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2020-09

Borges , P A V , Rigal , F , Ros-Prieto , A & Cardoso , P 2020 , ' Increase of insular exotic arthropod diversity is a fundamental dimension of the current biodiversity crisis ' , Insect Conservation and Diversity , vol. 13 , no. 5 , pp. 508-518 . <https://doi.org/10.1111/icad.12431>

<http://hdl.handle.net/10138/332450>

<https://doi.org/10.1111/icad.12431>

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Increase of insular exotic arthropod diversity is a neglected aspect of the current biodiversity crisis

Journal:	<i>Insect Conservation and Diversity</i>
Manuscript ID	Draft
Manuscript Type:	Special Issue Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Borges, Paulo; University of the Azores, Faculdade de Ciências e Engenharia do Ambiente Rigal, François; CNRS - Université de Pau et des Pays de l'Adour, Institut Des Sciences Analytiques et de Physico Chimie pour L'environnement et les Materiaux Ros-Prieto, Alejandra; CE3C – Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity Group Cardoso, Pedro; University of Helsinki, Finnish Museum of Natural History Zoology
Keywords:	arthropods, diversity, islands, long-term monitoring, sampling standardization, exotic species

1 **Target potential Journal: *Insect Conservation and Diversity***

2

3 Increase of insular exotic arthropod diversity is a neglected aspect of the current
4 biodiversity crisis

5 Running title: biodiversity crisis – exotic arthropod diversity

6

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27 Abstract:

- 28 1. A dramatic insect decline has been documented on the grasslands and forests of
29 European or North American mainland. However, other parts of the world and
30 other ecosystems remain much less studied with unknown patterns.
- 31 2. Using a unique time-series dataset, we investigate recent trends on abundance
32 and richness of arthropods sampled in Azorean native forest over six years
33 (2013-2018).
- 34 3. We test the hypothesis that biodiversity erosion drivers are changing the
35 diversity and relative species abundance structure (Species Abundance
36 Distribution, SAD) of endemics, native non-endemics and exotic species over
37 time. We also examine temporal trends in abundance for each individual species.
- 38 4. In contrast with mainland studies, we observed no decline in overall arthropod
39 diversity, but a clear increase on the diversity of exotic arthropods and some
40 evidence of a tendency for decreasing abundance for some endemic species. We
41 also document stronger species turnover for exotic species, but no specific
42 changes in the SAD.
- 43 5. We argue that many changes, particularly on unique systems such as islands,
44 will be noticed not at the richness but mostly at compositional level. Special
45 attention has to be given to exotic species which are known to be one of the
46 major drivers of biodiversity erosion on islands.

47
48 Keywords: arthropods, diversity, islands, long-term monitoring, sampling
49 standardization, exotic species

50

51 **Introduction**

52 Biodiversity loss is well recognized as a key challenge for this century (Sala *et al.*,
53 2000; Cardinale *et al.*, 2012). Although insect biodiversity in particular is an essential
54 component for ecosystem functioning (Allan *et al.*, 2015; Bennett *et al.*, 2015) and
55 biodiversity loss being a risk to both ecosystem sustainability and Human health and
56 well-being (Sandifer *et al.*, 2015), insect biodiversity loss or just plain changes in
57 population abundances tended to be relatively ignored by the public, policy-makers and

58 local and national authorities (Cardoso *et al.*, 2011). Yet, recently, insect population
59 declines have made the news, with multiple reports describing what appear to be
60 dramatic losses in richness, abundance and biomass (Halmann *et al.*, 2017; 2019, 2020;
61 Habel *et al.*; 2019; Homburg *et al.*, 2019; Seibold *et al.*, 2019; Wagner, 2020). There is
62 a recent call for urgent measures to be taken to avoid massive insect declines (e.g.
63 Cardoso *et al.*, 2020; Harvey *et al.*, 2020; Samways *et al.*, 2020) and obtain more long-
64 term standardized robust data (Cardoso & Leather, 2019, Thomas *et al.*, 2019). The
65 many insect population reports that are arriving from across the world do however
66 present a strong geographical bias, focusing on the European or North American
67 mainland. The rest of the world remains much less studied and to what point the current
68 findings are general is unknown.

69 The present biodiversity crisis is hitting islands disproportionately (Kier *et al.*,
70 2009), with impacts at all levels of biodiversity but also affecting Human populations
71 and economies (Chapin *et al.*, 2000; Weiss, 2015). This biodiversity crisis on islands
72 and elsewhere is a consequence of several biodiversity erosion drivers including land-
73 use changes, habitat degradation, pollution, invasive species and climatic changes
74 (Borges *et al.*, 2019a). In fact, historical human colonization of most isolated oceanic
75 archipelagos promoted whole island ecosystem extirpation, and at best, native habitats
76 fragmentation. Despite the evidences of historical losses in species diversity on islands
77 after Human occupation (e.g., Goodfriend *et al.*, 1994, Blackburn *et al.*, 2004; Triantis *et*
78 *al.*, 2010; Alcover *et al.*, 2015; Terzopoulou *et al.*, 2015; Kirch, 2015) there is no study
79 that investigates the recent temporal trends on species diversity and composition on
80 island native faunas.

81 In this contribution, we use a unique time-series dataset of arthropods sampled in
82 Azorean native forest over six years (2013-2018) (see Borges *et al.*, 2017; Matthews *et*
83 *al.*, 2019b) to investigate recent trends on arthropod diversity and composition. The
84 Azores is one of the world's most isolated archipelagos made of nine main islands
85 aligned on a WNW–ESE axis in the Atlantic Ocean. At the time of human colonization,
86 around AD 1440, the Azorean archipelago was almost entirely forest-covered. In less
87 than 600 years, 95% of the original native forest has been destroyed (Gaspar *et al.*,
88 2008) due to the development of an economy based on dairy and the plantation of
89 forests of exotic species. The protection of the remaining native forest fragments
90 became recently a priority for local authorities, since those fragments play a

91 fundamental role as refuges and source habitats for the endemic fauna and flora (Gaspar
92 *et al.*, 2011).

93 Several negative biodiversity erosion drivers are currently impacting Azorean
94 biota (Borges *et al.*, 2019b). For instance, Triantis *et al.* (2010) investigated the
95 possibility of an extinction debt attributable to the forest destruction in Azorean
96 arthropod fauna and have estimated that more than half of the extant native forest-
97 dependent arthropod species might eventually be driven to extinction. The current lack
98 of connectivity between forest patches (Aparício *et al.*, 2018) and potential enhanced
99 habitat fragmentation due to climatic changes (Ferreira *et al.*, 2016; Aparício *et al.*,
100 2018) is reducing the habitat quality for many arthropod species. Based on this previous
101 work and despite recent studies showing that there is a dominance of endemics (Ribeiro
102 *et al.*, 2005; Rego *et al.*, 2019) and possible resistance to invasions (Florencio *et al.*,
103 2016), we expect a visible decrease in endemics diversity over time most markedly in
104 abundance. Moreover, since exotic arthropod species are not in equilibrium and
105 consequently are more dynamic in space (Cardoso *et al.*, 2009; Rigal *et al.*, 2018) and
106 time (Matthews *et al.*, 2019b) than indigenous species, we also expect a temporal
107 positive signal for this group of species. Given the expected loss of endemics but gain
108 of exotics, overall richness and abundance would remain similar across time. We test
109 these predictions using the diversity metrics (Hill numbers), change in species
110 composition over time and Species Abundance Distribution (SAD) for all arthropod
111 species, endemics, native non-endemics and exotic species.

112

113 **Material and Methods**

114 **Study sites and sampling methods**

115 The Azorean archipelago is located in the North Atlantic, roughly between 37° to
116 40° N latitude and 25° to 3° W longitude. Terceira Island (Fig. 1), a roughly circular
117 island with an area of 402 km², contains the largest area of native pristine forests in the
118 Azores (Triantis *et al.*, 2010), with five main fragments of native forest distributed
119 across four main volcanic polygenetic complexes. The study was initiated in 2012 as
120 part of the EU-NETBIOME –ISLANDBIODIV (Cicconardi *et al.*; 2017; Borges *et al.*,
121 2018a) (Fig. 1). SLAM (Sea, Land, and Air Malaise) traps were setup in 10 plots for

122 long-term monitoring, maximizing the distance between plots within the continuous
123 forest patch. These traps are passive flight interception traps with approximately 110 x
124 110 x 110 cm, similar to Malaise traps, but allowing the interception of insects from all
125 directions (arthropods hit an area of black mesh and are funneled into a sampling
126 bottle). The collecting bottles, containing Propylene Glycol as preservative, operated
127 continually for six years, being collected and changed every three months; thus, each
128 sample covers one season of the year. Two of the original ISLANDBIODIV plots were
129 not considered due to the fact that some samples were missing in some of the years. In
130 total, 192 (8 plots x 4 seasons x 6 years) samples were considered for the study. A more
131 comprehensive outline of the study is provided in Borges *et al.* (2017) and Matthews *et*
132 *al.* (2019b).

133 **Species identification**

134 Arthropods were sorted to order level and to morphospecies by students working
135 as parataxonomists. One of the authors (PAVB) identified to species level the
136 morphospecies of the following arthropod classes: Diplopoda (Chordeumatida, Julida),
137 Chilopoda (Geophilomorpha, Lithobiomorpha, Scolopendromorpha), Arachnida
138 (Araneae, Opiliones, Pseudoscorpiones) and Insecta (Blattaria, Coleoptera, Hemiptera,
139 Microcoryphia, Neuroptera, Psocoptera, Thysanoptera, Trichoptera). All material is
140 stored at EDTP—Entomoteca Dalberto Teixeira Pombo, University of Azores, Angra
141 do Heroísmo, Portugal.

