species and because a high proportion of the species can be considered as vagrants, occurring only in one of the sampling periods with very low abundance. Chewers and predatory insects showed an inverse pattern with a high proportion of the species having a wide range. This is due to the broad distribution of most species of moths, carabids, staphylinids and chrysomelids, which tend to occur in three or more sites. Most of them are polyphagous herbivores (noctuid moth larvae) and polyphagous predators (carabids and staphylinids) with high vagility and colonization abilities. The smallest values of skew and kurtosis obtained for chewers and predatory insects mean not only that those groups are more widely distributed but also that the proportion of species in each range size category is more similar.

RANGE SIZE AND HERBIVORE DIET BREADTH

Table 1 shows the distribution of the number of species in each diet category throughout three range size categories. In the suckers, lumping the species into specialists and generalist, the distribution is contrary to the theoretical expectation, since a high proportion of specialist species have a wide range, while a large proportion of the generalists occupy few sites ($G = 5.638$, d.f. = 1, $p = 0.02$).

Table 1. Distribution of the number of herbivore species in each diet category throughout 3 range size categories.

Range size	Specialists		Generalists	
	Genus and species monophage	Family monophage	Oligophage	Polyphage
a) Suckers				
1 to 4	1	13	14	13
5 to 8	0	7	3	0
9 to 12	0	4	2	0
b) Chewers				
1 to 4	5	6	4	19
5 to 8	0	3	3	6
9 to 12	0	2	0	6

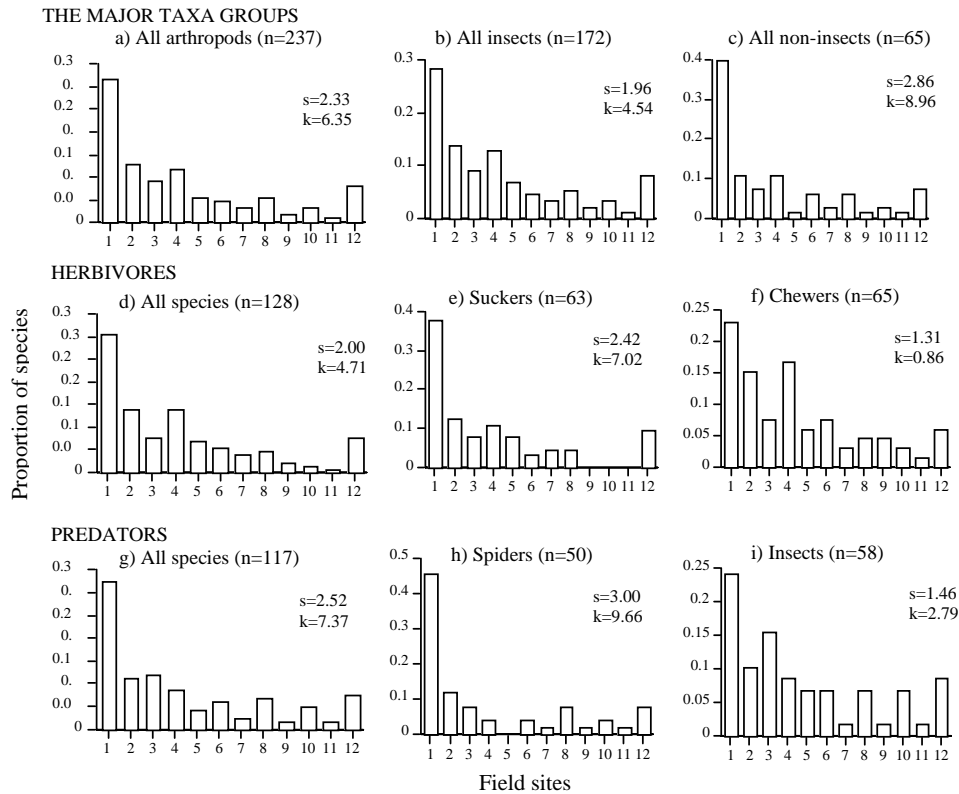


Fig. 1. Frequency histograms showing the proportion of species of several groups of arthropods occupying the 12 field sites; "n" gives the number of species. Values of skewness (s) and kurtosis (k) are given for each frequency distribution (see also text).

