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Regional patterns of biodiversity in New Guinea animals

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Abstract

Aim To assess regional patterns of biodiversity levels in the New Guinea region by counting numbers of species of different groups in 1° grid squares.

Location The New Guinea region.

Methods Panbiogeographical analysis [Craw, R.C., Grehan, J.R. & Heads, M.J. (1999) Panbiogeography: tracking the history of life. Oxford University Press, New York].

Results The following taxa were analysed: three genera of cicadas (Homoptera), freshwater fishes, snakes, and the four terrestrial orders of mammals in the region – monotremes, marsupials, bats and rodents. A total of 622 species (and subspecies) was analysed and the different centres of diversity in the various groups of animals are related to the three main geological regions of the country: Australian craton, accreted terranes, and Cainozoic volcanic arcs.

Main conclusions Freshwater fishes are most diverse in the lower Fly – Merauke region, on the southern, Australian craton portion of New Guinea. Marsupials are the only other group with a main massing on the craton (at the Kubor Mountains area). Snakes are most diverse in the trans-Fly region, like freshwater fishes, and also around Port Moresby. All the other groups have centres of diversity either on the craton margin or outboard of it on different accreted terranes of the New Guinea orogen. In the groups studied, only bats have a significant, albeit secondary, massing on the Bismarck Archipelago. Other terrestrial vertebrates with centres of diversity on the Bismarck Archipelago include the diverse frog genus *Platymantis*. The regions north and east of New Guinea (Bismarck Sea plate, Solomon Sea plate) are now occupied mainly by sea and volcanic island arcs, but biogeographers and geologists have suggested this as the site of earlier, more extensive land. The different centres of diversity in the different groups are suggested to derive from vicariant locations of early (Mesozoic – early Cainozoic) diversity rather than from different means of dispersal or other aspects of ecology.

Keywords
Biogeography, conservation, Pacific, tropics, rain forest, vertebrates.

INTRODUCTION

The tropical island of New Guinea is largely covered in rain forest and includes mountains up to 5000 m high. Not surprisingly it is one of the world's most biodiverse places and describing the plants and animals has been one of the great endeavours of systematics and ecology (Frodin & Gressitt, 1982).

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Confronted with a large island bearing what at first seems to be homogeneous rain forest, biologists in New Guinea, have often assumed that most species are widespread. Another well-known pattern, simple allopatry in a group with, say, a different species in each province would also result in the same levels of biodiversity throughout. But is biodiversity, if not the taxa themselves, really so evenly spread? This paper examines the distribution of biodiversity in different groups.

New Guinea is currently divided into a western half, the Indonesian province of Irian Jaya or West Papua, and an eastern half, the state of Papua New Guinea (PNG). Many areas in PNG, especially in the west of the country, remain poorly known zoologically. Irian Jaya is even less well-explored and although the coastal areas and the mountains are relatively well-collected, the areas between are very poorly known indeed. For example, there are practically no collections of any group from the 1° latitude by 1° longitude grid cell (approximately 100 km × 100 km) immediately south of the provincial capital, Jayapura. This sector includes the Nimboran Mountains and the site of a 'major transmigration settlement – planned or existing' (map in Supriatna, 1999). It is sometimes felt that the New Guinea biota is so hopelessly under-collected that valid generalizations about distribution there are impossible. It might be suspected that the maps probably provide a plotting of airstrips and roads rather than true distributions. However, the Archbold expeditions, for example, seldom used either, and collected hundreds of thousands of specimens in a series of transects across the island. Many other intensive collecting expeditions have been carried out and in many ways the biota is quite well-known. For example, the last new species of bird of paradise (Paradisaeidae) was discovered by the outside world in 1939, as was the last bowerbird (Ptilonorhynchidae). The idea of vast, unexplored rain forests with new species at every turn has a strong appeal and has been actively promoted by many visitors. Unfortunately it may have acted as a psychological barrier and delayed analysis.

Care is obviously needed in interpreting analyses of the fairly sketchy distribution data. However, collection-based data from modern taxonomic revisions is the best available information on biodiversity and up till now has seldom been analysed. Instead, published research has emphasized total species numbers for particular areas of different sizes.

METHODS

This study assesses regional levels of biodiversity in New Guinea animals by counting numbers of species in 1° grid cells. The figures were derived from recently published monographs of speciose groups which included maps. This method was first used in the 1960s to map species diversity in the very rich plant communities of southern Africa and Australia (references in Heads, 1997). Since then it has been applied around the world and the following groups have recently been analysed in this way: reptiles, birds and mammals in north-western Australia (Whitehead *et al.*, 1992; Woinarski, 1992); Crassulaceae in North America, Mexico and southern Africa (Jürgens, 1995; Thiede, 1995); *Banksia* L.f and *Hakea* Schrad. (Proteaceae) in south-western Australia (Groom & Lamont, 1996; Lamont & Connell, 1996); *Huperzia* Bernh (Lycopodiaceae) in the Neotropics (Øllgaard, 1996); pteridophytes in Iberia (Moreno Saiz *et al.*, 1996); plant and animal taxa in New Zealand (Heads, 1997, 1998, 1999); plants in New Guinea (Heads 2001a), and birds of paradise and bowerbirds in New Guinea (Heads, 2001b).

RESULTS

The results are presented in Figs 2–11, with the most diverse squares highlighted. In the next section the groups are discussed in sequence and related to the geological structure of New Guinea as shown in Fig. 1.

DISCUSSION

Homoptera

Duffels and de Boer have produced many excellent revisions of New Guinea cicadas; only three of the genera they have revised are analysed here.

Cosmopsaltria Stål (Duffels, 1983) (Fig. 2) has its main centres of massing in Irian Jaya around the middle Mamberamo Valley (including the upper Meervlakte) and Mount Wilhelmina (= Trikora). Despite high numbers in the Huon Peninsula, the Vogelkop and Milne Bay areas are both low in diversity. The pattern might be attributed to poor collecting in those areas, but this is unlikely as a related genus, treated next, is known to be diverse around Milne Bay.

