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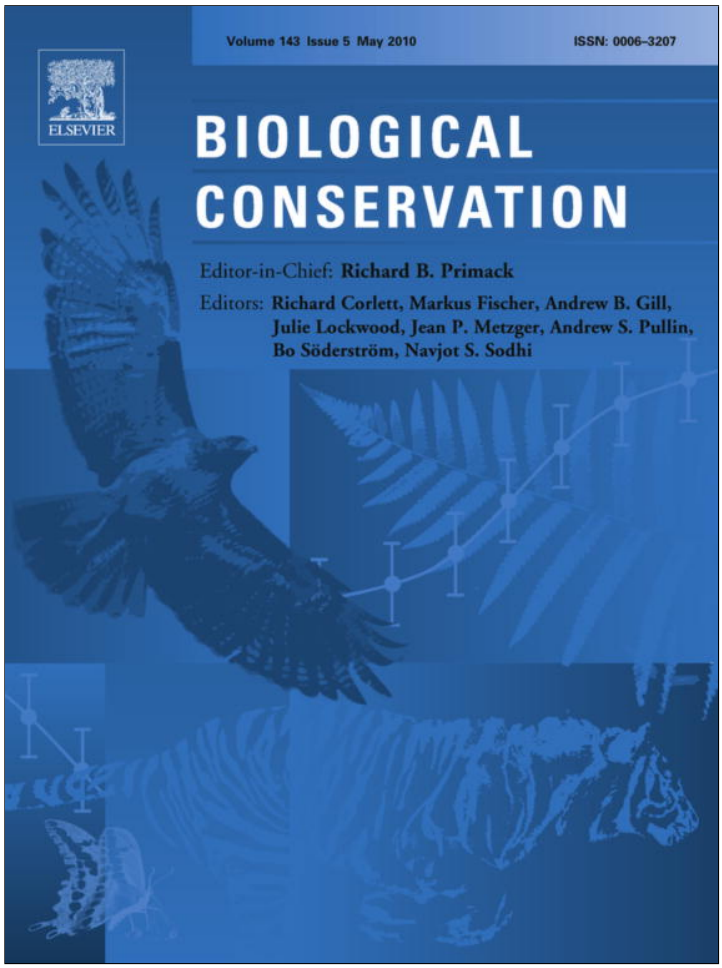

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Arthropods as surrogates of diversity at different spatial scales

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ABSTRACT

This study evaluates the effectiveness of taxonomic, colonization and trophic groups of arthropods from native forests of the Azores archipelago as surrogates of the diversity of other arthropod groups and of the remaining arthropods. Consistency in the performance of surrogates was tested across three spatial scales and using two measures of diversity. Pitfall and beating samples from 109 transects, 18 forest fragments and seven islands were analysed. The results showed that Araneae, Hemiptera and small orders taxonomic groups; native, endemic and introduced colonization groups; and the herbivores trophic group were consistent surrogates of the remaining diversity across the three spatial scales analysed, for both alpha and dissimilarity diversities. However, none of the subsets considered was significantly related with all of the other subsets at any of the three spatial scales. The effectiveness of surrogacy was dependent on the spatial level considered, and groups behaved inconsistently depending on the measure of diversity used. The value of a group as a diversity surrogate should be evaluated for a study area for a given spatial scale and diversity measure, in accordance with the scale and measure that will be used for biodiversity assessments and monitoring programs in that area.

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1. Introduction

A popular shortcut approach to assessing and monitoring the biodiversity of areas is the use of surrogates (e.g., Araújo et al., 2004; Balmford and Long, 1995; Gladstone, 2002; Rohr et al., 2007; Weaver, 1995), usually a set of species whose diversity or distribution can be used to predict the diversity or distribution of the remaining species. Such a predictive property, if it proves to be reliable, can offer a valuable tool for conservation planning and other purposes at a time when financial and time resources are limited.

Several species assemblages have been selected as surrogates based on characteristics that include, among others, their functional role, distribution, threat status or charismatic value (e.g., Bonn et al., 2002, 2004; Ozaki et al., 2006). Still, taxonomic groups are the most commonly applied surrogates. This preference is in part influenced by the ease with which specimens can be identified to a specific level because knowledge is required only for a group of related taxa.

Surrogates can also be selected based on the characteristic of the community that is to be predicted, whether that is diversity (diversity surrogate), co-occurrence (biotic indicator), habitat quality (environmental indicator) or taxa (higher-taxa surrogate) (e.g., Caro and O'Doherty, 1999; Gaston and Williams, 1993; Heino and Mykrä, 2006; Mac Nally et al., 2002; McGeoch, 1998; Rohr et al., 2007; Villaseñor et al., 2005). It is generally accepted that the predictive ability of a group will vary depending on the type of surrogate required (Caro and O'Doherty, 1999; Fleishman et al., 2000).

