CHANCE AND NECESSITY: LAND-SNAIL FAUNAS OF SÃO MIGUEL, AZORES, COMPARED WITH THOSE OF MADEIRA

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ABSTRACT

The land-snail faunas of 23 sites from forest, disturbed and open habitats were sampled on São Miguel, Azores archipelago. Collectively, the samples contained nearly all the known fauna of the island. Forest sites were the richest; while the number of non-endemic species differed little between habitats, forests held more endemic species, many of which were widely distributed. Open habitats have no unique endemic species. These results are compared with similar data from Madeira. Although the two islands are of the same size, and share the same *Laurisilva* forest cover, their faunas differ in important aspects of diversity. While many non-endemic species are common to both islands, and occur in similar numbers, endemic species are more numerous on Madeira, even though the numbers at individual forest sites are, on average, fewer than on São Miguel. Many endemics are confined to open, coastal habitats. These differences are discussed in terms of the islands' histories, the range of habitats available and the ease of dispersal from continental sources. Age, accidents of colonization and the range of natural habitats available must have major effects on the faunas, but present endemic faunal diversity is more a product of speciation and extinction than of immigration.

INTRODUCTION

Studies of island biogeography show a longstanding tension between the search for general rules, based on universal and testable processes, and the observation of the stubbornly idiosyncratic patterns shown in many particular cases. Hence, the elegance of MacArthur & Wilson's (1967) model has both stimulated new work, and attracted much criticism and modification; in Whittaker's (2001) phrase, it seems to be 'wrong in interesting ways'. Among the many modifications proposed, the challenges of non-equilibrium states and the extent of turnover (Whittaker, 2000), the non-random variation in species' capacity for dispersal and persistence (Lomolino, 2000a) and the separation of the effects of area and habitat diversity (Triantis *et al*., 2003; Triantis, Vardinoyannis & Mylonas, 2005) have been especially heuristic. A consensus appears to be forming that the demonstration of particular species–area relationships does not of itself advance our understanding of processes that may vary in importance between studies (Whittaker, 2000; Ward & Thornton, 2000; Lomolino, 2000b). On a broad scale, area and habitat diversity must be associated. Variation in area between islands can be factored out as a confounding variable, however, if the habitat diversity can be quantified.

Land mollusc faunas on islands have attracted considerable attention, and led to some thorough studies partitioning species richness and composition between causes (Cowie, 1996; Cowie & Holland, 2006). Within-island evolution and radiation is of particular importance in this group, and can result in very different results being obtained in islands of similar size and habitat diversity (Cameron, Cook & Hallows, 1996; Cameron, 2004).

São Miguel, the largest island of the Azores, and Madeira, the largest island in its archipelago, are almost exactly the same size. They share a volcanic, oceanic origin and are both isolated from the continents. Both are mountainous, and share an originally widespread vegetation type, the Macaronesian broadleaved but evergreen *Laurisilva* forests (Neves *et al*., 1996). They have a common human history. The important feature in which they differ is that São Miguel has fewer habitat types than Madeira. The land mollusc fauna of Madeira has been studied with great intensity for more than 150 years (Seddon, in press). Cameron & Cook (2001) have examined the diversity of molluscs within the island in terms of geographical, historical and habitat factors. Intensive study of the Azorean fauna started more recently, and knowledge of the endemic fauna may be less complete; nevertheless, a recent island-by-island checklist (Cunha *et al*., 2005) indicates that most of the fauna is now known, especially on São Miguel, the most populated and well-studied island in the group.

In this article, we present new data on the composition and richness of local faunas on São Miguel and we compare them with similar data for Madeira (Cameron & Cook, 2001). We examine them in the context of the island faunas as a whole, and what is known of the islands' history and origins. In particular we seek to see to what extent the necessary ecological constraints of a particular habitat impose similarity in richness and taxonomic composition on faunas of independent origin, and to what extent they are influenced by the chances of colonization and history. In addition to the endemic fauna, both islands hold a number of widespread species that can be used to establish the degree of similarity in ecological conditions.

MATERIAL AND METHODS

The Islands

Figure 1 shows the positions of São Miguel and Madeira relative to continental Africa and Europe, and within their archipelagos. In terms of similarities, both are oceanic, volcanic and mountainous islands never connected to a larger landmass. They are almost exactly the same size (*ca* 740 km^2). Both have, as nearest neighbours, a smaller, older, drier and more calcareous island (Porto Santo for Madeira, Santa Maria for São Miguel)

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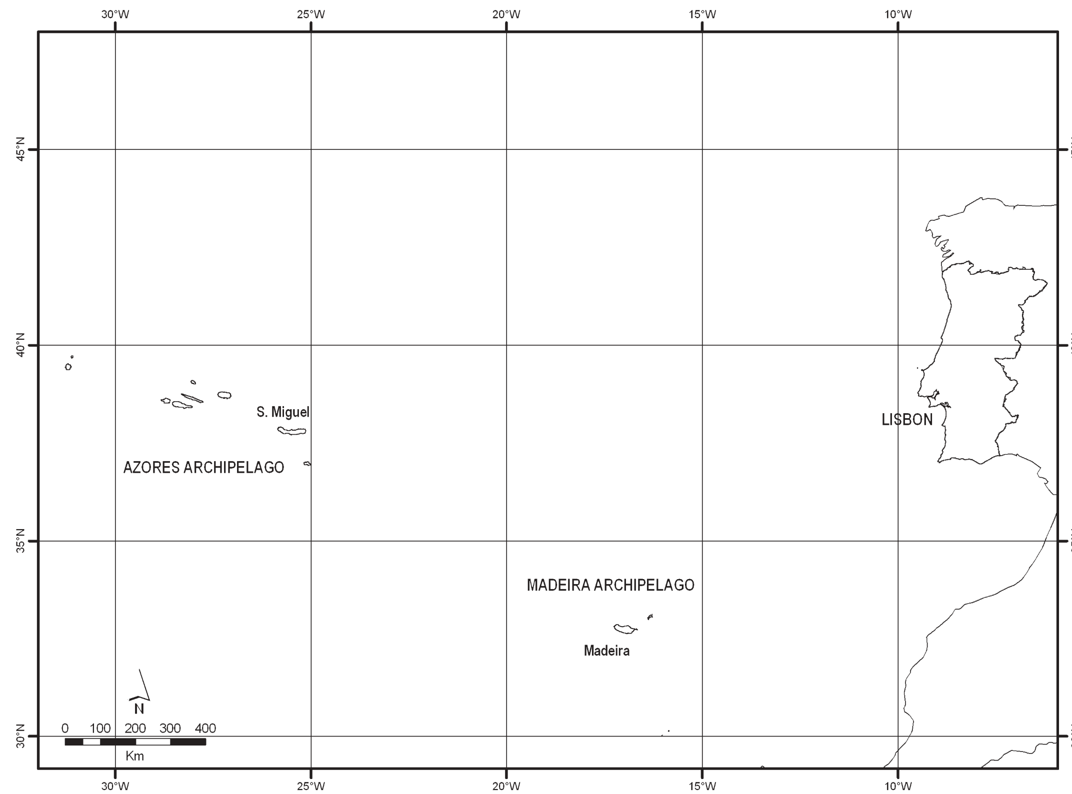

Figure 1. The position of São Miguel and Madeira relative to each other and the continents of Europe and Africa.

from which colonists might come. Both have very oceanic climates, with at least some parts of each receiving more than 1000 mm of rain each year, with no prolonged dry season. At sea level, Madeira is a little warmer (Funchal, mean January temperature, 16°, mean July temperature 21°) than São Miguel (Ponta Delgada, January, 14°, July, 20.5°), but at higher altitudes there is much overlap (Quental, 1989). Both have, as an important element in their natural vegetation, the broadleaved but evergreen *Laurisilva* forests, a relic of similar Tertiary forests in Southern Europe (Sjögren, 1972; Schäfer, 2003). Both islands were discovered and colonized by the Portuguese within a few years of each other (1420–1430), being previously uninhabited by humans. In both, there has been extensive replacement of natural vegetation by agriculture and commercial forestry. Both are now densely populated by humans, although the population of Madeira is roughly twice that of São Miguel.

