

Extinction debt on oceanic islands

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Habitat destruction is the leading cause of species extinctions. However, there is typically a time-lag between the reduction in habitat area and the eventual disappearance of the remnant populations. These “surviving but ultimately doomed” species represent an extinction debt. Calculating the magnitude of such future extinction events has been hampered by potentially inaccurate assumptions about the slope of species–area relationships, which are habitat- and taxon-specific. We overcome this challenge by applying a method that uses the historical sequence of deforestation in the Azorean Islands, to calculate realistic and ecologically-adjusted species–area relationships. The results reveal dramatic and hitherto unrecognized levels of extinction debt, as a result of the extensive destruction of the native forest: >95%, in <600 yr. Our estimations suggest that more than half of the extant forest arthropod species, which have evolved in and are dependent on the native forest, might eventually be driven to extinction. Data on species abundances from Graciosa Island, where only a very small patch of secondary native vegetation still exists, as well as the number of species that have not been found in the last 45 yr, despite the extensive sampling effort, offer support to the predictions made. We argue that immediate action to restore and expand native forest habitat is required to avert the loss of numerous endemic species in the near future.

In their natural state, oceanic islands typically support a substantial proportion of endemic species, many of which have been lost as a direct consequence of recent human habitation (Steadman 2006, Whittaker and Fernández-Palacios 2007). The biodiversity “crisis” is thus nowhere more apparent and in need of urgent action than on remote islands (Paulay 1994). The majority of the documented extinctions since ca AD 1600 are of species endemic to oceanic islands. Although the specific causes of these extinctions are often difficult to attribute (Whittaker and Fernández-Palacios 2007), the primary drivers are the habitat destruction and fragmentation universally associated with human colonization, in combination with other factors

such as the introduction of non-native species (Paulay 1994, May et al. 1995, Blackburn et al. 2004, Steadman 2006, Hanski et al. 2007, Whittaker and Fernández-Palacios 2007).

Habitat destruction is rarely absolute and typically results in many species being reduced to a few small, isolated populations, each susceptible to a variety of stochastic factors such as random fluctuations in demography, changes of the local environment and the erosion of genetic variability (Lande 1993). Hence, it can take several generations for the full impact of habitat destruction and fragmentation to be visible in the number of extinctions (Tilman et al. 1994, Helm et al. 2006, Vellend et al. 2006).

This time-lag represents an “extinction debt” (Tilman et al. 1994) – a future ecological cost of habitat destruction that may not be initially apparent in studies made shortly after habitat loss has occurred. For this reason it is probable that the true ecological costs of the historically recent spate of habitat destruction, disturbance and fragmentation on many oceanic islands are yet to be realised (Diamond 1989), i.e. there exist many extant but seriously imperilled species.

Developing methods to quantify the magnitude and taxonomic distribution of the extinction debt is clearly important for effective conservation planning and prioritization. However, accurate assessment of extinction rates and their extrapolation into the future requires robust long-term data on species occurrences – data which are rarely available, especially for less conspicuous taxa such as invertebrates. The lack of appropriate knowledge has led to an inevitable reliance on indirect measures and theoretical projections of extinctions (McDonald and Brown 1992, Heywood et al. 1994, May et al. 1995, Pimm et al. 1995, Brooks et al. 1997, Rosenzweig 2001, Brook et al. 2003, Whittaker et al. 2005, Kuussaari et al. 2009, Ladle 2009).

One of the most commonly used methods for estimating future extinctions is to extrapolate from the characteristic form of the classic island species–area relationship [$S = cA^z$, where S is the number of species, A is (island) area, and c and z are constants] derived from island biogeography theory (Preston 1962, MacArthur and Wilson 1967). The consequences of habitat loss under this framework can be predicted following the “rule of thumb” calculation that a 10-fold decrease in area results in a twofold decrease in species (Darlington 1957), or alternatively, when an area of habitat is reduced by 90%, the number of species eventually drops to one half. This approach has been applied at varying – sometimes very coarse – scales to forecast species losses as a function of habitat loss due to factors such as deforestation (Brooks et al. 2002) or future climate change (Thomas et al. 2004). Even though the accuracy of this approach critically rests upon accurate estimation of the slope (z) of the relationship (Rosenzweig 2001, Whittaker et al. 2005, Lewis 2006, Whittaker and Fernández-Palacios 2007), it has been commonplace to assume $z = 0.25$ across a range of different taxonomic groups, scales and ecogeographical systems (May et al. 1995, Brooks et al. 2002, Thomas et al. 2004).

Although arthropods represent the bulk of all known living species, the level of threat imposed by global environmental changes to arthropod diversity remains poorly documented (Brooks et al. 2006, Fonseca 2010). Dunn (2005) has estimated that roughly 44 000 insect extinctions have occurred in the last 600 yr, but the number of extinctions documented during this period is 61 species (IUCN 2009; the respective number for arachnids is zero). Here, we apply a method that uses the historical information on deforestation on the Azores (a remote Atlantic Ocean archipelago) to generate more accurate estimates of local extinctions or extirpations (hereafter extinctions) for the endemic forest-dependent species of three well-studied groups of arthropods from the Azores, namely the spiders (Araneae), the true bugs (Hemiptera) and the beetles (Coleoptera). This approach has been used in a few mainland systems (Pimm and Askins 1995, Helm et al.

2006, see also Kuussaari et al. 2009 for a recent review) but we are not aware of any similar study on islands, despite the widely accepted notion that islands and especially oceanic islands have suffered and will probably suffer increased extinctions following habitat loss.

The Azores constitute an ideal model system for assessing extinction debt because: 1) they have lost >95% of their original native forest during the six centuries of human occupation; 2) being one of the most isolated archipelagos on Earth they support a significant number of single island endemic species (SIE; i.e. endemic species restricted to one island) (Borges et al. 2005b, Borges and Hortal 2009, Cardoso et al. 2010); 3) the history of human settlement and deforestation is well known (Frutuoso 1963, Silveira 2007), and; 4) extensive distributional data exist for a range of taxa (Borges et al. 2005b).