142 Arthropods were grouped into three colonization categories: endemic (i.e.
143 restricted to the Azores); native non-endemic, i.e. species that arrived naturally to the
144 archipelago but are present both in the Azorean Islands and elsewhere; and exotic non-
145 native species, i.e., species whose original distribution range did not include the Azores
146 and that are believed to have been introduced in the Macaronesian region after human
147 settlement in the 15th century. The exotic status was inferred either from historical
148 records of detected species introductions or from their current distribution being closely
149 associated with human activity. For unidentified species, if other species in the same
150 genus, subfamily or family were present in the archipelago and all belonged to the same
151 colonization category (according to Borges *et al.*, 2010), the unknown species were
152 classified similarly. Otherwise, we assumed the species to be unclassified.

153 **Data Analysis**

154 For the current study, we used data sampled over the years 2013 –2018 (inclusive) and
155 pooled the data from the four seasons of each year to create yearly datasets for each of
156 the eight plots considered (temporal α diversity). We further pooled the eight plot trap
157 data to have yearly datasets at the regional scale (temporal γ diversity). Unless
158 otherwise stated, all the following analysis were performed with temporal γ diversity
159 (one value per year). A sensitivity analysis was performed previously by Matthews *et*
160 *al.* (2019b) to ensure our results were robust, namely sampling completeness estimates
161 for each year in each plot and an evaluation if a single SLAM trap was sufficient to
162 capture the relevant community properties, evaluating the results of three SLAM traps
163 setup in one of the plots during one year. In both cases the data was considered robust.

164 Our first set of analyses aimed to test whether species diversity of arthropod
165 assemblages show temporal trends over the six years period of sampling. We calculated
166 the Hill numbers at three different orders (q) of diversity with a q value of 0 for species
167 richness with all species having the same weight, $q = 1$ for the exponential of Shannon's
168 index with species being weighted exactly for their abundance in the community and
169 whereas $q = 2$ for the inverse of Simpson's index which favors abundant species. We
170 used a sample-size-based rarefaction approach to estimate the rate of increase in Hill
171 number with increasing number of individuals sampled, and then extrapolated the
172 observed accumulation curve using the rarefaction-extrapolation approach (Chao &
173 Jost, 2012). Second, we estimated accumulation rates in relation to the degree of
174 completeness of sampling effort, rather than just sample size, as recommended by Chao
175 & Jost (2012). Degree of completeness for each year was evaluated using the coverage
176 estimator (\hat{C}_n , Chao & Jost, 2012) which estimates the proportion of the total number of
177 individuals in an assemblage that belong to the species represented in the sample.
178 Sample coverage is considered to be an objective measure of completeness (Chao &
179 Jost, 2012). Hill numbers were subsequently calculated for endemic, native non-
180 endemic and exotic species separately. Generalized linear models with Quasi-Poisson
181 error and linear regression models with log-transformed data were used to examine the
182 relationships between diversity and years for species richness and the exponential of
183 Shannon's index and the inverse of Simpson's index respectively. This was carried out
184 for all species and for endemic, native non-endemic and exotic species. All
185 aforementioned analyses were also performed by averaging diversity across the eight

186 plots (mean temporal α diversity) to test whether trends found at regional scale were
187 congruent or not with patterns found at plot scales.

188 Our second set of analyses was to evaluate temporal trends in abundance per
189 individual species across the six years. We only selected species occurring in a
190 minimum of 4 years out of the six years and with a minimum of 5 individuals per year
191 of occurrence. We used this cut off because temporal changes of very rare species could
192 be caused by minor, chance events. Generalized linear models with Quasi-Poisson error
193 were run to test for the relation between the abundance and years.

194 Our third analysis aimed to examine β diversity patterns over time considering all
195 species together but also for endemic, native non-endemic and exotic species separately.
196 We used the Bray-Curtis index as a β diversity measure with square-root transformed
197 abundance. Relationships between β diversity and distance in time were tested with
198 Mantel permutation tests, based on 9,999 permutations and using Spearman's
199 correlation coefficient. We also tested for differences in β diversity values between
200 endemic, native non-endemic and exotic species using Kruskal-Wallis tests followed by
201 post-hoc pairwise Wilcoxon tests. Our fourth set of analyses was to evaluate temporal
202 changes in species abundance distribution (SAD) to further quantify the contribution of
203 endemic, native non-endemic and exotic species abundance patterns over time. We used
204 the Gambin model (Ugland *et al.*, 2007, Matthews *et al.*, 2014) to characterize the shape
205 of the SAD (Ugland *et al.*, 2007). The unimodal gambin model has a single free
206 parameter (α), which characterizes the distribution shape with low values indicating
207 logseries-distribution and higher values indicating more lognormal- distribution.
208 Gambin has been shown to provide good fits to a wide variety of empirical datasets
209 (Matthews *et al.*, 2014, 2019a). Recent developments (Matthews *et al.*, 2019a) have
210 derived the likelihood functions for multimodal gambin models (i.e. with one α per
211 mode) providing a means of easily assessing multimodality in SAD datasets. Therefore,
212 for each year, we fitted both unimodal and bimodal gambin models and used the
213 Bayesian information criterion (BIC) values to compare both models (Burnham &
214 Anderson, 2002). The bimodal model was considered to better fit the SAD if its BIC
215 value was lower than the unimodal model. We also recorded the χ^2 goodness-of-fit
216 statistic and its associated p-value for both one and bimodal models. Given that SAD
217 model parameters are sensitive to variations in sample size (McGill, 2011) and that we

218 were also interested in comparing parameter values across years, we used a procedure
219 where, for each sample, we subsampled 3000 individuals (the least abundant sample
220 having 3944 individuals), fitted the best gambin model (either uni- or bimodal) to this
221 subsample and stored the α parameter value(s). Given that this subsampling procedure is
222 stochastic, we repeated the process 100 times for each sample and took the mean α
223 value. Mean α values were regressed against years using linear regressions. Finally, we
224 calculated the mean weighted octaves (i.e. weighted with species number) for endemic,
225 native non-endemic and exotic species per year and (1) we used weighted t-tests to
226 examine whether mean weighted octaves differ between groups in each year and (2) run
227 linear regressions to test whether, for a given group, mean weighted octaves increase or
228 decrease over time. Statistical analyses were implemented within the R programming
229 environment (R Development Core Team, 2014) using the packages *vegan* (Oksanen *et al.*,
230 2013), *iNEXT* (Chao *et al.*, 2014), *BAT* (Cardoso *et al.*, 2015) and *gambin*
231 (Matthews *et al.*, 2014).

232

233 **Results**

234 A total of 30,875 arthropod specimens were collected and 159 (morpho) species
235 were identified, representing 17 orders. Of the 159 species, 32 were considered to be
236 endemic to Azores, 63 to be native (non-endemics) and 57 to be exotics while seven (7)
237 species were not assigned to any group. About 10% of the taxa were identified to
238 morphospecies rather than species. The number of species and total abundance per year
239 for all species and for the three species groups are presented in Table 1. Overall, we
240 found marginal significant differences in species richness over time between the three
241 groups (Friedman's test, $P=0.04$) with exotics representing a larger fraction of diversity
242 over time (Paired Wilcoxon post hoc test $P=0.036$).

243 Sample-size-based species accumulation curves (Fig. S1) indicated that the arthropod
244 fauna was well sampled for each year, but did not represent a complete census of
245 species. The majority of these unsampled species are likely to be rare (and potentially
246 vagrants) as coverage-based rarefaction revealed a sample completeness of almost
247 100% for the six years, suggesting that very few individuals of the community belonged
248 to species not represented in our samples. Therefore, we conclude that our sampling was
249 satisfactory for characterization of arthropod communities for each year (See Figure S1

250 and Table 1). Overall, we only detected a significant increase of gamma diversity with
251 time for exotic species, for both the exponential of Shannon's index ($R^2 = 0.81$, $P=0.01$)
252 and the inverse of Simpson's index ($R^2 = 0.84$, $P = 0.009$) (Figure 2; see detailed results
253 in Table S1). Similar results were obtained with mean α diversity (exotic species:
254 exponential of Shannon's index; $R^2 = 0.86$, $P=0.007$ and inverse of Simpson's index; R^2
255 $= 0.86$, $P = 0.007$) (See detailed results in Table S2).

256 Only 48 species were retained for the individual abundance analysis, representing
257 31% of the total species recorded in our study but 96% of the individuals (Figure 3).
258 Overall, average effect size was -0.064 ± 0.41 , -0.066 ± 0.417 and -0.066 ± 0.249 for
259 endemic, native non-endemic and exotic species respectively. However, 11 species
260 showed a significant decline in abundance, while only 3 species showed a significant
261 increase (Table S3).

262 We found significant and positive relationships between β diversity with distance
263 in time for overall, endemic and exotic species ($r_s = 0.85$; $P=0.002$; $r_s = 0.71$; $P= 0.016$
264 and $r_s = 0.60$; $P=0.011$ respectively, Figure 4) but not for native non-endemic species (r_s
265 $= 0.20$; $P= 0.247$). On average, β diversity values were strongly and significantly
266 different between the three species groups (Kruskal-Wallis; $H=36.25$; $P<0.001$) with
267 exotic species having the highest β diversity over time and endemics the lowest (Post-hoc
268 Pairwise Wilcoxon test: all pairs being significantly different, $P<0.001$, Figure 4). For
269 each of the six years, SADs was best represented by a bimodal gambin model according
270 to the χ^2 goodness-of-fit test and BIC (Figure 5 and see Table S4). Non-significant
271 relationships were detected between the mean α parameter values and time for both
272 modes ($R^2 = 0.15$, $P=0.44$ and $R^2 = 0.04$, $P=0.68$). Our weighted t-tests showed that,
273 regardless of the years, exotic species were always significantly associated to smaller
274 octaves (rare species, Table S5) than endemic species that were mostly represented in
275 higher octaves (dominant species). We did not detect any significant temporal trends in
276 the weighted mean octaves for endemic, native non-endemic or exotic species ($R^2 =$
277 0.04 , $P= 0.68$, $R^2 = 0.01$, $P=0.85$ and $R^2 = 0.003$, $P=0.91$ respectively).

