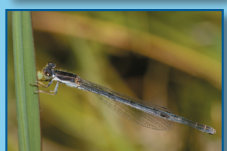
TERRESTRIAL ARTHROPODS OF MACARONESIA
BIODIVERSITY, ECOLOGY AND EVOLUTION

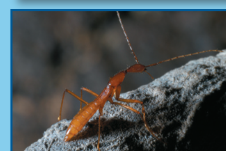




During the last few decades, a variety of studies dealing with terrestrial arthropods of Macaronesian islands reported valuable contributions to Science, emphasizing the unique value of these model systems for scientific research. The Macaronesian biodiversity has also been the subject of many activities aiming to raise the general public awareness for its outstanding value, and the need to address further efforts for its study and conservation.

This book aims to provide a synthesis of the recent developments made on the biology of Macaronesian terrestrial arthropods and to be a stimulus for further research in these islands. Through a series of essays it addresses various issues in the areas of island biodiversity, ecology and evolution and should be of interest for both students and researchers.





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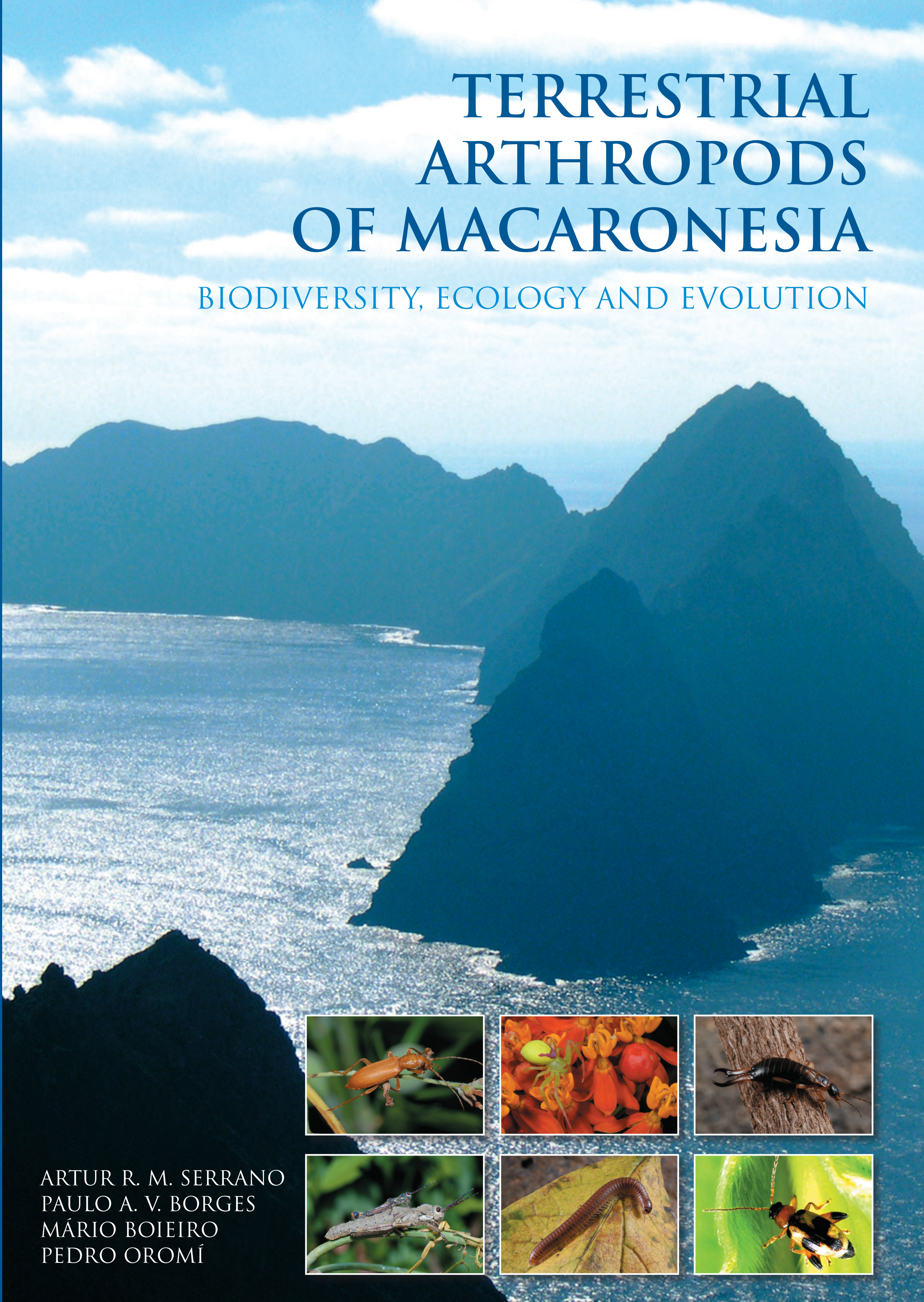