For chewers, there is no significant pattern in the distribution of the specialist-generalist species among the range size categories ($G = 0.331$, d.f. = 1, n.s.). All the sucker and chewer species of species/genus monophages consistently occurred in less than five sites, but there are few species and they are mainly restricted, so this distribution may not differ from random expectation (Table 1a) and b).

RANGE SIZE AND LOCAL ABUNDANCE

As Table 2 and Figure 2 show, for arthropods, there is a clear positive relationship between the range size of a species and its local abundance. Wide-ranging species tend to be, on average, more abundant locally, while narrowly distributed

species tend to have low densities where they occur. The log-linear model explained slightly more variance than the log-log model for all arthropods and herbivores (Table 2). In the predators and spiders, the fit of the log-log and log-linear models was very similar, but slightly better in the former. For arthropods (Fig. 2) the range of the r^2 's is 0.39 - 0.48 (Table 2), with the best fit for spiders (Table 2; see also Fig. 2d). Within each model, the slopes of the arthropods curves look very similar (pairwise t-tests for the differences showed that none is significant), suggesting that there is no difference in the way that the species' local abundance scales with distribution in the four groups of species studied.

Table 2. Statistics for linear regressions between abundance and range size distribution in the Summer 1994 for all arthropods, herbivores, all predators and spiders. The higher r^2 values are in bold; “n” gives the number of species; ** $p < 0.001$; *** $p < 0.0001$.

	Regression type	Equation	r^2	F
All arthropods (n = 96)	log-untransformed model	$\log y = -1.06+0.094x$	0.41	64.93***
	log-log model	$\log y = -1.07+0.86 \log x$	0.38	58.06***
Herbivores (n = 50)	log-untransformed model	$\log y = -1.098+0.112x$	0.46	41.26***
	Log-log model	$\log y = -1.108+1.02 \log x$	0.42	34.43***
All predators (n = 50)	log-untransformed model	$\log y = -1.043+0.079x$	0.37	28.50***
	log-log model	$\log y = -1.106+0.73 \log x$	0.39	30.38***
Spiders (n = 22)	log-untransformed model	$\log y = 1.013+0.082x$	0.48	18.47**
	log-log model	$\log y = -0.99+0.74 \log x$	0.48	18.76**

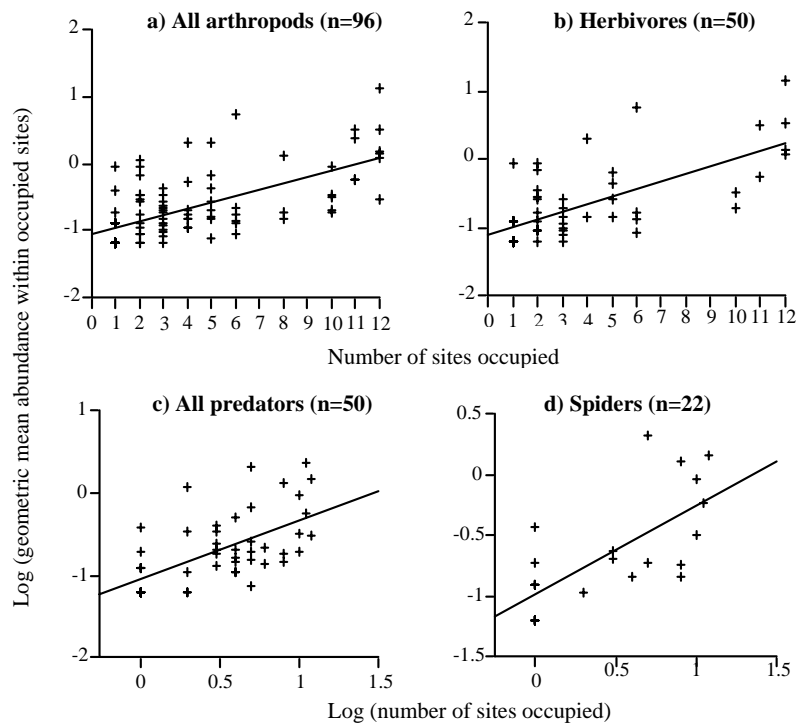


Fig. 2. Relationship between the logarithm of the geometric mean abundance within occupied sites and the number of sites occupied for a) all arthropods, b) herbivores, and the logarithm of the geometric mean abundance within occupied sites and the logarithm of the number of sites occupied for c) predators and d) spiders, in the Summer 1994. Note, several data points overlie one another. Statistics are presented in Table 2; “n” gives the number of species.