Species richness has been commonly used to evaluate groups of species as diversity surrogates (e.g., Pearson and Cassola, 1992; Wilsey et al., 2005; Wolters et al., 2006). However, the utility of diversity surrogates has been questioned in recent years because correlations of species richness between groups have been found to be highly variable across taxa and regions (e.g., Bilton et al., 2006; Prendergast, 1997). Several studies have suggested that complementary measures, taking other aspects of diversity into account, should be used in order to determine the surrogacy value of a group (Bilton et al., 2006; Su et al., 2004). A recently proposed approach is to look for congruence in community similarity, that is, the similarity in the species composition of the pairs of groups to be compared in different areas (Bilton et al., 2006; Su et al., 2004).

It has also been suggested that the effectiveness of a given surrogate could be influenced by spatial scale (Favreau et al., 2006; Weaver, 1995). Favreau et al. (2006) recommended treating spatial scale as an explanatory variable and evaluating the predictions of surrogates at multiple spatial scales. Indeed, spatial scale may be a crucial variable if the main aim is to define conservation plans which rely on surrogates to assess diversity or co-occurrence. Depending on the spatial scale at which a conservation plan will

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be applied, different surrogates may need to be used (Favreau et al., 2006). Still, the importance of spatial scale has seldom been formally tested (but see Weaver, 1995).

Islands of the Azores archipelago have remnants of a native forest composed of a high proportion of endemic plant and invertebrate (molluscs and arthropods) species. Most of the remnants were designated as protected areas for which conservation plans are needed in the near future. As in the majority of terrestrial habitats worldwide, the arthropods are the most diverse and abundant animals in the Azorean native forests. In recent years, an extensive standardised sampling protocol has been applied in most of the forest fragments of the archipelago, resulting in the largest standardised database of arthropods available for the Macaronesia region (comprising Azores, Madeira, Savage, Canaries and Cape Verde archipelagos in the North Atlantic Ocean) and one of the few worldwide at a regional scale. The 440 arthropod species recorded are distributed across 21 taxonomic orders, at least 104 families and 256 genera; cover distinct trophic groups; show different colonization histories; have dissimilar dispersal abilities; and have distinct abundances and variable distributional ranges (see also Gaspar et al., 2008). This extensive database gives the opportunity to test several methods to assess and monitor diversity at multiple spatial scales for a wide range of arthropod groups in a given region. Findings on the consistency in the performance of different groups as surrogates across multiple spatial scales using distinct measures of diversity can hopefully offer insights into the performance of arthropod groups in other regions of the world as well.

Previous studies based on these data have evaluated the effectiveness of arthropods as higher-taxa surrogates (Borges et al., 2002) and environmental indicators (Cardoso et al., 2007) in the Azores. Yet the evaluation of the effectiveness of arthropods as diversity surrogates has not been explored until the present. In this study, three factors commonly suggested to influence the assessment of the surrogacy value of a group were tested and compared: a wide range of taxonomic and non-taxonomic groups; multiple measures of diversity; and different spatial scales.

2. Methods

2.1. Study area

The study was conducted in native forests of the Azores, a volcanic archipelago in the North Atlantic Ocean (37–40°N, 25–31°W), composed of nine islands and islets. The climate is temperate humid at sea level and cold oceanic at higher altitudes. Humidity is high and temperatures have little variation throughout the year.

The native forest in the Azores, known as Laurisilva due to the presence of species of the Lauraceae family, is believed to be a relict of the forests that covered part of Europe in the Tertiary (but see Emerson, 2002). At present, Laurisilva only occurs in some islands of the Macaronesia region. In the Azores in particular, trees have a small stature, closed canopy and dense understory vegetation. Native forests are now restricted to high and steep areas in seven out of nine islands.

2.2. Sampling protocol

A total of 109 transects, each 150 m long and 5 m wide, were randomly established in 18 native forest fragments on seven islands during the summers of 1999–2004. Along each transect, a pitfall trap was placed in the soil every 5 m (30 traps in total) and beating samples were taken from the three most dominant tree and shrub species every 15 m (30 samples in total). A detailed description of the sampling methods applied is presented in Gaspar et al. (2008). A few transects had less than three woody plant species and only those species were considered. The endemic cedar, *Juniperus brevifolia* (Seub) Antoine (Cupressaceae), was the most common species, occurring on most transects.

All Araneae, Opiliones, Pseudoscorpiones, Myriapoda and Insecta (excluding Diptera and Hymenoptera) were considered for this study. Several taxonomists (see Acknowledgements) checked the identifications made.

