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The effects of land-use change on arthropod richness and abundance on Santa Maria Island (Azores): unmanaged plantations favour endemic beetles

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Abstract We study how endemic, native and introduced arthropod species richness, abundance, diversity and community composition vary between four different habitat types (native forest, exotic forest of *Cryptomeria japonica*, semi-natural pasture and intensive pasture) and how arthropod richness and abundance change with increasing distance from the native forest in adjacent habitat types in Santa Maria Island, the Azores. Arthropods were sampled in four 150 m long transects in each habitat type. Arthropods were identified to species level and classified as Azorean endemic, single-island endemic (SIE), native, or introduced. The native forest had the highest values for species richness of Azorean endemics, SIEs and natives; and also had highest values of Azorean endemic diversity (Fisher's alpha). In contrast, the intensive pasture had the lowest values for

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S. S. Meijer World Agroforestry Centre, Nairobi, Kenya endemic and native species richness and diversity, but the highest values of total arthropod abundance and introduced species richness and diversity. Arthropod community composition was significantly different between the four habitat types. In the semi-natural pasture, the number of SIE species decreased with increasing distance from the native forest, and in the exotic forest the abundance of both Azorean endemics and SIEs decreased with increasing distance from the native forest. There is a gradient of decreasing arthropod richness and abundance from the native forest to the intensive pasture. Although this study demonstrates the important role of the native forest in arthropod conservation in the Azores, it also shows that unmanaged exotic forests have provided alternative habitat suitable for some native species of forest specialist arthropods, particularly saproxylic beetles.

Keywords Arthropods · Azores · Conservation biogeography · Endemic species · Landscape matrix · Land use

Introduction

Humans are altering natural landscapes at an accelerating rate (Vitousek et al. 1997; Ramankutty and Foley 1999; Foley et al. 2005). Large-scale transformation and clearing of land have put ecosystems and biodiversity at serious risk (Tilman et al. 2001). The loss of natural habitats has led many species to become at risk of extinction (Pimm et al. 1995; Brook et al. 2003; Hanski et al. 2007) and some have claimed that habitat loss is causing a mass extinction of species (e.g. Myers 1992; Wilson 1992). Due to the timelag between habitat loss and extinction (Janzen 1986; Heywood et al. 1994), it is expected that many more species will go extinct in the future as a result of land conversion that has already taken place (Tilman et al. 1994; Brooks and Balmford 1996; Brooks et al. 1997, 1999a, b, 2002; Cowlishaw 1999; Grelle et al. 2005; Helm et al. 2006; Triantis et al. 2010).

As natural habitats get increasingly fragmented by human activities, it is important to understand the effects of this fragmentation on the distribution and survival of species in order to inform conservation strategies. The importance of protected areas in the conservation of biodiversity has been generally accepted (Margules and Pressey 2000; Bruner et al. 2001). This has been supported by classical ecological theories such as the theory of island biogeography (MacArthur and Wilson 1963, 1967) and metapopulation dynamics (Hanski 1998). However, these theories tend to view natural habitat patches as islands in a sea of uninhabitable matrix, which may be an unnecessarily pessimistic assumption in many cases (Bhagwat et al. 2008). As a result, the conservation of species has focussed mainly on the establishment of protected areas and the landscape outside of reserves has often been overlooked (Ricketts 2001; Whittaker and Fernández-Palacios 2007; Wiens 2007; Bhagwat et al. 2008).

Since further expansion of the existing network of protected areas might be constrained by competing claims for other land uses (Bhagwat et al. 2008) and their effectiveness in representing species diversity has been questioned (Rodrigues et al. 2004; Chape et al. 2005), it is important to start understanding which habitats besides natural vegetation can support viable populations of species. Various recent studies have examined the role of the landscape surrounding reserves and have indicated the importance of high quality matrix environments in supporting biodiversity (Gascon et al. 1999; Ricketts 2001; Vandermeer and Carvajal 2001; Hughes et al. 2002; Perfecto and Vandermeer 2002; Sekercioglu et al. 2002; Watson et al. 2005; Bhagwat et al. 2008). This switch of attention away from fragments to the matrix has been referred to as 'countryside biogeography' (Daily et al. 2001, 2003) or 'reconciliation ecology' (Rosenzweig 2003).

The Azorean archipelago has undergone drastic changes in land use since the first settlers arrived 600 years ago. Originally, the islands were covered mostly by *Laurisilva* forests. However, these have been reduced to small fragments restricted to higher altitudes (Borges et al. 2005a, 2006). The islands are now mainly occupied by non-native habitats, such as intensive pastures for cattle, areas for agricultural crop production, forest patches of exotic plant species, and abandoned agricultural land and pastures covered with invasive plants (Martins 1993). Since further increasing the protected area network and the area of the native forest presents many practical challenges, it is important to understand how the changes in land use have affected the Azorean biodiversity, and which habitats outside the original native forest are able to support indigenous species.

This study investigates how changes in land use have affected endemic, native and introduced arthropod richness and abundance on Santa Maria Island in the Azores. Santa Maria is the oldest island of the Azores, dating back 8.12 Myr (Abdel-Monem et al. 1975), which has resulted in higher numbers of endemic and native species compared to the other islands (Borges and Brown 1999; Borges and Hortal 2009). Arthropods were sampled using pitfall traps in four different habitat types (native forest, exotic forest, semi-natural pasture and intensive pasture) and classified as endemic (including the endemics from the target studied island, i.e. single-island-endemics-SIE), native nonendemic, or introduced. Native non-endemic species ("native" for simplicity) arrived in the Azores naturally and occur outside of the Azores as well. Introduced species are species that have been brought to the Azores by human activities. Where there was doubt over the colonisation status of a species, it was classified as native. In this study the following hypotheses will be tested: (i) species richness, abundance and diversity are highest in the native forest and lowest in the intensive pasture for Azorean endemic and native species, (ii) they are highest in the intensive pasture and lowest in the native forest for introduced species; (iii) the community composition of arthropods is different between the four habitat types; and (iv) an increase in distance to the native forest will result in a decrease in endemic, SIE and native arthropod richness and abundance in the other habitat types.

Materials and methods

Study area

This study was conducted in the Azores, an archipelago of nine islands situated in the North Atlantic (Fig. 1a). The islands are situated near the Mid-Atlantic Ridge and can be divided into three groups extending for 615 km: the western group (Flores and Corvo), the central group (Faial, Pico, São Jorge, Graciosa and Terceira) and the eastern group (São Miguel and Santa Maria). They are volcanic islands of recent origin, the youngest island is Pico (300,000 years) and Santa Maria is the oldest island (8.12 Myr) (Abdel-Monem et al. 1975; Borges and Hortal 2009). Santa Maria covers an area of 97 km² and the highest point is Pico Alto, with an elevation of 587 m. The temperate oceanic climate is strongly influenced by the proximity of the ocean and is characterised by high levels of humidity and small temperature fluctuations throughout the year. The average temperature on Santa Maria ranges between Fig. 1 Map of the region, showing **a** the nine islands of the Azores. Adopted from Borges et al. (2009); and **b** the four habitat types on Santa Maria and the position of the 16 transects (Land-use data extracted from DROTRH 2008)



14.3 and 17.5°C, with lowest temperatures in February and highest temperatures in August (Borges and Brown 1999). The average rainfall differs between the dry western part (752 mm year⁻¹) and wet eastern part (1,386 mm year⁻¹). January and February are generally the wettest months and August the driest (Borges and Brown 1999).

The original natural vegetation of the island is *Laurisilva* forest, a sub-tropical evergreen broadleaf laurel type forest, which now only covers a small part of the island (Fig. 1b). The small fragment of *Laurisilva* forest on Santa Maria covers about 9 ha (Gaspar et al. 2008) and the overstorey consists of the broadleaf species *Laurus azorica* and *Picconia azorica*, the short-leaf species *Erica azorica*, and the shrub *Vaccinium cylindraceum*, all of them Azorean endemics. In addition, this small fragment is now being invaded by the exotic invasive plants *Pittosporum*

undulatum and Hedychium gardneranum, which have both become abundant. The Laurisilva forests have been reduced since humans arrived on the islands in the fifteenth century. The rate of land conversion increased significantly after the Second World War, when the Government reforested parts of the islands with Cryptomeria japonica plantations and reinforced the development of cattleraising and great amounts of land were converted into pastures (Martins 1993). The vegetation on Santa Maria is now dominated by exotic forest (Cryptomeria japonica, Eucalyptus spp., Acacia spp. and Pittosporum undulatum), semi-natural pasture (not stocked year-round and with relatively low levels of fertilisation and introduced grass species) and intensive pasture (stocked year-round and with high levels of fertilisation and introduced grass and legume species).

Site selection

On the island of Santa Maria, four sites were selected in each of the four main habitat types: native forest, exotic forest (*Cryptomeria japonica* plantations), semi-natural pasture and intensive pasture, resulting in a total of 16 sites (Fig. 1b). The sites were selected so as to try and sample most of the island. However, the native forest is restricted to higher elevations in the central area of the island and reduced to a 9 ha fragment, whereas the intensive pastures tend to be located at lower elevations closer to the sea. The sites in the native forest of Pico Alto were sampled in August 1997 and June 2004 (Borges et al. 2005a; Gaspar et al. 2008), and data were collected in the other three habitat types in June 2009 (Appendix 1).