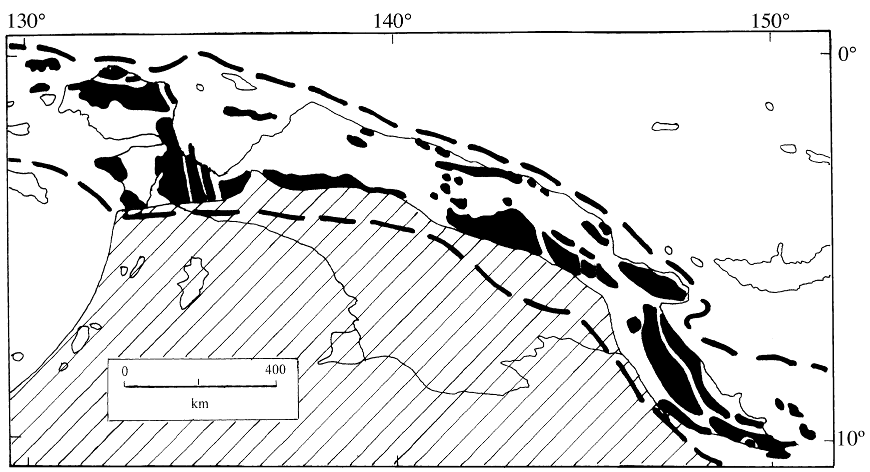

Figure 1 Geological map showing the Australian craton (hatched), the New Guinea orogen (between the heavy broken lines), and the accreted New Guinea terranes (black). The islands north of New Guinea comprise Palaeogene and Quaternary volcanic arcs (simplified from Pigram & Davies, 1987).

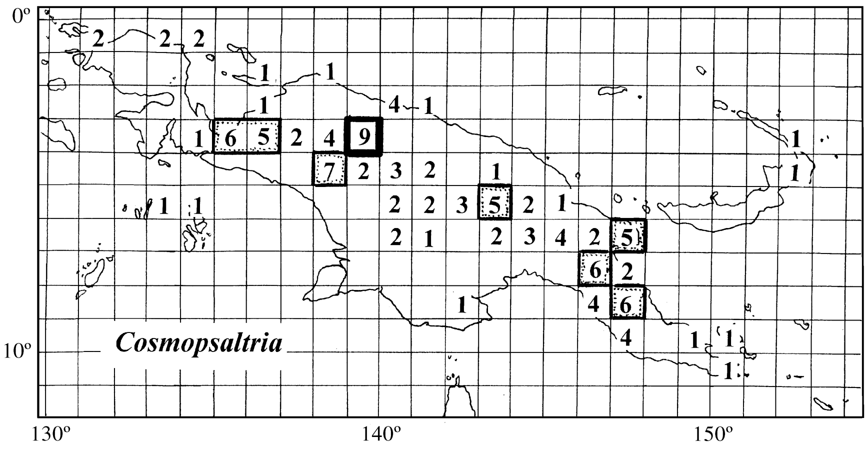

Figure 2 *Cosmopsaltria* (Homoptera) in New Guinea: numbers of species in 1° grid cells. Total number of New Guinea species = 20.

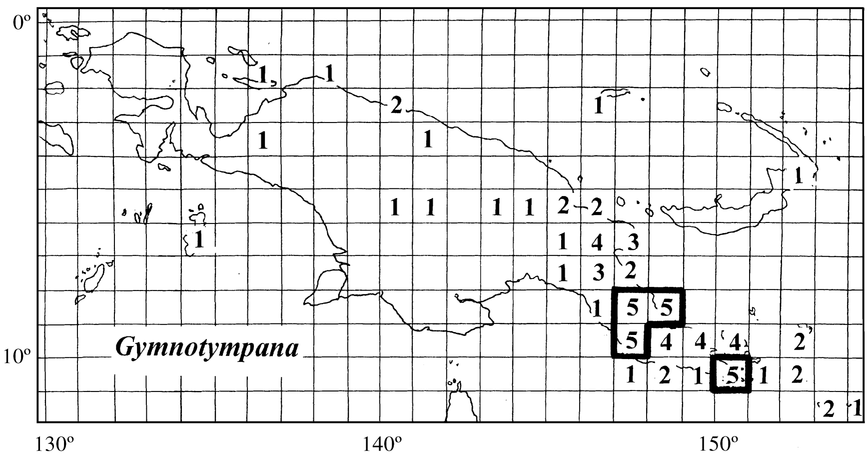

Figure 3 *Gymnotympana* (Homoptera) in New Guinea: numbers of species in 1° grid cells. Total number of New Guinea species = 15.

Gymnotympana Stål (de Boer, 1995b) (Fig. 3) has its main massing on the SE Papuan Peninsula from Mount Albert Edward to Milne Bay, an area made up of diverse accreted terranes comprising schists (Owen Stanley terrane), ultramafics (Bowutu terrane) and basalts (Kutu terrane) (Pigram & Davies, 1987). The low diversity of *Gymnotympana* recorded for Irian Jaya might be attributed to low collecting intensity there, but the related *Cosmopsaltria* is most diverse there, again indicating that normal biological vicariance is probably the explanation.

Papuapsaltria De Boer (de Boer, 1995a) (Fig. 4) has a main massing on the Wau grid square and a second massing in the nearby Crater Mountain – Goroka square, and so is mainly outboard of the craton margin lying between the massings of *Cosmopsaltria* in Irian Jaya, and *Gymnotympana* in the SE Papuan Peninsula.

Many other insect groups are distinctly northern in New Guinea: Miller *et al.* (1993) reported that tiger beetles (Carabidae: Cicindelinae) are most diverse on the south Morobe coast, adjacent to the Bowutu/Kuper Mountains which also comprise a centre of diversity for lizards (cited below). Miller *et al.* (1993) also noted that the adjacent lowlands of Oro (formerly Northern) Province are the most diverse area for several recently revised insect genera in Carabidae, Cicadidae, and Papilionidae.

Important centres of endemism for New Guinea butterflies (Parsons, 1999; Fig. 5) are all located outboard of the craton margin (except for the Weyland Mountains in Irian Jaya which straddle the margin), both in the New Guinea orogen and also in the volcanic island arcs.

Freshwater fishes

Although Allen's maps of freshwater fishes (1991) of New Guinea are fairly generalized, the large number of species maps make this work particularly valuable. Many centres of endemism, some very restricted, are clearly shown. The overall pattern of species diversity (Fig. 6) is striking, with a clear main massing in south-central New Guinea, mainly around the Fly River-Merauke area but extending west to the Digul and Lorentz Rivers. The Sepik River is a much less speciose secondary centre. The surprisingly depauperate fish fauna of this large river was also commented on by Van Zwieten (1990) and in fact most areas in New Guinea outboard of the craton are poor in freshwater fishes, especially the Papuan Peninsula and the Vogelkop.