Moreover, in the arthropods, there are no differences in the average abundance of species within each group (geometric mean of mean species abundances: all species = 0.21; herbivores = 0.22; predators = 0.19; spiders = 0.22).

Of course, there are some outliers. Some species occur in only a small proportion of sites, but are very abundant where they occur. This is the case for certain introduced species that occur in only some sites in the pastureland (e.g. the linyphiid spiders *Erigone atra* and *Oedothorax fuscus*). However, there are no cases of species occurring in only one site and being locally abundant. Moreover, all species that are widespread (occurring in 11 and 12 field sites of a maximum of 12) are locally abundant.

DISCUSSION

The present study considers patterns in regional occurrences of arthropod species (see also Borges & Brown 2001, 2004) rather than the entire geographic range of species (a more biogeographic approach). Therefore, this work covers only part of the geographic range of the species ("partial analyses" *sensu* Gaston & Blackburn 1996), as range size was measured in terms of number of sites occupied by each species.

The general result was a "hollow curve", repeated for several taxonomic and ecological (e.g. feeding groups) functional groups. The bimodal pattern was tested statistically and the right-hand mode was clearly not statistically significant. Narrowly distributed arthropod species are mainly endemic and tourist (or vagrant) species (note that some endemics can also be considered as tourists in the studied habitats). Moreover, for both endemics and tourists, local density is generally low (Gaston 1994a), a rule that was also confirmed in the present study. The low densities of endemics are probably due to a lack of adaptation to pasture management. However, some endemic species are persistent throughout the sampling periods, and some were indicator species of pasture communities (see Borges 1999). Nevertheless, endemic species are doubly at risk of extinction, because occupy few sites and attain low densities

where occur (Lawton 1993). However, the real range of those species is larger than obtained in the present study (see Borges et al. in press), and therefore the current results may be a consequence of a pasture being a sink habitat. This is probably true for the tourist species, a large group of species which are either habitat generalists (occupy several habitats in the islands) (e.g. some millipedes, moths, spiders and beetles) or habitat specialists (e.g. *Olisthopus inclavatus* and *Tarphius depressus* endemic forest dwellers) that accidentally colonize pastureland. For endemic species, at least in Santa Maria, the pastureland seems to be an alternative habitat as a result of the virtual absence of true natural areas (see Borges et al. 2005). Hence, the observed range probably accurately reflects their actual range. That is, those species genuinely occupy few sites at low densities. Concerning the tourist species, there are difficulties in correctly identifying them without having a total picture of their distribution in all the available habitats in the studied islands (but see Borges et al. in press, for a complete picture for Terceira Island). Their dynamics as "sink species" (Shmida & Wilson 1985) greatly increases the number of rare species in the community, which creates an artefactual increase in the left-hand mode of the frequency distributions of species (Gaston 1994b).

Species with wider distributions are predominantly habitat generalists, namely a) species with wide environmental tolerance, or b) species with high dispersal capacities (Brown 1984; Hanski et al. 1993; Lawton 2000). Considering habitat generalists, most species were also found to be abundant in both sown and semi-natural pastures, but there are exceptions. For instance, the endemic lycosid spider *Pardosa acoreensis* occurs in all the 12 sites but is mainly abundant in the semi-natural sites of Santa Maria and Pico ("source populations" *sensu* Shmida & Wilson 1985). Moreover, most of the species/genus monophage herbivores occur in a few sites, where they are never abundant. This result supports the "resource usage theory" (Brown 1984, 1995), but cannot rule out the 5th (resource availability) and 6th (habitat selection) models of Gaston et al. (1997), i.e. how generalist would a species have to be in these habitats to occupy all?; a) Species with wide environmental

tolerance: in accordance with the positive relationships found between range size and local abundance, arthropod species that are spatially ubiquitous (occur in 10-12 sites) must be highly tolerant to a wide array of environmental conditions. Such species also conform to the predictions of the "resource usage theory", being the generalist or broad-niched species of Brown (1984, 1995); b) Species with high dispersal capacities: most of the widespread and abundant predator species in these pasture communities are linyphiid spiders and staphylinids known for their good dispersal capacities. In the herbivores, dominant species are flying insects (e.g. leafhoppers, aphids and moths) also having good dispersal abilities.