Arthropod sampling

For the arthropod sampling the protocol followed since 1998 by Project BALA (see Borges et al. 2000, 2005a, Gaspar et al. 2008) was applied. At each site, 30 pitfall traps were used to capture arthropods along a transect of 150 m length. The pitfall traps were plastic cups with a top diameter of 42 mm and 78 mm deep. The traps were dug into the soil so that the rim of the cup was at the same level as the soil surface. Half of the traps were filled with 60 ml of an attractive solution (Turquin) and the other half with 60 ml of anti-freeze liquid with a small proportion of ethylene glycol. A few drops of liquid detergent were added to both solutions to reduce surface tension. A white plastic plate was placed 5 cm above the traps with two pieces of wire to protect the trap from rainfall. The traps were placed 5 m apart, starting the transect with a Turquin trap and alternating with ethylene traps. The traps were left in the field for 2 weeks and then the samples were taken to the laboratory. The specimens were sorted into morphospecies by para-taxonomists and then into species by a senior taxonomist (P. A. V. Borges). Due to non-availability of taxonomic expertise, Acari, Collembola, Hymenoptera and Diptera were excluded from this study. Based on expert opinions, the species were classified into three colonisation groups (see also Borges et al. 2005a): endemic (including the single-island endemics, or SIE), native (i.e. native but non-endemic species) and introduced species.

Data analysis

To test the first hypothesis, species richness, abundance, dominance and diversity were compared between the four habitat types (native forest, exotic forest, semi-natural pasture and intensive pasture) for Azorean endemic, native, introduced and total species. Due to the low replication of transects (n = 4) within each habitat type, tests of normality

could not be performed and the data were analysed using non-parametric Kruskal-Wallis tests in PASW Statistics 17. In transect T07 in the semi-natural pasture, 10 pitfall traps were lost as a result of trampling by cows, and therefore the abundance numbers in each transect were converted to average abundances by dividing the total abundance in the transect by the number of pitfall traps in that transect (20 traps for T07 and 30 for all other transects). It was assumed that the 20 pitfall traps in T07 were enough to give a representative number for species richness, diversity and dominance. The Berger-Parker Index was used as a measure of dominance and Fisher's Alpha as an indicator of diversity. The total number of species expected in each habitat type was calculated using a first-order Jack-knife estimator, selected because it is considered generally robust and insensitive to scale effects (see Hortal et al. 2006). For each habitat type, the observed number of species was divided by the expected number of species to obtain a completeness index. A value above 0.75 is generally accepted as representing a complete sampling effort (see also Borges and Brown 2003). Richness and abundance data for SIEs were also analysed with Kruskal-Wallis tests. SIEs are important species for conservation purposes since they are, by definition, restricted to Santa Maria Island.

Differences in species composition between the habitat types were compared with an analysis of similarities (ANOSIM) for Azorean endemic, native, introduced and total species composition to test the second hypothesis (Clarke 1993). The R statistic value ranges between 1 and -1and indicates the degree of difference between the groups, with a value of 1 signifying completely distinct communities. Detrended correspondence analyses (DCA) were carried out to illustrate the difference in species composition between the four habitat types for each group of Azorean endemic, native, introduced and total species (Oksanen and Minchin 1997). A DCA was used to remove the arch effect that was observed when using a correspondence analysis (analysis not shown). The number of axis rescalings was four and rare species were not down-weighted. The ANO-SIM and DCA were carried out in Community Analysis Package 4.0 (Henderson and Seaby 2007).

To assess the fourth hypothesis, that the increasing distance from the native forest results in a decrease in the richness and abundance of arthropod species in the adjacent habitat types, the distance to the native forest for each transect was correlated with the number of species and the number of individuals for Azorean endemic, SIE, native, introduced, and total species. The distance of each transect to the native forest was calculated using Google Maps. The intensive pastures were excluded from this analysis as they were not surrounding the native forest and were located at lower elevations. The data for the exotic forest and seminatural pasture were analysed together (eight sites) as well as separately (two groups of four sites). Non-parametric Spearman rank correlation (available in PASW Statistics 17) was used as the sample size was again too low to test for normality.

Results

In this study, a total of 12,513 arthropod specimens were identified to species level in the four habitat types on Santa Maria (see Appendix 2). These specimens belonged to 188 different species, of which 25 were considered endemic to the Azores (including 9 SIEs), 58 were native to the archipelago (excluding the endemics) and 105 were introduced species.

The species accumulation curves for each habitat type are starting to level off, with the intensive pastures closest to asymptote (Fig. 2a). This indicates that most of the species that occur in this habitat type have been sampled in this study, while a small number remain to be recorded in the other habitats. The same pattern can be observed for the completeness index of each habitat type, which was over or almost at the 0.75 level, indicating that about enough species were sampled to get a representative assessment of the composition and relative richness of each habitat (Appendix 3).

Species richness, abundance and diversity

Total species richness and abundance were significantly different between the four habitat types on Santa Maria (Kruskal–Wallis test, H = 8.032, P = 0.045 for species richness; H = 8.316, P = 0.040 for species abundance, Table 1). Species richness differed significantly between the four habitat types for Azorean endemics, native and introduced species (Kruskal–Wallis test, H = 12.555, P = 0.006; H = 10.296, P = 0.016; H = 12.192, P = 0.007, respectively). As hypothesised, Azorean endemic and native



Fig. 2 Species accumulation curves, showing **a** curves for the total number of species (1,000 randomisations) for each transect (each containing 30 pitfall traps) per habitat type (each containing 4 transects); **b** curves for the total number of species (1,000

randomisations) for each habitat type (each containing 4 transects with 30 pitfall traps) and **c** curves for the number of indigenous species (excluding the introduced species) (1,000 randomisations) for each habitat type (each containing 4 transects with 30 pitfall traps)

140

		Native forest	Exotic forest	Semi-natural pasture	Intensive pasture	Н	df	Р
Richness	Azorean endemic	10.0 (0.7)	5.3 (0.8)	4.0 (0.7)	1.5 (0.5)	12.555	3	0.006
	Native	15.8 (0.9)	14.0 (1.1)	13.3 (1.1)	7.5 (0.7)	10.296	3	0.016
	Introduced	14.8 (1.4)	15.5 (1.4)	28.3 (2.6)	35.8 (1.7)	12.192	3	0.007
	Total	40.5 (1.4)	34.8 (1.9)	45.5 (3.9)	44.8 (1.3)	8.032	3	0.045
Abundance	Azorean endemic	73.5 (25.0)	56.5 (34.6)	117.3 (52.1)	223.0 (111.0)	2.713	3	0.438
	Native	78.5 (8.3)	190.8 (48.5)	214.8 (71.1)	233.3 (154.4)	5.352	3	0.148
	Introduced	245.3 (64.8)	429.8 (117.0)	503.8 (141.6)	762.0 (135.1)	5.846	3	0.119
	Total	397.3 (82.7)	677.0 (124.3)	835.8 (171.6)	1218.3 (228.5)	8.316	3	0.040
Dominance	Azorean endemic	2.6 (0.3)	1.8 (0.4)	1.2 (0.1)	0.8 (0.3)	10.579	3	0.014
	Native	3.7 (0.1)	1.6 (0.3)	2.4 (0.5)	2.0 (0.7)	6.066	3	0.108
	Introduced	2.5 (0.1)	2.1 (0.3)	3.4 (0.7)	3.4 (0.9)	4.787	3	0.188
	Total	4.1 (0.2)	3.2 (0.8)	4.6 (0.5)	3.8 (0.9)	3.375	3	0.337
Diversity	Azorean endemic	3.6 (0.4)	2.2 (0.7)	0.9 (0.1)	0.3 (0.03)	10.975	3	0.012
	Native	6.1 (0.8)	3.7 (0.5)	3.8 (0.9)	2.0 (0.3)	11.184	3	0.011
	Introduced	3.5 (0.3)	3.2 (0.1)	6.7 (0.6)	8.0 (0.8)	12.044	3	0.007
	Total	11.7 (0.8)	8.0 (0.5)	10.5 (0.6)	9.7 (1.2)	7.013	3	0.071

Table 1 Mean $(\pm 1 \text{ SE})$ richness (number of species), abundance (number of individuals), dominance (1/Berger-Parker Index) and diversity (Fisher's alpha) values for Azorean endemic, native

(excluding endemics), introduced and total species for the four habitat types and results of the Kruskal-Wallis tests

In each habitat type, four 150 m long transects containing 30 pitfall traps were sampled

Probabilities in bold are significant at P < 0.05

species richness were both highest in the forest habitats (native and exotic forest) and lowest in the semi-natural and intensive pasture, while the number of introduced species was lowest in the native forest and highest in the intensive pasture (Fig. 3). Total species abundance was highest in the intensive pasture and lowest in the native forest. The same trend was apparent when the species were separated into Azorean endemic, native and introduced species (Fig. 3), although these differences were not significant.

Interestingly, when the species accumulation curves are plotted with all the species as one curve for each habitat type (Fig. 2b), the curve for the native forest comes out below that of the two pasture types. However, when the same curves are plotted for just the indigenous species (so excluding the exotic species) the native and exotic forest come out above the curves for the pastures (Fig. 2c). This indicates that the greater richness of the pasture sites is due to the non-natives and the curve levels when they are excluded.

