SPECIAL FEATURE

Functional biogeography of oceanic islands and the scaling of functional diversity in the Azores

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Analyses of species-diversity patterns of remote islands have been crucial to the development of biogeographic theory, yet little is known about corresponding patterns in functional traits on islands and how, for example, they may be affected by the introduction of exotic species. We collated trait data for spiders and beetles and used a functional diversity index (FRic) to test for nonrandomness in the contribution of endemic, other native (also combined as indigenous), and exotic species to functional-trait space across the nine islands of the Azores. In general, for both taxa and for each distributional category, functional diversity increases with species richness, which, in turn scales with island area. Null simulations support the hypothesis that each distributional group contributes to functional diversity in proportion to their species richness. Exotic spiders have added novel trait space to a greater degree than have exotic beetles, likely indicating greater impact of the reduction of immigration filters and/or differential historical losses of indigenous species. Analyses of species occurring in native-forest remnants provide limited indications of the operation of habitat filtering of exotics for three islands, but only for beetles. Although the general linear (not saturating) pattern of trait-space increase with richness of exotics suggests an ongoing process of functional enrichment and accommodation, further work is urgently needed to determine how estimates of extinction debt of indigenous species should be adjusted in the light of these findings.

island biogeography | saturation | arthropods | assembly rules | habitat destruction

In comparison with less-isolated settings, the biotas of oceanic island archipelagos are species poor, disharmonic, endemic-rich, and particularly sensitive to disturbance (1). Founded by strongly dispersal-filtered sets of colonists, some of which have since diversified, their precontact biotas represent the dynamic outcome of immigration, speciation, and extinction processes. Following human contact, they have experienced waves of anthropogenic species immigration, ecosystem transformation, indigenous species population reductions, and extinction (1). We may sustain such broad generalizations by reference to many case studies but, in so doing, disregard some intense debates within island biogeography: for instance, whether prehuman contact biotas can be regarded as equilibrial, what rules govern disassembly of precontact assemblages and the assembly of the novel combinations of indigenous and exotic species, how long it will take for the many ecological adjustments to play out before the tally of extinctions of declining indigenous species is clear, or indeed whether the net effect of anthropogenic interference (land-use change, species introductions, etc.) may be higher levels of species diversity (1, 2).

Although traditional island biogeographic analyses *sensu* MacArthur and Wilson (3) have identified notable differences between the emergent diversity patterns of endemic, other native, and exotic species across islands (4–6), they have so far failed to resolve the questions posed above. This failure may in part be because they mostly rely upon analyses in which species are treated as equivalent (but see, e.g., ref. 7). In contrast, case-study evidence suggests that the introduction of particular species possessing novel trait characteristics (e.g., mammalian predators, large herbivores) can have dramatic and disproportionate impacts on island ecosystems and assemblages (1, 8, 9). Such observations suggest that analyses based on functional traits ("components of an organism's phenotype that influence ecosystem level processes"; see ref. 10, p. 742) may provide especially valuable insights for island biogeographic theory (and perhaps vice versa).

Herein, we assess the scaling of functional diversity (FD) with island area and species richness (SR), testing for nonrandomness in the contributions of differing distributional groups of species. For exploratory purposes, we used the following distributional categories: endemics, natives (excluding endemics), indigenous (endemics plus natives), exotics, and all species, noting that the overlaps between categories renders certain tests nonindependent.

Significance

Biogeographic theory builds upon a long history of analyzing species-diversity patterns of remote islands, but no previous studies have attempted to investigate corresponding patterns in functional traits on islands. Our analyses of functional diversity (FD) for spiders and beetles in the Azorean archipelago reveal that FD increases with species richness, which, in turn scales with island area regardless of the taxa and distributional group considered (endemics, natives, and exotics). Our results also support the hypothesis that each group contributes to FD in proportion to their species richness and that, being dominant, exotic species have significantly extended the realized trait space of the Azorean islands. Further analyses in other archipelagos are needed to establish whether our findings are representative of oceanic islands.

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ECOLOGY

Our study system comprises the spiders and beetles of the Azorean archipelago, a uniquely well-specified oceanic island system. The Azores were originally almost fully forested, but, since human colonization (*ca*. A.D. 1440), native-forest cover has been reduced to <5% (11). Spiders are top predators among invertebrates and present an array of potentially important traits related to habitat structure and resource use. Beetles are the most diverse insect Azorean order (as they are globally), include a wide range of feeding ecologies and are prevalent in most habitats. Current estimates are that 22 spider species are endemic, 17 native, and 85 exotic, with respective values for beetles being 65, 134, and 325 (12, 13). It is likely that several endemic species are already globally extinct (14) and analyses of the Azorean "extinction debt" based on calibrated species-area models predict further extinctions to follow (2). However, the logic of those extinction-debt analyses is based on reductions in habitat area of native forest without adjustment for the role of exotics.

Several FD indices have been developed for the analysis of interspecific variation in functional traits for whole assemblages (15, 16). However, there have been few applications of these methods to island faunas (but see, e.g., ref. 8). More specifically, we are not aware of any work quantifying at island scale how functional-trait space of invertebrates has been changed, and with what consequences, by anthropogenic alteration of oceanic islands. Our goal is thus to explore the absolute and relative contribution of endemic, native, and exotic invertebrate species to functional-trait space at island and archipelagic scales in a system of nine oceanic islands spanning from 17 to 757 km^2 in area. We also test for nonrandomness of FD contributions at finer resolution within the remaining native-forest enclaves.

To estimate FD, we use FRic (a measure of functional richness) (17) calculated from input data based on seven traits for spiders and three traits for beetles. Given the broad differences in ecology (encompassing trophic status, flight ability, etc.) between these groups, the traits selected necessarily differ: the spider traits relate to size, feeding behavior, and habitat use whereas the beetle traits relate to size, feeding guild, and flight capabilities (*Materials and Methods*). We test for evidence of trait-space saturation with increasing island area and species richness for each distributional group and for all species (*Materials and Methods* and *SI Appendix*, Table S1). We also test for the contribution made by, and degree of overlap between, each distributional group by means of null-model simulations. We thus address a question of fundamental island- and conservation-biogeographical interest (e.g., refs. 18 and 19): Are the exotic species occupying and thus competing within essentially the same functional space as indigenous groups, or are they serving to expand the functional biodiversity of the archipelago?

Island species–area relationships (ISARs) typically show a positive trend, with slopes (z values) indicative of the process(es) establishing species richness and composition patterns (1, 5, 20). As we move from speciation-dominated systems (e.g., oceanic islands) to immigration–extinction dynamics (e.g., continental-shelf islands) and then to systems of little dispersal-limitation (e.g., inland islands), we generally observe lower values of z, as is also the case when comparing narrowly endemic species (higher z) to nonendemic natives (lower z) within oceanic archipelagos (5, 20). Recent work on functional traits has shown that FD, when measured as functional richness, is typically strongly related to SR (10, 17). Combining these insights, we next consider the implications for patterns of FD in an oceanic archipelago. As remote oceanic islands have strongly colonization-filtered ("disharmonic") biotas, we predict that, in the absence of large-scale trophic collapse driven by ecosystem transformers (9), anthropogenic introductions should add FD disproportionately with reference to native species and endemics and should therefore significantly expand the occupied functional-trait "space" of the archipelago. Because of the expected strong scaling between FD and area, we predict that smaller islands, possessing the fewest indigenous species, will see the greatest proportional gains in FD through the introduction of exotic species even if (compared with larger islands) comparatively few exotic species manage to arrive (less economic activity, less transport to the island) and establish (smaller human settlements) on those small islands. Higher proportional gains in smaller islands are expected because, with increasing richness (larger islands, more introductions), the chances of each new arrival adding truly novel trait combinations to the system diminishes. Therefore, the expansion of FD space by the addition of exotic species is predicted to decrease with island size. Based on the foregoing, we would predict that (*i*) log–log ISARs should increase in slope (z values) from exotics to natives and especially to endemics whereas (*ii*) the equivalent island functional diversity–area relationships (IFDARs) should increase in slope from exotics to indigenous species, with little difference between natives and endemics, as the latter groups experienced the same colonization filter in reaching the archipelago. By contrast, the rank order of "intercepts" (c values) may not be so readily predicted as a function of distributional groups, as much depends on the age and isolation of the islands and the extent of human transportation (1, 5).

Our analyses provide no support for the saturation of trait space at island level: Exotic species add FD approximately in proportion to increasing SR. This result holds for both spiders and beetles although exotic spiders appear to contribute more functional novelty than exotic beetles. Our predictions for the form of ISARs and IFDARs met with only equivocal support (for spider ISARs and beetle IFDARs). Finer scale analyses, restricted to species occurring in native-forest remnants, provide some intriguing indications of habitat filtering on particular islands for beetles, but not for spiders. Our results indicate that anthropogenic habitats and species introductions are combining to permit the persistence in these highly altered oceanic islands of much higher SR than might be anticipated from traditional applications of island theory while processes connected with habitat loss nonetheless continue to drive the attrition of the indigenous fauna (2, 14, 21).

Results

We first established that the significant log–log ISARs previously established for both spiders and beetles (2) hold, with some variation, for the distributional subsets (Fig. 1 and *SI Appendix*, Tables S2 and S3). For spiders, endemics display a steep ISAR, and natives a flat (nonsignificant) ISAR, but when the two categories are combined as "indigenous" species, the resulting ISAR is indistinguishable in slope from that of the exotic category whereas exotics have a higher intercept, reflecting their greater SR (Fig. 1 and *SI Appendix*, Table S3*A*). For beetles, the distributional subsets have indistinguishable slopes but differing intercepts [analysis of covariance (ANCOVA)] (*SI Appendix*, Table S3*B*). Having established that the traits we used are mostly complementary rather than redundant with one another (*SI Appendix*, Tables S1 and S4), we tested for the equivalent island functional diversity–area relationships (IFDARs). The IFDARs show that FD generally increases with island area, with the exception of the endemics subsets, for which no significant relationship was obtained (Fig. 1 and *SI Appendix*, Table S3*A*). For spiders, the slopes of the IFDARs for different subsets are indistinguishable, but the intercepts differ, whereas the between-group differences for beetles involve both intercept and slope (Fig. 1 and *SI Appendix*, Table S3*B*). Thus, in general, SR and FD each scale with island area, consistent with classic island theory (1, 3, 20) while statistical support for our specific predictions regarding ISAR and IFDAR form was limited to spider ISARs and beetle IFDARs.

