

Canopy insect herbivores in the Azorean Laurisilva forests: key host plant species in a highly generalist insect community

Sérvio P. Ribeiro, Paulo A. V. Borges, Clara Gaspar, Catarina Melo, Artur R. M. Serrano, João Amaral, Carlos Aguiar, Genage André and José A. Quartau

Ribeiro, S. P., Borges, P. A. V., Gaspar, C., Melo, C., Serrano, A. R. M., Amaral, J., Aguiar, C., André, G. and Quartau, J. A. 2005. Canopy insect herbivores in the Azorean Laurisilva forests: key host plant species in a highly generalist insect community. – *Ecography* 28: 315–330.

This article explores patterns of insect herbivore distribution in the canopy of the Laurisilva forests on seven islands in the Azores archipelago. To our knowledge, this is one of the first extensive study of this type in tree or shrub canopies of oceanic island ecosystems. One of the most frequently debated characteristics of such ecosystems is the likely prevalence of vague, ill-defined niches due to taxonomic disharmony, which may have implications for insect-plant interactions. For instance, an increase in ecological opportunities for generalist species is expected due to the lack of predator groups and reduced selection for chemical defence in host plants. The following two questions were addressed: 1) Are specialists species rare, and insect herbivore species randomly distributed among host plant species in the Azores? 2) Are the variances in insect herbivore species composition, frequency and richness explained by host plants or by regional island effects? We expect a proportional distribution of herbivore species between host plants, influenced by host frequency and distinct island effects; otherwise, deviation from expectation might suggest habitat preference for specific host tree crowns. Canopy beating tray samples were performed on seven islands, comprising 50 transects with 1 to 3 plant species each (10 replicates per species), giving 1320 samples from ten host species trees or shrubs in total. From a total of 129 insect herbivore species, a greater number of herbivore species was found on *Juniperus brevifolia* ($s = 65$) and *Erica azorica* ($s = 53$). However, the number of herbivore species per individual tree crown was higher for *E. azorica* than for any other host, on all islands, despite the fact that it was only the fourth more abundant plant. In addition, higher insect species richness and greater insect abundance were found on the trees of Santa Maria Island, the oldest in the archipelago. Insect species composition was strongly influenced by the presence of *E. azorica*, which was the only host plant with a characteristic fauna across the archipelago, whereas the fauna of other plant crowns was grouped by islands. The great insect occurrence on *E. azorica* reflects strong habitat fidelity, but only four species were clearly specialists. Our findings indicate a broadly generalist fauna. The simplicity of Azorean Laurisilva contributed to the understanding of insect-plant mechanisms in canopy forest habitats.

S. P. Ribeiro (e-mail: spribeiro@iceb.ufop.br), Lab. Ecologia Evolutiva de Herbívoros de Dossell/DECBI, Inst. de Ciências Exatas e Biológicas, Univ. Federal de Ouro Preto, Campus Morro do Cruzeiro, 35400-000, Ouro Preto, MG, Brasil. – P. A. V. Borges, C. Gaspar, C. Melo and J. Amaral, Dept de Ciências Agrárias, Univ. dos Açores, Terra-Chã, PT-9700-851 Angra do Heroísmo, Terceira, Açores, Portugal. – A. R. M. Serrano, C. Aguiar, G. André and J. A. Quartau, Fac. de Ciências de Lisboa (DBA), Centro de Biologia Ambiental, R. Ernesto de Vasconcelos, Ed. C2, 3º Piso, Campo Grande, PT-1749-016 Lisboa, Portugal.

Accepted 3 December 2004

Copyright © ECOGRAPHY 2005
ISSN 0906-7590

Patterns of spatial variation in species distribution, abundance and richness are central topics in community ecology (Gaston and Blackburn 2000). Presently, understanding the mechanisms influencing these species parameters, and their relationship with habitat conditions, have become important issues in ecological studies. Conversely, species diversity on oceanic islands is a poorly studied subject, except for some specific topics, including the species-area relationship and faunal taxonomic disharmony (lack of entire taxonomic groups which are expected in equivalent continental ecosystems) (Whittaker 1998). In particular, little is known about patterns of specialist versus generalist insect herbivore species in different host plant species, both within and between islands (Holloway 1996). Empirical data show a depauperate grassland insect herbivore fauna in the young isolated Azorean islands (Borges and Brown 1999). We suggest that such patterns may result from the relaxation of selective pressure for plant defence. Along with the lack of entire group of predators, this could increase opportunities for generalist insect herbivores.

The broadly discussed theory of insect-plant interactions based on co-evolutionary response at the level of chemical defence/resistance has over-emphasized the importance of specialist herbivores. Bernays and Funk (1999, but see Tune and Dussourd 2000) have discussed the likely uncommonness of polyphagy due to neural constraints. Nevertheless, the conventional wisdom that monophagy must have evolved as a response to deterrent effects of chemical secondary defences has been questioned by many authors, including Bernays and Graham (1988) and Bernays and Minkenberg (1997). Recent ecological surveys in the tropics (Basset et al. 1996, Novotny et al. 2002, Ribeiro 2003) and experimental studies (Bernays and Minkenberg 1997, Singer and Stireman 2003) have shown that generalists might be more important than previously thought.

However, Novotny et al. (2002) state clearly that the pattern of high proportion of generalists found in some tropical rainforests reflects specialization at the generic level. Chemical and mechanical evolutionary constraints for extreme polyphagy, combined with effects of plant traits and predator escape are likely mechanisms in favour of selection of specialisation, either in feeding behaviour or habitat preferences. In this context, the recent findings in the tropics are still consistent with the idea of the widespread presence of specialists, as far as the concept is applied in a broader sense, assuming oligophagy as a similar evolutionary output. As also stated by Novotny et al. (2002), the lack of closely related plant species could make species appear monophagous in certain plant communities. Ribeiro (2003) has discussed the possibility that the proportion of specialist/generalist insects may vary substantially with vegetation type, being specialists more frequent in harsh

scleromorphic plant communities (Fernandes and Price 1991, Price et al. 1998, Ribeiro and Brown 1999, Ribeiro et al. 1999).

There is not a straightforward relation between chemical deterrence and toxicity (Bernays and Minkenberg 1997). The evolution of specialist herbivores may also result from different pressures, such as predator or parasite escape (Bernays and Graham 1988, Gross and Price 1988, Losey and Denno 1998, Sabelis et al. 1999). In this case, the irreversibility of host specificity could depend on the maintenance of selective pressure at the third trophic level (Sabelis et al. 1999). Nevertheless, in highly heterogeneous tropical forest canopies, escape from predation and diseases, as well as adaptation to nutrient deficiency, may evolve by some other poorly understood ecological processes rather than host specialization, thus resulting in the noticeably high diversity of generalists.

Habitat simplification and taxonomic disharmony found on oceanic islands (Whittaker 1998) could be a distinct evolutionary cause of increased generalism evolution. The absence of sustainable herbivore populations during the early plant colonization releases the herbivory pressure on the evolution of defences in plant species. Subsequently, when herbivores eventually colonize these plants, only weak selective pressure would be expected favouring specialist genotypes, whatever the plant secondary chemicals that function as deterrent or host recognition mechanisms. Toxicity can result in significant loss of fitness for a non specialised insect herbivore species, but not for a specialist one (Hägele and Rowel-Rahier 2000). However, without such evolutionary advantage, there are few theoretical reasons to expect feeding specialization to evolve. Furthermore, known mechanisms of neo-specialists evolving on invading species, such as crop plants, result from a priori specialist herbivores in related host plants (Andow and Imura 1994), and thus would not apply to the Azorean insect community.

Relaxation of natural selection has been proposed as an important cause of evolution of generalists on oceanic islands, in various trophic levels (Givnish 1998). In addition, the lack of entire groups of predators (e.g. ants) could also be responsible for a high proportion of generalists (although the likely occupancy of predation vague niches by a large number of spider species needs further studies – Borges and Brown 2004). Hence, this community evolutionary process could result in a highly generalist insect herbivore guild.

Usually herbivore insect guilds have components which are locally absent in the Azores (Borges and Brown 2004). This fact could have implications for insect-plant interactions in a vague niche rich community, and eventually may reinforce a trend toward increase of generalist species. The present study aims to assess patterns of canopy phytophagous insect

distribution and species richness among island and host plants. In addition, we explore the possibility of insect species fidelity to the early successional shrub-arboreal species, *Erica azorica*, assuming as a null hypothesis the existence of a largely generalist insect herbivore guild. Specifically the following questions were addressed: 1) Are specialist species rare and randomly distributed among host plant species in an isolated oceanic archipelago like the Azores? 2) Are the variances in insect herbivore species composition, frequency and richness explained by host plant effects or regional island effects?

Assuming a highly generalist insect guild, the hypotheses predictions are: insect faunal composition, alpha diversity and local density should be constant among host species, or if they vary, 1) the occurrence of specialists should be rare and randomly distributed among host species; 2) at each island and in the area sampled they should be proportional to host species frequency.

To our knowledge, this is one of the first (but see Schowalter 1994, Schowalter and Ganio 1999) extensive surveys of distribution patterns, specialization and richness of phytophagous insect species in tree canopies of isolated oceanic island ecosystems.

Methods

Site description

This study was conducted in the Azores, an isolated northern Atlantic archipelago located at the junction of the North American, Eurasian and African plates. The archipelago shows recent volcanism and seismic activity and comprises nine islands, as well as several islets and seamounts distributed from northwest to southeast, roughly between 37° and 40°N and 24° and 31°W. The Azorean islands extend for ca 615 km and are situated across the Mid-Atlantic Ridge, which separates the western group (Flores and Corvo) from the central (Faial, Pico, S. Jorge, Terceira and Graciosa) and the eastern (S. Miguel and S. Maria) groups. The islands have a relatively recent volcanic origin, ranging from 8.12 Myr BP (S. Maria) to 300 000 yr BP (Pico) (Nunes 1999). The temperate oceanic climate is characterized by high relative humidity that can reach 95% at high altitude native forests, and low thermal variation throughout the year. Frequent storms come from the west, but the islands are also influenced by the “Leste”, a series of sand storms that originate in North Africa (Reis et al. 2002).

