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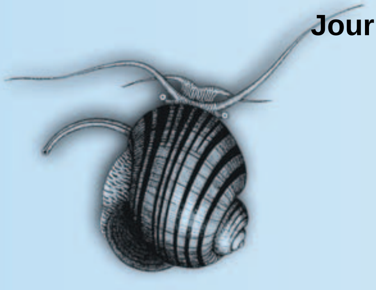

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LAND SNAIL FAUNAS ON SANTA MARIA (AZORES): LOCAL DIVERSITY IN AN OLD, ISOLATED AND DISTURBED ISLAND

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ABSTRACT

Sampling of land snails in 19 small sites on Santa Maria (Azores) in 2008 and 2011 yielded a total of 52 species; 26 were Macaronesian endemics, of which 23 are restricted to the Azores. These represent nearly all the described endemic fauna. Forest faunas were the richest and contained the highest proportion of endemic species. Widespread European species were the major components of assemblages in open habitats, subject to greater human disturbance, while secondary or heavily disturbed forests were intermediate. A small suite of endemic species showed no habitat preference and may represent a fauna living in relatively open conditions prior to human occupation. Within forests, congeneric species frequently occur in the same site. All seven endemic *Oxychilus* species recorded occurred in a single site; there is no evidence of allopatric replacement or restricted distribution other than that imposed by habitat. This may reflect the age of the island, the oldest in the archipelago. Nearly all forest endemics are found near the summit of the highest peak, a small area vulnerable to habitat destruction or climate change; even without these, there may be an extinction debt to be paid in the absence of conservation measures.

INTRODUCTION

As in other oceanic island archipelagos (Solem, 1984; Cowie, 1996; Seddon, 2008), the land snail fauna of the Azores contains a rich array of endemic species, many confined to single islands (Cunha *et al.*, 2005), a pattern seen in most of the fauna and flora of such islands (Whittaker & Fernández-Palacios, 2007). Consideration of within-island and within-archipelago evolution, and of the changes in size and topography of islands with age, has led to the development of general models (Triantis *et al.*, 2003; Whittaker, Triantis & Ladle, 2008; Hortal *et al.*, 2009) relating diversity to area and to the variety of available habitats or to the ages of the islands, the latter reflecting the sequence of emergence, growth, erosion and subsidence of oceanic islands (Whittaker & Fernández-Palacios, 2007). The habits and powers of dispersal of the taxa involved also influence the patterns observed (Borges & Hortal, 2009).

After colonization, the process of speciation generates this diversity and the age and environmental history of the islands will determine the patterns seen. Several patterns have been observed among snail faunas. One such is allopatric or parapatric replacement of sister species, as found by Cameron, Cook & Hallows (1996) on Porto Santo (Madeiran archipelago). Such patterns are not confined to oceanic islands (e.g. Solem, 1988). Gittenberger (1991) described them as examples of nonadaptive radiation, where the ecologies of each species were very similar. A vicariance model of repeated range fragmentation is often cited as the cause of such patterns, but rare dispersal events over barriers may also be involved, as in the occurrence of sister species on different islands within an archipelago (Rundell, 2008).

In other cases, sites may hold several congenerics and ranges do not give a clear signal as to how such diversity evolved. Solem (1984) suggested a slow build up of diversity within habitats that had persisted for a long time. By implication this involved isolation by distance and back migration. Such local co-existence may not require ecological differentiation. Dispersal limitation and fluctuating environments can allow equivalents to coexist (Auerbach & Shmida, 1987). Nekola, Coles & Bergthorsson (2009) report cases of multiple microsympatry in the *Vertigo gouldii* group of North America stemming from a Miocene radiation and Pokryszko *et al.* (2011) report a similar case in Caucasian *Leiostyla*. Cameron & Cook

(2001) found a similar situation in the snail fauna of Madeiran *Laurissilva* forests. We do not know if a theoretical upper limit to such syntopic diversity is ever reached, but we might expect lower site diversities on young islands on which diversity was still increasing.

Young islands also present us with the initial stages of diversification. Molecular studies on the Hawaiian *Succinea caduca* reveal a complex pattern of within-island vicariance and dispersal on the largest and youngest island in the chain (Holland & Cowie, 2007) and the anatomical study of differentiation within *Oxychilus atlanticus* on São Miguel (Azores) suggests similar processes (Martins, 2005).