278

279 **Discussion**

280 Contrasting with recent studies on the European and North American mainland,
281 our study shows no evidence of a decline of overall species diversity for endemic and
282 native non-endemic species, although the data are limited to six years of sampling.
283 However, our study clearly identified three important patterns: i) an increasing diversity
284 of exotic species over time; ii) the high temporal dynamism of exotic species (see also
285 Matthews *et al.*, 2019b) and iii) some evidence of a tendency for decreasing abundance
286 for some endemic species.

287 Therefore, all our predictions were generally confirmed, and here we clearly
288 identify exotic species as a potential driver of future biodiversity erosion on Azorean
289 native forests. This is partly similar to the pattern found by Seibold *et al.* (2019) in
290 German forests, where few initially abundant invasive (and potential pest) species
291 increased in abundance. In previous studies we observed that exotic species are already
292 permeating Azorean indigenous arthropod communities (Gaston *et al.*, 2006; Rigal *et*
293 *al.*, 2013), being however only abundant in anthropogenic habitats (Cardoso *et al.*,
294 2009). Rapid demographic fluctuations (Matthews *et al.*, 2019b) and contingent spatial
295 factors related with native forest fragmentation and land-use changes (Cardoso *et al.*,
296 2009; Florencio *et al.*, 2016) are surely involved on the increased diversity through time
297 of exotic species in the Azores. It is worth noting that the increasing diversity of exotic
298 species in six years is mostly due to juveniles. This suggests the increasing importance
299 of a source-sink dynamics between natural forests as sinks and other habitat types as
300 sources. The dispersion of juveniles from the surrounding matrix of semi-natural
301 grasslands and exotic plantations of *Cryptomeria japonica* towards native forests seems
302 to be more significant from year to year (see also Borges *et al.*, 2008). We have no data
303 yet to know what is causing this change, but it probably is only a matter of time before
304 many of the exotic species can establish and multiply healthy populations in native
305 forests, which might cause displacement or local extinctions of endemic and native non-
306 endemic species. Despite previous observations suggesting that Azorean canopies may
307 act as physical barriers to the colonization of exotic spiders (Florencio *et al.*, 2016), the
308 results obtained in this long-term study are less optimistic. If this process continues, we
309 may expect that in addition to the ongoing invasion of soil communities (see Cicconardi
310 *et al.*; 2017), the Azorean arthropod canopy communities are also under and a potential
311 process of ecological meltdown and homogenization.

312 The observation that there is a tendency for a decreasing abundance of some
313 endemic species is also of some concern. A recent assessment of the IUCN red list
314 status of Azorean endemic forest arthropods (Borges *et al.*, 2017, 2018c; see also
315 <http://www.maiisg.com/>), concluded that most species are threatened. There is no
316 current easy explanation for the observed trend in the endemic arthropod species, but it
317 can be associated with the current spread of invasive plants that are changing
318 dramatically the cover and structure of forest understory, namely the cover of ferns and
319 bryophytes in the forest floor (Borges *et al.*, 2017, 2018c). In addition, António Frias
320 Martins (pers. comm.) observed a tendency for a decrease in the cover of bryophytes on
321 the canopy of some endemic Azorean trees at high elevations in the last twenty years
322 with a consequent decrease in the abundance of endemic micro land snails. This
323 observation indicates an ongoing impact of climatic changes on Azorean native forest
324 and a tendency to change on habitat structure with impact on endemic invertebrates.

325 Continuing monitoring of island forest ecosystems is badly needed (Borges *et al.*,
326 2018b), on the Azores as well as other regions to avoid unexpected declines and
327 extinctions of native, often endemic, species.

328

329 **Conclusions**

330 In this study no major insect diversity decline was observed in the native forests
331 of a small Atlantic volcanic island in Azores (Portugal). In contrast, in addition to some
332 evidence of decreasing abundances of endemic species, the increase through time of the
333 diversity of exotic arthropods was the stronger pattern.

334 We can consider that our results are representative of the current situation on
335 Azorean native forests since we included most of arthropod orders encompassing
336 several trophic levels, even if excluding Acari, Collembola, Lepidoptera, Diptera and
337 Hymenoptera from our diversity measurements. The impact of exotic species on islands
338 is well known (Sax & Gaines, 2008), and as a result of this six-year study on Azores,
339 important management actions should be taken to tackle this problem (see also Harvey
340 *et al.*, 2020; Samways *et al.*, 2020).

341 This is therefore a different, complementary view of many studies showing insect
342 population declines. On islands, as studied extensively in the past, invasive species are

343 particularly relevant in a conservation context. This signal would have been missed if
344 species were not identified and classified according to their origin, masking a
345 worrisome pattern.

346

347

348 **Acknowledgments**

349 A large number of students financed by the EU Programs ERASMUS and
350 EURODYSSÉE sorted the samples prior to species assignment by one of us (PB), and
351 we are grateful to all of them: Adal Humberto Díaz Raya, David Rodilla Rivas, Daniel
352 Ehrhart, Juan Ignacio Pitarch Pérez, Juan Manuel Taboada Alvarez, Helena Marugán
353 Páramo, Laura Cáceres Sabater, Laura Gallardo, Marija Tomašić, Óscar García
354 Contreras, Percy de Laminne de Bex, Ruben Murillo Garcia, Sergio Fernandez, Sophie
355 Wallon, and William Razey. This manuscript was also partly financed by Portuguese
356 National Funds, through FCT – Fundação para a Ciência e a Tecnologia, within the
357 project UID/BIA/00329/2013-2020, the project from Direcção Regional do Ambiente -
358 PRIBES (LIFE17 IPE/PT/000010) and Portuguese FCT-NETBIOME –
359 ISLANDBIODIV grant 0003/2011. The Natural Park of Terceira (Azores) provided the
360 necessary authorization for sampling.

361 Author contributions – PAVB conceived the study and led the writing with the close
362 collaboration of FR and PC. FR preformed the statistical analysis. PAVB designed the
363 sampling methodology and collected the data with the help of ARP.

364 **Conflict of Interest**

365 The authors declare no conflict of interest

366

367 **References**

368 Alcover, J.A., Pieper, H., Pereira, F. & Rando, J.C. (2015) Five new extinct species of
369 rails (Aves: Gruiformes: Rallidae) from the Macaronesian Islands (North Atlantic
370 Ocean). *Zootaxa*, **4057**, 151-190.

- 371 Allan, E., Manning, P., Alt, F., Binkenstein, J., Blaser, S., Blüthgen, N., ... &
372 Kleinebecker, T. (2015) Land use intensification alters ecosystem
373 multifunctionality via loss of biodiversity and changes to functional
374 composition. *Ecology Letters*, **18**, 834-843.
- 375 Aparício, B.A., Cascalho, J., Cruz, M.J., Borges, P.A.V., Azevedo, E.B., Elias, R.B. &
376 Ascensão, F. (2018) Assessing the landscape functional connectivity using
377 movement maps: a case study with endemic Azorean insects. *Journal of Insect*
378 *Conservation*, **22**, 257-265.
- 379 Bennett, E. M., Cramer, W., Begossi, A., Cundill, G., Díaz, S., Egoh, B. N., ... & Lebel,
380 L. (2015) Linking biodiversity, ecosystem services, and human well-being: three
381 challenges for designing research for sustainability. *Current Opinion in*
382 *Environmental Sustainability*, **14**, 76-85.
- 383 Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L. & Gaston, K.J. (2004) Avian
384 extinction and mammalian introductions on oceanic islands. *Science*, **305**, 1955–
385 1958.
- 386 Borges, P.A.V., Cardoso, P., Fattorini, S., Rigal, F., Matthews, T.J., Di Biase, L.,
387 Amorim, I.R., Florencio, M., Borda-de-Água, L., Rego, C., Pereira, F., Nunes,
388 R., Carvalho, R., Ferreira, M.T., Lopez, H., Pérez Delgado, A.J., Otto, R.,
389 Fernández Lugo, S., Nascimento, L. de, Caujapé-Castells, J., Casquet, J.,
390 Danflous, S., Fournel, J., Sadeyen, A.-M., Elias, R.B., Fernández-Palacios, J.M.,
391 Oromí, P., Thébaud, C., Strasberg, D. & Emerson, B.C. (2018a) Community
392 structure of woody plants on islands along a bioclimatic gradient. *Frontiers of*
393 *Biogeography*, **10**, 1-31.
- 394 Borges, P.A.V., Cardoso, P., Kreft, H., Whittaker, R.J., Fattorini, S., Emerson, B.C.,
395 Gil, A., Gillespie, R.G., Matthews, T.J., Santos, A.M.C., Steinbauer, M.J.,
396 Thébaud, C., Ah-Peng, C., Amorim, I.R., Aranda, S.C., Arroz, A.M., Azevedo,
397 J.M., Boieiro, M., Borda-De-Água, L., Carvalho, J.C., Elias, R.B., Fernández-
398 Palacios, J.M., Florencio, M., González-Mancebo, J.M., Heaney, L.R., Hortal, J.,
399 Kueffer, C., Lequette, B., Martín-Esquivel, J.L., López, H., Lamelas-López, L.,
400 Marcelino, J., Nunes, R., Oromí, P., Patiño, J., Pérez, A.J., Rego, C., Ribeiro, S.P.,
401 Rigal, F., Rodrigues, P., Rominger, A.J., Santos-Reis, M., Schaefer, H., Sérgio,
402 C., Serrano, A.R.M., Sim-Sim, M., Stephenson, P.J., Soares, A.O., Strasberg, D.,
403 Vanderporten, A., Vieira, V. & Gabriel, R. (2018b) A Global Island Monitoring