The predominant vegetation form is the “Laurisilva”, a humid evergreen broadleaf and microphyllous (hereafter short-leaf) laurel type forest that originally covered most of western Europe during the Tertiary (Dias 1996). Dominant trees and shrubs include short-leaf *Juniperus brevifolia* (Cupressaceae) and *Erica azorica* (Ericaceae),

both endemics, and the broadleaf species *Ilex perado* Ait. ssp. *azorica* (Aquifoliaceae) (endemic), *Laurus azorica* (Lauraceae) (native) and the shrub *Vaccinium cylindraceum* (Ericaceae) (endemic). This type of forest is characterized by reduced tree stature (usually up to 5 m, rarely reaching 10 m), shaped by the shallow soil and fractured terrain, which is raised up to the tree tops in some points, and lowered five to six meters below in others. A high crown foliage density and thus low canopy openness is typical of these forests, as well as a particularly dense cover of moss and liverwort epiphytes. Some bryophytes also cover leaves in higher altitude humid forests.

Experimental design

In seven out of the nine Azorean islands native vegetation was surveyed within defined Natural Forest Reserves and/or NATURA 2000 protected areas. A total of 16 protected areas were investigated (Table 1). For more details on the protected areas considered see Borges et al. (2005). During the summer of 1999 and 2000 at least two 150 m long random transects were performed in each protected area, except in some large reserves where more transects were surveyed. In most cases the sampling was split equally between the two years. In each transect, ten replicates of the three most abundant and common woody plant species (trees and shrubs) were sampled. The sampling followed a block design in which one branch of each of the most common species was sampled at each 10 m interval along the transect. In most cases only three plant species clearly appeared to dominate over the remaining species and the choice was quite obvious. In some transects, however, less than three woody plant species were present and only those could be considered. Table 2 summarizes the plant species sampled in the protected areas. *Juniperus brevifolia* was the most common species in most of the study sites, occurring in 70% of the transects.

Arthropod sampling and identification

For the canopy arthropod sampling a modified beating tray was used, which consisted of an inverted cloth funnel pyramid of 1 m wide and 60 cm deep (after Bassett 1999a). A plastic bag was placed at the tip where arthropods, leaves and small branches were collected. For each selected plant, a branch was chosen at random, the beating tray placed beneath and the branch hit five times with a beating stick. Whenever possible, the sampling was performed on warm, sunny days, and always when the vegetation was dry. Sample bags were labelled and frozen until they were sorted. Finally, the sorted specimens were stored in 70% ethanol with glycerol.

Table 1. List of the studied reserves with its code, name, island of occurrence (FAI = Faial; PIC = Pico; STM = S. Maria; FLO = Flores; SJG = S. Jorge; SMG = S. Miguel; TER = Terceira), area, altitude (minimum and maximum), as well as the altitude and the list of the sampled trees or shrubs in each of the transects (Call = *Calluna vulgaris*; C = *Clethra arborea*; E = *Erica azorica*; J = *Juniperus brevifolia*; I = *Ilex perado azorica*; L = *Laurus azorica*; Myrs. = *Myrsine africana*; M = *Myrica faya*; P = *Picconia azorica*; V = *Vaccinium cylindraceum*).

Code	Name	Island	Area (ha)	Altitude (m)	No. transects	No. samples	Sampled plants and altitude (m)
STM-PA	Pico Alto	STM	4	470–575	2	60	(E; L; P; 530); (E; L; V; 530)
SMG-A	Atalhada	SMG	15	425–530	2	30	(J; I; 425); (I; 450)
SMG-G	Graminhais	SMG	27	850–925	2	60	(J; L; V; 870); (L; I; V; 925)
SMG-PV	Pico da Vara	SMG	742	400–1103	3	60	(E; C; 450); (J; L; I; 674) (E; 800)
TER-BF	Biscoito da Ferraria	TER	391	475–808	2	60	(J; V; Myrs.; 530); (J; L; I; 600)
TER-SB	Serra de St ^a Barbara e M. Negros	TER	1274	550–1025	7	240	(J; V; Myrs.; 630); (J; I; L; V; Myrs; 740) (J; I; Myrs; 760) (J; Call; 800); (J; I; L; V; Myrs; 910); (I; L; 971) (J; I; V; Myrs; 990)
TER-TB	Terra Brava	TER	450	600–700	2	30	(I; J; 630); (L; 659)
TER-M	Matela	TER	25	350–393	2	60	(J; E; L; 350); (E; L; V; 430)
FAI-CF	Cabeço do Fogo	FAI	54	400–529	2	30	(M; 425); (E; J; 510)
PIC-LC	Lagoa do Caiado	PIC	131	800–939	3	90	(J; E; Myrs.; 820); (J; I; V; 830); (J; I; V; 834)
PIC-MP	Mistério da Prainha	PIC	643	425–841	5	140	(E; L; I; V; 500); (J; L; I; 525); (I; 800); (J; E; I; 800); (J; E; I; 800)
PIC-C	Caveiro	PIC	199	850–950	2	60	(J; L; I; 900); (J; L; I; 920)
SJG-P	Pico Pinheiro	SJG	293	600–780	2	60	(J; V; Myrs.; 630); (E; J; V; 670)
SJG-T	Topo	SJG	2257	0–942	2	60	(J; I; V; 850); (J; I; V; 875)
FLO-FR	Caldeiras Funda e Rasa	FLO	459	350–600	4	70	(J; 400); (E; V; 450); (E; 487); (J; I; V; 500)
FLO-MA	Morro Alto e Pico da Sé	FLO	1558	300–915	8	200	(J; Call; 525); (J; 575); (J; L; Call; 600); (J; L; I; 625); (J; V; Call; 675); (J; V; Myrs.; 700); (J; V; Call; 700); (J; V; 890)

A total of 1320 samples were collected, Arthropod identification was performed in four stages: 1) trained parataxonomists sorted samples into morphospecies (or RTUs = recognizable taxonomic units, sensu Oliver and Beattie 1996) using a non-complete reference collection; 2) a senior taxonomist (P. A. V. Borges) performed a detailed correction in identification of each sorted sample, adding new species or morphospecies to the reference collection; 3) morphospecies were sent for formal identification to expert taxonomists (see acknowledgments); 4) specimens properly identified were used to correct datasheets and the reference collection prior to the second sampling year (Appendix

1). Immature stages were also considered in the identification process. Validation of the identification of immature forms was performed mainly in the second stage of the identification process, and based on previous experience of the taxonomists involved in the project (Borges 1999, Borges and Brown 1999). In spite of some recent criticism of immature identification (Derraik et al. 2002), such an approach was possible due to the low level of species richness found in this study.

The following insect phytophagous groups were investigated: Orthoptera, Hemiptera (Homoptera and Heteroptera), Thysanoptera, Coleoptera and Lepidoptera. The species sampled are only the free-living

Table 2. Number of transects per island in which each of the host plant species was sampled and the percentage of occurrence in all transects (n = 50).

Host plant species	Island								
	Endemic	Flores	S. Miguel	Terceira	Faial	S. Jorge	Pico	Sta. Maria	Total (%)
<i>Juniperus brevifolia</i>	yes	10	3	9	1	4	8	0	70
<i>Ilex perado azorica</i>	yes	2	4	8	0	2	9	0	50
<i>Vaccinium cylindraceum</i>	yes	6	2	6	0	4	3	1	44
<i>Laurus azorica</i>	no	2	3	8	0	0	4	2	38
<i>Erica azorica</i>	yes	2	2	2	1	1	4	2	28
<i>Myrsine africana</i>	no	1	0	6	0	1	1	0	18
<i>Calluna vulgaris</i>	no	4	0	1	0	0	0	0	10
<i>Myrica faya</i>	no	0	0	0	1	0	0	0	2
<i>Picconia azorica</i>	yes	0	0	0	0	0	0	1	2
<i>Clethra arborea</i>	no	0	1	0	0	0	0	0	2

chewing and sucking insect species captured with beating-trays, because surveying leaf-miners and stem-borers efficiently would require other sampling methods. Voucher specimens and all sorted data are housed in the insect reference collection in the Dept of Agriculture at the Univ. of the Azores.

Data analysis

ANOVA models were constructed using the General Linear Model Procedure of SPSS 11.5, in order to analyse arthropod species richness and abundance per tree and per island. Only the dominant host species were taken into account in order to achieve orthogonal combinations and to compensate for an unbalanced sample design. The unbalanced sample design was, unavoidable, due to the absence of all host species in some reserves or islands. To overcome this problem, two separate models were designed to test host and island factors on complementary data sets, without discarding information (Potvin 2001). In addition, an ANOVA design employing Type III sums of squares was chosen, as it is more appropriate to deal with unequal sample sizes (Shaw and Mitchell-Olds 1993, Potvin 2001). The lack of consistency in the relative densities of host plants, and hence the sample effort per plant did not affect the main conclusions (tested by comparing *E. azorica* and *J. brevifolia* in equal and different combinations of sample sizes on the same islands).

To reach a more balanced model, the islands of São Jorge, Pico and Faial were analyzed as a unique biogeographic set. This grouping procedure seems reasonable since these islands are much closer to each other than any further set of islands in the archipelago, and are of similar geological age (actually, it is the youngest group in the Azores).

Therefore, a combination of different models was used, in order to test hypotheses about the role of islands and host species on herbivore species richness and abundance. Two models were statistically tested: 1) all islands with the three dominant host species *Erica azorica*, *Laurus azorica perado* and *Vaccinium cylindraceum* and 2) all important host species *Erica azorica*, *Laurus azorica*, *Vaccinium cylindraceum*, *Ilex perado azorica* and *Juniperus brevifolia* on all islands but Santa Maria.