Within the Azores, Santa Maria is much the oldest island (França *et al.*, 2005). Endemic snail diversity is slightly higher than that of the younger São Miguel, which is eight times as large (Martins, 2011). This study set out to determine levels of local diversity, the existence, if any, of geographical replacements or ecologically distinct faunas and the extent of local coexistence of closely related species. A comparison is made with similar studies on São Miguel (Cameron, Cunha & Martins, 2007). The Azores have a large number of nonendemic species that are apparently native and our analyses include them in some cases. The study also places on record details of faunas which may no longer survive at the observed levels of diversity and which may have suffered losses prior to 2008.

MATERIAL AND METHODS

The island

Santa Maria is the easternmost island in the Azores archipelago. It is *c.* 97 km^2 in area, and its highest point (Pico Alto) is 587 m a.s.l. (Fig. 1). It is the oldest island in the archipelago; it holds rocks *c.* 8 Ma; the youngest date to *c.* 2 Ma (references in França *et al.*, 2005). It is *c.* 1,300 km from the European mainland, with no seamounts in between, and *c.* 90 km from São Miguel, the nearest island. Parts of São Miguel may be 4 Ma, although recent work suggests it may be much younger (Johnson *et al.*, 1998); other Azorean islands are also younger. Apart from the tiny Porto Santo (Madeiran archipelago), *c.* 14 Ma and 580 km from Santa Maria, the only potential source of early colonization nearer than the mainland is the now submerged Great Meteor seamount to the south (Fernández-Palacios *et al.*, 2011).

Santa Maria is the driest and warmest of the Azorean islands; the climate is very oceanic, with moderate rainfall (*c.* 600 mm/year), and only *c.* 6°C difference between mean July and January temperatures. While most of the island consists of volcanic rocks, there are some small areas of calcareous soils derived from shell sand blown on shore, especially near Praia on the south coast. These contain both marine and terrestrial fossil shells.

Uninhabited by humans until colonized by the Portuguese, Santa Maria had permanent residents by 1432 (Morton, Britton & Martins, 1998). It appears that the Azores were generally forested down to sea level prior to colonization, predominantly by *Laurissilva* (Fernández-Palacios *et al.*, 2011), although there are no detailed pollen or macrophytic records for Santa Maria. Forests were extensively cleared by humans (Martins, 1993; Triantis *et al.*, 2010); while small amounts of *Laurissilva* survive on São Miguel and on some other islands, native trees are now rare on Santa Maria. Forest cover on higher ground is mostly plantations of *Cryptomeria japonica*, or planted and regenerating *Pittosporum undulatum*, an introduced laurel-like species. In such forests the introduced *Hedychium gardneranum* usually dominates the herb layer unless the canopy is so dense as to suppress plant growth. At lower altitudes, forested patches are usually small and isolated, and contain a mixture of alien trees; eucalypt species are widely planted. Some patches are clearly secondary growth on previously open land. The herb layer is often dominated by brambles (*Rubus* spp.) or bracken. Open habitats are mainly grassy, but with introduced species such as prickly pear and agave. Rocks and dry stone walls provide cover for molluscs in such habitats.

Sampling

Seventeen samples were made in September 2008. For these, each site of *c.* 400 m^2 was searched for approximately two person-hours and *c.* 10 l of litter were sieved through a coarse mesh (10 mm) sieve (Cameron & Pokryszko, 2005). Material passing through the sieve was bagged, dried and sorted in the laboratory. Each site was located by using the Global Positioning System and a brief description of the habitat was