Methods

Study area

The first human settlements were established in the Azores (Supplementary material Fig. S1) around AD 1440. More than 550 yr of human presence has taken its toll on the local fauna and flora, 420 species of which (out of the 4467 total terrestrial taxa known from the Azores) are endemic to the archipelago (Borges et al. 2005b). Today, ca 70% of the vascular plant species and 58% of the arthropod species found in the Azores are exotic, many of them invasive (Borges et al. 2005b, 2006). The native “laurisilva”, a humid evergreen broadleaf laurel forest, was the predominant vegetation form in the Azores before human colonization in the 15th century (ca AD 1440). Here, we consider as “native forest” both the humid evergreen broadleaf laurel forest and other native forest types such as the *Juniperus brevifolia*- and *Erica azorica*-dominated forests. The Azorean laurisilva differs from that found on Madeira and on the Canary Islands as it includes just a single species of Lauraceae (*Laurus azorica*), although also featuring several species of sclerophyllous and microphyllous trees and shrubs (e.g. *J. brevifolia* and *E. azorica*), and luxuriant bryophyte communities, covering all available substrata (Gabriel and Bates 2005).

The destruction of the native forest in the Azores has followed a clear temporal sequence. At the time of human colonization the archipelago was almost entirely covered by forest (ca AD 1440) (Martins 1993, Silveira 2007). By 300 yr ago (ca AD 1700) human activities had restricted the native forest in most islands to areas above 300 m a.s.l. and by ca AD 1850, areas with native forest were mainly present above 500 m a.s.l. (Silveira 2007). The development of an economy dependent on milk production during the last decades of the 20th century drove a further reduction of native forest area, with the clearing of large fragments at mid- and high-altitude for pasture, further decreasing the native forest to its current extent of 2.5% of the total area of the archipelago (<58 km² in total). Thus, in <600 yr >95% of the original native forest has been destroyed (Gaspar 2007, Gaspar et al. 2008, Table 1).

Data

As a result of the exhaustiveness of taxonomic work, the relative poorness of the Azorean fauna, and the intensive sampling during the last ten years (see Supplementary material for an analytical description of the sampling method), the Borges et al. (2005b) checklist (updated also with recent unpublished data) includes virtually all arthropod species native to the Azores, reported and described from 1859 (Drouët 1859) up to today, as well as an accurate account of their presence or absence in all the islands of the archipelago. The data for the Araneae, Hemiptera and Coleoptera are particularly comprehensive (Borges et al. 2005b, Borges and Wunderlich 2008, Cardoso et al. 2010). In this context, even if more species remain to be discovered from the islands in the future (e.g. Borges and Wunderlich 2008), we can reasonably regard each island as being currently proportionally equally well-sampled.

In 1998, 60 native species (excluding Crustacea, Acari, Collembola, Hymenoptera and Diptera) were known to be SIE. During 1999 and 2000, 64 transects were set up, covering all remnants of native forest in the Azorean islands (BALA project) (Borges et al. 2005a, Ribeiro et al. 2005, Table 1). Eight species out of the original 60 SIE were found in other islands, but also 13 new species were described, nine of them being SIE (Borges and Wunderlich 2008). During 2003 and 2004, 38 new transects were set up in the same forest remnants (Gaspar 2007, Gaspar et al. 2008). After this intensive additional round of surveys, only one further species previously thought to be a SIE was found in another island, demonstrating the high reliability of the current checklist at the island level.

Based on previous work (Borges and Brown 1999, Borges et al. 2005a, 2006, 2008, Ribeiro et al. 2005, Gaspar 2007, Borges and Wunderlich 2008, Gaspar et al. 2008) the endemic arthropods were classified as native forest dependent and non-forest dependent species (e.g. cave-adapted species, native grassland specialists, species also surviving in exotic forests or other man-made habitats). A species was considered forest-dependent (i.e. forest specialist) when 85% or more of its individuals have been collected in native vegetation (see Forest dependent endemic species in Supplementary material Table S1). Only the forest-dependent species endemic to the archipelago (59 species in total) were considered for further analyses; these species represent 56% of all the endemic species of the taxa considered. Despite the intensive survey effort recently carried out in anthropogenic habitats on some of the islands (Terceira, Pico, Graciosa and Santa Maria; Borges and Brown 1999, Borges et al. 2005a, 2006, 2008, Borges and Wunderlich 2008; see also Supplementary material), none of the species considered as a native forest endemic here has been found to have large populations in any other type of land use (<15% of their total numbers of individuals, after standardising for sampling effort; see details in Supplementary material Table S1). The completeness and comparability of these surveys was verified using a number of sampling effort algorithms (see Sampling effort analysis in the Supplementary material).

The respective species lists of endemic forest specialists for the above three taxa were extracted for the areas of native

forest corresponding to four points in time (below). This step was undertaken using SQL-based queries on the ATLANTIS-Azores database by means of the Atlantis Tierra 2.0 software (Zurita and Arechavaleta 2003, Borges et al. 2005b, Table 2). The ATLANTIS-Azores database includes an exhaustive checklist created by many taxonomists, who have recently performed a detailed revision of the taxonomic status of many species, identified many synonyms and improved the list of Azorean arthropods (Borges et al. 2005b). This database includes the spatial distribution of all recorded species specimens in a 500 × 500 m grid, based on both literature and unpublished field data, hence allowing us to obtain the list of species for any region within any of the islands. Here we extracted four different species lists for each taxon, each one of them chosen to correspond to the extent of native forest at four known points in time before and since human colonization (Table 1; Fig. 2 with the island of Terceira as an illustration). They were as follows: a) for the total area of each island, i.e. all known forest specialist species reported from the island. This reflects the near 100% forest cover of the islands before the arrival of humans; AD 1440, herein T₁. b) For areas above 300 m, including only those species reported above this elevational limit and corresponding to the extent of the native forest ca AD 1700, T₂. c) For areas above 500 m, the extent of the native forest at ca AD 1850, T₃. d) for the present area occupied by native forest, including only those species currently reported from native forest remnants within each island, AD 2000, T₄.

The slight differences in the number of species denoted for (a), (b) and (c) are due to the fact that some species have been recorded only from the lowland areas which have been sequentially lost over time. As Raheem et al. (2009) have recently shown, the influence of pre-fragmentation patterns of species turnover can persist despite habitat loss and fragmentation, with the spatial pattern in species distribution before disturbance persisting to the present. Thus, we avoided considering each island as a priori biogeographically homogeneous before habitat destruction, in terms of species distribution in the different elevational zones considered. The differences between the species number for the total island area (a) and for the current extent of the native forest (d) (Table 2) are due to the inclusion in (a) of historical records of species presences in low and mid altitudes where the native forest is now absent. This means that if a species has been reported in the past from a lowland area where the native forest is now absent and this species is not found in any of the areas currently covered by native forest, the species was included in list (a) but not in list (d). Thus, for this latter category we are not following the simple elevational criterion used for (b) and (c) but we are instead using the actual distribution of the native forest patches.

