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Why may the same species have different elevational ranges at different sites in New Guinea?

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Summary.—Species in mountainous areas have characteristic elevational ranges, but with some variation from site to site. Such variation has been studied extensively elsewhere in the world, but not yet for New Guinea bird species. Hence, we examined five sources of that variation for New Guinea birds: latitude, competition, slope, the Massenerhebung effect, and physical barriers. Decreases of species elevational ranges with latitude are illustrated by three sets of examples: 20 species confined to New Guinea's mountains, but which descend to sea level at higher latitudes in Australia (joined to New Guinea at Pleistocene times of low sea level); 13 sea-level populations of some of the same New Guinea upland species on New Guinea's Fly River bulge; and 11 populations on the Aru Islands (part of Pleistocene New Guinea and Australia). Many New Guinea species contract or expand their elevational ranges, associated with the presence or absence of competing congenerics, which segregate by elevation at sites of sympatry. The flat Karimui Basin at an elevation of 1,110 m illustrates effects of slope, because the basin supports populations of many species otherwise characteristic of the flat lowlands, and lacks populations of many hill forest species characteristic of the sloping terrain found at that elevation elsewhere in New Guinea. We provide three sets of New Guinea examples of the Massenerhebung effect described for mountains elsewhere in the world: shifts of species to higher elevations on large high mountains far from the sea than on small coastal mountains or isolated mountains. Finally, we suggest that very steep high ridges boxing in a watershed on the Foja Mts. constitute dispersal barriers that have prevented 33 species expected at that watershed's elevation from arriving or establishing themselves.

The mountains of New Guinea rise to 4,884 m. No New Guinea bird species occupies the entire span of elevations from sea level to the highest summit. Instead, each species occurs mainly within a limited elevational range, which is so characteristic of the species that it is routinely mentioned in short species accounts in field guides. For example, the standard guide by Pratt & Beehler (2015) gives 3,800–4,200 m as the range of Snow Mountain Robin *Petroica archboldi*, and 0–100 m as the range of White-bellied Pitohui *Pseudorectes incertus*. We are unaware of any record of the former species below 3,800 m, or of the latter species above 100 m.

Nevertheless, most life characteristics of animal and plant species are subject to some variation, which often proves understandable, and is also true of elevational ranges. For example, our Table 4 will demonstrate that the elevational floor of the Island Leaf Warbler *Seicercus poliocephalus* varies from 366 to 1,866 m, and its elevational ceiling from 1,195 to 2,152 m, among New Guinea mountains, and that this large variation can be explained by three physical variables. There is a considerable literature on variation in elevational ranges, initially subjected to detailed study in the Alps, and subsequently in other parts of the world (e.g., Troll 1948, Richards 1952, Howard 1968, Grubb 1971, Whitmore 1990, Foster 2010,

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Bruijnzeel *et al*. 2010). However, this phenomenon has not received systematic attention in relation to New Guinea, although anecdotal reports exist.

This paper attempts an initial exploration of this phenomenon for New Guinea birds, based partly on analysis of already published information, and partly on our field experience of species elevational ranges on different New Guinea mountains, especially in the Van Rees Mts. and the Foja Mts. We shall discuss five sources of variation: latitude, competition, and terrain slope, which we discuss briefly; and the so-called Massenerhebung effect and barriers to dispersal, which we examine in more detail on the basis of our new field observations. Of course, there are surely other sources of variation that we do not discuss.

Methods

Our measurements of species elevational ranges were accumulated over the course of 27 expeditions to New Guinea and neighbouring islands since 1964 by JD, and of 86 expeditions since 1977 by KDB (e.g., Diamond 1972, Diamond & Bishop 2015, 2020, 2021a,b). Seventeen of those expeditions since 1986 have been joint efforts. JD collected bird specimens on six expeditions during 1964–74. Our subsequent records have been entirely observational, based both on sightings and (especially in forests) on vocalisations. We routinely measured elevations of all significant observations to the nearest 5 m using a Thommen altimeter (JD) or a Magellan or Garmin GPS (KDB). Elevations of fixed points along our transect were measured repeatedly on many days and at different times of day, and then averaged, to reduce the effect of variation due to atmospheric conditions. Our comparisons of species elevational ranges at different sites thus have the advantage of being based on measurements by the same observers using the same instruments. Our taxonomic nomenclature follows that of Beehler & Pratt (2016).

Latitude

South America and North America span 66 and 40 degrees of latitude, respectively. As a result, these continents offer innumerable examples of species elevational ranges decreasing with increasing latitude: species that are confined to high elevations on mountains at or near the equator shifting to lower elevations with increasing latitude, until they occur at sea level at high latitude.

