Biology Letters: accepted 20th May 2015. This version: as accepted but prior to copyediting, typesetting and proof correction. Please refer to final version of record where possible

Drivers of extinction: the case of Azorean beetles

Sofia Terzopoulou[1,2], Francois Rigal[2], Robert J. Whittaker[3,4], Paulo A.V. Borges[2] and Kostas A. Triantis[1,2,3]

[1]Department of Ecology and Taxonomy, Faculty of Biology, National and Kapodistrian University of Athens, Athens GR-15784, Greece
[2]CE3C–Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity Group and Universidade dos Açores, 9700-042, Angra do Heroísmo, Açores, Portugal
[3]Conservation Biogeography and Macroecology Programme, School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, UK.
[4]Center for Macroecology, Evolution and Climate, University of Copenhagen, Denmark.

Author for correspondence: Sofia Terzopoulou e-mail: s.terzopoulou9@gmail.com

Abstract

Oceanic islands host a disproportionately high fraction of endangered or recently extinct endemic species. We report on species extinctions among endemic Azorean beetles following 97% habitat loss since 1440AD. We infer extinctions from historical and contemporary records and examine the influence of three predictors: geographic range, habitat specialization and body size. Of 55 endemic beetle species investigated (out of 63), seven can be considered extinct. Single-island endemics (SIEs) were more prone to extinction than multi-island endemics. Within SIESs restricted to native habitat, larger species were more extinction-prone. We thus show a hierarchical path to extinction in Azorean beetles: species with small geographic range face extinction first, with the larger bodied ones being the most threatened. Our study provides a clear warning of the impact of habitat loss on island endemic biotas.

Keywords: Azores, body size, endemic beetles, extinction, habitat destruction, oceanic islands.

1. Introduction

The destruction and fragmentation of natural habitats have raised species extinctions significantly above background rates [1]. Extinction is non-random: differences in biology influence species' susceptibility to extinction [2-4]. Geographic range size, habitat specialization and body size are traits commonly identified to correlate with extinction risk, through their relationship with demographic parameters, abundance and population fluctuations [3-5].

Island – and especially oceanic island – biotas have provided the majority of recorded global species extinctions since 1600AD, as a result of extensive deforestation, transformation of natural habitats and introduction of non-natives [6]. Having evolved in isolation, oceanic island endemics occur in small geographic ranges, often have small overall population sizes, tend to be habitat specialists, and are more vulnerable to the introduction of non-native predators or competitors [1,7,8].

Insects represent nearly two-thirds of described species of animals and plants, but only 0.1% of the almost 1 million known insect species have been classified as globally extinct or threatened (i.e. Critically Endangered, Endangered or Vulnerable) [9, cf.10]. However, a significant number of insect species have most probably gone extinct unnoticed and, taking knowledge bias into account, invertebrates overall show much higher extinction rates and proportions of threatened species compared to better-known vertebrate taxa [11]. Beetles (Coleoptera) represent the largest order and about 40% of all described insect species, but just 1.6% of recorded extinct animal species [9].

Thus, there is an urgent need to focus on poorly studied taxa to address the extinction shortfall and quantify the extinction debt [12,13]. Based on the most extensive survey of arthropods in an oceanic archipelago, we use historical and contemporary records to infer extinctions of endemic Azorean beetles and examine the influence of: (i) the number of islands (single or multiple) where species occur as an estimate of geographic range size, (ii) the species dependence on native vegetation as an estimate of habitat specialization and (iii) body size. Since human settlement of the Azores in 1440AD, >97% of the natural forest has been destroyed: as a result it has been estimated that >50% of extant forest-dependent Azorean beetle species may already be committed to extinction [12].

2. Materials and Methods

(a) Study area

The Azores is one of the world's most isolated oceanic archipelagos (1580 km west of Iberia, 2150 km east of North America (Fig. S1)). Prior to human habitation, the islands were almost entirely clothed with Laurisilva, a type of humid, evergreen, broadleaf forest (dominated by *Laurus azorica*). Today, the remaining patches of natural forest (3%) are found only in isolated high elevation areas, surrounded by pasture and plantations. Parallel to the deforestation, the introduction of non-native species has radically altered the composition of the biota: almost 70% of vascular plant and 58% of arthropod species (60% of beetles) are exotic [14].

(b) Data

We used the checklist of Borges et al. [14] to determine the beetles of the archipelago. This source includes historical records dating back to the 19th century alongside extensive recent survey data (Details in Electronic Supplementary Material, ESM). Two long-term arthropod sampling projects, BALA in 1999–2000 and BALA2 in 2010, sampled the same 30 sites, covering all remnants of native forest on each island. Additional field surveys were conducted in all other major habitat types, both natural (e.g. caves, coastal areas) and anthropogenic (e.g. exotic forest, pastures, urban areas, see [15] and ESM) – a total of 383 sites. The intensive fieldwork and exhaustive taxonomic work involved have generated a comprehensive presence/absence dataset of species in each island and their distribution across habitat types: the most extensive oceanic island arthropod dataset yet compiled (See ESM for species distributions and species extinctions). Of the 63 endemic coleopteran species, eight cave-adapted, troglodyte species were excluded from analysis, due to their non-dependence on the native forest.

(c) Collection of traits

For geographic range and habitat specialization we classified each species into single-island endemics (SIE) and multi-island endemics (MIE; present in two or more islands); and into species strictly confined to native forest (SCL) and those also found in other habitat types (OHT), respectively. We calculated body size as the sum of the length of the thorax and the length of the abdomen. We measured ten individuals per species per island, using digital photography via a stereoscopic microscope; in the absence of specimens we used original descriptions and other literature references (See ESM for data and reliability of approach).