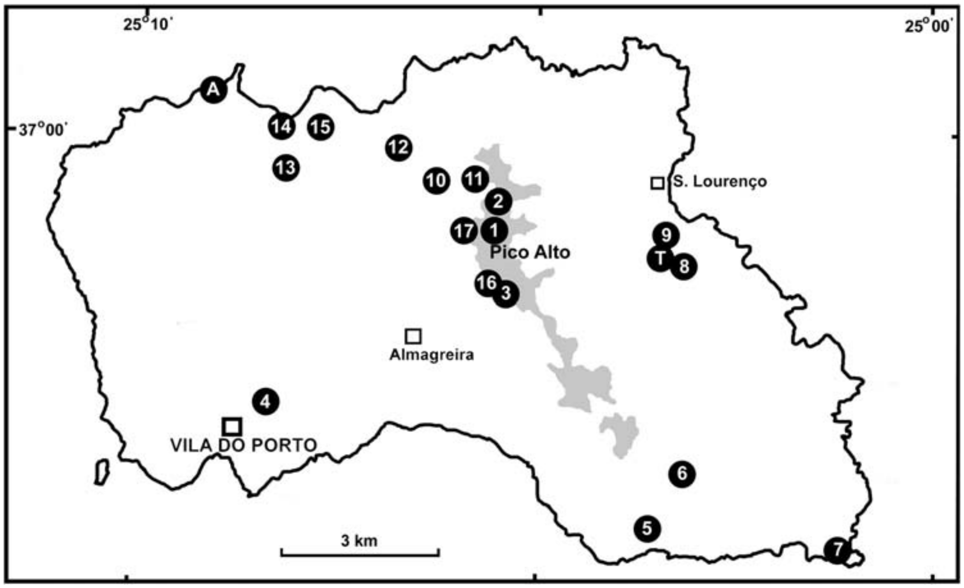

Figure 1. Map of Santa Maria showing the locations of sample sites. Land above 400 m is shaded grey.

made (Supplementary material Appendix S1). The distribution of sites is shown in Figure 1. All live snails and fresh, identifiable shells were identified and counted. Slugs are not included in our analyses, as the sampling methods used are not appropriate (Cameron & Pokryszko, 2005). All slugs recorded from Santa Maria are widespread species.

Two further samples (labelled A and T in Supplementary material Appendices and Fig. 1) were made in June 2011 to increase the number of sites in the open and in secondary woodland. These involved several person-hours search, but only small quantities of litter were examined. Only presence of species was recorded. These samples are omitted from some analyses.

Recent systematic work on the island fauna has revealed a number of as yet undescribed species (Martins, 2011). Where the diagnostic characters are known, we refer to them by notional generic name (thus '*Oxychilus*') and a number. Nomenclature follows Cunha *et al*. (2005) with later additions. Authorities are given in Supplementary material Appendix S2. Voucher specimens are held at the University of the Azores and in the Museum of Natural History, Wrocław.

Many of our analyses consider Azorean or Macaronesian endemics separated from species with a wider distribution. In this context, we treat *Balea heydeni* von Maltzan, 1881 as an Azorean endemic; although now widespread in Western Europe, there is good evidence to suggest that it originated in the Azores (Gittenberger *et al*., 2006). *Fauna Europaea* (Bank, 2010) regards *Zonitoides azoricus* Riedel, 1964 as a junior synonym of *Z. arboreus* (Say, 1817), but we have treated it as a distinct endemic. Among species with a wider distribution, there is no fossil evidence as to which are native and which are introduced by humans.

No natural *Laurissilva* remains on the island. We have split the habitats sampled into three types: forests with mature trees and closed canopy; more disturbed but partly wooded sites representing secondary succession on previously open land, or areas kept in a scrubby state by repeated cutting; and open sites in which there are at most only isolated bushes. Site 4, discussed below, was hard to fit into this scheme because it had a mix of exotic trees and evidence of grazing.

The number of sites on which this study is based is very modest. It was intended to make more samples at a later date. However, regular local monitoring over several decades has detected a decline in many species (A.M.F. Martins, unpubl.) and it was noticeably harder to find specimens in 2011 even than in 2008, an exceptionally dry period having intervened.

Analyses

Given this modest number of samples, and the great variations in numbers of individuals of any one species retrieved even from samples in the same habitat, we have used very simple analytical techniques rather than commonly used multivariate methods. The Kruskal–Wallace test is used to examine differences in number and proportions of species and individuals among habitats. For faunal similarity, we use the Simpson Index, taking the number of species held in common between two samples as a proportion of the numbers found in the least rich sample in the pair. Thus a sample that contains only an impoverished set of species present in another will yield an index of 100%. Given the range of species richness observed (12–31 species), and the manifold effects of disturbance, this gives a conservative estimate of faunal relationships.