Due to the unequal distribution of host species amongst sampling transects and reserves, no blocking effect could be analysed in either model. However, the effect of blocking environmental heterogeneity without a good understanding of the heterogeneity of the environment is of doubtful value. At the scale of tested hypothesis (i.e. the effect of host species distribution among islands) the effect of within-island heterogeneity

might also be impossible to explore (Potvin 2001), and therefore reserves may not be real independent variables.

The 10 host plants sampled in one transect were considered as a single sample set and an average value was calculated. Parameter estimates were used to test specifically the a priori hypothesis of differences between Santa Maria Island and other islands in model (1) using a t-test, based on confidence interval adjustment from the main factor. Post-hoc multiple comparisons based on least significant differences (LSD) was used to explore any differences found whether between islands or host species in model (2).

Further analysis of insect community composition was performed using Reciprocal Averaging multivariate analysis and clustering by Ward's method, using Bray-Curtis distances using the software CAP (Henderson and Seaby 2004).

To obtain an estimate of the level of specialization of each herbivore species to the host plant we applied the Lloyd index (L), as proposed by Basset (1999b). The Lloyd index was computed only for insect species represented by a minimum of 10 specimens, because these species could theoretically have been collected from ten possible plants. To standardize sampling effort among host plants, the number of specimens was averaged based on the samples available for each host plant, prior to applying the index. As the frequency distribution of abundance within each species was shown to be right skewed, the geometric mean was chosen instead of the arithmetic mean, since it provides a much more accurate representation of the central tendency (Zar 1996). The geometric mean also has the advantage of overcoming the problem of underestimating the mean due to high numbers of zeros. A species was considered to be a specialist (as opposed to a generalist) on a particular substrata if $L \geq 2.5$. A specialist species in the present context is only a species that showed preference for a particular host, the value of the index increasing for more specialized species (Basset 1999b).

Results

A total of 129 herbivore species were recorded in the present study. The cumulative number of herbivore species per host plant was greater on *Juniperus brevifolia* ($n=65$) and *Erica azorica* ($n=53$), although there was only a 31.3% similarity between the faunas of these two important host trees (Fig. 1). *Erica azorica* was sampled on all surveyed islands, comprising 10.7% of the sampled plants. *Juniperus brevifolia* was the most common tree species in mature forests, comprising 26.7% of the sampled plants, excluding Santa Maria Island, where the species does not occur in native vegetation patches (Table 2).

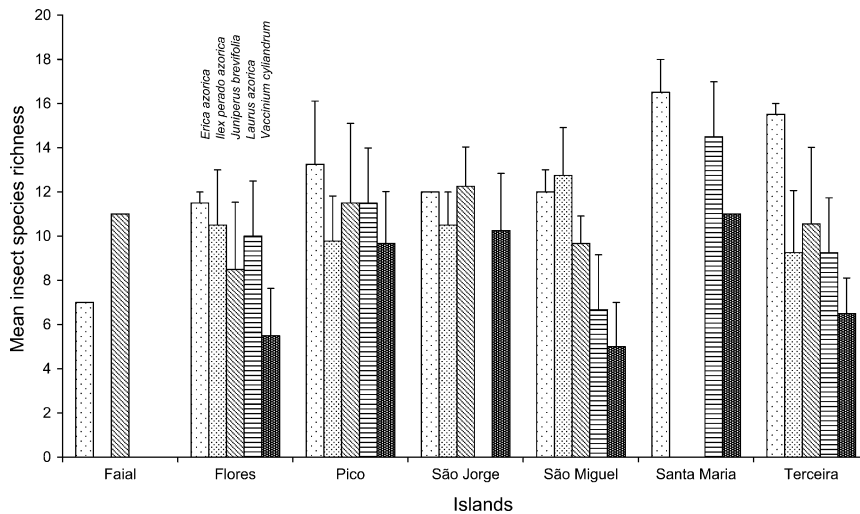


Fig. 1. Mean insect species richness per host plant species, for each studied island (+standard error), sampled in the summer of 1999 and 2000.

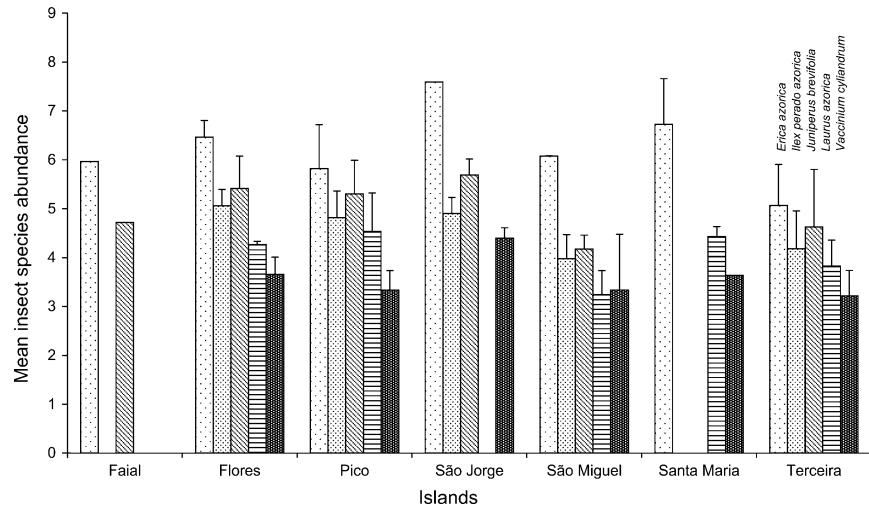
A great number of rare insect species was found. Indeed, 45% of sampled insect species were singletons (i.e. appeared just one time), and most species occurred scarcely. For instance, half of transects (=10 trees from one species) had 30–70% sampled trees with no herbivore insects. However, it is noticeable that such a pattern is not applicable to *E. azorica*, which had only 8% of its sampled trees lacking the herbivore guild. These data suggest that alpha diversity, taking individual crowns as local units, is higher for the insect herbivore fauna associated with this tree species than with any other, a pattern confirmed by the ANOVA models. The effect of *E. azorica* was remarkable, overcoming individual effects of islands and of other more frequent host species (*L. azorica*, *V. cylindraceum*, *J. brevifolia*, and *I. perado*; Table 2), and thus supporting the third hypothesis.

1) Model of all islands containing *Erica azorica*, *Laurus azorica* and *Vaccinium cylindraceum* – significant differences in insect species richness and abundance between hosts and between islands were found in these models (Table 3). However, island effect was strongly influenced by Santa Maria Island alone. Multiple comparisons confirmed that host trees on Santa Maria supported more species and individuals of insect herbivore species than trees on any other island (richness: $t = 2.49$, $p < 0.02$; abundance: $t = 2.15$, $p < 0.04$) (see also Figs 1 and 2). On the other hand, this pattern was influenced by the greatest number of insects on *E. azorica*, which resulted in no significant interaction effect between factors (Table 3; Fig. 2). Despite island idiosyncrasies in species composition, the pattern of higher insect species richness and abundance on

Table 3. ANOVA models designed using General Linear Procedures for (1) species richness and (2) log-transformed abundance of insect herbivores, testing *Erica azorica*, *Laurus azorica* and *Vaccinium cylindraceum* in all studied islands.

1) Species richness						
Source	SS	DF	MS	F-test	p	
Model	510.74	14	36.48	5,25	0.0001	
Islands	230.94	4	57.73	8,30	0.0001	
Host plants	207.33	2	103.66	14,91	0.0001	
Islands × Hosts	72.48	8	9,06	1,30	0.27	
Within cells	278.17	40	6,95			
Total	788.91	54	14,61			
2) Abundance						
Source	SS	DF	MS	F-test	p	
Model	66.70	14	4,76	8,56	0.0001	
Islands	14.11	4	3,52	6,33	0.0001	
Host plants	49.96	2	24,98	44,86	0.0001	
Islands × Hosts	2.64	8	0,33	0,59	0.78	
Within cells	22.27	40	0,56			
Total	88.98	54	1,65			

Fig. 2. Mean insect species abundance per host plant species, in each studied island (+standard error), sampled in the summer of 1999 and 2000.



E. azorica was consistent across the whole archipelago (Figs 1 and 2). Nonetheless, data suggests that geological age may play an important role, thus supporting the second hypothesis prediction.

2) Model of *Erica azorica*, *Laurus azorica*, *Vaccinium cylindraceum*, *Juniperus brevifolia*, and *Ilex perado azorica* in all studied islands except Santa Maria – this model showed that significant differences in insect herbivore species richness and abundance were found across host species (Table 4). *Erica azorica* had the greatest number of species per tree crown (12.75 ± 0.9 morphospecies per tree crown; LSD: mean differences varying from 2.3 to 5.3, $p < 0.05$), and *V. cylindraceum* the smallest (6.75 ± 0.7 morphospecies per crown; LSD: mean differences varying from 2.17 to 5.3, $p < 0.05$), while the remaining trees did not differ among species

(LSD: mean differences varying from 0.11 to 0.9, $p > 0.05$). Similarly, *E. azorica* had the greatest value of insect abundance per tree crown than other species, followed by *J. brevifolia*, and *I. perado azorica*, which had higher abundance than *L. azorica* and *V. cylindraceum* (LSD: mean differences varying from 0.9 to 2.9, $p < 0.05$). The latter two species did not differ in insect abundance (LSD: mean difference = 0.34, $p > 0.05$). The island factor had no effect on species richness without Santa Maria (Table 4), but Pico still had less abundance per averaged tree crown than other islands (4.16 ± 0.2 individuals per crown; LSD: mean differences varying from 0.6 to 1.5, $p < 0.05$).