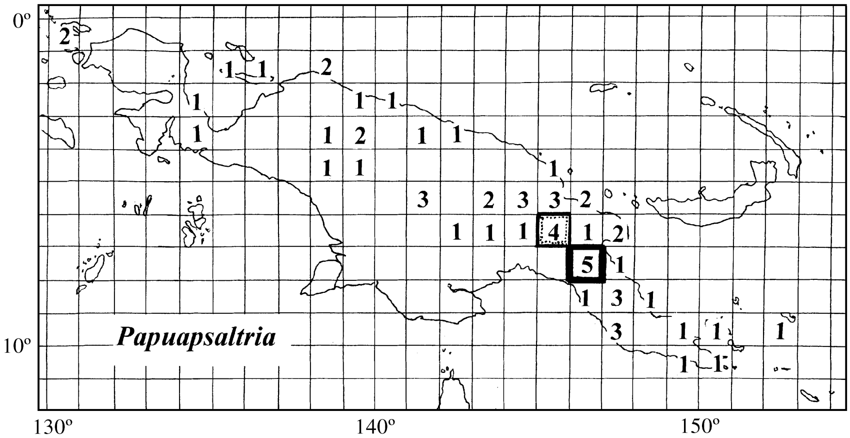

Figure 4 *Papuapsaltria* (Homoptera) in New Guinea: numbers of species in 1° grid cells. Total number of New Guinea species = 18.

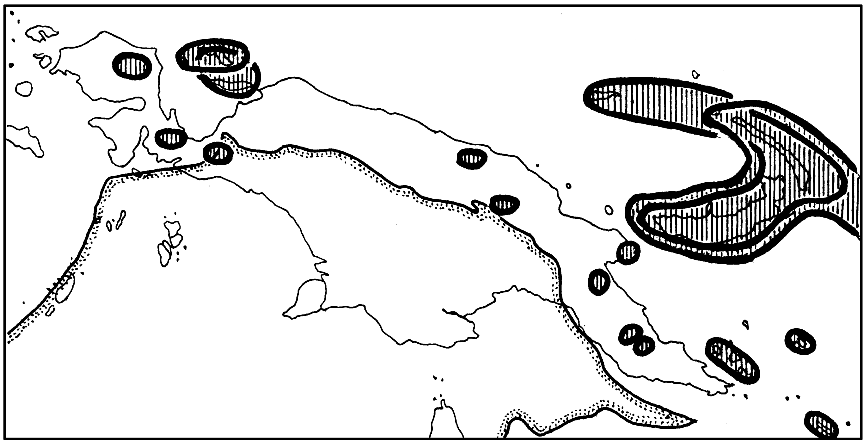

Figure 5 Butterflies in New Guinea: centres of endemism (from Parsons, 1999) shown in relation to the craton margin.

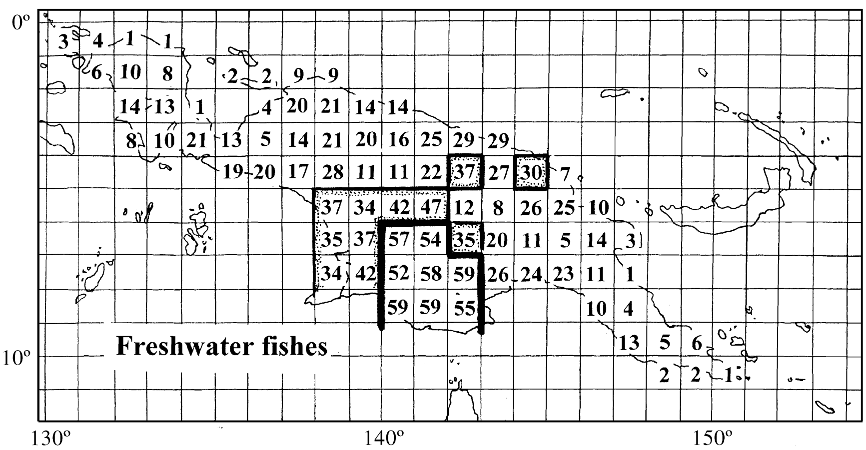

Figure 6 Freshwater fishes in New Guinea: numbers of species in 1° grid cells. Total number of New Guinea species = 219.

The diverse fishes on the Fly platform include genera endemic there, such as *Cochlefelis* Whitley, *Nedystoma* Ogilby, *Tetranesodon* Weber, *Oplotosus* Weber, and *Kiunga* Allen. Other groups (e.g. *Iriatherina* Meinken and *Denariusa* Whitley) are endemic to this region plus Cape York Peninsula (northern Queensland), and so are centred on a Torres Strait node (Heads, 1990). Several Fly platform groups (*Plotosus* Lacepède, *Zenarchopterus* Gill, *Strongylura* van Hasselt) are found elsewhere only in marine or brackish environments, but in New Guinea (and sometimes northern Australia) there are freshwater species.

Amphibia and reptilia

No modern, complete treatments of these groups in New Guinea are available, but maps have been published for some frog genera and for all the snakes (discussed separately below). Allison (1993) observed that the Bowutu Mountains/eastern Kuper Range (Bowutu terrane, consisting of the Papuan Ultramafic Belt) form a major centre of diversity for frogs and lizards, with 20 frogs endemic there and 10 lizards (New Guinea, like parts of South America, is a major centre of frog evolution and levels of endemism there are much higher in frogs than in lizards). Eastern Highlands Province is the second most diverse region, with 20 endemic frogs and six lizards; Chimbu Province is third with 18 endemic frogs and four lizards. The herpetofauna of the Hunstein Mountains/Central Mountains also seems particularly rich with a significant endemic element. All these areas lie in the accreted terrane portion of the New Guinea orogen, outboard of the craton margin.

Allison (1993) noted that the richest localities for all frogs, not just endemics, are mostly mountainous areas on the mainland and on Bougainville. Contradicting this general trend, the Huon Peninsula has most species overall although it apparently lacks a montane frog element. The lowlands and hill forests are rich in species and there are several endemics in the hills by the University of Technology, Lae.