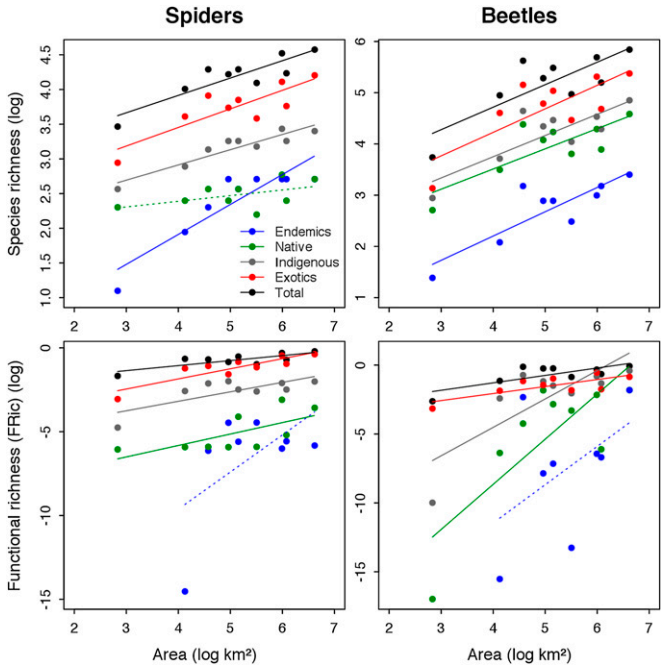

Fig. 1. Island species–area relationships (ISARs) and island functional diversity–area relationships (IFDARs) for Azorean spiders and beetles per island; $n = 9$ islands, except for the IFDAR endemics ($n = 8$), for which Corvo Island could not be included (*SI Appendix*, Table S2). FRic was computed based on six PCoA axes (81% total inertia) and seven PCoA axes (92%) for spiders and beetles, respectively. Dashed lines indicate nonsignificant regressions, all others being significant at $P < 0.05$ (see *SI Appendix*, Table S3 for details). Note that overplotting obscures some data points.

Comparison of linear and polynomial model fits for the FD–SR relationship provides a test for saturation in trait space with increasing SR across the nine islands (eight for endemics) (Fig. 2). Linear models are preferred [based on small sample size-corrected Akaike information criterion (AIC_c) values], with the following exceptions: for endemic spiders and native beetles, neither model is adequate (F statistic tests, $P > 0.05$); for endemic beetles, the ΔAIC_c between the linear and polynomial models is <2, indicating equivalence in fit, and, for native spiders, the fitted polynomial indicates increasing FD with higher SR rather than a tendency toward asymptote. Comparison with a sensitivity analysis indicates the patterns for endemics to be equivocal and unstable (Fig. 2 and *SI Appendix*, Fig. S1); in addition, a separate sensitivity test established that linear models are preferred for each distributional group of spiders upon reduction of the number of traits from seven (main analyses) down to three (as for beetles) (*SI Appendix*, *SI Materials and Methods*, and Table S5).

We next used a simulation approach to create null distributions of expected FD per island for each observed SR value. We report two such simulations (*SI Appendix*, Table S6). First, based on the entire archipelagic species pool, we found no deviation from the null expectation for either taxon for any distributional grouping; i.e., observed FD is simply a function of SR. Our second simulation was restricted to species occurring in the native forest (SONF), to assess the outcome of species assembly processes in the habitats where most remaining threatened endemic species occur. In this case, spider values did not depart from expected, but significantly lower than expected values were observed for six islands for native beetles (Faial, Pico, S. Jorge, S. Maria, S. Miguel, and Terceira) and for three islands for exotic beetles (S. Maria, S. Miguel, and Terceira). Lower values imply that, for the given SR, the FRic value is lower than expected were these species a random draw from the archipelagic SONF pool.

To further interrogate the trait-space occupancy and overlap among endemics, natives, and exotics, we undertook analyses of the whole archipelagic species pool (rather than per island) and estimated FRic as before, but using a slightly lower proportion of the derived trait data (*Materials and Methods* and *SI Appendix*,

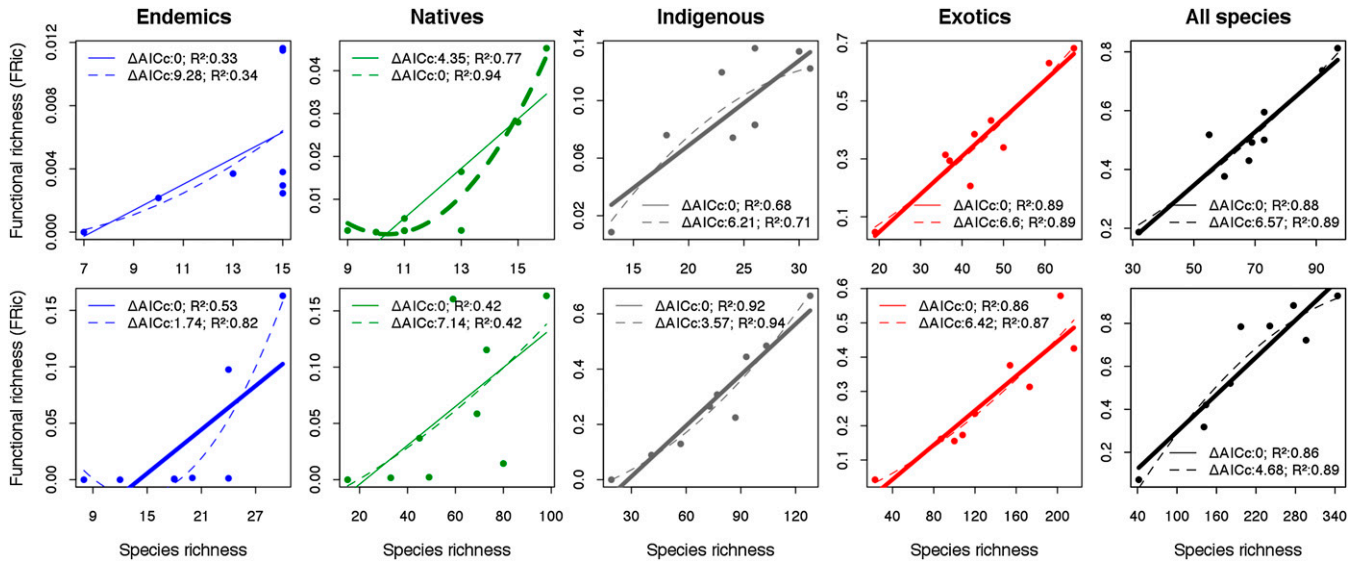

Fig. 2. The relationship between functional richness values (FRic, ref. 17) and species richness (SR) for Azorean spiders (*Upper*) and beetles (*Lower*) for each distributional category, where each data point represents an island ($n = 9$, except for endemics, where $n = 8$ as Corvo Island was excluded). Linear (full lines) and polynomial (dotted lines) fits and their respective ΔAIC_c and R^2 values are given. Bold lines indicate that the model is significant (F statistic test $P < 0.05$) and has the lowest ΔAIC_c value. In all cases, apart from endemic beetles, this is also the single "best" model and the preferred model (based on ΔAIC_c). Note that the polynomial model for endemic beetles is unrealistic in indicating negative FRic values, meaning that, even in this case, the linear model is preferable on grounds of ecological realism. FRic was computed based on six PCoA axes (81% total inertia) and seven PCoA axes (92%) for spiders and beetles, respectively.

Table S7 and Fig. S2). For spiders, 99.74% of the trait space is occupied by exotic species, 36.24% by natives, and 20.64% by endemics (Table 1). The endemic trait space is nested within that of natives, and natives within the exotics. By contrast, endemic (83.1%) and native (89.8%) beetles occupy far larger proportions relative to exotics (95.8%) although, again, the space occupancy is largely nested. The null simulations indicate that each distributional category contributes to the overall trait space as expected as a simple function of their SR. There are two marginal exceptions: First, endemic spiders occupy less functional space than expected and, second, the overlap between endemic and exotic spiders is less than expected. One corollary is that spider mean body size increases from endemic to native to exotic spiders (although only endemic body size is statistically distinct) whereas, for beetles, the three distributional categories are not distinguishable by body size (*SI Appendix*, *SI Results*, *Body Length*). These results indicate that the emergent patterns in FD can be related back to the underlying functional-trait data (compare *SI Appendix*, Fig. S2). Moreover, even when analyzing a single, common trait, there are differences between the two taxa in the relative contribution to FD made by endemics, natives, and exotics. The patterns in body size are also broadly as expected as larger bodied spiders are relatively unlikely to reach such remote islands naturally by ballooning, but may readily do so by human transportation (cargo in boats and planes). In contrast, beetles are less likely to demonstrate such a strong body size-related filter due to their active flight capability.

As the within-island habitat occupancy of the different groups may be crucial to the ecological interpretation (e.g., ref. 21), we undertook a further randomized simulation analysis of the species occurring in native forest, analyzing the degree of overlap in FD between exotic SONF and indigenous SONF and how this overlap compares with that expected if the exotic SONF were a random draw from the overall set of exotic species. This test showed only one deviation from the null expectation across the nine islands (Table 2). Only for beetles on Terceira Island is the overlap marginally lower than expected by chance, implying a degree of functional divergence between exotic SONF and indigenous SONF (Table 2). Thus, based on the traits assessed here, the assemblage of exotic species that has been observed in native-forest habitat in each island is (with that one exception) essentially a random subset of the exotics pool and not a pool of species filtered with respect to their similarity with indigenous species.

Table 1. Functional-space occupancy and overlap per distributional group, for all Azorean species (*n* values in *SI Appendix*, Table S2) based on FRic estimated from the first four PCoA axes using a Gower distance matrix

Distributional groups	Spiders	Beetles
Functional space		
Endemics	20.64 (−1.873)*	83.1 (0.550)
Natives	36.24 (0.567)	89.8 (−0.290)
Exotics	99.74 (0.687)	95.8 (−3.032)*
Overlap		
Endemics–natives	19.01 (−0.047)	76.3 (0.148)
Endemics–exotics	20.55 (−1.917)*	79.9 (0.263)
Natives–exotics	36.04 (0.696)	88.3 (−0.409)
Endemics–natives–exotics	18.98 (−0.019)	75.9 (0.123)

PCoA axes 1–4 account for 71% and 77% of the total inertia for spiders and beetles, respectively. Results were standardized by the full volume expressed as (Endemics + Natives + Exotics) − (Endemics ∩ Natives + Endemics ∩ Exotics + Natives ∩ Endemics − Endemics ∩ Natives ∩ Exotics), to sum to 100%, where ∩ is the intersection between pairs of volumes or among the volumes. In parentheses: deviation from the null expectation (given observed SR) for the functional-space overlap between categories and among the three categories measured by the standardized effect sizes (SESs), i.e., (O − M)/S, where O is the observed value and M and S are the mean and SD, respectively, of 1,000 randomizations of the trait distribution for that plot. Negative SESs mean functional spaces and overlaps are lower than expected by chance and positive SESs mean the opposite, where * indicates $0.01 < P < 0.05$ and, in all other cases, $P > 0.05$.

Table 2. Deviations expressed as standardized effect sizes (SESs) from the null expectation (given observed SR) for the functional overlap between exotic species occurring in native forest (SONF) and indigenous SONF for Azorean spiders and beetles species, based on the PCoA analyses reported in Table 1

Island	Spiders	Beetles
Corvo	0.237	−1.212
Faial	0.019	−1.045
Flores	0.702	0.279
Graciosa	1.290	−1.544
Pico	0.243	0.740
São Jorge	0.457	−0.736
São Miguel	0.691	−1.863
Santa Maria	0.538	−0.377
Terceira	−0.423	−2.416*

*$0.01 < P < 0.05$ and, in all other cases, $P > 0.05$.

Discussion

For most distributional groups, we obtained a strong positive relationship between island area and species richness (SR), with exotic SR exhibiting a similar but elevated ISAR to indigenous species, while FD also increases in proportion to both island area and SR across the nine islands of the archipelago. Thus, the principal effect of increasing SR by the addition of exotics is to generate a corresponding increase in FD, with no evidence of saturation. Whereas the ISARs vary mostly in their intercepts, the form of the IFDARs indicates that exotic spiders contribute an increasingly large proportion of FD with increasing island log-area. The pattern for beetles differs, with indigenous species showing comparable FD to exotics across the larger islands (Fig. 1).