No island-host plant interaction was found. This fact, along with the great insect occurrence on *E. azorica* in relation to the other host plants, on any island, was

Table 4. ANOVA models designed using General Linear Procedures for (1) species richness and (2) log- transformed abundance of insect herbivores, testing *Erica azorica*, *Juniperus brevifolia*, *Ilex perado azorica*, *Laurus azorica* and *Vaccinium cylindraceum* in all studied islands but Santa Maria.

1) Species richness						
Source	Type III SS	DF	MS	F-test	p	
Model	11047.02	20	552.35	69.92	0.00001	
Island	49.87	3	16.62	2.1	0.1	
Host species	251.17	4	62.79	7.95	0.00001	
Islands × Host species	160.75	12	13.39	1.69	0.08	
Within cells	710.98	90	7.9			
Total	11758	110				
2) Abundance						
Source	SS	DF	MS	F-test	p	
Model	2400.95	20	120.05	209.71	0.0001	
Island	13.24	3	4.415	7.71	0.0001	
Host species	42.714	4	10.68	18.65	0.0001	
Islands × Host species	3.034	12	0.25	0.44	0.94	
Within cells	51.524	90	0.57			
Total	2452.47	110				

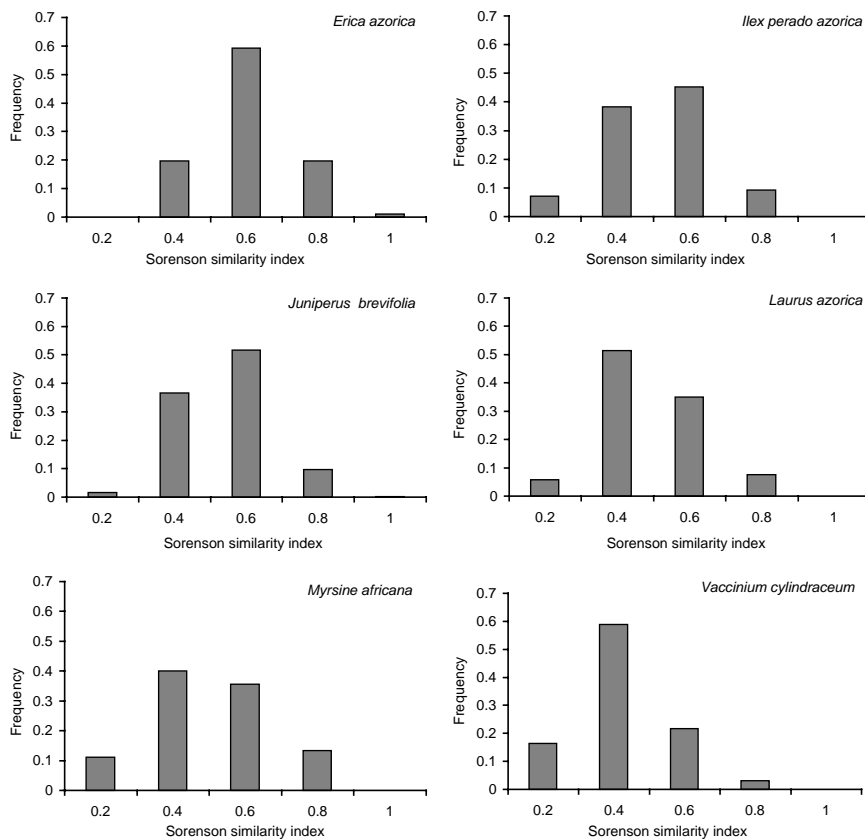


Fig. 3. Frequency distribution of Sorenson's similarity index values between transects for the most important host species, regardless of reserves and islands. A skewed distribution towards low similarity was observed in all studied plants except for *E. azorica*.

suggestive of strong host fidelity by its insect fauna, which was found to be highly similar between transects (Fig. 3). Other host species had a skewed distribution of insect species between transects, toward low similarity values, considering the similarity indexes between transect combination pairs, within and across islands (Fig. 3). In other words, in these host species the fauna found on the crowns seem to vary more in response to location than in *E. azorica*. For instance, *V. cylindraceum* had a mean similarity of 42% between transects, *L. azorica* 48%, *M. africana* 50%, *I. perado azorica* 51%, *J. brevifolia* 54%, while *E. azorica* had 61%, slightly skewed towards high similarities.

Reciprocal averaging (RA) analysis confirmed the pattern of high diversity and fidelity of the fauna on *E. azorica* compared with other species, and regardless of islands. RA for insect herbivore species frequency (Fig. 4) shows that each host plant species accumulates particular herbivore fauna in response to islands. *Erica azorica* is the exception, sustaining a uniform herbivore fauna across the archipelago and, consequently, trees of this species group together regardless of islands. Both insect fidelity to *E. azorica* and scarcity of species on other hosts may be influencing the patterns described by RA, as rare species were not down weighted in the analyses. A striking exception was Santa Maria Island,

which grouped all host trees in it, including *E. azorica* (Fig. 4). Yet, within this island *E. azorica* has a somewhat characteristic insect fauna compared with other plant species, and this species plot stands slightly displaced from others within the Santa Maria group (Fig. 4).

A likely explanation for the pattern found in Santa Maria Island could be the absence of *J. brevifolia*, which may then inflate the number of generalists in *E. azorica*, which are usually more frequent on the former species when it is present. Reciprocal averaging did not show an arch effect or data distortion, which are commonly associated with this technique.

Additional analyses on faunistic dissimilarity indices for all combinations of sampled trees on all islands reinforced that samples from *E. azorica* were more similar to each other despite islands of origin (in this analysis, only *E. azorica* from Pico island is not clustered with the other *E. azorica* samples from the remaining islands), while samples taken from other host species were clustered by islands (Fig. 5). No clear pattern of faunal dissimilarity increasing with distance or island size was found (Figs 4 and 5). Flores, the most distant and one of the smallest islands had high similarity with islands of the central group. A slight dissimilarity was found in São Miguel, the largest island. Therefore, apart

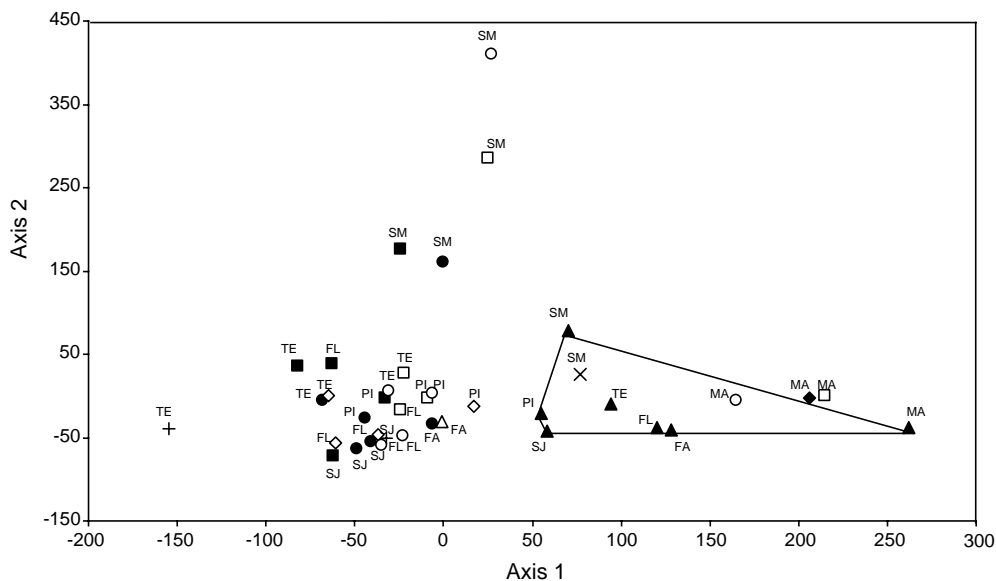


Fig. 4. Ordination plot based on Reciprocal Averaging analysis of insect species frequency on each host plant per islands, for the ordination axes 1 and 2. The letters of each code correspond to the island: FL – Flores, SJ – S. Jorge, PI – Pico, TE – Terceira, FA – Faial, SM – S. Miguel and MA – S. Maria. The plant species are represented by symbols: *Calluna vulgaris* (crosses), *Clethra arborea* (diagonal crosses), *Erica azorica* (filled triangles), *Ilex perado azorica* (filled squares), *Juniperus brevifolia* (filled circles), *Laurus azorica* (open squares), *Myrica faya* (open triangles), *Myrsine africana* (filled diamonds) and *Vaccinium cylindraceum* (open circles). The plant samples of *E. azorica* are linked with a perimeter line.

from the high species accumulation found in the oldest island, Santa Maria, no other clear biogeographic pattern was detected.

