Diversity and distribution of arthropods in native forests of the Azores archipelago

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Since 1999, our knowledge of arthropods in native forests of the Azores has improved greatly. Under the BALA project (Biodiversity of Arthropods of Laurisilva of the Azores), an extensive standardised sampling protocol was employed in most of the native forest cover of the Archipelago. Additionally, in 2003 and 2004, more intensive sampling was carried out in several fragments, resulting in nearly a doubling of the number of samples collected. A total of 6,770 samples from 100 sites distributed amongst 18 fragments of seven islands have been collected, resulting in almost 140,000 specimens having been caught. Overall, 452 arthropod species belonging to Araneae, Opilionida, Pseudoscorpionida, Myriapoda and Insecta (excluding Diptera and Hymenoptera) were recorded. Altogether, Coleoptera, Hemiptera, Araneae and Lepidoptera comprised the major proportion of the total diversity (84%) and total abundance (78%) found. Endemic species comprised almost half of the individuals sampled. Most of the taxonomic, colonization, and trophic groups analysed showed a significantly left unimodal distribution of species occurrences, with almost all islands, fragments or sites having exclusive species. Araneae was the only group to show a strong bimodal distribution. Only a third of the species was common to both the canopy and soil, the remaining being equally exclusive to each stratum. Canopy and soil strata showed a strongly distinct species composition, the composition being more similar within the same stratum regardless of the location, than within samples from both strata at the same location. Possible reasons for these findings are explored. The procedures applied in the sampling protocol are also discussed.

Key words: Biodiversity, canopy, endemism, Laurisilva, soil

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INTRODUCTION

Studies focusing on ecological patterns of diversity and distribution of arthropods in the Azores have a very recent history. The islands have been explored since 1850 and some studies on the biogeography and systematics of arthropods were undertaken (e.g. Drouët 1859; Wallace 1872; Fig. 1). However, probably due to the low diversity and inconspicuous fauna, arthropods from the Azorean islands were mostly disregarded until late in the last century (Fig. 2).

From 1975 to 1990, some autoecological studies were carried out focusing on agricultural pests and on their parasites, such as *Mythimna unipuncta* Haworth (Lepidoptera, Noctuidae; Tavares 1979); *Popillia japonica* Newman (Coleoptera, Scarabaeidae; Simões & Martins 1985) and *Trichogramma* sp. (Trichogrammatidae, Hymenoptera; Oliveira 1987). But it was only in 1990 that understanding of the ecology of arthropod communities started to develop in the

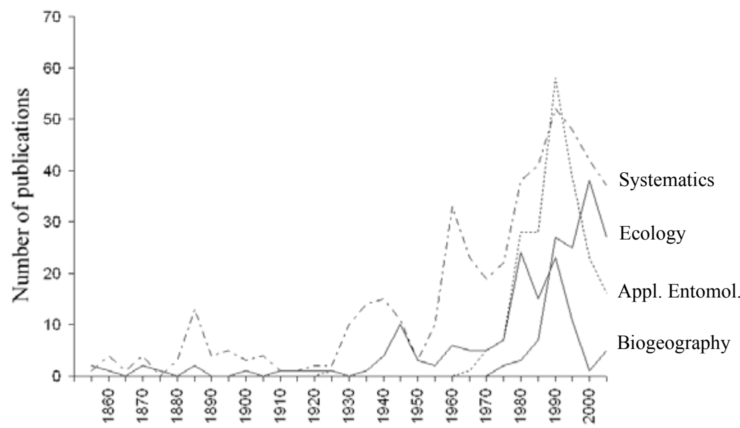


Fig. 1. Number of studies published regarding arthropods in the Azores archipelago through time, discriminated by subjects: Systematics, Ecology, Applied Entomology and Biogeography.

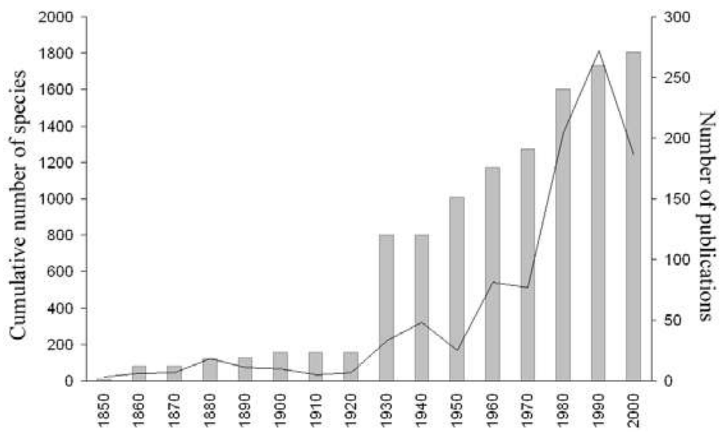


Fig. 2. Cumulative number of arthropod species recorded for the Azores archipelago (columns) in relation to the number of publications on arthropods through decades (line).

archipelago (Borges 1990, 1991a, 1991b, 1992; Fig. 1).

The arthropod fauna of native forests, in particular, had been neglected until less than a decade ago. Since 1999, a considerable effort has been made to study arthropod diversity and distribution across Azorean native forests. An extensive standardised sampling protocol was applied in most of the remnant forest fragments of the archipelago. The first years of field and laboratory work (1999-2002) involved a considerable number of researchers (see also Acknowledgments) and were developed under the BALA project (Biodiversity of Arthropods of Laurisilva of the Azores), headed by P. Borges.

Later years of more intensive sampling effort (2003 and 2004) in poorly prospected forest fragments were developed under another research project headed by CG and resulted in almost a duplication of the previous number of samples (3,140 samples against 3,640 samples from previous years).

Several studies based on these data have been published since then, focused on the distribution of insect herbivores (Ribeiro et al. 2005), selection of areas for conservation based on endemic (Borges et al. 2000) and soil arthropods (Borges et al. 2005a), relationship between endemic and introduced species (Borges et al. 2006), performance of species richness estimators (Hortal et al. 2006), abundance, spatial variance and occupancy of arthropods (Gaston et al. 2006) and a proposed biotic integrity index (Cardoso et al. 2007).

Yet none of these studies has explored the whole diversity, and the vertical and horizontal distribution of different arthropod groups in these native forests. It is important to look for such general patterns before additional studies are planned and resources used. Also, the outcome will be helpful to complement further conservation studies focused on the assessment of diversity and on the selection and management of areas. Here, arthropod data from the extensive standardised sampling protocol applied in native forests of the Azores archipelago are used to evaluate their diversity and distribution a) per taxonomic, colonization and trophic group, b) across sites, fragments and islands, c) between soil and canopy strata. Consideration was given to the sampling protocol design adopted in this study.

MATERIAL AND METHODS

STUDY AREA

The remote Azores archipelago extends for 615 km in the North Atlantic Ocean (37-40º N, 25-31º W), 1,584 km to the east (south Europe) and 2150 km to the west (north America) from the nearest mainland (Fig. 3). It comprises nine islands and islets of recent volcanic origin, ranging between 0.30 and 8.12 million years old (França et al. 2003). The archipelago is crossed by the Mid-Atlantic ridge and lies at the confluence of the American, Eurasian and African continental plates, resulting in frequent volcanic and seismic activities in the islands (Azevedo et al. 1991; Azevedo & Ferreira 1999). At sea level the climate is temperate humid (mean average temperature of 17 ºC, annual precipitation less than 1000mm), and at upper altitudes is cold oceanic (9 ºC, 4000mm) (IM 2005). Humidity is high, reaching 95% at higher altitudes and there are only relatively small temperature fluctuations throughout the year (8.5 ºC).

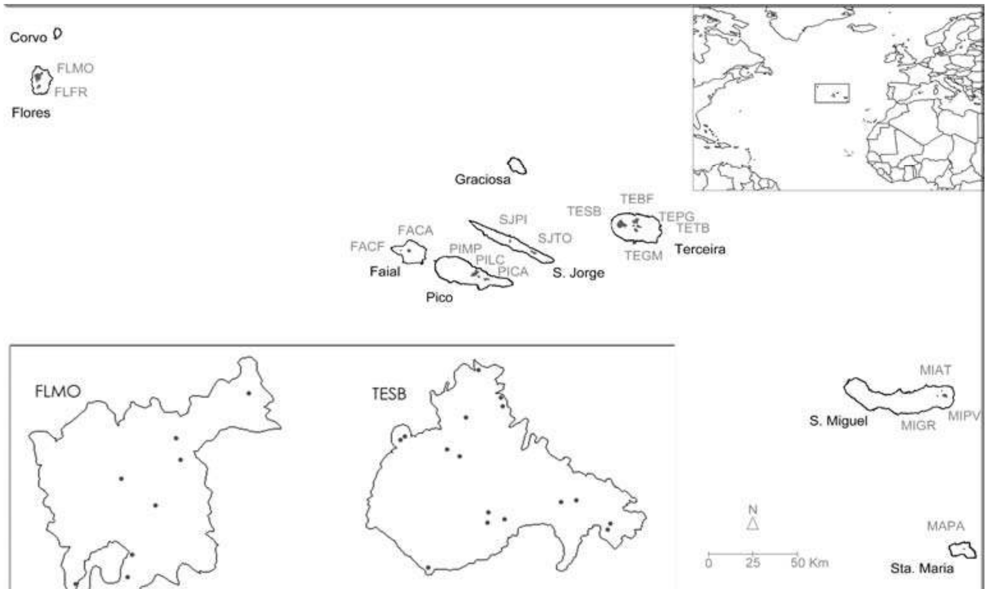
Native forest in the Azores is characterized by an association of native (many endemic) evergreen shrub and tree species (Table 1; Borges et al. 2005b). Commonly known as Laurisilva, due to the presence of Laurel species (Lauraceae family), this type of forest also occurs in other islands of the Macaronesia region (comprising Madeira, Savage, Canaries and Cape Verde archipelagos). It has been considered a relict of the Laurel forest that originally covered the Mediterranean basin and northwest of Africa during the Tertiary, but other studies support a more recent origin (Emerson 2002). It is distinguished from other Laurisilva forests of Macaronesia by a dense tree and shrub cover of small stature (trees have an average height of 3 m), closed canopy, high levels of humidity and low understorey light. Bryophytes are very abundant and cover vascular plants, volcanic rocks and soil to a great extent (Gabriel & Bates 2005).

Documents from the 15th century suggest that the Laurisilva covered all the islands 550 years ago, when the first human settlements were established in the archipelago. However, clearing for wood, agriculture and pasture, has markedly reduced its area and the native forest is now mostly restricted to high and steep areas where there are no economic interests (corresponding to less than 3% of the overall surface area of the archipelago). The smallest islands, Corvo and Graciosa, do not preserve native forest due to total clearance in mid 20th century.

SAMPLING PROTOCOL

Eighteen native forest fragments distributed across seven of the nine islands were sampled in this study (Fig. 4, Table 2). Altogether, they represent most of the native forest cover of the Azores, excluding highly fragmented, small patches (less than five hectares), located at low altitudes and/or strongly disturbed by exotic plants or cattle, which were not sampled.