(d) Statistical analysis

Initially, we considered all endemic species together (N=55). We fitted the three predictors (geographic range, habitat specialization and body size) independently to species extinction status (0=extant, 1=extinct) using a binomial generalized linear mixed model [16] including family and genus as nested random effects to account for phylogenetic relatedness between species. The statistical significance of each predictor was determined by likelihood ratio tests (LRT). Next, we included the three predictors in a global model and then simplified this model using backward elimination based on LRT [17]. Nagelkerke's R^2 was computed for both independent effect and multi-predictor models.

We also computed the same analyses as above but restricting analysis to SIE species (N =32). Consequently only habitat specialization and body size were included as predictors. Next, we restricted analysis to SIE+SCL species (N=18) and tested the independent effect of body size. For comparison, the analyses were re-run with phylogenetic generalized mixed models using a reconstructed calibrated phylogenetic tree at sub-family level (See ESM). While it would have been desirable to also examine interactions between predictors, the data structure limited our analysis to additive effects.

3. Results

Of the 55 endemic species, 32 were SIE, 54 occur in the native forest and 22 are restricted to this habitat type (SCL). Seven species, all SIE, were classified as Extinct in the Wild according to the IUCN criteria (Tables 1, S1, ESM for further details), hence geographic range significantly explained species status when all species where analyzed together (LRT: χ^2=6.32, P=0.01, R^2=0.22). SCL were more prone to extinction than OHT species (χ^2=4.94, P=0.03, R^2=0.18; Tables 1, S1), but there was no body size effect (χ^2=0.64, P=0.42, R^2=0.02). The best multi-predictor model included geographic range and body size, with the extinct species being larger (Table S2). When restricting our analysis to SIE species, body size became the most important predictor of species extinction status when tested independently and when included in a model with habitat specialization (χ^2=4.79, P=0.03, R^2=0.23, Table S2, Fig. 1), again with extinct species being larger. Considering SIE species occurring strictly in native forest (SIE+ SCL), body size was again related to species status (χ^2=8.25, P=0.004, R^2=0.52, Fig. 1). Results remained identical when using a phylogenetic generalized mixed model (Tables S3, S4).

4. Discussion

Extinction in Azorean beetles is linked to a confined geographic range (all extinct species being SIE), habitat specialization, and body size (Table S2). Species with large ranges also tend to have greater local abundances and larger numbers of spatially separated populations [1,18]. Larger populations are more resistant to stochastic fluctuations in demography compared to smaller ones, while metapopulation restocking effects can reduce the effect of local habitat loss [3,19]. Species with specialized resource requirements tend to be more vulnerable to threats such as habitat loss than are generalists: indeed, it has been shown that extinction of narrow-habitat specialists is more common in insects than in other taxa [20]. All but one of the species we considered extinct were forest-dependent. Of the extant endemic beetles of the Azores, 16 are forest-dependent and thus in urgent need of protection measures [12].

The link between larger body size and extinction risk is widely documented for several vertebrate taxa, e.g. birds, mammals [21], and in some cases for arthropods [22].

Larger species tend to occur in lower population densities, have slower reproductive rates and longer life spans [23] and to recover less rapidly from population declines than do rapidly growing populations of smaller species [3,7]. These tendencies are enhanced in arthropods due their more frequent fluctuations in population size compared to vertebrates. Although studies on correlates of extinction risk for insects are scarce, positive relationships between body size and extinction risk have been documented, either directly or as an interaction with other biological traits [22,24 but see 21]. We found that the role of large body size as a predictor of extinction became most evident when restricting the analysis to SIE species. This result was even stronger among the SIEs strictly dependent on native forest. This implies that while large body size might increase extinction risk, this threat can be counterbalanced by a wider distribution. However, an on-going research need is to determine whether records of endemic species found outside native forest might represent transient individuals (sink-populations) rather than self-sustaining populations.

Assuming these seven species of beetles really have gone extinct, they have done so within the last 141 years: an extinction rate of 4.96 species per century. As a large fraction of Azorean forest was cleared before the first reliable species records in the 1850s, the extinction of other disturbance-sensitive species probably went unrecorded [12]; e.g., the epigean relatives of seven of the eight *Trechus* cave beetle species are unknown [25]. Given that previous work has suggested that >50% of the endemic, forest-dependent beetles of the archipelago may be considered committed to extinction [12], the emerging picture presents a clear warning of the impact of habitat loss on the native Azorean biota.

Data accessibility. See the Supplementary Material.

Acknowledgements. We thank the numerous colleagues that contributed to BALA field and lab work since 1999.

Author contributions.

All authors designed the research and wrote the paper; FR and ST undertook the statistical analyses.

Funding statement. Direcção Regional dos Recursos Florestais (PROJ.17.01–080203), Fundação para a Ciência e a Tecnologia FCT-PTDC/BIA-BEC/100182/2008, FCT-PTDC/BIA-BIC/119255/2010.

Competing interests. No competing interests.

References

1. Ladle RJ, Whittaker RJ (Eds.). 2011 *Conservation biogeography*. John Wiley & Sons.
2. Purvis A, Agapow PM, Gittleman JL, Mace GM. 2000 Nonrandom extinction and the loss of evolutionary history. *Science* **288**, 328-330. (doi:10.1126/science.288.5464.328)
3. Lawton JH, May RM (Eds.). 1995 *Extinction rates*. Oxford, UK: Oxford University Press.
4. Hambler, C, Henderson PA, Speight MR. 2011 Extinction rates, extinction-prone habitats, and indicator groups in Britain and at larger scales. *Biol. Conserv*. **144**, 713–721. (doi:10.1016/j.biocon.2010.09.004)
5. Fisher DO, Owens IP. 2004 The comparative method in conservation biology. *Trends Ecol. Evol.* **19**, 391-398. (doi:10.1016/S0169-5347(04)00140-5)
6. Whittaker RJ, Fernández-Palacios JM. 2007 *Island biogeography: ecology, evolution, and conservation*. Oxford: Oxford University Press.
7. Gillespie RG. 1999 Naiveté and novel perturbations: conservation of native spiders on an oceanic island system. *J. Insect Conserv.* **3**, 263-272.
8. Purvis A, Gittleman JL, Cowlishaw G, Mace GM. 2000 Predicting extinction risk in declining species. *P. Roy. Soc. Lond. B: Bio.* **267**, 1947-1952. (doi:10.1098/rspb.2000.1234)
9. IUCN 2014. *The IUCN Red List of Threatened Species. Version 2014.3*. <http://www.iucnredlist.org>. Downloaded on 20 February 2015.