Our analyses of functional space occupancy and overlap show that exotic spiders have contributed much more to the increase in functional trait-space occupancy than have exotic beetles, both in absolute terms and in proportion to increasing SR (Table 1, Fig. 1, and *SI Appendix*, Fig. S3). Exotic spiders have added new taxonomic diversity to the Azores. For example, 13 of the 26 spider families now found on the archipelago are wholly comprised of exotics (13), including species bringing completely new foraging strategies to the regional functional space. For beetles, a rather lower proportion—18 of 54 families—are represented only by exotics (13), consistent with their making a lesser contribution to functional space across the archipelago. In summary, the most striking emergent pattern is that, for both taxa, FD scales up with the area and number of species per island, indicating that the present-day Azorean fauna appears to be largely unsaturated in terms of functional-trait space and consequently remains vulnerable to further colonization by newly introduced exotics (22).

These observations of expanding "biodiversity" contrast with claims (2, 14) of past and impending extinctions as a result of habitat alteration, yet these scenarios may be easily reconcilable with reference to the massive anthropogenic changes since colonization *ca.* A.D. 1440. The native habitats, on which many indigenous arthropods are dependent (23), have been reduced across the archipelago to <5% of their original cover, and an array of new agricultural, forestry, urban, and semiurban habitats have been created in their place. Concurrently, large numbers of exotic species have been introduced by anthropogenic means,

many of which occur wholly or predominantly in novel, anthropogenic habitats (24). The resulting ecological relationships between indigenous and exotic species must span the full gamut from closely co-occurring and interacting, to nonexistent, depending on the ecology and habitat occupancy of the particular species under consideration.

Previous work has shown evidence of source–sink dynamics operating between native and anthropogenic habitats in these islands. This process operates in both directions, with some endemic spiders and very few endemic beetles (see, e.g., ref. 23) spilling into novel sink habitats surrounding native forest whereas intensive pasture is the main habitat source of exotic species invading native forest (25). The success (i.e., abundance and spread) of such exotic "invasive" species has been found to vary between soil and canopy habitats. In particular, the canopies of Azorean endemic trees seem to be a specialized habitat, and few exotic insects and spiders maintain "source" populations there (12, 25, 26). These findings suggest that there may be assembly rules determined by a combination of functional traits and characteristics of the habitat template at local scales of analysis. In the present coarser-scaled analyses, we found no evidence for saturation at the island scale, and, when analyzing overlap between exotic and indigenous species occurring in native forest (SONF), we again found no deviation from expected, apart from the single case of beetles on Terceira (for which functional divergence was found). We did find slightly more extensive indications of lower FD than expected as a function of SR for native SONF in six islands and exotic SONF for three islands for beetles (Table 2 and *SI Appendix*, Table S6). These findings are intriguing. However, when endemic and native species are recombined to represent the whole indigenous assemblage of SONF, no departure from random is evident. The three islands showing lower than expected FD for exotic SONF are S. Maria, S. Miguel, and Terceira. These islands are the three richest islands in terms of exotic species and, on the basis of this test, would appear to show some evidence of saturation of native forest for exotics. Alternative explanations are possible; for example, these results might reflect the existence of large numbers of urban beetle species, or of recent arrivals that have yet to reach and enter the remaining native-forest fragments (24). It thus appears that multiscale analyses will be necessary, assessing species abundances and population trajectories, to determine how exotic species are influencing survival prospects of indigenous species in the remaining forest patches.

We recognize that FD values can be sensitive to properties such as the number and range of traits considered and that the outcome of certain FD analyses can also be sensitive to how the species pool is defined (15, 27). In the present analysis, we necessarily began by using the archipelagic species pool, as we lack a more realistic basis for defining a regional species pool. It is also important to note that we cannot be certain of the number, or trait selectivity, of extinctions of indigenous species that may have occurred without record, and which may have impacted on the functional trait-space occupancy and FD of indigenous groups (2, 13, 14) (*SI Appendix, SI Materials and Methods*). Moreover, a fuller picture of trait occupancy requires the use of additional FD indices that in essence interrogate the occupancy of the convex hull space analyzed herein (e.g., functional evenness or functional divergence) (17), and which make use of species-abundance data: unfortunately such data are lacking at a whole-island scale.

To conclude, it is apparent that exotic species have significantly expanded the realized trait space and FD of the Azorean islands, generating emergent FD patterns strikingly consistent with those of the indigenous fauna (compare ref. 4), while remaining largely dependent on the extensive anthropogenic habitats that have replaced the native forests. These findings suggest that, whereas island area strongly constrains both species richness and FD, the diversity levels observed are not indicative of a fixed area-dependent species carrying capacity. Rather, the capacity attainable has increased as the biological isolation of the islands has been progressively diminished by human agency. Although there is no evidence of saturation of the anthropogenic habitat space, endemic species are threatened in their native-forest enclaves (2), in which a degree of habitat filtering is apparent, at least for beetles. Further analyses of the functional biogeography, for other taxa and archipelagos, at multiple scales of analysis, are needed to establish whether the findings reported herein are representative of oceanic islands (compare ref. 28). In addition, long-term monitoring data are required to determine the extent to which indigenous species of the Azores can persist within the now much larger pool of species present on the islands.

Materials and Methods

In all cases, we undertook and reported separate analyses for spiders and for beetles, conducting statistical analyses implemented within the R programming environment (29) and the software FDiversity (30). Where significance tests are reported, the critical value used was <0.05.

Study Area. The Azores are volcanic, oceanic islands spanning the mid-Atlantic ridge, roughly 1,600 km from the European mainland. Humid evergreen broadleaf laurel forest (*laurisilva*) covered most of the land area before human colonization *ca.* A.D. 1440. Around 95% of these forests have since been destroyed by humans (11). The current major vegetation habitats across the archipelago comprise native forest, exotic forest, seminatural pasture, and intensively managed pasture (2, 21, 23, 25).

Functional Traits and Distributional Data. Data on the occurrence of species in each island and categorizations as endemic, native, or exotic were drawn from the latest compilations (13). We collated and/or recorded information for each spider species for (*i*) body length (average between females and males), (*ii*) web use, (*iii*) web architecture, (*iv*) foraging strategy, (*v*) prey range, (*vi*) vertical stratification, and (*vii*) circadian activity; and for each beetle species (*i*) body length, (*ii*) feeding guild, and (*iii*) wing morphology (see *SI Appendix, SI Materials and Methods* for details). Except for body length, all traits were coded as nominal variables. For analyses focused on species occurring in native forest (hereafter SONF), we used our distributional data (*SI Appendix, SI Materials and Methods*) to denote exotic SONF and indigenous SONF. As some of the exotic SONF may have been "tourists" or "sink populations," we avoided terming this group "invasive species."

Computing FD. Functional diversity (FD) was computed using the functional richness index FRic (17), which measures the multidimensional volume of trait space defined by using a convex hull volume. FRic does not require abundance data (which are unavailable in this study) and is not sensitive to species splitting; it is also effective for discriminating assembly rules (e.g., ref. 15) (see *SI Appendix, SI Materials and Methods* for details). First, Gower's distance was used to calculate multivariate distances between species based on the raw trait data. To avoid negative eigenvalues, the Gower's distance matrix was subject to primary square-root transformation (31). These distance data were then subject to principal coordinates analysis (PCoA)s and the resulting PCoA axes were used as new composite functional traits. FRic is then based on the minimum convex hull volume that contains all of the species selected for analysis (e.g., all endemics, exotic species on Faial Island, etc.). As the index requires that there are more species than there are traits (17) and in certain categories we have small numbers of species, we used only the first six (spiders, 81% total inertia) and seven (beetles, 92% total inertia) PCoA axes to estimate FRic for the island-by-island analyses. For endemics, as Corvo island has only three endemic spider and four endemic beetle species, we ran these analyses without Corvo (for subsidiary analyses including Corvo, see *SI Appendix, SI Results*). Due to computational restrictions, for analyses at the archipelago level (where very large numbers of species are involved), we used only the first four PCoA axes. We calculated FD (i.e., FRic) for five species groups: (*a*) endemics, (*b*) natives (i.e., excluding endemics), (*c*) indigenous (i.e., *a* plus *b*), (*d*) exotics, and (*e*) all species.

Relationships with Island Area. We estimated the log–log island species–area relationship (ISAR) and the equivalent island functional diversity–area relationship (IFDAR) for each distributional category. The significance of both linear and quadratic models was assessed using the *F* statistic. Differences

between the slopes and intercept between categories were estimated by analysis of covariance (ANCOVA), first considering endemics, native non-endemic, and exotics and, second, indigenous and exotic species.

Testing Redundancy. Potential presence of saturation/redundancy, for each grouping, was analyzed by means of the interisland SR–FD relationship. We used linear modeling and evaluated the relevance of a quadratic term (polynomial) to account for potential curvilinear relationships (i.e., indications of saturation) (32, 33). The significance of both linear and quadratic models was assessed using the *F* statistic. The additional information provided by the quadratic model was assessed on the basis of percentage of explained variance (R^2) and the small sample size-corrected AIC_c. The most parsimonious model has the lowest AIC_c, and thus $\Delta AIC_c = 0$. Models with ΔAIC_c between 0 and 2 were considered to have equivalent empirical support, and models with $\Delta AIC_c > 2$ were considered to have less support (34). Second, to distinguish whether FD was simply a product of SR, we used a simulations approach to create null distributions of FD for each observed SR value. Keeping SR constant for each island and category, we randomly selected species from the global pool of species without distinction between endemic, native, and exotic species. We repeated this procedure 999 times to produce a distribution of null FD values. The final null distribution included the 999 random values plus the observed value. Based on this null distribution, we computed the standardized effect size (SES) for each island to measure deviation of the observed FD from the null distribution. The *P* value associated with our null hypotheses, i.e., no deviation from a random assortment for species, was estimated per island. To avoid type I errors, we applied a false discovery rate analysis (FDR) (35) to account for multiple test comparisons.

Estimating Functional Space and Overlap. Overlap between endemic, native, and exotic functional space at the archipelago scale was estimated following ref. 36. The multidimensional volume (i.e., convex hull) for each set of species was estimated, allowing quantification of the intersection between two (or more) species assemblages. The overlap is maximal when the two functional spaces are equally similar or one is nested in the other and minimal (zero) when assemblages do not intersect in their functional spaces. Due to computational restrictions, analyses for the entire archipelagic pool of species were run using only the first four PCoA axes (see *Computing FD*), summarizing 71% and 77% of the total inertia present in the initial Gower distance matrix for spiders and beetles, respectively, and for each pairwise comparison of endemics, natives, and exotics. To determine whether outcomes are simply a function of SR variation between categories, two different hypotheses were tested: (*i*) Does the functional space for each category differ significantly from a random expectation for the given SR? (*ii*) Does functional pairwise overlap differ significantly from a random expectation for a given difference in SR? Expected distributions were obtained by 999 randomizations of the label of the distributional categories for each species (i.e., endemics, natives, and exotics) keeping SR constant. Statistical significance of the observed values was estimated by calculating the *P* value from the null distributions.

Functional Overlap Between Exotic and Indigenous Species Occurring in Native-Forest Habitat. To test whether the exotic species co-occurring with indigenous species in native-forest habitat are a random draw from the overall set of exotic species, we undertook a further test focusing only on species occurring in native forest (SONF). Expected distributions of the overlap between exotic SONF and indigenous SONF were obtained by measuring the overlap between indigenous SONF and random selections of all exotic species 999 times, keeping richness of the exotic SONF per island in the native habitat constant. Statistical significance was estimated as above.