Species dominance was significantly different between the four habitat types for Azorean endemic species (Kruskal–Wallis test, H = 10.579, P = 0.014), with the intensive pastures being most dominated by a few species and the native forest having the least dominance (Table 1). Species diversity was not significantly different between the four habitat types for total species richness (Kruskal– Wallis test, H = 7.013, P = 0.071), but did differ significantly for Azorean endemic, native and introduced species (Kruskal–Wallis test; H = 10.975, P = 0.012 for Azorean endemic species, H = 11.184, P = 0.011 for native species; and H = 12.044, P = 0.007 for introduced species). The native forest had the highest value of Fisher's alpha for Azorean endemic and native species, and the lowest for the intensive pasture. In contrast, introduced species diversity was highest in the intensive pasture, and lower in the forest habitats (Table 1).

Single-island endemics

Of the 25 Azorean endemic species found in this study on Santa Maria, nine species are single-island endemics (SIEs), i.e. only found on Santa Maria (Table 2). The number of SIEs differed between the four habitat types (Kruskal–Wallis test; H = 11.465, P = 0.009), with the highest number found in the native forest and none in the intensive pasture (Fig. 3). The abundance of the singe-island endemics was also significantly different between the four habitat types (Kruskal–Wallis test; H = 11.921, P = 0.008). The average abundance was highest in the native forest (Fig. 3), however, the highest abundance at transect level was recorded in one of the exotic forest transects, in which 145 individuals of the beetle *Tarphius pomboi* were found.

Species composition

In accordance with the third hypothesis, the total species composition of the arthropod communities was statistically different between the four habitat types (ANOSIM; Fig. 3 Mean $(\pm 1 \text{ SE})$ number of arthropod species and number of arthropod individuals per transect (four transects per habitat, each transect containing 30 pitfall traps) for Azorean endemic, native (excluding endemics), introduced and single-island endemic species found in the four habitat types



 Table 2
 The number of single-island endemic species and the percentage single-island endemics out of the total number of Azorean endemic species in the four habitat types on Santa Maria

	Native forest	Exotic forest	Semi-natural pasture	Intensive pasture	Total
Azorean endemics	17	13	8	3	25
Singe-island endemics	7	5	4	0	9
%	41.2	38.5	50.0	0.0	36.0

In each habitat type, four 150 m long transects containing 30 pitfall traps were sampled

R = 0.787, P = 0.001). The arthropod community in native forest has a larger proportion of Azorean endemic and native species compared to the other habitat types, whereas the semi-natural and intensive pasture have relatively more introduced species (Table 3). In addition, the

species composition was also different between the four habitat types for the three species groups (ANOSIM; R = 0.823, P = 0.001 for Azorean endemic species; R = 0.597, P = 0.001 for native species; and R = 0.602, P = 0.001 for introduced species), suggesting that the four habitat types have different Azorean endemic, native and introduced species. All pairwise comparisons were significant as well, except for Azorean endemic species composition in natural forest vs. exotic forest (ANOSIM; R = 0.146, P = 0.157) and for introduced species composition in exotic forest vs. semi-natural pasture (ANO-SIM; R = 0.302, P = 0.1).

The differences in species composition between the four habitat types were further supported by the detrended correspondence analysis (DCA). The ordination of the sites is a product of the distribution of species across the sites and the first two axes represent the two most prominent compositional gradients inherent to the data (Fig. 4). For **Fig. 4** Sites ordination plots by DCA for **a** endemic, **b** native and **c** introduced species composition. In each habitat type, four 150 m long transects containing 30 pitfall traps were sampled. *NF* native forest, *EF* exotic forest, *SNP* seminatural pasture, *IP* intensive pasture



the Azorean endemic species, the habitat types were clearly clustered and each habitat type formed a separate group. For native and introduced species composition there was more overlap between the four habitat types, suggesting that these species are more uniformly spread. The first axis of the ordination separates the forests from the pastures for Azorean endemic, native and introduced species (eigenvalues axis 1: 0.965; 0.972 and 0.741, respectively). The second axis separates the native forest from the exotic forest (eigenvalues axis 2: 0.277 for Azorean endemic species; 0.519 for native species and 0.245 for introduced species, Fig. 4).

	Azorean endemic			Native	Native				Introduced			
	NF	EF	SNP	IP	NF	EF	SNP	IP	NF	EF	SNP	IP
Total	17	13	8	3	28	27	22	18	32	28	49	67
Unique	9	4	1	1	9	1	3	5	6	1	7	28
% Unique	52.9	30.8	12.5	33.3	32.1	3.7	13.6	27.8	18.8	3.6	14.3	41.8

Table 3 The total number of Azorean endemic, native (excluding endemics) and introduced species in the four habitat types and the number and percentage of species that are unique to each habitat type

In each habitat type, four 150 m long transects containing 30 pitfall traps were sampled

NF native forest, EF exotic forest, SNP semi-natural pasture, IP intensive pasture

Species uniqueness

From the 17 Azorean endemic species that are found in the native forest, nine species occur exclusively in the native forest and in none of the other habitat types (Table 3). This means that for at least 50% of the Azorean endemic species on Santa Maria, the native forest is the only place where they occur. The exotic forest has four out of 13 Azorean endemic species that are unique to this habitat type, whereas in the semi-natural pasture only one out of 8 Azorean endemics is restricted to this habitat type. There are three Azorean endemic species that occur on the intensive pasture, of which one is unique to this type of habitat.

For the native species, nine out of 28 species found in the native forest were not found outside of this habitat type, which represents about one-third of the native species found in the native forest (Table 3). In the exotic forest, just one out of 27 native species seems to occur solely in this habitat type, whereas the semi-natural pasture has three out of 22 native species that are unique. Surprisingly, the intensive pasture is home to five native species that occur exclusively in this habitat type, which is more than one-fourth of the total of 22 native species found in the intensive pastures.

For the introduced species, there is an opposite trend (Table 3). The native forest has only six introduced species restricted to this habitat type out of a total of 32. In the exotic forest there is only one introduced species that does not occur in any of the other habitat types. The semi-natural pasture has seven out of 49 species that only occur in

this habitat type. The intensive pasture has the highest proportion of unique introduced species, with 28 out of 67 species (40%) only occurring in this habitat type.

Distance from the native forest

There was no significant correlation between the distance from the native forest and species richness and abundance when the exotic forest and semi-natural pasture were grouped together. However, when these two habitat types were analysed separately, there were some significant correlations that support the third hypothesis. In the seminatural pasture, the number of SIE species decreased with increasing distance from the native forest (Spearman correlation; r = -1, P < 0.01; Fig. 5a). For the exotic forest, the abundance of both Azorean endemics and SIEs decreased with increasing distance from the native forest (Spearman correlation; r = -1, P < 0.01, Fig. 5b).

Discussion

Our findings support the proposition that land use change has significantly affected arthropod species richness and abundance on Santa Maria. As hypothesised, the numbers of Azorean endemic and native species were highest in the native forest and they were lowest in the highly modified intensive pasture. In addition, the intensive pastures had the

Fig. 5 Relationship between distance to the native forest and a number of SIE species in the semi-natural pasture and b abundance of endemic and SIE species in the exotic forest. In each habitat type, four 150 m long transects containing 30 pitfall traps were sampled



highest introduced species richness and abundance. Following some recent work confirming the relevance of native forests for the conservation of Azorean endemic arthropod biodiversity (e.g. Borges et al. 2005a, 2006, 2008; Ribeiro et al. 2005; Gaspar et al. 2008; Cardoso et al. 2009), our findings reinforce the important role of the native forest in arthropod conservation on the Azores, with 7 out of 9 sampled SIEs being found in the native forest and 50% of the sampled Azorean endemic species being confined to this habitat type. There seems to be a gradient of land-use change effects on arthropods, where an increase in land-use intensity results in more negative impact on the indigenous (i.e. endemic and/or native) arthropod community. These results are in agreement with other studies in the Azores (Borges and Wunderlich 2008; Borges et al. 2008; Cardoso et al. 2009) and elsewhere (Driscoll 2005; Schweiger et al. 2005; Jana et al. 2006; Rainio and Niemelä 2006; Acevedo and Restrepo 2008; Schmidt et al. 2008), that have demonstrated negative effects of such land-use change for several taxa.

Although not as good habitat as the native forest, the exotic forest and semi-natural pasture performed better than the intensive pasture, which is in accordance with results obtained for Terceira Island (Cardoso et al. 2009). These two habitat types harboured higher numbers of Azorean endemics and native species and had a community composition more similar to the native forest compared to the intensive pasture. Similarly, other studies have found that habitat types other than pristine forest, such as agricultural fields and secondary forest can support certain species and help to maintain biodiversity (Burel et al. 1998; Toth and Kiss 1999; Grill et al. 2005). Our results support the notion that the quality of the matrix is important in species conservation, as suggested by several other studies (Ricketts 2001; Vandermeer and Carvajal 2001; Perfecto and Vandermeer 2002; Watson et al. 2005; Prugh et al. 2008; Muriel and Kattan 2009).