The current area of native forests for all the islands (Table 1) was estimated based on digital aerial photography of the islands and field work (Gaspar 2007, Gaspar et al. 2008).

Calculation of extinction debt

To explore the impact of native forest destruction on current levels of endemic arthropod species richness, we

Table 1. Basic characteristics of the islands of the Azores (main source: Borges and Hortal 2009; see also Methods). Latitude and longitude refer to the centre of the island, and are given in decimal degrees. Total area of the island approximates the forest cover before the arrival of humans; AD 1440, T₁; area above 300 m corresponds to the extent of the native forest ca AD 1700, T₂; area above 500 m, the extent of the native forest ca AD 1850, T₃; and the present area of forest remnants is for AD 2000, T₄. -: absence of native forest; *currently there is no primary native forest on Graciosa and Corvo Islands. On Graciosa only a very small patch of secondary native vegetation occurs; this patch is dominated by small-sized *Erica azorica*, an early successional endemic shrub.

Island	Latitude °N	Longitude °W	Altitude (m)	Total area of island (km ²), T ₁	Area above 300 m (km ²), T ₂	Area above 500 m (km ²), T ₃	Present area of forest remnants (km ²), T ₄	Maximum age (Ma)
Graciosa	39.0	27.6	398	62	3.48	–	–*	2.50
Corvo	39.4	31.0	718	17	9.33	5.44	–*	0.71
Santa Maria	36.9	25.1	587	97	13.19	0.21	0.09	8.12
Faial	38.6	28.5	1043	172	80.45	36.59	2.26	0.73
São Jorge	38.7	27.9	1053	246	170.56	90.35	2.93	0.55
São Miguel	37.7	25.5	1103	757	352.39	186.02	3.31	4.01
Pico	38.5	28.2	2351	433	261.66	188.30	9.52	0.25
Flores	39.4	30.9	915	142	95.18	52.58	15.71	2.90
Terceira	38.7	27.2	1023	402	177.60	70.09	23.45	3.52
Total				2328	1163.84	629.58	57.27	

Table 2. The number of forest-dependent endemic arthropod species in the four different habitat areas, corresponding to the extent of native forest at four known points in time, before and following human colonization (Supplementary material Table S2 and Methods for details).

Island	Coleoptera				Araneae				Hemiptera			
	Total area,	Area > 300 m,	Area > 500 m,	Present area,	Total area,	Area > 300 m,	Area > 500 m,	Present area,	Total area,	Area > 300 m,	Area > 500 m,	Present area,
	T ₁	T ₂	T ₃	T ₄	T ₁	T ₂	T ₃	T ₄	T ₁	T ₂	T ₃	T ₄
Graciosa	2	2	–	–	3	2	–	–	3	1	–	–
Corvo	1	1	1	–	0	0	0	–	2	2	2	–
Flores	8	7	6	6	11	11	11	10	5	5	4	3
Faial	4	3	3	3	8	8	7	7	5	5	5	3
Pico	14	13	13	13	10	10	10	10	4	4	4	4
São Jorge	4	4	4	4	11	11	11	11	6	6	6	4
Terceira	11	10	9	9	11	11	11	10	8	7	7	5
São Miguel	17	17	11	11	11	10	9	9	6	5	5	5
Santa Maria	14	13	12	12	7	7	6	6	3	3	3	3

assumed a multiple linear relationship between species number (S), area (A) and the geological age of each island (G), i.e. $\text{Log } S = b_1 + b_2 \text{Log } A + b_3 G$, for the endemic forest-dependent species of Araneae, Hemiptera and Coleoptera. For number of species and area we used the conventional logarithmic transformations (log_{10}) to estimate the equation parameters (Borges and Brown 1999, Borges and Hortal 2009, cf. Rosenzweig 2001). For the particular case of the single island, where the number of Araneae species was zero we used the conventional practice of raising the values for all islands by 0.5.

Inclusion of island age (Supplementary material) follows previous theoretical and empirical work showing that age can influence the evolutionary dynamics of oceanic islands, as reflected in levels of endemism (Whittaker et al. 2008, Borges and Hortal 2009). Including island age means that we do not assume that the islands were in a pure “ecological” immigration–extinction equilibrium prior to human colonization. Instead, the number of endemic forest species prior to human colonization is assumed to be a longer-term outcome of immigration, speciation and extinction dynamics.

We calculated our species–area–age relationships using four different “habitat areas” corresponding to the extent of native forest at four known points in time: AD 1440 (total area), AD 1700 (area above 300 m), AD 1850 (above 500 m) and AD 2000 (current extent) (see above). If “relaxation” of species numbers has not yet taken place or is incomplete (i.e. an extinction debt remains) then the best fitting species–area–age model will correspond to the remaining area of forest at some past time. However, which “past time” may not be the same for each taxon due to differences in their ecology and life history. Additionally, we tested the effectiveness of the applied model against a number of different models, e.g. including measures of island elevation, log-transformed age values, and considering quadratic models of geological age, i.e. $G + G^2$ (Whittaker et al. 2008).

An alternative explanation for the lack of relationship between the current extent of native forest and the number of forest dependent species is that larger islands originally had more species as a consequence of their larger area. Thus, due to their larger species pool, more species would be expected to be found in fragments within larger islands. To test this mechanism we evaluated the relationship between the number of the archipelagic endemic species of the three taxa considered here and the total area of each island and compared its explanatory power with the respective species–area–age relationship. If larger islands have more species, then the species–area model will be the best for the species

richness of the endemic taxa. We also tested the predictive accuracy of the two species–area–age models (for the total area and the area above 300 m) by testing the correlation between the observed and the predicted number of species.

Finally, in order to evaluate our predictions, we compare the average species abundance per transect (i.e. average number of individuals of archipelagic endemic forest-dependent species per transect) of Graciosa Island with the rest of the islands of the archipelago. Currently there is no primary native forest on Graciosa; only a very small patch of secondary native vegetation occurs, dominated by small-sized *Erica azorica*, an early successional endemic shrub. Hence we predict that the surviving forest-dependent species that are present in several islands will show smaller abundances within transects on Graciosa, indicative of a progressive reduction of their populations towards extinction. All analyses were carried out using STATISTICA 6.1 (StatSoft 2003).