During the summers of 1999 to 2004, transects 150 m long and 5 m wide were established in 100 sites (usually one transect per site). A linear direction was followed whenever possible but



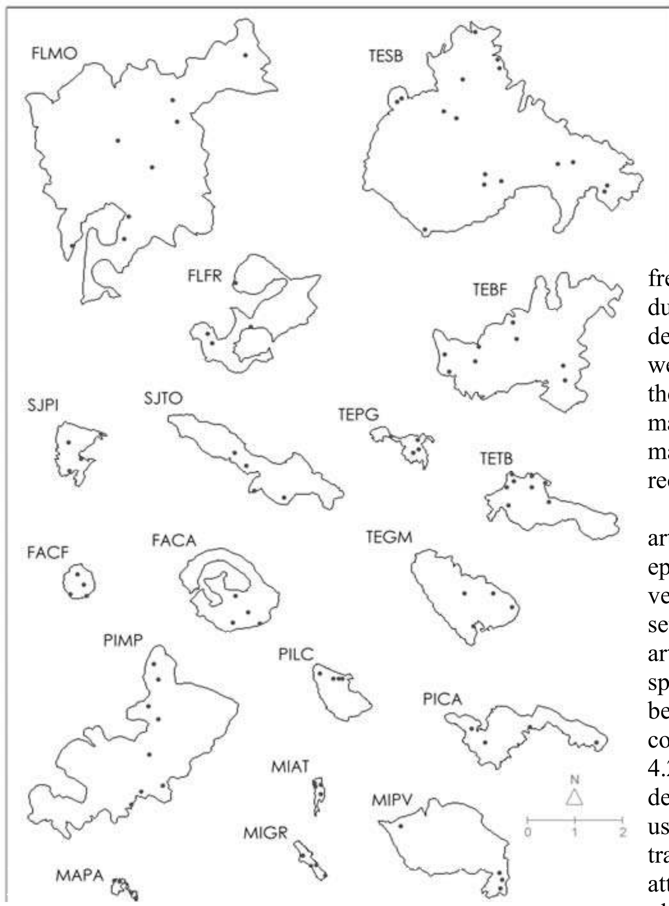


Fig. 3 (above). Location of islands and native forest fragments of the Azores archipelago. Fig. 4 (below). Location of the 100 sites from the 18 native forest fragments studied in the Azores. Precise positions and distances among fragments were changed for clarity. Forest fragments were delimited using DIVA-GIS software (Hijmans et al. 2005) and combined information on cartographic maps provided by IGP (see Acknowledgments), aerial photographs when available, and field data. Codes of fragments as in Table 2.

frequent deviations were needed due to uneven ground and very dense vegetation. All efforts were made to progress towards the core of the forest to avoid margin effects. Transects were marked with ropes to facilitate recognition.

Along each transect, arthropods from the soil (mainly epigean) and herbaceous vegetation were surveyed with a set of pitfall traps, while arthropods from woody plant species were sampled using a beating tray. Pitfall traps consisted of plastic cups with 4.2 cm diameter and 7.8 cm deep. Thirty pitfall traps were used per transect. Half of the traps were filled with a non-attractive solution (ethylene glycol antifreeze solution), and the remaining with a general attractive solution (Turquin), prepared mainly with dark beer and some preservatives (for further details see Turquin 1973, and Borges 1992).

Table 1. The most common woody plant species (trees and shrubs) present in Azorean native forests, ordered by the number of sites (out of 100) where each species was sampled; Col. – Colonization, E - Endemic, N – Native, I – Introduced.

N sites	Code	Species	FAMILY	Structure	Col.
74	JUN	*Juniperus brevifolia* (Seub.) Antoine	Cupressaceae	Tree	E
45	LAU	*Laurus azorica* (Seub.) Franco	Lauraceae	Tree	E
45	ILE	*Ilex perado* Aiton ssp. *azorica* (Loes.) Tutin	Aquifoliaceae	Tree	E
43	VAC	*Vaccinium cylindraceum* Sm.	Ericaceae	Shrub	E
38	ERI	*Erica azorica* Hochst. ex Seub.	Ericaceae	Tree/shrub	E
20	MYS	*Myrsine africana* L.	Myrsinaceae	Shrub	N
8	CAL	*Calluna vulgaris* (L.) Hull	Ericaceae	Shrub	N
3	FRA	*Frangula azorica* V. Grubov	Rhamnaceae	Tree	E
3	PIT	*Pittosporum undulatum* Vent.	Pittosporaceae	Tree	I
2	PIC	*Picconia azorica* (Tutin) Knobl.	Oleaceae	Tree/shrub	E
2	CLE	*Clethra arborea* Aiton	Clethraceae	Tree/shrub	I
1	MYC	*Myrica faya* Aiton	Myricaceae	Tree/shrub	N

Table 2. Main characteristics of the Azorean islands (bold) and native forest fragments considered in this study, including the area (hectares), the highest point (altitude, metres), distance to the nearest island/fragment (isolation, kilometres) and the oldest geological age of the soil (lava) substrate (million years BP).

Island	Fragment	Code	Area[a]	Altitude[a]	Isolation[b]	Age[c]
Flores		**FL**	**14102**	**911**	**236.43**	**2.16**
	Morro Alto e Pico da Sé	FLMO	1331	911	6.02	2.16
	Caldeiras Funda e Rasa	FLFR	240	773	6.02	2.16
Faial		**FA**	**17306**	**1043**	**34.26**	**0.73**
	Caldeira do Faial	FACA	190	934	4.67	0.73
	Cabeço do Fogo	FACF	36	597	4.67	0.60
Pico		**PI**	**44498**	**2350**	**32.42**	**0.30**
	Mistério da Prainha	PIMP	689	881	2.92	0.26
	Caveiro	PICA	184	1077	4.61	0.27
	Lagoa do Caiado	PILC	79	945	2.92	0.28
S.Jorge		**SJ**	**24365**	**1053**	**32.42**	**0.55**
	Topo	SJTO	220	946	15.13	0.55
	Pico Pinheiro	SJPI	73	717	15.13	0.55
Terceira		**TE**	**40030**	**1021**	**71.67**	**3.52**
	S. Bárbara e M. Negros	TESB	1347	1021	7.20	1.24
	Biscoito da Ferraria	TEBF	557	809	3.03	0.10
	Guilherme Moniz	TEGM	223	487	2.70	0.41
	Terra Brava	TETB	180	726	2.70	0.10
	Pico do Galhardo	TEPG	38	655	2.79	0.10
S.Miguel		**MI**	**74456**	**1105**	**97.53**	**4.01**
	Pico da Vara	MIPV	306	1105	3.42	3.20
	Graminhais	MIGR	15	930	4.02	3.20
	Atalhada	MIAT	10	500	3.42	4.01
S.Maria		**MA**	**9689**	**587**	**97.53**	**8.12**
	Pico Alto	MAPA	9	579	92.21	8.12

[a] based on the delimitation of forest fragments showed in Fig. 4. [b] determined by a geographic matrix of centroids using the DIVA-GIS software (Hijmans et al. 2005). [c] according to França et al. 2003 and J.C. Nunes (personal communication).

Table 3. Total number of sites, transects (including additional transects with only beating samples, defined as B) and samples considered for each forest fragment, island and for the overall archipelago. The number of plant species sampled (S), and the dominant plant species considered are also presented. Codes of plants are presented in Table 1, codes of fragments and islands in Table 2.

			Samples			**Plant species sampled**												
Code	**Sites**	**Transects**	Total	Soil	Can.	S	JUN	LAU	ILE	VAC	ERI	MYS	CAL	FRA	PIT	PIC	CLE	MYC
AZ	**100**	**114+15B**	**6770**	**3420**	**3350**	**12**	●	●	●	●	●	●	●	●	●	●	●	●
FL	**12**	**12**	**630**	**360**	**270**	**7**	●	●	●	●	●	●	●					
FLMO	8	8	440	240	200	6	●	●	●	●		●	●					
FLFR	4	4	190	120	70	4	●		●	●	●							
FA	**8**	**8**	**390**	**240**	**150**	**7**	●	●	●	●	●	●						●
FACA	4	4	210	120	90	5	●	●	●	●	●							
FACF	4	4	180	120	60	4	●				●	●						●
PI	**16**	**16+4B**	**1010**	**480**	**530**	**6**	●	●	●	●	●	●						
PIMP	8	8+1B	480	240	240	6	●	●	●	●	●	●						
PICA	4	4+1B	270	120	150	5	●	●	●	●		●						
PILC	4	4+2B	260	120	140	5	●	●		●	●	●						
SJ	**8**	**8**	**460**	**240**	**220**	**7**	●		●	●	●	●		●	●			
SJTO	4	4	230	120	110	4	●		●	●	●							
SJPI	4	4	230	120	110	7	●		●	●	●	●		●	●			
TE	**40**	**54+10B**	**3430**	**1620**	**1810**	**8**	●	●	●	●	●	●	●	●				
TESB	16	23+5B	1480	690	790	7	●	●	●	●	●	●	●					
TEBF	8	11+5B	760	300	460	8	●	●	●	●	●	●	●	●				
TEGM	4	5	260	150	110	3		●		●	●							
TETB	8	11	630	330	300	6	●	●	●	●	●	●						
TEPG	4	4	300	150	150	4	●	●	●	●								
MI	**12**	**12+1B**	**630**	**360**	**270**	**7**	●	●	●	●	●		●				●	
MIPV	4	4+1B	220	120	100	5	●	●	●		●						●	
MIGR	4	4	220	120	100	5	●	●	●	●			●					
MIAT	4	4	190	120	70	3	●	●	●									
MA	**4**	**4**	**220**	**120**	**100**	**5**		●		●	●				●	●		
MAPA	4	4	220	120	100	5		●		●	●				●	●		

A few drops of liquid detergent were added to both solutions to reduce surface tension. The traps were sunk in the soil (with the rim at the surface level) every 5 m, starting with a Turquin trap and alternating with the ethylene traps. They were protected from rain using a plastic plate, about 5 cm above surface level and fixed to the ground by two pieces of wire. The traps remained in the field for two weeks.

Canopy sampling was conducted during the period that pitfall traps remained in the field, when the vegetation was dry. A square 5 m wide was established every 15 m (10 squares in total per transect). In each square, a replicate of the three most abundant woody plant species was sampled. In most of the study sites, three species clearly dominated over the remaining plants and the choice was evident. However, in some transects, less than three were present and only those were considered. For each selected plant, a branch was chosen at random and a beating tray placed beneath. Five beatings were made using a stick. The tray consisted of a cloth inverted pyramid 1 m wide and 60 cm deep (adapted from Basset 1999), with a plastic bag at the end.