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1. Whittaker RJ, Fernández-Palacios JM (2007) *Island Biogeography: Ecology, Evolution, and Conservation* (Oxford Univ Press, Oxford), 2nd Ed.
2. Triantis KA, et al. (2010) Extinction debt on oceanic islands. *Ecography* 33:285–294.
3. MacArthur RH, Wilson EO (1967) *The Theory of Island Biogeography* (Princeton Univ Press, Princeton, NJ).
4. Sax DF, Gaines SD, Brown JH (2002) Species invasions exceed extinctions on islands worldwide: A comparative study of plants and birds. *Am Nat* 160(6):766–783.
5. Triantis KA, Mylonas M, Whittaker RJ (2008) Evolutionary species–area curves as revealed by single-island endemics: Insights for the inter-provincial species–area relationship. *Ecography* 31:401–407.
6. Price JP, Wagner WL (2011) A phylogenetic basis for species-area relationships among three Pacific Island floras. *Am J Bot* 98(3):449–459.
7. Borges PAV, Hortal J (2009) Time, area and isolation: Factors driving the diversification of Azorean arthropods. *J Biogeogr* 36:178–191.
8. Blackburn TM, Petchey OL, Cassey P, Gaston KJ (2005) Functional diversity of mammalian predators and extinction in island birds. *Ecology* 86:2916–2923.
9. Terborgh J (2010) *The Trophic Cascade on Islands: The Theory of Island Biogeography Revisited*, eds Losos JB, Ricklefs RE (Princeton Univ Press, Princeton), pp 116–142.
10. Petchey OL, Gaston KJ (2006) Functional diversity: Back to basics and looking forward. *Ecol Lett* 9(6):741–758.
11. Gaspar C, Borges PAV, Gaston KJ (2008) Diversity and distribution of arthropods in native forests of the Azores archipelago. *Arquipél Life Mar Sci* 25:1–30.
12. Borges PAV, Wunderlich J (2008) Spider biodiversity patterns and their conservation in the Azorean archipelago, with description of new taxa. *Syst Biodivers* 6:249–282.
13. Borges PAV, et al. (2010) *A List of the Terrestrial and Marine Biota from the Azores* (Princípia, Oeiras, Portugal).
14. Cardoso P, Arnedo MA, Triantis KA, Borges PAV (2010) Drivers of diversity in Macaronesian spiders and the role of species extinctions. *J Biogeogr* 37:1034–1046.
15. Mouchet MA, Villéger S, Mason NWH, Mouillot D (2010) Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Funct Ecol* 24:867–876.
16. Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's guide to functional diversity indices. *Ecol Monogr* 80:469–484.
17. Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89(8):2290–2301.
18. Lambdon PW, Lloret F, Hulme PE (2008) Do non-native species invasions lead to biotic homogenization at small scales? The similarity and functional diversity of habitats compared for alien and native components of Mediterranean floras. *Divers Distrib* 14:774–785.
19. Ladle RJ, Whittaker RJ, eds (2011) *Conservation Biogeography* (Wiley-Blackwell, Oxford).
20. Triantis KA, Guilhaumon F, Whittaker RJ (2012) The island species–area relationship: Biology and statistics. *J Biogeogr* 39:215–231.
21. Cardoso P, et al. (2009) A spatial scale assessment of habitat effects on arthropod communities of an oceanic island. *Acta Oecol* 35:590–597.
22. Borges PAV, et al. (2006) Invasibility and species richness of island endemic arthropods: A general model of endemic vs. exotic species. *J Biogeogr* 33:169–187.
23. Meijer SS, Whittaker RJ, Borges PAV (2011) The effects of land-use change on arthropod richness and abundance on Santa Maria Island (Azores): Unmanaged plantations favour endemic beetles. *J Insect Conserv* 15:505–522.
24. Borges PAV, et al. (2013) New records of exotic spiders and insects to the Azores, and new data on recently introduced species. *Arquipél Life Mar Sci* 30:57–70.
25. Borges PAV, Ugland KI, Dinis FO, Gaspar C (2008) Insect and spider rarity in an oceanic island (Terceira, Azores): True rare and pseudo-rare species. *Insect Ecology and Conservation*, ed Fattorini S (Research Signpost, Kerala, India), pp 47–70.
26. Ribeiro SP, Borges PAV (2010) Canopy habitat area effect on the arthropod species densities in the Azores: Pondering the contribution of tourist species and other life histories. *Terrestrial Arthropods Of Macaronesia: Biodiversity, Ecology And Evolution*, eds Serrano ARM, Borges PAV, Boieiro M, Oromí P (Sociedade Portuguesa de Entomologia, Lisbon), pp 89–114.
27. Lessard J-P, Belmaker J, Myers JA, Chase JM, Rahbek C (2012) Inferring local ecological processes amid species pool influences. *Trends Ecol Evol* 27(11):600–607.
28. Gillespie RG, Claridge EM, Roderick GK (2008) Biodiversity dynamics in isolated island communities: Interaction between natural and human-mediated processes. *Mol Ecol* 17(1):45–57.
29. R Development Core Team (2011) R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, Vienna, Austria). Available at www.R-project.org.
30. Casanoves F, Pla L, Di Rienzo JA, Díaz S (2011) FDiversity: A software package for the integrated analysis of functional diversity. *Methods Ecol Evol* 2:233–237.
31. Legendre P, Legendre L (1998) *Numerical Ecology* (Elsevier Science, Amsterdam), 2nd Ed.
32. Bihn JH, Gebauer G, Brandl R (2010) Loss of functional diversity of ant assemblages in secondary tropical forests. *Ecology* 91(3):782–792.
33. Mayfield MM, et al. (2010) What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Glob Ecol Biogeogr* 19:423–431.
34. Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (Springer, New York).
35. Benjamini Y, Yekutieli D (2001) The control of the false discovery rate in multiple testing under dependency. *Ann Stat* 29:1165–1188.
36. Villéger S, Novack-Gottshall PM, Mouillot D (2011) The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. *Ecol Lett* 14(6):561–568.

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Supporting Information

SI Materials and methods

Study area. The Azores is one of the world's most isolated archipelagos. Located in the North Atlantic (37–40° N, 25–31° W), the archipelago comprises nine islands aligned on a west/north-west to east/south-east axis (Flores and Corvo to the west, Faial, Pico, São Jorge, Terceira and Graciosa in the centre and São Miguel and Santa Maria to the east). The islands range in date of origin from 0.25 Ma for Pico to 8.12 Ma for Santa Maria. Azorean native forest (*laurisilva*) comprises an impoverished association of evergreen shrub and tree species, which almost entirely covered the islands before human settlement (*c.*AD 1440) (1). By 300 yr ago (*c.*AD 1700) anthropogenic clearance had restricted the native forest in most islands to areas above 300 m a.s.l. and by *c.*AD 1850 to areas above 500 m a.s.l. (2). Extensive dairy farming in the latter part of the 20th century led to widespread clearing at mid- and high-elevations for pasture, further decreasing the native forest to its current extent of about 5% of the total area of the archipelago (<58 km^2 in total), mostly in high and steep areas (2). Currently, four major habitats dominate: (i) native forests; (ii) exotic forests (*Cryptomeria japonica* and *Eucalyptus* monoculture plantations, monocultures and mixed forest of the invasive *Pittosporum undulatum*); (iii) semi-natural pastures (mid- and high- elevation pastures that maintain some indigenous plants); and (iv) intensively managed pastures mainly used for milk production (3–5). There are also small

patches of high elevation natural grassland and bogs (*Sphagnum* spp.), and low elevation agricultural fields, vines and orchards. Urban areas are mostly coastal in location.

Being remote oceanic islands, the Azores support a significant number of endemic species but the current biota is dominated by introduced exotic species, representing 80% of the flora (6) and 60% of the arthropods (7). Their introduction started during land-use changes commencing almost 600 hundred years ago, as the Portuguese settlers brought plants from all parts of the world and especially from mainland Portugal, South America and Africa.

Species distributions in the nine islands and in native and exotic habitats. The recently updated lists of Azorean arthropods derive from an unprecedented collaboration of more than 100 taxonomists (7), involving the update of taxonomic information, listing of synonyms, and quantification of the numbers of endemic, native and exotic species (available online at http://www.azoresbioportal.angra.uac.pt/ (see also 8). 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. Our data also include information derived from extensive standardized sampling (4, 5) of: native forest (100 sites in 7 islands), high elevation natural grasslands (20 sites, 5 islands), peat bogs (4 sites, 1 island), exotic forests (37 sites, 4 islands), semi-natural pastures (29 sites, 4 islands), and intensively managed pastures (38 sites, 4 islands). This distributional data set was used to attribute species as occurring in native forest (SONF) for the purposes of specific tests reported below.

Selection of taxa and functional traits. A recent study of the extinction debt attributable to the extensive destruction of the native forest of Azorean Islands, estimated that more than half of the

extant native forest-dependent arthropod species might eventually be driven to extinction (2). Among the three taxa considered in that analysis, spiders and beetles exhibited very high percentages of species 'committed' to future extinction and, consequently, we regard them as of particular ecological interest.

Spiders. Spiders (order Araneae) are one of the most diverse and abundant arthropod orders. They include more than 40,000 known species (9) and their relative abundance compared with other arthropod orders is particularly high in Macaronesia (e.g. 4, 5). Due to the almost complete absence of ants in native forests, spiders are the most important arthropod predators in the Azores (4). Theory predicts that higher trophic levels are more prone to extinction due to habitat change as, besides intrinsic factors, such species suffer from cascade effects from lower trophic levels (e.g. 10). Spiders in the Azores are relatively intolerant of the destruction and disturbance of mature forests on these islands because the replacement of native forest with intensively managed pastures, or with exotic forest of lower vegetation architecture, is restricting the availability of suitable sites for web-building (11, 12). Cardoso et al. (13) suggested that spider diversity patterns in the archipelago could best be explained by incorporating forest destruction as an explanatory factor, with past extinctions of endemic species playing a part in shaping these patterns at the island level. Additionally, exotic species may have caused past extinctions due to competition with indigenous species (13).

Beetles. Beetles (order Coleoptera) are the largest order of insects (constituting about 40% of all described insect species) and occupy a vast array of environments: the same is true of the Azores, where they constitute around 35% of the fauna (7). Beetles influence local communities by various roles in food webs, litter decomposition, and nutrient flow. The functional significance of

beetles is reflected in their diversity of foraging behaviors, and they may act as detritivores, herbivores, fungivores or predators (e.g. 14, 15, Table 1). In the Azores at least nine species became extinct during the last century (e.g. 2, 7).

Traits. Spider trait data were collected from a number of sources. When species-level information was not available we used the general characteristics of families or genera, acknowledging that some misattributions may thus be involved (16). Body length was collated from the literature, separately for males and females to address the possible effects of sexual dimorphism (e.g. 17). As females and males body lengths were highly correlated (Pearson correlation = 0.96; $P<0.001$), we used the mean value between females and males. For beetles, feeding guild and wing morphology traits data were obtained based on personal knowledge of many colleagues contacted due to their expertise in the life history of each beetle family and from monographs. To estimate mean body size, whenever possible, ten specimens were measured per species per island. When no specimens were available in the *Dalberto Pombo Insect Collection* of the University of Azores, we used body size data available from the literature and in a few cases we asked colleagues to measure specimens in their private collections. A description of the biological meaning of each trait is given in Table S1.