Results

For the total island area and the area above 300 m, the species–area–age model applied was significant ($p < 0.05$) for each of the arthropod taxa considered (Table 3), with most of the explained variance attributable to area. However, for the area above 500 m and the present area covered by native forest, neither the species–area–age relationships nor the respective species–area relationships were statistically significant for any of the three taxa considered (Supplementary material Table S2). We thus used the first two benchmark relationships, for total area (~AD 1440, T_1) and area above 300 m (~AD 1700, T_2) (Fig. 1 and 2B), to represent the baseline conditions for estimation of current extinction debt. Hence, we used the parameters estimated for the total area of the islands (Pred. 1; Table 4), and that of the area above 300 m (Pred. 2; Table 4) to estimate the number of endemic forest arthropods that “should” be present and, by direct comparison with the number of extant species, derive the number of species to go extinct (i.e. the extinction debt) for each taxon (Table 4 and Supplementary material S3).

For all three arthropod taxa considered, our results clearly indicate that the majority of the endemic forest-dependent species are expected to go extinct in time, especially on those islands on which the native forest has been restricted to small areas, namely Santa Maria, São Miguel, São Jorge and Faial, or on which it has been totally removed, namely Graciosa and Corvo (Table 1 and 4). Terceira, the island with the largest remnants of native

Table 3. The species–area–age equations used for predicting extinctions. S : number of forest-dependent archipelagic endemic species; A : area; G : geological age; b : standard error for non-standardized regression coefficients (see Methods for details). The degrees of freedom (DF), F and p -values are also presented. For all the models tested see Supplementary material Table S2.

Taxon/island area	Equation	SE intercept	SE b_A	SE b_G	DF	R^2	F-value	p-value
Coleoptera (total area)	$\text{Log } S = -0.915 + 0.678 \times \text{Log } A + 0.076 \times G$	0.288	0.126	0.025	2.6	0.87	20.14	<0.01
Coleoptera (>300 m)	$\text{Log } S = -0.383 + 0.471 \times \text{Log } A + 0.116 \times G$	0.198	0.092	0.026	2.6	0.86	18.78	<0.01
Araneae (total area)	$\text{Log } S = -0.979 + 0.780 \times \text{Log } A + 0.026 \times G$	0.189	0.170	0.03	2.6	0.79	11.06	0.01
Araneae (>300 m)	$\text{Log } S = -0.318 + 0.531 \times \text{Log } A + 0.067 \times G$	0.238	0.153	0.04	2.6	0.68	6.33	0.03
Hemiptera (total area)	$\text{Log } S = -0.060 + 0.321 \times \text{Log } A - 0.007 \times G$	0.184	0.080	0.016	2.6	0.73	7.96	0.02
Hemiptera (>300 m)	$\text{Log } S = -0.088 + 0.347 \times \text{Log } A + 0.016 \times G$	0.146	0.067	0.019	2.6	0.82	13.27	<0.01

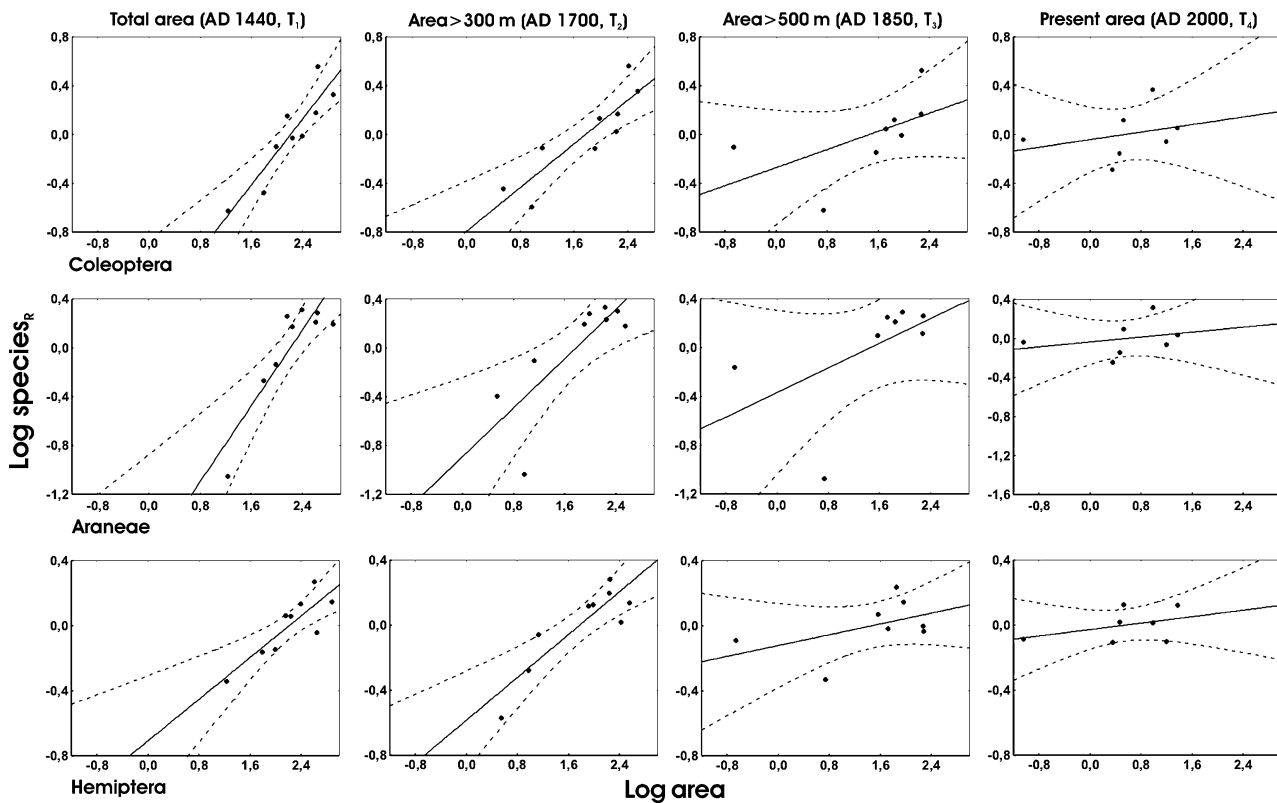


Figure 1. Species–area relationships for the endemic forest arthropods of the three groups studied (Coleoptera, Araneae, Hemiptera), for the areas of native forest corresponding to four known points in time (see text). In order to exclude the effect of island age on species richness, for purposes of visual representation we present the relationship between the residuals of the log (species)–age relationship, (i.e. geological age-independent richness) against log (area; km²). While the relationships for the total area (AD 1440, T₁) and the area above 300 m (AD 1700, T₂) were statistically significant for all taxa, for the area above 500 m (AD 1850, T₃) and the present area of the native forest (AD 2000, T₄) they are not statistically significant for any taxon (see Supplementary material Table S2 for details). Solid lines are regression trend-lines, and dashed lines are 95% confidence intervals. Non-significant relationships are shown here for purposes of comparison.