RESULTS

In total we found 52 species (24 Azorean and 2 Macaronesian endemics and 26 species with wider distribution). Of these, 51 among 9,201 shells were recovered from the quantitative samples made in 2008. Appendix S2 (Supplementary material) shows the numbers of each species found at each site for 2008 samples, and occurrences in the two samples from 2011. For the quantitative samples, none have less than 10 times as many individuals as species, and the mean and median Chao 1 estimator of missing species are both less than one (data not shown) (Cameron & Pokryszko, 2005). Thus although there is a positive association between the number of individuals and number of species among samples (Pearson's $r = 0.508$, $P < 0.05$) the inventories appear to be adequate for the analyses that follow. Table 1 shows the summary statistics by habitat and by the endemic *vs* widespread divide.

There are significant differences among habitats (Table 2). Forest sites hold more endemic species than do disturbed or open ones. Endemic species constitute a higher proportion of the total in forests, and are represented absolutely and relatively by more individuals. Differences between open and disturbed habitats are less marked; the disturbed sites have more endemic species in aggregate than do open sites and constitute a greater proportion of the faunas. Among widespread species, differences in richness and abundance are much smaller. Open sites have more such species overall, and on average per site, than others.

Table 1. Basic data from the samples from Santa Maria, given for endemic and widespread species separately, and overall.

	Forest	Disturbed	Open
Number of sites	9	4 (5)	4 (5)
Endemic total species	25	16	10
Endemic mean species/site	14.9	7.2	5.1
Endemic range species/site	11–20	4–9	2–8
Widespread total species	19	14	22
Widespread mean species/site	9.8	9.2	13.6
Widespread range species/site	8–15	6–11	9–19
Mean % endemic/site	60.4	43.4	27.1
Range % endemic/site	46.4–70.4	33.3–57.1	12.5–35.7
Endemic mean individuals/site	444	130	131
Endemic range individuals/site	273–625	91–184	49–219
Widespread mean individuals/site	196	284	314
Widespread range individuals/site	56–483	110–542	185–491
Mean % endemic/site	71.6	37.0	29.8
Range % endemic/site	41.3–88.8	14.4–53.9	17.1–54.2
Total all species	44	30	32
Mean all species/site	24.7	16.4	19.0
Range all species/site	19–31	12–20	14–27
Mean all individuals/site	641	414	445
Range all individuals/site	455–1051	230–633	287–623

For data on species, the two qualitative samples made in 2011 are included. This is not possible for data concerning individuals.

Table 2. Kruskal–Wallace tests for differences among habitats on Santa Maria.

Comparison	χ^2	P
No. of endemic species	14.0	<0.001
No. of widespread species	6.9	<0.05
% endemic species	14.7	<0.001
% endemic individuals	9.5	<0.01

χ^2 has two degrees of freedom.

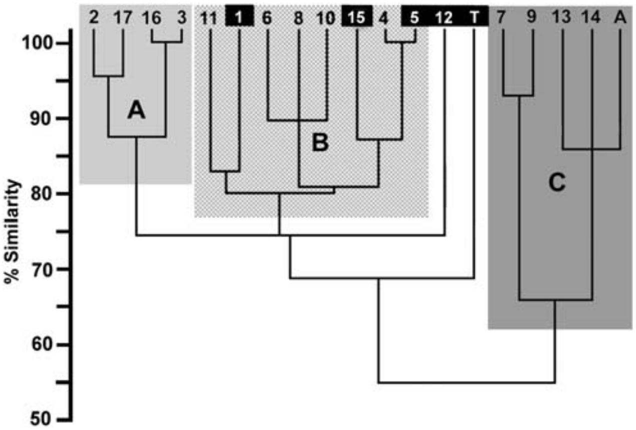

Figure 2. Dendrogram of site similarities estimated from the Simpson Index (UPGMA clustering). **A.** Forest sites from Pico Alto. **B.** Other forest and disturbed sites. Disturbed sites have white lettering on black. **C.** Open sites.