In terms of major differences, Madeira is considerably closer to a continental land-mass: 645 km from Morocco, as opposed to about 1300 km from Portugal for São Miguel (Morton, Britton & Martins, 1998), though even the shorter distance represents extreme isolation where land molluscs are concerned. More significantly, a series of seamounts lies between Madeira and mainland Portugal (Pereira, 1967; Pastouret *et al.*, 1980), indicating the possibility of a stepping stone colonization process over relatively short distances. The highest peaks on Madeira are considerably higher (up to 1850 m) than those on São Miguel (up to 1100 m), and there is a natural subalpine zone (Sjögren, 1972), albeit much disturbed. The combination of topography and prevailing winds on Madeira causes a rain shadow not found, generally, in the Azores, and the south side of the island has a variant of Mediterranean climate up to around 300 m above sea level (asl). This supports the *Aeonio-Lytanthion* plant alliance (Sjögren, 1972), which is only intermittently present, very close to sea level, in the north. It is predominantly open. Local topography and hydrology sometimes create very small-scale mixtures of open and forest associations. On São Miguel, although there are traces of such natural open communities very close to the sea, the original vegetation is overwhelmingly forest, with some altitudinal variation related to rainfall.

The two islands differ in their age. Whereas nearly all of Madeira has been above sea level for at least 4–5 My (Nascimento Prada & Serralheiro, 2000), with only very small-scale volcanic activity thereafter, São Miguel in its present form is very recent. While the eastern end was formed *ca* 4 My ago, the rest of the island formed from a set of later eruptions; the extreme west, formed around 0.5 My ago as a separate island, was joined to the remainder by later activity only 0.05 My ago. There have been major, caldera-forming eruptions within the last 0.05 My (summaries in Morton, Britton & Martins, 1998; França *et al.*, 2003).

In the case of Madeira, a Pleistocene/Holocene subfossil record indicates that about 20–25% of the endemic snail fauna may have been eliminated as a result of human activities; the species involved are mainly those of low, coastal areas with a Mediterranean type of climate (Goodfriend, Cameron & Cook, 1994; Cameron & Cook, 1996). There is no such record for São Miguel. Both have large numbers of non-endemic species in the present fauna, many of which are thought to have been introduced since human occupation, but some are undoubtedly native (Goodfriend *et al.*, 1996). One species, *Balea heydeni*, appears to have evolved on the Azores and invaded Europe and the Madeiran archipelago (Gittenberger *et al.*, 2006).

Sample sites on São Miguel

Figure 2 shows the location of sampling sites on the island. Although they are few relative to those made on Madeira

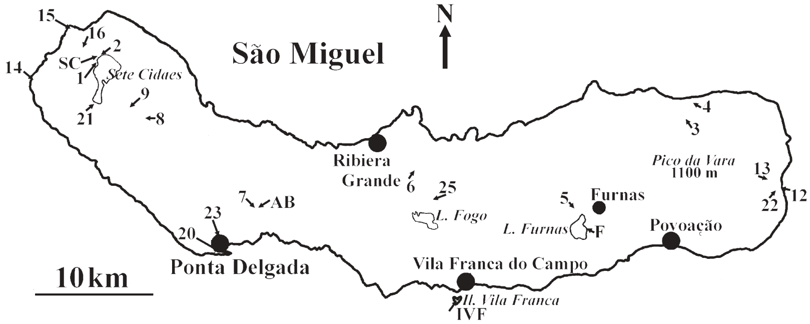

Figure 2. A map of São Miguel, showing the location of sampling sites (see text).

(Cameron & Cook, 2001), they span the whole length of the island. They have been allocated to three habitat categories. The 12 samples from forests come from sites with complete, or nearly complete canopy cover. Although most contain native tree species, they are generally dominated by the introduced conifer *Cryptomeria japonica*, and the herbaceous vegetation is often dominated by the introduced *Hedychium gardneranum*. The two sites with the most natural *Laurisilva* vegetation are AB and 22. Altitudes range from 130 to 700 m asl.

Seven samples come from more disturbed sites retaining some tree cover. These span a similar range of altitude (50–700 m asl). Most are partially cleared areas in the forest zone, with hedges, or scrub and fringes of *Cryptomeria* plantations. Site 25 is a damaged and heavily grazed remnant of *Laurisilva* at high altitude (600 m). This held much the poorest fauna within this group. Site 23 is in a tree-covered (mainly introduced species) part of the José do Canto park in the city of Ponta Delgada.

Four samples come from rather heterogeneous open habitats, all close to the coast. Sites 14 and 15 come from flat coastal platforms; site 15, at Mosteiros, was much more disturbed and closer to human habitation than site 14, from Ponta Ferraria. Site 20 was on and below the outer walls of the old fortress in Ponta Delgada, and Site IVF is an amalgamation of a series of samples from the small offshore Ilhéu de Vila Franca, all from scrubby or open vegetation.

Relative to Madeira, there is much less relatively undisturbed *Laurisilva* surviving intact, and penetration by alien plants is more extensive. The open and disturbed sites are dominated by alien vegetation, though remnants of natural communities persist at site IVF.

Sampling methods

Nineteen of the 23 samples made on São Miguel (numbered in Appendix 2) were made by RADC, using the same procedures as those used by Cameron & Cook (2001) on Madeira. Plots of *ca* 1000 m^2 were searched by eye for up to 2 h, and about 5 l of litter and soil were removed for inspection in the laboratory. All live animals, and all fresh shells were identified and included in the inventory. Three samples were made by RMTdaC (SC, AB and F) by regular monthly sampling of small plots by eye over 2 years. One (IVF) was sampled by AMFM, and represent collections on a small islet (Martins, 1995) made over several visits.

The lists for individual sites may well be incomplete (Cameron & Pokryszko, 2005), and the different sampling methods used may have effects. Inspection of the results, however, reveals that the only evident effect of repeated sampling (by RMTdaC and AMFM) is to increase greatly the chance of finding slugs. In our analyses, we have therefore omitted all non-endemic slugs (Stylommatophora: Arionidae, Agriolimacidae, Limacidae, Milacidae) without identifiable shells, as experiences here and elsewhere show that the sampling methodology used by RADC gives very variable detection rates (Cameron & Pokryszko, 2005). They are considered briefly where relevant. As sampling was generally qualitative, no corrections have been applied to estimate the number of missing species, but incompleteness is taken into account when discussing the results.