2.3. Data analyses

Arthropods were grouped by taxonomic (Araneae, Coleoptera, Hemiptera, Julida, Lepidoptera, Psocoptera, Thysanoptera, small orders), trophic (herbivores, predators, saprophages, fungivores) and colonization [introduced, native (indigenous minus endemic) and endemic species] categories. Fourteen taxonomic orders had less than four species and were combined in a group defined as *small orders* (Blattaria, Chordeumatida, Dermaptera, Ephemeroptera, Geophilomorpha, Litobiomorpha, Microcoryphia, Neuroptera, Opiliones, Orthoptera, Polydesmida, Pseudoscorpiones, Scolopendromorpha and Trichoptera). The arthropods with unknown colonization were excluded from the analyses. There was no overlap of species across groups within categories, so, for each category analysed, groups were independent from each other.

The terms spatial scale, spatial level and hierarchical level will be used interchangeably hereafter to refer to the nested transects, fragments, islands and archipelago. The term consistency will denote similar correlation results across different spatial scales or between diversity measures.

Presence–absence data on arthropods for each transect, fragment and island were used to calculate two measures of diversity: alpha species richness (Whittaker, 1960) and an adapted measure of beta diversity – the dissimilarity measure. Alpha species richness was determined as the total number of species present in a given transect, fragment or island. The dissimilarity measure was defined as the amount of variation in the species composition of a given transect, fragment or island in relation to the species composition of its next hierarchical level (its corresponding fragment, island or archipelago). In other words, if n is the hierarchical level to be analysed and alpha is defined as explained above, the dissimilarity measure (d) for a given i transect, fragment or island is:

$$d_{n,i} = \text{alpha } n + 1 - \text{alpha}_i n \quad (1)$$

The value of d is 0 when the species composition of the i-th unit at a given level represents all of the set of species present in the next higher level. This is based on the properties of additive partitioning of species richness (Lande, 1996; MacArthur et al., 1966) where:

$$\text{beta } n = \text{alpha } n + 1 - \text{alpha } n \quad (2)$$

The measure d (1) differs from the additive beta diversity definition (2) in that, for d, each i transect, fragment or island is compared individually ($\text{alpha}_i\, n$) with its next higher level, while *beta n* is based on the average alpha diversity from all samples (z) at a given level (alpha n). Thus, d is an individual measure of beta for each sample at a given level, while additive beta is the average of all values of d for that level:

$$\text{beta } n = \sum_{i=1}^{z} d_{n,i}/z \quad (3)$$

This measure of dissimilarity can determine if any arthropod group can act as a surrogate for the extent of contribution in species that a given transect, fragment or island has to the corresponding fragment, island or archipelago.

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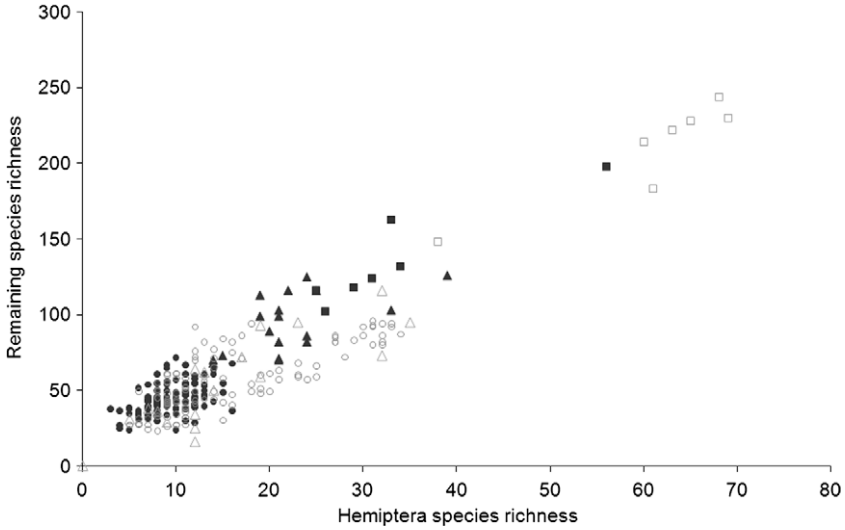

Fig. 1. Relationship between Hemiptera species richness and the species richness of the remaining groups for alpha (dark, closed symbols) and dissimilarity (grey, open symbols) at transect (circles), fragment (triangles) and island (squares) scales.

Table 1
Overall species richness (S), average alpha species richness (alpha) and average dissimilarity measure (d) found for the three spatial scales and the arthropod groups studied (subsets ordered by descending species richness).