A total of 6,770 samples (3,420 pitfall traps and 3,350 beating samples) were collected. Samples were sorted and the specimens preserved in 70% alcohol with glycerine. The selection of the arthropod taxa considered in this study was made taking into account the available taxonomists and the taxa which were readily separable by morphological criteria. All Araneae, Opilionida, Pseudoscorpionida, Myriapoda and Insecta (excluding Diptera and Hymenoptera) were assigned to morphospecies through comparison with a reference collection. Various taxonomists (see Acknowledgments) checked the assignment to morphospecies, made identifications and supplied additional ecological information.

Considerable efforts have been made to avoid lumping and splitting errors (see discussion), so it may be assumed in this study, with reasonable confidence, that morphospecies accurately represent species, and will be considered as species hereafter. All specimens and types are deposited in the *Arruda Furtado* entomological collection at the Department of Agrarian Science (University of the Azores).

DATA ANALYSES

Abundance matrices of arthropod species per island, fragment and site were used to compare the composition and abundance of different arthropod groups across areas. Arthropods were grouped by categories: taxonomic (orders Araneae, Blattaria, Chordeumatida, Coleoptera, Dermaptera, Ephemeroptera, Geophilomorpha, Hemiptera, Julida, Lepidoptera, Litobiomorpha, Microcoryphia, Neuroptera, Opilionida, Orthoptera, Polydesmida, Pseudoscorpionida, Psocoptera, Scolopendromorpha, Thysanoptera, Trichoptera), trophic (Herbivores, Predators, Saprophages, Fungivores), colonization (Introduced or non-indigenous - arrived as a result of human activities; Native - arrived by long distance dispersal, indigenous minus endemic; Endemic - only occur in the Azores as a result of speciation in the archipelago or extinction in other areas, indigenous minus native) and stratum preference (soil, canopy).

The modality in the frequency of species for each arthropod group across sites, fragments and islands was evaluated using the statistical test proposed by Tokeshi (1992; see also Barreto et al. 2003). Left (occurring in only one site, fragment or island) and right (occurring in all sites, fragments or islands) modality of the species-range distribution was evaluated and the null hypothesis of random or uniform distribution was rejected at $p<0.05$.

Hierarchical, agglomerative cluster analyses (Ward’s linkage method, 1-sorensen dissimilarity measure) were conducted using the Community Analysis Package (Seaby et al. 2004) to identify dissimilarities in the species composition for the canopy and soil strata across sites, fragments and islands studied.

Paired-sample t-tests were performed to look for differences in the species richness and abundance per site between canopy and soil strata. Also, one-way ANOVAs were conducted to evaluate the effect of plant species on the average number of species and individuals of arthropods found per sample. Abundance data were log (x+1) transformed to satisfy the assumption of normal distribution of data. Paired-sampled t-tests and ANOVAs were performed using MINITAB v13 (2000).

RESULTS

A total of 139,476 identifiable specimens, distributed amongst 21 orders, at least 106 families, 261 genera and representing 452 species were collected in the native forests of the Azores. A detailed list of the species recorded is presented in Appendix. Adults (69,300 individuals, 50%) and immatures (67,096 indiv., 48%) contributed in similar proportions to the total number of individuals recorded. The majority of the genera recorded (210 of 261 genera identified) were only represented by a single species, most of the remaining genera (34 of 51 genera remaining) being represented by two species per genus.

SPECIES RICHNESS AND ABUNDANCE PER TAXONOMIC, TROPHIC AND COLONIZATION GROUP

The great majority of the species (379 spp, 84% of the overall species richness) belonged to four taxonomic orders (Fig. 5). Altogether, Coleoptera, Hemiptera, Araneae and Lepidoptera also comprised the major proportion of the total abundance found (108,634 individuals, 78%). Coleoptera, with the highest number of species

(137 spp) had the lowest number of individuals of the four most diverse taxa (7,196 indiv., Fig. 5). On the other hand, Araneae with 74 species, had the highest abundance overall (40,938 indiv., Fig. 5). The remaining 17 orders had very low species richness (Fig. 5). In fact, all except Psocoptera (21 spp), Thysanoptera (18 spp) and Julida (9 spp) were represented by three or less species (Fig. 5). However, the abundance of some of those taxa was relatively high, such as the Opilionida, represented by only two species but with more than 6,700 individuals collected, a number close to the abundance of the most diverse order (Fig. 5).

Araneae was one of the taxa with the lowest ratios of adults per immatures (1:3; 9,358 adults against 31,564 immatures). Overall, Araneae contributed to 47% of the total number of immatures found in this study.

The herbivore species were slightly more diverse and abundant (208 spp, 67,047 individuals) than predators (165 spp, 56,666 indiv.; Fig. 6a). Together, they represented 83% of the species and 89% of the individuals found (Fig. 6a). The remaining species were mostly saprophages (64 spp, 13,932 indiv.). Fungivores were the least well represented in this study (13 spp, 1,829 indiv.; Fig. 6a).

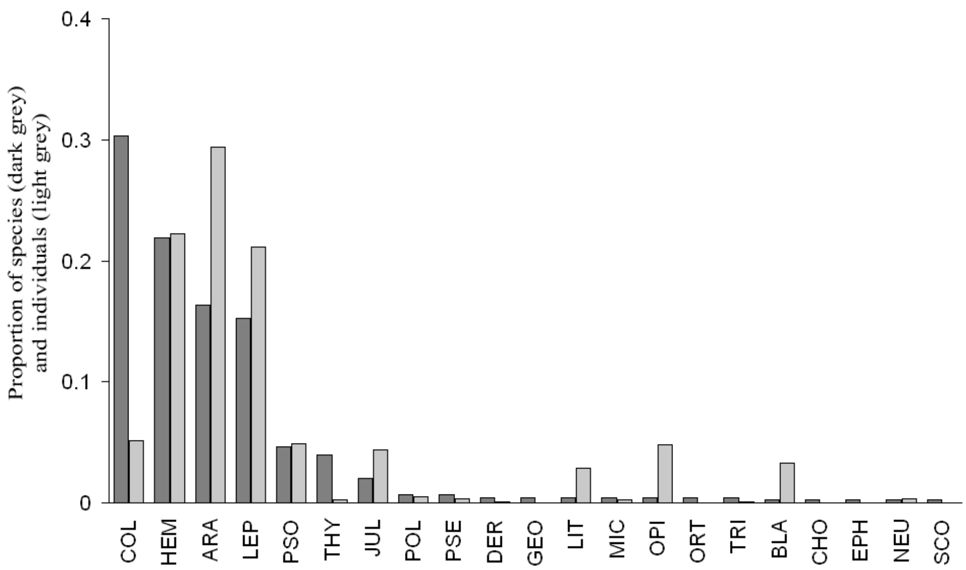


Fig. 5. Contribution of each taxon (order) to the overall number of species and individuals found (COL - Coleoptera, HEM - Hemiptera, ARA - Araneae, LEP - Lepidoptera, PSO - Psocoptera, THY - Thysanoptera, JUL - Julidae, POL - Polydesmida, PSE - Pseudoscorpionida, DER - Dermaptera, GEO - Geophilomorpha, LIT - Lithobiomorpha, MIC - Microcoryphia, OPI - Opilionida, ORT - Orthoptera, TRI - Trichoptera, BLA - Blattaria, CHO - Chordeumatida, EPH - Ephemeroptera, NEU - Neuroptera and SCO - Scolopendromorpha).

Grouped by colonization categories, more than half of the species (257 spp, 57%) were indigenous (endemic plus native, Fig. 6b). Of those, native species were more diverse (149 spp) but less abundant (54,669 indiv.) than endemics (108 spp, 68,138 indiv.; Fig. 6b). Endemic species alone comprised nearly half of the overall abundance found (Fig. 6b). Grouped with natives, indigenous species included 88% of the total number of individuals (Fig. 6b). The abundance of non-indigenous species (15,956 indiv., 11%) was relatively low when compared with native or endemic species, but the species richness (155 spp, 34%) was considerably higher (Fig. 6b).

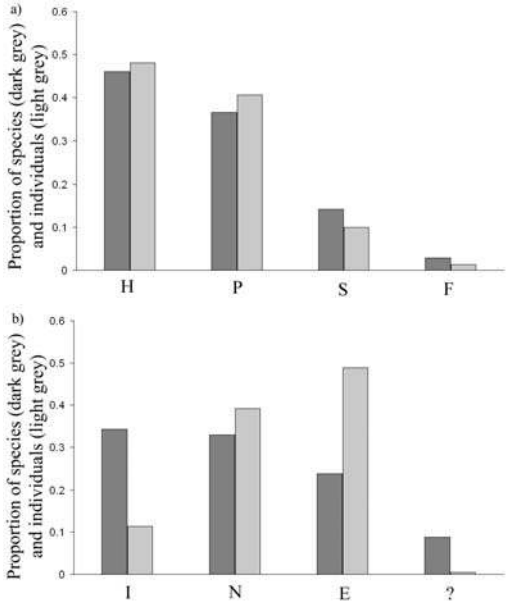


Fig. 6a (above). Contribution of each trophic group, and Fig. 6b (below), colonization group, to the overall number of species and individuals found (H-herbivores, P-predators, S-saprophages, F-fungivores; I-introduced, N-native, E-endemic, ?-unknown origin).

SPECIES RICHNESS AND ABUNDANCE ACROSS SITES, FOREST FRAGMENTS AND ISLANDS

A high proportion of the species occurred in only one island (45% of the species, Fig. 7a), one fragment (38%, Fig. 7b) or even one site (31%, Fig. 7c). The Tokeshi (1992) test for modality supports this finding showing a strong left unimodal distribution of species for the three spatial scales analysed (Pl < 0.001 and Pr > 0.98). All fragments and islands had locally restricted species although the fragment MAPA and Terceira Island had the highest number of exclusive species (Table 4). In fact, a considerable proportion of the total number of species (167 spp, 37%) was considered to be very rare (doubletons: 51 spp, 11%; singletons: 116 spp, 26%).

The general pattern of strong left unimodality was also observed when species were grouped by taxa, trophic and colonization categories, whether at the island, fragment or site scale (Table 5). The only exception was for the species distribution of the Araneae, which was found to be strongly bimodal across islands (Table 5, Fig. 8).

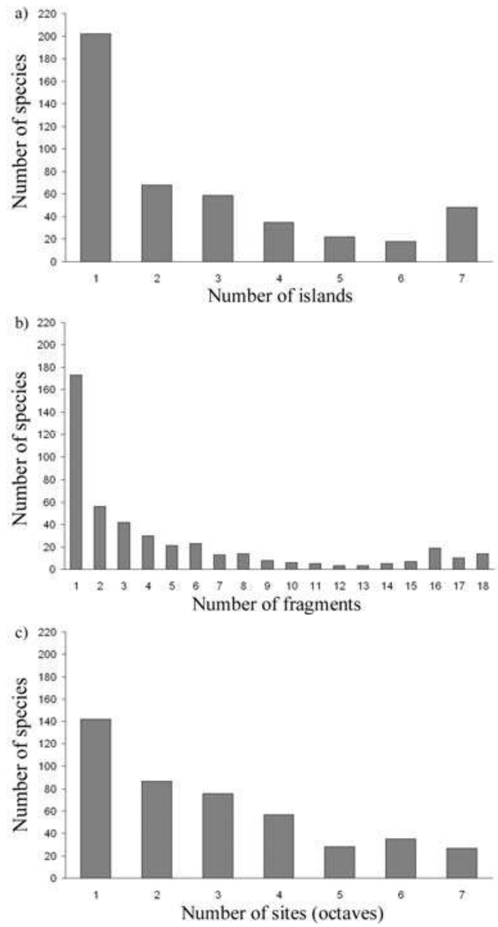


Fig. 7. Distribution range of the species for the (a) seven islands, (b) 18 fragments and (c) 100 sites studied (for the latter, the x-axis was transformed on an octave scale for clarity).