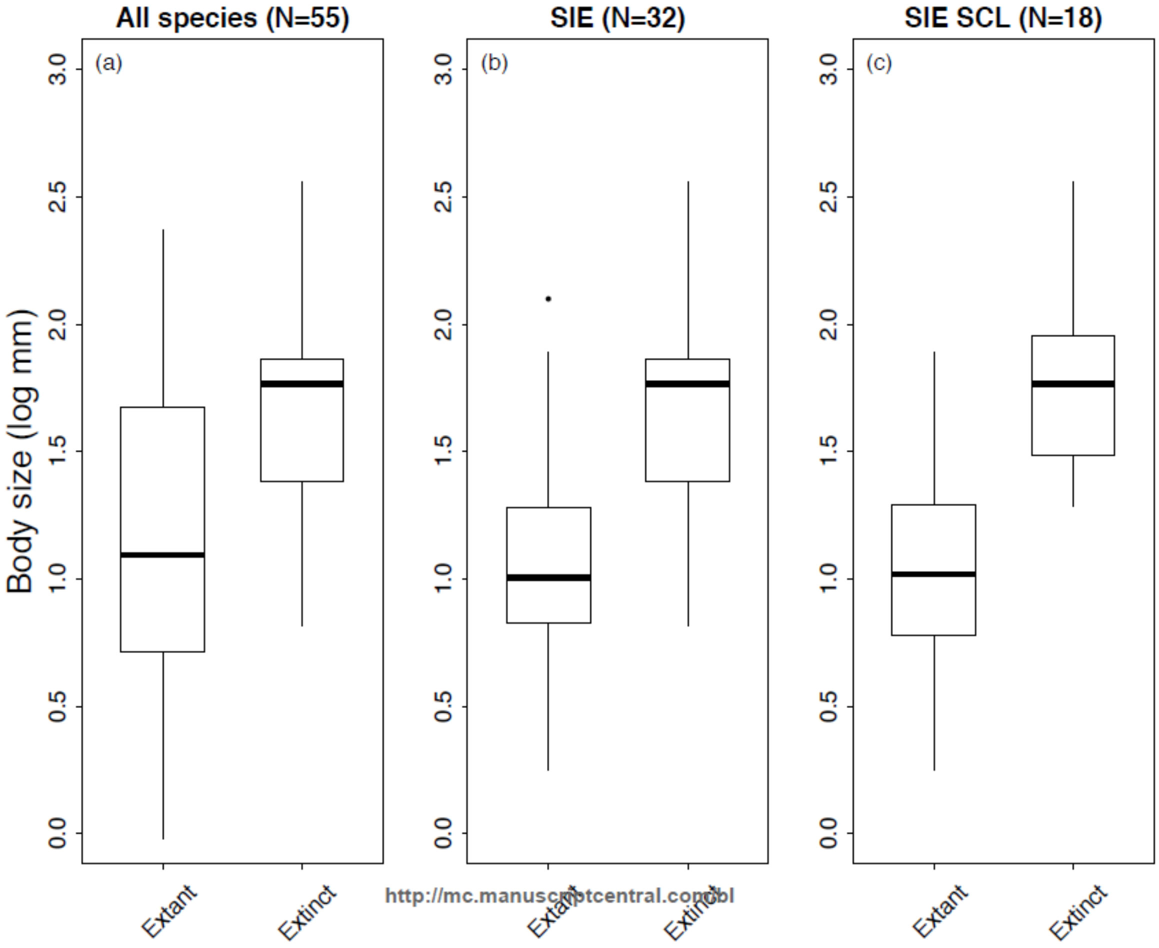
10. Cardoso P, Borges, PAV Triantis KA, Ferrández MA, Martín JL. 2011 Adapting the IUCN red listing criteria for invertebrates. *Biol. Conserv*. **144**, 2432-2440. (doi:10.1016/j.biocon.2011.06.020)
11. McKinney ML. 1999 High rates of extinction and threat in poorly studied taxa. *Conserv. Biol.* **13**, 1273–1281. (doi:10.1046/j.1523-1739.1999.97393.x)
12. Triantis KA, Borges PAV, Ladle RJ, Hortal J, Cardoso P, Gaspar C, Dinis F, Mendonça E, Silveira LMA, Gabriel R, et al. 2010 Extinction debt on oceanic islands. *Ecography* **33**, 285-294. (doi:10.1111/j.1600-0587.2010.06203.x)
13. Tedesco PA, Bigorne R, Bogan AE, Giam X, Jézéquel C, Hugueny B. 2014 Estimating how many undescribed species have gone extinct. *Conserv. Biol*. **28**, 1360-1370. (doi:10.1111/cobi.12285)
14. Borges PAV, Costa A, Cunha R, Gabriel R, Gonçalves V, Martins AF, Melo I, Parente M, Raposeiro P, Rodrigues P, et al. 2010 *List of the terrestrial and marine biota from the azores*. Princípia, Cascais.
15. Borges PAV, Aguiar C, Amaral J, Amorim IR, André G, Arraiol A, Baz A, Dinis F, Enghoff H, Gaspar C, et al. 2005 Ranking protected areas in the Azores using standardised sampling of soil epigean arthropods. *Biodivers. Conserv*. **14**, 2029-2060. (doi:10.1007/s10531-004-4283-y)
16. Bates D, Maechler M, Bolker B, Walker S. 2014 lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-6. http://CRAN.R-project.org/package=lme4.
17. Crawley MJ. 2012 *The R book*. John Wiley & Sons.

