



# A herpetofauna with dramatic endemism signals an overlooked biodiversity hotspot

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## Abstract

The Milne Bay Region of southeasternmost Papua New Guinea comprises a small portion of mainland New Guinea and several offshore islands, totaling 15,000 km<sup>2</sup> in land area. I numerically summarize the literature and findings from my field surveys of the region's herpetofauna and show that it contains the greatest known assemblage of range-restricted endemic herpetofauna globally for such a small area. Further, most of these species occupy only one or two of 11 small areas of local endemism within the region. I compare the number and density of endemic herpetofauna in the Milne Bay Region to other regions of notable endemic biodiversity and find it to be far larger than that in the large majority of these other "hotspots", despite the much larger sizes of those areas. Herpetofaunal surveys within the Milne Bay Region are more complete than for other taxa, but it is clear that this region holds a large trove of range-restricted endemic species within less well-studied groups too. The driver of this endemic diversity is the ongoing geological dismemberment and uplift of the region resulting from the opening of the Woodlark Rift. Prior ignorance of the biodiversity importance of this region stems from decades of classifying New Guinea as a "tropical wilderness area", which has deprived that region of the conservation focus accorded the more famous "hotspots". One effect of this is that some of the areas of local endemism identified here are under immediate pressure for habitat conversion, especially Woodlark Island, which is threatened by both mining and virtually complete conversion to oil palm, posing a high extinction risk for scores of endemic species.

**Keywords** Amphibians · Milne Bay · Papua New Guinea · Priority-setting · Reptiles · Woodlark Rift

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## Introduction

Biological diversity is not evenly distributed in space, with a minority of the planet's terrestrial surface holding a majority of its species (e.g., Myers 1988; Mittermeier et al. 2004; Lamoreaux et al. 2006). Differing classification systems have been used to identify and highlight these denser regions of "irreplaceability", including biodiversity hotspot regions, endemic bird areas, global 200 ecoregions, crisis ecoregions, key biodiversity areas, and Last of the Wild regions (Olson and Dinerstein 1998; Stattersfield et al. 1998; Myers et al. 2000; Eken et al. 2004; Mittermeier et al. 2004; Hoekstra et al. 2005). Conservation priorities are often based on these regions (Brooks et al. 2006; Grenyer et al. 2006; Wilson et al. 2006), but these classification schemes work at vastly different spatial scales. Furthermore, several rely on distributions of species richness, but richness measures alone are insufficient for preserving the world's biodiversity (Myers 1988; Veach et al. 2017; Shrestha et al. 2019). Hence, considerable attention has also been placed on identifying areas of concentrated endemism having many species unique to a particular region. Because all species are endemic at some level—if only at the level of planet Earth—the term necessarily varies by reference to a specific geographic scale or an area with a unitary geological history. Importantly, at least in terrestrial vertebrates, high rates of endemism are not well correlated with overall species richness (Orme et al. 2005; Grenyer et al. 2006; Lamoreaux et al. 2006), endemism in other classes (Leroux and Schmiegelow 2007), nor threat level (Orme et al. 2005), and, unsurprisingly, congruence is less as spatial scales become finer (Grenyer et al. 2006). Areas of endemism are hierarchically nested, so sizes of such defined areas will also vary, requiring that, for setting conservation priorities, the term must be referenced in some manner to geographical scale (Peterson and Watson 1998).

Despite these complications with identifying important areas of endemism for conservation purposes, there nonetheless remains the valid concern that species and communities with very restricted ranges be identified and made a focus of conservation efforts because of their irreplaceability (Brooks et al. 2006; Kier et al. 2009; Lamoreaux et al. 2006; Carrara et al. 2017; Veach et al. 2017). As a substitute for the scale-dependent term "endemic" it is sometimes more accurate to simply refer to such species as "range-restricted" species (Peterson and Watson 1998; Carrara et al. 2017; Veach et al. 2017; Shrestha et al. 2019). Even doing so, however, still leaves open the question of how restricted a range must be to warrant such a label, and the term is used with about as much areal elasticity as is "endemic", although some have advocated applying the term to species with range sizes of < 50,000 km<sup>2</sup> (Bibby et al. 1992), and this cut-off size has been used in identifying some conservation priority areas (e.g., Eken et al. 2004; Veach et al. 2017).