- 404 Scheme (GIMS) for the long-term coordinated survey and monitoring of forest
405 biota across islands. *Biodiversity and Conservation*, **27**, 2567–2586.
- 406 Borges, P.A.V., Costa, A., Cunha, R., Gabriel, R., Gonçalves, V., Martins, A.F., Melo, I.,
407 Parente, M., Raposeiro, P., Rodrigues, P., Santos, R.S., Silva, L., Vieira, P. &
408 Vieira, V. (Eds.) (2010) *A list of the terrestrial and marine biota from the Azores*.
409 Príncipeia, Cascais, 432 pp.
- 410 Borges, P.A.V., Gabriel, R. & Fattorini, S. (2019a) Biodiversity erosion: causes and
411 consequences. *Life on Land. Encyclopedia of the UN Sustainable Development*
412 *Goals*. (ed. by Leal Filho W., Azul A., Brandli L., Özuyar P., Wall T.), pp. 1-10.
413 The Springer Nature, Switzerland. DOI: 10.1007/978-3-319-71065-5_78-1.
- 414 Borges, P.A.V., Lamelas-López, L., Amorim, I.R., Danielczak, A., Nunes, R., Serrano,
415 A.R.M., Boeiro, M., Rego, C., Hochkirch, A. & Vieira, V. (2017) Conservation
416 status of the forest beetles (Insecta, Coleoptera) from Azores, Portugal.
417 *Biodiversity Data Journal*, **5**, e14557.
- 418 Borges, P.A.V., Pérez Santa-Rita, J.V., Nunes, R., Danielczak, A., Hochkirch, A.,
419 Amorim, I.R., Lamelas-López, L., Karsholt, O. & Vieira, V. (2018c) Species
420 conservation profile of moths (Insecta, Lepidoptera) from Azores, Portugal.
421 *Biodiversity Data Journal*, **6**, e23311.
- 422 Borges, P.A.V., Pimentel, R., Carvalho, R., Nunes, R., Wallon, S. & Ros Prieto, A.
423 (2017) Seasonal dynamics of arthropods in the humid native forests of Terceira
424 Island (Azores). *Arquipelago Life and Marine Sciences*, **34**, 105-122.
- 425 Borges, P.A.V., Santos, A.M.C., Elias, R.B. & Gabriel, R. (2019b). The Azores
426 Archipelago: Biodiversity Erosion and Conservation Biogeography. *Encyclopedia*
427 *of the World's Biomes -Earth Systems and Environmental Sciences*. Reference
428 Module in Earth Systems and Environmental Sciences, Elsevier, pp. 1-18.
429 Amsterdam, Netherlands. DOI: 10.1016/B978-0-12-409548-9.11949-
- 430 Borges, P.A.V., Ugland, K.I, Dinis, F.O. & Gaspar, C. (2008). Insect and spider rarity
431 in an oceanic island (Terceira, Azores): true rare and pseudo-rare species. *Insect*
432 *Ecology and Conservation* (ed. by Fattorini, S.). pp. 47-70. Research Signpost,
433 Kerala, India. ISBN: 978-81-308-0297-8, pp. 317.

- 434 Burnham, K.P. & Anderson, D.R. (2002) *A practical information-theoretic approach*.
435 *Model selection and multimodel inference*, 2nd ed. Springer, New York.
- 436 Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P.,
437 Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C.,
438 Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012)
439 Biodiversity loss and its impact on humanity. *Nature*, **486**, 59-67.
- 440 Cardoso, P. & Leather, S.R. (2019) Predicting a global insect apocalypse. *Insect*
441 *Conservation and Diversity*, **12**, 263-267.
- 442 Cardoso, P., Lobo, J.M., Aranda, S.C., Dinis, F., Gaspar, C. & Borges, P.A.V. (2009) A
443 spatial scale assessment of habitat effects on arthropod communities of an oceanic
444 island. *Acta Oecologica-International Journal of Ecology*, **35**, 590-597.
- 445 Cardoso, P., Barton, P.S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T.,
446 Fukushima, C.S., Gaigher, R., Habel, J.C., Hallmann, C.A., Hill, M.J., Hochkirch,
447 A., Kwak, M.L., Mammola, S., Noriega, J.A., Orfinger, A.B., Pedraza, F., Pryke,
448 J.S., Roque, F.O., Settele, J., Simaika, J.P., Stork, N.E., Suhling, F., Vorster, C. &
449 Samways, M.J. (2020) Scientists' warning to humanity on insect extinctions.
450 *Biological Conservation*, in press.
- 451 Cardoso, P., Rigal, F. & Carvalho, J. C. (2015) BAT–Biodiversity Assessment Tools, an
452 R package for the measurement and estimation of alpha and beta taxon,
453 phylogenetic and functional diversity. *Methods in Ecology and Evolution*, **6**, 232-
454 236.
- 455 Chao, A. & Jost, L. (2012). Coverage-based rarefaction and extrapolation: standardizing
456 samples by completeness rather than size. *Ecology*, **93**, 2533-2547.
- 457 Chao, A., Chiu, C.H. & Jost, L. (2014) Unifying species diversity, phylogenetic diversity,
458 functional diversity, and related similarity and differentiation measures through Hill
459 numbers. *Annual Review of Ecology, Evolution, and Systematics*, **45**, 297-324.
- 460 Chapin III, F.S., Zaveleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Lavorel, S.,
461 Reynolds, H.L., Hooper, D.U., Sala, O.E., Hobbie, S.E., Mack, M.C. & Diaz, S.
462 (2000) Consequences of changing biotic diversity. *Nature*, **405**, 234-242.
- 463 Cicconardi, F., Borges, P.A.V., Strasberg, D., Oromí, P., López, H., Perez-Delgado, A.J.,
464 Casquet, J., Caujape-Castells, J, Fernandez-Palacios, J.M., Thebaud, C. & Emerson,

- 465 B.C. (2017) MtDNA metagenomics reveals large-scale invasion of belowground
466 arthropod communities by introduced species. *Molecular Ecology*, **26**, 3104-3115.
- 467 Ferreira, M.T., Cardoso, P., Borges, P.A.V., Gabriel, R., Azevedo, E.B., Reis, F., Araújo,
468 M.B. & Elias, R.B. (2016) Effects of climate change on the distribution of
469 indigenous species in oceanic islands (Azores). *Climatic Change*, **138**, 603-615.
- 470 Florencio, M., Rigal, F., Borges, P.A.V., Cardoso, P., Santos, A.M.C. & Lobo, J.M.
471 (2016) The role of plant fidelity and land-use changes on island exotic and
472 indigenous canopy spiders at local and regional scales. *Biological Invasions*, **18**,
473 2309-2324.
- 474 Gaspar, C., Borges, P.A.V. & Gaston, K.J. (2008) Diversity and distribution of arthropods
475 in native forests of the Azores archipelago. *Arquipelago Life and marine Sciences*,
476 **25**, 1-30.
- 477 Gaspar, C., Gaston, K.J., Borges, P.A.V. & Cardoso, P. (2011) Selection of priority areas
478 for arthropod conservation in the Azores archipelago. *Journal of Insect*
479 *Conservation*, **15**, 671–684.
- 480 Gaston, K.J., Borges, P.A.V., He, F. & Gaspar, C. (2006) Abundance, spatial variance
481 and occupancy: arthropod species distribution in the Azores. *Journal of Animal*
482 *Ecology*, **75**, 646-656.
- 483 Goodfriend, G.A., Cameron, R.A.D. & Cook, L.M. (1994) Fossil evidence of recent
484 human impact on the snail fauna of Madeira. *Journal of Biogeography*, **21**, 309–
485 320.
- 486 Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., ... &
487 Goulson, D. (2017) More than 75 percent decline over 27 years in total flying insect
488 biomass in protected areas. *PloS one*, **12**, e0185809.
- 489 Hallmann, C.A., Ssymank, A., Sorg, M., Jongejans, E. & de Kroon, H. (2019) 5. Biomass
490 declines predict diversity loss in a hoverfly community. *A tragedy of the common*,
491 63. In press
- 492 Hallmann, C.A., Zeegers, T., van Klink, R., Vermeulen, R., van Wielink, P., Spijkers,
493 H., van Deijk, J., van Steenis, W., Jongejans, E. (2020) Declining abundance of
494 beetles, moths and caddisflies in the Netherlands. *Insect Conservation and*
495 *Diversity* In press
- 496 Harvey, J.A. Heinen, R., Klein, A-M., Armbrrecht, I., Basset, Y., Baxter-Gilbert, J.H.,
497 Bezemer, M., Böhm, M., Bommarco, R., Borges, P.A.V., Cardoso, P. et al. (2020)