Table S1. Functional traits for spiders and beetles used in the study

Spiders	Trait	Modalities	Description
	Body size	-	Prey size is often correlated with body size in spiders as in other organisms.
	Web use	Capture web, sensing web and no-web	Different web types capture different prey and usually it is only possible for spiders to capture prey much larger than themselves using capture webs.
	Web architecture	Tube web, sheet web, space web, orb web or no-web and particular combinations (tube+sheet and space+sheet)	Different web shapes capture different prey as, e.g., tube and sheet webs are usually effective for crawling insects while orb webs are more effective for flying insects.
	Foraging strategy	Ambush hunter, active hunter, generalist hunter and non-hunter	Different hunting strategies are used for different prey as, e.g., active searching is more effective for capturing crawling insects while ambushing is often more effective with flying insects.
	Prey range	Stenophagous and euryphagous	Stenophagous spiders feed on a small variety of prey, euryphagous spiders are generalist predators.
	Vertical stratification	Ground, vegetation and micro-habitat generalist	Hunting within different strata provides access to different insect assemblages.
	Circadian activity	Diurnal, nocturnal and circadian generalist	Hunting at different times of day provides access to different insect assemblages.
Beetles	Body size	-	Prey size is often correlated with body size in invertebrates. In addition smaller species tend to disperse passively and attain high densities.
	Feeding guild	Predator, herbivore, fungivore, saprophagus and polyphagus	Beetle feeding habits vary widely. Different types of feeding imply a different placement within the trophic webs and different use of resources.
	Wing morphology	Macropterous, brachypterous, apterous and dimorphic	Wing morphology is an important surrogate of dispersal ability in beetles.

The above traits for beetles were listed for all but six (1.2%) species of the 524 currently known from the archipelago (7): the six species lacking data were excluded from the analysis. We measured the correlations for each pair of traits for both spiders and beetles in order to estimate the level of redundancy in our functional information. We first computed the distance matrices for each trait and then we calculated the Spearman rank correlations between every possible pair of distance matrices (see *Supplementary Results*, Table S4, below). Here we used Gower's distance, a metric that accommodates continuous and nominal variables (18, 19), following the general formula:

$$D_{ij} = \sqrt{1 - \frac{\sum_{k=1}^{n} s_{ijk}\delta_{ijk}w_k}{\sum_{k=1}^{n} \delta_{ijk}w_k}}$$

where D_{ij} is the Gower's dissimilarity between species i and j, n is the number of variables (traits), s_{ijk} is the similarity between species i and j for the trait k, $\delta_{ijk} = 0$ if information is missing for at least one species and 1 if the information is available for the two species (here fixed at 1) w_k is the variable weights (here fixed at 1).

Functional diversity assessment. Functional diversity (FD) was assessed by a multidimensional continuous measure based on a distance matrix summarizing pair-wise difference between species computed using Gower's distance. To estimate the independent contributions of each trait to the global Gower's distance, we applied the method proposed by Pavoine et al. (20), in which squared distance matrices for each trait are correlated with the global squared distance. Independent contributions are as follows: for spiders, body size: 26%; the use of the web: 84%;

architecture of the web: 70%; foraging strategy: 80%; prey range: 11%; and vertical stratification: 36%. For beetles, body size: 46%; wing morphology: 66% and feeding guild: 61%.

Although there are several options for calculating continuous measurement of FD none is optimal for all cases (see 21). As species abundance data are lacking at the island level, we used a metric that mostly captures the notion of richness, i.e. amount of functions contained in a given community, based on presence/absence data. There are several such indices, each with limitations. For example, the Functional Attribute Diversity index (FAD2) and its modified version (MFAD), are extremely sensitive to species splitting and then increase exponentially with species richness, meaning that they do not correctly translate the degree of redundancy among species (e.g. 21, 22). Petchey and Gaston's dendrogram-based index (23) has similarly attracted criticisms (e.g. 24). Herein we use the FRic index of functional richness (25), which has been shown to be efficient at detecting assembly rules in simulation tests (21). FRic estimates the multidimensional trait space within the convex hull volume. For instance, in a two dimensional space, the convex hull volume represents the smallest polygon that encloses all species. As our functional information is summarized in the Gower distance matrix, we first analyzed this distance matrix through a principal coordinates analysis (PCoA) and used the resulting PCoA axes as the new traits to compute FRic (26). To avoid negative eigenvalues being returned by the PCoA, Gower distance matrices were primary square-root transformed (27).

One constraint of using FRic is that the number of species must always exceed the number of traits (herein PCoA axes scores). As there are only three endemic spiders and four endemic beetles on Corvo Island, we could only use two and three PCoA axes respectively, to estimate FRic for Corvo. Hence, we excluded Corvo from the analyses for endemics presented in the text, but include subsidiary analyses below including Corvo, based on two (55% inertia) and three (69% inertia) axes, respectively, for spiders and beetles. By removing Corvo, the second lowest

species richness values in the dataset were for Graciosa for spiders and beetles, with seven and eight endemic species, respectively. We therefore used the first six PCoA axes for spiders and the first seven axes for beetles in the main island-by-island analyses, capturing respectively 81% and 92% of total inertia.

Sensitivity to number of traits for spiders. Identifying functionally important traits and excluding functionally unimportant traits is always subject to uncertainty (28). To test the robustness of our results to the particular selection of traits included in the analyses for spiders (for which the seven traits listed in Table S1 were used), we conducted a sensitivity analysis by calculating FD and the SR–FD relationship based on all possible combinations of three, four, five and six traits. For each distributional category we first investigated the Pearson's correlation between the observed FD values (i.e. computed with the seven traits) for the nine islands (expect for endemic species, for which Corvo was excluded) with the averaged FD values arising from all possible combinations for a given number of traits (i.e. for three, four, five and six traits). Second, we re-fitted the SR–FD relationship for each distributional category and determined the best fit between linear and polynomial forms using ΔAIC_c and R^2 (as described in the main text). The results showed FD values and the outcome of subsequent analytical steps to be robust (*Supplementary Results, Table S5*) and so for all further analyses the full seven-trait data set was used. For beetles, since we only used three traits in the analyses, no such sensitivity analysis was performed.

Supplementary Results

Functional diversity of endemics. In the main results we were obliged to exclude Corvo Island from analysis of the FD–SR relationship for endemics because of low species number. Here we report the results including Corvo Island and based on two PCoA axes for spiders and three for beetles, respectively. In contrast to the results reported in Fig. 2, both linear and polynomial models provide significant fits, with polynomial models having higher R^2 values but being indistinguishable in fit from the linear model based on ΔAIC_c values (Fig. S1). This result shows that the pattern for endemics is unstable and is dependent on the amount of trait space and/or the inclusion of the least rich island.

Body length. Many life-history traits of animals, such as growth rate, clutch size, or life span, are strongly correlated with body size. Thus, body size represents an important surrogate for other ecological attributes across species and environments, and is considered a synthetic functional trait (29, 30). Moreover, dispersal range for small species of spiders may be far greater than for larger ones owing to their increased ballooning ability (e.g. 31, 32) and thus we expected indigenous species (endemics and natives), which arrived by their own means on this isolated archipelago, to be smaller (on average) than exotics. For both spiders and beetles, we compared the body sizes of endemic, native and exotic species using Kruskal-Wallis one-way analysis of variance. For spiders, we used the mean body size of males and females. For spiders, the average body size for exotic species was 5.02±3.24 (range: 1.4–15 mm), for natives 3.91±2.20 (range: 1.45–9.88 mm) and for endemics 3.14±2.49 (range: 1–10.5 mm). For beetles, the average body length for exotic species was 4.12±3.30 (range: 0.50–23.88 mm), for natives 3.70±3.48 (range: 0.58–18.63 mm) and for endemics 3.96±2.58 (range: 0.98–12.92 mm). Body size of endemic,

native and exotic spider species were significantly different (Kruskal-Wallis: χ^2=13.43; df=2, *P* =0.001), with endemics being significantly smaller than the other two similar groups (*a posteriori* test). For beetle species, no significant differences between the three categories (Kruskal-Wallis: χ^2=5.60; df=2, *P*=0.061) were found. When only species occurring in native habitats were considered, difference in body size for spiders and beetles between the three categories were consistent, with a significant difference found for spiders (Kruskal-Wallis: χ^2=10.52; df=2, *P* =0.006, with only endemics being different from natives and exotics) and an absence of difference for beetles (Kruskal-Wallis: χ^2=0.98; df=2, *P* =0.616).

Other Supplementary Results. Additional results follow below in Tables S2–S7 and in Figures S1–S3, as described in the relevant legends and cited in the main text.

Table S2. Area, species richness (SR) and functional diversity (FD) per island for each distributional category for Azorean spiders and beetles.

Spiders	Area	Endemic			Native		Indigenous		Exotic		All	
Island	km^2	SR	FD	FD*	SR	FD	SR	FD	SR	FD	SR	FD
Corvo	17	3	-	0.004	10	0.002	13	0.009	19	0.047	32	0.187
Faial	172	13	0.004	0.664	13	0.016	26	0.083	47	0.433	73	0.595
Flores	142	15	0.011	0.833	11	0.003	26	0.136	42	0.207	68	0.430
Graciosa	62	7	0.000	0.644	11	0.003	18	0.076	37	0.294	55	0.518
Pico	433	15	0.004	0.663	11	0.006	26	0.083	43	0.385	69	0.492
S. Jorge	246	15	0.012	0.831	9	0.003	24	0.074	36	0.314	60	0.377
S. Miguel	757	15	0.003	0.706	15	0.028	30	0.134	67	0.682	97	0.812
S. Maria	97	10	0.002	0.654	13	0.003	23	0.120	50	0.339	73	0.501
Terceira	402	15	0.002	0.661	16	0.045	31	0.122	61	0.631	92	0.737
All islands	2328	22			17		39		85		124	
Beetles	Area	Endemic			Native		Indigenous		Exotic		All	
Island	km^2	SR	FD	FD*	SR	FD	SR	FD	SR	FD	SR	FD
Corvo	17	4	-	0.013	15	0.000	19	0.000	23	0.060	42	0.099
Faial	172	18	0.001	0.851	69	0.003	88	0.220	154	0.155	243	0.604
Flores	142	18	0.000	0.657	59	0.026	77	0.178	120	0.145	198	0.476
Graciosa	62	8	0.000	0.416	33	0.004	41	0.119	100	0.094	141	0.207
Pico	433	24	0.001	0.710	49	0.000	74	0.214	108	0.154	182	0.563
S. Jorge	246	12	0.000	0.679	45	0.001	57	0.134	87	0.086	144	0.284
S. Miguel	757	30	0.163	0.914	98	0.000	130	0.503	216	0.165	347	0.905
S. Maria	97	24	0.098	0.886	80	0.000	106	0.405	173	0.147	280	0.741
Terceira	402	20	0.002	0.876	73	0.007	93	0.392	203	0.165	296	0.547
All islands	2328	65			130		195		323		518	
Real total		65			134		199		325		524	

Natives are indigenous species excluding those that are endemic to the Azores. For beetles, from a total of 524 species recorded in Azores, we were able to obtain trait data for 518 of them. The remaining six (four native and two exotic species) were thus excluded from all trait calculations. Therefore, in the row “all islands”, we give the species richness corresponding to the number of species used

to compute FD and also give in the row denoted “real total” the total number of species recorded in the Azores, providing the values used in the species–area computation for all species. FD was computed by using the index of functional richness FRic (25). Respectively, 6 PCoA axes (81% total inertia) and 7 PCoA axes (92 % inertia) were used to estimate FRic for spiders and beetles. For FD, Corvo was excluded from the computation for endemics (See SI Material and methods and main text for further details). All FRic values are standardized by the global FRic, which includes all species, such that FRic is constrained between 0 and 1. FD* refers to FRic computed for endemic species with Corvo included, but based on only 2 (55% inertia) and 3 (69%) PCoA axes for spiders and beetles, respectively.