The observed pattern of herbivore fidelity to *E. azorica* seems to result from two independent causes: gathering of a great number of generalists, and a higher

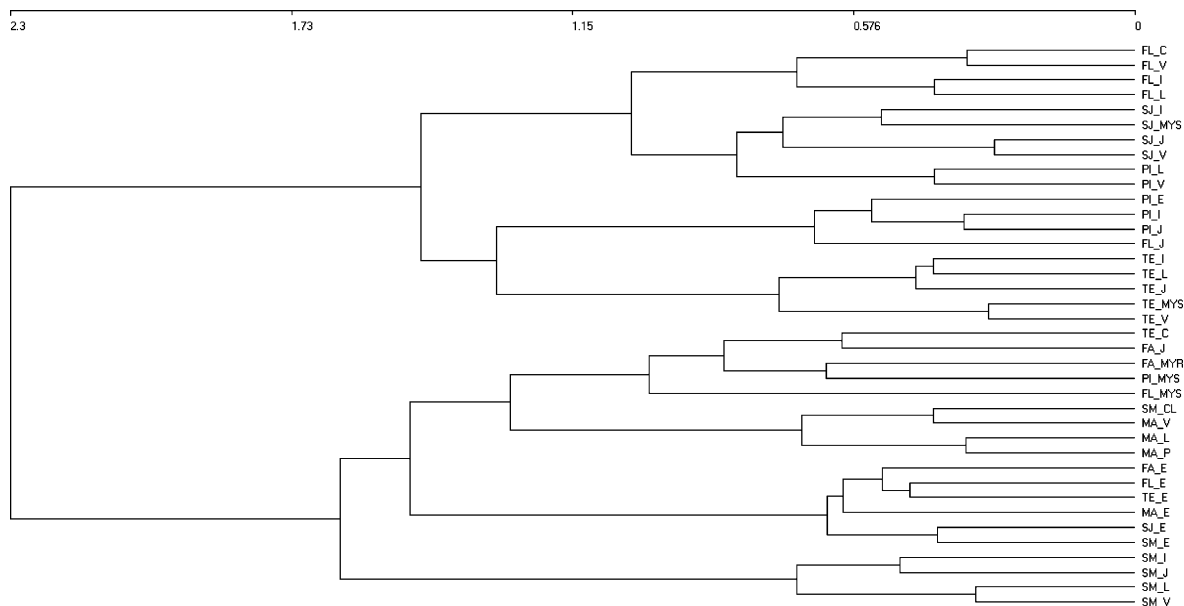


Fig. 5. Dissimilarity clustering between host species grouped by island (Ward's method, using Bray-Curtis distances). Legend for island-host codes as follows: the first two letters of each code correspond to the island: FL – Flores, SJ – S. Jorge, PI – Pico, TE – Terceira, FA – Faial, SM – S. Miguel and MA – S. Maria. The remaining letters are the plant species: C – *Calluna vulgaris*, V – *Vaccinium cylindraceum*, J – *Juniperus brevifolia*, L – *Laurus azorica*, MYR – *Myrica faya*, MYS – *Myrsine africana*, P – *Picconia azorica* and E – *Erica azorica*.

Table 5. Herbivorous insect species considered specialists by the Lloyds Index (cut point at 2.5). The geomean abundance of each specialist per host plant species, as well as the respective mean and variance abundance for all host plant species are also presented. Plant legend as in Table 1.

Species	Order	Family	Endemic	Host plant species											Mean	Var	Lloyd
				V	P	MYRS	M	L	J	I	E	C	CALL				
<i>Cleora fortunata azorica</i>	Lepidoptera	Geometridae	yes	1.7	2.0	0.0	1.0	1.4	2.0	1.0	1.0	25.4	1.0	0.0	4.4	71.7	4.41
<i>Argyresthia atlanticella</i>	Lepidoptera	Yponomeutidae	yes	11.3	11.0	3.5	31.0	5.0	61.0	8.7	8.7	252.6	5.0	45.9	43.5	5783.3	4.03
<i>Kleidocerys ericae</i>	Hemiptera	Lygaeidae	no	2.0	21.0	0.0	0.0	3.3	2.0	1.7	49.7	3.0	0.0	11.8	327.2	3.25	
<i>Heliothrips haemorrhoidalis</i>	Thysanoptera	Thripidae	no	2.0	0.0	0.0	0.0	1.7	4.0	0.0	1.5	23.0	0.0	0.0	6.4	86.6	2.93
<i>Toxoptera auranti</i>	Hemiptera	Aphididae	no	0.0	0.0	0.0	0.0	0.0	4.0	4.0	162.0	0.0	0.0	83.0	12482.0	2.80	
<i>Cixius azoforesis</i>	Hemiptera	Cixiidae	yes	4.4	0.0	9.0	0.0	10.8	66.6	32.9	3.0	0.0	2.4	18.4	560.5	2.60	
<i>Anaspis proteus</i>	Coleoptera	Anaspidae	no	1.0	0.0	2.5	0.0	3.2	2.1	3.7	17.6	1.0	0.0	4.4	34.9	2.54	
<i>Rhopobota naevana</i>	Lepidoptera	Tortricidae	no	1.2	0.0	0.0	0.0	2.0	1.5	1.5	13.5	1.7	0.0	4.0	28.2	2.53	
<i>Cyclophora pupillaria granti</i>	Lepidoptera	Geometridae	yes	3.0	4.0	0.0	0.0	1.4	1.0	1.0	18.0	0.0	0.0	5.5	50.4	2.49	

frequency of oligophagous compared to other host species. Indeed, only 10 out of the 131 herbivore species sampled could be considered specialists according to the Lloyd index, and half of them were specialized on *E. azorica* (Table 5). Furthermore, three out of the four endemic species considered to be specialists were specialized on *E. azorica*.

Partially, the prediction of a low number of specialist species was upheld, but uniform distributions among host species was not, due to a biased distributions towards *E. azorica*, this suggests that habitat preference, related to this species crown and leaf traits, may confound other island effects.

Discussion

Herbivore species accumulation on islands and polyphagy

Studies of community structure of canopy arthropods are virtually absent in the Azores, let alone in any other Atlantic islands, or even in oceanic islands in general (Holloway 1996). Our study, covering seven islands, ten vascular plants (five Azorean endemics) and a large sampling effort, is the first quantitative survey of free-living tree or shrub insects in an oceanic Atlantic archipelago.

This study suggests that free-living insect herbivores are mainly generalists, as expected for a relatively young and isolated volcanic archipelago. This pattern of a high proportion of generalists was also found by Olesen et al. (2002) for Azorean pollinators and is common for other island guilds of phytophagous insects (e.g. Lepidoptera), as in Norfolk Island (Holloway 1996). Olesen et al. (2002) explain the super-generalization of pollinators in the Azores by the low interspecific competition. This same explanation, along with generally low predation and parasitic pressures, could also account for the generalization found among the free-living herbivore insects foraging in the canopies of native and endemic shrubs and trees of the Azores.

Given the high incidence of generalist species in this community, it becomes imperative to understand the processes involved in their evolution. A problem of studying polyphagy in the wild is that most revisions or experimental trials to test phytochemical toxicity have been done using herbivore insects associated with ruderal plant communities or cultivated species. These systems do not cover the variety of habitat constraints and/or biochemical background such as that found in a tropical forest, or a Macaronesian Laurisilva canopy environment. Host plant physiological adaptations to shallow, poor, or extremely heterogeneous soils, along with the predictability and complexity of the canopy habitat, must provide a suite of completely different

selective forces on insect feeding patterns. Why should insects in such a complex environment have neural constraints to recognize food sources and why should specialisation become an advantage? How do sensory systems interact with a variable and complex, versus a predictable and simple habitat? Many important questions like these will remain unanswered until researchers perceive the importance of linking studies between macroecology and experimental insect-plant interaction, particularly those performed in the wild rather than in disturbed urban or agricultural ecosystems.

Despite the common belief in the widespread advantage of monophagy, high numbers of generalists have been reported in many tropical forests, as well as in temperate natural forests of the Azores. Selective pressure favouring specialist herbivores may be less common than previously expected, or at least more important in particular types of vegetation. For instance, specialists seem to be more frequent in evolutionarily old communities, adapted to harsh abiotic and nutritional conditions (Price et al. 1998, de Souza Mendonça 2001, Ribeiro and Brown 2002, Novotny et al. 2002, Ribeiro 2003). Host-shifting in these plant communities is likely to affect patterns of insect speciation, even though all new species end up with a restricted feeding behaviour due to increased reproductive success (de Souza Mendonça 2001, Novotny et al. 2002) or larval developmental constraints, mainly in endophagous insects. Therefore, changes in host choice may become a mechanism of herbivore species radiation rather than of increasing generalism. Ribeiro (2003) argues that such insect communities may have evolved strictly in response to severe feeding constraints, and that generalists may predominate in many other types of vegetation.

Bernays and Graham (1988) discuss potential ecological advantages related to host plant fidelity in oligophagous species, such as sequestration of chemical protection, which is an adaptative (though reversible) trait, strictly related to constant feeding on the same or similar host plants. Micro-habitat conditions may also contribute to general host plant fidelity. Nevertheless, the same mechanism of protection against predators (or parasitoids) can result in a mixed diet and phagostimulation by secondary compounds which should favour either specialists or polyphagous insects (Bernays et al. 2000, Singer and Stireman 2003).

***Erica azorica* as a predictable and widespread habitat for insects**

A small-scale high plant density may result in herbivore accumulation, as described by Straw (1994). Such a process is also compatible with the present pattern of species accumulation and generalist-with-fidelity insect herbivore guilds, found in *E. azorica*. Crawley (1983)

among others (Straw and Ludlow 1994, Krüger and McGavin 2000) argued that a widespread host plant may support more insect species due only to "sampling" various local faunas, which might be the case of *J. brevifolia* in the present study. However, it is not expected that such tree species would support more herbivores per individual crown than a similar-sized host plant in the same place. In this study, *J. brevifolia* accumulated a greater number of herbivore species than *E. azorica*, although the latter supported higher species richness per tree crown.

Moreover, in this study the highest densities of the few specialist species were recorded in *E. azorica*. Among those, both *Argyresthia atlanticella* Rebel (Lepidoptera, Yponomeutidae) and *Cleora fortunata azorica* (Lepidoptera, Geometridae) cause substantial impact on plant architecture, with potential consequences for its competitive success during the successional process (Ribeiro et al. 2003). Dense populations of specialist herbivore insects may act as a significant selective force in preventing the dominance of *E. azorica* in climax Laurisilva forest, as well as acting as an evolutionary force favouring both the evolution of arborescence in *E. azorica* and herbivory resistance or tolerance (Givnish 1998, Ribeiro et al. 2003, Ribeiro et al. unpubl.).