	Overall	Transect (n = 109)		Fragment (n = 18)		Island (n = 7)	
	S	Alpha	d	Alpha	d	Alpha	d
All	440	54	72	116	71	170	270
Coleoptera	134	7	18	22	21	38	96
Hemiptera	94	10	16	22	16	33	61
Araneae	72	17	14	29	10	36	36
Lepidoptera	67	8	11	17	11	25	42
Small orders	25	6	6	11	5	15	10
Psocoptera	21	4	5	8	3	10	11
Thysanoptera	18	1	3	3	4	6	12
Julida	9	2	1	3	1	5	4
Herbivores	203	21	32	48	32	72	131
Predators	162	24	28	48	27	67	95
Saprophages	64	8	11	18	10	26	38
Fungivores	13	1	2	3	2	4	9
Introduced	147	12	23	32	27	54	93
Native	146	21	25	44	24	62	84
Endemic	108	20	18	34	13	44	64

Correlation analyses to compare the diversity measures for a given category between pairs of arthropod groups and between an arthropod group and the remaining diversity (for all cases, total diversity minus the diversity of the group to be analysed), were carried out with Spearman's rank correlation (r_s) using the SPSS 12.0 software (SPSS Inc., 2004). A non-parametric correlation technique was used since several datasets were not normally distributed. Spearman was also applied to data that were normally distributed so that correlation coefficients could be compared. Two-tailed significance tests were considered significant when $p < 0.05$. Although sequential Bonferroni correction is commonly used to adjust significance values of correlation analyses when multiple comparisons are made, there are some mathematical and practical objections in its application, as explained by Moran (2003). Thus, in this study, no adjustment was applied. The recommendations of Moran (2003) were followed and marginal values of significance (values approaching $p = 0.05$) were analysed with caution.

Since only one archipelago was considered in this study, the alpha diversity of the archipelago (alpha $n + 1$) was the same for all of the islands, and thus, for the island scale, $d_{n,i}$ was proportional to its respective alpha$_i$ n. This meant that, for the island scale, although the values for alpha and dissimilarity measures were different, their correlation coefficients were the same. Both sets of results are presented in the results tables to facilitate comparisons of each measure at the three scales.

3. Results

Overall, 128,101 individuals corresponding to 440 arthropod species were recorded (a detailed list of the species is presented in Gaspar et al., 2008). Average alpha increased proportionally across higher hierarchical levels (Table 1). For average values of dissimilarity, transect and fragment spatial scales showed similar values, while a very high increase was found for the island scale (Table 1).

Coleoptera was the taxonomic order with the highest species richness (Table 1). The average alpha for Coleoptera per transect and fragment was low in relation to other orders, only compensated by the highest values of average dissimilarity (Table 1). For the island scale, though, both alpha and dissimilarity of Coleoptera had the highest values of all orders considered (Table 1). Araneae, although not having the highest species richness overall, showed the highest average alpha per transect and fragment, and one of the highest averages of alpha for the island scale (Table 1). Values of average dissimilarity for Araneae at all scales were relatively low (Table 1). Hemiptera showed similar values of average dissimilarity for transect and fragment scales but one of the highest values at the island level (Table 1). Herbivores and predators showed similar total species richness and average values of alpha and dissimilarity across the three spatial scales (Table 1). Native and endemic arthropods, corresponding to indigenous species, had nearly twice the richness of the introduced species (Table 1).

Alpha and dissimilarity measures of diversity did not show consistency in surrogacy for many of the arthropod groups considered at transect or fragment scales (Tables 2–4). In general, the dissimilarity measure showed a higher number of correlated groups (Table 5), with higher correlation coefficients (r_s) and significance values (p; Tables 2–4).

Regardless of the taxonomic, trophic and colonization categories and of the diversity measures considered, none of the arthropod subsets was significantly correlated across the three spatial scales with all of the remaining groups of a given category (Tables

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Table 2
Spearman correlation coefficients and their significance values among arthropod taxonomic groups for alpha diversity (upper right triangle) and dissimilarity measure (lower left triangle). ARA – Araneae, COL – Coleoptera, HEM – Hemiptera, JUL – Julida, LEP – Lepidoptera, PSO – Psocoptera, THY – Thysanoptera, SOR – small orders, REM-remaining overall species richness excluding that of the focal group analysed.