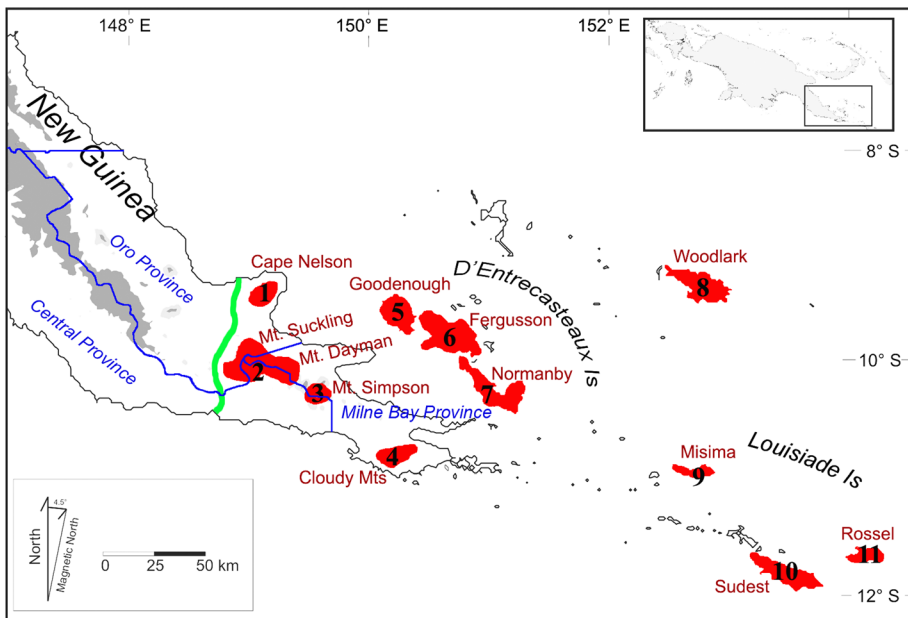
It is the focus of this report to bring attention to what is apparently the largest assemblage of range-restricted endemic reptiles and amphibians on the globe. The limited dispersal capabilities and narrow physiological tolerances of many reptile and amphibian species make them prone to having small ranges; hence, they are ideal candidates to use in identifying concentrations of range-restricted endemics. The hotspot (*sensu lato*) of herpetofaunal endemism identified here occurs in a small region that also holds large numbers of other endemic species, though diversity in those taxa is less well surveyed. Hence, the herpetofauna signals an area of dramatic endemic diversity, yet overall this biota remains poorly known, and the region has been virtually neglected for conservation purposes. It is to be hoped that recognition of the biodiversity values of this area will increase attention to its conservation importance and result in protective measures in this region, important portions of which are under immediate conservation threat.

Beyond the primary goal of highlighting the conservation value of this region, there is no comparative assessment of the relative density of range-restricted species in amphibians and reptiles at a global level. Identifying those areas most important for conservation of range-restricted reptiles and amphibians will remain largely an ad hoc affair until such time as comprehensive comparisons are made across regions. By comparing the focal region of this report to other biodiverse areas around the globe I also begin that larger effort here.

## Materials and methods

The region of concern—herein referred to as the Milne Bay Region—comprises a terrestrial area of 15,000 km<sup>2</sup> covering the southeasternmost tip of New Guinea and a number of immediately offshore islands, of which seven, ranging from 202 to 1437 km<sup>2</sup>, are large enough to host many endemic species. This region is here defined as that portion of New Guinea and associated islands east of the Musa Divide, a low-elevation break in the southern end of the Owen Stanley Mountains that serves as an important migration barrier for mid-elevation and upper-elevation species (Fig. 1). The majority of this region lies within Milne Bay Province, but small adjacent portions of Central Province and Oro Province are also involved (Fig. 1).

I summed numbers of endemic herpetofauna for the Milne Bay Region based primarily on my own field and taxonomic work in Papua New Guinea, involving 18 expeditions totaling 48 weeks of field surveys from 2002 to 2018, inclusive. I supplemented



**Fig. 1** Map of southeastern Papua New Guinea, showing the Milne Bay Region, here defined as everything mainland and insular east of the Musa Divide (green line) in the southern Owen Stanley Mountains. Areas of local endemism are shown in red, their numbers corresponding to the names in Table 1. Provinces are outlined in blue

that with literature information for eight species that I have not personally collected or studied and taxonomic conclusions of colleagues for nine taxa I have not personally investigated. Several of the narrowly endemic species used in this study remain to be described, although most already have been (Online Resource 1).

I used Google Earth to determine the approximate size of the mainland montane areas of endemism by drawing a polygon for each around the approximate lowest limit at which I have found endemic species characterizing each of those areas. Sizes of the islands came from the UN System-wide Earthwatch web site (<http://islands.unep.ch/Tiarea.htm>).