- 498 International scientists formulate a roadmap for insect conservation and recovery.
499 *Nature Ecology and Evolution* **4**, 174–176.
- 500 Homburg, K., Drees, C., Boutaud, E., Nolte, D., Schuett, W., Zumstein, P., ... &
501 Assmann, T. (2019) Where have all the beetles gone? Long-term study reveals
502 carabid species decline in a nature reserve in Northern Germany. *Insect*
503 *Conservation and Diversity*, **12**, 268-277.
- 504 Kier, G., Kreft, H., Ming, T., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J. & Barthlott,
505 W. (2009) A global assessment of endemism and species richness across island and
506 mainland regions. *Proceedings of the National Academy of Sciences*, **23**, 9322–
507 9327.
- 508 Kirch P. (2015) Human ecodynamics in the Mangareva Islands: a stratified sequence from
509 Nenega-Iti Rock Shelter (site AGA-3, Agakautai Island). *Archaeology and*
510 *physical anthropology in Oceania*, **50**, 23-42.
- 511 Matthews, T.J., Borregaard, M., Gillespie, C., Ugland, K., Rigal, F., Krüger, R., Marques,
512 R., Sadler, J., Borges, P.A.V. & Whittaker, R.J. (2019a). Extension of the gambin
513 model to multimodal species abundance distributions. *Methods in Ecology and*
514 *Evolution*, **10**: 432–437.
- 515 Matthews, T.J., Borregaard, M.K., Ugland, K., Borges, P.A.V., Rigal, F., Cardoso, P. &
516 Whittaker, R.J. (2014). The gambin model provides a superior fit to species
517 abundance distributions with a single free parameter: evidence, implementation and
518 interpretation. *Ecography*, **37**, 1002–1011.
- 519 Matthews, T., Sadler, J.P., Carvalho, R., Nunes, R. & Borges, P.A.V. (2019b).
520 Differential turnover rates and temporal beta-diversity patterns of native and non-
521 native arthropod species in a fragmented native forest landscape. *Ecography*, **42**:
522 45–54.
- 523 McGill, B.J. (2011) Species abundance distributions. *Biological Diversity: Frontiers In*
524 *Measurement & Assessment*, **M2**, 105-122.
- 525 Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., ...
526 & Oksanen, M. J. (2013) Package 'vegan'. Community ecology package, version,
527 2(9), 1-295.

- 528 Ribeiro, S.P., Borges, P.A.V., Gaspar, C., Melo, C., Serrano, A.R.M., Amaral, J.,
529 Aguiar, C., André, G. & Quartau, J.A. (2005) Canopy insect herbivores in the
530 Azorean Laurisilva forests: key host plant species in a highly generalist insect
531 community. *Ecography*, **28**, 315-330.
- 532 Rigal, F., Cardoso, P., Lobo, J.M., Triantis, K.A., Whittaker, R.J., Amorim, I.R. &
533 Borges, P.A.V. (2018) Functional traits of indigenous and exotic ground-dwelling
534 arthropods show contrasting responses to land-use changes in an oceanic island,
535 Terceira, Azores. *Diversity and Distributions*, **24**, 36-47.
- 536 Rigal, F., Whittaker, R.J., Triantis, K.A. & Borges, P.A.V. (2013) Integration of non-
537 indigenous species within the interspecific abundance-occupancy relationship.
538 *Acta Oecologica-International Journal of Ecology*, **48**, 69–75.
- 539 Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-
540 Sanwald, E., Huenneke, L.F., Jackson, R., Kinzig, A., Leemans, R., Lodge, D.,
541 Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M.
542 & Wall, D.H. (2000). Global biodiversity scenarios for the year 2100. *Science*,
543 **287**, 1770-1776.
- 544 Samways, M.J., Barton, P.S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T.,
545 Fukushima, C.S., Gaigher, R., Habel, J.C., Hallmann, C.A., Hill, M.J., Hochkirch,
546 A., Kwak, M.L., Maes, D., Mammola, S., Noriega, J.A., Orfinger, A.B., Pedraza,
547 F., Pryke, J.S., Roque, F.O., Settele, J., Simaika, J.P., Stork, N.E., Suhling, F.,
548 Vorster, C. & Cardoso, P. (2020) Scientists solutions to conserve insects. *Biological*
549 *Conservation*, in press.
- 550 Sandifer, P.A., Sutton-Grier, A.E. & Ward, B. P. (2015) Exploring connections among
551 nature, biodiversity, ecosystem services, and human health and well-being:
552 opportunities to enhance health and biodiversity conservation. *Ecosystem Services*,
553 **12**, 1-15.
- 554 Sax, D. F. & Gaines, S.D. (2008) Species invasions and extinction: the future of native
555 biodiversity on islands. *Proceedings of the National Academy of*
556 *Sciences*, **105**(Supplement 1), 11490-11497.
- 557 Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., ... &
558 Linsenmair, K.E. (2019) Arthropod decline in grasslands and forests is associated
559 with landscape-level drivers. *Nature*, **574**, 671-674.

- 560 Terzopoulou, S., Rigal, F., Whittaker, R.J., Borges, P.A.V. & Triantis, K.A. (2015)
561 Drivers of extinction: the case of Azorean beetles. *Biology Letters*, **11**, 1-4.
- 562 Thomas, C.D., Jones, T.H., Hartley, S.E. (2019). “Insectageddon”: a call for more
563 robust data and rigorous analyses. *Global Change Biology*, **25**, 1891–1892.
- 564 Triantis, K.A., Borges, P.A.V., Ladle, R.J., Hortal, J., Cardoso, P., Gaspar, C., Dinis, F.,
565 Mendonça, E., Silveira, L.M.A., Gabriel, R., Melo, C., Santos, A.M.C., Amorim,
566 I.R., Ribeiro, S.P., Serrano, A.R.M., Quartau, J.A. & Whittaker, R.J. (2010)
567 Extinction debt on oceanic islands. *Ecography*, **33**, 285-294.
- 568 Ugland, K.I., Lamshead, P.J.D., McGill, B., Gray, J.S., O’Dea, N., Ladle, R.J. &
569 Whittaker, R.J. (2007) Modelling dimensionality in species abundance
570 distributions: description and evaluation of the Gambin model. *Evolutionary*
571 *Ecology Research*, **9**, 313-324.
- 572 Wagner, D.L. (2020) Insect declines in the Anthropocene. *Annual Review of*
573 *Entomology*, **65**. 457-480.

574 Weiss, K.R. (2015). Before we drown we may die of thirst. *Nature*, **526**, 624–627.
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578 **Figure legends**

579

580 **Figure 1.** A map of the eight out of the ten originally sampled 50m x 50m plots and
581 areas of native forest on the island of Terceira, Azores.

582

583 **Figure 2.** Relationships between species diversity and years. Analyses were performed
584 with first three Hill numbers namely species richness, the exponential of Shannon and
585 the inverse Simpson and for all species and endemic, native (non-endemic) and exotic
586 species separately. Generalized linear model with Quasi-Poisson error and linear
587 regression models with log-transformed data were used to examine the relationships
588 between diversity and years for species richness and the exponential of Shannon’s index

589 and the inverse of Simpson's index respectively. Dotted red lines indicate non-
590 significant relationships while solid red lines indicate significant ones.

591

592 **Figure 3.** Effect sizes of the relationships between individual species abundance with
593 years. Effect size refers to the standardized slope of the relationship extracted from the
594 Generalized linear models with Quasi-Poisson error fitted to the data. Analyses were
595 performed only for the species occurring in a minimum of 4 years out of the six years
596 and with a minimum of 5 individuals per year of occurrence. In total, 48 species were
597 considered representing 31% of the species sampled across the six years but 96% of all
598 individuals. Horizontal lines indicate the confidence interval at 95% calculated for each
599 effect size. Negative effect size indicates decline in abundance over the six years while
600 positive effect size indicates an increase in abundance. Endemic, native (non-endemic)
601 and exotic species per octave are indicated with different colors. Species for which the
602 effect size was significant are labelled.

603

604 **Figure 4.** Results of the β diversity analyses over time for all species, endemic, native
605 (non-endemic) and exotic species. β diversity was computed with the Bray-Curtis index.
606 (A) Relationship between β diversity and distance in years. Relationships were tested
607 using Mantel test with Spearman correlation. Dotted red lines indicate non-significant
608 relationships while solid red lines indicate significant ones. (B) Distribution of the β
609 diversity values between endemic, native and exotic species. Differences were tested
610 with Kruskal-Wallis test. The test was significant and post-hoc pairwise Wilcoxon test
611 showed that all groups differed between each other.

612

613 **Figure 5.** Species abundance distribution (SADs) histograms for arthropods, with
614 predicted values of the bimodal gambin model (black dots), for each year. The
615 following binning system was used: bin 1 corresponds to the number of species with 1
616 individual per species, bin 2 corresponds to the number of species with 2–3 individuals
617 per species, bin 3 corresponds to the number of species with 4–7 individuals per
618 species, etc. Number of endemic, native (non-endemic) and exotic and unclassified
619 species per octave are indicated with color code.

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1 **Table 1.** Degree of completeness estimated with coverage (\hat{C}_n) and number of species and individuals for all species (ALL) and for the endemic
 2 (END), native (non-endemic) (NAT) and exotic (EXO) species separately. The coverage estimator estimates the proportion of the total number of
 3 individuals in an assemblage that belong to the species represented in the sample.