forest, has the smallest number of predicted future extinctions. The estimated proportion of extinctions per island varies from 50 to 99% for Coleoptera, 60 to 99.5% for Araneae and 49 to 85% for Hemiptera. Amongst the three taxa, Hemiptera are at the lowest overall risk of extinction. The mean predicted percentage of extinctions for all the islands is: Coleoptera, 91.56% ($\pm 5.68\%$; Pred. 1) and 74% ($\pm 15.82\%$; Pred. 2), Araneae, 94.81% ($\pm 4.41\%$; Pred. 1) and 80.81% ($\pm 10.73\%$; Pred. 2), and Hemiptera, 68.56% ($\pm 12.42\%$; Pred. 1) and 67% ($\pm 13.06\%$; Pred. 2). These projections are in accordance with the distribution of the taxa across the island group since the percentage of endemic forest-dependent species present in three or fewer islands is 72% for Coleoptera, 47% for Araneae and 36% for Hemiptera.

In the multiple regression models applied, the age parameter was statistically significant only in the case of Coleoptera; hence, when it was excluded from the models applied for spiders and Hemiptera, the predictions remained the same (without any statistically significant difference for the values presented). However, we applied the species–area–age model in all cases for purposes of comparison (Table 3). Note that this does not affect the statistical significance of the relationships used, i.e. the relationships estimated based on the area above 500 m and the current area of the native forest remain statistically

non-significant even when only area is considered (Supplementary material Table S2), and the calculated parameters remain statistically indistinguishable for the cases where age has no significant contribution (Supplementary material Table S2). Additionally, the models we report were always better, based on the adjusted R² values and the Akaike's information criterion values (AIC), than were models considering elevation or quadratic age (results not shown).

The species–area model for the archipelagic endemic species was the best model (i.e. lower value of AIC) only for Araneae (see Alternative mechanism in Supplementary material and Table S4), indicating that at least for Coleoptera and Hemiptera, the hypothesis that larger islands have more species, independent of the current area of the native forests, can be ruled out.

The general pattern arising from the cross-checking of the predictive accuracy of the two species–area–age models used (Supplementary material Table S5) demonstrates that using the parameter estimations from the species–area–age model of the areas > 300 m over-predicts the number of species that are present when applied to the total area of the islands, while the use of the parameters arising from the species–area–age model for the total area leads to an underestimation of the species present in areas above 300 m (Supplementary material Table S5 and further discussion in the Supplementary material). In all cases

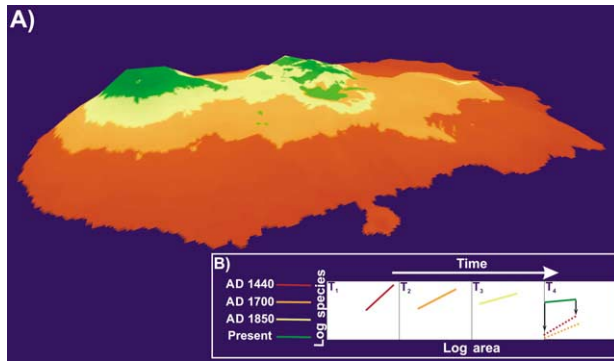


Figure 2. The sequential reduction of the native forest and the respective species–area relationships. (A) The elevational distribution of native forest in historical times for the island of Terceira (Azores; using Atlantis Tierra 2.0 software and Silveira 2007). Red (total area, T_1): before human occupation, (almost complete coverage of island's area); orange (area >300 m, T_2): ca 300 yr ago (300–500 m); yellow (area >500 m, T_3): ca 160 yr ago (above 500 m); green (present area, T_4): current distribution. (B) A schematic representation of the effects of the sequential reduction of the native forest on the species–area relationships of endemic forest arthropods. The dashed line in T_4 represents the future species–area relationships, extrapolated from T_1 and T_2 (see text). The magnitude of the extinction debt is represented by the difference between current species richness (solid green line) and the future predictions (dashed lines).

the Durbin-Watson test, applied to detect the presence of autocorrelation, indicates that the residuals are not positively autocorrelated, except for the Araneae >300 m dataset, for which the test is not conclusive (Supplementary material Table S6) and the coefficient of determination (R^2) of the relationship between observed and predicted number of species (log-transformed values) was higher than 0.65.

The results of the comparison of species average abundance on Graciosa Island with the rest of the islands, where native forest still exists, clearly indicate that for the clear majority of the eight species for which available data exists, there is a clear pattern of lower abundances in Graciosa Island (Supplementary material Table S7).

Discussion

Brook et al. (2003), studying a wide range of terrestrial and freshwater taxa from Singapore, inferred that 34–87% of species identified as forest specialists had gone extinct following deforestation in Singapore. They referred to these as catastrophic extinctions and warned that 13–42% of regional populations in south east Asia will be lost over the next century due to habitat loss, in the absence of remedial action. Our estimates for the magnitude of the extinction debt among forest-dependent endemic arthropods in the Azores are even higher than these startling figures and suggest that more than half of the extant species might eventually be driven to extinction due to habitat loss; a habitat loss which is almost complete ($>95\%$ of the original extent of the native forest) and has occurred in <600 yr. The severity of the deforestation, both in terms of the spatial extent and the temporal scale, has clearly reduced

Table 4. Predicted extinctions. Number of forest-dependent archipelagic endemic arthropods of Coleoptera, Araneae and Hemiptera for the nine Azorean Islands and the respective predicted number of species that should be found based on the species–area–age models calculated using the total area of each island (Pred. 1) and the area of each island above 300 m (i.e. area occupied by native forest ca 300 yr ago; Pred. 2). Currently there is no native forest on Graciosa and Corvo Islands. The lower and upper bound of 95% confidence limits for both predicted responses are presented in Supplementary material Table S3.