Nomenclature and systematic issues

Appendix 1 provides a systematic list of names and authorities for all species named in the text and tables. For Azorean species, we have followed Cunha *et al.* (2005), and for those from Madeira, Seddon (in press). For species held in common, we follow Cunha *et al.* (2005). It should be noted that somewhat different nomenclature is provided by Bank, Groh & Ripken (2002). Their list is available electronically, and is in a state of ongoing revision. In general, differences in nomenclature do not reflect disagreements about species-level status.

Analyses of endemic (to the archipelago) and non-endemic species are often separated. In this context, we note three particular problems. There are four species on São Miguel that are not endemic to the Azores, but which are restricted to some or all of the Macaronesian archipelagos (Azores, Madeira, Canaries, Cape Verde). Of these, two, *C. microspora* and *Hydrocena gutta* are regarded as natural occupants, and classed as endemics. They are widespread in *Laurisilva*. The other two, *Heterostoma paupercula* and *Leptaxis erubescens*, are confined to a few very anthropogenic sites, and are regarded as human introductions from Madeira (Backhuys, 1975), hence as non-endemics. Similarly, *C. microspora*, *H. paupercula* and *L. erubescens* are regarded as endemic to Madeira (*H. gutta* is absent there).

There are four described endemic species on São Miguel, *Punctum azoricum*, *Acanthinula azorica*, *Spermodea monas* and *Z. azoricus*, all of which have very closely related congenerics in continental Europe or N. America. Three of these continental species, *P. pygmaeum*, *A. aculeata* and *Z. arboreus*, are recorded as non-endemics on Madeira, but material from that island has not been subject to recent taxonomic review. All are found in Madeiran *Laurisilva*.

Lauria anconostoma, listed by Cunha *et al.* (2005), is recorded both on São Miguel and Madeira. Cameron & Cook (2001) identified all *Lauria* (other than *L. fanalensis*) found on Madeira as the widespread species *L. cylindracea*. We treat these taxa as equivalent non-endemic species.

Finally, we note that there are several species on São Miguel that show geographical or interdemic variation on the island, sometimes related to its geological history (Van Riel *et al.*, 2003; Martins, 2005). This infraspecific differentiation is not incorporated in analyses, but is considered in discussion.

Table 1. Basic data on species richness of endemic, non-endemic and whole land-snail faunas for habitats and sites on São Miguel.

São Miguel	Forest	Disturbed	Open	Total
No. of samples	12	7	4	23
Endemic species	20	18	4	21
Mean/site	11.3	6.3	1.7	
Non-endemic species	20	23	23	30
Mean/site	10.9	11.9	11.0	
All species	40	41	27	51
Mean/site	22.2	18.2	12.7	
Endemic overall %	50.0	43.9	14.8	
Mean endemic/site %	51.0	34.6	13.4	
Percentage of all endemics	95.2	85.7	19.0	
Percentage of all non-endemics	66.7	76.7	76.7	

The last two rows record percentages of the fauna found in the survey, not of all known species on the island.

RESULTS

Within São Miguel

Appendix 2 shows the species found at each site. Non-endemic slugs are listed separately (see above). fifty-seven species were found altogether, of which six were non-endemic slugs. Table 1 shows the basic data relating to species richness of the faunas, both by habitat, and by the status of the species. Forest is the richest habitat, and contains roughly equal numbers of endemic and non-endemic species, both overall and site-by-site. Disturbed sites with some tree cover are slightly poorer overall at site level; this impoverishment is entirely due to a significant drop in the mean number of endemic species per site. Open coastal sites, which are rather heterogeneous in overall richness and character, are poorer still in endemic species, but retain similar numbers of non-endemics to the other habitats both overall and per site. Within the forest and disturbed series, a few endemics show altitudinal trends, *Oxychilus miguelinus* and *O. volutella* being found mainly below 400 m, while *Leptaxis azorica* is more frequent above that altitude. There are no detectible geographical trends in faunal similarity (examined with the Nei index, data not shown).

Twenty of the 21 endemic species found overall were found in forest. The single exception, *Zonitoides azorica*, was found in one disturbed site only. Thus, all endemics found in the open were also found in the forest. Among non-endemics, however, 10 of the 30 species found were missing from the forests (Table 3). The distribution of non-endemics between habitats reflects closely their known habitats in other parts of their ranges. However, with 28 species recorded in the open and forest categories combined, 15 are common to both.

The recorded fauna of São Miguel (Cunha *et al*. 2005) contains 57 species other than littoral species and non-endemic slugs (six out of 11 of the latter were found in our samples). Fifty one of these were found in the samples considered here. Three recorded endemics, *L. caldeirarum*, *Leiostyla vermiculosa* and *Plutonia brevispira*, and three non-endemics, *Otala lactea*, *Theba pisana* and *Aegopinella nitidula* were missing. The set of 23 sites therefore includes the great majority of the known fauna.

Comparison with Madeira

Comparisons with Madeiran sites use the data presented in Cameron & Cook (2001), and the sites/species matrix is available from those authors. Table 2 shows figures for Madeiran habitat and geographical divisions as for São Miguel in Table 1. Note that while forest sites are categorized by altitude and disturbance, coastal sites are categorized geographically. If they were amalgamated, it would greatly increase the overall number and proportion of endemic species involved, because there are many cases of allopatric replacement around the island.

With the exception of category D, which contained intimate mixtures of open and forest microhabitats within sample plots, mean overall richness per plot is generally lower than in São Miguel. This is most evident when forest comparisons are made, between the forest and disturbed categories on São Miguel and categories E, F and G representing the *Laurisilva* on Madeira. The striking difference between the two islands is

Table 2. Basic data for land-snail faunas of sites and habitats/regions on Madeira, as for São Miguel in Table 1.

	Madeira									
	Open, Coastal						Forest			Total
	A	B	I	H	C	D	E	F	G	
No. of samples	5	3	11	9	9	3	12	8	14	74
Endemic species	19	14	19	26	17	27	21	19	24	61
Mean/site	11.0	9.7	6.2	11.1	6.8	18.0	6.4	8.5	7.6	
Non-endemics	13	8	19	13	13	14	15	10	10	34
Mean/site	7.8	2.7	7.6	4.0	6.3	7.7	5.8	5.9	2.5	
All species	32	22	38	39	30	41	36	29	34	95
Mean/site	18.8	12.3	13.7	15.1	13.1	25.7	12.2	14.4	10.1	
Endemics overall %	59.4	63.6	50.0	66.7	56.7	65.9	58.3	65.5	70.6	
Mean % endemics	58.5	78.9	45.3	73.5	51.9	70.0	52.5	59.0	75.2	
Percentage of all endemics	31.1	22.9	31.1	42.6	27.9	44.3	34.4	31.1	39.3	
Percentage of all non-endemics	38.2	23.5	55.9	38.2	38.2	41.2	44.1	29.4	29.4	

Categories A–C represent sections of the open, coastal environments. Category D represents sites in a section of the north coast with mixtures of open and forested habitats. Category E represents disturbed forests below 600 m. F represents *Laurisilva* 600–900 m asl, and G the same between 900 and 1200 m. Data from Cameron & Cook (2001). Note that categories J and K in that paper (high cleared slopes and subalpine) are omitted here.