The community composition of the arthropods differed between the four habitat types, with higher proportions of Azorean endemics in the forest habitats and more introduced species in the pastures. This is in agreement with the third hypothesis. When clustering the four habitat types according to species composition for each colonisation group, the clustering was most clear for the Azorean endemic species, suggesting that the habitat types harboured different endemic species. The overlap in species composition was most obvious for introduced species, which indicates that introduced species are able to occupy several habitat types on the island and spread easily. In doing so, introduced species form one of the major threats to terrestrial biodiversity in the Azores (Martins 1993; Borges et al. 2006, 2008, 2009).

Interestingly, the total abundance of Azorean endemic species was highest on the intensive pastures and not in the

native forest, which is not in accord with the first hypothesis. However, this was almost entirely the consequence of the great abundance of one beetle species, Heteroderes azoricus, of which 868 individual specimens were collected in the intensive pastures. Of the eight Azorean endemic species occurring in the semi-natural pasture, the spider Pardosa acorensis was also highly abundant, a pattern found in most of the Azorean islands (see also Borges and Wunderlich 2008; Cardoso et al. 2009). The number of Azorean endemic species inhabiting the pastures is low, yet these two generalist species are able to maintain populations with higher abundances than most endemic species in the native forest. The same pattern was found in a recent study on Terceira Island in the Azores (Cardoso et al. 2009), where these two species were found in high numbers in the pastures as well. Similar to our findings, Azorean endemic and native species richness on Terceira were also highest in the native forest and the intensive pasture had the highest number of introduced species. Cardoso et al. (2009) conclude that these two habitat types are the main drivers of the species composition of a particular site, with semi-natural pastures and exotic forests functioning as 'connector habitats' between natural forests. However, in the case of Santa Maria, exotic Cryptomeria japonica plantations seem to have a quite different role, accumulating a high density of endemic saproxylic beetles (see also below).

In addition to the endemic abundant and widespread Heteroderes azoricus and Pardosa acorensis, other endemic species are particularly important in Santa Maria, notably the nine SIE species exclusive to Santa Maria. The semi-natural pastures harboured four SIEs (Tarphius pomboi, Tarphius rufonodulosus, Catops velhocabrali, Olisthopus inclavatus), three of which are saproxylic beetle species. The exotic forest is home to five SIE saproxylic beetle species (Tarphius serranoi, Tarphius pomboi, Tarphius rufonodulosus, Catops velhocabrali, Caulotrupis parvus), of which the species Tarphius pomboi was particularly abundant. This might be explained by the fact that this species feeds on wood-inhabiting fungi and is able to benefit from the decaying wood found in the exotic forest in Santa Maria, as has been shown for other saproxylic beetle species in northern Europe (Okland et al. 1996; Kaila et al. 1997; Martikainen et al. 2000; Jonsson et al. 2005).

The fact that so many SIE forest-specialist beetles are found in both exotic forest and semi-natural pasture sites surrounding the native forest fragment of Santa Maria is a novel finding in the Azores. Patterns of endemic species distribution in other Azorean islands are not so positive, with most of the endemic species being restricted to native forest or having only sink populations in nearby human modified habitats (see Borges et al. 2008). The management practices in Santa Maria in both exotic Cryptomeria japonica plantations and semi-natural pastures are obviously different compared to similar habitats on the other islands. In fact, particularly in C. japonica plantations, the management is less intensive or even almost absent, leading to a more diverse vegetation and high density of dead wood favourable for many dead-wood and fungi-eating endemic saproxylic beetles. The C. japonica plantations surrounding the Pico Alto native forest fragment were planted in the 1960s to catch water from the fog and improve water collection for human use. Consequently, the past and current management of these human-modified exotic forests has a positive effect on the diversity of endemic arthropods on Santa Maria. Despite the fact that Santa Maria has only 0.2% of the total area of native forest in the Azores (Gaspar et al. 2008), it is home to 57 endemic arthropod species (ATLANTIS database consulted in July 2009), which makes up 20% of the total number of Azorean endemic arthropod species. As such, Santa Maria can be considered as a 'hotspot' among the Azorean islands (see also Borges and Brown 1999; Borges et al. 2005a, b; Borges and Hortal 2009).

In accordance with the fourth hypothesis, our results showed also that with increasing distance from the native forest, the abundance of both Azorean endemics and SIEs decreased in the exotic forest and the number of SIE species decreased in the semi-natural pasture. Similar patterns of decreasing species numbers with increasing distance from natural forest have been found elsewhere (e.g. Klein et al. 2006). This suggests that the favorability of these two habitats is not general within the island, since their ability to support arthropods important to conservation depends on where they are located relative to the native forest. In addition, it is not clear what will be the long-term management of the C. japonica plantations surrounding the Pico Alto native forest fragment, casting some doubts on the successful conservation of saproxylic invertebrates on this island.

This study has some important implications for conservation management activities on Santa Maria. We clearly demonstrated the importance and uniqueness of the native forest for arthropod conservation and recommend that efforts should be made to protect the small patches of native forest that are left on the island. This small area of native forest is critical for the conservation of both archipelagic and single-island endemic species (Borges et al. 2005a). This study clearly showed that the exotic forest and semi-natural pasture are better habitats for these arthropods than the intensive pastures (see also Borges et al. 2008; Cardoso et al. 2009). Our results indicate that it would be better to replace disappearing native forest or abandoned fields with less intensively managed habitats such as exotic forest and semi-natural pasture, rather than intensive

pastures (see also Cardoso et al. 2009), although conservation of the original habitats is of course by far the best option.

The species accumulation curves suggest that not all arthropod species that occur in the different habitat types have been sampled in this study, and this is particularly true for the native forest for which the accumulation curve is only just about to start levelling off. The latter is probably due to the fact that a lower number of individuals was captured in the native forest, but this should not be considered a bias. The fact that not all arthropod species have been sampled is not a problem for this study, as the aim was not to obtain a complete list of species for Santa Maria, but to compare arthropod species richness and abundance between the different habitat types. This finding does suggest that further sampling is likely to find more species on Santa Maria, especially in the native forest. Moreover, it is important that the arthropods on the Azores are the subject of long-term studies, as the effects of native habitat that has been lost already might become pronounced in the future. Due to this so-called 'extinction debt' (Tilman et al. 1994), many more arthropods might be on the brink of extinction than current studies have shown (Triantis et al. 2010).

Implications for the conservation of S. Maria endemic arthropods

A regional strategy for the long-term persistence of SIEs from S. Maria is needed. We suggest: (i) it is important to monitor the abundance of SIEs in the different habitats over the following decades following the Long-Term Ecological Research (LTER) strategy (see e.g. Pereira and Cooper 2006); (ii) removal of *P. undulatum* and other plant invaders and its progressive replacement by native woody species; (iii) in addition, pastures and forest plantations surrounding the small area on native forest at Pico Alto should retain their current low-intensity management in such a way that they will be able to support species that will otherwise be driven to extinction in the long term.

This study demonstrates that the matrix quality in the form of less intensive agricultural management is important for the conservation of rare endemic saproxylic invertebrates in the Azores. The studied native forest fragment and part of the surrounding area is now a protected area named as Santa Maria Park using the IUCN Protected Areas Management Categories System (see Borges et al. 2005a). The Pico Alto area was classified as Category IV (protected area for the management of habitats and species), which implies some restrictions on human activities. Our results support the importance of maintaining the diverse matrix surrounding Pico Alto, to ensure the continuing availability of wood in several stages of decay, essential for saproxylic arthropods.

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Appendix 1

See Table 4.

sorting and identification of the arthropods. Enésima Mendonça is thanked for her help in preparing the map of Santa Maria, and Kostas Triantis for giving useful comments on the introduction. This study was supported by a Huygens Scholarship Programme (HSP) grant and a VSB Foundation grant to S. S. M. and financial support in the Azores was provided by project "Consequences of land-use change on Azorean fauna and flora—the 2010 Target" (Ref: Direcção Regional da Ciência e Tecnologia M.2.1.2/I/003/2008) to P. A. V. B.

Table 4 Information on all transects in the four habitat types on Santa Ma	iria
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Name	Transect	Sampled	Habitat	Longitude	Latitude	Elevation (m)
Pico Alto	T01	August 1997	Native forest	669927	4094384	530
Pico Alto	T02	August 1997	Native forest	669823	4094394	530
Pico Alto	T03	June 2004	Native forest	670257	4094043	479
Pico Alto	T04	June 2004	Native forest	670170	4094140	479
Aeroporto-Cabrestantes	T05	June 2009	Intensive pasture	662662	4096328	43
Pico do Facho	T06	June 2009	Intensive pasture	665588	4090185	52
Casas Velhas	T07	June 2009	Semi-natural pasture	671945	4091662	379
Fonte Jordão	T08	June 2009	Intensive pasture	673963	4090920	271
Pico Alto-L	T09	June 2009	Exotic forest	670185	4094194	464
Cruzamento Pico Alto	T10	June 2009	Exotic forest	670608	4093423	419
Pico Alto-PSN	T11	June 2009	Semi-natural pasture	670417	4093748	482
Fontinhas—PSN	T12	June 2009	Semi-natural pasture	671513	4092040	448
Fontinhas	T13	June 2009	Exotic forest	671308	4092293	419
St. Espírito	T14	June 2009	Exotic forest	673033	4091592	318
Ponta do Norte	T15	June 2009	Intensive pasture	672741	4096864	219
Alto da Nascente	T16	June 2009	Semi-natural pasture	669313	4095181	296

Long/Lat coordinates are presented in UTMs

Appendix 2

See Table 5.