I quantitatively compared the diversity of range-restricted endemic herpetofauna in the Milne Bay Region to two sets of other, well-recognized regions of biological diversification: (1) 26 of Conservation International's (CI) "hotspots" (*sensu stricto*, meaning limited to areas having high plant endemism and high habitat loss), and (2) 14 insular areas (mostly offshore, but including one set of continental sky islands) known for their biodiversity. I ignored the remaining ten CI hotspots because they are both much larger (13–158 times larger) and more diverse areas that add nothing to the conclusions made here with the other 26 areas. I obtained numbers of endemic reptiles and amphibians for 24 of the original CI hotspots from Mittermeier et al. (2004) and for the Forests of East Australia and North American Coastal Plain hotspots (both added since Mittermeier et al. 2004) from Williams et al. (2011) and the Critical Ecosystems Partnership Fund (CEPF, <https://www.cepf.net/our-work/biodiversity-hotspots>), respectively. Information on species numbers provided in Mittermeier et al. (2004) is outdated: their reptile information came from data synthesized by Olson et al. (2001), published near the end of that year, and their amphibian information from the IUCN red-list assessments, which I assumed to be current through 2003. Hence, to update the numbers for the 24 original CI hotspots I added to each area the new species of endemic reptiles described from the years 2002–2019, inclusive, and the new species of endemic amphibians described from the years 2004–2019, inclusive. For the more recently added Forests of East Australia hotspot, I added data since August, 2006 (Williams et al. 2011). I took these data from Amphibian Species of the World (<https://amphibiansoftheworld.amnh.org/>), AmphibiaWeb (<https://amphibiaweb.org/>), and The Reptile Database (<http://www.reptile-database.org/>), and I summed total numbers of endemic reptiles and amphibians for each CI hotspot through the end of 2019. The sole exception was for New Zealand, for which van Winkel et al. (2018) is more accurate because it includes a large number of recognized but yet-undescribed species. For the second comparative set of 14 areas of insular endemism, I took numbers of endemic species from the published literature and again supplemented those numbers with data gleaned from Amphibian Species of the World, AmphibiaWeb, and The Reptile Database since the publication of those literature sources.

I took geographical sizes for the 24 original CI hotspots from Mittermeier et al. (2004), for the Forests of East Australia hotspot from Williams et al. (2011), for the North American Coastal Plain from the CEPF website, and for the 14 other regions from either the CIA World Factbook (<https://www.cia.gov/the-world-factbook/>) or the Wikipedia account for the region, with preference given to the former when data were available there. In Minitab 14, I compared numbers of endemic species between the Milne Bay Region and all these other biodiverse areas with least-squares regression analyses of species numbers vs. log-transformed areal extents so as to readily illustrate the degree to which numbers of endemic species in the Milne Bay Region diverge from trends across these other biodiverse regions. I contrasted densities of endemic species for each area by dividing numbers of endemic species in each area by that area's total land extent.

## Results

A total of 161 species of amphibians and reptiles is currently known to be endemic to the Milne Bay Region (Online Resource 1). Of these, 88 are frogs, 52 are lizards, and 21 are snakes. The large majority of these species (136 of 161) is found within one or more of eleven areas of local endemism within the broader Milne Bay Region (Table 1, Fig. 1). The remaining 25 species occur either in other limited areas not identified here as a major center of endemism (i.e., on one of three small islands) or occur more broadly within the region. Of these range-restricted endemics, 109 are confined to one or more of the islands of Milne Bay Province (Table 1, plus 8 species that don't fall in those categories). Considerable taxonomic activity on the species of the Milne Bay Region over the past 17 years has resulted in the description of 82 of these 161 species, but 53 of them remain to be scientifically described, although ten are under active research by me or others. In contrast to these 161 endemic species, only approximately 105 additional, non-endemic species comprise the remainder of the known herpetofauna of the Milne Bay Region. Hence, the endemic species form approximately 60% of the regional herpetofauna.

Of the eleven areas of local endemism, seven comprise the major offshore islands of Milne Bay Province. Four montane areas on the mainland complete this set. The areal extents of the seven islands are self-evident; those of the mainland areas are more approximate because the limits of those montane areas could be defined at different elevations. The eleven areas of local endemism that I identify comprise in total approximately 9603 km<sup>2</sup> (Table 1), which is 64% of the land area of the Milne Bay Region.

To put this concentration of range-restricted endemic herpetofauna in a global context, the numbers found in the Milne Bay Region are larger (and typically far larger) than the numbers of reptiles and amphibians endemic to 21 of the 26 Conservation International “hotspots” contrasted here (Table 2, Fig. 2a), even though these hotspots encompass much

**Table 1** Areas of local endemism within the Milne Bay Region and the numbers of range-restricted endemic amphibians and reptiles found in each

Area number	Area name	Area (km <sup>2</sup> )	No. endemic amphibians	No. endemic reptiles	Total
1	Cape Nelson	965	7	1	8
2	Mt. Suckling/Mt. Dayman	2200	12	2	16
3	Mt. Simpson	630	6	4	10
4	Cloudy Mountains	440	2	1	3
5	Goodenough	687	3	1	4
6	Fergusson	1437	2	2	4
7	Normanby	1040	3	4	7
8	Woodlark	874	7	7	14
9	Misima	202	4	8	12
10	Sudest	866	11	9	20
11	Rossel	262	7	13	20
5+6+7	D'Entrecasteaux Islands	3164	5	8	13
9+10+11	Louisiade Islands	1330	4	3	7
Total		9603	73	63	136

An additional 25 endemic species are not confined to these areas but range more widely across the region ( $n=21$ ) or are restricted ( $n=4$ ) to smaller islands