18. Lawton JH. 1993 Range, population abundance and conservation. *Trends Ecol. Evol*. **8**, 409-413.
19. Hanski I. 1999 Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos **87**, 209–19. (doi:10.2307/3546736)
20. Dunn RR. 2005 Modern insect extinctions, the neglected majority. *Conserv*. *Biol*. **19**, 1030–1036. (doi:10.1111/j.1523-1739.2005.00078.x)
21. Gaston KJ, Blackburn TM. 1996 Conservation implications of geographic range size–body size relationships. *Conserv. Biol.* **10**, 638-646. (doi:10.1046/j.1523-1739.1996.10020638.x)
22. Seibold S, Brandl R, Buse J, Hothorn T, Schmidl J, Thorn S, Müller J. 2015 Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conserv. Biol*. **29**, 382–390. (doi:10.1111/cobi.12427)
23. McKinney ML. 1997 Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annu. Rev. Ecol. Syst.* **28**, 495-516. (doi:10.1146/annurev.ecolsys.28.1.495)
24. Mattila N, Kaitala V, Komonen A, Kotiaho JS, Päeivinen J. 2006 Ecological determinants of distribution decline and risk of extinction in moths. *Conserv. Biol.* **20**, 1161-1168. (doi:10.1111/j.1523-1739.2006.00404.x)
25. Borges PAV, Oromí P, Serrano ARM, Amorim IR, Pereira F. 2007 Biodiversity patterns of cavernicolous ground-beetles and their conservation status in the Azores, with the description of a new species: *Trechus isabelae* n. sp. (Coleoptera, Carabidae, Trechinae). *Zootaxa* **1478**, 21-31.

Table 1. Number of endemic Azorean beetle species (extinct in parenthesis) by geographic range and habitat specialization (species confined to native forest (SCL) and those also found in other habitat types (OHT).

Predictors	Habitat specialization		
Geographic range	Specialists (SCL)	Generalists (OHT)	Total
Single-Island endemics	18 (6)	14 (1)	32 (7)
Multi-Island endemics	4	19	23
Total	22	33	55 (7)

Figure 1. Body size distribution for extant and extinct Azorean endemic beetle species: (a) all species (N=55), (b) single island endemic species (SIE; N=32) and (c) SIE native-forest specialist species (SIE+SCL; N=18).



http://mc.manuscriptcentral.com/bl

Electronic Supplementary Material

Drivers of extinction: the case of Azorean beetles

Sofia Terzopoulou et al.

2 Species distributions in the Azores.

The recently updated list of Azorean arthropods derive from an unprecedented collaboration of more than 100 taxonomists [1,2], involving the update of taxonomic information, listing of synonyms, and quantification of the numbers of endemic, native non-endemic and exotic species (available online at http://www.azoresbioportal.angra.uac.pt/ [3]. Sources included an exhaustive literature review of taxonomical and distributional data, in addition to data from museum collections (e.g. the University of Azores entomological collections), BA, MSc and PhD theses and expert field reports.

Over the last 15 years, intensive fieldwork and exhaustive taxonomic efforts have also been undertaken in the Azores. Specifically, two long-term ecological research projects, ‘Biodiversity of Arthropods from the Laurisilva of the Azores’ (BALA), BALA in 1999-2000 [4,5,6] and BALA2 in 2010, have involved sampling in seven islands of the archipelago (excluding Corvo and Graciosa due to the current absence of native forest in these islands), covering all remnants of the native forest of the Azores. The same sampling sites were surveyed in both projects (30 sites). Additional field surveys were also conducted in both native forest (70 sites) and in all the other habitat types present in Azores (283 sites), natural (e.g. caves, coastal areas) or anthropogenic (e.g. exotic forest, pastures, urban areas), [7,8]. In total 383 sites have been surveyed, with 30 of them sampled twice, ten years apart.

To assess the species likely to have gone extinct, we compared historical recordings with current findings of the species presence/absence in all islands of the archipelago. As extinct we considered all the endemic species with historical records of presence in the archipelago that were not found during the recent extensive fieldworks implemented since the start of 1999–2000 (all information collected from taxonomic work and fieldwork on Azorean species is compiled in the ATLANTIS-Azores database [9, 10]). Although endemic species originally occurred in the native forest, currently some of them are found also in the anthropogenic habitats. Thus, considering data from surveys conducted on those habitats, we were able to determine whether or not species absent from the native forest patches could be persisting elsewhere within the islands. Those species not observed since the start of the fieldwork in 1999 were classified as extinct. This approach is fully concordant with the definition used by IUCN for species listed as Extinct in the wild '*EXTINCT IN THE WILD (EW) A taxon is Extinct in the Wild when it is known only to survive in cultivation, in captivity or as a naturalized population (or populations) well outside the past range. A taxon is presumed Extinct in the Wild when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time frame appropriate to the taxon's life cycle and life form*' [11]. In our case (i) there are also no captive populations for any of the species considered extinct and (ii) despite the exhaustive recent surveys, we have no record of the presumed extinct species, namely *Bembidion derelictus*, *Bradycellus chavesi*, *Calathus extensicollis*, *Calathus vicenteorum, Trechus torretassoi, Neocnemis occidentalis* and *Nesotes azoricus*, since 1888, 1918, 1930, 1985, 1985, 1865 and 1930, respectively: a minimum of 25 years since the last record, far exceeding the average life cycle of beetles.

3 Reliability of measurements and mean body size.

Since most specimens are held in alcohol and some have been collected more than 20 years ago, the head is in many cases disconnected from the thorax. Thus, we decided to measure the body size as the sum of the length of the thorax and the length of the abdomen. This was applied to all the individuals considered.