N/E/I	Code MF	Species	Class	Order	Family	NF	EF	SNP	IP
Е	MF134	Gibbaranea occidentalis Wunderlich	Arachnida	Araneae	Araneidae	3		1	
Е	MF17	Pardosa acorensis Simon	Arachnida	Araneae	Lycosidae	4	1	410	23
Е	MF5	Rugathodes acoreensis Wunderlich	Arachnida	Araneae	Theridiidae		6		
Е	MF50	Lepthyphantes acoreensis Wunderlich	Arachnida	Araneae	Linyphiidae	6			
Е	MF526	Neon acoreensis Wunderlich	Arachnida	Araneae	Salticidae		1		
Ι	MF1014	Gen. sp.	Arachnida	Araneae	Salticidae				2
Ι	MF1047	Heliophanus kochi Simon	Arachnida	Araneae	Salticidae				4
Ι	MF1100	Zelotes tenuis (C.L. Koch)	Arachnida	Araneae	Gnaphosidae				3
Ι	MF1071	Chalcoscirtus infimus (Simon)	Arachnida	Araneae	Salticidae				5
Ι	MF1118	Micaria pallipes (Lucas)	Arachnida	Araneae	Gnaphosidae				10

Table 5 continued

N/E/I	Code MF	Species	Class	Order	Family	NF	EF	SNP	IP
I	MF122	Clubiona terrestris Westring	Arachnida	Araneae	Clubionidae	1		6	
Ι	MF127	Steatoda grossa (C.L. Koch)	Arachnida	Araneae	Theridiidae	1			
Ι	MF133	Metellina merianae (Scopoli)	Arachnida	Araneae	Tetragnathidae	3			
Ι	MF140	Ero furcata (Villers)	Arachnida	Araneae	Mimetidae	1	1		
Ι	MF21	Tenuiphantes tenuis (Blackwall)	Arachnida	Araneae	Linyphiidae	125	49	65	9
Ι	MF233	Oedothorax fuscus (Blackwall)	Arachnida	Araneae	Linyphiidae			378	664
I	MF234	Erigone autumnalis Emerton	Arachnida	Araneae	Linyphiidae			5	67
I	MF24	Eperigone fradeorum (Berland)	Arachnida	Araneae	Linyphiidae				17
I	MF250	Xysticus nubilus Simon	Arachnida	Araneae	Thomisidae			4	66
Ι	MF28	Dysdera crocata C. L. Koch	Arachnida	Araneae	Dysderidae	12	5	7	25
I	MF330	Meioneta fuscipalpis (C.L. Koch)	Arachnida	Araneae	Linyphiidae				32
Ι	MF333	Ostearius melanopygius (O. PCambridge)	Arachnida	Araneae	Linyphiidae		1	1	4
Ι	MF334	Gen. sp.	Arachnida	Araneae	Linyphiidae			2	
I	MF34	Erigone atra (Blackwall)	Arachnida	Araneae	Linyphiidae				2
I	MF488	Achaearanea acoreensis (Berland)	Arachnida	Araneae	Theridiidae		1	5	4
Ι	MF489	Lycosoides coarctata (Dufour)	Arachnida	Araneae	Agelenidae				2
Ι	MF701	Haplodrassus signifer (C. L. Koch)	Arachnida	Araneae	Gnaphosidae				1
I	MF988	Oecobius similis Kulczynski	Arachnida	Araneae	Oecobiidae				6
Ι	MF998	Zelotes aeneus (Simon)	Arachnida	Araneae	Gnaphosidae				38
I	MF688	Clubiona genevensis L. Koch	Arachnida	Araneae	Clubionidae				30
Ν	MF117	Lathys dentichelis (Simon)	Arachnida	Araneae	Dictynidae	1			
Ν	MF2	Tenuiphantes miguelensis Wunderlich	Arachnida	Araneae	Linyphiidae	34	18		
Ν	MF20	Palliduphantes schmitzi (Kulczynski)	Arachnida	Araneae	Linyphiidae	9	15	2	
Ν	MF33	Homalenotus coriaceus (Simon)	Arachnida	Opiliones	Phalangiidae	61	24	139	11
Ν	MF103	Chthonius tetrachelatus (Preyssler)	Arachnida	Pseudoscorpiones	Chthoniidae	2		5	
Ν	MF38	Chthonius ischnocheles (Hermann)	Arachnida	Pseudoscorpiones	Chthoniidae	1	6		
Ν	MF26	Geophilus truncorum Bergsoe & Meinert	Chilopoda	Geophilomorpha	Geophilidae				17
Ν	MF27	Lithobius pilicornis pilicornis Newport	Chilopoda	Lithobiomorpha	Lithobiidae		1		
Ν	MF1006	Lithobius sp.	Chilopoda	Lithobiomorpha	Lithobiidae				4
Ι	MF336	Scutigera coleoptrata (Linnaeus)	Chilopoda	Scutigeromorpha	Scutigeridae				42
Ν	MF468	Haplobainosoma lusitanum Verhoeff	Diplopoda	Chordeumatida	Haplobainosomatidae	3			
I	MF309	Choneiulus palmatus (Nemec)	Diplopoda	Julida	Blaniulidae	83		2	
I	MF9	Ommatoiulus moreletii (Lucas)	Diplopoda	Julida	Julidae	218	194	330	93
I	MF48	Blaniulus guttullatus (Fabricius)	Diplopoda	Julida	Blaniulidae	305	101		
I	MF62	Brachviulus pusillus (Leach)	Diplopoda	Julida	Julidae	3	30	9	2
Ν	MF282	Cylindroiulus propinguus (Porat)	Diplopoda	Julida	Julidae	15	20	11	14
Ν	MF49	Nopoiulus kochii (Gervais)	Diplopoda	Julida	Blaniulidae	16	2		
Ν	MF53	Proteroiulus fuscus (Am Stein)	Diplopoda	Julida	Blaniulidae	26	8	1	
Ν	MF544	Cylindroiulus latestriatus (Curtis)	Diplopoda	Julida	Julidae	5			
I	MF71	Oxidus gracilis (C.L.Koch)	Diplopoda	Polydesmida	Paradoxosomatidae	20	82	33	1
Ν	MF37	Polydesmus coriaceus Porat	Diplopoda	Polydesmida	Polydesmidae	19	510	40	
Ν	MF59	Zetha vestita (Brullé)	Insecta	Blattaria	Polyphagidae	32	10	35	9
Ν	MF1113	Loboptera decipiens (Germar)	Insecta	Blattaria	Blattellidae				803
Е	MF107	Atlantocis gillerforsi Israelson	Insecta	Coleoptera	Ciidae		2		
Е	MF1098	Olisthopus inclavatus Istaelson	Insecta	Coleoptera	Carabidae			6	
Е	MF128	Caulotrupis parvus Israelson	Insecta	Coleoptera	Curculionidae	6	1	-	
Е	MF138	Athous pomboi Platia & Borges	Insecta	Coleoptera	Elateridae	3			
Е	MF244	Alestrus dolosus (Crotch)	Insecta	Coleoptera	Elateridae				1
		~ /		-					