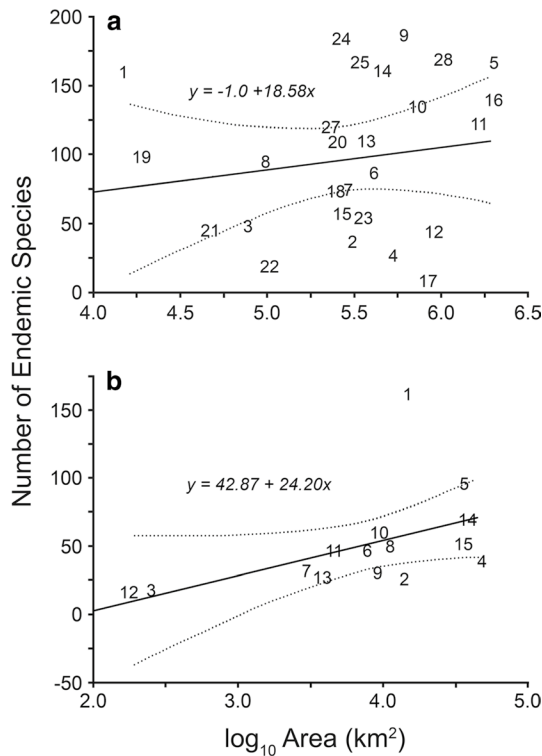
**Table 2** Land areas and numbers of endemic reptiles and amphibians in the 26 CI hotspots and 14 other insular areas with high biodiversity values that are herein compared to the Milne Bay Region

Location	Size (km <sup>2</sup> )	Number endemic amphibians	Number endemic reptiles	Total number endemics	Density of endemics (species/km <sup>2</sup> )	Sources
Milne Bay Region (total)	15,000	87	74	161	0.010733	Online Resource 1
<i>Conservation international hotspots</i>						
California Floristic Region	293,804	29	9	38	0.000129	CEPF, ASW, AW, RD
Cape Floristic Region	78,555	26	26	52	0.000662	CEPF, ASW, AW, RD
Caucasus	532,658	5	23	28	0.000053	CEPF, ASW, AW, RD
Cerrado	2,031,990	83	85	168	0.000083	CEPF, ASW, AW, RD
Chilean-Valdivian Forests	397,142	36	52	88	0.000222	CEPF, ASW, AW, RD
Coastal Forests East Africa	291,250	13	63	76	0.000261	CEPF, ASW, AW, RD
East Melanesian Islands	99,384	39	57	96	0.000966	CEPF, ASW, AW, RD
Forests of East Australia	253,200	44	78	122	0.000481	Williams et al. (2011), ASW, AW, RD
Guinean Forests West Africa	620,314	118	70	188	0.000303	CEPF, ASW, AW, RD
Himalayas	741,706	72	62	134	0.000181	CEPF, ASW, AW, RD
Horn of Africa	1,659,363	7	114	121	0.000073	CEPF, ASW, AW, RD
Irano-Anatolia	899,773	4	43	47	0.000052	CEPF, ASW, AW, RD
Japan	373,490	77	33	110	0.000295	CEPF, ASW, AW, RD
Madrean Pine-Oak Woodlands	461,265	86	75	161	0.000349	CEPF, ASW, AW, RD
Maputaland/Pondoland/Albany	274,136	16	43	59	0.000215	CEPF, ASW, AW, RD
Mediterranean Basin	2,085,292	44	97	141	0.000068	CEPF, ASW, AW, RD
Mountains of Central Asia	863,362	1	6	7	0.000008	CEPF, ASW, AW, RD
Mountains of SW China	262,446	45	30	75	0.000286	CEPF, ASW, AW, RD
New Caledonia	18,972	0	99	99	0.005218	CEPF, AW, RD
New Zealand	270,197	3	107	110	0.000407	CEPF, ASW, AW, RD
North American Coastal Plain	1,130,000	57	113	170	0.000150	CEPF
Polynesia/Micronesia	47,239	3	44	47	0.000995	CEPF, ASW, AW, RD

**Table 2** (continued)

Location	Size (km <sup>2</sup> )	Number endemic amphibians	Number endemic reptiles	Total number endemics	Density of endemics (spe- cies/km <sup>2</sup> )	Sources
Southwest Australia	356,717	20	35	55	0.000154	CEPF, ASW, AW, RD
Succulent Karoo	102,691	3	17	20	0.000195	CEPF, ASW, AW, RD
Tumbes-Chocó-Magdalena	274,597	58	128	186	0.000677	CEPF, ASW, AW, RD
Wallacea	338,494	35	132	167	0.000493	CEPF, ASW, AW, RD
<i>Other insular areas noted for endemism</i>						
Bahamas	13,962	0	25	25	0.001791	AW, RD
Bay Islands, Honduras	250	0	18	18	<b>0.072000</b>	McCranie and Valdés Orellana (2014); AW, RD
Bismarek/Admiralty Islands	49,700	23	16	39	0.000785	Kraus, unpubl. data
Eastern Arc Mts of Africa	36,770	58	37	95	0.002584	Burgess et al. (2007); ASW, AW, RD
Galapagos	7880	0	47	47	0.005964	AW, RD
Gulf of Guinea islands	2998	13	17	30	0.010007	Jones (1994); Juste and Fa (1994); ASW, AW, RD
Jamaica	10,991	21	28	49	0.004458	ASW, AW, RD
Puerto Rico	9104	14	17	31	0.003405	ASW, AW, RD
Puerto Rican Bank	9389	18	40	58	0.006177	ASW, AW, RD
Ryukyu Islands	4642	16	29	45	0.009694	Ota (1998); ASW, AW, RD
Seribuat Archipelago, Malaysia	178	1	15	16	<b>0.089888</b>	Grismer et al. (2006)
Socotra	3796	0	27	27	0.007113	Rösler and Wranglik (2006); Sindaco et al. (2012); ASW, AW, RD
Solomon Islands	37,800	28	40	68	0.001799	Boehme (2003); McCoy (2006); Brown and Richards (2008); Pikacha et al. (2008); ASW, AW, RD
Taiwan	36,175	25	26	51	0.001410	ASW, AW, RD