Most of the species-based studies on correlates of extinction risk generally assume that phenotypic means of characters (e.g. body size) are species-specific traits; implicitly requiring that intraspecific variation is smaller than interspecific variation. We tested this assumption with our data for 37 of the 55 endemic beetles species considered in the study, for which at least two distinct individuals have been measured (a total of 394 individuals). This was accomplished by using the method developed by de Bello et al. [12], which decomposes variance between intra- and inter-specific variability by quantifying variance with the Rao Quadratic Index. For further details on the method, see [12]. Results showed that 96% of the body size variation among the 394 individuals was attributed to difference between species and, therefore, difference between individuals within species was negligible (i.e. 4%). This result supports the reliability of using the mean body size in our analysis.

Measurements of body length (i.e. sum of the length of the thorax and the length of the abdomen) were taken after the individuals were photographed with a camera installed on a stereoscopic microscope and images were mounted with the software Auto–Montage Pro ® [13].

4 Phylogenetic generalized linear mixed models

All analyses performed with binomial generalized linear mixed model were re-run using phylogenetic generalized linear mixed models.

1 Tree reconstruction

To perform the phylogenetic mixed models, we reconstructed a phylogenetic tree at sub-family level using taxonomic classification of species in subfamilies as in [14]. Sequences of 18S and COI were retrieved from GenBank for the 28 sub-families considered in our study. We also included four families of early diverging Coleoptera lineages as outgroups, Hydroscaphidae, Sphaeriusidae, Torridincolidae (Myxophaga) and Cupepidae (Archostemata) [15]. Sequences of 18s were aligned with BlastAlign [16] and sequences of COI with CodonCode Aligner[1], using the default settings. An ultrametric tree was inferred under an uncorrelated lognormal relaxed clock in BEAST 1.8 [17] using a coalescent tree prior with constant size. The dataset was partitioned by marker (18S and COI) and substitution and clock models were unlinked across partitions, whereas the partition trees were linked. We assigned a GTR+ G + I model of sequence evolution following analyses with Modeltest v. 2.2 [18]. Because the phylogenetic generalized linear mixed models analyses require only that trees be calibrated to relative time-scales, default parameter priors were used except for the mean of branch rates parameter (ucld.mean), which was fixed to 1.0, reflecting the absence of calibration dates: this resulted in time being measured in units that have been arbitrarily chosen so that 1 time unit corresponds to the mean time required for the accumulation of 1 substitution per site. In the analysis, a set of constrains were imposed according to [15, see Fig. S2 herein]. Two independent runs were conducted of 20 million generations each (sampling every 1000th generation). The convergence and mixing of the Markov chain Monte Carlo chains were assessed by inspection of the trace plots and the effective sample sizes using TRACER 1.5 [17]. Samples from the two independent runs were then pooled

---

[1] CodonCode Corporation, www.codoncode.com

after removing a 10% burn-in using LogCombiner 1.6.2 [17] and the means of node heights were summarized on a ‘maximum clade credibility’ tree using TreeAnnotator 1.6.2 [17].

The consensus calibrated trees using relative time generated for the 28 sub-families is presented in Fig. S2. Subsequently, species were grafted to their sub-families using the function *bind.tree* from the R package ape [19] and were then treated as polytomies.

2 Modelling

Phylogenetic generalized linear mixed models were implemented with the function MCMCglmm [20] in R using species status, treated as a binary variable (family = “categorical”), as the response variable. We used a parameter-expanded prior, with V=1, m=1000, α.μ=0 and α.V=1 for the random effects following the recommendation of [21], while for the fixed effect(s), we used a weakly informative Gelman prior [22]. The residual variances were fixed to 1 because they are not identifiable in binary models. We ran each analysis for 5000000 iterations with a burn-in of 10000 and thinning interval of 1000, which resulted in more than 1000 posterior distribution samples of model parameter estimates, from which mean parameter estimates were calculated, and 95% credible intervals were constructed. For each model, we checked the convergence by visually inspecting trace plots of MCMC chains and using Gelman-Rubin tests in the R package *coda* [23]. For the Gelman-Rubin test we ran each analysis three times and used the Gelman-Rubin statistic (potential scale reduction factor; PSR) to compare within- and between-chain variance. When models have converged the PSR <1.1 and in all our analyses PSR was <1.04 and autocorrelation was <0.1 for all models. Effective sample sizes for all fixed and random effects were all greater than 1000.

We performed the complete set of analyses implemented with Binomial generalized linear mixed models (See main text). Full models were simplified by sequentially removing the least significant variable (based on the pMCMC values) until only significant ones remained. Results are given in Table S3 for the independent effect of each predictor and in Table S4 for the best models.

References

26. Borges PAV, Costa A, Cunha R, Gabriel R, Gonçalves V, Martins AF, Melo I, Parente M, Raposeiro P, Rodrigues P, et al. 2010. *A list of the terrestrial and marine biota from the Azores*. Principia, Cascais, Portugal.
27. Assing V. 2013: A revision of Palaearctic *Medon* IX. New species, new synonymies, a new combination, and additional records (Coleoptera: Staphylinidae: Paederinae). *Entomologische Blätter und Coleoptera*, **109**, 233-270.
28. Borges PAV, Gabriel R, Arroz A, Costa A, Cunha R, Silva L, Mendonça E, Martins AF, Reis F, Cardoso P. 2010 The Azorean Biodiversity Portal: an internet database for regional biodiversity outreach. *Syst. Biodivers*. **8**, 423-434. (doi:0.1080/14772000.2010.514306)
29. Borges PAV, Serrano AR, Quartau JA. 2000 Ranking the Azorean Natural Forest Reserves for conservation using their endemic arthropods. *J. Insect Conserv*. **4**, 129-147. (doi:10.1023/A:1009629012205)
30. Borges PAV, Aguiar C, Amaral, J, Amorim IR, André G, Arraiol A, Baz A, Dinis F, Enghoff H, Gaspar C, et al. 2005 Ranking protected areas in the Azores using

standardised sampling of soil epigean arthropods. *Biodivers. Conserv.* **14**, 2029-2060. (doi:10.1007/s10531-004-4283-y)