Lizards, like frogs, have the highest total numbers (including endemics) on the Huon Peninsula and also in the Ramu-Sepik basin (61 species each). Third most speciose areas are the Bewani Mountains and Torricelli Mountains (50 species each). Allison (1993) also noted that the savanna region around the national capital Port Moresby is an important area for restricted range lizards. The high number of species recorded here may be partly because of the area being relatively well-collected, but Allison's analysis suggested that the region is also an important centre of endemism.

In contrast with freshwater fishes and snakes (next), frogs and lizards are clearly a 'northern' group on the New Guinea mainland and are massed on the accreted terranes of the New Guinea orogen, although they show low endemism further north on the islands of the Bismarck Archipelago.

The maps of snakes (O'Shea, 1996) indicate a clear centre of diversity in the lower Fly region (Fig. 7), as in freshwater fishes, and another across the Gulf of Papua in the Port Moresby – Kairuku – Biaru area.

Birds

Although birds are the best-known group of animals, few detailed maps have been published. Coates (1990) has rather generalized maps of species ranges on the mainland, with more detail shown for the islands. Even for the best-known bird group in New Guinea, the birds of paradise, detailed dot-maps became available only recently (Frith & Beehler, 1998). The bowerbirds have also been mapped, but in much less detail (Cooper & Forshaw, 1977; Coates, 1990). Both groups were analysed (Heads, 2001) and are shown to be most diverse in the Mount Hagen – Wahgi Valley grid cell, which is traversed by the craton margin. However, while birds of paradise have secondary massings in mountains on the craton, bowerbirds have secondary massings north of the craton margin on accreted terranes.

Mammals

The mammals of New Guinea and the New Guinea islands have been mapped by Flannery (1995a,b), and Bonaccorso (1998) has given a detailed treatment of PNG bats.

Monotremes

The two New Guinea genera show southern (cratonic) and northern (accreted terrane) distributions, respectively, and overlap along the margin of the craton (Fig. 8). The form on the craton (*Tachyglossus* Illiger) is shared with Australia but in the north barely occupies the Huon Peninsula and is absent from the Vogelkop and the Owen Stanley Range. The northern form (*Zaglossus* Gill) is currently restricted to New Guinea (known in Australia from fossils only), with records

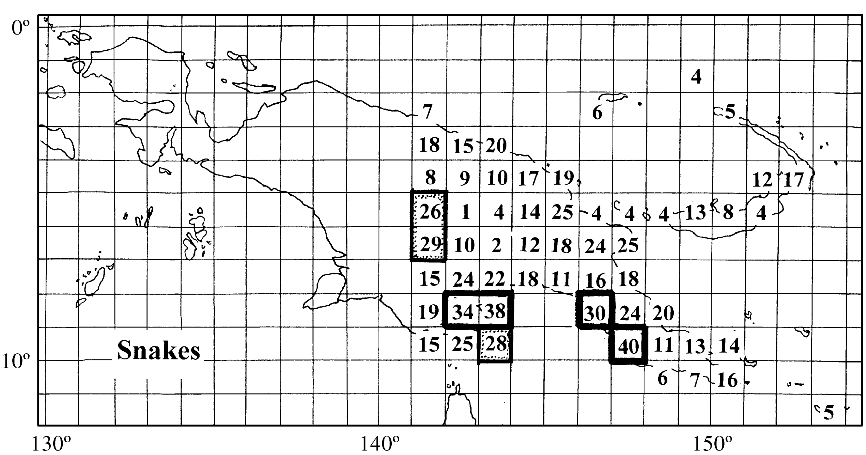

Figure 7 Snakes in Papua New Guinea: numbers of species and subspecies in 1° grid cells. Total number of New Guinea species = 92.

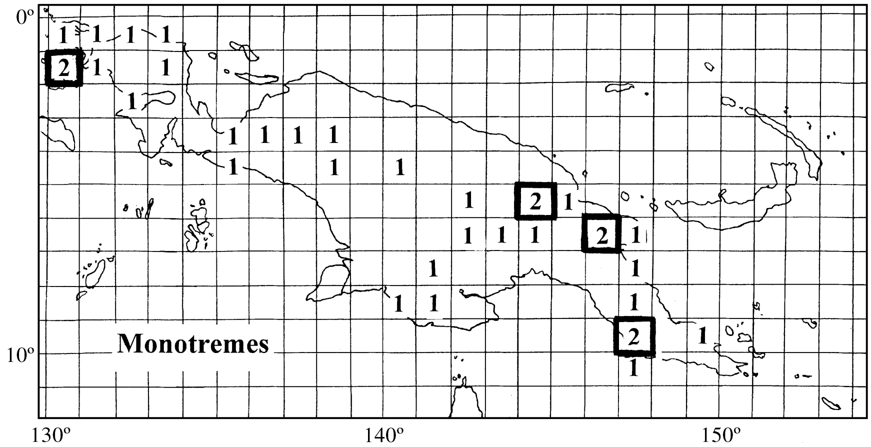

Figure 8 Monotremes in New Guinea: numbers of species in 1° grid cells. Total number of New Guinea species = 2.

in the Vogelkop and Huon Peninsulas and in the Owen Stanley Range. The monotremes, like other characteristic mainland groups such as birds of paradise, appear to be totally absent from the Bismarck Archipelago.

Marsupials

The marsupials are most diverse in the Kubor Mountains 1° grid cell, south of the craton margin as might be expected for a largely Australian group. The 'southern beeches' (*Nothofagus* Bl.) are also most diverse in this grid cell (data from Read & Hope, 1996) and are another southern group, present in Australia, New Caledonia, New Zealand and South America. Other centres of marsupial diversity occur around Mount Hagen – Wahgi Valley (cf. birds of paradise and bowerbirds), the Port Moresby – Mount Victoria square, and Tufi – Collingwood Bay around the schists of the Dayman terrane. The highest marsupial diversity in Irian Jaya is recorded in the Weyland Mountains, where the Dasyuridae have their main New Guinea centre. Flannery (1994) recorded the most diverse site in New Guinea for possums (Phalangeroidea) in oak forest at 1500–2000 m just west of Telefomin, and in the grid cell analysis the Telefomin square has 16 possum species, the maximum number for New Guinea (Fig. 9).

