Updated estimates of biotic diversity and endemism for Madagascar—revisited after 20 years

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Abstract The terrestrial and marine biotypes of Madagascar are critical priorities for conservation, with almost unparalleled levels of endemism, species diversity and human threat for a land area of its size. Field inventories and molecular-based research conducted from the mid 1980s to present have greatly expanded knowledge of the country's biota, for some groups with nearly exponential growth in measures of species diversity. I provide updated measures of estimated species diversity between a book with 289 contributors, published in 2003 (*The Natural History of Madagascar*), and a full-scale update with 539 contributors, published in 2022 (*The New Natural History of Madagascar*). I compare biodiversity information presented in the new book with data from the earlier book, providing insight into scientific advancements, and revised estimates of species richness and endemism of a range of taxonomic groups.

Keywords Biodiversity, conservation priorities, endemicity, Madagascar, marine, measures of species richness, terrestrial

Measures of species diversity and levels of endemism are important components in determining conservation priorities. In numerous countries, islands and biomes, biological exploration has advanced considerably since 1980 and ongoing field inventories, combined with systematic studies using classical techniques and more modern molecular biology, are modifying previous estimates of biotic diversity, such as those concerning endemism and species richness. With almost unparalleled levels of endemism, species diversity and human threat, Madagascar is one of the most critical global priorities for conservation, and has been designated one of the most important biodiversity hotspots (Myers et al., 2000; Groombridge & Jenkins, 2002). This island nation, with a surface area of 594,150 km², retains, depending on definitions and analyses, between 15% and < 10% of the natural forests that existed before human colonization (Vieilledent et al., 2018; Global Forest Watch, 2022), estimated by some scholars to have been > 10,000 years ago (Hansford et al., 2018; Godfrey & Douglass, 2022). Of particular importance associated with conserving the forest-dwelling biota of Madagascar is that the annual deforestation rate during 2010–2014 was nearly 100,000 ha/year, and nearly half of the remaining forest area is located < 100 m from the forest edge (Vieilledent et al., 2018).

Since the 1980s, considerable advances have been made in biological research on Madagascar, including the exploration of scientifically unknown or poorly known areas, and subsequent studies of associated specimens. As previously summarized by Goodman & Benstead (2005) based on *The Natural History of Madagascar* (Goodman & Benstead, 2003), for a country such as Madagascar, with its considerable and poorly documented levels of biotic diversity and endemism, the measures used in biodiversity analyses are in constant need of revision. However, given the remarkable number of new species being described across a wide variety of taxonomic groups and considerable changes in geographical distribution, it is difficult for any single research team to maintain up-to-date data for the island. The recalculation of these values depends on the hundreds of specialists working on the island's biota. The recent publication of *The New Natural History of Madagascar* (Goodman, 2022), a synthesis by 539 contributors from a range of disciplines, provides the means to update these estimates. Here, I give revised data for species richness and endemism of a wide variety of marine and terrestrial taxonomic groups on Madagascar (Table 1; comparisons between the 2003 and 2022 books are only for groups treated in both volumes).

For many marine organisms occurring within Malagasy waters, with a few exceptions, the current state of knowledge is still insufficient to estimate species richness. There appear, however, to be few local marine endemics, although at a regional level (western Indian Ocean) the numbers are higher. Earlier assessments of the vascular plant diversity suggested 10,000–12,000 species (Koechlin et al., 1974; Phillipson, 1994; Schatz et al., 1996), with rates of endemism of c. 85%. A more recent estimate is 14,000 species and endemism of nearly 87% (Lowry et al., 2018), with even higher endemism amongst trees and large shrubs. On the basis of the nine plant families covered in both books (Table 1), the level of endemism in 2003 for these groups was 92%, and 90% in 2022. For these nine families, 677 species new to science have been described, with 573 endemic. For the 21 non-marine invertebrate groups covered in both books,

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TABLE 1 Estimates of species richness and endemism (where available) of Malagasy plants and animals over the course of nearly 2 decades. The 2003 data are from *The Natural History of Madagascar* (Goodman & Benstead, 2003), and those of 2022 from *The New Natural History of Madagascar* (Goodman, 2022), and sources (author names and associated page numbers) within each of these volumes are given. Species tallies from 2022 that are preceded by an asterisk (*) include confirmed candidate species. In most cases the 2022 data were tabulated in 2020 or the first half of 2021 and for certain groups there has been the subsequent description of new species, the majority being endemics.