Densities in bold are those two insular areas with greater densities of endemic herpetofauna than the Milne Bay Region  
 CEPF Critical Ecosystem Partnership Fund, ASW Amphibian Species of the World, AW AmphibiaWeb, RD The Reptile Database



**Fig. 2** Numbers of endemic species by geographic area for the Milne Bay Region versus **a** 26 of Conservation International's 36 biodiversity hotspots, and **(b)** 14 other insular areas noted for their biodiversity values. For **(a)**, 1=Milne Bay Region, 2=California Floristic Region, 3=Cape Floristic Region, 4=Caucasus, 5=Cerrado, 6=Chilean-Valdivian Forests, 7=Coastal Forests of East Africa, 8=East Melanesian Islands, 9=Guinean Forests of West Africa, 10=Himalayas, 11=Horn of Africa, 12=Irano-Anatolia, 13=Japan, 14=Madrean Pine-Oak Woodlands, 15=Maputaland/Pondoland/Albany, 16=Mediterranean Basin, 17=Mountains of Central Asia, 18=Mountains of Southwest China, 19=New Caledonia, 20=New Zealand, 21=Polynesia/Micronesia, 22=Succulent Karroo, 23=Southwest Australia, 24=Tumbes-Chocó-Magdalena, 25=Wallacea, 26=Forests of East Australia, and 27=North American Coastal Plain. For **b**, 1=Milne Bay Region, 2=Bahamas, 3=Bay Islands, Honduras, 4=Bismarck/Admiralty Islands, 5=Eastern Arc Mts of Africa, 6=Galapagos, 7=Gulf of Guinea islands, 8=Jamaica, 9=Puerto Rico, 10=Puerto Rican Bank, 11=Ryukyu Islands, 12=Seribuat Archipelago, Malaysia, 13=Socotra, 14=Solomon Islands, and 15=Taiwan

greater areas. The five hotspots in Fig. 2a that hold more endemic herpetofaunal species (168–188) than the Milne Bay Region range from 274,597 to 2,031,990 km<sup>2</sup>, areas 18–135 times larger than the Milne Bay Region. Across these hotspots there is no compelling relationship between area and numbers of herpetofaunal endemics, with the best linear regression ( $y = -1.0 + 18.58x$ ) explaining very little of the data ( $R^2 = 0.03$ ), yet the regression line and the location of the Milne Bay Region outside the 95% confidence limits of this relationship makes its outlying nature immediately obvious. If the Milne Bay Region is removed from these comparisons, the linear regression improves slightly ( $R^2 = 0.12$ ), confirming its importance as an outlier.

Similarly, one may compare endemic herpetofauna in the Milne Bay Region to other insular areas noted for their biodiversity values and for which sufficient information on reptiles and amphibians is available. The Milne Bay Region holds a dramatically greater



number of range-restricted endemic reptiles and amphibians compared to these areas (Table 2, Fig. 2b), with the best linear regression among these points ( $y = 42.87 + 24.20x$ ) again performing poorly ( $R^2 = 0.23$ ). Once again, the Milne Bay Region lies well outside the 95% confidence intervals for this regression, and if it is removed from these comparisons, the linear relationship improves considerably ( $R^2 = 0.47$ ).

Of the 40 global areas of endemism compared by me to the Milne Bay herpetofauna, only two have densities of endemic herpetofauna greater than that in the Milne Bay Region, though both have far fewer species (Table 2). The Seribuat Archipelago in Malaysia has one endemic amphibian and 15 endemic reptiles in an area of 178 km<sup>2</sup>, for a density of 0.089888 species/km<sup>2</sup>; the Bay Islands of Honduras have 18 endemic reptile species in an area of 250 km<sup>2</sup>, for a density of 0.072000 species/km<sup>2</sup>. The Gulf of Guinea Islands in Africa have a density of endemic herpetofauna almost as great as that of the Milne Bay Region, though again with far fewer total species (Table 2).