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Chapter 2

The provisional status of terrestrial arthropod inventories in the Macaronesian islands

Jorge M. Lobo & Paulo A. V. Borges

Introduction

The Macaronesian archipelagos of Cape Verde, Madeira, the Selvagens, the Canary Islands and the Azores are among the richest regions in fungi, plant and animal diversity, and these islands are part of the Mediterranean Hotspot (Myers *et al*., 2000). As a consequence of their isolation and geological history, these archipelagos harbour many endemic taxa (Fernández-Palacios & Whittaker, 2008; Borges & Hortal, 2009). Approximately 10 years ago, the Government of the Canary Islands started the BIOTA project with the goal of mapping the biodiversity of these Atlantic islands (see Izquierdo *et al.,* 2001). As a consequence of this important project, plant and animal species checklists are available for the Azores (Borges *et al*., 2005a), Madeira and the Selvagens (Borges *et al*., 2008), the Canary Islands (Izquierdo *et al*., 2001, 2004) and Cape Verde (Arechavaleta *et al*., 2005). These recent inventories now allow us to compare the biodiversity of the different archipelagos, but such comparisons require an assessment of the reliability of the data, principally when the data of hyper-diverse groups, such as arthropods, are examined. The current inventory of each archipelago depends on the "true" number of species inhabiting the islands, but also on the discovery process. This discovery process is a function of the strength of the taxonomical work that described and discovered the species. Unfortunately, the lack of taxonomic and biogeographical knowledge (the so-called 'Linnean' and 'Wallacean' shortfalls; Whittaker, *et al*., 2005), as well as the general lack of financial resources to efficiently study biodiversity (see Weeks & Gaston, 1997; Green, 1998), suggests that a great and still un-quantified proportion of Macaronesian diversity remains undescribed (Borges *et al*., 2005b). Moreover, taxonomic revisions and monographs are lacking for most of the Macaronesian taxa and the main question remains: "How many species are out there?" (see May, 1988).

We examined the available data on the most hyper-diverse group of terrestrial animals (the arthropods) with the aim to assess the general reliability of these Macaronesian inventories. First, we describe the main differences between archipelagos in the year of species description. These calculations allow us to compare the temporal pattern of the taxonomic process in the four archipelagos depending on the origin and range size of the species. Subsequently, we examine the shape and characteristics of discovery curves in order to obtain a provisional picture of the taxonomic completeness of current inventories and the amount of work that still needs to be completed. Lastly, we discuss the implications of our results on our current knowledge of Macaronesian arthropods for each archipelago.

Data analysis

The Macaronesian region is composed of four Atlantic archipelagos (the Azores, Madeira including the Selvagens, the Canary Islands and Cape Verde) that vary both in their isolation (approximately 100 km from the mainland in the Canaries to 1450 in the Azores) and latitudinal location (from 15ºN in Cape Verde to 40º N in the Azores). For each one of these archipelagos, we extracted the year of species/subspecies description for all arthropod taxa included in the recent catalogues of Izquierdo *et al*. (2004), Arechavaleta *et al*. (2005) and Borges *et al*. (2005a and 2008). The species included in these catalogues were grouped into three categories: endemic, native and exotic species. Endemic species are those described and only occurring in one of the four archipelagos. Native species would have arrived to each archipelago by long-distance dispersal (including dispersal by wind, water and animals) and are also present in other Macaronesian archipelagos and/or on the continents. Exotic species are those believed to have arrived to the archipelagos as a result of human activities. All unclassified species were assumed to be native.

The median year of species description for these three types of species was estimated for each archipelago and Kruskal-Wallis non-parametric tests were used to evaluate if there were differences between archipelagos and species categories. We estimated the rate of increase in the accumulated number of described species for each archipelago using simple linear regressions. We also examined the shape of the growth curve of the cumulative number of species as a function of the year of description (see Steyskal, 1965; Bebber *et al*., 2007 and references therein). We used the Species Accumulation Functions freeware (Díaz-Francés & Soberón, 2005) which generate improved model parameters by likelihood nonlinear regression functions. We used this software to compare the exponential and Clench functions (the two main species-accumulation functions) and estimations of an asymptotic value (Soberón & Llorente, 1993). The value of these asymptotes can be used to estimate the number of species still undescribed, although these values are based on a number of assumptions (Steyskal, 1965; Cabrero-Sañudo & Lobo, 2003). Unless a high proportion of the species have been already described, the asymptotic values should be used with caution in assessing the relative completeness of current species inventories (see Bebber *et al*., 2007). Because the year of the first citation for each species was not available, we used the year of species description to examine the temporal accumulation of species. In the case of endemic species, the collecting year may be considered equivalent to the year of species description. However, in the case of native and especially for exotic species, this temporal accumulation curve will almost always show a more asymptotic shape because any newly collected species would have been described many years ago. Thus, the addition of new native or exotic species will not change the last part of the asymptotic curve unless these species have been recently described. Hence, completeness values for exotic species, and partially for native ones, should be considered estimates of the recently described species that may remain to be discovered in the future on each archipelago. However, the estimates for endemic species can provide an idea of the amount of taxonomical work that still needs to be conducted for this hyper-diverse group. In the future, the addition of new taxonomical descriptions will permit the validation of the behaviour of these curves.