There is a drop-off in marsupial diversity in the Vogelkop (even in the well-explored Arfak Mountains), along the north New Guinea coast, and in the mountains of the eastern Huon Peninsula. There is also a markedly lower diversity on the PNG islands than on the adjacent mainland, which for Flannery 'clearly indicates that marsupials are, in general, very poor over-water dispersalists'. However, there is minor but significant marsupial endemism on the islands: *Petaurus biacensis* Ulmer on Biak; the distinctive *Spilocuscus kraemeri* (Schwartz) on Manus, Ninigo and Wuvulu Islands; the very distinctive *Dorcopsis atrata* van Deusen on Goodenough Island in montane forest ('undoubtedly a relic species only distantly related to the New Guinea species'); *Dactylopsila tatei* Laurie above 600 m on Fergusson Island; *Echymipera davidi* Flannery on the Trobriand Islands (the bandicoots on Goodenough, Fergusson and Normanby may also belong to this species); and *Phalanger lullulae* Thomas, with 'perhaps the most unusual coat pattern of any marsupial', on Woodlark Island and nearby Alcester.

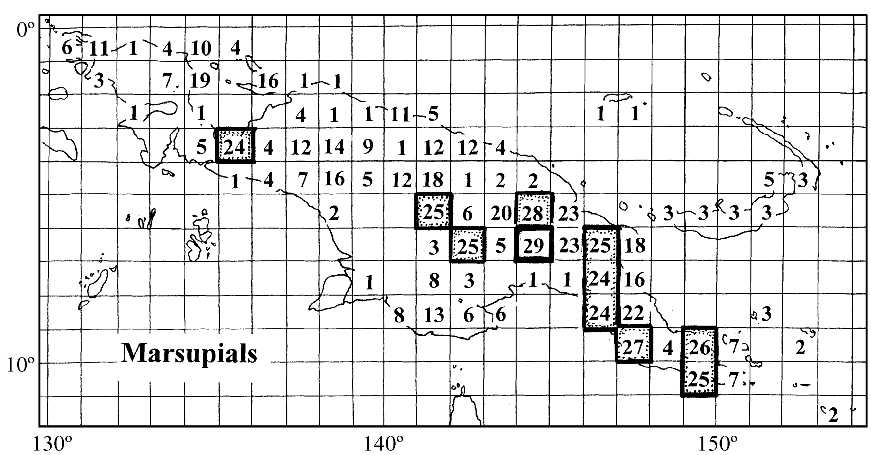

Figure 9 Marsupials in New Guinea: numbers of species in 1° grid cells. Total number of New Guinea species = 69.

Bats

Bonaccorso's (1998) maps of the bats of PNG and Flannery's (1995b) of the bats of Irian Jaya are analysed here. The main massings all lie outboard of the craton margin, on the New Guinea orogen and the Bismarck Archipelago. Highest diversity is recorded in the Port Moresby – Mount Victoria square which may be partly due to greater intensity of collecting here, but the region is also an important centre of endemism for many groups. For example, the vespertilionid bat *Pharotis* Thomas is known only from Kemp Welch River and Kapakapa, 40 km south-east of Port Moresby [Bonaccorso's (1998) map record from the Western Highlands is erroneous – Dr F. Bonaccorso, pers. comm.]. For plants, Fortune-Hopkins & Menzies (1995) listed six species endemic to the Port Moresby region and others include *Alyxia sogerensis* S. Moore (Middleton, 2000) and *Decaisnina pedicellata* (Danser) Barlow (Barlow, 1993) both endemic at Sogeri, and *Tetradyas* Danser at Sogeri and Lala River (Barlow, 1974) (Fig. 10).

The bats are the only group analysed here that shows numerically important centres in the Bismarck Archipelago, although other groups, such as the frog family Ranidae with the diverse genus *Platymantis* Guenther have their main diversity there (Allison, 1996). The strong northern massing of Chiroptera (they are also diverse on Bougainville) may be derived from an early, ancestral diversity in the area north of New Guinea currently occupied by the Bismarck Sea (the Bismarck Sea plate) and Solomon Sea (the Solomon Sea plate). This would also explain why the bat fauna of the islands includes significant endemism; it is not simply a collection of widespread, 'weedy' taxa. Compatible with this idea is Flannery's (1995b) the suggestion that bats are a 'very old' group in New Guinea, and that the Megachiroptera underwent an early Tertiary radiation on the proto-New Guinea archipelago.

There is an interesting anomaly in the distribution of the New Guinea bats: the pteropodid fruit-bats have a high degree of endemism on the New Guinea islands, while the insectivorous bats have relatively few endemics there. This 'remains unexplained' (Flannery, 1995a), but resembles the distribution of the frog families, with Hylidae and Microhylidae massing on the mainland, and Ranidae on the Bismarcks and Solomons. Like the 'inexplicable' absence of birds of paradise and bowerbirds from the islands, these patterns of vicariance and different locations of main massings are not explained by 'means of dispersal'.

Rodents

The New Guinea rodents, all Muridae but with endemic genera, have a main centre of massing in the Crater Mountain – Goroka grid cell, where the Uromyini (38 New Guinea species) and Murinae (12 New Guinea species) are both most diverse. The craton margin runs through this grid cell, as it does through the Hagen – Wahgi cell, also an important centre. The Moresby region and the Mount Wilhelmina grid cell in Irian Jaya are also diverse for rodents. In summary, the rodents are diverse through the mountains of the New Guinea orogen, on both cratonic and accreted terrane sectors (Fig. 10).