## Discussion

### Comparative patterns

Here I have shown that the Milne Bay Region of Papua New Guinea hosts the largest, yet previously unrecognized, assemblage of range-restricted endemic reptiles and amphibians in the world, in an area smaller than El Salvador, Fiji, Kuwait, New Jersey, or Slovenia. These numbers and density are far higher than those seen in the majority of Conservation International's much-publicized biodiversity hotspots and in most other insular (offshore as well as mainland) areas noted for their biodiversity values (Fig. 2). The ten of 36 CI hotspots not compared here comprise areas 13–158 times larger than the Milne Bay Region and contain yet larger numbers of species: 172–939 endemics based even on outdated 1994 data. Detailed comparison of the Milne Bay herpetofauna to those areas, therefore, serves no purpose. Furthermore, the large majority of the Milne Bay endemics are restricted to local areas of endemism ranging from 200 to 2200 km<sup>2</sup> (Table 1) and, so, have very small ranges. The larger areas of the CI hotspots mean that many of their endemic species are not necessarily narrow-range endemics, but have much greater geographic ranges than do the Milne Bay species. That geographic area provides a poor explanation of numbers of endemic herpetofauna (Fig. 2a) is unsurprising inasmuch as these areas include temperate as well as tropical regions and were not defined on the basis of faunal diversity but of floral diversity and extent of deforestation (Myers 1988; Mittermeier et al. 1998).

High as the demonstrated concentration of range-restricted endemic herpetofauna in the Milne Bay Region is, it is a conservative estimate, and future research will undoubtedly show the number to be higher for three reasons. First, I have been conservative in estimating numbers of range-restricted endemics in poorly known genera that still require major taxonomic revision, such as *Hylophorbus*, *Papurana*, and *Tropidonophis*. Second, several portions of this region that hold promise for discovery of additional new species remain unsurveyed. Lastly, herpetofaunal surveys in most of the 11 areas of local endemism that I have identified here are incomplete, and I am confident that additional species await discovery in several of them. For example, I heard at least two frogs with unique advertisement calls in regions 1 and 6 (Fig. 1) that I never heard elsewhere, but I could not capture them. Surveys in most of these 11 areas have so far encompassed only brief visits, and more thorough surveys will undoubtedly discover additional endemics.

The rich density of range-restricted endemic species identified here is not an anomaly restricted to the herpetofauna. I am able to press the case for this region's biotic importance because my surveys and research since 2002 have made its herpetofauna among the most comprehensively studied biotic elements. In fact, there are also many range-restricted endemic aquatic insects (Polhemus and Polhemus 2004, 2006; Polhemus and Allen 2007; Polhemus 2011, 2020), land snails (Slapcinsky unpubl. data), fish (Polhemus and Allen 2007), and plants (Johns et al. 2009) in the region whose endemism is concordant with that seen in the herpetofauna. For quantitative comparison, 139 endemic plant taxa are known from the Milne Bay islands alone (Johns et al. 2009), although a similarly thorough synthesis of the flora of the mainland portion of this region is unavailable. Several endemic bird ( $n=9$ ) and mammal ( $n=6$ ) species are also known from the islands of this region (Flannery 1995; Pratt and Beehler 2015). For these other taxa, the islands have been better studied than the mainland portion of the region, so numbers of range-restricted endemics are generally not available for the latter.

Beyond this, I have provided a comparison of endemic reptile and amphibian numbers across many regions of the globe recognized for their biodiversity importance, and this serves as an initial step toward a global evaluation of the most important areas of endemism for the global herpetofauna. Doing so has shown that two small archipelagoes have densities of endemic herpetofauna even higher than that in the Milne Bay Region, though far fewer species (Table 2). The fact that my diversity estimate for the Milne Bay Region's endemic herpetofauna is conservative no doubt applies to many other poorly surveyed areas of the tropics as well (e.g., Meegaskumbura et al. 2002; Gillespie et al. 2005; Surasinghe 2009; Vieites et al. 2009; Koch 2011; Swenson et al. 2012). However, most of those areas are in the large CI hotspots (e.g., Indo-Burma, Madagascar, Sundaland, Tropical Andes) not compared in this paper because asymptotic estimates of the sizes of their endemic herpetofauna are unavailable due to incomplete survey work, and those areas are far larger in any event (600,460–2,373,000 km<sup>2</sup>). The task within each of those areas is to determine what concentrations of range-restricted endemics might occur in much smaller portions of those vast hotspots. It is also important to recognize that most of the high-biodiversity areas used in my comparisons are among the better-surveyed areas of the tropics and subtropics, and the numbers of undiscovered endemic herpetofauna in those areas are unlikely to increase dramatically enough to negate the general comparative findings of this study.