General differences in the year of species descriptions

Taking into account all the recognised arthropod species, the median year of species description significantly differs between the four considered archipelagos (Kruskal-Wallis median test, KW = 391.9, N = 13166, P<0.0001). Multiple post-hoc comparisons of mean ranks show that the year of species description (YSD) significantly differs between all pair-wise archipelagos (Table I). Thus, the species present in the Canary Islands were, in general, described more recently, while those occurring in the Azorean islands were described earlier. However, this pattern changed when the differences in YSD were analyzed according to the origin and range-size of species (endemic, native and exotic species).

Table I. Median year of species description in each Macaronesian archipelago for endemic, native, exotic or total arthropod species. The years between the brackets are the upper and lower quartiles, while the inferior rows represent the number of species and their percentage of total species (in brackets). Median years of each archipelago with the same letter are not-statistically different (P<0.001) according to post-hoc comparisons of a Kruskal-Wallis median test.

	Endemic	Native	Exotic	Total
Azores	1979 (1940-1992)	1835 (1794-1857) [C]	1840 (1796-1875)[C, D]	1850 (1803-1914)
	267 (20%)	328 (24%)	746 (56%)	1341
Madeira-Selvagens	1938 (1858-1982)	1845 (1818-1895) [B]	1856 (1813-1895)[B, E, F]	1865 (1836-1938)
	979 (39%)	891 (35%)	643 (26%)	2513
Cape Verde	1958 (1898-1982) [A]	1870 (1837-1915)	1849 (1795-1888)[D, E, G]	1884 (1843-1952)
	476 (25%)	1302 (68%)	147 (8%)	1925
Canary Islands	1963 (1903-1987) [A]	1861 (1833-1910)	1856 (1803-1901)[F, G]	1899 (1847-1964)
	3079 (42%)	3744 (51%)	564 (8%)	7387

The YSD of endemic species was always more recent (Table I) than those of native and exotic species in all the archipelagos. However, these values varied greatly between the four archipelagos (KW = 105.8, N = 4801, P<0.0001), showing post-hoc statistically significant differences between all pair-wise comparisons except in the case of Cape Verde and the Canary Islands (Table I). On average, Azorean endemic species were described more recently than those of the other archipelagos, and Madeira endemics were described almost half a century earlier. The native species were also described after the exotic ones both in Cape Verde and in the Canary Islands, but interestingly, the YSD of native species did not significantly differ from exotic ones in the Azores and Madeira (see Table I). Again, the YSD of native species significantly differed between the archipelagos (KW = 209.1, N = 6265, P<0.0001) but in this case, all pair-wise post-hoc comparisons were statistically significant. The earliest native YSDs appeared in the northernmost archipelagos (first in the Azores and later in Madeira) and around thirty years later in the southern archipelagos (first in the Canary Islands and later in Cape Verde). The median YSD of exotic species also differed significantly between the archipelagos (KW = 31.7, N = 2100, P<0.0001), but the only two significant post-hoc differences were between the Azores and the Canary Islands and the Azores and Madeira; the median year of description of the exotic species was on average sixteen years earlier in the Azores.

Within archipelagos patterns in endemics

The YSD for endemic species showed a well-defined pattern both in the Canary and in Azorean islands. The only significant differences appeared between the western-most islands (El Hierro and Corvo, respectively) and the eastern-most (Fuerteventura-Lanzarote and São Miguel-Santa Maria, respectively; see Table II). Thus, in these archipelagos, the number of endemic arthropod species recently described was lower in the islands farthest from the continent compared to the nearest ones. In the Madeira archipelago, the mean date of species description was more recent in the greater island (Madeira) and even most recent in the isolated Selvagens (Table II). In the case of Cape Verde, there was not a clear geographic pattern, except that smaller islands did not seem to have recently described species.

Table II. Number of endemic arthropod species (S), mean, minimum and maximum year of species description (± 95% confidence interval) for each archipelago. Islands are ordered according to their mean year of species description.