Table 3. Similarity and differences between the non-endemic land-snail faunas recorded on each island.

Non-endemics	Forest	Open	Overall
São Miguel			
Species	20	23	30
Joint with Madeira	10	16	22
Joint %	50	69	73
Joint: different habitat	5	2	–
Equivalent congeneric	2	3	5
Unique	3	2	3
Unique %	15	9	10
Madeira			
Species	17	27	34
Joint with São Miguel	10	16	22
Joint %	59	59	65
Joint: Different habitat	1	3	–
Equivalent congeneric	5	4	6
Unique	1	4	6
Unique %	6	15	18

For the forest comparison, the forest series of São Miguel is compared to groups E, F and G on Madeira. The open comparison compares the open coastal series of São Miguel with groups A, B, C, I and H on Madeira. The overall comparison uses the recorded non-endemics from all samples. There is one species unique to group D on Madeira, and two for the disturbed series on São Miguel. Data for Madeira comes from Cameron & Cook (2001).

that, overall, the Madeiran sites contain nearly three times as many endemic species, but roughly the same number of non-endemics. The contrast is due to the much higher proportion of endemics in open habitats on Madeira. Even if all Madeiran forest groups (E, F and G) are combined, they hold only 32 endemics (52%). Open coastal sites on Madeira hold around the same proportion of endemics at both category and site levels as do forest sites, especially taking into account that category I includes many sites in a semi-urban environment around Funchal, and has an exceptional number of non-endemics.

The only Macaronesian endemic common to samples from both islands is *Columella microspora* (discounting *L. erubescens* and *Heterostoma paupercula* as introduced from Madeira). Non-endemics, however, show a great degree of overlap. Table 3 shows the distribution of non-endemics between the two islands, comparing forest and open habitats separately, and the aggregate total. There is a greater difference between open and forest faunas on Madeira (10 species in common, 30% of the total recorded non-endemic fauna) than on São Miguel (15 in common, 53%), but within each habitat and overall, species held in common are never less than 50% of the fauna of each. Furthermore, a significant proportion of species unique to one or other island/habitat category have congeneric equivalents on the other, or are found on the other island, but in a different habitat category. Some of these congenerics are endemic equivalents of more widely distributed species (see above). Only six species in the Madeiran series and three from São Miguel appear to lack equivalents (Table 4); one of these, *T. pisana*, is known from São Miguel (Cunha *et al.*, 2006) but was not recorded in our samples, and *Balea heydeni*, though not known from Madeira, is found on the nearby Porto Santo (Gittenberger *et al.*, 2006; Seddon, in press). The non-endemic faunas of the two islands are very similar, though the universal presence of *Discus rotundatus* in São Miguel forests is a distinctive feature; the related, and endemic, *D. guerinianus* on

Table 4. Non-endemic land-snail species in each island series unique to each, and lacking congeneric equivalents.

Madeira	São Miguel
Truncatellina callicratis†	*Discus rotundatus**
Vallonia excentrica†	*Balea heydeni**
*Plagyrona placida**	*Oestophora barbula*†
Hawaiia minuscula†	
Ferussacia folliculus†	
Theba pisana†	

*These are mainly forest species, relatively frequent in each forest series.
†These are open country species, usually less frequent.

Madeira is very rare, and until recently thought to be extinct (Cameron & Cook, 1999).

The fauna of Madeira as a whole is much richer than that of São Miguel. There are some differences of view as to the number of species-level taxa present (Waldén, 1983; Bank, Groh & Ripken, 2002; Seddon, in press), and a number of non-endemic species appear to be confined closely to very anthropogenic environments, or to be known only as single finds, which may represent transient introductions. Nevertheless, taking the very conservative figures used by Cameron & Cook (1996), the 61 endemic species recorded by Cameron & Cook (2001), omitting two confined to the subalpine zone, represent *ca* 75% of the 80 species recorded live at any time on the island. Thus, the 74 sites from Madeira used here hold a smaller proportion of the known endemic fauna than do the 23 sites sampled on São Miguel.

Excluding non-endemic slugs (most species of which are recorded on both islands), there are *ca* 45 non-endemic species on Madeira (again, a conservative figure), of which 34, again *ca* 75%, are represented in the samples considered here. Twenty-five species are held in common with São Miguel, and a further six are represented by endemic or very similar congeners on the other island. Taking the two archipelagos as a whole, there are very few non-endemic species unique to each, and most of these have very restricted distributions (Cunha *et al.*, 2005; Seddon, in press).

Taxonomically, there are substantial differences between the endemic faunas in terms of the representation of families or equivalent higher groups (Table 5). Apart from the relatively small numbers of endemic species in families found only on one island (Clausiliidae on Madeira, Enidae on São Miguel), the principal differences lie in the Helicoidea and Pupillidae where the Madeiran fauna is much richer than that of São Miguel. This is reflected both in overall recorded faunas on each island, and in the samples analysed above. However, as

Table 5. Numbers of endemic land-snail species in selected higher taxa on each island, both overall, and as recorded in this study and in Cameron & Cook (2001).

	São Miguel		Madeira	
Endemic species	Total	This study	Total	Cameron & Cook
Non-pulmonates	2	2	5	4
Clausiliidae	0	0	5	4
Enidae	3	3	0	0
Helicoidea	3	2	30+	23
Pupillidae	4	3	22	14
Vitrinidae	4	3	5	5
Zonitidae *s.l.*	4	4	2	2

Table 6. The number of endemic species of (A) helicoid and (B) pupillid snails in forested and disturbed habitats on Madeira and São Miguel, and the mean number of such species recorded per site.

	Madeira		São Miguel	
	E	F & G	Disturbed	Forest
(A)				
Helicoids				
No. of species	8	5	2	2
Mean per site	2.0	1.4	1.0	1.3
(B)				
Pupillidae				
No. of species	4	9	2	3
Mean per site	0.4	1.6	1.4	1.9

For E, F and G, see Table 2.

discussed in Cameron & Cook (2001), helicoids on Madeira are predominantly species of open or relatively dry, scrubby habitats. Of the 23 species recorded by them overall, only 10 were found in the forest categories E, F and G (Table 6A). Category E, disturbed and at low altitudes, held the most species, all of which, with the exception of *Leptaxis membranacea*, were also found in the open coastal regions. F and G held fewer species, and only *L. membranacea* occurred at high frequency. The mean number of species per site in these forests is about the same as on São Miguel.

The same does not hold true for the Pupillidae. Of the 14 species recorded on Madeira by Cameron & Cook (2001), only three were missing from categories E, F and G. Furthermore, both the number of species, and the frequency of their overall occurrence were much lower in E than in F and G. Even in the latter, with nine species recorded, the mean number of species per site is less than that in the forest series on São Miguel (Table 6B), where two of the three species recorded are nearly universal.