Years	\hat{C}_n	S_{ALL}	S_{END}	S_{NAT}	S_{EXO}	N_{ALL}	N_{END}	N_{NAT}	N_{EXO}
2013	0.9944	83	24	32	24	5894	3858	1646	217
2014	0.9969	87	29	30	27	7026	4469	2357	199
2015	0.9949	75	26	29	19	3944	2479	1336	128
2016	0.9964	76	22	30	23	4120	2683	1274	160
2017	0.9947	80	20	29	29	3933	2358	1430	140
2018	0.9960	86	24	30	31	5958	3042	2729	186

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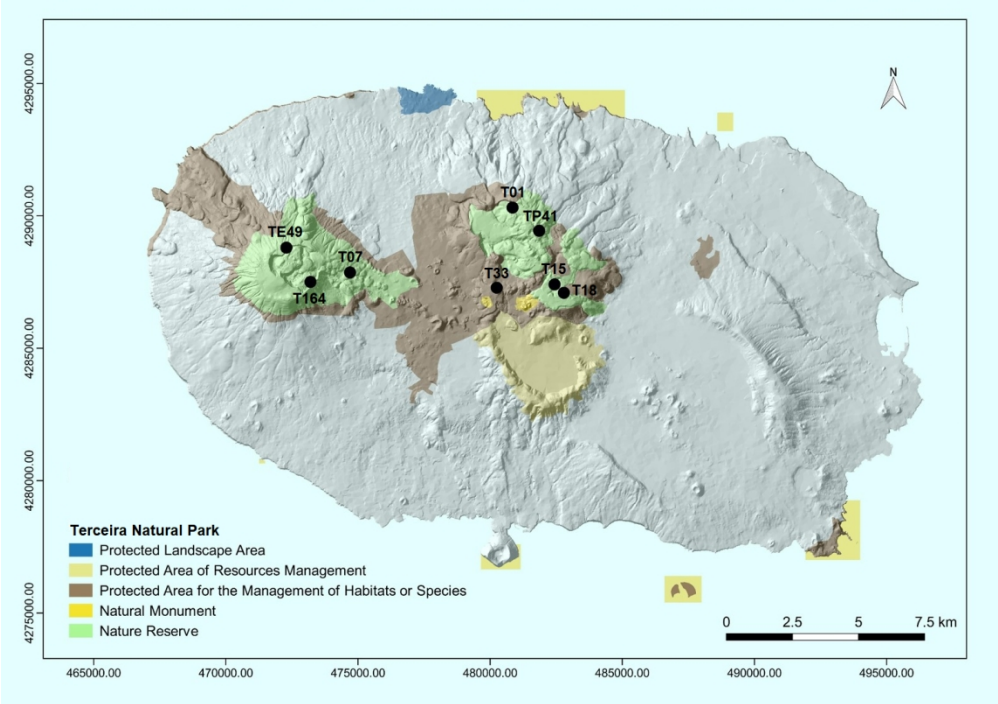


Figure 1. A map of the eight out of the ten originally sampled 50m x 50m plots and areas of native forest on the island of Terceira, Azores.

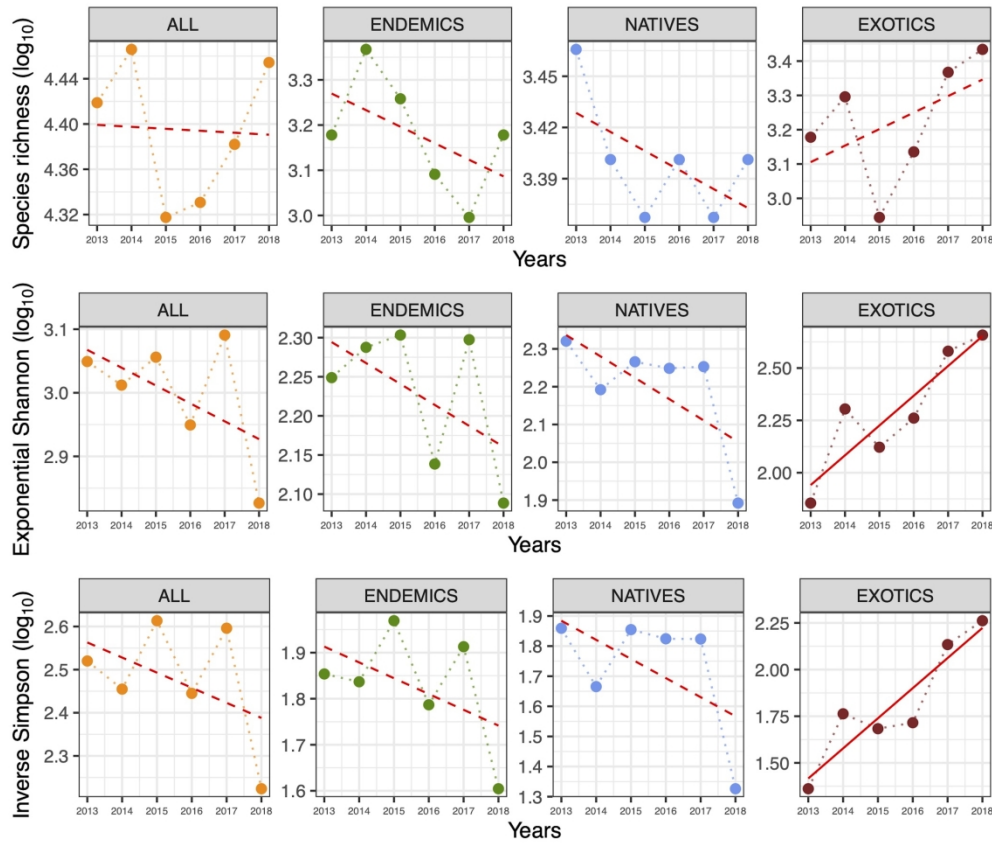


Figure 2. Relationships between species diversity and years. Analyses were performed with first three Hill numbers namely species richness, the exponential of Shannon and the inverse Simpson and for all species and endemic, native (non-endemic) and exotic species separately. Generalized linear model with Quasi-Poisson error and linear regression models with log-transformed data were used to examine the relationships between diversity and years for species richness and the exponential of Shannon’s index and the inverse of Simpson’s index respectively. Dotted red lines indicate non-significant relationships while solid red lines indicate significant ones.

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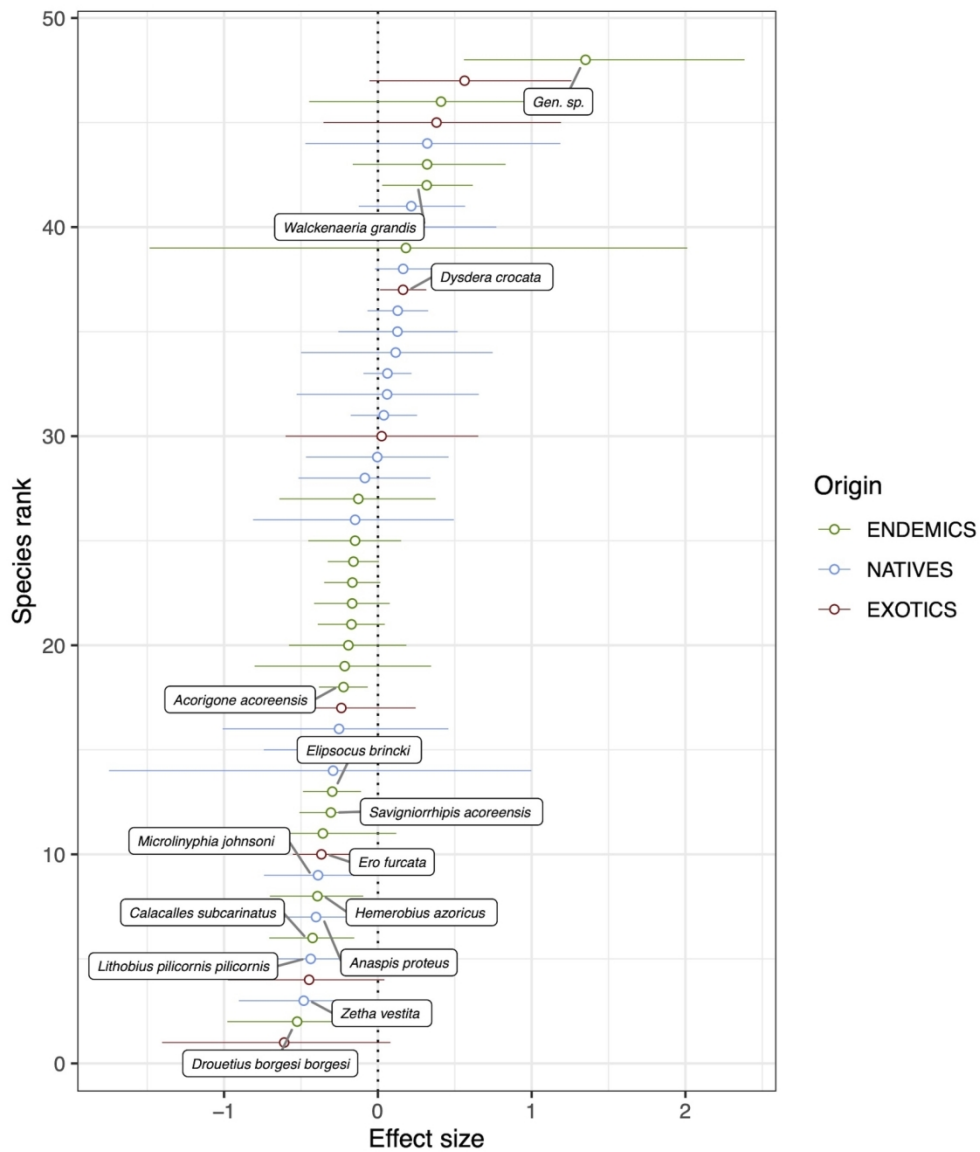


Figure 3. Effect sizes of the relationships between individual species abundance with years. Effect size refers to the standardized slope of the relationship extracted from the Generalized linear models with Quasi-Poisson error fitted to the data. Analyses were performed only for the species occurring in a minimum of 4 years out of the six years and with a minimum of 5 individuals per year of occurrence. In total, 48 species were considered representing 31% of the species sampled across the six years but 96% of all individuals. Horizontal lines indicate the confidence interval at 95% calculated for each effect size. Negative effect size indicates decline in abundance over the six years while positive effect size indicates an increase in abundance. Endemic, native (non-endemic) and exotic species per octave are indicated with different colors. Species for which the effect size was significant are labelled.