That is, most of the species of Araneae, when restricted in their distribution, occurred in only one island; while those that had a wide distribution tended to occur in all islands (Fig. 8).

SPECIES RICHNESS AND ABUNDANCE IN CANOPY AND SOIL

The canopy and soil samples captured similar proportions of the overall number of species recorded (304 spp, 67% and 296 spp, 65% respectively; Table 6), although only a third of the species (148 spp, 33%) was common to both

Table 4. Ranking of the Azorean fragments and islands according to the number of exclusive species (Excl.); the number of exclusives that were endemic (End.) is also presented. Codes of fragments as in Table 2

Fragment	Excl.	End.	Island	Excl.	End.
All frag.	173	33	All isl.	202	48
MAPA	31	10	TE	65	8
TESB	18	2	FL	33	10
FLFR	15	0	MA	31	10
TETB	15	1	MI	26	6
FLMO	13	6	PI	24	7
MIAT	11	1	SJ	14	4
PIMP	10	3	FA	9	3
TEPG	7	1			
SJPI	7	1			
TEBF	6	0			
FACF	6	2			
MIGR	6	0			
MIPV	6	4			
TEGM	5	0			
PICA	5	1			
PILC	5	0			
SJTO	5	1			
FACA	2	0			

Table 5. Significance values for the modality test (Tokeshi 1992) of the species distribution grouped by taxa, trophic and colonization categories, with respective subgroups, across islands, fragments and sites (** p<0.001, * p<0.01); P l – Left, P r - right.

	Island		Fragment		Site	
Taxa	P l	P r	P l	P r	P l	P r
Coleoptera	**	1.000	**	1.000	**	0.748
Hemiptera	**	0.955	**	0.976	**	0.630
Araneae	**	*	**	0.120	**	0.525
Lepidoptera	**	0.668	**	0.338	**	0.500
Trophic						
Herbivores	**	0.970	**	0.946	**	0.876
Predators	**	0.669	**	0.816	**	0.810
Saprophages	**	0.711	**	0.697	**	0.474
Colonization						
Introduced	**	1.000	**	0.993	**	0.789
Endemic	**	0.085	**	0.394	**	0.662
Native	**	0.653	**	0.727	**	0.776

strata (Fig. 9). Most of the individuals (104,716 indiv., 75%) were found in the canopy (Table 6). The strata had a similar fraction of rare species (singletons and doubletons; canopy: 124 spp, 41%,

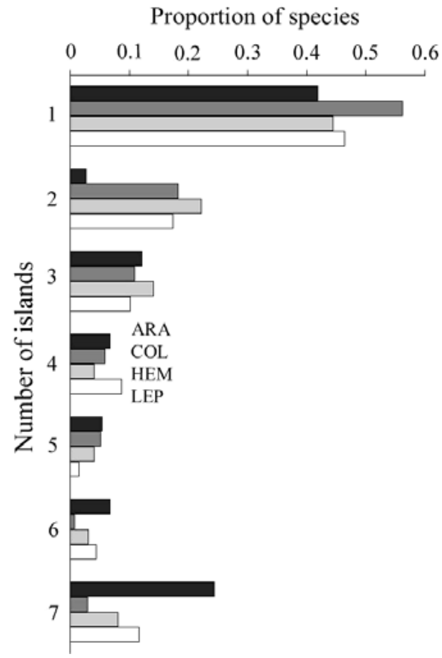


Fig. 8. Distribution range of the species across islands, grouped by the four most dominant taxonomic orders (ARA-Araneae, COL-Coleoptera, HEM-Hemiptera and LEP-Lepidoptera).

soil: 116 spp, 39%). But considering the species that were exclusive to each stratum, canopy had a higher proportion of rare species than soil (canopy: 93 spp, 60%; soil: 69 spp, 47%). The species common to both methods only showed a small proportion of doubletons (5 spp, 3%).

Grouped by taxonomic orders, a higher number of species and a major proportion of individuals of Araneae, Hemiptera and Lepidoptera were found in the canopy, while Coleoptera showed a higher number of species and much more abundance on the soil (Table 6). In fact, most of the species of Coleoptera were found exclusively in the soil stratum (Fig. 9). Instead, Hemiptera and Lepidoptera had more species exclusively from the canopy. Species of Araneae were mostly common to both soil and canopy (Fig. 9).

Herbivore species were more dominant (in number of species and individuals) in canopy (Table 6), and most of them were exclusive to canopy (Fig. 9).

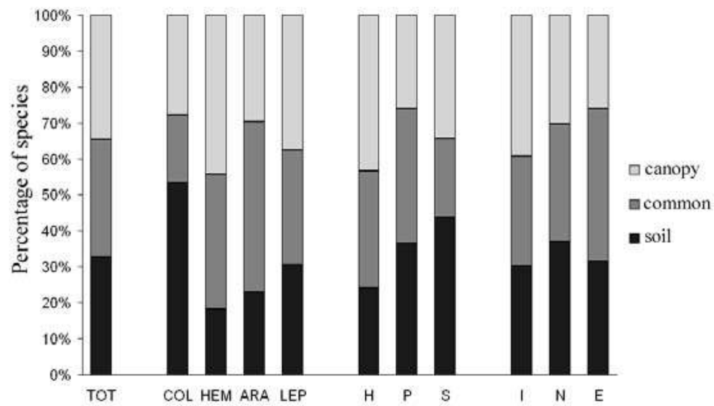


Fig. 9. Percentage of the number of species that were exclusively from soil, canopy, or that were common to both soil and canopy samples. Results are shown for the total number of species (TOT) and grouped by taxa (COL-Coleoptera, HEM-Hemiptera, ARA-Araneae, LEP-Lepidoptera), trophic (H-Herbivores, P-Predators, S-Saprophages) and colonization (I-Introduced, N-Native, E-Endemic) groups.

Table 6. Number of species and individuals found in canopy and soil strata. Data are presented for the overall arthropods collected (Total) and separated by taxonomic, trophic and colonization categories.

	Species richness		Abundance	
Canopy	x		x	
Soil		x		x
Total	304	296	104716	34760
Taxonomic				
Coleoptera	64	99	942	6254
Hemiptera	81	55	28688	2310
Araneae	57	52	34187	6751
Lepidoptera	48	43	27669	1833
Trophic				
Herbivores	158	118	57950	9097
Predators	105	122	35079	21587
Saprophages	36	42	11628	2304
Colonization				
Introduced	108	94	5856	10100
Native	94	104	36746	17923
Endemic	74	80	61834	6304

Conversely, predators were more dominant in soil rather than in canopy (Table 6) and few species were exclusive to canopy (Fig. 9).

Non-indigenous had a higher number of species in the canopy than on soil, contrary to endemics or natives (Table 6). The abundance of non-indigenous in the canopy was smaller than in soil (Table 6). Endemic species were more abundant in the canopy (Table 6). Most of the non-indigenous species were exclusive to the canopy, while most of the endemics were common to both strata (Fig. 9).

The local number of species and individuals found per site was significantly higher in the canopy stratum than in the soil (paired-sample *t*-tests, species richness: t=8.40, d.f.=98, p<0.001; abundance: t=10.16, d.f.=98, p<0.001). Notwithstanding, canopy and soil strata showed a strongly distinct species composition, the composition being more similar within the same stratum regardless of the location, than within samples from both strata at the same location. This pattern was clear when comparing the two strata across islands (canopy and soil samples with a 1-sorensen dissimilarity measure of d=1.76, Fig. 10), across fragments (d=4.54, not presented) or even across sites (d=26.4, not presented).

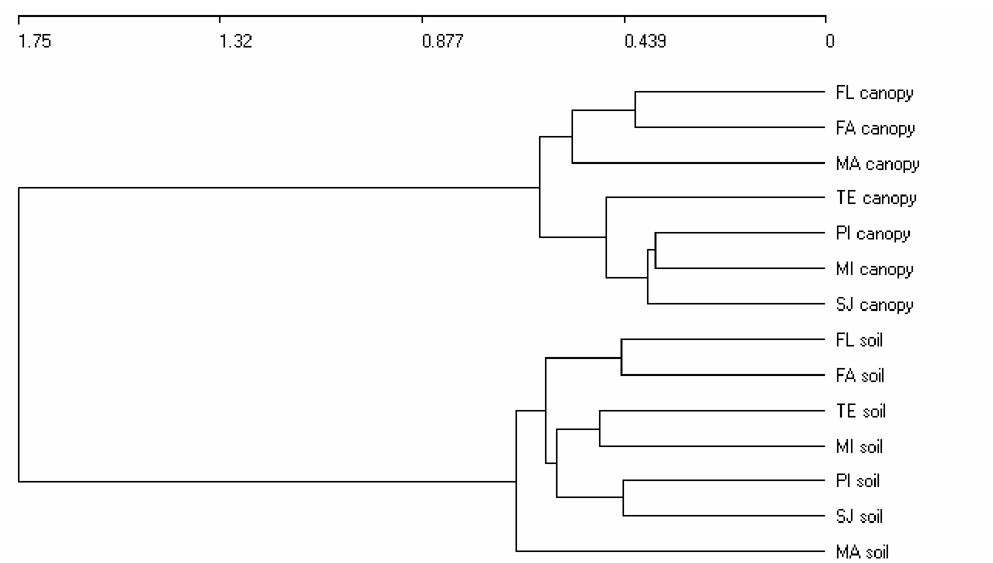


Fig. 10. Hierarchical, agglomerative cluster analysis (Ward's linkage, 1-sorensen dissimilarity measure) for the canopy and soil strata across the seven islands studied. Code of islands as in Table 2.

The mean number of arthropod species and individuals collected per sample was found to be significantly different among plant species (ANOVA, species richness: F=47.9, p<0.001, d.f.=11, 3,338; abundance: F=143.6, p<0.001, d.f.=11, 3,338). *Erica azorica* and *Juniperus brevifolia* were two of the plant species with the highest species richness and abundance per sample while *Calluna vulgaris* had the lowest number of species and individuals (Fig. 11).

Despite the effect of plant species on the number of species and individuals of arthropods found per sample, the composition of arthropods did not seem to be related with plant species, instead, samples tended to be more similar within each island rather than grouped per plant species (Fig. 12).