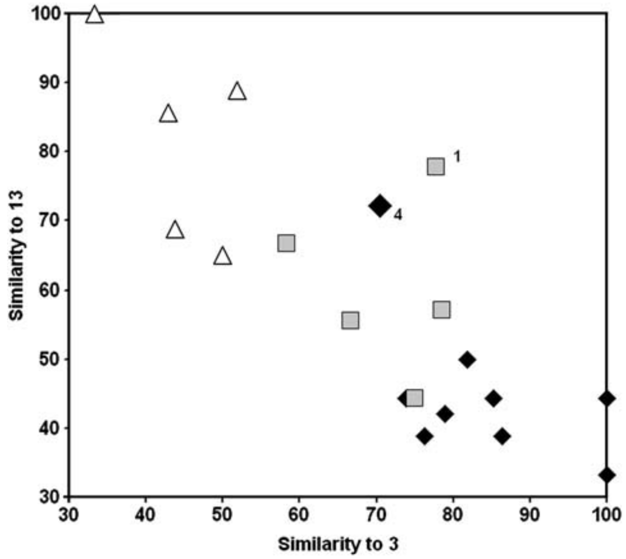

Figure 3. The scatter of site faunas on Simpson similarities to those of sites 3 and 13, the least similar in the array from Santa Maria (see text). Symbols: black diamonds, forests; grey squares, disturbed; open triangles, open habitats.

Individual sites in all habitats contain between a third and three quarters of all species recorded for their habitat. Potentially some pairs of sites could have no species in common. The matrix of Simpson Index similarities shows that this is not the case (Supplementary material Appendix S3); the smallest value is 33.3% and the mean 68.1%. Figure 2 shows the clustering of sites. Faunas from open sites (Group C) are clearly distinct from forest and disturbed sites, but associate together finally at a rather low level of similarity. Among the forest and disturbed sites, Group A contains four forest sites close together around the summit of Pico Alto. These, the richest faunas, are concentrated around the only area where substantial forest stands survive. Group B and the outliers (12 and T) are more geographically dispersed (Fig. 1). Among the disturbed sites, the fauna of site 5 is simply a reduced version of that in site 4, and site 1 is disturbed scrub at the summit of Pico Alto.

This clustering reflects the difference between the richest forest faunas and those typical of entirely open habitat, as shown in Figure 3. Disturbed forest site faunas fall between these two extremes and lack distinctive species. Figure 3 highlights the peculiarity of site 4, a rich fauna (28 species) with large numbers of both endemic and widespread species. Site 1, on the summit of Pico Alto, has fewer endemic species than surrounding forest, but has not acquired a richer fauna of widespread species.

The relatively high mean level of similarity among sites arises because there are some species that are found in all or most sites (Table 3). Two species, *Oxychilus draparnaudi* and *Cochlicopa lubricella*, were found in all sites. Given the small number of samples involved, only the most extreme differences in proportion of sites occupied among habitats would yield statistically significant differences. However, we note that among species occurring in at least 60% of samples in at least one habitat (Table 3), there are both widespread and endemic species that appear not to discriminate among habitats, and also some which run counter to the overall trend for endemics to be more frequent in forests and widespread species to be more frequent in the open. Thus *Nesovitrea hammonis*, *Carychium minimum*, *C. ibazoricum* and *Columella aspera* show primarily forest distributions among the widespread species, while among endemics *Leptaxis sanctaemariae*, *Napaeus tremulans* and *N. hartungi* show no discrimination, and *Lauria fasciolata* is most frequent in the open. These four endemics are the only ones to occur in large numbers in any open site (Supplementary material Appendix S2). The only endemic not recorded in forests, *Moreletina obruta*, occurred in only one site. By comparison, 16 out of the 26 endemic species were not recorded from any open site.

There are no indications of geographical patterns in distribution other than those resulting from environmental constraints. Twenty-one out of the 25 endemic species recorded in forests occur in the three sites near the summit and south-western slopes of Pico Alto (2, 3 and 16). The remaining four were all very infrequent and with the exception of *Spermodea monas* were found in very small numbers. *Moreletina obruta*, the only endemic not found in forests, was found only at site A, but it is known from other open coastal sites and is found subfossil at Praia on the south coast. Congeneric endemic species are frequently found together at the same sites; all seven endemic *Oxychilus* species found were present at site 16 and six in both sites 2 and 3. The two *Napaeus* species, both very widely distributed, were usually found together.