	ARA	COL	HEM	JUL	LEP	PSO	THY	SOR	REM
(a) Transect scale (n=109)									
ARA	–	0.02	0.25**	-0.05	0.25**	0.30**	0.21*	0.15	0.29**
COL	0.62***	–	0.17	0.20*	0.08	0.40***	0.16	0.21*	0.28**
HEM	0.64***	0.62***	–	0.23*	0.19*	0.29**	0.17	0.43***	0.47***
JUL	0.17	0.23*	0.24*	–	0.15	0.04	0.01	0.26**	0.20*
LEP	0.64***	0.68***	0.57***	0.20*	–	0.29**	-0.09	0.24*	0.31***
PSO	0.46***	0.47***	0.60***	0.26**	0.39***	–	0.19*	0.18	0.52***
THY	0.45***	0.49***	0.60***	0.00	0.26**	0.57***	–	0.11	0.20*
SOR	0.51***	0.47***	0.57***	0.20*	0.39***	0.44***	0.57***	–	0.44***
REM	0.73***	0.74***	0.75***	0.29**	0.69***	0.60***	0.59***	0.60***	–
(b) Fragment scale (n=18)									
ARA	–	0.30	0.50*	0.07	0.66**	0.09	0.28	0.39	0.47*
COL	0.56*	–	0.41	0.33	0.46	0.46	0.33	0.68**	0.71***
HEM	0.60**	0.84***	–	0.38	0.27	0.33	0.52*	0.51*	0.62**
JUL	0.37	0.32	0.26	–	0.19	0.08	0.13	0.21	0.38
LEP	0.45	0.91***	0.73***	0.24	–	0.12	0.09	0.35	0.55*
PSO	0.39	0.81***	0.67**	0.29	0.67**	–	0.65**	0.60**	0.52*
THY	0.54*	0.79***	0.76***	0.19	0.72***	0.88***	–	0.60**	0.57*
SOR	0.69**	0.49*	0.50*	0.56*	0.38	0.46	0.42	–	0.75***
REM	0.61**	0.90***	0.84***	0.41	0.83***	0.79***	0.82***	0.54*	–
(c) Island scale (n=7)									
ARA	–	0.56	1.00***	-0.56	0.77*	0.49	0.56	0.85*	0.86*
COL	0.56	–	0.56	-0.06	0.46	0.41	0.82*	0.71	0.63
HEM	1.00***	0.56	–	-0.56	0.77*	0.49	0.56	0.85*	0.93**
JUL	-0.56	-0.06	-0.56	–	-0.28	-0.29	-0.47	-0.30	-0.42
LEP	0.77*	0.46	0.77*	-0.28	–	0.82*	0.56	0.73	0.72
PSO	0.49	0.41	0.49	-0.29	0.82*	–	0.70	0.51	0.58
THY	0.56	0.82*	0.56	-0.47	0.56	0.70	–	0.59	0.73
SOR	0.85*	0.71	0.85*	-0.30	0.73	0.51	0.59	–	0.93**
REM	0.86*	0.63	0.93**	-0.42	0.72	0.58	0.73	0.93**	–

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

Table 3
Spearman correlation coefficients and their significance values among arthropod trophic groups for alpha diversity (upper right triangle) and dissimilarity measure (lower left triangle). FUNG – fungivores, HERB – herbivores, PRED – predators, SAPR – saprophages, REM – remaining overall species richness excluding that of the focal group analysed.

	FUNG	HERB	PRED	SAPR	REM
(a) Transect scale (n = 109)					
FUNG	–	0.16	0.21*	0.30**	0.26**
HERB	0.25**	–	0.50***	0.59***	0.62***
PRED	0.33***	0.79***	–	0.43***	0.55***
SAPR	0.35***	0.78***	0.74***	–	0.61***
REM	0.33***	0.83***	0.82***	0.81***	–
(b) Fragment scale (n = 18)					
FUNG	–	0.27	0.39	0.36	0.33
HERB	0.53*	–	0.81***	0.79***	0.86***
PRED	0.49*	0.86***	–	0.72***	0.82***
SAPR	0.63**	0.89***	0.90***	–	0.80***
REM	0.57*	0.92***	0.89***	0.96***	–
(c) Island scale (n = 7)					
FUNG	–	0.45	0.29	0.83*	0.45
HERB	0.45	–	0.96***	0.65	0.96***
PRED	0.29	0.96***	–	0.51	0.61
SAPR	0.83*	0.65	0.51	–	0.65
REM	0.45	0.96***	0.61	0.65	–

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

Table 4
Spearman correlation coefficients and their significance values among arthropod colonization groups for alpha diversity (upper right triangle) and dissimilarity measure (lower left triangle). END – endemic, INT – introduced, NAT – native, REM – remaining overall species richness excluding that of the focal group analysed.

	END	INT	NAT	REM
(a) Transect scale (n = 109)				
END	–	0.37***	0.27**	0.35***
INT	0.74***	–	0.56***	0.57***
NAT	0.77***	0.79***	–	0.45***
REM	0.79***	0.81***	0.83***	–
(b) Fragment scale (n = 18)				
END	–	0.61**	0.46	0.57*
INT	0.77***	–	0.81***	0.85***
NAT	0.78***	0.96***	–	0.68**
REM	0.78***	0.93***	0.94***	–
(c) Island scale (n = 7)				
END	–	0.86*	0.75	0.82*
INT	0.86*	–	0.68	0.79*
NAT	0.75	0.68	–	0.77*
REM	0.82*	0.79*	0.77*	–