There is another difference between the faunas that is not conspicuous in Table 5. In the whole Madeiran archipelago there are only two endemic zonitids, *Janulus bifrons* and *J. stephanophora*. *Janulus* is a relict genus, a palaeoendemic surviving on Madeira, but found in tertiary deposits in Europe (Waldén, 1983). There are no native *Oxychilus* species. On São Miguel, there are three endemic species of this genus and, in the Azores as a whole, at least 13 (Cunha *et al.*, 2005).

DISCUSSION

In terms of the overall endemic snail fauna, Madeira and São Miguel differ considerably. Not only is the former much richer than the latter, but the taxonomic composition also differs at family level both in occurrence and in representation of species within families. On the other hand, at site level, endemic faunas in forest habitats on São Miguel are generally slightly richer than those on Madeira, despite the predominance of introduced plant species. The balance between local and regional faunas (Srivastava, 1999) clearly differs between the two islands. Area *per se* cannot account for these differences. Age, accidents of colonization and the range of natural habitats available must have major effects.

It is clear that a substantial part of the difference in overall diversity is due to the natural occurrence of open, scrubby and dry habitats on Madeira. Not only are many endemic species confined to such habitats, but these have fluctuated in extent and connectedness, resulting in the build up of allopatric diversity, especially among the large, thick-shelled helicoids (Cameron & Cook, 2001). No endemic on São Miguel is specific to open habitats. Within forest, the differences are much less marked. The great overlap in non-endemic species or closely related equivalents suggests a similarity in ecological conditions. Among helicoids, there is a striking similarity in the thin-shelled morphology of the two abundant forest species (*Leptaxis membranacea* on Madeira, *L. azorica* on São Miguel), reflecting the rather acid, calcium-poor soils present. Although endemic species found in forests overall are more numerous on Madeira, several, especially helicoids in the lower, more disturbed sites, can be considered as local invaders from the open-country fauna, which is not present on São Miguel. Both in the helicoids, and in the Pupillidae, the mean number of species per site is at least as high on São Miguel as it is on Madeira, where there are many infrequent species with patchy distributions. Although sampling error may contribute to this, many samples from both islands were made by the same person, using the same methods.

Age also has an effect. Within Madeira, the *Laurisilva* has probably remained as a single block throughout Pliocene/Pleistocene climatic shifts (Cameron & Cook, 2001). Unlike in the coastal faunas, it is common to find a number of congeners in close sympatry, or syntopy: occurring at the same site. On São Miguel, the island's history, and especially the existence of two separate islands until around 0.05 Ma is reflected in the allopatric/parapatric distribution of genetically distinct forms of some species (Van Riel *et al.*, 2003, 2005). Others, for example *Oxychilus atlanticus*, (Martins, 2005) show strong interdemic variation in morphological characters with no discernable geographical pattern. In other subtropical or tropical forests of greater age than most of São Miguel, but perhaps comparable to Madeira, local, site, diversity seems to have built up within a region by isolation by distance followed by differentiation and back migration (Solem, 1984; Cameron, Pokryszko & Wells, 2005; Pokryszko & Cameron, 2005). The coexistence of similar congeners may indicate a lack of competitive interactions, or a metapopulation structure that sustains equivalents even in a resource-limiting situation (Hubbell, 2001). In this context, neither Cook (1996) nor Cameron & Cook (2001) could find evidence of negative interactions between endemic and non-endemic species on Madeira and on São Miguel the evidence points the same way. Habitat, or its destruction, explains the number of coexisting endemic species, not the number of non-endemics present. In particular, endemic and non-endemic species of *Oxychilus* are frequently found syntopically on São Miguel. Densities are generally low, and species populations patchy in these forests, in contrast to the more calcareous open habitats, where cases of parapatry amongst congeners are much more frequent.

Finally, there are accidents of colonization. For Madeira, it is clear that at least 20 separate colonization events are required to account for the endemic fauna (Cameron & Cook, 1992; Pokryszko & Waldén, 1992); many genera are palaeoendemic relics of a more widespread late tertiary fauna (Waldén, 1983). Some, at least, of the non-endemic species are natural colonizers (Goodfriend *et al.*, 1996), adding to this number. The large helicoids, for which passive dispersal over considerable sea distances is particularly hard, are easily the most numerous group. The existence of numerous seamounts (Pastouret *et al.*, 1980) between Madeira and Portugal suggests an easier route for such species. No such seamounts straddle the even greater distance between the continent and the Azores. Only two genera of helicoids with endemic species are present in the archipelago, *Leptaxis*, including the aberrant species previously distinguished as *Helixena sanctaemariae* (Van Riel *et al.*, 2005) and *Moreletina* (Cunha *et al.*, 2005). While the environment of São Miguel may always have been hostile to the open-country genera found on Madeira, just the same two genera, represented by four extant and one recently extinct species are found on the nearby Santa Maria, which is drier, more calcareous and has certainly supported more open vegetation. By contrast, Porto Santo, less than half the size of Santa Maria, holds at least 37 helicoid species in at least 11 genera (Cameron & Cook, 1996); more species are known as quaternary fossils.

Around 14 separate colonization events appear to account for the endemic fauna of the Azores. Of these, four, involving the genera *Punctum*, *Acanthinula*, *Spermodea* and *Zonitoides*, involve species represented by more widespread congeners on Madeira (subject to taxonomic revision). Excluding these, it seems likely that there have been around twice as many successful colonizations in the Madeiran archipelago as in the Azores, a product both of greater age and shorter distance to the mainland. Subsequent evolution has multiplied these initial colonizations more on Madeira than on São Miguel in some of the families. There has been more time for it to occur.

Other differences between the two islands appear to be due to chance, or to the character of continental sources. Thus, while introduced, western European *Oxychilus* are present on both, endemics are found only on São Miguel (and on the Azores as a whole); on the basis of vegetation, climate and the non-endemic fauna generally, there is no obvious reason why the genus did not reach, or survive, on Madeira long enough ago to differentiate. Enidae missed Madeira, while reaching both the Azores and the Canaries (Waldén, 1983). Among the non-endemics of São Miguel, *Discus rotundatus* is nearly universal in forests, and often occurs in large numbers. It is recorded only as a restricted, anthropophilic introduction on Madeira. It appears to have reached the Azores sufficiently long ago to spread, but not so as to differentiate.

Whittaker (2000) provides a useful representation of island biotas on two axes: equilibrium/non-equilibrium and dynamic/static, the second relating to the extent of turnover. Although limited to the last 0.2–0.5 My, the fossil record for both Madeira (Goodfriend, Cameron & Cook, 1994; Goodfriend *et al*., 1996) and Porto Santo (Cameron *et al*., 2006) suggests that turnover other than that caused by humans is low. The islands are large relative to the minimum population areas needed by snails. In terms of non-equilibrium, Whittaker distinguishes between the dynamic, disturbed state, where fauna tracks changes in the island's environment (conceived as occurring in ecological time), and the static, relictual case (Brown, 1971) where an island is slowly shedding diversity inherited from an original continental connection.