Table 5 continued

N/E/I	Code MF	Species	Class	Order	Family	NF	EF	SNP	IP
Е	MF540	Heteroderes azoricus Tarnier	Insecta	Coleoptera	Elateridae		2	42	868
Е	MF64	Tarphius serranoi Borges	Insecta	Coleoptera	Zopheridae	108	5		
Е	MF70	Tarphius pomboi Borges	Insecta	Coleoptera	Zopheridae	103	176	3	
Е	MF73	Metophthalmus occidentalis Israelson	Insecta	Coleoptera	Lathridiidae	4			
Е	MF76	Tarphius rufonodulosus Israelson	Insecta	Coleoptera	Zopheridae	1	7	3	
Е	MF77	Pseudechinosoma nodosum Hustache	Insecta	Coleoptera	Curculionidae	10	3		
Е	MF84	Catops velhocabrali Blas & Borges	Insecta	Coleoptera	Leiodidae		1	1	
Е	MF85	Tarphius depressus Gillerfors	Insecta	Coleoptera	Zopheridae	6	20	3	
Ι	MF108	Cryptamorpha desjardinsii (Guérin-Méneville)	Insecta	Coleoptera	Silvanidae		1	21	
Ι	MF1097	Gen. sp.	Insecta	Coleoptera	Lyctidae		2		
Ι	MF1099	Carpophilus sp.	Insecta	Coleoptera	Nitidulidae			1	
Ι	MF1101	Gen. sp.	Insecta	Coleoptera	Cucujidae				40
Ι	MF1105	Bruchus sp.	Insecta	Coleoptera	Chrysomelidae				2
Ι	MF1106	Sitona sp.	Insecta	Coleoptera	Curculionidae				1
Ι	MF1110	Gen. sp.	Insecta	Coleoptera	Corylophidae			1	
Ι	MF1111	Gen. sp.	Insecta	Coleoptera	Curculionidae			2	2
Ι	MF1114	Calamosternus granarius (Linnaeus)	Insecta	Coleoptera	Aphodiidae				28
Ι	MF1117	Gen. sp.	Insecta	Coleoptera	Chrysomelidae				2
Ι	MF1120	Notiophilus quadripunctatus Dejean	Insecta	Coleoptera	Carabidae				1
Ι	MF113	Typhaea stercorea (Linnaeus)	Insecta	Coleoptera	Mycetophagidae	1	2	2	10
Ι	MF120	Coccotrypes carpophagus (Hornung)	Insecta	Coleoptera	Curculionidae	6		1	
I	MF142	Cilea silphoides (Linnaeus)	Insecta	Coleoptera	Staphylinidae		1		1
I	MF145	Cryptophagus sp.	Insecta	Coleoptera	Cryptophagidae	1		5	108
I	MF161	Amara aenea (De Geer)	Insecta	Coleoptera	Carabidae				2
I	MF162	Atheta amicula (Stephens)	Insecta	Coleoptera	Staphylinidae	2			
I	MF247	Aleochara bipustulata (Linnaeus)	Insecta	Coleoptera	Staphylinidae			1	7
I	MF266	Chaetocnema hortensis (Fourcrov)	Insecta	Coleoptera	Chrysomelidae			3	
I	MF268	Carpophilus sp.	Insecta	Coleoptera	Nitidulidae				1
I	MF271	Anotylus sp. 2	Insecta	Coleoptera	Staphylinidae			1	
I	MF275	Agonum muelleri muelleri (Herbst)	Insecta	Coleoptera	Carabidae			3	2
I	MF308	Stelidota geminata (Say)	Insecta	Coleoptera	Nitidulidae	2	824	115	56
I	MF341	Philonthus politus politus (Linnaeus)	Insecta	Coleoptera	Staphylinidae				1
I	MF342	Cercyon sp.	Insecta	Coleoptera	Hydrophilidae		1	1	3
I	MF344	Sitona discoideus Gyllenhal	Insecta	Coleoptera	Curculionidae			1	10
T	MF386	Sitona puberulus Reitter	Insecta	Coleoptera	Curculionidae			1	10
T	MF395	Psylliodes marcidus (Illiger)	Insecta	Coleoptera	Chrysomelidae			10	1
T	MF45	Anisodactylus hinotatus (Eabricius)	Insecta	Coleoptera	Carabidae			50	2
T	MF502	Omosita colon (Linnaeus)	Insecta	Coleoptera	Nitidulidae			20	- 1
T	MF51	Paranchus albines (Fabricius)	Insecta	Coleoptera	Carabidae	8	258	128	97
T	MF52	Cordalia obscura (Gravenhorst)	Insecta	Coleoptera	Staphylinidae	1	1	6	6
T	MF523	Sphenophorus abbreviatus (Fabricius)	Insecta	Coleoptera	Dryophthoridae	1	1	0	2
T	MF541	Hirticomus auadriguttatus (Rossi)	Insecta	Coleoptera	Anthicidae				407
T	MF57	Atheta atramentaria (Gyllenhal)	Insecta	Coleoptera	Staphylinidae		2	7	107
T	ME570	Meligethes geneus (Espricius)	Insecta	Coleoptera	Nitidulidae		-	,	1
T	MF61	Enuraea higuttata (Thunberg)	Insecta	Coleontera	Nitidulidae	3	0	30	1
T	MF65	Sericoderus lateralis (Gyllenhal)	Insecta	Coleontera	Corvlophidae	5	1	200	7
1 T	MF66	Amischa analis (Gravenhoret)	Insecta	Coleontera	Stanhylinidae	6	2	200	3
1 T	ME603	Gen sn	Insecto	Coleoptera	Curculionidae	0	4	1	5
T	1075	oun. sp.	msceta	Colcopiera	Curcunomuae			1	

Table 5 continued

N/E/I	Code MF	Species	Class	Order	Family	NF	EF	SNP	IP
I	MF703	Nephus helgae Fursh	Insecta	Coleoptera	Coccinellidae				36
Ι	MF72	Ptenidium pusillum (Gyllenhal)	Insecta	Coleoptera	Ptiliidae	1	1	3	
Ι	MF74	Pseudophonus rufipes (DeGeer)	Insecta	Coleoptera	Carabidae	1		2	1
Ι	MF758	Gen. sp.	Insecta	Coleoptera	Anthicidae		1		11
Ι	MF764	Harpalus distinguendus (Duftschmidt)	Insecta	Coleoptera	Carabidae				11
Ι	MF767	Oligota parva Kraatz	Insecta	Coleoptera	Staphylinidae			1	3
Ι	MF771	Astenus lyonessius (Joy)	Insecta	Coleoptera	Staphylinidae				3
Ι	MF777	Gen. sp.	Insecta	Coleoptera	Anthicidae				37
Ι	MF823	Coproporus pulchellus (Erichson)	Insecta	Coleoptera	Staphylinidae				1
Ι	MF828	Carpophilus hemipterus (Linnaeus)	Insecta	Coleoptera	Nitidulidae	1			1
Ι	MF885	Oxytelus sculptus Gravenhorst	Insecta	Coleoptera	Staphylinidae			2	3
Ι	MF888	Gen. sp.	Insecta	Coleoptera	Ptiliidae			2	
Ι	MF89	Tachyporus chrysomelinus (Linnaeus)	Insecta	Coleoptera	Staphylinidae	1	23	110	25
Ι	MF944	Gen. sp.	Insecta	Coleoptera	Laemophloeidae				1
Ι	MF99	Phloeonomus sp.3	Insecta	Coleoptera	Staphylinidae		3	2	
Ι	MF153	Atheta sp.2	Insecta	Coleoptera	Staphylinidae			3	
Ι	MF16	Atheta fungi (Gravenhorst)	Insecta	Coleoptera	Staphylinidae	147	21	123	
Ι	MF354	Orthochaetes insignis (Aubé)	Insecta	Coleoptera	Curculionidae			5	
Ι	MF673	Mecinus pascuorum (Gyllenhal)	Insecta	Coleoptera	Curculionidae				2
Ι	MF708	Aridius sp.	Insecta	Coleoptera	Lathridiidae			1	
Ν	MF102	Pseudophloeophagus tenax (Wollaston)	Insecta	Coleoptera	Curculionidae	3	6	1	
Ν	MF1086	Gen. sp.	Insecta	Coleoptera	Curculionidae		1		12
Ν	MF1104	Rhyzobius litura (Fabricius)	Insecta	Coleoptera	Coccinellidae				11
Ν	MF1115	Psilothrix viridicoerulea (Geoffroy)	Insecta	Coleoptera	Dasytidae				5
Ν	MF23	Phloeonomus sp.	Insecta	Coleoptera	Staphylinidae		1		
Ν	MF25	Pseudophloeophagus aenopiceus (Boheman)	Insecta	Coleoptera	Curculionidae		1		
Ν	MF262	Rugilus orbiculatus orbiculatus (Paykull)	Insecta	Coleoptera	Staphylinidae		1	204	3
Ν	MF68	Sepedophilus lusitanicus (Hammond)	Insecta	Coleoptera	Staphylinidae	1			
Ν	MF69	Stilbus testaceus (Panzer)	Insecta	Coleoptera	Phalacridae			4	1
Ν	MF78	Anaspis proteus (Wollaston)	Insecta	Coleoptera	Scraptiidae			10	
Ν	MF79	Quedius curtipennis Bernhauer	Insecta	Coleoptera	Staphylinidae		5	261	
Ν	MF82	Proteinus atomarius Erichson	Insecta	Coleoptera	Staphylinidae	2	4	5	
Ν	MF88	Ocypus olens (Muller)	Insecta	Coleoptera	Staphylinidae		3		
Ν	MF94	Anommatus duodecimstriatus (Muller)	Insecta	Coleoptera	Bothrideridae		1		
Ν	MF98	Placonotus sp.1	Insecta	Coleoptera	Laemophloeidae		9	2	
Ν	MF15	Ocys harpaloides (Audinet-Serville)	Insecta	Coleoptera	Carabidae		23		
Ν	MF691	Otiorhynchus cribicollis Gyllenhal	Insecta	Coleoptera	Curculionidae		85	1	2
Ν	MF360	Gen. sp.	Insecta	Coleoptera	Corylophidae				11
Ι	MF352	Euborellia annulipes (Lucas)	Insecta	Dermaptera	Anisolabididae	18	89	246	741
Ι	MF56	Forficula auricularia Linnaeus	Insecta	Dermaptera	Forficulidae	2	7	21	9
Е	MF8	Aphrodes hamiltoni Quartau & Borges	Insecta	Hemiptera	Cicadellidae	30			
Е	MF925	Cixius azomariae Remane & Asche	Insecta	Hemiptera	Cixiidae	3			
Ι	MF155	Pseudacaudella rubida (Borner)	Insecta	Hemiptera	Aphididae	2			
Ι	MF335	Rhopalosiphum insertum (Walker)	Insecta	Hemiptera	Aphididae			1	
Ι	MF501	Loricula coleoptrata (Fallén)	Insecta	Hemiptera	Microphysidae				1
Ι	MF521	Brachysteles parvicornis (A. Costa)	Insecta	Hemiptera	Anthocoridae				23
Ι	MF818	Dysaphis plantaginea (Passerini)	Insecta	Hemiptera	Aphididae			1	1
Ι	MF676	Microplax plagiata (Fieber)	Insecta	Hemiptera	Lygaeidae				119
				-					