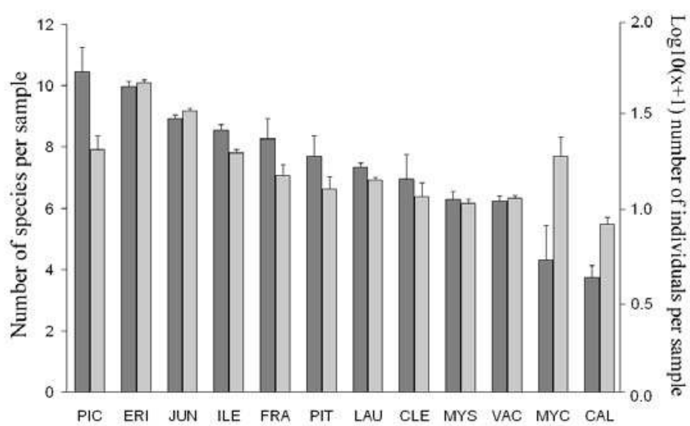


Fig. 11. Mean number of species (dark grey) and individuals (light grey, log10 transformed) per sample for each plant species studied. Standard errors are presented. Codes of plant species as in Table 1.

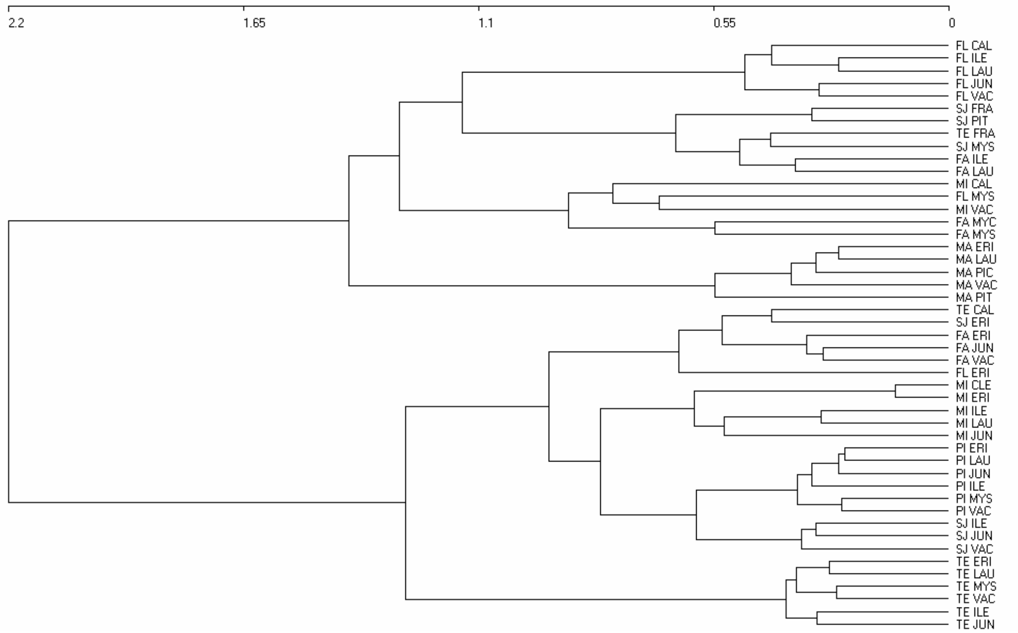


Fig. 12. Hierarchical, agglomerative cluster analysis (Ward's linkage, 1-sorensen dissimilarity measure) for the samples of the 12 plant species across the seven islands studied. Codes of islands are presented in Table 2, codes of plant species in Table 1.

DISCUSSION

As in the majority of terrestrial habitats worldwide, the arthropods are the most diverse and abundant animals in the Azores. However, their diversity in these islands (2,209 spp of which 267 spp are endemic, Borges et al. 2005b) is relatively low compared with the other archipelagos of the Macaronesia region (e.g. the Canary islands with 6,843 spp of which 2,704 spp are endemic, Martín et al. 2001). This is likely a consequence of the greater isolation from the mainland and the more recent geological origin (Borges & Brown 1999; Borges et al. 2005b). Also, the poor knowledge of highly diverse taxa in the Azores, such as Hymenoptera, may under-estimate to some extent the overall diversity of this archipelago (Borges et al. 2005b).

Arthropod diversity in Azorean native forests in particular is low (452 spp). The fragments of native forest are likely to be influenced not only by physical factors such as the isolation, geological age and area of the islands themselves, but also by the fragmentation and shrinkage that have shaped the fragments directly over the last 550 years. Nonetheless, the arthropod diversity of the native forests still represents one third of the arthropod species ever recorded (which includes extinct species) in all habitats of the archipelago (1297 spp listed for the same taxonomic orders considered in this study, Borges et al. 2005b), including 104 of the 162 endemic arthropod species listed for the overall archipelago.

The relatively low arthropod diversity in the Azores meant that a large sampling scheme could be implemented resulting in more than 6,700 samples from 100 sites distributed amongst 18 fragments of seven islands. The most representative terrestrial arthropod orders present in these forests were considered (except Diptera, Hymenoptera, Acari and Collembola) resulting in nearly 140,000 specimens being identified. Despite the low diversity, the protocol required a considerable effort that had never been made before in these islands. The uneven volcanic ground and the closed canopy made the progress through the forests difficult. The isolation of the islands was also a logistical constraint. The effort, however, was valuable: it is at present the largest standardised database of arthropods available for the Macaronesia region and one of the few worldwide for arthropods at a regional scale.

The extensive sampling effort and high number of specimens caught, along with the poor knowledge of arthropods in Azorean native forests when the BALA project started, made indispensable the use of a rapid and efficient shortcut for identification. The use of morphospecies has become a common strategy to include poorly known taxa in conservation studies (Oliver & Beattie 1994; Derraik et al. 2002; Krell 2004). However, errors caused by splitting and lumping often occur. It is believed that accuracy in assignment to morphospecies may vary greatly among different groups of arthropods (Derraik et al. 2002) and with different life stages or sexes considered (Oliver & Beattie 1993). Yet, errors may be considerably reduced if some precautions are taken, namely: (1) some previous training is given to the parataxonomists (Oliver & Beattie 1994; Derraik et al. 2002), (2) the same parataxonomists are used throughout the process, (3) some tools to assist parataxonomists are available (Oliver & Beattie 1997; Beattie & Oliver 1999; Oliver et al. 2000) and (4) taxonomic validation is applied in a further step (Borges et al. 2002). In this study, all of these precautions were taken. A senior researcher trained several students, and checked the assignment to morphospecies made by students for all specimens. Identification keys were made by taxonomists or students (and then checked by the senior researcher) to ease distinction of many morphotypes. A conservative approach was adopted, and when in doubt a new morphotype was created. All morphotypes were checked by taxonomists, with most of them identified to the species (301) and genus level (53). For those that still remain unnamed at a species or genus level (most of them are new records for the archipelago or new species to science and waiting to be described by taxonomists), precautions were taken to ensure that they corresponded to unique species, distinct from others unnamed or described in the collection. With such a considerable effort to avoid lumping and splitting, it is believed that morphospecies accurately represent species.

Diptera, Hymenoptera and Acari and Collembola orders were not considered in this sampling protocol since their assignment to morphospecies, besides being more time consuming than for other orders, results in many lumping and splitting errors. More taxonomic expertise is required and a greater investment needs to be made to train parataxonomists. Moreover, the sampling methods used here were not adequate for these particular orders. While other flying insects, such as Coleoptera and Hemiptera, tend to fall or remain still when taking a beating sample, Diptera and Hymenoptera are very agile and tend to escape easily from the beating tray before closing the collecting bag. Malaise traps would be preferable but they are difficult to set in the field due to dense understorey vegetation in these native forests. Likewise, Collembola and Acarina orders would be more effectively sampled using extracting methods of soil and litter. Berlese funnels were used experimentally in several transects but they proved to be ineffective, probably due to the high water saturation of the soil (further discussion of sampling methods by Gaspar et al. is under scientific scrutiny at the moment). It is widely recognised that the species diversity recorded in a given site will greatly depend on the sampling effort and on the sampling methods applied in the field (Moreno & Halffter 2001; Longino et al. 2002; Romo et al. 2006). The influence of the sampling methods used in this study on the results here obtained will be explored in detail elsewhere in future work. However, regardless of the sampling methods used, a standardised protocol allows accurate comparability among places sampled, which was the main aim of this work.

The use of immatures in diversity studies has been criticized due to common lumping and splitting errors. However, in the Azores, as the diversity is low (Borges et al. 2005b) and most of the genera are monospecific (80%), identification errors are less likely to occur (Borges et al. 2002). Furthermore, and as a result of the large number of individuals caught, the Azorean collection includes voucher specimens to account for the polymorphism that has been observed across islands, and much expertise has been gained during the process and from previous studies as well (e.g., Borges 1990; Borges 1999; Borges & Brown 2001). Araneae, in particular, which accounted for nearly half of the overall abundance of immatures, is one of the arthropod groups that has received more attention from taxonomists in the Azores (e.g. Berland 1917; Bacelar 1937; Machado 1982; Wunderlich 1994; Borges & Wunderlich 2008). Apart from all these precautions, only late instars were considered to avoid any errors.

Although corresponding to the same type of habitat (Laurisilva), each site has a particular composition and structure (relative abundance) of woody plant species. This is a consequence of local climatic conditions, past geological events and vegetation succession processes (Dias 1996; Gabriel 2000). As a result, it was not possible to compare directly the diversity and distribution of arthropods for a given plant species across all sites. Instead, each site was compared with others based on the combined dominant plant species present. Actually, results showed that the arthropod diversity for a given plant species was more similar to the arthropod composition of other plant species within the same site than to composition of the same plant species from different sites. In a previous study, Ribeiro et al. (2005) found the same pattern except for *Erica azorica*, which showed a characteristic arthropod diversity across the archipelago. In this study, using more data, not even *Erica azorica* was an exception. In fact, the particular structure and composition of the combined plant species within each site is expected to have an effect on the proportion of organic matter and acidity of the soil, in the intensity of light, density of the understorey vegetation and humidity inside the forest, and thus, may influence the composition and abundance of arthropods. This supports the use of arthropod data from plant species combined rather than using the arthropod information for each plant species independently. The differences in the arthropod diversity collected using dominant or non-dominant plant species will be evaluated in detail in the near future.

Araneae species had the highest abundance of the 21 arthropod orders studied, corresponding to 30% of the overall abundance found. Also, it was the only group of the four most diverse orders to show a bimodal distribution of occurrences. This is likely a result of the high dispersal ability (ballooning capacity of species from the Linyphiidae family, 34 spp) and low habitat specificity of many species of Araneae.