DISCUSSION

It is possible that not only have we missed some species present at our sites, but that decline in abundance and occurrence in recent decades has removed some species present at the sites in the recent past. Nevertheless, the 26 Macaronesian endemics recorded here represent all but two of the described species known from the island (*Acanthinula azorica* and *Leiostyla fuscidula*). We failed to find three known but undescribed taxa (an *Oxychilus*, a *Napaeus* and a helicoid related to *Moreletina*), but found all remaining known but undescribed species (Supplementary material Appendix S2). Rather more of the widespread species known to occur on the island were not found, almost exclusively rather large species strongly associated with human activity. Our survey represents an adequate sample of the snail fauna, especially of forests.

Taking all species together, levels of local species richness in forests are on a par with those recorded in continental studies off limestone (Pokryszko & Cameron, 2005; Stanisic *et al.*, 2007). They are marginally richer than those on São Miguel and have a higher proportion of endemic species (Cameron *et al.*, 2007). On Corvo (*c.* 0.71 Ma; França *et al.*, 2005), forest

Table 3. Occurrences by habitat of snail species recorded in more than 60% of samples in any one habitat on Santa Maria.

	Total	Forest	Disturbed	Open
Sites	19	9	5	5
Widespread				
Cochlicopa lubricella	**19**	**9**	**5**	**5**
Oxychilus draparnaudi	**19**	**9**	**5**	**5**
Vitrea contracta	**17**	**9**	**4**	**4**
Cochlicopa lubrica	15	8	4	3
Nesovitrea hammonis	**14**	**7**	**5**	**2**
Discus rotundatus	13	3	5	5
Euconulus fulvus	13	6	4	3
Lauria cylindracea	12	5	2	5
Carychium minimum	**12**	**9**	**3**	**0**
Carychium ibazoricum	**10**	**6**	**2**	**2**
Testacella maugei	8	5	0	3
Vallonia pulchella	7	3	0	4
Vertigo pygmaea	6	1	1	4
Helix aspersa	6	0	3	3
Columella aspera	**5**	**3**	**2**	**0**
Otala lactea	5	0	0	5
Candidula intersecta	3	0	0	3
Cochlicella barbara	4	0	0	4
Endemic				
Leptaxis sanctaemariae	**17**	**9**	**4**	**4**
Napaeus tremulans	**16**	**9**	**3**	**4**
Napaeus hartungi	**14**	**7**	**2**	**5**
Balea heydeni	14	9	4	1
Craspedopoma hespericum	13	8	3	2
Lauria fasciolata	**12**	**4**	**3**	**5**
'*Oxychilus*' sp. 1	12	8	2	2
Punctum azoricum	12	7	3	1
Oxychilus brincki	12	9	3	0
Columella microspora	12	9	3	0
Oxychilus spectabilis	11	8	3	0
Oxychilus lineolatus	8	7	1	0

Species in bold show either no trend with habitat, or a trend opposite to that shown by the group (endemic or widespread) as a whole.

sites held 10–11 endemic species each (A.M.F. Martins *et al.*, unpubl.). A very intensive study of a larger patch of montane forest on the island of Hawaii (*c.* 0.5 Ma) involving the collection of more than 12,000 shells revealed 16 species, 15 of which were endemic (Cowie *et al.*, 1995). While this total of endemics does not differ greatly from the 21 endemic species found around the summit of Pico Alto, we note that Hawaii has older islands nearby from which multiple colonizations could take place. Allowing for such colonizations, younger islands appear to have poorer local endemic faunas.