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

2–4). In fact, for each category, few pairs of groups showed consistency in their performance as surrogates across the three spatial scales. For alpha diversity, only the groups Araneae-Hemiptera, Araneae-Lepidoptera, Hemiptera-small orders, endemic-introduced and herbivores-predators showed consistency across scales (Tables 2–4). For the dissimilarity measure, a few other groups were also consistent across spatial scales: Araneae-small orders, Coleoptera-Thysanoptera, Hemiptera-Lepidoptera, Lepidoptera-Psocoptera and fungivores-saprophages (Tables 2–4). Araneae

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Table 5
Number of significant correlations of each group (compared with the remaining groups of each category) that are consistent at one, two or three spatial scales, for alpha and dissimilarity measures. *n* is the number of comparisons possible within each category for the three spatial scales.

	Alpha				*d*			
	1	2	3	Total	1	2	3	Total
n = 24								
Araneae	3	–	3	12	1	3	3	16
Coleoptera	3	2	–	7	1	6	1	16
Hemiptera	3	1	3	14	1	3	4	19
Julida	4	–	–	4	5	1	–	7
Lepidoptera	1	3	1	10	2	4	2	16
Psocoptera	4	3	–	10	3	4	1	14
Thysanoptera	4	2	–	8	1	5	1	14
Small orders	5	1	2	13	3	2	3	16
n = 12								
Fungivores	2	1	–	4	–	3	1	9
Herbivores	–	1	2	8	–	2	2	10
Predators	1	2	1	8	–	3	1	9
Saprophages	–	4	–	8	–	3	1	9
n = 9								
Endemic	1	–	2	7	–	1	2	8
Introduced	–	1	2	8	–	1	2	8
Native	1	1	1	6	–	2	1	7

and Lepidoptera were significantly correlated for alpha but were not correlated for dissimilarity. The orders Coleoptera, Julida, Psocoptera and Thysanoptera for alpha diversity, and Julida for dissimilarity, did not significantly correlate for all scales with any of the other groups (Table 2).

Despite no consistency across scales for a group in relation to all the other subsets independently, some groups still showed consistency across spatial scales and diversity measures with the remaining diversity combined: Araneae, Hemiptera (Fig. 1), small orders; herbivores (Fig. 2); introduced, native (Fig. 3) and endemic.

Hemiptera showed higher correlation coefficients and significance values than Araneae at all scales both for alpha and for dissimilarity (Table 2). Hemiptera was also equally or better correlated and with higher significance values than small orders for all scales and diversity measures except for alpha at the fragment level (Table 2).

For the trophic groups studied, only herbivores showed a significant relationship with the remaining diversity across scales, both for alpha and dissimilarity, with an increasing correlation coefficient the greater the hierarchical level (Table 3). Predators, saprophages and fungivores had increasing, though not always significant, values of correlation from transect to fragment level, but at island scale the coefficients were lower and never significant (Table 3).

Alpha and dissimilarity diversities from the three colonization groups studied were correlated with remaining diversity (Table 4). For both transect and fragment scales, introduced species had higher association values for alpha diversity than native or endemic, while for dissimilarity, native species had higher correlations than the other groups. At island scale, endemics had higher coefficient values than introduced or native species (Table 4).

4. Discussion

Alpha and dissimilarity diversities gave different correlation results for 25% of the total number of pairs of arthropod groups analysed. Coleoptera and Araneae at the transect scale, for example, showed an association for dissimilarity but not for alpha diversity. That is, a transect contributing more to the Araneae species richness of the fragment also corresponded to a transect that contributed more to Coleoptera species richness of the fragment, but a transect rich in Araneae was not necessarily rich in Coleoptera. This may occur because Araneae species are well distributed across transects (also across fragments and islands) but Coleoptera have an unequal distribution across sites, shown by the low values of average dissimilarity for Araneae and the high values for Coleoptera at all scales. The dissimilarity diversity may be proportional for all transects but alpha for Coleoptera may be lower than for Araneae for one transect and higher for another. Similarly, this pattern was observed between other groups of arthropods. And the opposite pattern, in which alpha diversity is correlated but dissimilarity diversity is not, also occurred (for example, Araneae and Lepidoptera at fragment scale). Thus, what may seem to be a good surrogate using dissimilarity diversity (e.g., Araneae vs Coleoptera at transect and fragment scales) may not be adequate using alpha species richness. Inconsistent results were also found in other studies when comparing species richness and other measures to assess diversity surrogates (e.g., Bilton et al., 2006; Prendergast, 1997; Su et al., 2004). Several authors advised that species richness is highly variable across taxa and sites, and that other measures