Indigenous species, including native and endemic, corresponded to more than half of the species recorded and almost 90% of the abundance found. The low abundance of non-indigenous species may suggest that some of these species may be vagrants in native forests, dispersing from surrounding habitats, such as pastures or exotic forests. The proportion of singletons and doubletons for non-indigenous species (45%), however, was not much higher than that for indigenous species (31%) and even lower than for the group with unknown colonization (55%). A study is being developed comparing the arthropod diversity and abundance within native forests and from surrounding habitats that will hopefully help to clarify this (Borges et al. in press).

The arthropod composition in soil and canopy strata seems to be considerably different. Canopy and soil strata shared only a third of common arthropod species, and arthropod composition seems to aggregate more strongly per stratum than per location (islands, fragments or even sites). This is surprising, taking into account the particular characteristics that each site presents, as discussed above. Both strata have a prevalence of species with high dispersal ability (65% for soil and 70% for canopy), so this may be a result of dissimilar niche requirements rather than a constraint in dispersal ability of soil arthropods. Also, due to the uneven ground, it is common to see canopy strata at the ground level, and still, despite the opportunity given to soil arthropods to disperse to canopy both strata remain distinct in their arthropod composition.

More than one third of the arthropod species occurred in only one island, one fragment or one site, being the exclusive species distributed across all fragments and islands. Thus, each site has a unique contribution to the overall diversity found. This finding has important implications to the selection and management of areas for arthropod conservation in the archipelago. This outcome and possible factors that may be driving it (e.g. differential colonization, extinction, speciation, habitat specificity) will be explored in different perspectives elsewhere. Notwithstanding, further studies are needed to effectively evaluate processes that may be driving this general pattern in the Azores.

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APPENDIX

Table 1. List of the arthropod species recorded in the Azorean native forests, ordered alphabetically by major taxon (Order). Col. - Colonization group (I-Introduced, N-Native, E-Endemic); Tro. - Trophic group (P-Predator, H-Herbivore, S-Saprophage, F-Fungivore); Disp. - Dispersal ability (High, Low). Taxa with no information or followed by ? are waiting for identification or confirmation, but were recognized by taxonomists as different taxonomic units. Endemic species are highlighted in grey.

Order	FAMILY	Species	Col.	Tro.	Disp.
Araneae					
	ARANEIDAE				
		Araneus sp.	I	P	Low
		Gen. sp.	I ?	P	Low
		Gibbaranea occidentalis Wunderlich	E	P	Low
		Mangora acalypha (Walckenaer)	I	P	Low
	CLUBIONIDAE				
		Cheiracanthium erraticum (Walckenaer)	I	P	Low
		Cheiracanthium floresense Wunderlich	E	P	Low
		Cheiracanthium jorgeense Wunderlich	E	P	Low
		Clubiona decora Blackwall	N	P	Low
		Clubiona genevensis L. Koch	I ?	P	Low
		Clubiona terrestris Westring	I	P	Low
		Gen. sp.	I ?	P	Low

Table 1. Arthropod species from Azorean native forests (continuation, 2/13)

Order	FAMILY	Species	Col.	Tro.	Disp.
	DICTYNIDAE				
		Dictyna (Emblyna) acoreensis (Wunderlich)	E	P	Low
		Lathys dentichelis (Simon)	N	P	Low
		Nigma puella (Simon)	I	P	Low
	DYSDERIDAE				
		Dysdera crocata C.L. Koch	I	P	Low
	LINYPHIIDAE				
		Acorigone acoreensis (Wunderlich)	E	P	High
		Acorigone zebraneus Wunderlich	E	P	High
		Agyneta decora (O.P.-Cambridge)	I	P	High
		Agyneta depigmentata Wunderlich	E	P	High
		Agyneta rugosa Wunderlich	E	P	High
		Agyneta sp.	?	P	High
		Araeoncus n. sp.	E	P	High
		Eperigone bryantae Ivie & Barrows	I	P	High
		Eperigone fradeorum (Berland)	I	P	High
		Eperigone sp. 1	I	P	High
		Eperigone sp. 3	I	P	High
		Eperigone trilobata (Emerton)	I	P	High
		Erigone atra (Blackwall)	I	P	High
		Erigone autumnalis Emerton	I	P	High
		Erigone dentipalpis (Wider)	I	P	High
		Erigone sp.	?	P	High
		Gen. sp. 1	E ?	P	High
		Gen. sp. 2	?	P	High
		Lepthyphantes acoreensis Wunderlich	E	P	High
		Lessertia dentichelis (Simon)	I	P	High
		Meioneta fuscipalpis (C.L. Koch)	I	P	High
		Microlinyphia johnsoni (Blackwall)	N	P	High
		Minicia floresensis Wunderlich	E	P	High
		Neriene clathrata (Sundevall)	I	P	High
		Oedothorax fuscus (Blackwall)	I	P	High
		Ostearius melanopygius (O.P.-Cambridge)	I	P	High
		Palliduphantes schmitzi (Kulczynski)	N	P	High
		Pelecopsis parallela (Wider)	I	P	High
		Porrhomma borgesi Wunderlich	E	P	High
		Prinerigone vagans (Audouin)	I	P	High
		Savigniorrhipis acoreensis Wunderlich	E	P	High
		Tenuiphantes miguelensis Wunderlich	N	P	High
		Tenuiphantes tenuis (Blackwall)	I	P	High
		Walckenaeria grandis (Wunderlich)	E	P	High
	LYCOSIDAE				
		Pardosa acorensis Simon	E	P	Low
	MIMETIDAE				
		Ero furcata (Villers)	I	P	Low
	OECOBIIDAE				
		Oecobius navus Blackwall	I	P	Low
	OONOPIDAE				
		Orchestina furcillata Wunderlich	E	P	Low

Table 1. Arthropod species from Azorean native forests (continuation, 3/13)

Order	Family	Species	Col.	Tro.	Disp.
	PISAURIDAE				
		Pisaura acoreensis Wunderlich	E	P	Low
	SALTICIDAE				
		Macaroeris cata (Blackwall)	N	P	Low
		Macaroeris sp.	I ?	P	Low
		Neon acoreensis Wunderlich	E	P	Low
		Pseudeuophrys vafra (Blackwall)	I	P	Low
	TETRAGNATHIDAE				
		Metellina merianae (Scopoli)	I	P	Low
		Sancus acoreensis (Wunderlich)	E	P	Low
	THERIDIIDAE				
		Achaearanea acoreensis (Berland)	I	P	Low
		Argyrodes nasicus (Simon)	I	P	Low
		Gen. sp. 1	E ?	P	Low
		Gen. sp. 2	?	P	Low
		Gen. sp. 3	?	P	Low
		Lasaeola oceanica Simon	E	P	Low
		Neottiura bimaculata (Linnaeus)	I	P	Low
		Rugathodes acoreensis Wunderlich	E	P	Low
		Steatoda grossa (C.L. Koch)	I	P	Low
		Theridion musivivum Schmidt	N	P	Low
		Theridion sp.	I	P	Low
	THOMISIDAE				
		Xysticus cor Canestrini	N	P	Low
		Xysticus nubilus Simon	I	P	Low
	ZODARIIDAE				
		Zodarion atlanticum Pekár & Cardoso	I	P	Low
Blattaria					
	POLYPHAGIDAE				
		Zetha vestita (Brullé)	N	S	High
Chordeumatida					
	HAPLOBAINOSOMATIDAE				
		Haplobainosoma lusitanum Verhoeff	N ?	S	Low
Coleoptera					
	Fam ?				
		Gen. sp.	?	S/H	High
	ANTHICIDAE				
		Gen. sp.	I	S	High
	CARABIDAE				
		Acupalpus dubius Schilsky	N	P	High
		Acupalpus flavicollis (Sturm) ?	N	P	High
		Amara aenea (De Geer)	I	P	High
		Anisodactylus binotatus (Fabricius)	I	P	High
		Calathus lundbladi Colas	E	P	Low
		Cedrorum azoricus azoricus Borges & Serrano	E	P	Low
		Cedrorum azoricus caveirensis Borges & Serrano	E	P	Low
		Laemosthenes complanatus Dejean	N	P	High
		Ocys harpaloides (Audinet-Serville)	N ?	P	High
		Paranchus albipes (Fabricius)	I	P	High
		Pseudanchomenes aptinoides Tarnier	E	P	Low

Table 1. Arthropod species from Azorean native forests (continuation, 4/13)

Order	FAMILY	Species	Col.	Tro.	Disp.
		Pseudophonus rufipes (DeGeer)	I	P/H	High
		Pterostichus (Argutor) vernalis (Panzer)	I	P	High
		Pterostichus aterrimus aterrimus (Herbst)	N	P	High
		Stenolophus teutonus (Schrank)	I	P	High
		Trechus terrabravensis Borges, Serrano & Amorim	E	P	Low
	CERAMBYCIDAE				
		Crotchiella brachyptera Israelson	E	H	High
	CHRYSOMELIDAE				
		Chaetocnema hortensis (Fourcroy)	I	P	High
		Epitrix hirtipennis Melsham	I	H	High
		Gen. sp.	I ?	H	High
	CIIDAE				
		Atlantocis gillerforsi Israelson	E	F	Low
	COCCINELLIDAE				
		Clitostethus arcuatus (Rossi)	I	P	High
		Coccinella undecimpunctata undecimpunctata L.	I	P	High
		Gen. sp.	I	P	High
		Rhyzobius lophanthae (Blaisdell)	I	P	High
	CORYLOPHIDAE				
		Gen. sp.	?	P	High
		Sericoderus lateralis (Gyllenhal)	I	P	High
	CRYPTOPHAGIDAE				
		Cryptophagus sp. 1	I	S	High
		Cryptophagus sp. 2	I	S	High
		Cryptophagus sp. 3	I	S	High
		Cryptophagus sp. 4	I	S	High
		Cryptophagus sp. 5	I	S	High
		Gen. sp.	I	S	High
	CURCULIONIDAE				
		Calacalles subcarinatus (Israelson)	E	H	High
		Caulotrupis parvus Israelson	E	H	Low
		Coccotrypes carpophagus (Hornung)	I	H	High
		Gen. sp. 1	I ?	H	High
		Gen. sp. 2	I	H	High
		Gen. sp. 3	?	H	High
		Drouetis borgesi Machado	E	H	Low
		Otiorhynchus rugosostriatus (Goeze)	N	H	Low
		Phloeosinus gillerforsi Bright	E	H	High
		Pseudechinosoma nodosum Hustache	E	H	Low
		Pseudophloeophagus tenax (Wollaston)	N	H	High
		Sitona discoideus Gyllenhal	I	H	High
		Sitona sp.	I	H	High
		Tychius sp.	I ?	H	High
		Xyleborinus saxesenii (Ratzeburg)	I	H	High
	DRYOPHTHORIDAE				
		Sitophilus oryzae (Linnaeus)	I	H	High
		Sphenophorus abbreviatus (Fabricius)	I	H	High
	DRYOPIDAE				
		Dryops algiricus Lucas	N	H	High
		Dryops luridus (Erichson)	N	H	High

Table 1. Arthropod species from Azorean native forests (continuation, 5/13)