Table 5 continued

N/E/I	Code MF	Species	Class	Order	Family	NF	EF	SNP	IP
I	MF926	Anoscopus albifrons (Linnaeus)	Insecta	Hemiptera	Cicadellidae	2		54	45
Ν	MF1119	Triatoma rubrofasciata (De Geer)	Insecta	Hemiptera	Reduviidae				1
Ν	MF124	Cyphopterum adcendens (HerrSchaff.)	Insecta	Hemiptera	Flatidae	4			
Ν	MF232	Acyrthosiphon pisum Harris	Insecta	Hemiptera	Aphididae			11	
Ν	MF254	Megamelodes quadrimaculatus (Signoret)	Insecta	Hemiptera	Delphacidae			64	
Ν	MF326	Buchananiella continua (White)	Insecta	Hemiptera	Anthocoridae	1			
Ν	MF60	Rhopalosiphonimus latysiphon (Davidson)	Insecta	Hemiptera	Aphididae	8	1	20	
Ν	MF83	Plinthisus brevipennis (Latreille)	Insecta	Hemiptera	Lygaeidae	1	3	34	
Ν	MF890	Euscelidius variegatus (Kirschbaum)	Insecta	Hemiptera	Cicadellidae				6
Ν	MF101	Geotomus punctulatus (Costa)	Insecta	Hemiptera	Cydnidae	2			6
Ν	MF1096	Gen. sp.	Insecta	Hemiptera	Lygaeidae		2		
Ν	MF118	Scolopostethus decoratus (Hahn)	Insecta	Hemiptera	Lygaeidae	38	1		
Ν	MF119	Gen. sp.	Insecta	Hemiptera	Coccidae	1			
Ν	MF132	Gen. sp.	Insecta	Hemiptera	Coccidae	1			
Ν	MF156	Gen. sp.	Insecta	Hemiptera	Coccidae	8		6	
Ν	MF54	Gen. sp.	Insecta	Hemiptera	Margarodidae	10			
Ν	MF58	Gen. sp.	Insecta	Hemiptera	Coccidae	3			
Е	MF12	Cyclophora pupillaria granti Prout	Insecta	Lepidoptera	Geometridae	2			
Е	MF130	Brachmia infuscatella Rebel	Insecta	Lepidoptera	Gelechiidae	1			
Е	MF19	Argyresthia atlanticella Rebel	Insecta	Lepidoptera	Yponomeutidae	3			
Е	MF90	Ascotis fortunata azorica Pinker	Insecta	Lepidoptera	Geometridae	1			
Ι	MF1	Gen. sp.	Insecta	Lepidoptera	Tortricidae		6		
Ι	MF918	Blastobasis sp.3	Insecta	Lepidoptera	Blastobasidae	1			
Ν	MF10	Mythimna unipuncta (Haworth)	Insecta	Lepidoptera	Noctuidae	3	2	2	16
Ν	MF126	Chrysodeixis chalcites (Esper)	Insecta	Lepidoptera	Noctuidae	1			
Ν	MF220	Noctua pronuba (Linnaeus)	Insecta	Lepidoptera	Noctuidae			1	
Ν	MF365	Gen. sp.	Insecta	Lepidoptera	Pyralidae	1			
Ι	MF123	Gryllus bimaculatus (De Geer)	Insecta	Orthoptera	Gryllidae	2			3
Ι	MF245	Eumodicogryllus bordigalensis (Latreille)	Insecta	Orthoptera	Gryllidae				38
Ν	MF319	Gen. sp.	Insecta	Orthoptera	Gryllidae				1
Е	MF184	Elipsocus azoricus Meinander	Insecta	Psocoptera	Elipsocidae		1		
Ν	MF121	Ectopsocus briggsi McLachlan	Insecta	Psocoptera	Ectopsocidae	1			
Ν	MF36	Lachesilla greeni (Pearman)	Insecta	Psocoptera	Lachesillidae	1			
Ι	MF135	Nesothrips propinquus (Bagnall)	Insecta	Thysanoptera	Phlaeothripidae	1			

In the first column *E* endemic from the Azores, *I* introduced species, *N* native non-endemic. Land-uses are coded as follows: *NF* native forest, *EF* exotic forest, *SNP* semi-natural forest, *IP* intensive pasture

Appendix 3

See Table 6.

 Table 6 Completeness index (observed number of species divided by the expected number of species) for the four habitat types (four transects per habitat, each transect containing 30 pitfall traps)

	Native forest	Exotic forest	Semi-natural pasture	Intensive pasture
Observed nr of species	81	69	82	95
Expected nr of species	108.8	92.8	103.8	116.8
Completeness Index	0.74	0.74	0.79	0.81

The expected number of species was calculated using a first-order Jack-knife estimator

References

- Abdel-Monem AA, Fernandez LA, Boone GM (1975) K–Ar ages from the eastern Azores group (Santa Maria, São Miguel and the Formigas Islands). Lithos 8:247–254
- Acevedo MA, Restrepo C (2008) Land-cover and land-use change and its contribution to the large-scale organization of Puerto Rico's bird assemblages. Diversity Distrib 14:114–122
- Bhagwat SA, Willis KJ, Birks HJB, Whittaker RJ (2008) Agroforestry: a refuge for tropical biodiversity? Trends Ecol Evol 23:261–267
- Borges PAV, Brown VK (1999) Effect of island geological age on the arthropod species richness of Azorean pastures. Biol J Linn Soc 66:373–410
- Borges PAV, Brown VK (2003) Estimating species richness of arthropods in Azorean pastures: the adequacy of suction sampling and pitfall trapping. Graellsia 59:5–22
- Borges PAV, Hortal J (2009) Time, area and isolation: factors driving the diversification of Azorean arthropods. J Biogeogr 36:178– 191
- Borges PAV, Wunderlich J (2008) Spider biodiversity patterns and their conservation in the Azorean archipelago, with description of new taxa. Syst Biodivers 6:249–282
- Borges PAV, Serrano ARM, Quartau JA (2000) Ranking the Azorean Natural Forest Reserves for conservation using their endemic arthropods. J Insect Conserv 4:129–147
- Borges PAV, Aguiar C, Amaral J, Amorim IR, André G, Arraiol A, Baz A, Dinis F, Enghoff H, Gaspar C, Ilharco F, Mahnert V, Melo C, Pereira F, Quartau JA, Ribeiro S, Ribes J, Serrano ARM, Sousa AB, Strassen RZ, Vieira L, Vieira V, Vitorino A, Wunderlich J (2005a) Ranking protected areas in the Azores using standardized sampling of soil epigean arthropods. Biodivers Conserv 14:2029–2060
- Borges PAV, Cunha R, Gabriel R, Martins AF, Silva L, Vieira V, Dinis F, Lourenço P, Pinto N (2005b) Description of the terrestrial Azorean biodiversity. In: Borges PAV, Cunha R, Gabriel R, Martins AMF, Silva L, Vieira V (eds) A list of the terrestrial fauna (Mollusca and Arthropoda) and flora (Bryophyta, Pteridophyta and Spermatophyta) from the Azores. Direcção Regional de Ambiente and Universidade dos Açores, Horta, Angra do Heroísmo and Ponta Delgada, pp 21–68
- Borges PAV, Lobo JM, de Azevedo EB, Gaspar C, Melo C, Nunes LV (2006) Invasibility and species richness of island endemic arthropods: a general model of endemic vs. exotic species. J Biogeogr 33:169–187
- Borges PAV, Ugland KI, Dinis FO, Gaspar C (2008) Insect and spider rarity in an oceanic island (Terceira, Azores): true rare and pseudo-rare species. In: Fattorini S (ed) Insect ecology and conservation. Research Signpost, Kerala, pp 47–70
- Borges PAV, Amorim IR, Cunha R, Gabriel R, Martins AF, Silva L, Costa A, Vieira V (2009) Azores. In: Gillespie R, Clague D (eds) Encyclopedia of Islands. University of California Press, California, pp 70–75
- Brook BW, Sodhi NS, Ng PKL (2003) Catastrophic extinctions follow deforestation in Singapore. Nature 424:420–423
- Brooks T, Balmford A (1996) Atlantic forest extinctions. Nature 380:115
- Brooks TM, Pimm SL, Collar NJ (1997) Deforestation predicts the number of threatened birds in insular Southeast Asia. Conserv Biol 11:382–394
- Brooks TM, Tobias J, Balmford A (1999a) Deforestation and bird extinctions in the Atlantic Forest. Anim Conserv 2:211–222
- Brooks TM, Pimm SL, Kapos V, Ravilious C (1999b) Threat from deforestation to montane and lowland birds and mammals in insular South-east Asia. J Anim Ecol 68:1061–1078