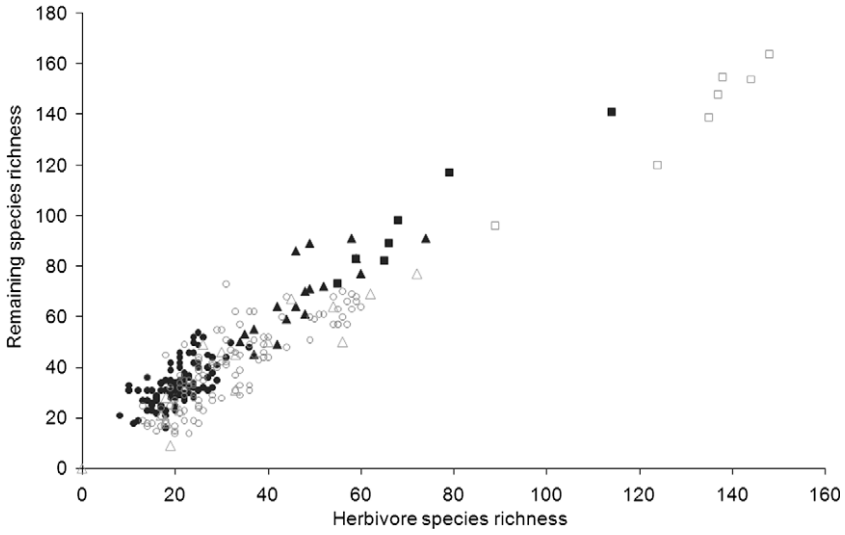

Fig. 2. Relationship between herbivore species richness and the species richness of the remaining groups for alpha (dark, closed symbols) and dissimilarity (grey, open symbols) at transect (circles), fragment (triangles) and island (squares) scales.

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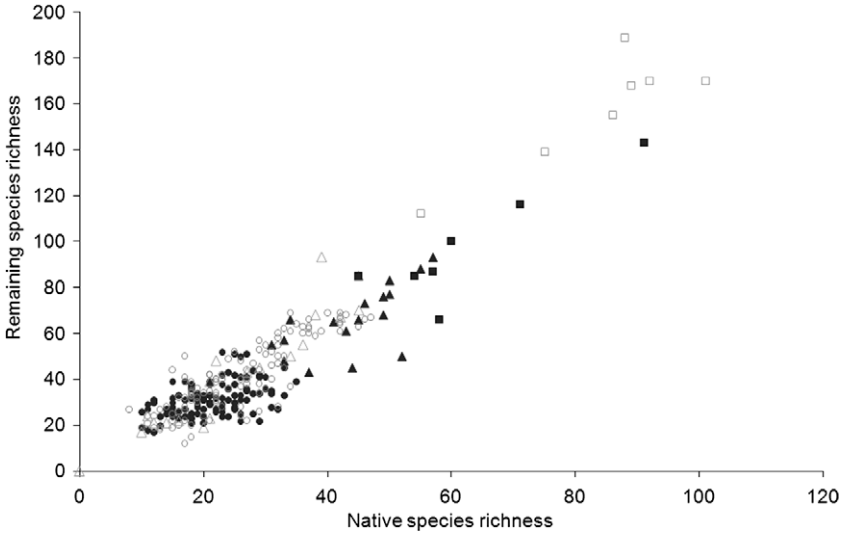

Fig. 3. Relationship between native species richness and the species richness of the remaining groups for alpha (dark, closed symbols) and dissimilarity (grey, open symbols) at transect (circles), fragment (triangles) and island (squares) scales.

taking species composition into account showed more consistent results across sites and should be preferred (e.g., Bilton et al., 2006; Prendergast, 1997). It is expected that different measures, by capturing different aspects of diversity, may give different outcomes in the assessment of the surrogacy value of a group (Reyers and van Jaarsveld, 2000), and Su et al. (2004) suggest choosing the more appropriate assessment technique in accordance with the approach adopted for conservation planning in that area. A complementary study made with the same arthropod database in native forests of the Azores (Gaspar et al., unpublished data) showed that beta diversity contributes greatly to the overall diversity at the three spatial scales analysed here, so the dissimilarity measure may be a relevant measure of diversity to include in a surrogate assessment plan and then to assess and monitor diversity in these areas.