Table S3. Model details and comparisons for the island species–area relationships (ISARs) and for the island functional diversity–area relationships (IFDARs) for spiders and beetles using the log–log model, for the five distributional categories, for the Azorean archipelago.

a) Model parameters and fits

Spiders	ISAR	C	SE	z	SE	df	*F*	R^2	*P*
	Endemics	0.185	0.398	0.432	0.076	1,7	31.916	0.820	**<0.001**
	Natives	2.062	0.279	0.082	0.054	1,7	2.322	0.249	0.174
	Indigenous	2.034	0.169	0.220	0.032	1,7	46.030	0.868	**<0.001**
	Exotics	2.383	0.336	0.268	0.065	1,7	17.199	0.711	**0.004**
	All species	2.915	0.260	0.250	0.050	1,7	25.146	0.782	**0.002**
	IFDAR	C	SE	z	SE	df	*F*	R^2	*P*
	Endemics	-18.473	7.217	2.213	1.328	1,6	2.776	0.316	0.147
	Natives	-8.552	1.474	0.682	0.283	1,7	5.818	0.454	**0.047**
	Indigenous	-5.447	0.951	0.565	0.183	1,7	9.561	0.577	**0.018**
	Exotics	-4.267	0.648	0.604	0.124	1,7	23.509	0.771	**0.002**
	All species	-2.257	0.438	0.299	0.084	1,7	12.686	0.644	**0.009**
Beetles	ISAR	C	SE	z	SE	df	*F*	R^2	*P*
	Endemics	0.307	0.567	0.474	0.109	1,7	18.910	0.730	**0.003**
	Natives	1.934	0.582	0.394	0.112	1,7	12.446	0.640	**0.009**
	Indigenous	2.087	0.565	0.417	0.108	1,7	14.760	0.678	**0.006**
	Exotics	2.390	0.722	0.459	0.139	1,7	10.951	0.610	**0.013**
	All species	2.960	0.646	0.440	0.124	1,7	12.576	0.642	**0.009**
	IFDAR	C	SE	z	SE	df	*F*	R^2	*P*
	Endemics	-22.576	11.073	2.779	2.038	1,6	1.859	0.237	0.222
	Natives	-21.762	5.025	3.276	0.965	1,7	11.531	0.622	**0.012**
	Indigenous	-12.765	3.038	2.061	0.583	1,7	12.488	0.641	**0.010**
	Exotics	-4.101	0.857	0.509	0.165	1,7	9.565	0.577	**0.017**
	All species	-3.446	0.883	0.539	0.170	1,7	10.114	0.591	**0.015**

Where, C is the intercept, z the slope, SE Standard errors, df the degree of freedom, *F* the *F* statistic, R^2 the fit, and *P* indicates the significance level; n = 9 islands, except for the endemics category, wherein Corvo island was excluded; species numbers are as given in Table S2.

b) Analyses of covariance (ANCOVA) comparing the ISARs and the IFDARs from part (a) using two ways of grouping species into distributional categories.

	Categories tested	Intercept			Slopes		
Spiders	ISAR	df	*F*	*P*	df	*F*	*P*
	Endemics–Natives–Exotics	2,21	114.031	**<0.001**	2,21	7.081	**<0.001**
	Indigenous–Exotics	1,14	57.315	**<0.001**	1,14	0.449	0.514
	IFDAR	df	*F*	*P*	df	*F*	*P*
	Endemics–Natives–Exotics	2, 20	24.361	**<0.001**	2,20	1.671	0.213
	Indigenous–Exotics	1, 14	32.980	**<0.001**	1, 14	0.031	0.863
Beetles	ISAR	df	*F*	*P*	df	*F*	*P*
	Endemics–Natives–Exotics	2,21	59.739	**<0.001**	2,21	0.123	0.885
	Indigenous–Exotics	1,14	7.354	**0.017**	1,14	0.058	0.813
	IFDAR	df	*F*	*P*	df	*F*	*P*
	Endemics–Natives–Exotics	2, 20	9.844	**0.001**	2, 20	2.275	0.128
	Indigenous–Exotics	1, 14	1.324	0.269	1, 14	6.561	**0.023**

The degrees of freedom (df), *F* statistic and corresponding *P* value are given for both intercept and slope. For the spider ISARs, the slopes do not differ when natives and endemics are aggregated into indigenous species and compared with exotics, but do when the three separate categories are compared. This reflects differences in the form of the ISAR for natives and endemics (Fig. 1). For the spiders IFDARs, the intercepts differ for both comparisons but the slopes do not. For the beetle ISARs, the intercept differs for both the endemics–natives–exotics and indigenous-exotics comparison but the slopes do not. For the beetles IFDARs, the intercepts differ for the endemics–natives–exotics comparison and the slopes differ for the indigenous–exotics comparison.

Table S4. Spearman rank correlations between Gower's distance matrices implemented for each trait, where the traits and their various states (modalities) are as given in Table S1. For spiders n = 124, and for beetles n = 518.

Spiders						
Traits	Body size	Web use	Web architecture	Foraging strategy	Prey range	Vertical stratification
Use of the web	0.021					
Architecture of the web	0.058	0.754				
Foraging strategy	0.000	0.880	0.614			
Prey range	-0.022	-0.049	-0.118	0.005		
Vertical stratification	0.062	0.055	0.053	0.052	0.016	
Circadian activity	0.117	-0.008	-0.103	0.022	-0.030	0.044
Beetles						
Traits	Body size	Wing morphology				
Wing morphology	0.044					
Feeding guild	0.024	0.013				

Table S5. Summary of sensitivity analyses of all possible number and combination from three to six traits for spiders in the estimation of the functional diversity index FRic and the relationship between FRic and species richness.

Distributional groups	3 traits (35; 81%)	4 traits (35; 82%)	5 traits (21; 83%)	6 traits (7; 82%)
Endemics				
r	**0.925****	**0.931****	**0.971*****	**0.989*****
ΔAIC_c linear	0.000	0.000	0.000	0.000
ΔAIC_c polynomial	8.655	8.650	9.196	9.318
R^2 linear	**0.568***	**0.570***	0.472	0.414
R^2 polynomial	**0.603***	**0.605***	0.481	0.416
Natives				
r	0.667	**0.771***	**0.800***	**0.921*****
ΔAIC_c linear	0.000	0.000	0.000	0.000
ΔAIC_c polynomial	7.198	7.063	6.948	3.476
R^2 linear	**0.641***	**0.742****	**0.767****	**0.840****
R^2 polynomial	**0.641***	**0.745****	**0.773****	**0.894*****
Indigenous				
r	**0.947*****	**0.979*****	**0.969*****	**0.995*****
ΔAIC_c linear	0.000	0.000	0.000	0.000
ΔAIC_c polynomial	6.987	5.976	7.037	6.768
R^2 linear	**0.449***	**0.606***	**0.508***	**0.627***
R^2 polynomial	0.462	**0.656***	**0.517***	**0.644***
Exotics				
r	**0.928*****	**0.944*****	**0.974*****	**0.992*****
ΔAIC_c linear	0.000	0.000	0.000	0.000
ΔAIC_c polynomial	4.119	4.742	6.742	7.197
R^2 linear	**0.786****	**0.816****	**0.846*****	**0.879*****
R^2 polynomial	**0.848****	**0.860****	**0.853****	**0.879****
All species				
r	**0.948*****	**0.956*****	**0.980*****	**0.995*****
ΔAIC_c linear	0.000	0.000	0.000	0.000
ΔAIC_c polynomial	5.636	6.576	7.169	7.137
R^2 linear	**0.770****	**0.748****	**0.781****	**0.842*****
R^2 polynomial	**0.806****	**0.765****	**0.781****	**0.844****

Results are for nine islands, except for the endemic grouping (eight Azorean islands, as Corvo was excluded). Bold values indicate significance, where * indicates $0.01<P<0.05$; ** $0.001< P <0.01$, *** $P <0.001$ while in all other cases, $P >0.05$. For a given number of traits, the mean of

the FD values was calculated with all the combinations of those traits. The number of PCoA axes used to measure FRic was selected to ensure around 80% trait inertia in each case (in line with our main analyses), resulting in the use of varying numbers of PCoA axes within this sensitivity analysis. The number of combinations as well as the average inertia retained is given in parentheses in the column headers. Pearson correlations (*r*) were calculated between mean FD values and the observed FD (i.e. computed with the seven traits) for each distributional category. The mean FD from all the combinations was used to re-fit the SR–FD relationship and the preferred model between linear and polynomial models was assessed by using ΔAIC_c and R^2 (see details in Materials and methods). FD is shown to be robust to the number of traits used and in all cases, the linear model is preferred according to the ΔAIC_c values, although this does not necessarily mean they are all significant. These analyses indicate that patterns obtained do not show any evidence of saturation and appear generally robust to the number of traits used in the analysis of spiders: elsewhere we report only the full results using 7 traits.

Table S6. Results of the null model tests exploring deviations in functional richness (FRic) from the null expectation for each island given observed SR, for spiders and beetles on the Azorean islands. Deviations, expressed as standardized effect sizes (SES) and *P* values are given for five distributional groups under two distinct null models (below).