	S	Mean ± CI 95%	Minimum	Maximum
Canary Islands				
El Hierro	532	1921 ± 5	1758	2006
La Palma	863	1927 ± 3	1758	2003
Gomera	860	1927 ± 3	1758	2003
Tenerife	1687	1932 ± 2	1758	2006
Gran Canaria	1117	1932 ± 3	1758	2007
Lanzarote	429	1934 ± 5	1832	2006
Fuerteventura	484	1935 ± 5	1802	2003
Azorean Islands				
Corvo	24	1929 ± 15	1859	1991
Graciosa	44	1944 ± 15	1833	2003
Flores	102	1947 ± 8	1833	2005
Faial	96	1949 ± 8	1833	2005
Pico	113	1950 ± 7	1833	2005
São Jorge	89	1951 ± 8	1833	2007
São Miguel	155	1952 ± 6	1822	2005
Terceira	136	1957 ± 7	1833	2006
Santa Maria	74	1958 ± 10	1833	2005

	S	Mean ± CI 95%	Minimum	Maximum
Madeira islands				
Porto Santo	153	1901 ± 7	1834	2004
Desertas	104	1904 ± 12	1775	2008
Madeira	827	1920 ± 15	1758	2008
Selvagens	44	1935 ± 17	1854	2008
Cape Verde				
Ilhéu Branco	5	1888 ± 87	1843	2002
Santa Luzia	17	1893 ± 18	1867	1984
Ilhéu Raso	4	1901 ± 87	1843	1955
São Vicente	128	1914 ± 9	1843	2002
Brava	68	1919 ± 11	1843	1989
Fogo	100	1922 ± 10	1850	2002
Santo Antão	174	1932 ± 7	1843	2002
Sal	72	1938 ± 11	1843	2002
Maio	39	1938 ± 15	1843	2002
São Nicolau	116	1938 ± 8	1843	2002
Boavista	62	1940 ± 12	1843	2002
Santiago	208	1941 ± 7	1845	1996

Temporal variation in species descriptions

The rate of species description per year varied between archipelagos according to the type of species (Table III). In the Canary Islands, this rate was almost four times higher than in the other archipelagos both for endemic and native species, but not in the case of exotic ones. The Canary Islands also showed the highest current rate of endemic species descriptions.

Interestingly, the overall rate was higher in Madeira than Azores and intermediate in Cape Verde (Table III). This same pattern also occurred during the last ten years (Table III). The rates of description of exotic species were always low, although in the Azorean archipelago the rate was higher than those for endemic or native species.

Table III. Coefficient value (*B*) of the simple linear regression between the accumulated number of species and the year of species description (± 95% confidence interval) and *t* value measuring the statistical significance of this slope for each archipelago and type of arthropod species. This coefficient represents the number of described species added per year. This value for the ten last years is in brackets. The Spearman rank correlation coefficient values (*rs*) between the year of species description and the number of islands in which the species are present was also included.

	endemic		**Native**		**exotic**	
	B	*t*	*B*	*T*	*B*	*t*
Canary Islands	15.6 ± 2.4 (18.3)	13.41***	17.9 ± 0.4 (3.4)	47.75***	2.5 ± 0.1 (0.8)	49.08***
	rs = -0.42, *P*<0.0001		*rs* = -0.32, *P*<0.0001		*rs* = -0.36, *P*<0.0001	
Azorean Islands	1.6 ± 0.2 (2.6)	18.94***	1.6 ± 0.1 (0.1)	36.96***	3.5 ± 0.1 (0.3)	54.65***
	rs = -0.24, *P*<0.001		*rs* = -0.15, *P*<0.01		*rs* = 0.02 *P*= ns	
Madeira islands	4.3 ± 0.2 (9.9)	42.55***	4.1 ± 0.1 (0.9)	59.98***	3.0 ± 0.1 (0.3)	72.26***
	rs = -0.18, *P*<0.01		*rs* = -0.17, *P*<0.01		*rs* = -0.14, *P*<0.01	
Cape Verde	2.9 ± 0.1 (5.5)	21.36***	6.3 ± 0.1 (0.3)	110.56***	0.8 ± 0.01 (0)	62.55***
	rs = -0.26 *P*<0.0001		*rs* = -0.22, *P*<0.0001		*rs* = -0.22, *P*<0.01	

The variation in the rates of species description over time (Figure 1) allowed us to visualise the previously mentioned patterns. The shapes of the accumulation curves together with the estimated total number of species (TNS) showed that an asymptotic trend was hardly reached, such that estimates are inflated. Further taxonomical work in the Canary Islands may considerably increase the number of endemic species, and there may be almost double the number of native species. Both in the Azores and in Madeira, current figures of endemics are far below the "real" species numbers, and additional taxonomical effort is necessary to provide a reliable estimation of arthropod biodiversity. This situation is not so dramatic for the native species: the current number of described species oscillated between 30% (in the Azores) to 80% (in Madeira). The current number of endemic species documented in Cape Verde could be half the total number of extant endemics. In general, this archipelago had the highest completeness values for all considered species groups. Species with larger distributions in the archipelagos (measured by the number of islands inhabited) had earlier years of description, except in the case of exotic Azorean species (Table III).