The island faunas described here seem to fit neither case at all closely. With much evolution at species level occurring within each, they rather resemble the faunas of many continental areas with a slow accumulation of richness, further advanced in old Madeira than in younger São Miguel where, nevertheless, the build up of diversity can be seen at infraspecific level. Disturbance, both volcanic and climatic, appears to create opportunities for speciation, rather than to reduce the fauna (Cameron, Cook & Hallows, 1996; Cook, 1996; Martins, 2005). We have no direct means of knowing whether there is a saturated, equilibrium level, or whether it has been reached on Madeira. The slightly richer site faunas seen in forests on São Miguel than on Madeira suggest that, despite greater differentiation within genera, yet more species could be packed into the latter. Any pre-human equilibrium would seem likely to be more like that envisioned by Hubbell (2001), a balance between extinction and speciation, than between extinction and colonization as conceived by MacArthur & Wilson (1967). For snails, islands of this size are truly continents, although very young ones depend on immigration to start the process of diversification. What happens thereafter depends on the details of island history.

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REFERENCES

BACKHUYS, W. 1975. *Land and freshwater molluscs of the Azores*. Backhuys & Meesters, Amsterdam.

BANK, R.A., GROH, K. & RIPKEN, T.E.J. 2002. Clecom Project: catalogue and bibliography of the non-marine Mollusca of Macaronesia. In: *Collectanea Malacologica, Festschrift für Gerhard Falkner* (M. Falkner, K. Groh & M.C.D. Speight, eds), 89–235. Conch Books, Hackenheim.

BROWN, J.H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. *American Naturalist*, **105**: 467–478.

CAMERON, R.A.D. 2004. From continents to quadrats: species/area relationships in land mollusc faunas. *Journal of Conchology, Special Publication*, **3**: 39–54.

CAMERON, R.A.D. & COOK, L.M. 1992. The development of diversity in the land snail fauna of the Madeiran archipelago. *Biological Journal of the Linnean Society*, **46**: 105–114.

CAMERON, R.A.D. & COOK, L.M. 1996. Diversity and durability: responses of the Madeiran and Porto-Santan snail faunas to natural and human-induced environmental change. *American Malacological Bulletin*, **12**: 3–12.

CAMERON, R.A.D. & COOK, L.M. 1999. Island land snail relocated. *Journal of Molluscan Studies*, **65**: 273–274.

CAMERON, R.A.D. & COOK, L.M. 2001. Madeiran snails:–faunal differentiation on a small island. *Journal of Molluscan Studies*, **67**: 257–267.

CAMERON, R.A.D., COOK, L.M., GOODFRIEND, G.A. & SEDDON, M.B. 2006. Fossil land snails of Porto Santo, Madeiran Archipelago: change and stasis. *Malacologia*., **49**: 25–60.

CAMERON, R.A.D., COOK, L.M. & HALLOWS, J.D. 1996. Land snails on Porto Santo: adaptive and non-adaptive radiation. *Philosophical Transactions of the Royal Society of London, Series B*, **351**: 309–327.

CAMERON, R.A.D. & POKRYSZKO, B.M. 2005. Estimating the species richness and composition of land mollusc communities: problems, consequences and practical advice. *Journal of Conchology*, **38**: 529–547.

CAMERON, R.A.D., POKRYSZKO, B.M. & WELLS, F.E. 2005. Alan Solem's work on the diversity of Australasian land snails: an unfinished project of global significance. *Records of the Western Australian Museum, Supplement*, **68**: 1–10.

COOK, L.M. 1996. Habitat, isolation and evolution of Madeiran landsnails. *Biological Journal of the Linnean Society*, **59**: 457–470.

COWIE, R.H. 1996. Pacific island land snails: relationships, origins and determinants of diversity. In: *The origin and evolution of Pacific island biotas, New Guinea to eastern Polynesia: patterns and process* (A. Keast & S.E. Miller, eds), 347–372. SPB Academic, Amsterdam.

COWIE, R.H. & HOLLAND, B.S. 2006. Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. *Journal of Biogeography*, **33**: 193–198.

CUNHA, R., MARTINS, A.M.F., LOURENCO, P. & RODRIGUES, A. 2005. List of molluscs. In: *A list of the terrestrial fauna (Mollusca and Arthropoda) and flora (Bryophyta, Pteridophyta and Spermatophyta) from the Azores* (P.A.V. Borges, R. Cunha, R. Gabriel, A.F. Martins, L. Silva & V. Viera, eds), 157–161. Direcção Regional do Ambiente and Universidade dos Açores, Angra do Heroismo and Ponta Delgada.

FRANÇA, Z., CRUZ, J.V., NUNES, J.C. & FORJAZ, V.H. 2003. Geologia dos Açores: uma perspectiva actual. *Açoreana*, **10**: 11–140.

GITTENBERGER, E., GROENENBERG, D.S.J., KOKSHOORN, B. & PREECE, R.C. 2006. Molecular trails from hitch-hiking snails. *Nature*, **439**: 409.

GOODFRIEND, G.A., CAMERON, R.A.D. & COOK, L.M. 1994. Fossil evidence of recent human impact on the snail fauna of Madeira. *Journal of Biogeography*, **21**: 309–320.

GOODFRIEND, G.A., CAMERON, R.A.D., COOK, L.M., COURTY, M.-A., FEDEROFF, N., KAUFMAN, N., LIVETT, E. & TALLIS, J. 1996. The Quaternary eolianite sequence of Madeira: stratigraphy, chronology, and paleoenvironmental interpretation. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **120**: 195–234.

HUBBELL, S.P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton.

LOMOLINO, M.V. 2000a. A species-based theory of insular zoogeography. *Global Ecology and Biogeography*, **9**: 39–58.

LOMOLINO, M.V. 2000b. Ecology's most general, yet protean pattern: the species–area relationship. *Journal of Biogeography*, **27**: 17–26.

MACARTHUR, R.H. & WILSON, E.O. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ.

MARTINS, A.M.F. 1995. Terrestrial molluscs of Ilhéu de Vila Franca do Campo, São Miguel, Azores – an illustrated list. *Açoreana, Suplemento Maio de 1995*, 249–260.

MARTINS, A.M.F. 2005. The shaping of a species: the Azorian *Drouetia* Gude (Pulmonata: Zonitidae: *Oxychilus*) as a model. *Records of the Western Australian Museum, Supplement*, **668**: 143–157.

MORTON, B., BRITTON, J.C. & MARTINS, A.M.F. 1998. *Coastal ecology of the Açores*. Sociedade Afonso Chaves, Ponta Delgada.

NASCIMENTO PRADA, S. & SERRALHEIRA, A. 2000. Stratigraphy and evolutionary model of Madeira island. *Bocagiana*, **200**: 1–13.

NEVES, H.C., VALENTE, A.V., FARIA, B.F., DA SILVA, I.G., MARQUES, J.C., GOUVEIA, N.A., DA SILVA, P.G. & OLIVIERA, P.J. 1996. *Laurissilva da Madeira*. Parque Natural da Madeira, Funchal.

PASTOURET, L., AUZENDE, J.-M., LE LANN, A. & OLIVET, J.-L. 1980. Temoins des variations glacio-eustatiques du niveau marin et des mouvements tectoniques sur le banc de Gorringe (Atlantique du Nord-Est). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **32**: 99–118.