	2003		2022		
Taxonomic group	Reference	Number of species/ endemics (% endemism)	Reference	Number of species/ endemics (% endemism)	Changes in number of species/endemics between 2003 & 2022
Marine					
Fishes (including elasmobranchs)	Cooke et al., p. 179	c. 1,110	Cooke et al., p. 311	1,708	+c. 598
Porifera (sponges)	Cooke et al., p. 179	> 300	A. Cooke, unpubl. data	318	+18
Cnidaria (corals & anemones)	Cooke et al., p. 179	> 400	A. Cooke, unpubl. data	> 650	+> 250
Octocorallians (soft corals, sea fans, etc.)	Cooke et al., p. 179	222	A. Cooke, unpubl. data	222	0
Hexacorallians (hard corals)	Cooke et al., p. 179	208	Cooke et al., p. 311	400–450	+192–242
Mollusca (molluscs)	Cooke et al., p. 179	c. 1,500	A. Cooke, unpubl. data	> 1,712	+c. 212
Crustacea (crustaceans)	Cooke et al., p. 179	c. 800	A. Cooke, unpubl. data	835	+35
Marine algae	Cooke et al., p. 179	c. 200	Cooke et al., p. 311	c. 500	+c. 300
Chelonidae (sea turtles)	Ratsimbazafy, p. 210	5	Walker et al., p. 391	5	0
Cetacea (whales & dolphins)	Rosenbaum, p. 213	25 (12 confirmed, 13 suspected)	Cerchio et al., p. 411	26 (all confirmed)	+1
Sirenia (dugongs)	Rosenbaum, p. 213	1	Davis et al., p. 400	1	0
Non-marine plants					
Aquatic plants	Andrianasetra Ranarijaona, p. 250	338/128 (38)	Manjato et al., p. 470	489/240 (49)	+151/+112
Moraceae (*Ficus*)	Dalecky et al., p. 322	25/15 (60)	Rasplus et al., p. 617	24/15 (63)	−1/0
Bombaceae *(Adansonia)*	Baum, p. 339	7/6 (86)	Karimi et al., p. 706	7/6 (86)	0/0
Sapotaceae	Gautier, p. 342	84/81 (96)	Gautier et al., p. 726	*125/122 (98)	+41/+41
Leguminosae	Labat & Moat, p. 346	573/459 (80)	Phillipson et al., p. 598	668/455 (77)	+95/−4
Melastomataceae	Almeda, p. 375	321/318 (99)	Almeda et al., p. 668	346/342 (99)	+25/+24
Euphorbiaceae	Hoffman & McPherson, p. 379	c. 700 (mostly endemic)	New circumscription & not comparable		
Anacardiaceae	Randrianasolo, p. 398	41/38 (93)	Randrianasolo, p. 681	75/68 (91)	+34/+30
Rubiaceae	Davis & Bridson, p. 431	c. 650/637 (98)	Razafimandimbison et al., p. 744	*1,010 (c. 99)	+360
Arecaceae (palms)	Dransfield & Beentje, p. 448	170/167 (98)	Rakotoarinivo et al., p. 567	208/204 (98)	+38/+37
Pandanaceae (*Pandanus*)	Callmander & Laivao, p. 460	99/99 (100)	Callmander et al., p. 551	84/84 (100)	−15/−15
Poaceae, Bambuseae (bamboos)	Dransfield, p. 467	34/34 (100)	Vorontsova et al., p. 585[1]	38/37 (97)	+4/+3
Non-marine invertebrates					
Gastropoda (terrestrial snails)	Pearce, p. 529	671/671 (100)	Griffith & Herbert, p. 860	*1,123/1,089 (97)	+452/+418
Scorpiones (scorpions)	Lourenço, p. 575	41/40 (98)	Lourenço et al., p. 873	101/100 (99)	+60/+60
Araneae (spiders)	Griswold, p. 579	459/390 (85)	Wood & Griswold, p. 878	771/678 (88)	+312/+288
Ixodida (ticks)	Klompen, p. 588	27/25 (93)	Klompen & Apanaskevich, p. 894	*51/46 (90)	+24/+21
Atyidae (freshwater shrimps)	Short & Doumenq, p. 603	27/20 (75)	Short, p. 899	31/24 (77)	+4/+4