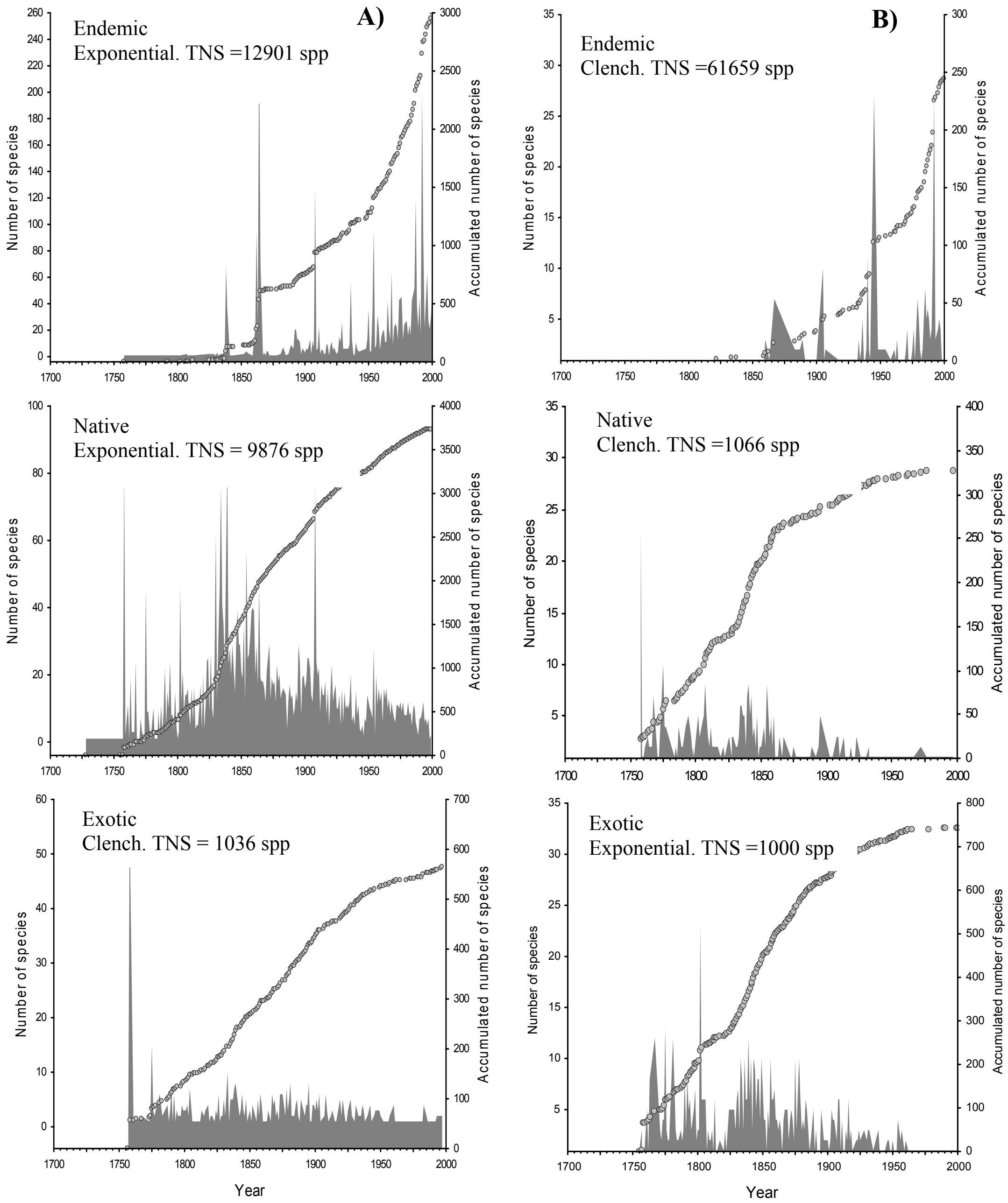

Figure 1 (cont.). Number of described of endemic, native or exotic species (grey areas) and variation in their accumulated number (circles) according to the year in which they were described for the Canary Islands (A) and the Azores (B). The accumulated curves were adjusted to logarithmic or Clench functions to estimate the asymptotic value or total number of species (TNS).