The higher r^2 obtained for the spiders in the range size/abundance relationship (Fig. 2d) is a consequence of the fact that spiders are a more closely related ecological group of species than the predator or herbivore assemblages (Brown 1984; Gaston 1994a). In fact, within the spider assemblage, there are only two main ways of using resources, the "web-building way" and the "wandering way". The predator assemblage, as it was designed in the present study, includes the spider foraging strategies mentioned above and also the feeding behaviours of centipedes, ground-beetles and rove-beetles. The herbivore assemblage includes sucker and chewer species and within these two main groups there are different ways of using resources (e.g. root-feeders, leaf-feeders, xylem sap feeders, phloem sap feeders, pollen feeders, etc.). However, the fact that the correlation obtained with the predators was the weakest of the four computed correlations for the arthropods may reflect a sampling artefact, since estimates of abundance were based on a suction method (Vortis machine) that is not suitable for the larger predatory species (e.g. centipedes, night-dwelling ground-beetles and rove-beetles, and larger spiders). However, the inclusion of pitfall data implies the inclusion of additional errors for the herbivorous functional groups and was not considered (see Methods).

Gaston et al. (1997) proposed eight mechanisms that govern the positive relationship between abundance and range size (see also Introduction). Metapopulation models assume that distance between patches (or sites) should be

small enough in order for all species to move between them (see also Gaston 1994a). This condition is not fulfilled in the case of oceanic islands separated by sea, where over-water dispersal is very low. Moreover, this study was not designed to test the phylogenetic non-independence, range position, habitat selection and vital rate models, and will not be further considered. As previously suggested in this manuscript, the "resource usage model" fits very well with the characteristics of the species/genus monophage herbivores and wide ranging species. Brown's (1984) model also predicts that "consumers" (e.g. predators) should use the environment on a larger spatial scale with lower densities but wider distributions than "producers" (e.g. herbivores). Despite the fact that on average the widespread herbivores are more abundant than the widespread predators (geometric mean of the mean abundances of the species that occur in eight or more sites: herbivores = 1.31 m⁻²; predators = 0.51 m⁻²), which conforms with the model, when the slopes of curves are compared, there was no evidence to suggest that the predators have a wider distribution than the herbivores. Moreover, looking for Figures 1d) and 1g), and for the skew and kurtosis values therein, contrary to the prediction, herbivore species are more widely distributed than the predators. However, this is largely a consequence of the spider distribution pattern, since the predatory insects showed very low values of skewness and kurtosis and therefore some tendency for wider distributions. As a great proportion of the spiders can be considered tourist species, probably Brown's (1984) predictions are best applied to the arthropod community under study.

As mentioned above, the slopes of the regression lines relating abundance to range size were very similar for the different assemblages of species. This is a very important result (Gregory & Gaston 2000). Since the slope of the regression line relating distribution to abundance increases as the number of resources per locality increases (Maurer 1990), the similar slopes obtained for the several assemblages of species may imply a tight connection between the different trophic groups.

The unexpected result obtained with the sucker species (*viz.* a high proportion of specialist

species have a wide range, while a large proportion of the generalists occupy few sites), may be explained because a great proportion of the sucker species are family monophages adapted to feed on Leguminosae and perennial grasses common throughout all the measured range. Hence, patterns in the distribution of the lower trophic level are constraining the distribution of herbivore sucker species. On the other hand, the reason why a large proportion of the generalist sucker species occupy few sites may be related to the fact they need a variety of resources not available in all the measurable range, or they are recent introduced species and therefore, they have a more limited distribution (Gaston 1994a). This conforms with the "resource availability model" (Gaston et al. 1997), that is, attainment of higher local abundances and wider distributions by species with greater resource availability.

CONCLUDING REMARKS

With this study it is clear that even in human-altered habitats two commonly ecological patterns are found for arthropods: i) narrowly distributed species dominate and very few species are widespread, and this was repeated for several taxonomic and ecological (e.g. feeding groups) functional groups; ii) there is a positive relationship between mean abundance and the distribution of species. Moreover, the slopes of the regression lines relating abundance to range size were very similar for the different assemblages of species, which supports the "resource availability model".

These results call attention for the fact that arthropod communities in the Azorean pastures are well structured and that in spite of most species being exotic, the communities are commonly dominated by rare species and the few widespread species attain high local densities.

We suggest that more work needs to be conducted in order to evaluate the relationship between arthropod diet breadth, habitat specialization and range size in the islands in several types of habitats.

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