31. Gaspar C, Borges PAV, Gaston K. 2008 Diversity and distribution of arthropods in native forests of the Azores archipelago. *Arquipélago - Life Mar Sci*. **25**, 1–30.
32. Cardoso P, Aranda SC, Lobo JM, Dinis F, Gaspar C, Borges PAV. 2009 A spatial scale assessment of habitat effects on arthropod communities of an oceanic island. *Acta Oecol.* **35**, 590-597. (doi:10.1016/j.actao.2009.05.005)
33. Borges PAV, Hortal J. 2009 Time, area and isolation: factors driving the diversification of Azorean arthropods. *J. Biogeogr.* **36**, 178-191. (doi:10.1111/j.1365-2699.2008.01980.x)
34. Zurita NA, 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.
35. Borges PAV, Gabriel R, Arroz A, Costa A, Cunha R, Silva L, Mendonça E, Martins AF, Reis F., Cardoso P 2010. The Azorean Biodiversity Portal: an internet database for regional biodiversity outreach. *Syst. Biodivers.* **8**, 423-434. (doi:10.1080/14772000.2010.514306)
36. IUCN 2014. *The IUCN Red List of Threatened Species. Version 2014.3*. <http://www.iucnredlist.org>. Downloaded on 20 February 2015.
37. de Bello F, Lavorel S, Albert CH, Thuiller W, Grigulis K, Dolezal J, Janeček Š, Lepš J. 2011 Quantifying the relevance of intraspecific trait variability for functional diversity. *Methods Ecol. Evol*. **2**, 163-174. (doi:10.1111/j.2041-210X.2010.00071.x)

38. Syncroscopy. Auto-Montage Pro, version 5.03.0061. Syncroscopy, a Division of Synoptics Ltd. Information; 1997. Available from: http://www.syncroscopy.com/auto-montage.

39. Löbl I, Smetana A (Eds.). 2003-11 *Catalogue of the Palearctic Coleoptera Volume I-VI*. Apollo Books, Stenstrup.

40. Hunt T, Bergsten J, Levkanicova Z, Papadopoulou A, John OS, Wild R, Hammond, PM, Ahrnes D, Balke M, Caterino, MS, et al. 2007 A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science*, **318**, 1913-1916. (doi:10.1126/science.1146954)

41. Belshaw R, Katzourakis A. 2005 BlastAlign: a program that uses blast to align problematic nucleotide sequences. *Bioinformatics* **21**, 122-123. (doi:10.1093/bioinformatics/bth459)

42. Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012 Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.* **29**, 1969-1973. (doi:10.1093/molbev/mss075)

43. Posada D, Crandall KA. 1998 Modeltest: testing the model of DNA substitution. *Bioinformatics* **14**, 817-818. (doi:10.1093/bioinformatics/14.9.817)

44. Paradis E, Claude J, Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289-290. (doi:10.1093/bioinformatics/btg412)

45. Hadfield JD. 2010 MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. *J. Stat. Softw.* **33**, 1-22.

46. De Villemereuil P, Gimenez O, Doligez B. 2013 Comparing parent-offspring regression with frequentist and Bayesian animal models to estimate heritability in wild populations:

a simulation study for Gaussian and binary traits. *Methods Ecol. Evol.* **4**, 260–275. (doi:10.1111/2041-210X.12011)

47. Gelman A, Jakulin A, Pittau MG, Su YS. 2008 A weakly informative default prior distribution for logistic and other regression models. *Ann. Appl. Stat.* **2**, 1360–1383. (doi:10.1214/08-AOAS191)
48. Plummer M, Best N, Cowles K, Vines K. 2006 CODA: Convergence Diagnosis and Output Analysis for MCMC. R News **6**, 7-11.

Table S1. Data on the extinction status (0=extant, 1=extinct), body length (mm) and the geographic range (single- or multi- island endemics, native forest specialists or generalists species) of the endemic beetles of Azores considered in the study. Single-island endemic species (SIE) and species strictly confined to native forest (SCL) are marked with 1; when otherwise (i.e. multi-island endemic species and species occurring also in other habitat types (OHT)) are marked with 0.

Family	Species	Extinct	Body length (mm)	Single-island endemic (SIE)	Species confined to native forest (SCL)
Carabidae	*Bembidion derelictus*	1	5.86	1	1
	Bradycellus chavesi	1	4.41	1	1
	Calathus carvalhoi	0	5.52	1	0
	Calathus extensicollis	1	7.06	1	1
	Calathus lundbladi	0	6.61	1	1
	Calathus vicenteorum	1	5.84	1	1
	Cedrorum azoricus	0	10.71	0	0
	Olisthopus inclavatus	0	3.96	1	0
	Pseudanchomenus aptinoides	0	9.46	0	1
	Trechus terrabravensis	0	2.58	1	1
	Trechus torretassoi	1	2.26	1	0
Cerambycidae	*Crotchiella brachyptera*	0	8.12	0	0

Chrysomelidae	*Mniophilosoma obscurum*	0	1.45	1	0
Ciidae	*Atlantocis gillerforsi*	0	1.51	0	0
Curculionidae	*Calacalles azoricus*	0	3.59	1	1
	Calacalles droueti	0	4.47	0	1
	Calacalles subcarinatus	0	1.95	0	0
	Caulotrupis parvus	0	1.96	1	0
	Donus multifidus	0	5.16	1	1
	Drouetius azoricus	0	6.38	0	0
	Drouetius borgesi	0	7.68	0	0
	Drouetius oceanicus	0	8.44	0	0
	Neocnemis occidentalis	1	3.61	1	1
	Phloeosinus gillerforsi	0	2.18	0	1
	Pseudechinosoma nodosum	0	2	0	0
Dasytidae	*Gietella faialensis*	0	2.8	1	0
Dytiscidae	*Agabus godmani*	0	7	0	0
	Hydroporus guernei	0	3.22	0	0
Elateridae	*Alestrus dolosus*	0	5	0	0