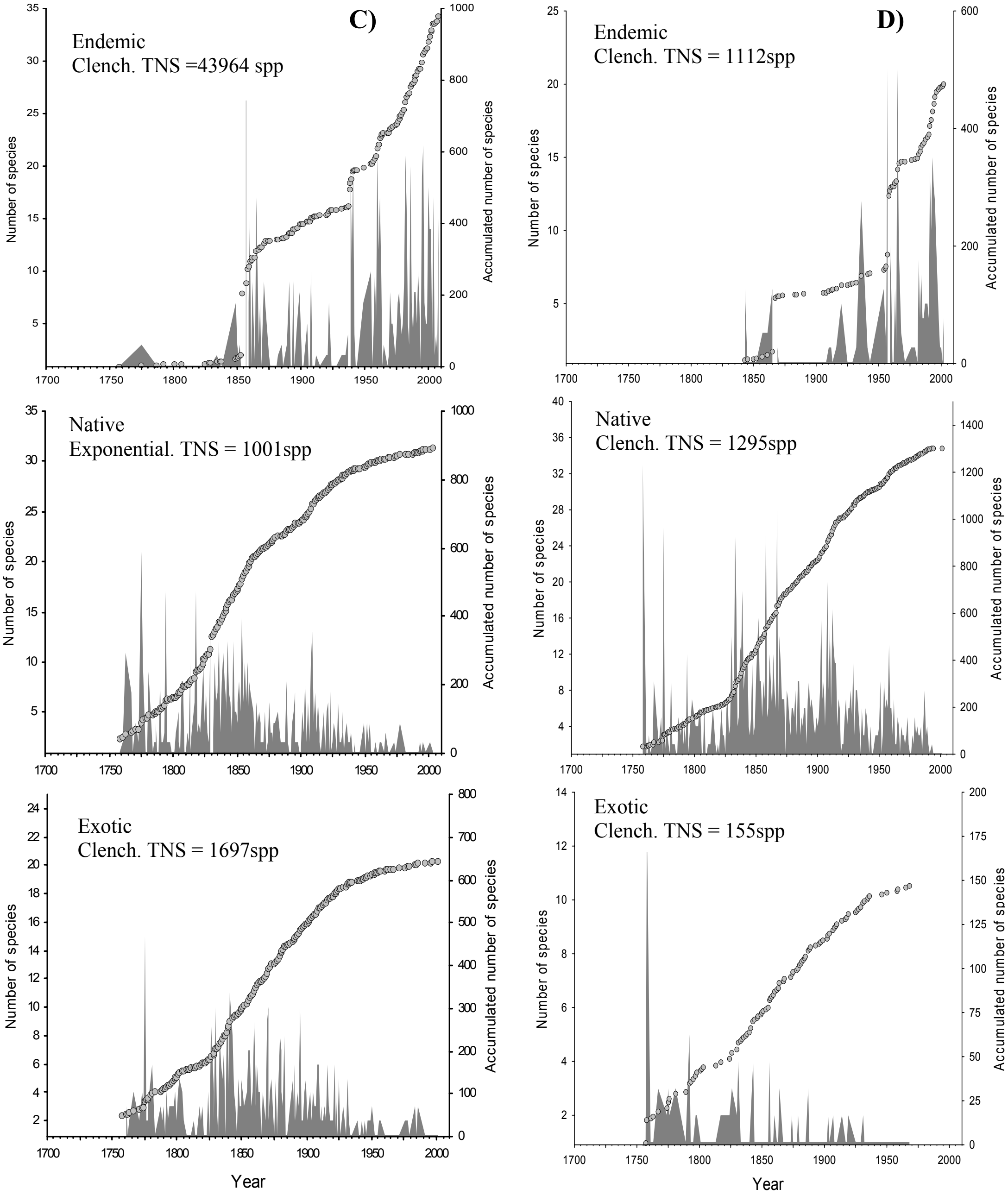

Figure 1 (cont.). Number of described of endemic, native or exotic species (grey areas) and variation in their accumulated number (circles) according to the year in which they were described for the Madeira-Selvagens (C) and Cape Verde (D). The accumulated curves were adjusted to logarithmic or Clench functions to estimate the asymptotic value or total number of species (TNS).

Discussion

Despite long-standing interest in documenting global biodiversity (e.g. May, 1988; Odegaard, 2000), the terrestrial diversity of Macaronesian archipelagos has only recently been catalogued (Izquierdo *et al*., 2001, 2004; Arechavaleta *et al*., 2005; Borges *et al*., 2005a, 2008). These checklists have confirmed the high biodiversity of these archipelagos and the large number of endemic species. However, our results indicate that current taxonomical knowledge is far from complete, and that many species of terrestrial arthropods may be discovered in the near future. We also showed that species catalogues can be used to depict the temporal evolution of taxonomical knowledge and that a careful examination of the structure of this information reveals interesting patterns.