Island	Coleoptera	Pred. 1 (ALL)	Pred. 2 (>300)	Species loss (%)	Araneae	Pred. 1 (ALL)	Pred. 2 (>300)	Species loss (%)	Hemiptera	Pred. 1 (ALL)	Pred. 2 (>300)	Species loss (%)
Graciosa	2	0.19	0.81	90.5–59.5	3	0.12	0.71	96–76	3	0.83	0.90	72–70
Corvo	1	0.14	0.50	86–50	0	0.11	0.54	–	2	0.86	0.84	57–58
Flores	8	1.15	2.69	86–67	11	1.02	2.90	91–74	5	2.11	2.30	58–54
Faial	4	0.25	0.75	94–81	8	0.21	0.83	97–83	5	1.13	1.13	77
Pico	14	0.59	1.29	96–91	10	0.62	1.65	94–83.5	4	1.80	1.79	55
São Jorge	4	0.28	0.81	93–80	11	0.25	0.93	98–92	6	1.23	1.21	80
Terceira	11	1.92	4.68	82.5–57.5	11	1.52	4.42	86–60	8	2.40	2.96	54–49
São Miguel	17	0.56	2.11	97–88	11	0.34	1.69	97–85	6	1.28	1.43	79–76
Santa Maria	14	0.10	1.17	99–92	7	0.03	0.47	99.5–93	3	0.46	0.48	85–84

the opportunities for forest-dependent species to cope with the changes in their environment.

At face value, these figures constitute a powerful warning to island conservationists that the worst of the extinction crisis is by no means over. Furthermore, in spite of the fact that some archipelagic endemic species may benefit from a degree of population reinforcement between habitat fragments or islands (see also Borges et al. 2008), the parallel reduction of the native forest across all islands in the last 600 yr has greatly diminished the probability of such source-sink dynamics rescuing species from global extinction. Hence, we would also anticipate a correspondingly large number of archipelagic-scale species extinctions for Azorean endemic arthropods in the future as the extinction debt is settled.

Amongst the three studied taxa, our analyses suggest that Araneae and Coleoptera are at greater risk of extinction per island, compared to Hemiptera. This may be partially related to the ecological characteristics and requirements of the species in each group, with Hemiptera typically exhibiting higher dispersal abilities and having a smaller proportion of species endemic to a single island (SIE: 6%). In contrast, both Araneae and Coleoptera have high proportions of SIEs, 19.4 and 18.9% respectively. Additionally, spiders, the most important arthropod predators in the Azores, are expected to be relatively intolerant to the destruction and disturbance of natural forests on these islands (Cardoso et al. 2007, 2010) as shown for other high trophic level taxa (Whittaker and Fernández-Palacios 2007). We recognise that other processes may be involved in the extinctions to come apart from habitat loss, but at the same time these area-based models can offer an effective descriptor of the combined effects of other causes (see also Hanski et al. 2007, Yaacobi et al. 2007). One such additional factor is undoubtedly the significant pressure exerted by exotic species (Blackburn et al. 2004, Whittaker and Fernández-Palacios 2007), which already comprise 58% of the total Azorean arthropod fauna (68% of Araneae, 60% of Coleoptera and 47% of Hemiptera, Borges et al. 2005b, 2006).

The figures that we report here are likely to be more accurate than previous predictions because we have focused our attention on endemic forest species that have evolved in and are only found in association with the native forest. Endemic forest dependent species are unlikely to show a range expansion to anthropogenic habitats under land-use changes. Hence, we avoid additional “noise” caused by generalist species that may well be able to survive in other (i.e. anthropogenic) habitats. For example, there is no evidence that the endemic forest arthropods on Terceira can establish viable populations within other forest or vegetation types on the island (Borges and Wunderlich 2008, Borges et al. 2008, see also Methods). Furthermore, we base our predictions on two baseline curves, and not on a single one as usually applied, an approach providing fairly conservative estimates of the present extinction debt, taking into account the crude but reasonably well-founded habitat distributional data available. However, it should also be recognised that the projected extinctions arising from the use of the species–area models involve several uncertainties (May et al. 1995, Lewis 2006, Vellend et al. 2006, Whittaker and Fernández-Palacios 2007, Kuussaari et al.

2009, Ladle 2009) and can never completely replace species-level assessments for the identification of extinction threat (Kotiaho et al. 2005, Whittaker et al. 2005, Kuussaari et al. 2009). Nevertheless, for many species of conservation concern the collection of appropriately detailed information is an unrealistic target. It is therefore important that we develop more realistic indirect measures and theoretical projections of extinctions, based on as pragmatic a set of assumptions as possible (Heywood et al. 1994, May et al. 1995, Whittaker et al. 2005). Here, by using taxon-specific z -values derived from species–area relationships of the same taxon in the same island system, we would argue that our extinction estimates are likely to prove more realistic and robust than previous analyses (see Yaacobi et al. 2007 for a similar example on habitat islands).

It is highly probable that since the original settlement of humans on the Azores a number of arthropods and other poorly known taxa have already become extinct due to deforestation (cf. Brook et al. 2003, Hanski et al. 2007, Cardoso et al. 2010). Thus, given that a large fraction of the island’s forest had already been cleared before the first reliable standardized sampling (Borges et al. 2005a, 2006, 2008, Ribeiro et al. 2005, Gaspar 2007, Gaspar et al. 2008, Borges and Wunderlich 2008), the extinction of species most sensitive to disturbance probably went unrecorded (Cardoso et al. 2010). In point of fact, at least five SIE beetle species (*Bradycellus chavesi*, *Calathus extensicollis*, *Calathus vicenteorum*, *Nesotes azorica*, *Ocydromus derelictus*), recorded early in the 20th century, have not been recorded since 1965 and might therefore be considered extinct (Borges et al. 2000). Moreover, many other SIEs are extremely rare and under threat (Borges et al. 2006), and are particularly scarce in standardized samples (Supplementary material Table S1 for Terceira Island). While seven individuals of *Calathus lundbladi*, an endemic species of São Miguel, were found in four traps during 1989, just one individual was collected in 120 traps in the 1999–2000 survey (Borges et al. 2005a). The case of Graciosa Island is in accord with the above (Supplementary material Table S7); although species abundance responses to forest loss and fragmentation can be strikingly idiosyncratic (Fahrig 2001), and phenomena like density compensation as a result of the extinction of competitors and/or predators cannot be excluded (Whittaker and Fernández-Palacios 2007; Supplementary material Table S7), the very small fragment of secondary native vegetation in Graciosa, which is highly disturbed, can be considered as the “last refuge” for the endemic forest-dependent species on that island. These species are already on an ecological trajectory towards extinction. Although, it is possible that some forest specialist species might be able to find a refuge in exotic forests (Supplementary material Table S1), the durability and viability of these populations are probably limited (Borges, unpubl.). Conclusively proving the extinction of a small arthropod species will be practically impossible within such a large area as the Azorean archipelago (2328 km²), but we concur with others (Hanski et al. 2009, Ladle 2009), that given the great importance of understanding the processes and rates of species extinctions, analyses based on indirect evidence can be informative.