A possible mechanistic explanation for the evolution of the pattern discussed above may be drawn from a metapopulation hypothesis of Hanski (1994, see also Krüger and McGavin 2000). This hypothesis predicts a decrease in local extinction due to regional immigration, thus causing a positive correlation between distribution and abundance (Gaston and Blackburn 2000). Taken in a proper temporal context, the idiosyncratic evolutionary history of each island may be overcome by the widespread and long term presence of *E. azorica*. The hypothesis states that the presence and, particularly, the local dominance of this host species results in insect habitat similarities, hence allowing a particular section of the insect community to be widely distributed, by following conditions created by *E. azorica*.

In fact, an evolutionarily old host species could accumulate an enormous diversity of herbivore species on it (Birks 1980, Kennedy and Southwood 1984), by the simplest fact of being a predictable habitat. In this sense, evolutionary time may mask other island biogeographical factors (Borges and Brown 1999) that otherwise could appear as a typical null hypothesis output (taking biogeographic theory as a neutral theory, sensu Hubbell 2001). On the contrary, the Azorean canopy herbivore guild seems to respond to more directed evolutionary and ecological forces, which clearly define patterns of species diversity and survival after colonization far beyond a possible explanation based on MacArthur and Wilson's neutral assumptions. Hence, it is expected that such species populations will evolve in response to this insect pressure, but that may or may not result in

accumulation of specialists, which instead depends on how long the species have been in the ecosystem (Ribeiro and Brown 1999). Therefore, host and habitat fidelity (which varies from oviposition sites, to food resources, lack of predator/parasitism, or even feeding speciality) could be one of the most reasonable explanations for faunistic association with this plant species – *Erica azorica*.

Conclusions

The results described here agree with the general pattern of community simplification in island ecosystems: dominance of generalist species and strong island regional effects on species composition (Borges and Brown 1999). However, one early successional plant species, *E. azorica*, seems to play an important functional role by hosting a common set of phytophagous insect species throughout most of the Azorean islands. Polyphagy in these free-living herbivore insects may have a strong correlation with the high floristic similarity found among all the Azorean islands, and is compatible with an expected ecological community shaped by taxonomic disharmony.

Regardless of the strong effect of habitat caused by *E. azorica*, other patterns of insect herbivore species distribution were not clearly distinct from those found in canopy ecosystems of world continental biomes. The pattern of low tree individual occupancy was similar to those found in tropical savannas. On the other hand, the mean number of herbivore species per tree crown was two and half fold lower than in Brazilian savanna vegetation, which is a species-poor tropical plant community, at least concerning free-living herbivores (Ribeiro et al. 2003). On the other hand, the high proportion of local singletons (45%) was similar to that found by Novotny and Basset (2000) in tropical rainforest in Papua New Guinea. The patterns described here are supported by a large comprehensive data base for forest canopies in the Azores, and may contribute to understanding of general insect-plant mechanisms which might shape insect herbivore guild structures in any canopy forest habitat of the world.

Acknowledgements – Thanks are due to the Azorean Forest Services, for their support and guidance to the field sites. Also to A. Arraiol, F. Pereira, L. Vieira and A. Vitorino for the valuable help during the field and laboratory work. We are in debt to all the taxonomists who help us to identify the morphospecies: A. Baz (Univ. de Alcalá, Spain), H. Enghoff (Zoological Museum, Univ. of Copenhagen, Denmark), F. Ilharco (Estação Agronómica Nacional, Portugal), V. Manhart (Museum d'Histoire Naturelle, Switzerland), J. Ribes, A. B. Sousa (SPEN-Sociedade Portuguesa de Entomologia, Lisbon, Portugal), R. Z. Strassen (Germany), V. Vieira (Dept Biology, Univ. Azores, Portugal) and J. Wunderlich (Germany). L. Fagan and R. Didham contributed for language style and text improvement. Brazilian Council for Science Development,

CNPq, funded SPR, in the scope of PROFIX programme. Pro-rectory of Research and post-graduation in the Fed. Univ. Ouro Preto funded partially SPR. SPR was also funded by CITA-UA in his visit to the Univ. of Azores in 2002. CM was funded by Fundação para a Ciência e a Tecnologia for a Masters grant. CG was supported by Fundação para a Ciência e a Tecnologia, BD/11049/2002. Overall funding for this study was provided by “Direcção Regional dos Recursos Florestais” (“Secretaria Regional da Agricultura e Pescas”) through the Project “Reservas Florestais dos Açores: Cartografia e Inventariação dos Artrópodes Endémicos dos Açores” (PROJ. 17.01 – 080203).

References

- Andow, D. A. and Imura, O. 1994. Specialization of phytophagous arthropod communities on introduced plants. – *Ecology* 75: 296–300.
- Basset, Y. 1999a. Diversity and abundance of insect herbivores collected on *Castanopsis acuminatissima* (Fagaceae) in New Guinea: relationships with leaf production and surrounding vegetation. – *Eur. J. Entomol.* 96: 381–391.
- Basset, Y. 1999b. Diversity and abundance of insect herbivores foraging on seedlings in a rainforest in Guyana. – *Ecol. Entomol.* 24: 245–259.
- Basset, Y. et al. 1996. How many species of host-specific insects feed on a species of tropical tree? – *Biol. J. Linn. Soc.* 59: 201–216.
- Bernays, E. A. and Graham, M. 1988. On the evolution of host specificity in phytophagous arthropods. – *Ecology* 69: 886–892.
- Bernays, E. A. and Minkenbergh, O. P. J. M. 1997. Insect herbivores: different reasons for being a generalist. – *Ecology* 78: 1157–1169.
- Bernays, E. A. and Funk, D. J. 1999. Specialists make faster decisions than generalists: experiments with aphids. – *Proc. R. Soc. Lond. B.* 266: 1320–1326.
- Bernays, E. A., Chapman, R. F. and Singer, M. S. 2000. Sensitivity to chemically diverse phagostimulants in a single gustatory neuron of a polyphagous caterpillar. – *J. Comp. Physiol. A* 186: 13–19.
- Birks, H. J. B. 1980. British trees and insects: a test of the time hypothesis over the last 13,000 years. – *Am. Nat.* 115: 600–605.
- Borges, P. A. V. 1999. Plant and arthropod species composition of sown and semi-natural pasture communities of three Azorean islands (S. Maria, Terceira and Pico). – *Arquipélago* 17: 1–21.
- Borges, P. A. V. and Brown, V. K. 1999. Effect of island geological age on the arthropod species richness of Azorean pastures. – *Biol. J. Linn. Soc.* 66: 373–410.
- Borges, P. A. V. and Brown, V. K. 2004. Arthropod community structure in pastures of an island archipelago (Azores): looking for local-regional species richness patterns at small-scales. – *Bull. Entomol. Res.* 94: 111–121.
- Borges, P. A. V. et al. 2005. Ranking protected areas in the Azores using standardized sampling of soil epigeal arthropods. – *Biol. Conserv.*, in press.
- Crawley, M. J. 1983. Herbivory: the dynamics of animal – plant interactions. – Blackwell.
- Derraik, J. G. B. et al. 2002. Arthropod morphospecies versus taxonomic species: a case study with Araneae, Coleoptera, and Lepidoptera. – *Conserv. Biol.* 16: 1015–1023.
- Dias, E. 1996. Vegetação Natural dos Açores: Ecologia e Sintaxonomia das Florestas Naturais. – Ph.D. thesis, Univ. dos Açores, Angra do Heroísmo.
- Fernandes, G. W. and Price, P. W. 1991. Comparison of tropical and temperate galling species richness: the roles of environmental harshness and plant environmental status. – In: Price, P. W. et al. (eds), *Plant – animal interactions:*