	Athous azoricus	0	8.45	0	0
	Athous pomboi	0	8.16	1	0
	Heteroderes azoricus	0	7.93	0	0
Hydraenidae	*Ochthebius frey*	0	1.65	0	0
Laemophloeidae	*Cryptolestes azoricus*	0	1.5	1	1
Latridiidae	*Metophthalmus occidentalis*	0	0.98	0	0
Leiodidae	*Catops velhocabrali*	0	3.06	1	0
Ptinidae	*Sphaericus velhocabrali*	0	1.75	1	0
Staphylinidae	*Aleochara freyi*	0	3.32	1	1
	Atheta floresensis	0	3.07	1	0
	Atheta caprariensis	0	2.83	1	1
	Atheta dryochares	0	1.78	0	0
	Geostiba melanocephala	0	2.7	1	1
	Phloeostiba azorica	0	1.95	0	1
	Phytosus schatzmayri	0	2.08	1	1
	Medon varamontis	0	4	1	1
Scydmaenidae	*Euconnus azoricus*	0	1.28	1	1

Tenebrionidae	*Nesotes azoricus*	1	12.92	1	1
Zopheridae	*Tarphius acuminatus*	0	2.29	1	1
	Tarphius azoricus	0	2.92	0	0
	Tarphius depressus	0	3.28	0	0
	Tarphius pomboi	0	2.54	1	0
	Tarphius rufonodulosus	0	2.4	1	0
	Tarphius serranoi	0	2.37	1	0
	Tarphius tornvalli	0	4.17	0	0
	Tarphius wollastoni	0	2.73	1	0
Total		**7**		**32**	**22**

Table S2. Results of the model selection for the first and second groupings of the endemic beetles of Azores considered in the study (All species and SIE only). Full Binomial GLMM models were simplified by sequentially removing the least significant variable according to a likelihood ratio test (LRT) until only significant variables remained. For each model, the χ^2 and its associated P-value from LRT are given as well as the Nagelkerke's R^2. SIE/MIE = Single / Multi Island Endemic species; SCL/OHT = species strictly confined to native forest (SCL) and those also found in other habitat types (OHT), respectively. Significant effects are indicated in bold.

Grouping	χ^2	P
All species (N=55)		
Full model (R^2 = 0.426)		
Geographic range (SIE/MIE)	**6.582**	**0.010**
Habitat specialization (SCL/OHT)	1.760	0.185
Body size	3.434	0.064
Reduced model (R^2 = 0.374)		
Geographic range (SIE/MIE)	**10.468**	**0.001**
Body size	**4.791**	**0.029**
SIE species (N=32)		
Full model (R^2 = 0.301)		
Habitat specialization (SCL/OHT)	1.760	0.185
Body size	3.434	0.064
Reduced model (R^2 = 0.226)		
Body size	**4.791**	**0.029**

Table S3. Results of the Phylogenetic generalized linear mixed models based on *MCMCglmm* for the three groupings of the Azorean endemic beetles in the study when considering the independent effect of each predictor in explaining species extinction status (N = number of species in each grouping). For each model, the posterior mean, the associated 95% confidence interval (Lower and upper CI) and the pMCMC (*P*-value) are given. SIE/MIE = Single / Multi Island Endemic species; SCL/OHT = species strictly confined to native forest (SCL) and those also found in other habitat types (OHT), respectively. Significant effects are indicated in bold.

Grouping	Posterior mean	Lower CI	Upper CI	pMCMC
All species (N=55)				
Geographic range (SIE/MIE)	**4.120**	**0.492**	**8.1421**	**0.006**
Habitat specialization (SCL/OHT)	**2.740**	**0.438**	**5.154**	**0.013**
Body size	1.327	-0.372	3.138	0.123
SIE (N = 32)				
Habitat specialization (SCL/OHT)	2.312	-0.354	5.006	0.071
Body size	**2.935**	**0.5792**	**5.5464**	**0.010**
SIE SPC (N=18)				
Body size	**4.640**	**1.103**	**8.673**	**0.004**

Table S4. Results of the model selection using Phylogenetic generalized linear mixed models for the first and second groupings of the endemic beetles of Azores considered in the study (All species and SIE only) for which more than one predictor was available for the analysis. MCMCglmm Models are simplified by sequentially removing the least significant variable based on the pMCMC until only significant ones remained. For each predictor, posterior mean, its associated 95% confidence interval (Lower and upper CI) and pMCMC (P-value) are given. SIE/MIE = Single / Multi Island Endemic species; SCL/OHT = Strict / Non-Strict native forest species. Significant effects are indicated in bold.