Precise estimation of the time to extinction of each species under threat remains an unrealistic aim, for it will vary from island to island and from species to species. The scarce available information suggests that delayed extinctions are more likely to occur in species with longer generation times, e.g. mammals as opposed to insects, (see review in Kuussaari et al. 2009), but recent studies on invertebrates (Raheem et al. 2009, Sodhi et al. 2009) have shown a resilience of some invertebrate species to the effects of forest loss; with many species requiring only very small areas to persist for extended periods (see also discussion in Samways 2006). These results suggest a need for caution in generalizing about relaxation and species loss based on data for ecologically different taxa, such as vertebrates and especially birds. Despite the extensive destruction of the Azorean native forest, the remaining network of patches within some of the islands and the overall remaining area in the archipelago might be sufficient for delaying relaxation for long periods of time or even sustain viable populations for some species. Hence, the time lag may be considerable, even for invertebrates of short life cycles.

We conclude that large-scale conservation efforts need to be implemented if the high extinction debt we have identified is to be deferred or avoided. Human-induced fragmentation, land-use changes and invasive species have already been identified as important threats to Azorean biodiversity (Martins 1993, Borges et al. 2000, 2006, Borges and Wunderlich 2008). Our analyses strongly reinforce this message: the conservation of the Azorean natural heritage, and that of many other oceanic islands, will largely depend on establishing an integrated large-scale strategy to manage both indigenous and non-indigenous species while simultaneously protecting the remnants of native habitat (i.e. forest in the Azorean context) and, ideally, increasing their extent. This point is corroborated by the case of the Azorean bullfinch *Pyrrhula murina*, an endemic passerine bird species confined to eastern São Miguel and living almost exclusively in the laurel forest. The species, locally abundant in the second half of 19th and early 20th century, has suffered through widespread loss of native forest and invasion by exotic vegetation, which has largely overrun the remaining patches of natural vegetation within the bullfinch's breeding range. This led to a dramatic decline, to <100 individuals, in the late 1970s. Following the implementation in 2003 of a five-year LIFE-Nature project, a central objective of which was to increase the habitat of the Azores bullfinch, mainly through promoting the regeneration of the laurel forest and the control of the exotic flora (Ramos 1996, 2005, Guimarães and Olmeda 2008), the population had increased to an estimated 400 pairs by the year 2006 (Guimarães and Olmeda 2008).

In the absence of focused and well-resourced interventions, the legacy of past and current deforestation on oceanic islands will be an inexorable process of biodiversity loss stretching well into the future. Many extant species may already have passed crucial thresholds of population size and/or genetic diversity that typically precede extinction, meaning that the species are becoming highly sensitive to demographic and environmental stochasticity (Schoener et al. 2003). The approach to estimating extinction debt outlined in this work may be suitable for application to many other analogous systems, including numerous oceanic

archipelagos that have experienced anthropogenic habitat loss (Mueller-Dombois and Fosberg 1998, Rolett and Diamond 2004, Steadman 2006) and where the temporal sequence of habitat loss can be at least crudely estimated.

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References

- Blackburn, T. M. et al. 2004. Avian extinction and mammalian introductions on oceanic islands. – *Science* 305: 1955–1958.
- Borges, P. A. V. and Brown, V. K. 1999. Effect of island geological age on the arthropod species richness of Azorean pastures. – *Biol. J. Linn. Soc.* 66: 373–410.
- Borges, P. A. V. and Wunderlich, J. 2008. Spider biodiversity patterns and their conservation in the Azorean archipelago, with descriptions of new species. – *Syst. Biodivers.* 6: 249–282.
- Borges, P. A. V. and Hortal, J. 2009. Time, area and isolation: factors driving the diversification of Azorean arthropods. – *J. Biogeogr.* 36: 178–191.
- Borges, P. A. V. et al. 2000. Ranking the Azorean natural forest reserves for conservation using their endemic arthropods. – *J. Insect Conserv.* 4: 129–147.
- Borges, P. A. V. et al. 2005a. Ranking protected areas in the Azores using standardised sampling of soil epigeal arthropods. – *Biodivers. Conserv.* 14: 2029–2060.
- Borges, P. A. V. et al. 2005b. A list of the terrestrial fauna (Mollusca and Arthropoda) and flora (Bryophyta, Pteridophyta and Spermatophyta) from the Azores. – Direcção Regional de Ambiente and Univ. Azores.
- Borges, P. A. V. et al. 2006. Invasibility and species richness of island endemic arthropods: a general model of endemic vs. exotic species. – *J. Biogeogr.* 33: 169–187.
- Borges, P. A. V. et al. 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, India, pp. 47–69.
- Brook, B. W. et al. 2003. Catastrophic extinctions follow deforestation in Singapore. – *Nature* 424: 420–423.
- Brooks, T. M. et al. 1997. Deforestation predicts the number of threatened birds in insular southeast Asia. – *Conserv. Biol.* 11: 382–394.
- Brooks, T. M. et al. 2002. Habitat loss and extinction in the hotspots of biodiversity. – *Conserv. Biol.* 16: 909–923.
- Brooks, T. M. et al. 2006. Global biodiversity conservation priorities. – *Science* 313: 58–61.