- evolutionary ecology in tropical and temperate regions. Wiley, pp. 91–115.
- Gaston, K. J. and Blackburn, T. M. 2000. Pattern and process in macroecology. – Blackwell.
- Givnish, T. J. 1998. Adaptive plant evolution on islands: classical patterns. – In: Grant, P. R. (ed.), *Evolution on islands*. Oxford Univ. Press, pp. 281–304.
- Gross, P. and Price, P. W. 1988. Plant influences on parasitism of two leafminers: a test of enemy-free space. – *Ecology* 69: 1506–1516.
- Hägele, B. F. and Rowel-Rahier, M. 2000. Choice, performance and heritability of performance of specialist and generalist insect herbivores towards cacalol and seneciophylline, two allelochemicals of *Adenostyles alpina* (Asteraceae). – *J. Ecol. Biol.* 13: 131–142.
- Hanski, I. 1994. A practical model of metapopulation dynamics. – *J. Anim. Ecol.* 63: 151–162.
- Henderson, P. A. and Seaby, R. M. H. 2004. CAP – Community Analysis Package, ver. 3.0. – Pisces Conservation.
- Holloway, J. D. 1996. The Lepidoptera of Norfolk Island, actual and potential. Their origins and dynamics. – In: Keast, A. and Miller, S. E. (eds), *The origin and evolution of Pacific island biotas, New Guinea to eastern Polynesia: patterns and processes*. SPB Academic Publ., pp. 123–151.
- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. – Princeton Univ. Press.
- Kennedy, C. E. J. and Southwood, T. R. E. 1984. The number of species of insects associated with British trees: a re-analysis. – *J. Anim. Ecol.* 53: 455–478.
- Krüger, O. and McGavin, G. C. 2000. Macroecology of local insect communities. – *Acta Oecol.* 21: 21–28.
- Losey, J. E. and Denno, R. F. 1998. The escape response of pea aphids to foliar-foraging predators: factors affecting dropping behaviour. – *Ecol. Entomol.* 23: 53–61.
- Novotny, V. and Basset, Y. 2000. Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. – *Oikos* 89: 564–572.
- Novotny, V. et al. 2002. Low host specificity of herbivorous insects in a tropical forest. – *Nature* 416: 841–844.
- Nunes, J. C. C. 1999. A actividade vulcânica na ilha do Pico do Plistocénico Superior ao Holocénico: mecanismo eruptivo e Hazard vulcânico. – Ph.D thesis, Univ. dos Açores.
- Olesen, J. M., Eskildsen, I. and Venkatasamy, S. 2002. Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. – *Div. Distribut.* 8: 181–192.
- Oliver, T. and Beattie, A. J. 1996. Invertebrate morphospecies as surrogates for species: a case study. – *Conserv. Biol.* 10: 99–109.
- Potvin, C. 2001. ANOVA. Experimental layout and analysis. – In: Scheiner, S. M. and Gurevitch, J. (eds), *Design and analysis of ecological experiments*, 2nd ed. Oxford Univ. Press, pp. 63–76.
- Price, P. W. et al. 1998. Global patterns in local number of insect galling species. – *J. Biogeogr.* 25: 581–592.
- Reis, M. A. et al. 2002. Comparison of continental Portugal and Azores Islands aerosol during a Sahara dust storm. – *Nucl. Instrum. Meth. Phys. Res. B* 189: 272–278.
- Ribeiro, S. P. 2003. Insect herbivores in the canopies of savannas and rainforests. – In: Basset, Y. et al. (eds), *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy*. Cambridge Univ. Press, pp. 348–359.
- Ribeiro, S. P. and Brown, V. K. 1999. Insect herbivory within tree crowns of *Tabebuia aurea* and *T. ochracea* (Bignoniaceae): contrasting the Brazilian cerrado with the wetland “Pantanal Matogrossense”. – *Selbyana* 120: 159–170.
- Ribeiro, S. P. and Brown, V. K. 2002. Tree species monodominance or species-rich savannas: the influence of abiotic factors in designing plant communities of the Brazilian cerrado and the Pantanal matogrossense – a review. – *Ecotropica* 8: 31–45.
- Ribeiro, S. P. et al. 1999. Leaf polyphenols in Brazilian Melastomataceae: sclerophylly, habitats, and insect herbivores. – *Ecotropica* 5: 137–146.
- Ribeiro, S. P., Borges, P. A. V. and Gaspar, C. 2003. Ecology and evolution of the arborescent *Erica azorica* Hochst. (Ericaceae). – *Arquipélago Ciên. Agr.* 1: 41–50.
- Sabelis, M. W. et al. 1999. The evolution of direct and indirect plant defence against herbivorous arthropods. – In: Olff, H., Brown, V. K. and Drent, R. H. (eds), *Herbivores: between plants and predators*. Blackwell, pp. 109–165.
- Schowalter, T. D. 1994. Invertebrate community structure and herbivory in a tropical rain forest canopy in Puerto Rico following hurricane Hugo. – *Biotropica* 26: 312–319.
- Schowalter, T. D. and Ganio, L. M. 1999. Invertebrate communities in a tropical rain forest canopy in Puerto Rico following Hurricane Hugo. – *Ecol. Entomol.* 24: 191–201.
- Shaw, R. G. and Mitchell-Olds, T. 1993. ANOVA for unbalanced data: an overview. – *Ecology* 74: 1638–1645.
- Singer, M. S. and Stireman, III, J. O. 2003. Does anti-parasitoid defense explain host-plant selection by a polyphagous caterpillar? – *Oikos* 100: 554–562.
- de Souza Mendonça, Jr. 2001. Gall insects diversity patterns: the resource synchronisation hypothesis. – *Oikos* 95: 171–176.
- Straw, N. A. 1994. Species-area relationships and population dynamics: two sides of the same coin. – In: Leather, S. R. et al. (eds), *Individuals, populations and patterns*. Intercept, pp. 276–286.
- Straw, N. A. and Ludlow, A. R. 1994. Small-scale dynamics and insect diversity on plants. – *Oikos* 71: 188–192.
- Tune, R. and Dussourd, D. E. 2000. Specialized generalists: constraints on host range in some plusiine caterpillars. – *Oecologia* 123: 543–549.
- Whittaker, R. J. 1998. *Island biogeography – ecology, evolution and conservation*. – Oxford Univ. Press.
- Zar, J. H. 1996. *Biostatistical analysis*, 3rd ed. – Prentice-Hall.

Subject Editor: John Spence.

Appendix 1. Abundance per plant in each island of most common (more than 10 specimens) sampled herbivore arthropod species. For each species information is given concerning its colonization status (Col.: E =endemic, N =native; I =introduced), taxonomic affiliation, morphospecies code (MF), Lloyd's Index and number of plants occurrence. For each island (FLO = Flores; FAI = Faial; PIC = Pico; SJG = S. Jorge; TER = Terceira; SMG = S. Miguel; SMA = S. Maria) the number of transects for each plant is given in brackets.

MF	Species	Col.	Order	Family	Lloyd	No. plants	<i>Calluna</i>		<i>Clectra</i>		<i>Ilex</i>				<i>Juniperus</i>													
							FLO (3)	TER (1)	SMG (1)	FAI (1)	FLO (2)	PIC (4)	SJG (1)	SMG (2)	STM (2)	TER (2)	FLO (2)	PIC (9)	SJG (2)	SMG (4)	TER (8)	FAI (1)	FLO (10)	PIC (8)	SJG (4)	SMG (3)	TER (9)	
MF90	<i>Cleora fortunata azorica</i>	E	Lepidoptera	Geometridae	4.41	8	0	0	1	109	57	59	11	23	95	75	0	1	0	0	0	2	0	0	0	0	0	0
MF19	<i>Argyresthia atlanticella</i>	E	Lepidoptera	Yponomeutidae	4.03	10	326	5	5	291	400	1562	0	436	351	328	89	192	46	39	36	60	2665	1018	1512	27	127	
MF167	<i>Kleidocerys ericae</i>	N	Hemiptera	Lygaeidae	3.25	7	0	0	3	29	785	1	0	151	1880	27	3	1	0	5	2	7	9	2	1	5	0	
MF276	<i>Heliothrips haemorrhoidalis</i>	I	Thysanoptera	Thripidae	2.93	5	0	0	23	0	2	0	1	1	0	5	0	0	0	0	0	0	0	0	0	4	0	
MF534	<i>Toxoptera aurantii</i>	I	Hemiptera	Aphididae	2.80	2	0	0	0	0	0	0	0	0	0	0	0	162	0	0	0	0	0	4	0	0	0	
MF316	<i>Cixius azofloresi</i>	E	Hemiptera	Cixiidae	2.60	7	10	0	0	0	6	0	0	0	0	0	69	0	0	0	0	0	752	0	0	0	0	
MF78	<i>Anaspis proteus</i>	N	Coleoptera	Anaspidae	2.54	7	0	0	1	0	0	61	3	19	0	0	2	9	0	0	21	0	1	10	0	0	10	
MF211	<i>Rhopobota naevana</i>	I	Lepidoptera	Tortricidae	2.53	5	0	0	0	0	0	1	1	0	0	3	7	198	5	45	137	0	1	5	2	0	0	
MF12	<i>Cyclophora pupillaria granti</i>	E	Lepidoptera	Geometridae	2.49	5	0	0	0	0	0	0	5	0	45	0	0	0	0	0	0	0	0	0	0	0	2	
MF176	<i>Cyclophora azorensis</i>	E	Lepidoptera	Geometridae	2.16	8	0	0	2	0	10	13	2	26	0	3	1	8	1	4	4	1	18	21	3	0	22	
MF141	<i>Calacalles subcarinatus</i>	E	Coleoptera	Curculionidae	2.16	6	0	0	0	0	0	2	2	0	0	0	57	39	0	28	20	0	1	3	1	2	1	
MF412	Gen. sp.	?	Lepidoptera	?	2.12	6	0	0	0	0	0	0	0	0	2	0	0	6	17	0	0	0	0	91	123	0	0	
MF195	<i>Trioza laurissilvae</i>	N	Hemiptera	Psyllidae	2.01	9	2	0	4	0	0	5	0	1	19	6	9	29	5	17	10	0	20	20	6	12	8	
MF44	<i>Cinara juniperi</i>	N	Hemiptera	Aphididae	1.93	7	0	11	0	0	0	2	0	0	0	0	1	5	0	2	7	58	39	494	28	55	1211	
MF587	<i>Cixius azopifajo azojo</i>	E	Hemiptera	Cixiidae	1.93	5	0	0	0	0	0	0	0	0	0	0	0	190	0	0	0	0	0	0	135	0	0	
MF118	<i>Scolopostethus decoratus</i>	N?	Hemiptera	Lygaeidae	1.90	3	0	0	0	1	0	0	0	0	76	0	0	0	0	0	0	0	0	0	0	0	0	
MF557	<i>Strophingia hartensi</i>	E	Hemiptera	Psyllidae	1.88	8	0	0	5	6	46	125	0	44	125	9	0	19	0	1	0	0	0	2	3	2	0	
MF7	<i>Cixius azoterceirae</i>	E	Hemiptera	Cixiidae	1.83	7	0	1	0	0	0	0	0	0	0	15	0	0	0	0	325	0	0	0	0	0	223	
MF7	<i>Cixius azomariae</i>	E	Hemiptera	Cixiidae	1.65	4	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	
MF137	<i>Pinalitus oronii</i>	E	Hemiptera	Miridae	1.63	10	4	0	4	7	0	161	0	33	83	1	2	123	6	14	10	7	181	175	89	3	30	
MF9	<i>Ommatoiulus moreleti</i>	I (?)	Diplopoda	Julidae	1.58	7	6	1	0	37	65	56	0	1	0	8	6	16	2	0	5	8	26	37	6	4	13	
MF487	Gen. sp.	?	Hemiptera	Margaroidae	1.53	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	
MF413	Gen. sp.	?	Lepidoptera	Blastobasidae	1.49	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	20	0	0	6	
MF124	<i>Cyphopterum adscendens</i>	N	Hemiptera	Flatidae	1.49	9	1	0	8	0	1	13	0	22	1	3	23	65	0	17	79	18	226	38	65	7	84	
MF414	<i>Xanthorhoe inaequata</i>	E	Lepidoptera	Geometridae	1.35	8	0	0	3	0	0	43	0	75	17	5	0	4	1	3	2	0	2	19	3	0	2	
MF295	<i>Cixius azopifajo</i>	E	Hemiptera	Cixiidae	1.27	6	0	0	0	0	0	154	0	0	0	0	0	459	0	0	0	0	0	341	0	0	0	
MF255	<i>Cixius insularis</i>	E	Hemiptera	Cixiidae	1.19	6	0	0	2	0	0	0	0	44	0	0	0	0	0	224	0	0	0	0	0	85	0	
MF636	Gen. sp.	E?	Hemiptera	Aleyrodidae	1.01	3	0	0	0	0	0	11	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	
MF363	<i>Popillia japonica</i>	I	Coleoptera	Scarabaeidae	0.88	3	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	3	
MF671	<i>Isoneurothrips australis</i>	I	Thysanoptera	Thripidae	0.87	3	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	