## Origins

The high diversity and areal concordance of range-restricted endemics across many taxa in 11 areas of local endemism in the Milne Bay Region is a direct result of the region's recent geological history. The continued opening of the Woodlark Rift—which began approximately 6 MYA (Taylor et al. 1999; Miller et al. 2012) and whose westernmost extension now runs northwestward under the Papuan Peninsula (Bird 2003; Baldwin et al. 2012)—has resulted in an ongoing process of geological extension that has isolated the southern end of the Owen Stanley Mts into the current Louisiade Archipelago via submergence of the intervening Pocklington Rise, separated Woodlark and Misima islands from formerly close proximity, created the uplands of the D'Entrecasteaux Islands and Mt. Suckling/Mt. Dayman Massif via exhumation of metamorphic core complexes, and produced the volcanism that created the peaks of the Cape Nelson Peninsula (Baldwin et al. 1993, 2012; Taylor et al. 1999; Polhemus and Polhemus 2004; Daczko et al. 2009; Davies 2012). Consequently, the region has been variously uplifted and/or dismembered over the past six

million years, resulting in a burst of vicariant speciation across its biota. This vicariant geological history has created all of the eleven areas of local endemism within the Milne Bay Region (Fig. 1) with the possible exception of Mt. Simpson. Unsurprisingly, the dramatic explosion of range-restricted endemics has closely tracked this vicariant sundering of biotic communities in a tropical region of high background diversity. This pattern supports the correlation between endemic richness and plate-tectonic activity found by Pellissier et al. (2018).

## Conservation implications

The Milne Bay Region's biodiversity values are not matched by conservation efforts there. This stems in part because New Guinea has not received the conservation attention accorded to areas highlighted decades ago as biodiversity "hotspots". When the latter were defined, three large tropical areas with less-dramatic habitat loss at the time (Amazon, Congo Basin, New Guinea) were relegated to the separate class of "wilderness areas" (Mittermeier et al. 1998; Myers et al. 2000), implying that large amounts of original habitat were then available, allowing time for conservation at a later date. But those large wilderness areas hide numerous areas of local or regional endemism (e.g., New Guinea: Alcorn et al. 1993; Amazon: da Silva et al. 2005; Morrone 2014) or lack much local endemism (e.g., Congo: Linder 2001; Jetz et al. 2004; Fjelds  2003). Of these three tropical wilderness areas, the Amazon region has received considerable conservation attention from a host of other governmental and non-governmental organizations because of the region's just fame for biodiversity and the effects that loss of its forests would have on regional and world climate (e.g., Davidson and Artaxo 2004; Marengo et al. 2011). The Congo Basin has also benefitted from conservation efforts focused around its charismatic megafauna.

However, New Guinea and immediately surrounding islands lack these attractions and, consequently, have enjoyed less conservation attention. For example, the CEPF, which does not provide conservation funding for New Guinea and immediately adjacent islands, instead restricts its regional funding to the less-diverse CI hotspots. Further, the biota of New Guinea and adjacent islands remains less well known because the region's accretional geological history and extremely mountainous nature have created high beta diversity of range-restricted endemics (e.g., Flannery 1995; Polhemus and Allen 2007; Pratt and Beehler 2015; Kraus unpubl. data; Fig. 1). This creates a need for geographically dense surveys to effectively understand the biota, but that activity is seriously hindered by the sparse infrastructure (roads, airfields) for survey access and the region's safety concerns, which dampen research interest. Beyond that, effective conservation in New Guinea must involve lengthy collaborative work with local inhabitants because of the traditional, community-based form of land ownership, and this may not be attractive to many international organizations that prefer to work with governments to achieve top-down conservation actions. That approach cannot work effectively in Melanesia. This confluence of funding, logistical, institutional, and safety constraints has made conservation action in New Guinea limited compared to the other large tropical wilderness areas. Because of that, funding opportunities for community-based efforts to protect the hyper-diverse Milne Bay Region have been sparse. Yet funding in New Guinea is greatly needed for further survey work to identify additional areas of local endemism and for follow-up community-based conservation programs to protect the biodiversity discovered.

Even were New Guinea better recognized as a biodiversity hotspot under increasing threat of deforestation (e.g., Shearman et al. 2008; Bryan and Shearman 2015), the high beta diversity in the Papuan region (e.g., Fig. 1) makes it easy to miss important local areas of endemism in broad-scale priority-setting exercises, highlighting the need for the finer-scale approach taken here. Identification of the conservation needs here could potentially be captured by the Key Biodiversity Areas (KBAs) system because one criterion used to identify KBAs is geographic restriction of biodiversity elements (Eken et al. 2004). Of the > 13,000 KBAs globally, the Milne Bay Region hosts 13 (<http://www.keybiodiversityareas.org/site/mapsearch>), and 11 of those overlap with the 11 areas of local endemism identified herein, albeit only partially in most cases. In some cases, recognized KBAs omit critical habitat for endemic species (e.g., East Fergusson, Goodenough) or omit the best remaining habitat (e.g., Misima). More importantly, two areas of high endemism identified here are not registered as KBAs. These include Sudest, holding at least 62 endemic species, and Woodlark, with at least 48 (Johns et al. 1999; Polhemus and Allen 2007; Polhemus 2011; Pratt and Beehler 2015; Slapcinsky unpubl. data; Tennant unpubl. data; Table 1). Only 11 of the 161 endemic reptiles and amphibians identified herein were considered when constructing the KBAs in the Milne Bay Region, and each KBA was identified on the basis of containing 1–12 range-restricted biotic elements that served as “triggers” for area identification. But eight of the 11 herpetofaunal species used were actually wide-ranging amphibians of low conservation value or (in one instance) with a misunderstood distribution. When these non-range-restricted species are removed, each KBA is recognized based on holding only 1–6 range-restricted species, with the exception of Rossel Island, which contains 11. Clearly, the evidence presented herein provides much stronger cases for KBA recognition in the Milne Bay Region, the addition of new KBAs, and the modification of some KBA boundaries. Even with a more solid foundation for delimiting local KBAs, such recognition must be followed by effective on-the-ground conservation, a task that only a single small NGO (Eco Custodians, based in Alotau) is focused on.