- Cardoso, P. et al. 2007. Biotic integrity of the arthropod communities in the natural forests of Azores. – *Biodivers. Conserv.* 16: 2883–2901.
- Cardoso, P. et al. 2010. Drivers of diversity in Macaronesian spiders and the role of species extinctions. – *J. Biogeogr.* 37, doi: 10.1111/j.1365-2699.2009.02264.x.
- Darlington, P. J. 1957. *Zoogeography: the geographical distribution of animals.* – Wiley.
- Diamond, J. M. 1989. The present, past and future of human-caused extinctions. – *Phil. Trans. R. Soc. B* 325: 469–477.
- Drouët, H. 1859. Coléoptères Açoréens. – *Rev. Mag. Zool.* 11: 243–259.
- Dunn, R. R. 2005. Modern insect extinctions, the neglected majority. – *Conserv. Biol.* 19: 1030–1036.
- Fahrig, L. 2001. How much habitat is enough? – *Biol. Conserv.* 100: 65–74.
- Fonseca, R. C. 2010. The silent mass extinction of insect herbivores in biodiversity hotspots. – *Conserv. Biol.* 23: 1507–1515.
- Frutuoso, G. 1963. *The sixth book on longing for the land.* – Inst. Cultura de Ponta Delgada.
- Gabriel, R. and Bates, J. W. 2005. Bryophyte community composition and habitat specificity in the natural forests of Terceira, Azores. – *Plant Ecol.* 177: 125–144.
- Gaspar, C. S. 2007. *Arthropod diversity and conservation planning in native forests of the Azores archipelago.* – Ph.D. thesis, Univ. Sheffield.
- Gaspar, C. et al. 2008. Diversity and distribution of arthropods in native forests of the Azores archipelago. – *Arquipélago-Life Mar. Sci.* 25: 1–30.
- Guimarães, A. and Olmeda, C. 2008. Management of Natura 2000 habitat. 9360 *Macaronesian laurel forests (*Laurus, Ocotea*). – European Commission.
- Hanski, I. et al. 2007. Deforestation and apparent extinctions of endemic forest beetles in Madagascar. – *Biol. Lett.* 3: 344–347.
- Hanski, I. et al. 2009. Deforestation and tropical insect extinctions. – *Biol. Lett.* 5: 653–655.
- Helm, A. et al. 2006. Slow response of plant species richness to habitat loss and fragmentation. – *Ecol. Lett.* 9: 72–77.
- Heywood, V. H. et al. 1994. Uncertainties in extinction rates. – *Nature* 368: 105.
- IUCN 2009. IUCN Red List of Threatened Species. Version 2009.2. – <www.iucnredlist.org>.
- Kotiaho, J. S. et al. 2005. Predicting the risk of extinction from shared ecological characteristics. – *Proc. Nat. Acad. Sci. USA* 102: 1963–1967.
- Kuussaari, M. et al. 2009. Extinction debt: a challenge for biodiversity conservation. – *Trends Ecol. Evol.* 24: 564–571.
- Ladle, R. J. 2009. Forecasting extinctions: uncertainties and limitations. – *Diversity* 1: 133–150.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. – *Am. Nat.* 142: 911–927.
- Lewis, O. T. 2006. Climate change, species–area curves and the extinction crisis. – *Phil. Trans. R. Soc. B* 361: 163–171.
- MacArthur, R. H. and Wilson, E. O. 1967. *The theory of island biogeography.* – Princeton Univ. Press.
- Martins, A. M. F. 1993. The Azores – westernmost Europe: where evolution can be caught red-handed. – *Bol. Mus. Municipal Funchal* S2: 181–198.
- May, R. M. et al. 1995. Assessing extinction rates. – In: Lawton, J. H. and May, R. M. (eds), *Extinction rates.* Oxford Univ. Press, pp. 1–24.
- McDonald, K. A. and Brown, J. H. 1992. Using montane mammals to model extinctions due to global change. – *Conserv. Biol.* 6: 409–415.
- Mueller-Dombois, D. F. and Fosberg, F. R. 1998. *Vegetation of the tropical Pacific islands.* – Springer.
- Paulay, G. 1994. Biodiversity on oceanic islands: its origin and extinction. – *Am. Zool.* 34: 134–144.
- Pimm, S. L. and Askins, R. A. 1995. Forest losses predict bird extinctions in eastern North America. – *Proc. Nat. Acad. Sci. USA* 92: 9343–9347.
- Pimm, S. L. et al. 1995. The future of biodiversity. – *Science* 269: 347–350.
- Preston, F. W. 1962. The canonical distribution of commonness and rarity: part I. – *Ecology* 43: 185–215.
- Raheem, D. C. et al. 2009. Fragmentation and pre-existing species turnover determines land-snail assemblages of tropical rain forest. – *J. Biogeogr.* 36: 1923–1938.
- Ramos, J. A. 1996. Introduction of exotic tree species as a threat to the Azores bullfinch population. – *J. Appl. Ecol.* 33: 710–722.
- Ramos, J. A. 2005. *The Priolo and the natural altitude forest*, 2nd ed. – Câmara Municipal de Nordeste.
- Ribeiro, S. P. et al. 2005. Canopy insect herbivores in the Azorean laurisilva forests: key host plant species in a highly generalist insect community. – *Ecography* 28: 315–330.
- Rolett, B. and Diamond, J. 2004. Environmental predictors of pre-European deforestation on Pacific islands. – *Nature* 431: 443–446.
- Rosenzweig, M. L. 2001. Loss of speciation rate will impoverish future diversity. – *Proc. Nat. Acad. Sci. USA* 98: 5404–5410.
- Samways, M. J. 2006. Insect extinctions and insect survival. – *Conserv. Biol.* 20: 245–246.
- Schoener, T. W. et al. 2003. Life-history models of extinction: a test with island spiders. – *Am. Nat.* 162: 558–573.
- Silveira, L. M. A. 2007. *Learning with history: interaction with nature during the human colonization in Terceira Island.* – M.Sc. thesis, Univ. Azores.
- Sodhi, N. S. et al. 2009. Insect extinctions on a small denuded Bornean island. – *Biodivers. Conserv.* 19: 485–490.
- StatSoft 2003. STATISTICA (data analysis software system), version 6.1. – StatSoft, Tulsa, OK.
- Steadman, D. W. 2006. *Extinction and biogeography of tropical Pacific birds.* – Univ. Chicago Press.
- Thomas, C. D. et al. 2004. Extinction risk from climate change. – *Nature* 427: 145–148.
- Tilman, D. et al. 1994. Habitat destruction and the extinction debt. – *Nature* 371: 65–66.
- Vellend, M. et al. 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. – *Ecology* 87: 542–548.
- Whittaker, R. J. and Fernández-Palacios, J. M. 2007. *Island biogeography: ecology, evolution, and conservation*, 2nd ed. – Oxford Univ. Press.
- Whittaker, R. J. et al. 2005. Conservation biogeography: assessment and prospect. – *Divers. Distrib.* 11: 3–23.
- Whittaker, R. J. et al. 2008. A general dynamic theory of oceanic island biogeography. – *J. Biogeogr.* 35: 977–994.
- Yaacobi, G. et al. 2007. Habitat fragmentation may not matter to species diversity. – *Proc. R. Soc. B* 274: 2409–2412.
- Zurita, N. A. and Arechavaleta, M. 2003. Database of the biodiversity of the Canary Islands (Banco de datos de Biodiversidad de Canarias). – *Bol. Soc. Entomol. Aragonesa* 32: 293–294.

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