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Table 1 (*Cont.*)

Taxonomic group	2003 Reference	2003 Number of species/ endemics (% endemism)	2022 Reference	2022 Number of species/ endemics (% endemism)	Changes in number of species/endemics between 2003 & 2022
Palaemonidae (freshwater shrimps)	Short & Doumenq, p. 603	13/5 (39)	Short, p. 899	15/4 (27)	+2/−1
Parasitacidae (freshwater crayfish)	Crandall, p. 608	6/6 (100)	Crandall et al., p. 908	7/7 (100)	+1/+1
Potamonautidae (freshwater crabs)	Cumberlidge & v. Sternberg, p. 612	12/12 (100)	Cumberlidge, p. 913	18/18 (100)	+6/+6
Diplopoda (millipedes)	Enghoff, p. 617	160/123 (77)	Wesener & Enghoff, p. 918	266/227 (85)	+106/+104
Collembola (springtails)	Betsch, p. 627	69/64 (93)	Cipola et al., p. 934	*109/76 (70)	+40/+12
Ephemeroptera (mayflies)	Elouard et al., p. 639	> 100/100 (c. 100)	Elouard et al., p. 947	c. *130/130 (100)	+30/+30
Odonata (dragonflies & damselflies)	Donnelly & Parr, p. 645	181/132 (73)	Dijkstra, p. 953	c. *200/186 (93)	+19/+54
Cincindelidae (tiger beetles)	Cassola, p. 669	203/201 (99)	Moravec, p. 1014	233/231 (99)	+30/+30
Scarabaeidae, Melolonthinae, Eneriini (scarab beetles)	Andriamampianina, p. 677	148/148 (100)	Lacroix & Andriamampianina, p. 1051	148/148 (100)	0/0
Siphonoptera (fleas)	Duchemin et al., p. 687	24/21 (88)	Duchemin et al., p. 1074	49/42 (86)	+25/+21
Culicidae (mosquitoes)	Duchemin et al., p. 708	178/80 (45)	Robert et al., p. 1089	237/140 (59)	+59/+60
Tabanidae (horse flies)	Chainey, p. 721	75/71 (95)	Zeegers, p. 1101	*105/101 (96)	+30/+30
Trichoptera (caddisflies)	Gibon, p. 740	c. 500/c. 495 (c. 99)	Gibon, p. 1135	c. 700/c. 672 (96)	+200/+177
Lepidoptera (butterflies & moths)	Lees & Minet, p. 748	4,530	Lees & Minet, p. 1141	*5,016/4,514 (90)	+486
Formicidae (ants)	Fisher, p. 811	393/379 (96)	Fisher, p. 1173	*1,252/c. 1,179 (94)	+859/+800
Freshwater fishes	Sparks & Stiassny, p. 849	143/93 (65)	Sparks & Stiassny, p. 1245	*178/122 (69)	+35/+29
Land vertebrates					
Amphibia (frogs)	Glaw & Vences, p. 883	199/197 (99)	Glaw et al., p. 1305	*365/363 (99)	+166/+166
Reptiles (snakes & lizards)	Raxworthy, p. 934	340/314 (92)	Glaw et al., p. 1423	*436/417 (96)	+96/+103
Birds (breeding)	Hawkins & Goodman, p. 1019	209/109 (52)	Safford et al., p. 1553	210/110 (52)	+1/+1
Mammals (native non-volant)	Goodman et al., p. 1181	101/101 (100)	Goodman & Soarimalala, p. 1737	174/174 (100)	+73/+73
Mammals (bats)	Eger & Mitchell, p. 1287	30/18 (60)	Goodman et al., p. 1894	46/36 (78)	+16/+18

[1]Concerns bamboos in the Bambusoideae.