		Spiders		Beetles	
Groups	Islands	All	SONF	All	SONF
Endemics	Corvo	-0.981	-0.995	-0.268	-0.210
	Faial	-0.983	-0.860	-0.433	-0.482
	Flores	-1.015	-1.018	-0.425	-0.543
	Graciosa	-0.369	-0.325	-0.073	-0.131
	Pico	-1.208	-1.085	-0.655	-0.849
	S. Jorge	-0.988	-1.041	-0.250	-0.366
	S. Miguel	-1.286	-1.122	1.993	1.124
	S. Maria	-0.617	-0.493	1.899	1.184
	Terceria	-1.211	-1.119	-0.485	-0.443
Natives	Corvo	-0.382	-0.361	-0.398	-0.403
	Faial	0.088	0.129	-1.579	**-1.918***
	Flores	-0.560	-0.501	-0.467	-1.423
	Graciosa	-0.550	-0.509	-0.916	-1.019
	Pico	-0.279	-0.425	-1.415	**-1.126***
	S. Jorge	0.281	-0.052	-0.921	**-1.400***
	S. Miguel	0.015	1.070	-1.820	**-2.246*****
	S. Maria	-0.730	-0.547	-2.280	**-2.189*****
	Terceria	0.230	0.975	-1.304	**-2.185***
Indigenous	Corvo	-0.603	0.017	-0.520	-0.624
	Faial	-0.970	-1.026	-1.103	-0.794
	Flores	-0.437	-0.617	-0.067	-0.905
	Graciosa	0.119	0.357	-0.167	-0.061
	Pico	-1.087	-1.073	-0.264	-0.260
	S. Jorge	-0.972	-0.945	-0.597	-0.636
	S. Miguel	-0.862	-0.669	0.870	0.281
	S. Maria	-0.025	0.141	0.265	0.022
	Terceria	-1.175	-0.873	0.361	0.006
Exotics	Corvo	-0.842	-0.129	0.640	0.929
	Faial	0.439	1.257	-2.132	-2.238
	Flores	-1.197	-0.647	-1.928	-1.999
	Graciosa	0.274	-0.261	-1.865	-1.901
	Pico	0.105	1.619	-2.015	-1.556
	S. Jorge	0.178	2.402	-1.461	-1.810

	S. Miguel	0.655	1.520	-3.397	**-2.994*** **
	S. Maria	-0.724	0.651	-3.340	**-2.583***
	Terceria	0.778	0.972	-1.592	**-3.070***
All species	Corvo	-0.690	1.183	-0.416	-0.420
	Faial	-0.552	0.561	-0.185	-0.872
	Flores	-1.506	-0.489	0.617	-1.538
	Graciosa	0.302	0.791	-1.991	-2.440
	Pico	-1.399	0.271	-1.569	-0.376
	S. Jorge	-1.458	-0.138	-1.390	-2.180
	S. Miguel	-0.496	1.182	0.255	0.632
	S. Maria	-1.258	0.822	0.346	-0.457
	Terceria	-0.547	-0.218	-2.109	-2.392

Null model 'All' is for all habitats and all species. In null model 'SONF' only species occurring in native forest (whether indigenous or exotic) were considered. Which species qualify as SONF was determined from systematic field data (above (4, 5)). Except for endemic species for Corvo, FD was calculated by using FRic index based on 6 and 7 PCoA axes for spiders and beetles, respectively. Null simulations for Corvo were run by retaining only 2 and 3 PCoA axes for spiders and beetles, respectively. SES values are calculated as (O-M)/S where O is the observed value and M and S are the mean and standard deviation respectively of 999 randomizations of the traits distribution. Negative SESs indicate that FRic is lower than expected by chance while positive SESs mean the opposite. *P* values are calculated as a two tailed-test. We applied the false discovery rate correction (FDR, (33)) to correct for multiple comparisons. Bold values indicate significance, where * indicates $0.01<P<0.05$; ** $0.001< P <0.01$, *** $P <0.001$ while in all other cases, $P >0.05$.

Table S7. Pearson correlations between body size and the position of each species within the first six and seven axes of the principal coordinates analysis (PCoA) of the Azorean traits data for spiders and beetles, respectively.

(Spiders)		(Beetles)	
Axes	Body size	Axes	Body size
PCoA 1 (40.8%)	0.125	PCoA 1 (28.8%)	-0.112
PCoA 2 (14.3%)	-0.387	PCoA 2 (22.8%)	-0.208
PCoA 3 (9.6%)	-0.043	PCoA 3 (17.5%)	-0.088
PCoA 4 (7%)	-0.212	PCoA 4 (9.1%)	0.444
PCoA 5 (5.3%)	-0.436	PCoA 5 (5.5%)	-0.172
PCoA 6 (4.7%)	-0.269	PCoA 6 (5.4%)	-0.778
		PCoA 7 (3.4%)	0.061

Percentages of inertia explained by each PCoA axis are presented in parentheses. Where island-level calculations are undertaken we used six axes for spiders and seven for beetles, but for archipelago-level analysis using the whole species pool, computational restrictions meant we could use only the first four axes for each taxon. Further analyses demonstrating the loadings of other traits in the PCoA space are presented in Fig. S2 (below).

Supporting Figures

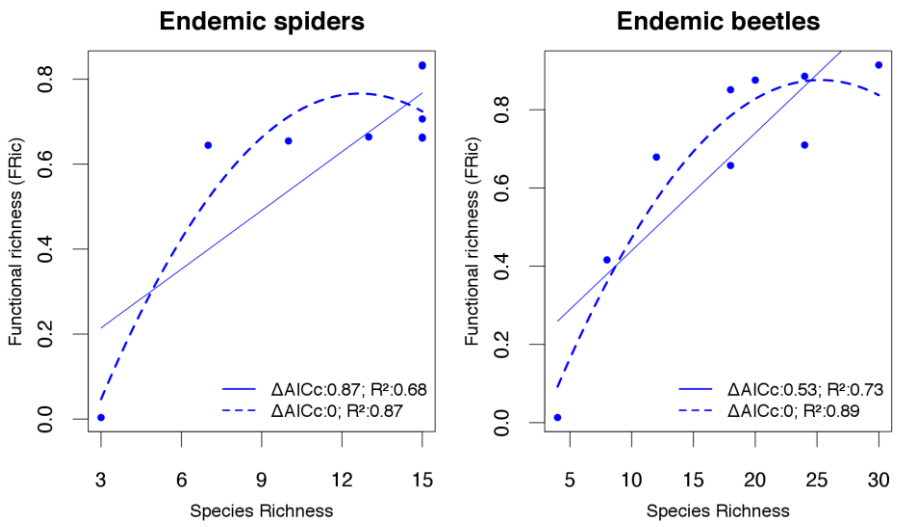

Figure S1. The relationship between FD (using FRic (25)) and species richness (SR) for endemic Azorean spiders (left panel) and beetles (right panel). In contrast to Fig. 2, the island of Corvo was included in the analysis (i.e. n = 9 islands, although only 7 points can be seen for spiders because of over-plotting). FRic was therefore computed based on only the first two PCoA axes for spiders and the first three axes for beetles, representing 55 and 69% of total inertia for spiders and beetles, respectively (See *Materials and methods* for further details). Linear (full lines) and polynomial (dotted lines) fits are given, with their respective ΔAIC_c and R^2. Both linear and polynomial models provide significant fits (*F* statistic test $P < 0.05$). The models with the lowest ΔAIC_c values are given in bold, but as they differ from the alternative model by <2.0, we are unable to distinguish a single best model in either case. The outcome of this analysis is thus equivocal for both taxa.

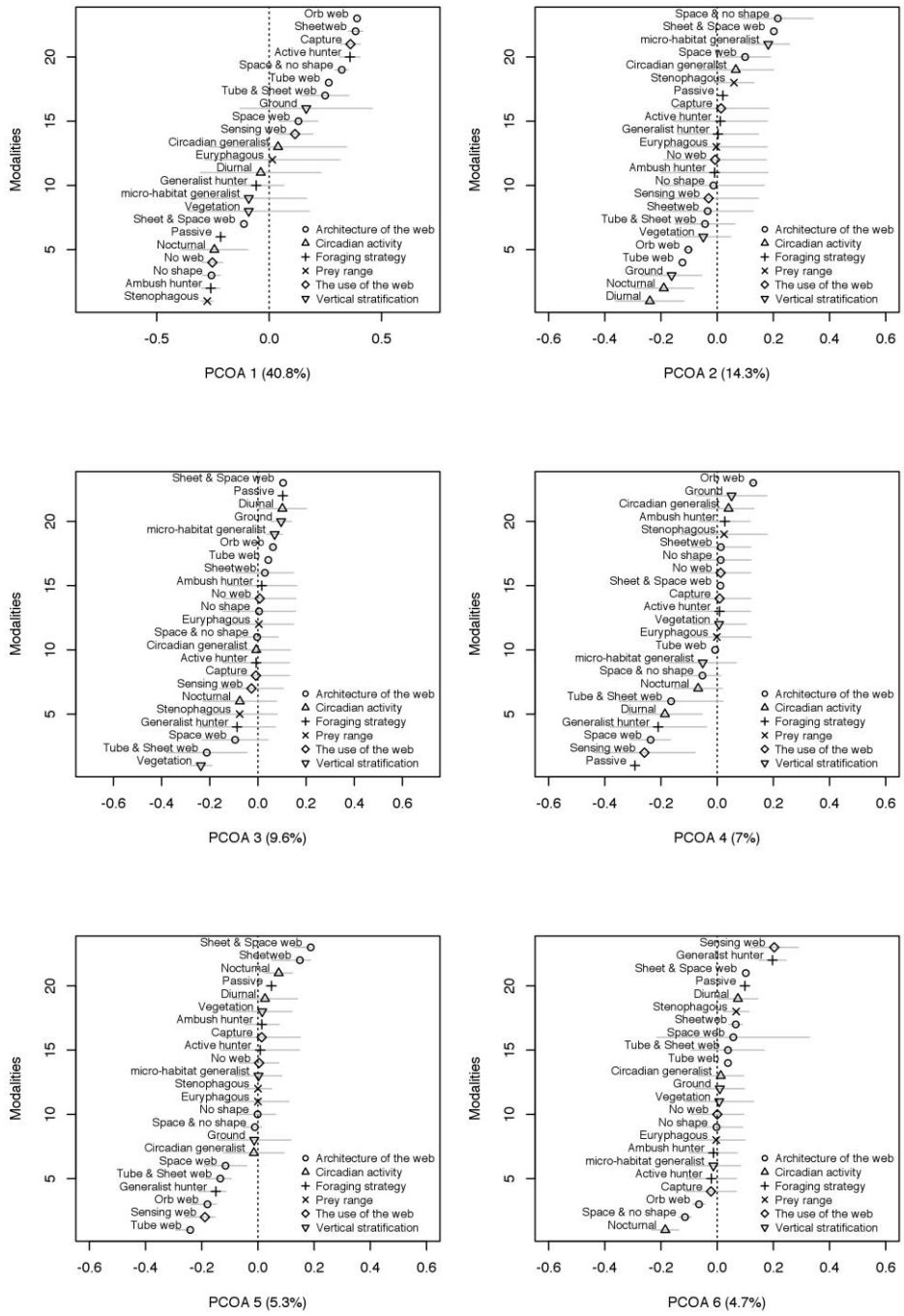

Figure S2. Trait loadings on the PCoA axes, showing how the derived traits relate to the underlying functional traits: (a) Trait loadings for spiders for the first six axes of the principal coordinates analysis (PCoA) based on the global distance matrix, for the 124 species of Azorean spiders**.** The different modalities (character states) of each trait are placed on each PCoA axis at the center of gravity of their associated species, with the lines representing the standard deviation around the center of gravity. The values in parentheses indicate the inertia represented in each axis.