New Guinea's mountains span a much smaller range of latitude: from *c*.01°S for the Tamrau Mts. of north-west New Guinea to only *c*.10.5°S for the southernmost mountains of south-east New Guinea. Our own field experience of New Guinea mountains extends only from 01.1°S in the Arfak Mts. to 08.4°S on Mt. Albert-Edward. The modest differences in species elevational ranges that we measured for those two mountains proved to be in the opposite direction to expectations based on latitude: elevational ranges are somewhat higher, rather than lower, at the higher-latitude site of Mt. Albert-Edward (*cf*. *Seicercus poliocephalus* in Table 4), probably because the effect of the small difference in latitude is overshadowed by a big difference in the Massenerhebung effect to be discussed later.

However, a much greater range of latitude is available for study when one considers Pleistocene land connections. The floor of the shallow Arafura Sea separating New Guinea from Australia today (Fig. 1 of Diamond & Bishop 2021b) emerged intermittently as dry land (the 'Arafura Shelf') during Pleistocene times of low sea level. New Guinea and Australia were then joined in a single continent extending from the equator to 44°S at the south coast of Tasmania, which was also joined to Australia in Pleistocene periods of low sea level. The 44° latitudinal span of the former single Australasian continent is greater than

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TABLE 1
Species or superspecies of New Guinea mountains that breed at sea level in Australia. Lists the species or superspecies that in New Guinea are largely confined to the mountains (at least in northern New Guinea), but which in Australia have breeding populations at sea level.

		Different allospecies?	**Only Cape York?**
Lewin's Rail	*Lewinia pectoralis*		
Eurasian Coot	*Fulica atra*		
Pygmy Eagle	*Hieraaetus weiskei*	A	
Nankeen Kestrel	*Falco cenchroides*		
Fan-tailed Cuckoo	*Cacomantis flabelliformis*		
Black-eared Catbird	*Ailuroedus melanotis*		Y
Masked Bowerbird	*Sericulus* [*aureus*]	A	
Papuan Treecreeper	*Cormobates placens*	A	
Tropical Scrubwren	*Sericornis beccarii*		t
Papuan Logrunner	*Orthonyx novaeguineae*	A	
Barred Cuckooshrike	*Coracina lineata*		
Papuan Sittella	*Daphoenositta papuensis*	A	
Black-headed Whistler	*Pachycephala monacha*	A	
Trumpet Manucode	*Phonygammus keraudrenii*		t
Black-winged Monarch	*Monarcha frater*		t
Yellow-legged Flyrobin	*Kempiella griseoceps*		t
Papuan Scrub Robin	*Drymodes beccarii*	A	t
Ashy Robin	*Heteromyias* [*albispecularis*]	A	Y
White-faced Robin	*Tregellasia leucops*		t
Russet-tailed Thrush	*Zoothera heinei*		

[ ]: New Guinea populations considered to belong to two or three different allospecies of the same superspecies.

A: New Guinea and Australian populations currently considered, by Beehler & Pratt (2016) and others, to belong to different allospecies of a superspecies. These taxonomic decisions are in a state of flux; in most cases the populations were until recently considered conspecific.

Y, t: Australian breeding populations of the superspecies confined to the Cape York Peninsula (Y), or even just to the peninsula's northern tip (t).

that of North America (40°). Hence, when one examines bird elevational ranges on New Guinea and Australia together, one finds examples of species or superspecies confined to high elevations on modern New Guinea mountains near the equator, at least in northern New Guinea, but which occur at sea level at higher latitudes in modern Australia—just as in North and South America.

Table 1 lists the 20 examples that we recognise. For example, Nankeen Kestrel *Falco cenchroides* is confined in New Guinea as a breeding species to elevations above 3,200 m on New Guinea's highest mountains, but it is widespread in the lowlands of Australia. As another example, Fan-tailed Cuckoo *Cacomantis flabelliformis* is confined in New Guinea to mountain forests at about 1,500–3,000 m, but is widespread in the lowlands of eastern and southern Australia, including Tasmania in the far south. Eight of the 20 species are confined

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in Australia today to the Cape York Peninsula, and six of those eight to the peninsula's northern tip, i.e., the part of Australia closest to New Guinea.