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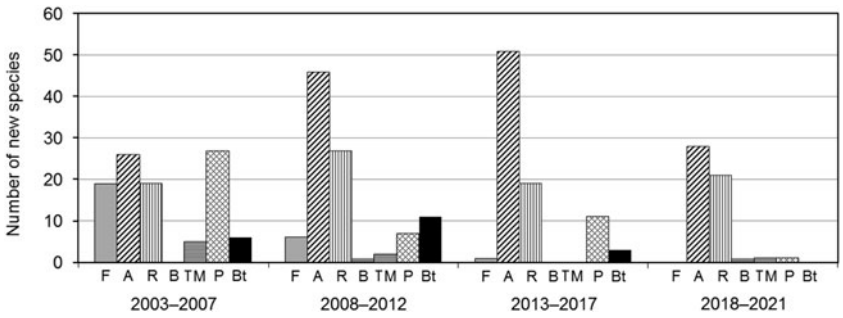

FIG. 1 The number of endemic non-marine vertebrate species described as new to science between 2003 and 2021, in 5-year intervals (4 years for 2018–2021). The levels of endemism for each group and associated acronyms are: F, freshwater fishes (69%); A, amphibians (99%); R, reptiles (95%); B, birds (52%); TM, non-primate terrestrial mammals (100%); P, primates (100%); Bt, bats (78%). Confirmed candidate species are not included in these calculations.

endemism in 2003 (slightly > 5,800 species) was 86% and in 2022 (slightly < 10,570 species) it was 91%. For virtually all groups covered in both books, there were notable increases in species diversity, but these were most dramatic in ants, with an additional 859 species (93% endemics), and in terrestrial snails, with 452 new species (93% endemics). With these increases in species diversity, as well as in other invertebrate groups such as spiders, millipedes and caddisflies, it is clear that large-scale inventories and subsequent systematic studies of the island's invertebrates (Fisher, 2022) are making important contributions to improving knowledge of these groups.

Madagascar's vertebrate fauna has received considerable attention from field biologists, taxonomists and the conservation community. The data from the 2003 book included 879 land vertebrates, with 739 (84%) endemic. In the 2022 book, the total is 1,234, of which 1,100 (89%) are endemic; when breeding birds (52% endemic) are excluded from these comparisons, rates of endemism rise to 97%. A total of 339 new species of endemic Malagasy land vertebrates were described as new to science between 2003 and 2022 (Fig. 1). For terrestrial vertebrates, rates of endemism are 95–100%, and those for flying vertebrates (bats and birds) are 52–78%.

Since 2003, there has been a dramatic increase in the number of Malagasy researchers undertaking field studies and students presenting higher degrees in the national university system in fields related to conservation biology. For example, in the botany chapter of the 2003 book, the number of contributions with Malagasy authors was 6 of 45 (13%), with a total of 15 Malagasy co-authors; in the 2022 book, these figures are, respectively, 20 of 45 (40%) and 47 Malagasy co-authors (Gautier et al., 2022). The same pattern occurs in the mammal chapters, with < 12% of the contributors being Malagasy in the 2003 book, and 45% in the 2022 book (Goodman & Soarimalala, 2022).

The data presented here further highlight Madagascar as a critical component of our global biological heritage. An overwhelming majority of the island's terrestrial species occur in the original and widely differing forest formations. These forests are shrinking at an alarming rate (Vieilledent et al., 2018; Global Forest Watch, 2022) and are clearly in need of conservation action, which needs a multifaceted approach to be effective (Jones et al., 2022). Major advances in the park and reserve system have been made over the past 2 decades, which in 2003 included 46 legally protected areas, comprising c. 17,000 km² or 3% of the island's land area (Randrianandianina et al., 2003). By 2018 the number of protected areas increased to 122, comprising nearly 12% of the island (Ranivo Rakotoson & Razafimahatratra, 2018). Although it is important not to disregard various historical and modern problems in the maintenance of the unique biodiversity of Madagascar represented in these protected areas (Gardner et al., 2018; Jones et al., 2022), remarkable progress has been made over the past 2 decades in the network of marine and terrestrial sites.

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