Grouping	Posterior mean	Lower CI	Upper CI	pMCMC
All species (N=55)				
Full model				
Geographic range (SIE/MIE)	**4.173**	**0.325**	**8.243**	**0.016**
Habitat specialization (SCL/OHT)	1.706	-0.951	4.196	0.180
Body size	2.198	-0.116	4.505	0.050
Reduced model				
Geographic range (SIE/MIE)	**4.990**	**1.300**	**9.142**	**0.002**
Body size	**2.441**	**0.276**	**4.707**	**0.023**
SIE species (N=32)				
Full model				
Habitat specialization (SCL/OHT)	1.771	-1.083	4.583	0.202
Body size	**2.688**	**0.138**	**5.357**	**0.032**
Reduced model				
Body size	**4.640**	**1.103**	**8.673**	**0.004**

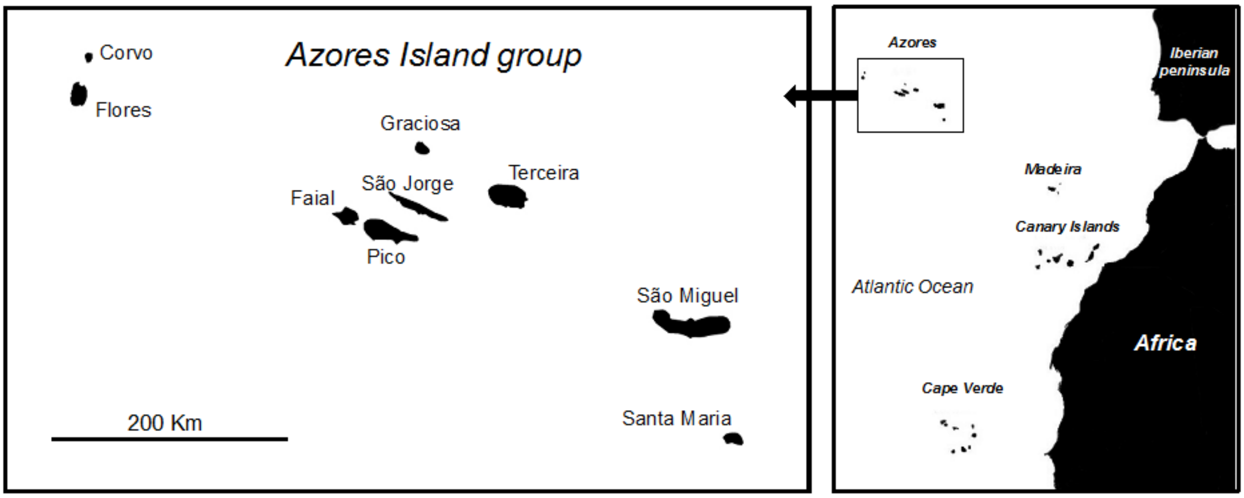


Figure S1. Location map of the Azores.

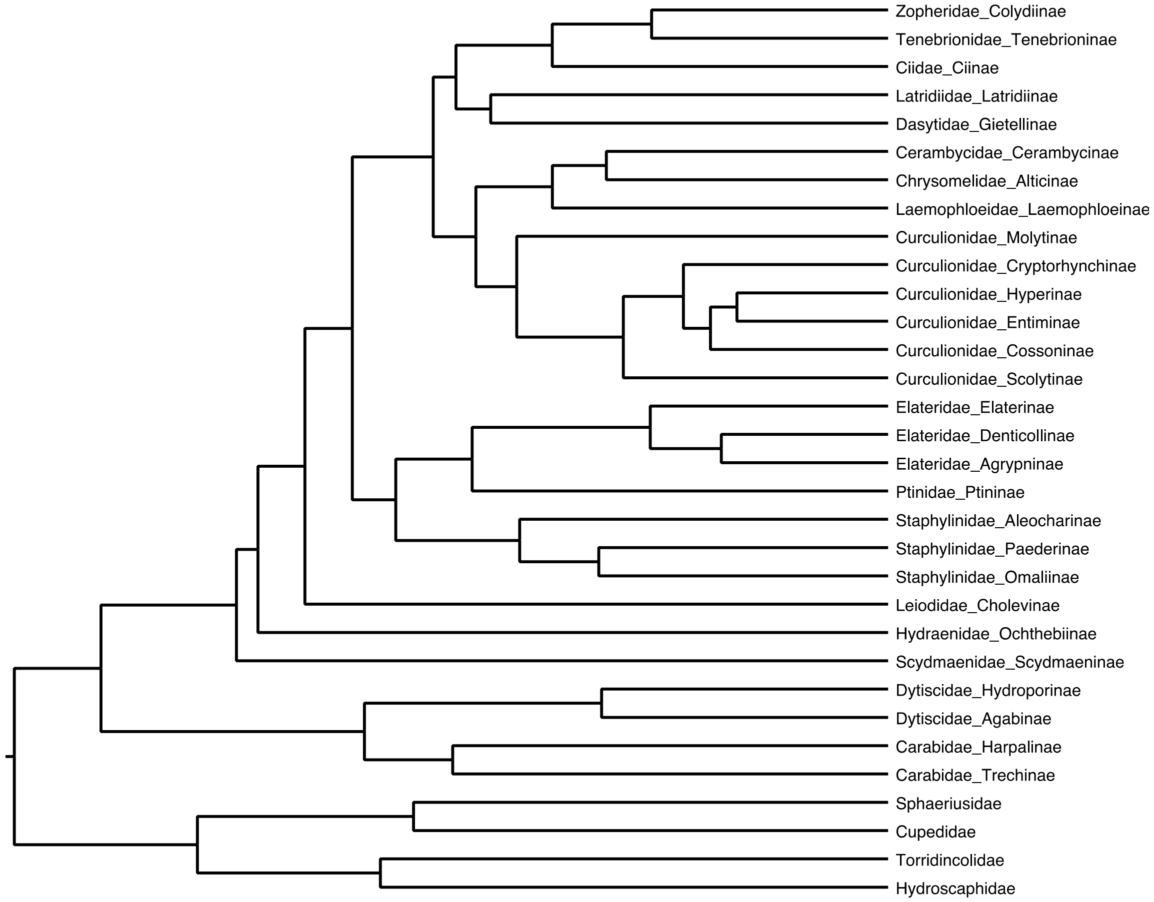


Figure S2. The consensus calibrated trees based on 18S and COI genes for the 28 sub-families of Coleoptera found in our study and the four outgroups, Hydroscaphidae, Sphaeriusidae, Torridincolidae and Cupepidae. Names of the tips indicate first the family and second the sub-family of the species included in the study. For the four outgroups, only the family name is given.