In general, the averaged delay in the description of the exclusive and characteristic species of these archipelagos was around of 75 years with regard to native or exotic faunas. This pattern indicates that the taxonomic effort spent in these Macaronesian archipelagos at the early stages of taxonomic work was lower than in continental areas. Apparently, the rate of description of endemic species has increased in recent times, but according to the non-asymptotic shape of the species accumulation curves, this effort has been insufficient. Although uncertain and imprecise (Bebber *et al*., 2007), the estimates provided by these curves suggest that a huge number of species still remain undescribed, especially in the northernmost archipelagos (the Azores and Madeira), but also in the Canary Islands and Cape Verde where the “real” number of arthropod species could be double or quadruple the number currently documented. In a previous study, Borges *et al*. (2005b) suggested that the documented number of endemic arthropods in the Azores was probably a poor estimate of the true number. This underestimation is particularly critical to biodiversity conservation because many native habitats are threatened by human activities, and unknown species could potentially disappear before being discovered. Thus, our results suggest that a lot of taxonomical work is still needed to fully document arthropod diversity and that the current effort is clearly insufficient. For example, most of the cave-adapted fauna in the Macaronesian islands were only described in the last 30 years through the efforts of specialised fieldwork in the subterranean environment. In addition, many new Azorean spiders were found in the canopy habitat after employing a standardised sampling of this particular habitat (see Ribeiro *et al*., 2005; Borges & Wunderlich, 2008). We suspect that additional surveys directed at the canopies of endemic trees in Madeira and the Canary Islands will produce the discovery of many new arthropod species. From a management point of view, our lack of reliable information both on the taxonomic composition and geographical distributions of Macaronesian arthropods creates the need to establish conservation designs devoted to protect the undescribed invertebrate species. Increasing the amount of protected areas, establishing micro-reserves, protecting microhabitat characteristics, controlling invaders and regulating the use of chemical compounds in agriculture and cattle farming practices may be fundamental strategies to enhance the protection of Macaronesian biodiversity.

Borges & Wunderlich (2008) recently demonstrated that the newly described Azorean endemic spider species have very restricted ranges, where they occur only in particular micro-habitats in isolated fragments of native habitats. Our results corroborate this pattern because those species restricted to one or a few islands are generally described later (see Gaston 1994; Gaston *et al*., 1995), suggesting that a large part of the undiscovered endemic and native species probably inhabit highly isolated conditions. Interestingly, the only non-significant correlation between the year of species description and the number of islands inhabited was in the case of Azorean exotic species, which was probably a consequence of the recent inclusion of these species in the archipelago inventories and their relatively modern description in the continent. Exotic species were described on specimens collected outside the considered archipelagos, and the addition of these species may be due to their recent description in another region and the subsequent collection in the archipelago or, alternatively, by the synonymisation of formerly endemic or native Macaronesian described species. This synonymisation may be more frequent with future taxonomic revisions.

In spite of these general patterns, each Macaronesian archipelago seems to have followed a distinctive pattern in species description. These differences may due to changes in the available taxonomical resources over time, differences in isolation, diversity, and endemicity or the interest of foreign taxonomists. In the case of the Azores, exploration in the islands began in 1850, but the taxonomic knowledge of the arthropod fauna is characterised by the recent description of endemic species. Almost a third of the total number of endemic species were described after 1990, probably due to the low diversity, inconspicuous fauna and the difficult access to some isolated native forest fragments. In fact, arthropods from the Azorean islands were mostly disregarded until late in the last century, which may have been due to the recent interest in the Azorean fauna by foreign entomologists and, to a greater extent, the collaborative work conducted through the efforts of the University of the Azores. Moreover, since 1999, a considerable effort has been made to study arthropod diversity and distribution across Azorean native forests (Borges *et al*., 2005c; Ribeiro *et al*., 2005), generating many new taxa. However, both current and total rates of species description are the lowest of all archipelagos, indicating that the recent process of description of the most singular Azorean species is far from being enough (see e.g. Borges *et al*., 2005b; Borges & Wunderlich, 2008). The most important case of a 'Linnean' shortfall in the Azores is the inventory of Hymenoptera, for which there are more unnamed "morphospecies" recently catalogue in biodiversity studies (see e.g. Santos *et al*., 2005) than species listed in the 2005 catalogue of species (see also Borges *et al.*, 2005b). Interestingly, the description rate of native species was also the lowest of all archipelagos, while the description rate of exotic species was the greatest. This result corresponds to the high effort devoted to inventory the invader species on the Azorean archipelago. Future taxonomical effort should also be directed towards the approximately two thirds of the Azorean native arthropod species that still remain undiscovered for this archipelago (particularly in Collembola, Diptera and Hymenoptera; see Borges *et al.*, 2005b), and species described in a particular inventory many years ago probably have higher ecological tolerances and wider range sizes. Azorean exotic species also had earlier description dates, but their rate of description was comparatively high. This rate may be related to the high proportion of exotics inventoried on this archipelago that come from mainland territories and have been well known for a long time. Because exotic species are generally described earlier (Gaston, 1994), the overall early dates of description of the Azorean arthropods were probably a result of the archipelago harbouring the highest number and percentage of exotic species (see Borges *et al*., 2005b). The introduction of many of these exotic species is related to the fact that the Azores was a strategic passage for all boats coming from the Americas to Europe and vice-versa. Additionally, the Portuguese brought plants from all over the world to their private gardens, particularly in the most populated islands (S. Miguel, Terceira and Faial).