In a comparison of the faunas of Madeira and São Miguel, Cameron *et al.* (2007) attributed the extreme rarity of endemics in open habitats in the latter to the absence of natural open habitats. *Laurissilva* is thought to have extended to sea level in the Azores prior to human colonization (Fernández-Palacios *et al.*, 2011). In contrast, natural vegetation resembling Mediterranean maquis occupied low altitudes along the south coast of Madeira (Sjögren, 1972); it holds a characteristic suite of endemic species (Cameron & Cook, 2001). Although only one endemic, *Moreletina obruta*, was unique to our open sites, the number of endemics found overall was greater, and the mean per site higher, than on São Miguel. Only one out of four endemic species recorded in the open on São Miguel, *Napaeus vulgaris*, occurred in more than half the open sites. The very similar Santa Marian *N. hartungi* was one of three species showing no clear habitat preference. Although the evidence is sparse, there appears to be a small suite of endemic species capable of living in open habitats. Apart from the known occurrence of *Moreletina obruta* in the open on the south coast, there are undated subfossil shells of this species, the two *Napaeus* species and others that are associated with *Otala lactea* and *Cochlicella barbara*, two widespread species typical of open habitats. The deposits also contain the endemic but apparently recently extinct *Leptaxis vetusta* (Morelet & Drouet, 1857), a large, heavy-shelled species resembling open habitat species of the same genus on Madeira and Porto Santo, and very different from the forest dwelling *Leptaxis* species in either archipelago (Callapez, Soares & Marquez, 2003). The tall-spired *Leptaxis sanctaemariae* also tolerates open habitats and is one of the most abundant and widespread species on the island. All other Azorean *Leptaxis* are strictly forest species. *Leptaxis sanctaemariae* evolved within the Azorean *Leptaxis* clade and is not an outlier (Jordaens *et al.*, 2009). We tentatively suggest that some low-lying parts of Santa Maria were less fully forested prior to human colonization than on São Miguel and that, as in Madeira, elements of the endemic fauna found there were capable of surviving in deforested, anthropogenic habitats.

There is no trace of any pattern of allopatric replacement of sister species. While this might reflect extinctions in parts of the island in which forest has been destroyed together with such sister species, we note that the great majority of endemic forest species are found together around the summit of Pico Alto, the only high-altitude ridge on the island. All seven endemic *Oxychilus* species recorded were found in the same site. While the island is small, it is three times the size of Porto Santo, where such replacements are common (Cameron *et al.*, 1996) and can be related to repeated fragmentation of suitable habitats. Both for *Oxychilus* and for the as yet undescribed helicoids related to *Moreletina*, Santa Maria is richer in species than the larger but younger islands further west (Martins, 2011). The pattern resembles that seen in continental regions where suitable habitats have remained continuous for millions of years (Solem, 1984; Pokryszko *et al.*, 2011), and provides no evidence of competitive exclusion. As Santa Maria is the oldest of the Azorean islands and very isolated from mainland sources, it seems likely that this syntopic diversity has evolved *in situ*; divergence can occur in a very small area.

We do not know which of the widespread species are native, or how long they have been present. They generally show habitat preferences similar to those known from other parts of their ranges and most are also found on São Miguel (Cameron *et al.*, 2007). The larger species occupying open habitats are almost certainly introduced, as is *Oxychilus draparnaudi*. The smaller species occurring most frequently in forests are more likely to be native. We note that some endemics such as *Punctum azoricum* and *Spermodea monas* are very similar to their continental congenerics, suggesting a relatively recent arrival. Only molecular analyses can give us estimates of the timing or sequence of lineage divergence. There is no evidence of any competitive replacement. On Madeira the presence of widespread species appeared to have no effect on the number of endemic species (Cameron & Cook, 2001) and Chiba *et al.* (2009) report an absence of connection between numbers of indigenous and introduced species on Hahajima (Ogasawara Islands, Japan).

Oceanic island snail faunas are notoriously vulnerable to extinction by habitat destruction and introduced predators (Solem, 1990; Paulay, 1994; Lydeard *et al.*, 2004). While the Madeiran fauna has proved more resilient than those on many other archipelagos (Cameron & Cook, 1996), we have no firm evidence for the Azores, other than the presumed recent extinction of *Leptaxis vetusta*. Certainly, the endemic forest faunas on Santa Maria appear to be rich, especially around Pico Alto, despite the secondary nature of most forests. By contrast Chiba *et al*. (2009) document a drastic decline in local endemic faunal richness in areas of earlier forest clearance on the Ogasawara Islands, even though regeneration has taken place subsequently. The areas in which such faunas survive on Santa Maria are very small; Triantis *et al*. (2010) demonstrate for Azorean arthropods that present richness may be much greater than that which is sustainable in the absence of restoration and conservation measures; there is a time lag between habitat modification and multiple extinctions, an extinction debt that has yet to be paid. While the recent unquantified decline in distribution and abundance of some endemic species on Santa Maria may in part reflect short-term climatic changes, our study emphasizes the vulnerability of species now confined to small, isolated pockets of suitable habitats.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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