- Brooks TM, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Rylands AB, Konstant WR, Flick P, Pilgrim J, Oldfield S, Magin J, Hilton-Tailor C (2002) Habitat loss and extinction in the hotspots of biodiversity. Conserv Biol 16:909–923
- Bruner AG, Gullison RE, Rice RE, da Fonseca GAB (2001) Effectiveness of parks in protecting tropical biodiversity. Science 291:125–128
- Burel F, Baudry J, Butet A, Clergeau P, Delettre Y, Le Coeur D, Dubs F, Morvan N, Paillat G, Petit S, Thenail C, Brunel E, Lefeuvre JC (1998) Comparative biodiversity along a gradient of agricultural landscapes. Acta Oecol 19:47–60
- Cardoso P, Aranda SC, Lobo JM, Dinis F, Gaspar C, Borges PAV (2009) A spatial scale assessment of habitat effects on arthropod communities of an oceanic island. Acta Oecol 35:590–597
- Chape S, Harrison J, Spalding M, Lysenko I (2005) Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. Philos Trans R Soc Biol Sci 360:443–455
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143
- Cowlishaw G (1999) Predicting the pattern of decline of African primate diversity: an extinction debt from historical deforestation. Conserv Biol 13:1183–1193
- Daily GC, Ehrlich PR, Sánchez-Azofeifa GA (2001) Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. Ecol Appl 11:1–13
- Daily GC, Ceballos G, Pachego J, Suzán G, Sánchez-Azofeifa A (2003) Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. Conserv Biol 17:1814–1826
- Driscoll DA (2005) Is the matrix a sea? Habitat specificity in a naturally fragmented landscape. Ecol Entomol 30:8–16
- DROTRH (2008) Carta de ocupação do solo da região Autónoma dos Açores—projecto SUEMAC. Secretaria Regional do Ambiente. Direcção Regional do Ordenamento do território e dos Recursos Hídricos, Ponta Delgada
- Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global consequences of land use. Science 309:570–574
- Gascon C, Lovejoy TE, Bierregaard RO Jr, Malcolm JR, Stouffer PC, Vasconcelos HL, Laurance WF, Zimmerman B, Tocher M, Borges S (1999) Matrix habitat and species richness in tropical forest remnants. Biol Cons 91:223–229
- Gaspar C, Borges PAV, Gaston KJ (2008) Diversity and distribution of arthropods in native forests of the Azores Archipelago. Arquipélago, Life Marin Sci 25:1–30
- Grelle CEV, Alves MAS, Bergallo HG, Geise L, Rocha CFD, Van Sluys M, Caramaschi U (2005) Prediction of threatened tetrapods based on the species-area relationship in Atlantic Forest, Brazil. J Zool Soc Lond 265:359–364
- Grill A, Knoflach B, Cleary DFR, Kati V (2005) Butterfly, spider, and plant communities in different land-use types in Sardinia, Italy. Biodivers Conserv 14:1281–1300
- Hanski I (1998) Metapopulation dynamics. Nature 396:41-49
- Hanski I, Koivulehto H, Cameron A, Rahagalala P (2007) Deforestation and apparent extinctions of endemic forest beetles in Madagascar. Biol Lett 3:344–347
- Helm A, Hanski I, Pärtel M (2006) Slow response of plant species richness to habitat loss and fragmentation. Ecol Lett 9:72–77
- Henderson PA, Seaby RMH (2007) Community Analysis Package 4.0. Pisces Conservation Ltd. Available via www.pisces-conservation. com

Heywood VN, Mace GM, May RM, Stuart SN (1994) Uncertainties in extinction rates. Nature 368:105

- Hortal J, Borges PAV, Gaspar C (2006) Evaluating the performance of species richness estimators: sensitivity to sample grain size. J Anim Ecol 75:274–287
- Hughes JB, Daily GC, Ehrlich PR (2002) Conservation of tropical forest birds in countryside habitats. Ecol Lett 5:121–129
- Jana G, Misra KK, Bhattacharya T (2006) Diversity of some insect fauna in industrial and non-industrial areas of West Bengal, India. J Insect Conserv 10:249–260
- Janzen DH (1986) The future of tropical ecology. Ann Rev Ecol Syst 17:305–324
- Jonsson BG, Kruys N, Ranius T (2005) Ecology of species living on dead wood—lessons for dead wood management. Silva Fenn 39:289–309
- Kaila L, Martikainen P, Punttila P (1997) Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. Biodivers Conserv 6:1–18
- Klein AM, Steffan-Dewenter I, Tscharntke T (2006) Rain forest promotes trophic interactions and diversity of trap-nesting Hymenoptera in adjacent agroforestry. J Anim Ecol 75:315–323
- MacArthur RH, Wilson EO (1963) An equilibrium theory of insular zoogeography. Evolution 17:373–387
- MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton
- Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243–253
- Martikainen P, Siitonen J, Punttila P, Kaila L, Rauh J (2000) Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biol Conserv 94:199–209
- Martins AMF (1993) The Azores—Westernmost Europe: where evolution can be caught red-handed. Bol Mus Mun Funchal 2:181–198
- Muriel SB, Kattan GH (2009) Effects of patch size and type of coffee matrix on Ithomiine butterfly diversity and dispersal in cloudforest fragments. Conserv Biol 23:948–956
- Myers N (1992) The primary source: tropical forests and our future. W.W. Norton, New York
- Okland B, Bakke A, Hagvar S, Kvamme T (1996) What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodivers Conserv 5:75–100
- Oksanen J, Minchin PR (1997) Instability of ordination results under changes in input data order: explanations and remedies. J Veg Sci 8:447–454
- Pereira HM, Cooper HD (2006) Towards the global monitoring of biodiversity change. Trends Ecol Evol 21:123–129
- Perfecto I, Vandermeer J (2002) Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. Conserv Biol 16:174–182
- Pimm SL, Russell GJ, Gittleman JL, Brooks TM (1995) The future of biodiversity. Science 269:347–350
- Prugh LR, Hodges KE, Sinclair ARE, Brashares JS (2008) Effect of habitat area and isolation on fragmented animal populations. Proc Natl Acad Sci 105:20770–20775
- Rainio J, Niemelä J (2006) Comparison of carabid beetle (Coleoptera: Carabidae) occurrence in rain forest and human-modified sites in south-eastern Madagascar. J Insect Conserv 10:219–228

- Ramankutty N, Foley JA (1999) Estimating historical changes in global land cover: croplands from 1700 to 1992. Glob Biochem Cycles 13:997–1027
- Ribeiro SP, Borges PAV, Gaspar C, Melo C, Serrano ARM, Amaral J, Aguiar C, André G, Quartau JA (2005) Canopy insect herbivores in the Azorean Laurisilva forests: key host plant species in a highly generalist insect community. Ecography 28:315–330
- Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. Am Nat 158:87–99
- Rodrigues ASL, Andelman SJ, Bakarr MI, Boitani L, Brooks TM, Cowling RM, Fishpool LDC, da Fonseca GAB, Gaston KJ, Hoffmann M, Long JS, Marquet PA, Pilgrim JD, Pressey RL, Schipper J, Sechrest W, Stuart SN, Underhill LG, Waller RW, Watts MEJ, Yan X (2004) Effectiveness of the global protected area network in representing species diversity. Nature 428:640–643
- Rosenzweig ML (2003) Reconciliation ecology and the future of species diversity. Oryx 37:194–205
- Schmidt MH, Thies C, Nentwig W, Tscharntke T (2008) Contrasting responses of arable spiders to the landscape matrix at different spatial scales. J Biogeogr 35:157–166
- Schweiger O, Maelfait JP, Van Wingerden W, Hendrickx F, Billeter R, Speelmans M, Augenstein I, Aukema B, Aviron S, Bailey D, Bukacek R, Burel F, Diekötter T, Dirksen J, Frenzel M, Herzog F, Liira J, Roubalova M, Bugter R (2005) Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. J Appl Ecol 42:1129–1139
- Sekercioglu CH, Ehrlich PR, Daily GC, Aygen D, Goehring D, Sandi RF (2002) Disappearance of insectivorous birds from tropical forest fragments. Proc Natl Acad Sci 99:263–267
- Tilman D, May RM, Lehman CL, Nowak MA (1994) Habitat destruction and the extinction debt. Nature 371:65–66
- Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhamer D (2001) Forecasting agriculturally driven global environmental change. Science 292:281–284
- Toth F, Kiss J (1999) Comparative analyses of epigeic spider assemblages in northern Hungarian winter wheat fields and their adjacent margins. J Arachnol 27:241–248
- Triantis KA, Borges PAV, Ladle RJ, Hortal J, Gaspar C, Dinis F, Mendonça E, Silveira LMA, Gabriel R, Cardoso P, Melo C, Santos AMC, Amorim IR, Ribeiro SP, Serrano ARM, Quartau JA, Whittaker RJ (2010) Extinction debt on oceanic islands. Ecography 33:285–294
- Vandermeer J, Carvajal R (2001) Metapopulation dynamics and the quality of the matrix. Am Nat 158:211–220
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. Science 277:494–499
- Watson JEM, Whittaker RJ, Freudenberger D (2005) Bird community responses to habitat fragmentation: how consistent are they across landscapes? J Biogeogr 32:1353–1370
- Whittaker RJ, Fernández-Palacios JM (2007) Island biogeography: ecology, evolution, and conservation, 2nd edn. Oxford University Press, Oxford
- Wiens J (2007) The dangers of black-and-white conservation. Conserv Biol 21:1371–1372
- Wilson EO (1992) The diversity of life. Harvard University Press, Cambridge