In the other northern archipelagos (Madeira and the Selvagens), the average year of description of endemic species was almost forty years earlier than in the Azores, while exotic and native species were described a little more recently. Between 1854 and 1871, Thomas Vernon Wollaston published a major landmark study of the arthropods from Madeira and the Selvagens (Machado, 2006). In spite of the notable current increase in the rate of species descriptions, the accumulation curves also indicate that a high proportion of the endemic species remain undiscovered. Thus, taxonomical work in Madeira needs to increase in order to recognise and describe their high biodiversity, and these efforts should take advantage of Madeira's long tradition of taxonomical studies. A key factor for improving the knowledge of arthropod inventories in the Azores and Madeira may be a diversification in the taxonomical and habitat scope of future studies. For example, taxonomists seem to have devoted a high effort to the description and collection of Azorean Acari species but a low effort to Hymenoptera (Fig. 2) (see also Borges *et al*., 2005b). Together, these two archipelagos have not described a single species in one fourth of the arthropod families recognised in the best-studied archipelago (the Canary Islands).

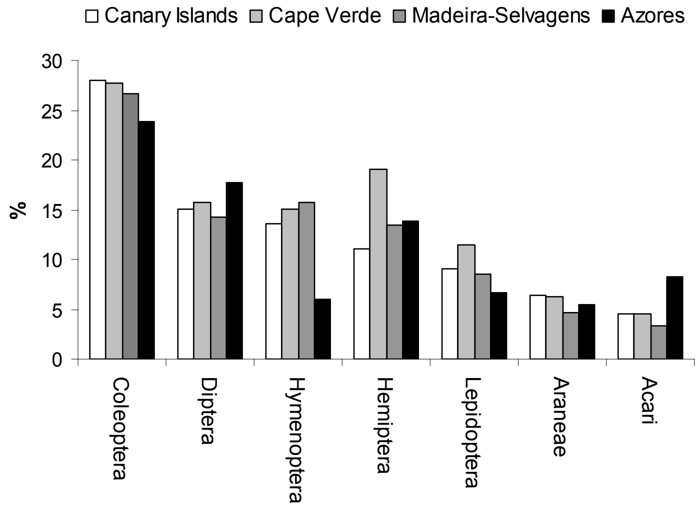

Figure 2. Percentage of species of the most hyper-diverse groups according to the total number of arthropod species inventoried in each of the Macaronesian archipelagos.

The results indicate that in Cape Verde, the current number of described endemic species is approximately one half the total number of arthropod species probably present in this archipelago. The observed number of arthropod species and the current rate of endemic species description were similar but intermediate compared with the Azores and Madeira (Tables I and III). However, our results suggest that the number of undescribed endemic species is not as large as in the other Macaronesian archipelagos, and that overall arthropod species richness of this archipelago could be lower. Future taxonomical effort should be directed toward Coleoptera and Diptera (see Figure 2). The discovery curves for native and exotic species showed an almost asymptotic shape. As the addition of new native or exotic species would not change this asymptotic tendency unless they were recently described, this ceiling could be due to the lack of recently described species in the catalogue. The median year of species description of the Cape Verde exotic species was not significantly different from other archipelagos (Table I). Consequently, we suggest that most of the undiscovered native and exotic species were probably described many years ago in the mainland or other regions.

The Canary Islands have the highest number of arthropod species and the highest proportion of endemic species. In this case, the taxonomic work seems to be characterised by the comparatively recent description of the three types of species considered, in spite of being an archipelago with a long tradition of taxonomical studies. Certainly, the favourable climatic conditions of these islands as well as their proximity to Europe have been decisive factors for their taxonomical attractiveness. However, although both total and current rates of endemic and native species descriptions are the highest, our results suggest that only a fourth of the total endemics and a third of the native species would have been described.

In spite of the known difficulties with extrapolation methods, our results clearly show that it is highly probable that many new species of arthropods will continue to be discovered in all the Macaronesian archipelagos. In practice, this will occur from i) detailed revisions of previously lumped taxa; ii) standardised sampling of unexplored habitats and/or regions; and iii) investment in the sampling of and taxonomic work on understudied taxa (e.g. Collembola, Acari, Diptera, Hymenoptera).

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