Order	Family	Species	Col.	Tro.	Disp.
	DYTISCIDAE				
		Agabus bipustulatus (Linnaeus)	N	P	High
		Agabus godmani Crotch	E	P	High
		Hydroporus guernei Régimbart	E	P	High
	ELATERIDAE				
		Aeolus melliculus moreleti Tarnier	E	S	High
		Alestrus dolosus (Crotch)	E	H	High
		Athous pomboi Platia & Borges	E	H	High
	HYDROPHILIDAE				
		Cercyon haemorrhoidalis (Fabricius)	I	S	High
		Sphaeridium bipustulatum (Fabricius)	I	S	High
	LAEMOPHLOEIDAE				
		Gen. sp.	N ?	P	High
		Placonotus sp. 1	N	P	High
	LATHRIDIIDAE				
		Cartodere (Aridius) nodifer (Westwood)	I	S	High
		Gen. sp. 1	E ?	S	High
		Gen. sp. 2	?	S	High
		Lathridius australicus (Belon)	I	S	High
		Metophthalmus occidentalis Israelson	E	S	High
	LEIODIDAE				
		Catops coracinus coracinus Kellner	N	S	High
	MYCETOPHAGIDAE				
		Typhaea stercorea (Linnaeus)	I	F	High
	NITIDULIDAE				
		Carpophilus fumatus Boheman	I	S	High
		Carpophilus hemipterus (Linnaeus)	I	S	High
		Carpophilus sp. 2	I	S	High
		Epuraea biguttata (Thunberg)	I	H	High
		Meligethes aeneus (Fabricius)	I	H	High
		Meligethes sp. 2	I	H	High
		Meligethes sp. 3	I	S	High
		Stelidota geminata (Say)	I	S	High
	PHALACRIDAE				
		Gen. sp.	I ?	S	High
		Stilbus testaceus (Panzer)	N	S	High
	PTILIIDAE				
		Acrotrichis sp. 1	N ?	S	High
		Ptenidium pusillum (Gyllenhal)	I	S	High
	SCARABAEIDAE				
		Onthophagus taurus (Schreber)	I	S	High
	SCRAPTIIDAE				
		Anaspis proteus (Wollaston)	N	H	High
	SCYDMAENIDAE				
		Cephennium distinctum Besuchet	N ?	S	High
	SILVANIDAE				
		Cryptamorpha desjardinsii (Guérin-Méneville)	I	P	High
	STAPHYLINIDAE				
		Aleochara bipustulata (Linnaeus)	I	P	High
		Aloconota sulcifrons (Stephens)	N	P	High

Table 1. Arthropod species from Azorean native forests (continuation, 6/13)

Order	FAMILY	Species	Col.	Tro.	Disp.
		Amischa analis (Gravenhorst)	I	P	High
		Anotylus nitidifrons (Wollaston)	I	P	High
		Anotylus sp. 2	I	P	High
		Atheta amicula (Stephens)	I	P	High
		Atheta atramentaria (Gyllenhal)	I	P	High
		Atheta dryochares Israelson	E	P	High
		Atheta fungi (Gravenhorst)	I ?	F	High
		Atheta sp. 3	E	P	High
		Atheta sp. 4	E ?	P	High
		Carpelimus corticinus (Gravenhorst)	N	P	High
		Cilea silphoides (Linnaeus)	I	P	High
		Cordalia obscura (Gravenhorst)	I	P	High
		Gabrius nigritulus (Gravenhorst)	I	P	High
		Gen. sp. 1	N ?	P	High
		Gen. sp. 2	N ?	P	High
		Gen. sp. 3	E ?	P	High
		Gen. sp. 4	N	H	High
		Habrocerus capillaricornis (Gravenhorst)	N	P	High
		Medon sp. 2	N	P	High
		Ocypus (Pseudocypus) aethiops (Waltl)	N	P	High
		Ocypus olens (Muller)	N	P	High
		Oligota parva Kraatz	I	P	High
		Philonthus sp.	N ?	P	High
		Phloeonomus n. sp. ?	E	P	High
		Phloeonomus sp. 1	N	P	High
		Phloeonomus sp. 3	I	P	High
		Phloeonomus sp. 4	?	P	High
		Phloeopora sp. 1	N	P	High
		Phloeopora sp. 4	N ?	P	High
		Phloeostiba azorica (Fauvel)	E	P	High
		Proteinus atomarius Erichson	N	P	High
		Quedius curtipennis Bernhauer	N	P	High
		Quedius simplicifrons (Fairmaire)	N	P	High
		Rugilus orbiculatus orbiculatus (Paykull)	N	P	High
		Scopaeus portai Luze	N ?	P	High
		Sepedophilus lusitanicus (Hammond)	N	P	High
		Stenus guttula guttula Müller	N	P	High
		Tachyporus chrysomelinus (Linnaeus)	I	P	High
		Xantholinus longiventris Heer	I	P	High
		Xantholinus sp.	I	P	High
	ZOPHERIDAE				
		Tarphius acuminatus Gillerfors	E	F	Low
		Tarphius azoricus Gillerfors	E	F	Low
		Tarphius depressus Gillerfors	E	F	Low
		Tarphius pomboi Borges	E	F	Low
		Tarphius rufonodulosus Israelson	E	F	Low
		Tarphius serranoi Borges	E	F	Low
		Tarphius tornvalli Gillerfors	E	F	Low
		Tarphius wollastoni Crotch	E	F	Low

Table 1. Arthropod species from Azorean native forests (continuation, 7/13)

Order	Family	Species	Col.	Tro.	Disp.
Dermaptera					
	Anisolabididae				
		Euborellia annulipes (Lucas)	I	P	Low
	Forficulidae				
		Forficula auricularia Linnaeus	I	P	Low
Ephemeroptera					
	Baetidae				
		Cloeon dipterum (Linnaeus)	N ?	H	High
Geophilomorpha					
	Geophilidae				
		Geophilus truncorum Bergsoe & Meinert	N	P	Low
	Linotaeniidae				
		Strigamia crassipes (C.L. Koch)	N ?	P	Low
Hemiptera					
	Fam ?				
		Gen. sp.	E ?	H	High
	Aleyrodidae				
		Gen. sp. 1	N ?	H	High
		Gen. sp. 2	N ?	H	High
		Gen. sp. 3	?	H	High
		Gen. sp. 4	?	H	High
		Gen. sp. 5	?	H	High
		Gen. sp. 6	E ?	H	High
		Gen. sp. 7	E ?	H	High
		Gen. sp. 8	E ?	H	High
		Gen. sp. 9	E ?	H	High
		Gen. sp. 10	E ?	H	High
		Gen. sp. 11	E ?	H	High
		Gen. sp. 12	E ?	H	High
		Gen. sp. 13	E ?	H	High
	Anthocoridae				
		Brachysteles parvicornis (A. Costa)	I	P	High
		Buchananiella continua (White)	N	P	High
		Orius (Orius) laevigatus laevigatus (Fieber)	N	P	High
	Aphididae				
		Acyrthosiphon pisum Harris	N	H	High
		Amphorophora rubi (Kaltenbach) *sensu latiore*	N	H	High
		Aphis craccivora Koch	N	H	High
		Aphis sp.	?	H	High
		Aulacorthum solani (Kaltenbach)	N	H	High
		Covariella aegopodii (Scopoli)	I	H	High
		Dysaphis plantaginea (Passerini)	I	H	High
		Gen. sp. 1	I ?	H	High
		Gen. sp. 2	I ?	H	High
		Gen. sp. 3	I	H	High
		Longiunguis luzulella Hille Ris Lambers ?	I	H	High
		Myzus cerasi (Fabricius)	I	H	High
		Neomyzus circumflexus (Buckton)	I	H	High
		Pseudacaudella rubida (Borner)	I	H	High
		Rhopalosiphonimus latysiphon (Davidson)	N	H	High

Table 1. Arthropod species from Azorean native forests (continuation, 8/13)

Order	FAMILY	Species	Col.	Tro.	Disp.
		Rhopalosiphum insertum (Walker)	I	H	High
		Rhopalosiphum padi (Linnaeus)	I	H	High
		Rhopalosiphum rufiabdominalis (Sasaki)	I	H	High
		Toxoptera aurantii (Boyer de Fonscolombe)	I	H	High
		Uroleucon erigeronense (Thomas)	N ?	H	High
	CERCOPIDAE				
		Philaenus spumarius (Linnaeus)	N ?	H	High
	CICADELLIDAE				
		Anoscopus albifrons (Linnaeus)	I ?	H	High
		Aphrodes hamiltoni Quartau & Borges	E	H	High
		Eupteryx azorica Ribaut	E	H	High
		Gen. sp.	?	H	High
		Opsius stactogallus Fieber	N ?	H	High
	CIXIIDAE				
		Cixius azofloresi Remane & Asche	E	H	High
		Cixius azomariae Remane & Asche	E	H	High
		Cixius azopifajo azofa Remane & Asche	E	H	High
		Cixius azopifajo azojo Remane & Asche	E	H	High
		Cixius azopifajo Remane & Asche	E	H	High
		Cixius azoricus azoricus Lindberg	E	H	High
		Cixius azoricus azoropicoi Remane & Ashe	E	H	High
		Cixius azoterceirae Remane & Asche	E	H	High
		Cixius insularis Lindberg	E	H	High
	COCCIDAE				
		Gen. sp. 1	?	H	Low
		Gen. sp. 2	?	H	Low
		Gen. sp. 3	?	H	Low
		Gen. sp. 4	?	H	Low
		Gen. sp. 5	N	H	Low
		Gen. sp. 6	?	H	Low
		Gen. sp. 7	N ?	H	Low
	CYDNIDAE				
		Geotomus punctulatus (Costa)	N ?	H	High
	DELPHACIDAE				
		Gen. sp. 1	N ?	H	High
		Gen. sp. 2	?	H	High
		Megamelodes quadrimaculatus (Signoret)	N	H	High
		Muellerianella sp. 1	N	H	High
		Muellerianella sp. 2	N ?	H	High
		Muellerianella sp. 3	N ?	H	High
	DREPANOSIPHIDAE				
		Anoecia corni (Fabricius)	I	H	High
		Theriaphis trifolii (Monell)	N	H	High
	FLATIDAE				
		Cyphopterum adcendens (Herr.-Schaff.)	N	H	High
	LACHNIDAE				
		Cinara juniperi (De Geer)	N	H	High
	LYGAEIDAE				
		Beosus maritimus (Scopoli)	N ?	H	High
		Gastrodes grossipes grossipes (De Geer)	I	H	High

Table 1. Arthropod species from Azorean native forests (continuation, 9/13)