Inconsistencies in correlation results were also observed across the spatial scales analysed. In general, the higher the hierarchical level, the smaller the number of groups associated and the lower the significance values. The results of this study were in accordance with the predictions of Favreau et al. (2006) regarding the confounding effect that spatial scale may have on the effectiveness of surrogates. Their discussion was based on the scale dependency of co-occurrence of species in which higher scales would usually show higher species co-occurrence and thus higher numbers of correlated groups. Conversely, in this study, higher spatial levels showed a smaller number of diversity surrogates. This may be explained by the fact that higher hierarchical levels reflect increasing accumulated dissimilarities in species richness among groups and scale units (Weaver, 1995). Some groups are well distributed across small scales and thus the next scale does not add many new species while others are very dissimilar across sites (Weaver, 1995). In addition, at higher scales, other factors may influence the species richness of each group differently (Chalcraft et al., 2004; Corney et al., 2004) and species may not be added at the same rate for all groups (Weaver, 1995). In a review of studies focusing on the relationship of species richness between different taxa, Wolters et al. (2006) noticed that invertebrates seem to have higher predictive values at smaller scales. Alongside the implications that different diversity measures may influence the selection of good surrogates, different spatial scales may also give inconsistent results in surrogacy. Therefore, it is also fundamental to define the scale that will be used for assessment and monitoring programs (Weber et al., 2004) and then to determine surrogate groups for that scale. For the Azorean Laurisilva, from a conservation planning perspective, since native forests are highly fragmented and remnants are distributed across islands, the fragment scale seems to be the only effective unit of management. The effectiveness of diversity surrogates in the selection of priority areas for conservation at the fragment scale in comparison with the overall arthropod diversity will be addressed and discussed elsewhere.

Despite the differences found in the surrogacy results across diversity measures and spatial scales, some arthropod groups showed a significant consistent association with the remaining arthropod diversity, across all spatial scales and measures of diversity used. The Araneae, Hemiptera and small orders taxonomic groups, the colonization groups introduced, native, and endemic, and the herbivorous trophic group were correlated with the remaining diversity. This may be related to the vacant niches occurring in the Azorean habitats, from transect to island level, where inter-specific competition is less evident (no significant negative correlations for species richness were found among groups), such that sites favourable for one group can also support other arthropod groups. In these islands, saturation does not seem to occur even at smaller scales. The non-saturation of habitats in the Azores archipelago has already been suggested in previous studies (Borges et al., 2006; Ribeiro et al., 2005). Another explanation that could be suggested for the consistent correlations of some groups with the remaining diversity is the similar response of the groups to an environmental gradient, but further studies are needed to evaluate this hypothesis. A previous study in one of the Azorean islands evaluating the effect of environmental variables on endemic and introduced species richness (Borges et al., 2006) showed that endemic species were mainly affected by climatic and geomorphological variables, whereas introduced species were mainly driven by habitat disturbance factors. And after accounting for all environmental variables, part of the unexplained variance in the species richness of one group was still explained by the species richness of the other group (Borges et al., 2006). For this study, the ubiquity of Araneae, Hemiptera and small orders, and the many functional roles (Araújo et al., 2004; Heino and Mykrä, 2006) occurring for Hemiptera and small orders may be some of the reasons that these taxonomic groups, and not others, represent the remaining diversity. The type of colonization of arthropods does not seem to influence the surrogacy effectiveness of a group, as the three

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colonization groups studied predict the remaining diversity. This implies that at all scales there is a positive relationship between indigenous (endemic and native) and non-indigenous species, a pattern that has also previously been observed for large scales on Terceira island (Borges et al., 2006).

The selection of a diversity surrogate group among several alternative options should take into account the ease of sampling and identifying the group as well as the ecological information that is to be predicted. Because identification knowledge is required only for a group of related taxa, taxonomic groups are commonly preferred; but trophic or colonization groups may be useful to predict the diversity of other groups providing specific ecological information (for example, endemic species as diversity surrogates of introduced species). In this study, consistent correlations across the two measures of diversity and the three spatial scales were only found for some groups in relation to the remaining diversity. In this case, in order to predict the remaining diversity, it would be easier to select as a diversity surrogate one of the taxonomic groups (Araneae, Hemiptera or small orders) rather than a trophic (herbivorous) or colonization (introduced, native, or endemic) group. Although the correlation coefficients for the small orders group were higher and the species richness was smaller than coefficients and richness of Araneae or Hemiptera, the small orders group includes 14 distinct orders, which requires more taxonomic knowledge as well as a wide variety of sampling methods to capture all of the diversity. Hemiptera (with higher coefficients and significance values and lower average alpha species richness than Araneae) and Araneae (with lower total species richness and greater ease of identifying specimens than Hemiptera) may be more promising surrogates of arthropod diversity for the Azorean native forests at transect, fragment and island scales and using alpha and dissimilarity diversity measures.

Further studies should be conducted in some native forests of the Azores to test the predictive ability of other animal and plant groups in relation to arthropods and the overall diversity and the benefit in considering a combination of groups to predict the remaining diversity (multi-taxa approach, Wolters et al., 2006). Efforts should also be made to improve the knowledge of hyper-diverse orders of arthropods such as Hymenoptera and Diptera (see Borges et al., 2005). The effectiveness of arthropod surrogates at different time scales (months, years) should also be assessed as recommended by Favreau et al. (2006).

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