PEREIRA, E.C.N. 1967. *Ilhas de Zargo*, Edn 3. Vol. I. Câmara Municipal, Funchal.

POKRYSZKO, B.M. & CAMERON, R.A.D. 2005. Geographical variation in the composition and richness of forest snail faunas in northern Europe. *Records of the Western Australian Museum, Supplement.*, **68**: 115–132.

POKRYSZKO, B.M. & WALDÉN, H. 1992. Anatomical, biometrical and phylogenetic studies on the genus *Leiostyla* (Gastropoda, Pulmonata). In: *Proceedings of the Tenth International Malacological Congress (Tübingen, 1989)* (C. Meier-Brook, ed.), 565–570. Unitas Malacologica, Tübingen.

QUENTAL, R. 1989. *Laurissilva. A floresta da Madeira*. Editorial Correio da Manhã, Funchal.

SCHÄFER, H. 2003. The chorology and diversity of the Azorean flora. *Dissertationes Botanicae*, **374**: 1–130.

SEDDON, M.B. *Illustrated guide to the land-snails of the Madeiran Islands. Studies in terrestrial and freshwater biodiversity and systematics. BIOTIR reports 2*. National Museums and Art Galleries of Wales, Cardiff, in press

SJÖGREN, E. 1972. Vascular plant communities of Madeira. *Boletim do Museu Municipal do Funchal*, **26**: 46–125.

SOLEM, A. 1984. A world model of land snail diversity and abundance. In: *World-wide snails: biogeographical studies on non-marine Mollusca* (A. Solem & A.C. Van Bruggen, eds), 6–22. Brill, Leiden.

SRIVASTAVA, D.S. 1999. Using local–regional richness plots to test for species saturation: pitfalls and potentials. *Journal of Animal Ecology*, **68**: 1–16.

TRIANTIS, K.A., MYLONAS, M., LIKA, K. & VARDINOYANNIS, K. 2003. A model for the species-area-habitat relationship. *Journal of Biogeography*, **30**: 19–27.

TRIANTIS, K.A., VARDINOYANNIS, K. & MYLONAS, M. 2005. Area and habitat relationships in island land snail faunas: an Aegean case study. *Records of the Western Australian Museum, Supplement*, **68**: 133–142.

VAN RIEL, P., JORDAENS, K., VERHAGEN, R., MARTINS, A.M.F. & BACKELJAU, T. 2003. Genetic differentiation reflects geological history in the Azorean land snail *Leptaxis azorica*. *Heredity*, **91**: 239–247.

VAN RIEL, P., JORDAENS, K., VAN HOUTTE, N., MARTINS, A.M.F., VERHAGEN, R. & BACKELJAU, T. 2005. Molecular systematics of the endemic Leptaxini (Gastropoda: Pulmonata) on the Azores islands. *Molecular Phylogenetics and Evolution*, **37**: 132–143.

WALDÉN, H.W. 1983. Systematic and biogeographical studies in the terrestrial Gastropoda of Madeira. With an annotated Check-list. *Annales Zoologici Fennici*, **20**: 255–275.

WARD, S.A. & THORNTON, I.W.B. 2000. Chance and determinism in the development of isolated communities. *Global Ecology and Biogeography*, **9**: 7–18.

WHITTAKER, R.J. 2000. Scale, succession and complexity in island biogeography: are we asking the right questions? *Global Ecology and Biogeography*, **9**: 75–85.

WHITTAKER, R.J. 2001. Wrong in interesting ways. *Journal of Biogeography*, **28**: 1441–1442.

APPENDICES

Appendix 1. Systematic list of species mentioned in text, tables and appendix 2, listed alphabetically by genus.

Acanthinula aculeata (Müller, 1774)
Acanthinula azorica Pilsbry, 1926
Aegopinella nitidula (Draparnaud, 1805)
Balea heydeni Maltzan, 1881
Candidula intersecta (Poiret, 1801)
Caracollina lenticula (Michaud, 1831)
Carychium ibazoricum Bank and Gittenberger, 1985
Carychium minimum Müller, 1774
Cecilioides acicula (Müller, 1774)
Cochlicella barbara (Linnaeus, 1758)
Cochlicopa lubrica (Müller, 1774)
Cochlicopa lubricella (Porro, 1838)
Columella aspera Waldén, 1966
Columella microspora (Lowe, 1852)
Craspedopoma hespericum (Morelet & Drouët, 1857)
Discus guerinianus (Lowe, 1852)
Discus rotundatus (Müller, 1774)
Euconulus fulvus (Müller, 1774)
Ferussacia folliculus (Gmelin, 1790)
Hawaiia minuscula (Binney, 1840)
Helicodiscus singleyanus (Pilsbry, 1890)
Helix aspersa (Müller, 1774)
Heterostoma paupercula (Lowe, 1831)
Hydrocena gutta (Shuttleworth, 1852)
Janulus bifrons (Lowe, 1831)
Janulus stephanophora (Deshayes, 1835)
Lauria anconostoma (Lowe, 1831)
Lauria cylindracea (Da Costa, 1778)
Lauria fasciolata (Morelet, 1860)
Leiostyla fuscidula (Morelet, 1860)
Leiostyla rugulosa (Morelet, 1860)
Leiostyla vermiculosa (Morelet, 1860)
Leptaxis azorica (Albers, 1852)
Leptaxis caldeirarum (Morelet & Drouët, 1857)
Leptaxis erubescens (Lowe, 1831)
Leptaxis membranacea (Lowe, 1852)
Leptaxis sanctaemariae (Morelet & Drouët, 1857)
Microxeromagna armillata (Lowe, 1852)
Moreletina horripila (Morelet & Drouët, 1857)
Napaeus delibutus (Morelet & Drouët, 1857)
Napaeus pruninus (Morelet & Drouët, 1857)
Napaeus vulgaris (Morelet & Drouët, 1857)
Nesovitrea hammonis (Ström, 1765)
Oestophora barbula (Rossmässler, 1838)
Otala lactea (Müller, 1774)
Oxychilus alliarius (Miller, 1822)
Oxychilus atlanticus (Morelet & Drouët, 1857)
Oxychilus cellarius (Müller, 1774)
Oxychilus draparnaudi (Beck, 1837)
Oxychilus miguelinus (Pfeiffer, 1856)
Oxychilus volutella (Pfeiffer, 1856)
Plagyrona placida (Shuttleworth, 1852)
Plutonia atlantica (Morelet, 1860)
Plutonia brevispira (Morelet, 1860)
Plutonia brumalis (Morelet, 1860)
Plutonia laxata (Morelet, 1860)
Punctum azoricum (De Winter, 1988)
Punctum pygmaeum (Draparnaud, 1801)
Rumina decollata (Linnaeus, 1758)
Spermodea monas (Morelet, 1860)
Testacella maugei (Férussac, 1819)
Theba pisana (Müller, 1774)
Toltecia pusilla (Lowe, 1831)
Truncatellina callicratis (Scacchi, 1833)
Vallonia costata (Müller, 1774)
Vallonia excentrica (Sterki, 1892)
Vallonia pulchella (Müller, 1774)
Vertigo pygmaea (Draparnaud, 1801)
Vitrea contracta (Westerlund, 1871)
Zonitoides arboreus (Say, 1816)
Zonitoides azoricus (Riedel, 1964)

Appendix 2. Species of snail (above) and non-endemic slug (below) recorded at each site on São Miguel.