Order	Family	Species	Col.	Tro.	Disp.
		Heterogaster urticae (Fabricius)	N ?	H	High
		Kleidocerys ericae (Horváth)	N	H	High
		Microplax plagiata (Fieber)	I ?	H	High
		Nysius atlantidum Horváth	E	H	High
		Plinthisus brevipennis (Latreille)	N	H	High
		Plinthisus minutissimus Fieber	N	H	High
		Scolopostethus decoratus (Hahn)	N ?	H	High
	MARGARODIDAE				
		Gen. sp. 1	?	H	Low
		Gen. sp. 2	?	H	Low
		Gen. sp. 3	?	H	Low
	MICROPHYSIDAE				
		Loricula (Loricula) elegantula (Bärensprung)	I	H	High
		Loricula (Myrmedobia) coleoptrata (Fallén)	I	H	High
	MIRIDAE				
		Campyloneura virgula (Herrich-Schaeffer)	N ?	H	High
		Closterotomus norwegicus (Gmelin)	N	H	High
		Heterotoma planicornis (Pallas)	N	P	High
		Monalocoris filicis (Linnaeus)	N	H	High
		Pinalitus oromii J. Ribes	E	H	High
		Polymerus (Poeciloscytus) cognatus (Fieber)	N	H	High
	NABIDAE				
		Nabis pseudoferus ibericus Remane	N	P	High
	PENTATOMIDAE				
		Nezara viridula (Linnaeus)	I	H	High
	PSYLLIDAE				
		Acizzia uncatoides (Ferris & Klyver)	I	H	High
		Cacopsylla pulchella (Low)	I	H	High
		Strophingia harteni Hodkinson	E	H	High
	REDUVIIDAE				
		Empicoris rubromaculatus (Blackburn)	N ?	P	High
	SALDIDAE				
		Saldula palustris (Douglas)	I	H	High
	TINGIDAE				
		Acalypta parvula (Fallén)	N	H	High
	TRIOZIDAE				
		Trioza (Lauritrioza) laurisilvae Hodkinson	N	H	High
Julida					
	BLANIULIDAE				
		Blaniulus guttullatus (Fabricius)	I ?	S	Low
		Choneiulus palmatus (Nemec) ?	I	S	Low
		Nopoiulus kochii (Gervais)	N ?	S	Low
		Proteroiulus fuscus (Am Stein)	N ?	S	Low
	JULIDAE				
		Brachyiulus pusillus (Leach)	I ?	S	Low
		Brachyiulus sp.	N ?	S	Low
		Cylindroiulus latestriatus (Curtis)	N ?	S	Low
		Cylindroiulus propinquus (Porat)	N	S	Low
		Ommatoiulus moreletii (Lucas)	I ?	H	Low

Table 1. Arthropod species from Azorean native forests (continuation, 10/13)

Order	FAMILY	Species	Col.	Tro.	Disp.
Lepidoptera					
	Fam ?				
		Gen. sp. 1	?	H	Low
		Gen. sp. 2	?	H	High
		Gen. sp. 3	?	H	Low
		Gen. sp. 4	N ?	H	Low
		Gen. sp. 5	?	H	Low
		Gen. sp. 6	N ?	H	Low
		Gen. sp. 7	E ?	H	Low
		Gen. sp. 8	?	H	High
		Gen. sp. 9	I ?	H	Low
		Gen. sp. 10	E ?	H	Low
		Gen. sp. 11	N ?	H	Low
		Gen. sp. 12	N ?	H	Low
		Gen. sp. 13	N ?	H	Low
		Gen. sp. 14	N	H	Low
		Gen. sp. 15	N	H	Low
		Gen. sp. 16	N ?	H	Low
		Gen. sp. 17	N ?	H	Low
		Gen. sp. 18	N ?	H	Low
		Gen. sp. 19	N ?	H	Low
	BLASTOBASIDAE				
		Blastobasis sp. 1	I ?	H	High
		Blastobasis sp. 3	I	H	High
		Neomariania sp.	?	H	High
	GELECHIIDAE				
		Brachmia infuscatella Rebel	E	H	High
	GEOMETRIDAE				
		Ascotis fortunata azorica Pinker	E	H	Low
		Cyclophora azorensis (Prout)	E	H	Low
		Cyclophora pupillaria granti Prout	E	H	Low
		Gen. sp.	E ?	H	Low
		Orthomana obstipata (Fabricius)	N	H	Low
		Xanthorhoe inaequata (Warren)	E	H	Low
	GRACILLARIIDAE				
		Caloptilia schinella (Walsingham)	I	H	High
		Micrurapteryx bistrigella (Rebel)	E	H	High
		Phyllocnistis citrella Stainton	I	H	High
	NIMPHALYDAE				
		Hipparchia azorina occidentalis (Sousa)	E	H	High
		Hipparchia miguelensis (Le Cerf)	E	H	High
	NOCTUIDAE				
		Agrotis ipsilon (Hufnagel)	N	H	High
		Agrotis sp.	N	H	Low
		Chrysodeixis chalcites (Esper)	N	H	Low
		Gen. sp. 1	?	H	High
		Gen. sp. 2	N ?	H	Low
		Gen. sp. 3	N ?	H	Low
		Gen. sp. 4	N ?	H	Low
		Gen. sp. 5	N ?	H	Low

Table 1. Arthropod species from Azorean native forests (continuation, 11/13)

Order	Family	Species	Col.	Tro.	Disp.
		Gen. sp. 6	N ?	H	Low
		Gen. sp. 7	I	H	Low
		Mesapamea storai (Rebel)	E	H	High
		Mythimna unipuncta (Haworth)	N	H	High
		Phlogophora interrupta (Warren) ?	E	H	Low
		Xestia c-nigrum (Linnaeus)	N	H	High
	PYRALIDAE				
		Eudonia luteusalis (Hampson)	E	H	High
		Gen. sp. 1	N ?	H	Low
		Gen. sp. 2	?	H	High
		Gen. sp. 3	?	H	High
		Scoparia coecimaculalis Warren	E	H	High
		Scoparia semiamplalis Warren	E	H	High
		Scoparia sp. 1	E	H	Low
		Scoparia sp. 2	E ?	H	High
		Scoparia sp. 3	?	H	High
		Scoparia sp. 4	E	H	High
	TINEIDAE				
		Oinophila v-flava (Haworth)	I	H	High
		Opogona sacchari (Bojer)	I	H	High
		Opogona sp.	?	H	High
	TORTRICIDAE				
		Gen. sp. 1	I	H	Low
		Gen. sp. 2	I	H	Low
		Gen. sp. 3	I	H	Low
		Gen. sp. 4	I	H	Low
		Gen. sp. 5	I	H	Low
		Gen. sp. 6	N ?	H	Low
		Rhopobota naevana Huebner	I	H	High
	YPONOMEUTIDAE				
		Argyresthia atlanticella Rebel	E	H	High
Litobiomorpha					
	LITHOBIIDAE				
		Lithobius pilicornis pilicornis Newport	N	P	Low
		Lithobius sp.	N	P	Low
Microcoryphia					
	MACHILIDAE				
		Dilta saxicola (Womersley)	N	S	Low
		Trigoniophthalmus borgesi Mendes et al.	E	S	Low
Neuroptera					
	HEMEROBIIDAE				
		Hemerobius azoricus Tjeder?	E	P	High
Opilionida					
	PHALANGIIDAE				
		Homalenotus coriaceus (Simon)	N	P	Low
		Leiobunum blackwalli Meade	N	P	Low
Orthoptera					
	GRYLLIDAE				
		Gryllus bimaculatus (De Geer)	I	S	High

Table 1. Arthropod species from Azorean native forests (continuation, 12/13)

Order	FAMILY	Species	Col.	Tro.	Disp.
	CONOCEPHALIDAE				
		Conocephalus chavesi (Bolivar)	N ?	H	High
Polydesmida					
	PARADOXOSOMATIDAE				
		Oxidus gracilis (C.L. Koch)	I	S	Low
	POLYDESMIDAE				
		Brachydesmus superus Latzel	N	S	Low
		Polydesmus coriaceus Porat	N	S	Low
Pseudoscorpionida					
	CHTHONIIDAE				
		Chthonius ischnocheles (Hermann)	N	P	Low
		Chthonius tetrachelatus (Preyssler)	N	P	Low
	NEOBISIIDAE				
		Neobisium maroccanum Beier	I	P	Low
Psocoptera					
	Fam ?				
		Gen. sp. 1	?	S	High
		Gen. sp. 2	?	S	High
		Gen. sp. 3	?	S	Low
	CAECILIUSIDAE				
		Valenzuela burmeisteri (Brauer)	N	S	High
		Valenzuela flavidus (Stephens)	N	S	High
	ECTOPSOCIDAE				
		Ectopsocus briggsi McLachlan	N	S	High
		Ectopsocus strauchi Enderlein	N	S	High
	ELIPSOCIDAE				
		Elipsocus azoricus Meinander	E	S	High
		Elipsocus brincki Badonnel	E	S	High
		Bertkauia lucifuga (Rambur)	N	S	High
	LACHESILLIDAE				
		Lachesilla greeni (Pearman)	N	S	High
	PERIPSOCIDAE				
		Peripsocus milleri (Tillyard)	N	S	High
		Peripsocus phaeopterus (Stephens)	N	S	High
		Peripsocus subfasciatus (Rambur)	N	S	High
	PSOCIDAE				
		Atlantopsocus adustus (Hagen)	N	S	High
	TRICHOPSOCIDAE				
		Trichopsocus clarus (Banks)	N	S	High
	TROGIIDAE				
		Cerobasis cf sp. A	E	S	Low
		Cerobasis n. sp.	E ?	S	Low
		Cerobasis sp. A	E	S	Low
		Gen. sp.	N ?	S	Low
		Lepinotus reticulatus Enderlein	N	S	Low
Scolopendromorpha					
	CRYPTOPIDAE				
		Cryptops hortensis Leach	N ?	P	Low

Table 1. Arthropod species from Azorean native forests (continuation, 13/13)

Order	Family	Species	Col.	Tro.	Disp.
Thysanoptera					
	Aeolothripidae				
		Aeolothrips collaris Priesner	N	P	High
		Aeolothrips gloriosus Bagnall	I	P	High
	Phlaeothripidae				
		Apterygothrips ? *canarius* (Priesner)	I	H	High
		Apterygothrips n. sp. ?	E	H	High
		Eurythrips tristis Hood	I	H	High
		Gen. sp.	?	H	High
		Hoplandrothrips consobrinus (Knechtel)	I	H	High
		Hoplothrips corticis (De Geer)	N	F	High
		Hoplothrips ulmi (Fabricius)	N	F	High
		Nesothrips propinquus (Bagnall)	I	H	High
	Thripidae				
		Aptinothrips rufus Haliday	N	H	High
		Ceratothrips ericae (Haliday)	N	H	High
		Frankliniella sp.	N	H	High
		Heliothrips haemorrhoidalis (Bouché)	I	H	High
		Hercinothrips bicinctus (Bagnall)	I	H	High
		Isoneurothrips australis Bagnall	I	H	High
		Thrips atratus Haliday	N	H	High
		Thrips flavus Schrank	N	H	High
Trichoptera					
	Fam ?				
		Gen. sp.	?	P	Low
	Limnephilidae				
		Limnephilus atlanticus Nybom ?	E	P	High