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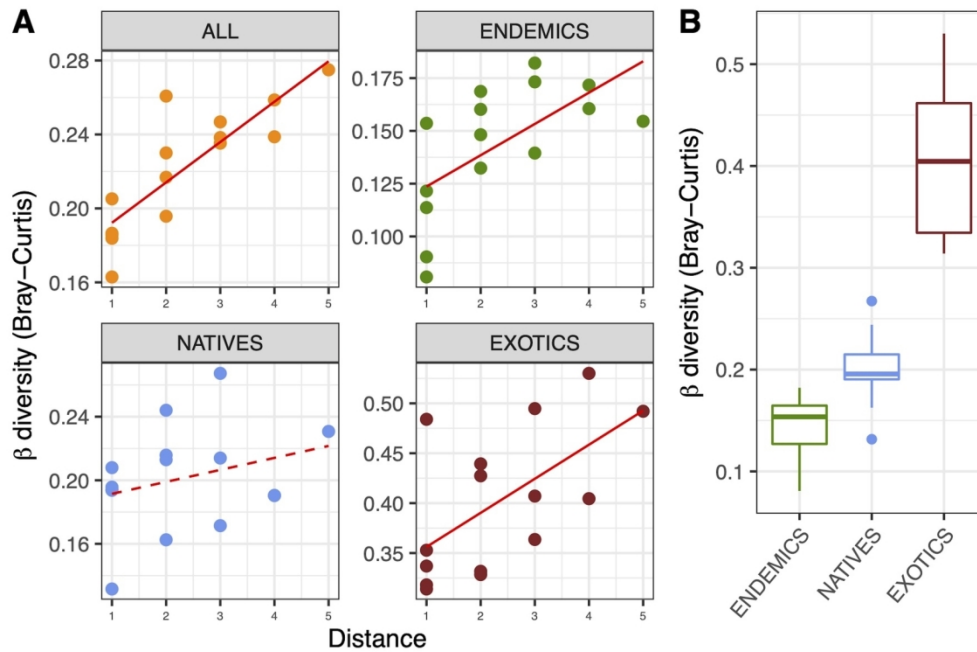


Figure 4. Results of the β diversity analyses over time for all species, endemic, native (non-endemic) and exotic species. β diversity was computed with the Bray-Curtis index. (A) Relationship between β diversity and distance in years. Relationships were tested using Mantel test with Spearman correlation. Dotted red lines indicate non-significant relationships while solid red lines indicate significant ones. (B) Distribution of the β diversity values between endemic, native and exotic species. Differences were tested with Kruskal-Wallis test. The test was significant and post-hoc pairwise Wilcoxon test showed that all groups differed between each other.

152x101mm (300 x 300 DPI)

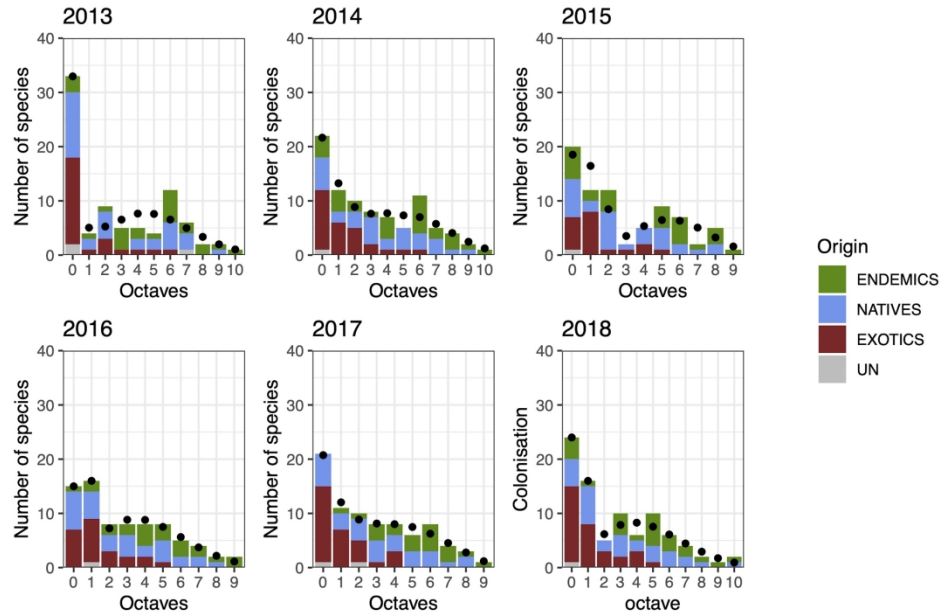


Figure 5. Species abundance distribution (SADs) histograms for arthropods, with predicted values of the bimodal gambin model (black dots), for each year. The following binning system was used: bin 1 corresponds to the number of species with 1 individual per species, bin 2 corresponds to the number of species with 2–3 individuals per species, bin 3 corresponds to the number of species with 4–7 individuals per species, etc. Number of endemic, native (non-endemic) and exotic and unclassified species per octave are indicated with color code.

406x254mm (300 x 300 DPI)

Supplementary Material

Increase of insular exotic arthropod diversity is a neglected aspect of the current biodiversity crisis

Paulo A.V. Borges François Rigal Alejandra Ros-Prieto & Pedro Cardoso

For Review Only

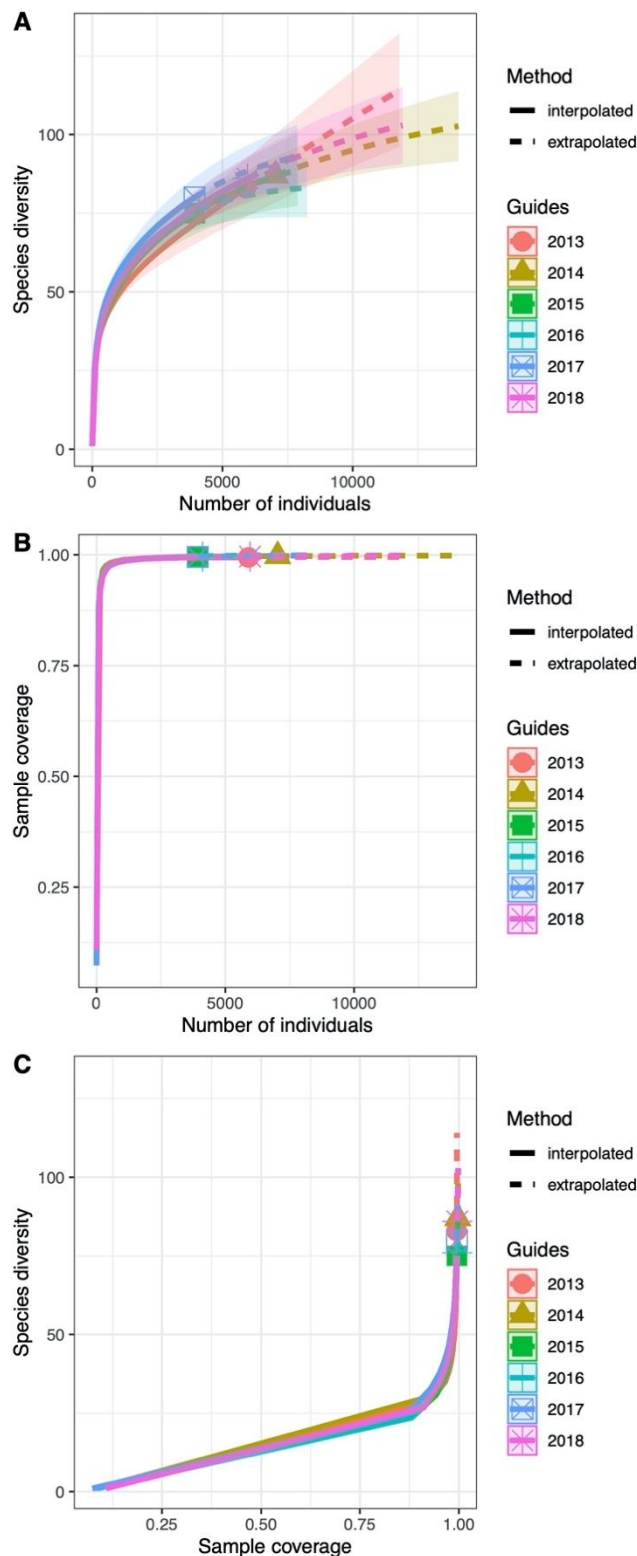


Figure S1. (A) Sample-size-based rarefaction (solid lines) and extrapolation (dotted lines, up to twice the sample size actually taken) of arthropod species richness per year of sampling, along with 95% unconditional confidence intervals (color shading). The symbols indicate the full sampling extent for each year (See Table 1 for the total abundance per year). (B) The sample-completeness plot with 95% confidence interval for rarefied samples (solid line) and extrapolated samples (dashed line) as a function of the number of individuals (See Table 1 for coverage value per year). (C) Coverage-based rarefaction (solid line) and extrapolation

(dashed line) with 95% unconditional confidence intervals. All 95% confidence intervals in three panels were obtained by a bootstrap method based on 100 replications.

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Table S1. Relationships between species diversity of arthropods and years. Species diversity was calculated using Hill numbers at three different orders (q) of diversity with a q value of 0 for species richness, $q = 1$ for the exponential of Shannon's index and $q = 2$ for the inverse of Simpson's index. Generalized linear models (GLM) with Quasi-Poisson error were used to examine the relationships between species richness and years while linear regression (LM) models with log-transformed data were used for the exponential of Shannon's index and the inverse of Simpson's index. The effect size (standardized coefficient of the effect of year) with its associated standard error (SE) is given as well as the R^2 and the P -value of the χ^2 and F -test for GLM and LM respectively. For GLM, R^2 was calculated as one minus ratio between residuals deviance and null deviance.