	Forest sites listed from west to east												
Site	1	2	SC	21	9	7	AB	6	F	3	22	13	tot
Altitude (m)	260	260	260	570	750	130	130	250	320	400	200	270	
Snails													
Hydrocena gutta	X	X	X	X	X	X	X		X	X	X	X	11
Craspedopoma hespericum		X											1
Carychium ibazoricum	X	X	X	X	X	X	X	X	X	X	X	X	12
Carychium minimum				X	X			X		X	X		5
Cochlicopa lubrica	X	X	X	X	X	X	X		X	X	X	X	11
Cochlicopa lubricella	X	X						X		X	X	X	6
Columella moreletina	X	X	X	X	X		X	X	X	X	X		10
Columella aspera	X			X	X			X			X	X	6
Vertigo pygmaea											X		1
Leiostyla fuscidula	X	X	X	X	X	X	X		X	X	X		10
Leiostyla rugulosa	X												1
Lauria fasciolata	X	X	X	X	X	X	X	X	X	X	X	X	12
Lauria cylindracea		X		X	X	X		X		X	X	X	8
Vallonia pulchella											X		1
Vallonia costata													0
Acanthinula azorica				X	X			X				X	4
Spermodea monas			X	X	X		X		X				5
Napaeus pruninus	X	X	X			X	X		X		X	X	8
Napaeus vulgaris	X		X	X	X	X	X	X	X		X		9
Napaeus delibutus										X			1
Punctum azoricum	X				X	X		X		X	X	X	7
Toltecia pusilla													0
Discus rotundatus	X	X	X	X	X	X	X	X	X	X	X	X	12
Plutonia brumalis								X		X			2
Plutonia laxata	X	X	X	X	X	X	X	X	X	X	X	X	12
Plutonia atlantica										X			1
Helicodiscus singleyanus	X	X		X	X	X		X					6
Vitrea contracta	X	X	X	X	X	X	X		X	X	X	X	11
Nesovitrea hammonis	X	X	X	X	X	X	X	X	X	X	X	X	12
Oxychilus draparnaudi	X	X	X	X		X	X		X		X		8
Oxychilus cellarius	X			X	X	X		X				X	6
Oxychilus alliarius													0
Oxychilus miguelinus	X	X	X			X	X		X	X	X	X	9
Oxychilus atlanticus	X	X	X	X	X	X	X	X	X	X		X	11
Oxychilus volutella			X			X	X				X	X	5
Zonitoides azoricus													0
Euconulus fulvus			X	X	X		X		X				5
Cecilioides acicula													0
Rumina decollata													0
Balea heydeni	X	X	X			X	X		X				6
Testacella maugei		X	X			X	X		X		X		6
Helix aspersa	X					X					X	X	4
Caracollina lenticula													0
Oestophora barbula							X						1
Microxeromagna armillata													0
Candidula intersecta													0
Cochlicella barbara			X				X				X	X	4
Heterostoma paupercula													0
Moreletina horripila	X	X	X	X		X	X	X	X	X	X	X	11
Leptaxis azorica				X	X					X	X	X	5
Leptaxis erubescens													0
Total species	24	22	22	23	22	23	23	18	20	21	27	22	40
Total endemics	12	10	12	10	10	11	12	8	11	13	12	10	19
Slugs													
Arion distinctus			X		X		X		X	X	X	X	7
Milax gagates			X										1
Limax maximus			X				X	X					3
Lehmannia valentiana	X	X	X				X	X	X		X	X	8
Deroceras reticulatum	X	X	X				X	X		X	X		7
Deroceras panormitanum													0

(*Continued*)

Appendix 2. *Continued*

	Disturbed with some trees								Low open sites near sea				
Site	16	8	23	25	5	4	12	tot	15	14	20	IVF	tot
Altitude (m)	250	700	40	600	520	120	50		40	50	10	30	
Snails													
Hydrocena gutta	X							1					0
Craspedopoma hespericum								0					0
Carychium ibazoricum	X	X	X		X	X	X	6					0
Carychium minimum	X	X	X		X	X		5		X			1
Cochlicopa lubrica	X	X	X	X	X	X	X	7					0
Cochlicopa lubricella	X		X		X	X	X	5		X			1
Columella microspora		X		X				2					0
Columella aspera		X			X		X	3					0
Vertigo pygmaea				X				1		X		X	2
Leiostyla fuscidula	X	X				X	X	2				X	1
Leiostyla rugulosa								0					0
Lauria fasciolata	X	X	X		X	X	X	6		X		X	2
Lauria cylindracea	X	X	X			X		4		X	X	X	3
Vallonia pulchella		X	X					2		X	X	X	3
Vallonia costata			X					1					0
Acanthinula azorica		X						1					0
Spermodea monas								0					0
Napaeus pruninus		X						1					0
Napaeus vulgaris	X		X				X	3	X	X	X		3
Napaeus delibutus		X			X			2					0
Punctum azoricum			X		X	X		3				X	1
Toltecia pusilla			X			X		2		X		X	2
Discus rotundatus	X	X	X	X		X	X	6	X	X		X	3
Plutonia brumalis		X			X			2					0
Plutonia laxata							X	1					0
Plutonia atlantica		X		X	X			3					0
Helicodiscus singleyanus	X						X	2		X	X		2
Vitrea contracta	X	X	X	X	X	X	X	7	X	X		X	3
Nesovitrea hammonis	X	X	X	X	X	X	X	7					0
Oxychilus draparnaudi	X	X	X		X	X	X	6		X	X	X	3
Oxychilus cellarius		X		X		X		3		X			1
Oxychilus alliarius								0		X		X	2
Oxychilus miguelinus						X	X	2					0
Oxychilus atlanticus	X	X					X	3					0
Oxychilus volutella	X					X		2					0
Zonitoides azoricus			X					1					0
Euconulus fulvus							X	1				X	1
Cecilioides acicula			X					1				X	1
Rumina decollata								0	X				1
Balea heydeni	X		X			X		3					0
Testacella maugei								0				X	1
Helix aspersa	X	X	X		X	X	X	6	X	X	X		3
Caracollina lenticula								0				X	1
Oestophora barbula			X					1		X			1
Microxeromagna armillata								0	X	X		X	3
Candidula intersecta								0			X		1
Cochlicella barbara	X		X				X	3	X	X	X	X	4
Heterostoma paupercula								0			X		1
Moreletina horripila			X		X	X	X	4					0
Leptaxis azorica		X		X	X			3					0
Leptaxis erubescens			X					1					0
Total species	19	22	23	9	16	19	19	41	7	18	9	18	27
Total endemics	6	9	5	3	7	6	7	17	1	2	1	3	4
Slugs													
Arion distinctus	X	X	X		X	X		5					0
Milax gagates		X						1					0
Limax maximus		X			X			2					0
Lehmannia valentiana		X	X		X	X		4				X	1
Deroceras reticulatum	X	X	X		X	X	X	6		X		X	2
Deroceras panormitanum		X	X		X	X		4				X	1