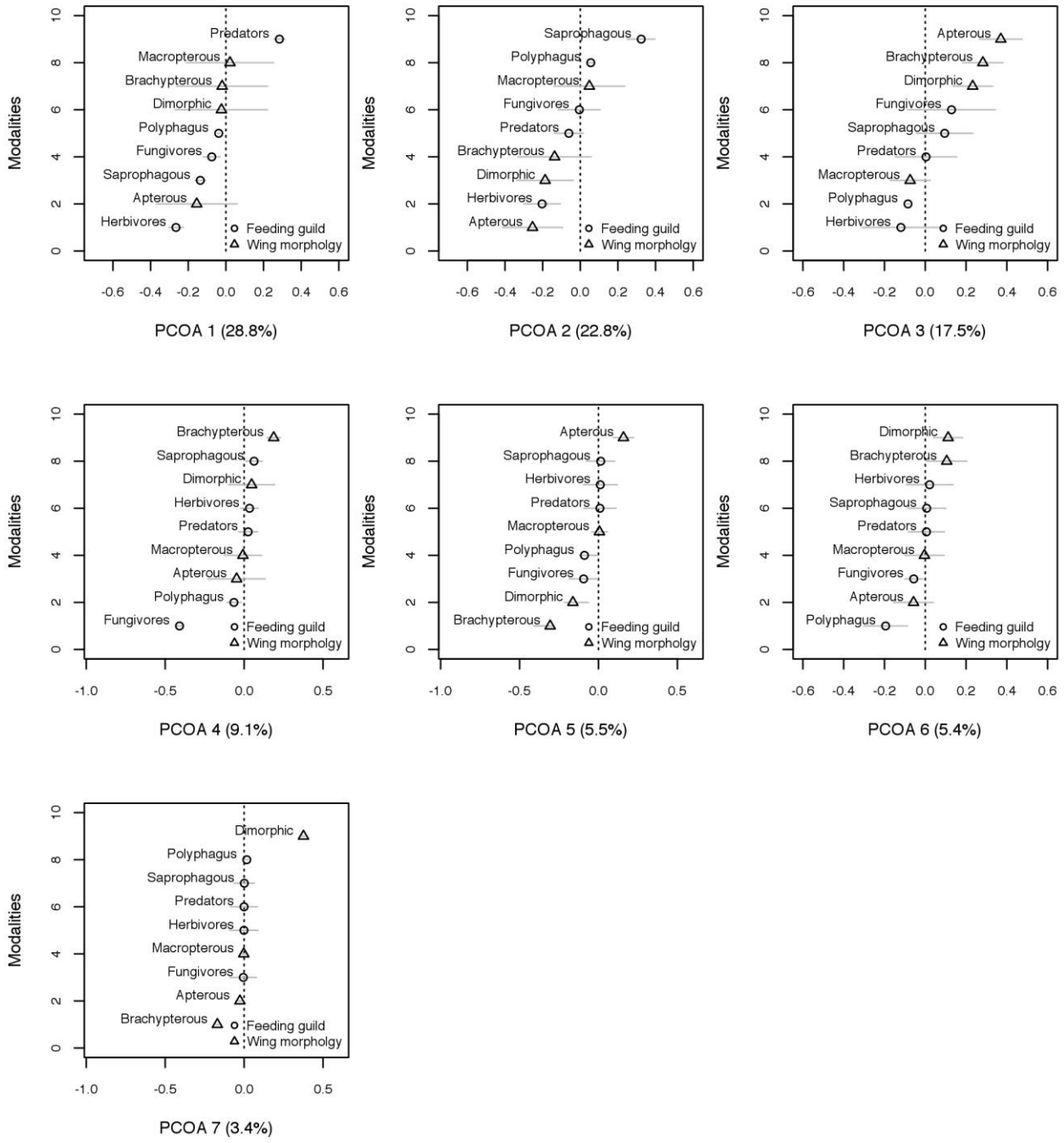

Figure S2 continued: (b) Trait loadings for beetles for the first seven axes of the principal coordinates analysis (PCoA) based on the global distance matrix, for 518 species of Azorean beetles. These diagrams provide ecological insight into the trait space described by the PCoA analyses for the interested reader.

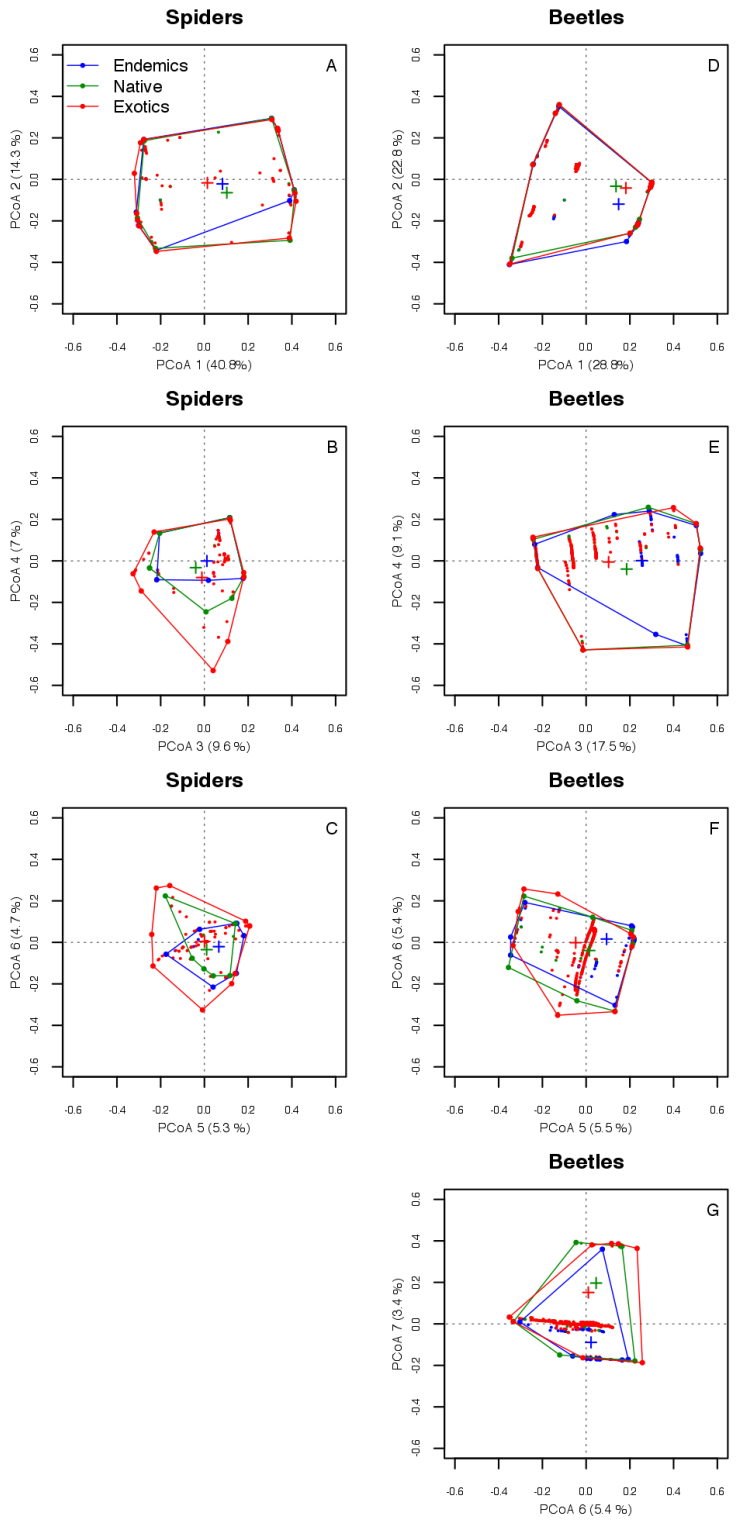

Figure S3. Projections of the convex hull functional space of endemics (blue), natives (green) and exotics (red) estimated by the first six PCoA axes for spiders (left) and by the first seven PCoA axes for beetles. Percentages of inertia summarized per axis are given in parentheses alongside the x and y axes. Crosses represent the center of gravity of the volume occupied while colored dots indicate species.

Supplementary References:

1. Borges PAV, et al. (2005) Ranking protected areas in the Azores using standardised sampling of soil epigean arthropods. *Biodivers Conserv* 14:2029−2060.
2. Triantis KA, et al. (2010) Extinction debt on oceanic islands. *Ecography* 33:285–294.
3. Gaspar C, Borges PAV, Gaston KJ (2008) Diversity and distribution of arthropods in native forest of the Azores archipelago. *Arquipél Life Mar Sci* 25:1−30.
4. Borges PAV, Ugland KI, Dinis FO, Gaspar C (2008) Insect and spider rarity in an oceanic island (Terceira, Azores): true rare and pseudo-rare species. *Insect Ecology and Conservation*, ed Fattorini S (Research Signpost, Kerala, India), pp. 47–70.
5. Cardoso P, et al. (2009) A spatial scale assessment of habitat effects on arthropod communities of an oceanic island. *Acta Oecol* 35:590−597.
6. Shaefer H, (2003) Chorology and diversity of the Azorean flora. *Diss bot* 374:1−130.
7. Borges PAV, et al. (2010) *A list of the terrestrial and marine biota from the Azores* (Princípia, Oeiras).
8. Borges PAV, et al. (2010) The Azorean Biodiversity Portal: an internet database for regional biodiversity outreach. *Syst Biodivers* **8**:423−434.
9. Platnick NI, Merrett P, Cameron HD, Reddy D. (2003) *The world spider catalog, version 3.5.* (American Museum of Natural History, New York). http://research.amnh.org/iz/spiders/catalog/
10. Holt RD (1996) Food webs in space: an island biogeographic perspective. *Food Webs: Contemporary Perspectives*, eds Polis G, Winemiller K (Chapman and Hall), pp 313–323.
11. Borges PAV, Wunderlich J (2008) Spider biodiversity patterns and their conservation in the Azorean archipelago, with description of new taxa. *Syst Biodivers* 6:249–282.

12. Cardoso P, Borges PAV, Gaspar C (2007). Biotic integrity of the arthropod communities in the natural forests of Azores. *Biodivers Conserv* 16:2883−2901.

13. Cardoso P, Arnedo MA, Triantis KA, Borges PAV (2010) Drivers of diversity in Macaronesian spiders and the role of species extinctions. *J Biogeogr* 37:1034−1046.

14. Lawrence JF, Britton EB (1994) *Australian Beetles.* (Melbourne University Press, Melbourne).

15. Lassau SA, Hochuli DF, Cassis G, Reid CAM (2005) Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? *Divers Distrib* 11:73−82.

16. Cardoso P, Pekar S, Jocqué R, Coddington JA (2011) Global patterns of guild composition and functional diversity of spiders. *PLoS ONE* 6: e21710.

17. Coddington JA, Hormiga G, Scharff N (1997) Giant female or dwarf male spiders? *Nature* 385:687−688.

18. Podani J, Schmera D (2006) On dendrogram-based measures of functional diversity. *Oikos* 115:179−185.

19. Gower JC (1971) A general coefficient of similarity and some of its properties. *Biometrics* 27: 857−874.

20. Pavoine S, Vallet J, Dufour A, Gachet S, Daniel H (2009) On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos* 118:391–402.

21. Mouchet MA, Villéger S, Mason NWH, Mouillot D (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Funct Ecol* 24:867–876.

22. Petchey OL, Hector A, Gaston KJ (2004) How do different measures of functional diversity perform? *Ecology* 85:847–857.

23. Petchey OL, Gaston KJ (2002) Functional diversity (FD), species richness, and community composition. *Ecol Lett* 5:402–411.

24. Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's guide to functional diversity indices. *Ecol Monogr* 80:469–484.

25. Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290–2301.

26. Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305.

27. Legendre P, Legendre L (1998) *Numerical* ecology. Second English edition. (Elsevier Science, Amsterdam, The Netherlands).

28. Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. *Ecol Lett* 9:741–758.

29. Peters RH (1983) *The ecological implications of body size* (Cambridge University Press, Cambridge).

30. Gaston KJ, Blackburn TM (2000) *Pattern and process in macroecology* (Blackwell Science, Oxford).

31. Greenstone MH, Morgan CE, Hultsch AL, Farrow RA, Dowse JE (1987) Ballooning spiders in Missouri, USA, and New South Wales, Australia: family and mass distributions. *J Arachnol* 15:163–170.

32. Entling W, Schmidt-Entling MH, Bacher S, Brandl R, Nentwig W (2010) Body size–climate relationships of European spiders. *J Biogeogr* 37:477–485.

33. Benjamini Y, Yekutieli D (2001) The control of the false discovery rate in multiple testing under dependency. *Ann Stat* 29:1165–1188.