As is monotremes and marsupials, the rodent faunas of the New Guinea islands are strikingly less diverse than those of the adjacent mainland. Nevertheless, again like marsupials, there is minor but significant endemism there: *Melomys matambuai* Flannery, Colgan & Trimble on Manus; *Rattus mordax sanila* Flannery & White (extinct), now considered a distinct species (Flannery, 1995b), on New Ireland; and *Uromys neobrittanicus* Tate & Archbold, *Hydromys neobrittanicus* Tate & Archbold, and *Melomys* cf. *levipes* (Thomas) on New Britain. The few rodents on the islands SE of New Guinea are all widespread elsewhere in New Guinea, apart from *Chiruromys forbesi* Thomas known only from the three D'Entrecasteaux Islands and SE New Guinea. However, on Bougainville there are three rodents – *Melomys bougainville* Troughton, *Solomys ponceleti* Troughton ('most unusual appearance… very striking') and *S. salebrosus* Troughton – known only from there and Choiseul, in the neighbouring Solomon Islands. Flannery (1995a) stressed that the murid fauna of the Bismarck Archipelago is 'surprisingly impoverished' but in a group of such notoriously good dispersers this cannot be explained by lack of

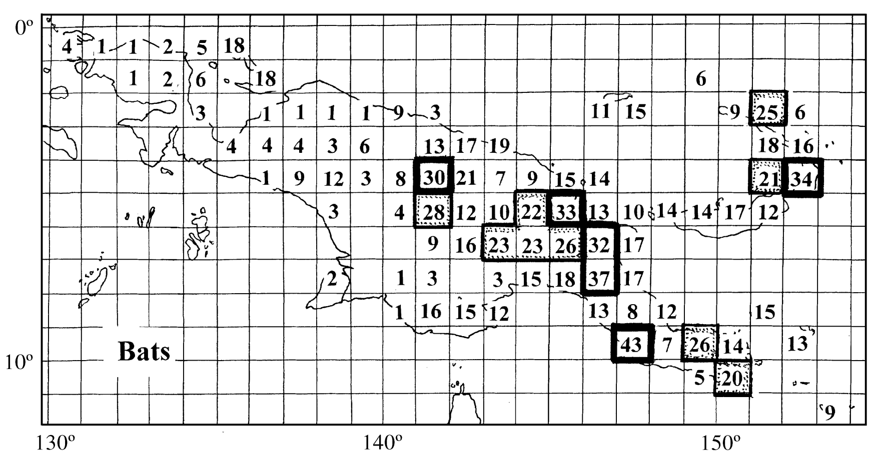

Figure 10 Bats in New Guinea: numbers of species and subspecies in 1° grid cells. Total number of New Guinea species = 118.

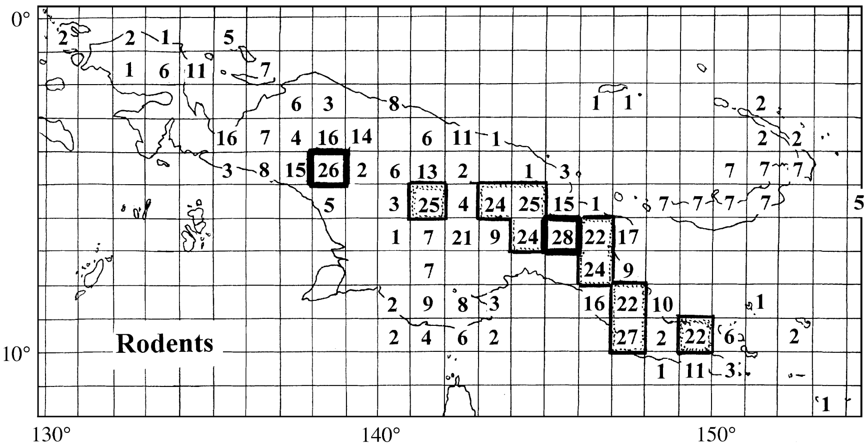

Figure 11 Rodents in New Guinea: numbers of species in 1° grid cells. Total number of New Guinea species = 69.

efficient 'means of dispersal' or suitable environment. Thus the paucity of murids is seen as surprising and a 'biogeographical problem'. However, the situation is actually even more problematic for dispersal theory as many other mobile groups, such as birds of paradise and bowerbirds, are also absent there, while conversely, terrestrial groups such as the frog genus *Platymantis* have their major centre there.

Recently global conservation groups have focused their attention on resolving patterns of biodiversity in the New Guinea region. A Conservation Biodiversity Workshop for PNG initiated by Conservation International brought experts in the different groups together for discussion. The results were published as a Conservation Needs Assessment (CNA) for the country (Beehler, 1993). The project, which cost an estimated $US 500,000 (Groombridge & Jenkins, 1996), produced 'a broad consensus of expert opinion on conservation priorities [which] can be used to wield more influence on government opinion than if a narrow sectoral approach is used'. One of the main results of the workshop was a politically useful consensus in the form of a map of 'nationally important areas.' Scientifically, it is important to understand how these areas were derived.

The CNA recognized that assessing regional levels of biodiversity is best done by analysing and synthesizing available data, rather than actually going into the field and counting species in plots. The second approach is the one taken by many conservation workers, but biogeographers have hardly begun to analyse the thousands of distribution records already available in taxonomic monographs and checklists.

The authors contributing to the CNA proposed areas with high levels of biodiversity in their respective groups, and gave estimates (or 'guesstimates' – Johns, 1993) of species numbers there as well as other valuable data, some cited above. However, despite the plea in the Introductory chapter for analyses that can be replicated, none of the papers really explained how the areas used were demarcated to begin with and so the exercise is not readily testable.

A Conservation Priorities Workshop for Irian Jaya (Supriatna, 1999) also suggested priority areas but again did not explain how these had been derived from the data. However, this publication also included a valuable data base of specimens on a CD-ROM and maps of these would be very useful.

Another recent map of biodiversity priority areas in PNG (Margules & Pressey 2000) gave very different results from those in Beehler (1993). It aimed at representing 608 environmental domains, 564 vegetation types, 10 species assemblages and 12 rare and threatened species. However, the analysis of priority areas aimed at minimizing foregone opportunities for timber extraction, minimizing the number of areas currently used for intensive agriculture, and gave preference to areas previously identified by experts as biodiversity priority areas.

With the recent publication of mapped treatments of invertebrates, freshwater fishes, snakes, birds of paradise, and mammals it is now possible to evaluate what is known of regional levels of biodiversity in a well-studied sample of the New Guinea fauna, using an explicit methodology that can be repeated in different groups. Areas with levels of high biodiversity are shown in the figures above, whether or not they are desirable for forestry or agriculture or have previously been identified as priority areas by experts.