The need for immediate conservation engagement in the Milne Bay Region remains pressing because most of the 11 areas of local endemism identified here are under moderate to serious threat of habitat loss. This is perhaps clearest for Woodlark Island, which has been variously threatened for the past 20 years by schemes for mining, logging, and development of oil-palm plantations, each of which would degrade large portions of Woodlark should those plans come to complete fruition (Barry 2008; Hance 2014; Kraus 2017; Cerullo 2019, 2020). The island is currently threatened with virtually complete deforestation to plant oil palm—a proposal upheld by a PNG national court in early 2020 (Robby 2020)—which would virtually guarantee the extinction of many of the 48+ endemic forest-dwelling species on that island of only 874 km<sup>2</sup> extent. And an active gold mine operates in the center of the island, with approximately half the island under active lease for further exploration, providing conflicting claims for exploitation with the proposed oil-palm venture. Mining interest is, however, not limited to Woodlark. A significant area of Misima was degraded by a now-closed gold mine. And recent exploration permits and applications involve nine of the 11 areas of local endemism identified herein, including more than half of Misima and Normanby, and with almost all of Fergusson under lease or application for lease (PNG Mineral Resources Authority 2021). Although each mining permit is issued for a limited time, renewal and swapping of permits between companies is common and can extend mining threats for decades (D. Mitchell pers. comm.).

Beyond this, population growth rate in the Milne Bay Region averages 2.5%/year (McMurray and Lavu 2020), providing a population doubling time of 28 years, and this pressure is already recognized by many local inhabitants to be a threat to their natural

resources and future sustainability (Butler et al. 2014). Rapid population growth places increased pressure to convert forest to gardens and shortens fallow periods between cutting regimes, leading to progressive forest degradation. Tree-cover loss has been extensive throughout the region, including in all 11 areas of local endemism, and five of these areas currently feature active forestry concessions as well (Climate Change and Development Authority 2021). Cultivated land in Milne Bay Province was already 40% of total land area by 1987 (Saunders 1993), and that number is certainly higher now. As one example of deforestation threats, most of Misima Island below < 400 m elevation was already converted to gardens or mine sites by the time of my visit in January 2003, leaving only ca. 20% of the island (ca. 4200 ha) covered by primary rainforest. Smaller islands suffer larger degrees of deforestation (Shearman et al. 2008; Bryan and Shearman 2015), and some of these hold endemic species as well (e.g., *Panaeati*, Trobriands).

It is clear from these considerations that deforestation threat throughout the Milne Bay Region—and, in particular, in its 11 areas of local endemism—is high and increasing, whether or not it yet reaches the 70% forest-loss threshold used by CI for official "hotspot" recognition (Myers et al. 2000; Mittermeier et al. 2004). Given the very small sizes of the local areas of endemism and the rapid doubling time of the Milne Bay population, it should be clear that little time remains to take strong conservation actions to preserve the region's terrestrial diversity.

Beyond concerns specifically with New Guinea or the Milne Bay Region, this study makes a first step toward a much-needed global assessment to identify priority areas for conservation of narrow-range endemic herpetofauna, much as has been done effectively for birds (Stattersfield et al. 1998; BirdLife International 2014). This study identifies the Milne Bay Region, Bay Islands of Honduras, Seribuat Archipelago, and Gulf of Guinea islands as all holding outstanding concentrations of endemic herpetofauna in very small areas. Additional concentrations of range-restricted endemics can be expected to lie hidden within the much larger tropical "hotspots" and "wilderness areas" already identified through the work of Conservation International, but others lie outside these areas (e.g., Clausnitzer et al. 2012). The IUCN red-list system for categorizing species endangerment (IUCN 2012) is insufficient to identify these areas because concentrations of endangered taxa will not necessarily occur in areas of high local endemism; for example, none of the species considered herein (Online Resource 1) is flagged as of IUCN concern. But work to identify additional local centers of endemism or to supplement recognized KBAs with information from additional taxa should go some way toward better focusing conservation efforts within the large CI hotspots to more practical scales for conservation action. Further, tighter coordination between organizations identifying areas of critical biodiversity importance and taxonomists working in those regions—as IUCN does with its red-listing process—would also help improve recognition of additional important areas for which data are already available.

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