MF102	<i>Pseudophloeophagus tenax</i>	N	Coleoptera	Curculionidae	0.60	6	0	0	0	0	1	1	0	0	0	0	0	0	5	1	1	4	3	2	3		
MF372	Gen. sp.	I	Lepidoptera	Tortricidae	0.60	2	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0	9	2	0	0		
MF440	<i>Eudonia melanographa</i>	E	Lepidoptera	Pyralidae	0.55	5	0	0	0	0	0	0	0	0	0	11	28	8	8	13	0	2	11	3	4	11	
MF42	<i>Orthomana obstipata</i>	N	Lepidoptera	Geometridae	0.53	9	0	0	2	0	0	3	0	0	2	1	0	4	0	6	1	0	0	1	0	0	4
MF630	Gen. sp.	E?	Lepidoptera	?	0.50	5	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	17	5	1	0	
MF116	<i>Scoparia coecimaculalis</i>	E	Lepidoptera	Pyralidae	0.46	6	0	0	0	0	0	5	0	0	0	0	0	5	0	2	0	0	3	2	1	0	0
MF519	Gen. sp.	I	Lepidoptera	Tortricidae	0.45	4	0	0	0	0	1	2	0	0	11	10	0	0	0	0	0	0	0	0	0	0	0
MF418	Gen. sp.	I	Lepidoptera	Tortricidae	0.41	5	0	0	0	0	0	2	0	0	0	0	0	2	0	0	3	0	4	8	0	0	15
MF476	<i>Monalocoris filicis</i>	N	Hemiptera	Miridae	0.32	5	0	0	0	0	1	0	0	0	0	4	0	1	0	1	0	0	2	2	0	0	0

Appendix 1. Cont.

MF	Species	Col.	Order	Family	Lloyd	No. plants	<i>Laurus</i>				<i>Myrica</i>		<i>Myrsine</i>		<i>Picconia</i>		<i>Vaccinium</i>						
							FLO (2)	PIC (4)	SMG (3)	STM (2)	TER (8)	FAI (1)	FLO (1)	PIC (1)	SJG (1)	TER (6)	STM (1)	FLO (6)	PIC (3)	SJG (4)	SMG (2)	STM (1)	TER (6)
MF90	<i>Cleora fortunata azorica</i>	E	Lepidoptera	Geometridae	4.41	8	0	1	0	2	0	1	0	0	0	0	2	0	0	0	0	3	1
MF19	<i>Argyresthia atlanticella</i>	E	Lepidoptera	Yponomeutidae	4.03	10	32	50	5	11	36	31	0	33	30	13	11	154	35	192	8	8	28
MF167	<i>Kleidocerys ericae</i>	N	Heteroptera	Lygaeidae	3.25	7	2	1	1	55	1	0	0	0	0	0	21	4	1	2	0	11	1
MF276	<i>Heliothrips haemorrhoidalis</i>	I	Thysanoptera	Thripidae	2.93	5	0	3	0	0	1	0	0	0	0	0	0	4	0	0	0	0	1
MF534	<i>Toxoptera aurantii</i>	I	Homoptera	Aphididae	2.80	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MF316	<i>Cixius azofloresi</i>	E	Homoptera	Cixiidae	2.60	7	22	0	0	0	0	0	9	0	0	0	28	0	0	0	0	0	0
MF78	<i>Anaspis proteus</i>	N	Coleoptera	Anaspidae	2.54	7	0	1	0	0	10	0	1	8	0	2	0	1	0	0	0	1	0
MF211	<i>Rhopobota naevana</i>	I	Lepidoptera	Tortricidae	2.53	5	0	0	2	0	2	0	0	0	0	0	0	1	1	0	0	3	
MF12	<i>Cyclophora pupillaria granti</i>	E	Lepidoptera	Geometridae	2.49	5	0	0	0	3	0	0	0	0	0	0	4	0	0	0	0	0	3
MF176	<i>Cyclophora azorensis</i>	E	Lepidoptera	Geometridae	2.16	8	1	15	0	0	14	16	0	1	1	15	0	1	2	3	0	0	1
MF141	<i>Calacalles subcarinatus</i>	E	Coleoptera	Curculionidae	2.16	6	1	4	1	0	2	0	0	0	0	2	0	2	1	0	0	0	1
MF412	Gen. sp.	?	Lepidoptera	?	2.12	6	0	7	0	0	0	0	0	0	1	1	0	0	0	30	0	0	0
MF195	<i>Triozia laurisilvae</i>	N	Homoptera	Psyllidae	2.01	9	48	164	48	122	106	0	0	0	0	2	19	0	26	3	6	5	7
MF44	<i>Cinara juniperi</i>	N	Homoptera	Aphididae	1.93	7	0	0	1	0	6	0	1	2	0	8	0	0	0	2	0	0	1
MF587	<i>Cixius azopifajo azojo</i>	E	Homoptera	Cixiidae	1.93	5	0	0	0	0	0	0	0	0	6	0	0	0	0	27	0	0	0
MF118	<i>Scolopostethus decoratus</i>	N?	Heteroptera	Lygaeidae	1.90	3	0	0	0	3	0	0	0	0	0	0	1	0	0	0	0	0	0

MF557	<i>Strophingia hartensi</i>	E	Homoptera	Psyllidae	1.88	8	0	3	2	23	46	0	0	4	0	0	11	0	1	2	0	3	0	
MF7	<i>Cixius azoterceirae</i>	E	Homoptera	Cixiidae	1.83	7	0	0	0	0	109	0	0	0	0	36	0	0	0	0	0	0	39	
MF7	<i>Cixius azomariae</i>	E	Homoptera	Cixiidae	1.65	4	0	0	0	10	0	0	0	0	0	0	12	0	0	0	0	2	0	
MF137	<i>Pinalitus oronii</i>	E	Heteroptera	Miridae	1.63	10	2	70	1	2	14	16	1	5	9	7	3	25	13	28	1	1	27	
MF9	<i>Ommatolulus moreleti</i>	I (?)	Diplopoda	Julidae	1.58	7	4	16	2	1	5	0	0	1	0	1	0	12	3	5	0	0	1	
MF487	Gen. sp.	?	Homoptera	Margaroidae	1.53	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
MF413	Gen. sp.	?	Lepidoptera	Blastobasidae	1.49	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
MF124	<i>Cyphopterum adscendens</i>	N	Homoptera	Flatidae	1.49	9	16	44	0	12	48	0	0	0	56	61	25	21	30	55	0	1	38	
MF414	<i>Xanthorhoe inaequata</i>	E	Lepidoptera	Geometridae	1.35	8	0	1	1	4	7	0	0	2	2	2	3	2	2	6	0	2	0	
MF295	<i>Cixius azopifajo</i>	E	Homoptera	Cixiidae	1.27	6	0	75	0	0	0	0	0	18	0	0	0	0	19	0	0	0	0	
MF255	<i>Cixius insularis</i>	E	Homoptera	Cixiidae	1.19	6	0	0	225	0	0	0	0	0	0	0	0	0	0	0	74	0	0	
MF636	Gen. sp.	E?	Homoptera	Aleyroridae	1.01	3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	
MF363	<i>Popillia japonica</i>	I	Coleoptera	Scarabaeidae	0.88	3	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	
MF671	<i>Isoneurothrips australis</i>	I	Thysanoptera	Thripidae	0.87	3	0	0	0	5	0	0	0	0	0	0	1	0	0	0	0	0	0	
MF102	<i>Pseudophloeophagus tenax</i>	N	Coleoptera	Curculionidae	0.60	6	0	0	0	0	2	0	0	0	0	3	0	1	0	1	0	0	0	
MF372	Gen. sp.	I	Lepidoptera	Tortricidae	0.60	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
MF440	<i>Eudonia melanographa</i>	E	Lepidoptera	Pyralidae	0.55	5	2	3	1	0	8	0	0	0	2	4	0	0	1	3	0	0	6	
MF42	<i>Orthomana obstipata</i>	N	Lepidoptera	Geometridae	0.53	9	0	0	0	2	12	3	1	1	1	5	2	0	1	0	0	0	3	
MF630	Gen. sp.	E?	Lepidoptera	?	0.50	5	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
MF116	<i>Scoparia coecimaculalis</i>	E	Lepidoptera	Pyralidae	0.46	6	0	2	2	0	2	0	0	1	0	0	0	2	1	1	5	0	1	
MF519	Gen. sp.	I	Lepidoptera	Tortricidae	0.45	4	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0
MF418	Gen. sp.	I	Lepidoptera	Tortricidae	0.41	5	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
MF476	<i>Monalocoris filicis</i>	N	Heteroptera	Miridae	0.32	5	0	1	0	0	3	0	0	0	0	0	0	0	0	1	0	0	0	