CONCLUSIONS

Freshwater fishes are most diverse in the lower Fly – Merauke region, on the southern, Australian craton portion of New Guinea. Marsupials are the only other group with a main massing on the craton (in the Kubor Mountains area). Snakes are most diverse in the trans-Fly region, like freshwater fishes, and also around Port Moresby. All the other groups have centres of diversity either on the craton margin or outboard of it on different accreted terranes of the New Guinea orogen. In the groups studied, only bats have a significant, albeit secondary, massing on the Bismarck Archipelago. Other terrestrial vertebrates with centres of diversity on the Bismarck Archipelago include the diverse frog genus *Platymantis*.

The different locations of main massing in the various groups of animals on the three main geological regions of the country (craton, accreted terranes, Palaeogene and

Quaternary volcanic arcs) probably have more to do with prior (Mesozoic – early Cenozoic) locations of main diversity than with means of dispersal or other aspects of ecology. The region north-east of New Guinea is currently occupied mainly by sea and the only land consists of volcanics and limestones. However, the area has long been suggested to be the site of earlier, extensive land, both by biogeographers (Gressitt, 1958) and geophysicists (Nur & Ben-Avraham, 1981). Pigram & Davies, 1987) interpretation of the New Guinea orogen as a collage of allochthonous terranes which have moved in from the Pacific, rather than the result of a simple continent/island arc collision, also accords well with this idea. Hall's (1998, 2001) reconstruction of the region for 30 Ma shows the east Philippines, northern Moluccas and north New Guinea terranes (including New Britain) forming a relatively continuous arc, running parallel with and 1–2000 km north of New Guinea, before moving south and west and docking. This would go some way to explain the close connections among these regions and also the great difference between New Britain and the New Guinea mainland.

The magnificent suite of recent publications on New Guinea vertebrates discussed above is a little offset by the lack of detailed maps for the best-known group, the birds. Of the vast collections of New Guinea birds held in museums in Europe, the USA and Australia only a minute fraction have been mapped. If these countries could map their collections, this would be of great assistance in orienting conservation strategy in New Guinea.

There is more to conservation than just locating the most biodiverse areas; in many places it is more important to focus on particular threats. Nevertheless, it does seem that biogeographical and conservation studies in the New Guinea region would benefit from undertaking further analyses of the data already published in taxonomic monographs. This data, in the form of classifications and distribution maps, is itself the result of extensive analysis and synthesis but is often not presented in a framework readily understood from the biogeographical/conservation viewpoint. Often there are simply too many maps, and usually there is very little synthesis beyond the maps and perhaps a key or cladogram.

Another limitation of the approach used in this paper is the use of species numbers in large taxa only. It would also be of interest to map diversity in and of genera and families. A more detailed 1° grid analysis of marsupials as mentioned above, for example, shows interesting differences between the families, with Dasyuridae most diverse in Irian Jaya, Petauridae with a similar pattern (diverse east to Telefomin), and Phalangeridae and Macropodidae most diverse in PNG. Acrobatidae, Petauridae and Burramyidae are more or less evenly spread throughout the main ranges, while Pseudocheiridae are evenly spread through the central New Guinea mountains but are less diverse in the Vogelkop and Milne Bay.

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REFERENCES

Allen, G. R. (1991) *Field guide to the freshwater fishes of New Guinea*. Christensen Research Institute, Madang.

Allison, A. (1993) Biodiversity of the fishes, amphibians, and reptiles of Papua New Guinea. In: *Papua New Guinea conservation needs assessment*, Vol. 2. *A biodiversity analysis for Papua New Guinea* (ed. by B.M. Beehler), pp. 57–226. Biodiversity Support Program, Washington, DC & Department of Environment and Conservation, Boroko, PNG.

Allison, A. (1996) Zoogeography of amphibians and reptiles of New Guinea and the Pacific region. In: *The origin and evolution of Pacific Island biotas, New Guinea to Eastern Polynesia: patterns and processes* (ed. by A. Keast and S. E. Miller), pp. 407–436. SPB. Academic Publishing, Amsterdam.

Barlow, B. A. (1974) A revision of the Loranthaceae of New Guinea and the south-western Pacific. *Australian Journal of Botany*, **22**, 531–621.

Barlow, B. A. (1993) Conspectus of the genera *Amylotheca, Cyne, Decaisnina, Lampas, Lepeostegeres,* and *Loxanthera* (Loranthaceae). *Blumea*, **38**, 65–126.

Beehler, B. M. (ed.) (1993) *A biodiversity analysis for Papua New Guinea. Papua New Guinea conservation needs assessment*, Vol. 2. Biodiversity Support Program, Washington, DC & Department of Environment and Conservation, Boroko, PNG.

de Boer, A. J. (1995a) The taxonomy and biogeography of the cicada genus *Papuapsaltria* gen. n. (Homoptera, Tibicinidae). *Tijdschrift voor Entomologie*, **138**, 1–44.

de Boer, A. J. (1995b) The taxonomy, phylogeny and biogeography of the cicada genus *Gymnotympana* Stål, 1861 (Homoptera: Tibicinidae). *Invertebrate Taxonomy*, **9**, 1–81.

Bonaccorso, F. (1998) *Bats of Papua New Guinea*. Conservation International, Washington, DC.

Coates, B. J. (1990) *The birds of Papua New Guinea including the Bismarck Archipelago and Bougainville*, 2 Volumes. Dove Publications, Alderley, Queensland.

Cooper, W. T. & Forshaw, J. M. (1977). *The birds of paradise and bowerbirds*. Collins, Sydney.

Duffels, J. P. (1983) Taxonomy, phylogeny and biogeography of the genus *Cosmopsaltria*, with remarks on the historic biogeography of the subtribe Cosmopsaltriaria (Homoptera: Cicadidae). *Pacific Insect Monogrraphs*, **39**, 1–127.

Flannery, T. (1994) *Possums of the World: a monograph of the Phalangeroidea*. Geo, Sydney.

Flannery, T. (1995a) *Mammals of the south-west Pacific and Moluccan Islands*. Reed, Chatswood, New South Wales.

Flannery, T. (1995b) *Mammals of New Guinea*, 2nd edn. Reed, New South Wales, and Cornell University Press, Ithaca.

Fortune-Hopkins, H. & Menzies, J. I. (1995) *The flora of Motupore island*. University of Papua New Guinea Press, Port Moresby.

Frith, C. B. & Beehler, B. M. (1998). *Birds of paradise*. Oxford University Press, New York.