Metrics	Groups	Effect sizes	SE	R^2	P
$q = 0$	All species	-0.003	0.029	0.003	0.920
	Endemics	-0.064	0.051	0.283	0.278
	Natives	-0.020	0.014	0.347	0.219
	Exotics	0.088	0.066	0.297	0.256
$q = 1$	All species	-0.028	0.022	0.297	0.264
	Endemics	-0.027	0.020	0.299	0.261
	Natives	-0.056	0.030	0.470	0.133
	Exotics	0.142	0.035	0.809	0.015
$q = 2$	All species	-0.035	0.034	0.214	0.356
	Endemics	-0.034	0.029	0.259	0.303
	Natives	-0.063	0.046	0.325	0.238
	Exotics	0.161	0.034	0.848	0.009

Table S2. Relationships between mean plot species diversity of arthropods and years. Species diversity was calculated using Hill numbers at three different orders (q) of diversity with a q value of 0 for species richness, $q = 1$ for the exponential of Shannon's index and $q = 2$ for the inverse of Simpson's index. Generalized linear models (GLM) with Quasi-Poisson error were used to examine the relationships between species richness and years while linear regression (LM) models with log-transformed data were used for the exponential of Shannon's index and the inverse of Simpson's index. The effect size (standardized coefficient of the effect of year) with its associated standard error (SE) is given as well as the R^2 and the P -value of the χ^2 test of deviance and F-test for GLM and LM respectively. For GLM, R^2 was calculated as one minus ratio between residuals deviance and null deviance.

Metrics	Groups	Effect sizes	SE	R^2	P
$q = 0$	All species	-0.009	0.031	0.020	0.789
	Endemics	-0.042	0.030	0.340	0.226
	Natives	-0.022	0.031	0.116	0.508
	Exotics	0.097	0.045	0.531	0.098
$q = 1$	All species	-0.017	0.031	0.071	0.609
	Endemics	-0.026	0.033	0.134	0.475
	Natives	-0.079	0.046	0.430	0.158
	Exotics	0.149	0.036	0.810	0.014
$q = 2$	All species	-0.017	0.052	0.025	0.763
	Endemics	-0.021	0.043	0.058	0.645
	Natives	-0.106	0.061	0.430	0.157
	Exotics	0.157	0.032	0.858	0.008

Table S3. Relationships between abundance and years for the 48 individual species selected (See main text). Relationships were examined using generalized linear models (GLM) with Quasi-Poisson error. For each of the 48 species, the order, the name, the colonization group, the effect size (standardized coefficient of the effect of year) with its associated standard error (SE) is given as well as the R^2 and the P-value of χ^2 test of deviance. R^2 was calculated as one minus ratio between residuals deviance and null deviance.

Order	Species names	Group	Effect sizes	SE	R^2	P-value
Coleoptera	<i>Drouetius borgesii borgesii</i>	Endemics	-0.525	0.222	0.595	0.014
Coleoptera	<i>Calacallesubcarinatus</i>	Endemics	-0.425	0.141	0.688	0.002
Neuroptera	<i>Hemerobiusazoricus</i>	Endemics	-0.393	0.154	0.601	0.009
Microcoryphia	<i>Trigoniophthalmusborgesii</i>	Endemics	-0.358	0.248	0.378	0.143
Araneae	<i>Savigniorrhipisacoreensis</i>	Endemics	-0.306	0.103	0.681	0.003
Psocoptera	<i>Elipsocusbrincki</i>	Endemics	-0.297	0.096	0.711	0.002
Araneae	<i>Acorigoneacoreensis</i>	Endemics	-0.223	0.081	0.667	0.005
Hemiptera	<i>Strophingiaharteni</i>	Endemics	-0.216	0.289	0.118	0.453
Araneae	<i>Pisauraacoreensis</i>	Endemics	-0.191	0.194	0.192	0.320
Hemiptera	<i>Pinalitusoromii</i>	Endemics	-0.172	0.111	0.374	0.121
Araneae	<i>Sancusacoreensis</i>	Endemics	-0.167	0.125	0.283	0.181
Araneae	<i>Rugathodesacoreensis</i>	Endemics	-0.166	0.093	0.431	0.074
Araneae	<i>Gibbaraneaoccidentalis</i>	Endemics	-0.159	0.085	0.468	0.060
Hemiptera	<i>Cixiusazoterceirae</i>	Endemics	-0.148	0.153	0.192	0.333
Psocoptera	<i>Elipsocusazoricus</i>	Endemics	-0.127	0.256	0.058	0.620
Araneae	<i>Canariphantesacoreensis</i>	Endemics	0.182	0.806	0.015	0.820
Araneae	<i>Walckenaeriagrandsis</i>	Endemics	0.318	0.150	0.522	0.032
Coleoptera	<i>Athetadryochares</i>	Endemics	0.320	0.251	0.242	0.196
Hemiptera	<i>Eupteryxazorica</i>	Endemics	0.411	0.450	0.135	0.351
Hemiptera	<i>Gen.sp.</i>	Endemics	1.350	0.455	0.755	0.000
Blattaria	<i>Zethavestita</i>	Natives	-0.482	0.207	0.597	0.016
Lithobiomorpha	<i>Lithobiuspilicornis pilicornis</i>	Natives	-0.437	0.158	0.668	0.005
Coleoptera	<i>Anaspisproteus</i>	Natives	-0.402	0.208	0.501	0.048
Araneae	<i>Microlinyphiajohnsoni</i>	Natives	-0.389	0.174	0.580	0.023
Psocoptera	<i>Bertkauialucifuga</i>	Natives	-0.291	0.655	0.046	0.653
Hemiptera	<i>Kleidocerysericae</i>	Natives	-0.283	0.227	0.245	0.208
Psocoptera	<i>Valenzuelaflavidus</i>	Natives	-0.253	0.366	0.106	0.487
Hemiptera	<i>Monalocorisfilicis</i>	Natives	-0.148	0.327	0.052	0.650

Thysanoptera	<i>Hoplothripscorticis</i>	Natives	-0.085	0.217	0.036	0.697
Coleoptera	<i>Catopscoracinus</i>	Natives	-0.004	0.234	0.000	0.987
Coleoptera	<i>Pseudophloeophagustenax</i>	Natives	0.039	0.110	0.031	0.725
Araneae	<i>Tenuiphantesmiguelensis</i>	Natives	0.060	0.298	0.010	0.840
Araneae	<i>Lathysdentichelis</i>	Natives	0.062	0.080	0.132	0.435
Araneae	<i>Xysticuscor</i>	Natives	0.116	0.313	0.023	0.711
Hemiptera	<i>Triozalaurisilvae</i>	Natives	0.127	0.196	0.094	0.516
Hemiptera	<i>Cinarajuniperi</i>	Natives	0.129	0.100	0.287	0.199
Araneae	<i>Macaroeriscata</i>	Natives	0.164	0.094	0.434	0.078
Opiliones	<i>Leiobunumblackwalli</i>	Natives	0.203	0.280	0.116	0.466
Hemiptera	<i>Cyphopterumadcendens</i>	Natives	0.217	0.176	0.273	0.214
Psocoptera	<i>Trichopsocusclarus</i>	Natives	0.321	0.411	0.136	0.429
Psocoptera	<i>Ectopsocusbriggsi</i>	Exotics	-0.609	0.371	0.374	0.085
Araneae	<i>Cheiracanthiumerraticum</i>	Exotics	-0.447	0.257	0.348	0.074
Araneae	<i>Erofurcata</i>	Exotics	-0.367	0.094	0.798	0.000
Julida	<i>Ommatoiulusmoreletii</i>	Exotics	-0.238	0.249	0.186	0.337
Araneae	<i>Tenuiphantestenuis</i>	Exotics	0.025	0.314	0.001	0.937
Araneae	<i>Dysderacrocata</i>	Exotics	0.164	0.077	0.528	0.033
Coleoptera	<i>Tachyporusnitidulus</i>	Exotics	0.381	0.385	0.205	0.312
Coleoptera	<i>Athetaaeneicollis</i>	Exotics	0.564	0.329	0.408	0.075

Table S4. Comparison between the performance of the unimodal and bimodal gambin model in fitting species abundance distribution (SAD) of arthropods species per year. Comparison was performed using its BIC value as well as χ^2 goodness-of-fit statistic and its associated p-value. The α parameter of each mode is also given. For each of the six years, SADs was best represented by a bimodal gambin model.

Years	Unimodal gambin model				Bimodal gambin model				
	χ^2	P	BIC	α	χ^2	P	BIC	α_1	α_2
2013	56.325	0.000	372.475	0.95	11.147	0.346	344.536	0.11	7.35
2014	22.490	0.013	399.620	1.53	3.606	0.963	391.415	1.04	10.55
2015	29.487	0.001	334.209	1.48	7.571	0.578	323.496	3.07	15.62
2016	8.207	0.513	335.067	1.86	1.058	0.999	334.934	6.26	5.68
2017	15.144	0.087	353.441	1.61	1.128	0.999	348.076	0.70	11.53
2018	16.893	0.077	378.642	1.25	4.106	0.942	372.887	2.96	5.59

Table S5. Mean weighted octaves for endemic, native non-endemic and exotic species and P-values for the weighted t-tests testing pairwise differences in mean weighted octaves between species groups. For a given species group, the mean weighted octave is calculated by averaging octave values, each being weighted by its associated species number.

	Mean weighted octave			P-values of the weighted <i>t</i> -tests		
	Endemics	Natives	Exotics	End-Nat	End-Exo	Nat-Exo
2013	4.708	2.812	1.042	0.126	<0.001	0.096
2014	4.345	3.567	1.370	0.500	0.002	0.010
2015	3.846	2.966	1.368	0.440	0.020	0.072
2016	4.591	2.833	1.435	0.106	<0.001	0.130
2017	5.150	3.138	1.034	0.054	<0.001	0.031
2018	4.417	3.200	1.194	0.299	0.003	0.050