Frodin, D. G. & Gressitt, J. L. (1982) Biological exploration of New Guinea. In: *Biogeography and ecology of New Guinea* (ed. J.L. Gressitt), pp. 87–130. Dr W. Junk, The Hague.

Gressitt, J. L. (1958) New Guinea and insect distribution. *Proceedings of the Tenth International Congress of Entomology*, pp. 767–773.
Groom, P. K. & Lamont, B. B. (1996) Ecogeographical analysis of *Hakea* (Proteaceae) in south-western Australia, with special reference to leaf morphology and life form. *Australian Journal of Botany*, **44**, 527–542.
Groombridge, B. & Jenkins, M. D. (eds) (1996) *Assessing biodiversity status and sustainability*. World Conservation Press, Cambridge.
Hall, R. (1998) The plate tectonics of Cenozoic SE Asia and the distribution of land and sea, pp. 99–131. In: *Biogeography and geological evolution of SE Asia* (eds R. Hall & J.D. Holloway). Backhuys Publishers, Leiden.
Hall, R. (2001) Cenozoic reconstructions of SE Asia and the SW Pacific: changing patterns of land and sea. In: *Faunal and floral migrations and evolution in SE Asia and Australia* (ed I. Metcalfe), 35–56. Balkema, Rotterdam.
Heads, M. (1990) Mesozoic tectonics and the deconstruction of biogeography: a new model of Australasian biology. *Journal of Biogeography* **17**, 223–225.
Heads, M. J. (1997) Regional patterns of biodiversity in New Zealand: one degree grid analysis of plant and animal distributions. *Journal of the Royal Society of New Zealand*, **27**, 337–354.
Heads, M. J. (1998) Biodiversity in the New Zealand divaricating tree daisies *Olearia* sect. nov. (Compositae). *Botanical Journal of the Linnean Society*, **127**, 239–285.
Heads, M. J. (1999) Vicariance biogeography and plate tectonics in the Pacific: an analysis of *Abrotanella* (Compositae). *Biology Journal of the Linnean Society*, **67**, 391–432.
Heads, M. J. (2001a) Regional levels of biodiversity in New Guinea plants. *Botanical Journal of the Linnean Society*, **136**, 67–73.
Heads, M. J. (2001b) Regional levels of biodiversity in birds of paradise and bowerbirds. *Journal of Zoology [London]*, **255**, 331–339.
Johns, R. J. (1993) Biodiversity and conservation of the native flora of Papua New Guinea. In: *Papua New Guinea conservation needs assessment*, Vol. 2. *A biodiversity analysis for Papua New Guinea* (ed. B.M. Beehler), pp. 15–76. Biodiversity Support Program, Washington, DC & Department of Environment and Conservation, Boroko, PNG.
Jürgens, N. (1995) Contributions to the phytogeography of *Crassula*. In: *Evolution and systematics of the Crassulaceae* (eds H. Hart and U. Eggli), pp. 136–150. Backhuys, Leiden.
Lamont, B. B. & Connell, S. W. (1996) Biogeography of *Banksia* in southwestern Australia. *Journal of Biogeography*, **23**, 295–309.
Margules, C. R. & Pressey, R. L. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.
Middleton, D. J. (2000) Revision of *Alyxia* (Apocynaceae). Part 1: Asia and Malesia. *Blumea*, **44**, 27–120.
Miller, S. E., Cowie, C., Polhemus, D. & Eldredge, L. (1993) Biodiversity and conservation of the nonmarine invertebrate fauna of Papua New Guinea. In: *Papua New Guinea conservation needs assessment*, Vol. 2. *A biodiversity analysis for Papua New Guinea* (ed B.M. Beehler), pp. 227–325. Biodiversity Support Program, Washington, DC & Department of Environment and Conservation, Boroko, PNG.
Moreno Saiz, J. C., Castro Parga, I., Humphries, C. J. & Williams, P.H. (1996) Strengthening the national and natural park system of Iberia to conserve pteridophytes. In: *Pteridology in perspective* (eds J.M. Camus, M. Gibby and R.J. Johns), pp. 101–124. Royal Botanic Gardens, Kew.
Nur, A. & Ben-Avraham, Z. (1981) Lost Pacifica continent: a mobilistic speculation. In: *Vicariance biogeography: a critique* (ed. G. Nelson and D.E. Rosen), pp. 341–358. Columbia University Press, New York.
O'Shea, M. (1996) *A guide to the snakes of Papua New Guinea*. Independent Publishing, Port Moresby.
Øllgaard, B. (1996) Neotropical *Huperzia* (Lycopodiaceae) – distribution of species richness. In: *Pteridology in perspective* (ed. J.M. Camus, M. Gibby and R.J. Johns), pp. 93–100. Royal Botanic Gardens, Kew.
Parsons, M. J. (1999) *The butterflies of Papua New Guinea: their systematics and biology*. Academic Press, London.
Pigram, C. J. & Davies, P. J. (1987) Terranes and the accretion history of the New Guinea orogen. *BMR Journal of Australian Geology and Geophysics*, **10**, 193–212.
Read, J. & Hope, G. S. (1996) Ecology of *Nothofagus* forests of New Guinea and New Caledonia. In: *The ecology and biogeography of Nothofagus forests* (ed. T.T. Veblen, R.S. Hill and J. Read), pp. 200–256. Yale University Press, New Haven.
Supriatna, J. (ed.) (1999) *The Irian Jaya biodiversity conservation priority-setting workshop*. Conservation International, Washington, DC.
Thiede, J. (1995) Quantitative phytogeography, species richness, and evolution of American Crassulaceae. In: *Evolution and systematics of the Crassulaceae* (ed. H.Hart and U.Eggeli), pp. 89–123. Backhuys, Leiden.
Van Zwieten, P. (1990) *Distribution, altitudinal range and abundance of the fish species in the lower order streams of the Sepik-Ramu catchment*. Unpublished Report. FAO, Rome.
Whitehead, P. J., Bowman, D.M.J.S. & Tideman, S.C. (1992) Biogeographic patterns, environmental correlates and conservation of avifauna in the Northern Territory. *Journal of Biogeography*, **19**, 151–161.
Woinarski, J. C. Z. (1992) Biogeography and conservation of reptiles, mammals and birds across north-western Australia: an inventory and base for planning an ecological reserve system. *Wildlife Research*, **19**, 665–705.

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