Besides Australia, there are two other pieces of the intermittent combined continent of New Guinea / Australia where 17 species confined to mountains in the rest of New Guinea (or at least in northern New Guinea) now occur at sea level. One is southern New Guinea's Fly River bulge at *c.*09ºS (the highest-latitude part of modern New Guinea except the south-east peninsula), where 13 species confined to mountains over most of the rest of New Guinea have sea-level populations. The other piece is the low-elevation Aru Islands at 05.5–07ºS, the only surviving exposed fragment of the Pleistocene Arafura Shelf, where 11 species confined to mountains in the rest of New Guinea have sea-level populations. (Fig. 1 of Diamond & Bishop 2021b shows the location of the Fly River bulge and the Aru Islands.) Table 6 of Diamond & Bishop (2020) lists these Fly River and Aru Island populations. They are presumably relicts established during the cooler Pleistocene, when they and some other species now largely or entirely confined in New Guinea to the mountains shifted downslope. At that time those species maintained lowland populations variously extending from what is now lowland southern New Guinea, across the now-submerged and then-dry Arafura Shelf encompassing what are now the Aru Islands, to the lowlands of Australia. As post-Pleistocene climates warmed, and as the sea level rose and drowned the Arafura Shelf except for the Aru Islands, these species retreated in New Guinea again to the mountains, and survived in the lowlands mainly just in those two patches (plus Australia in ten cases).

Competition

Many New Guinea species belong to altitudinal sequences of two, three, four, or even five congeneric species that replace each other with elevation, often with sharp elevational transitions (Diamond 1972). Competition plays a role in maintaining the sequences. This is illustrated by the fact that, on mountains where one member of a sequence is absent, the congener whose elevational range is abutting on mountains of sympatry often expands its elevational range to occupy that of the missing congener (Diamond 1972, 1973).

For example, two closely related, ecologically similar, congeneric honeyeaters, Rufous-backed Honeyeater *Ptiloprora guisei* and Grey-streaked Honeyeater *P. perstriata*, occur sympatrically on mountains in New Guinea's Eastern Highlands and parts of south-east New Guinea. On those mountains of sympatry (e.g., Mt. Michael in the Eastern Highlands, which JD studied in 1964), the two species segregate altitudinally, *P. perstriata* occurring at approximately 2,400–3,750 m, *P. guisei* at 1,750–2,400 m. On the Huon Peninsula, where *P. perstriata* is absent, *P. guisei* occurs at least 800 m higher, to at least 3,200 m. In western New Guinea, where *P. guisei* is absent, *P. perstriata* occurs as much as 850 m lower, down to 1,550 m.

Similar examples of contractions or expansions of elevational ranges associated with presence or absence of competing species have been documented in New Guinea for species in the genera *Amblyornis*, *Megapodius*, *Melanocharis*, *Pachycephalopsis*, *Paradisaea*, *Psittacella*, *Rallicula*, *Rhipidura*, *Talegalla* and *Toxorhamphus* (e.g., Diamond 1972, 1973). These New Guinea examples have been noted anecdotally but not analysed systematically. Even more examples have been found in the Andes, where Terborgh (1971) and Terborgh & Weske (1975) did analyse them systematically. They found that at least 71% of Andean bird species expand their elevational ranges in the absence of congeners.

Terrain slope

Whilst the New Guinea lowlands include huge expanses of flat terrain, most land in New Guinea's mountains is instead sloping, often steeply. Extensive flat areas are infrequent in the mountains. One such area studied by JD in 1964–65 is the Karimui Basin, a large flat plain at an elevation of about 1,110 m connecting the bases of two extinct Pleistocene volcanoes, and rimmed by mountains pierced by a river gorge (Diamond 1972). In three respects Karimui's avifauna resembles that of the flat lowlands, rather than of the sloping terrain usually present at that elevation elsewhere in New Guinea.

One is the abundance at Karimui of lowland forest species that are uncommon or absent elsewhere in New Guinea at the same elevation, such as King Bird of Paradise *Cicinnurus regius*, Large Fig Parrot *Psittaculirostris desmarestii* and at least 23 other lowland forest species (Table 2). Almost as soon as JD started up the steep slopes of Mt. Karimui and left the flat basin floor, most (18 of the 25) of these lowland forest species disappeared (absent in JD's zone 1 of mountain surveys at 1,220–1,280 m: Diamond 1972), and all but two of the 25 species were absent in JD's zone 2 of mountain surveys at 1,341–1,448 m (Table 2, columns 2–3). JD's observations in Karimui's unusual flat terrain at 1,110 m may be compared with his observations at his collecting site of Okasa, only 95 km east of Karimui, at a comparable elevation (1,082–1,296 m), and surveyed twice by JD, only one week after his first visit to Karimui in 1964 and one week before his second visit in 1965. Unlike Karimui, Okasa is in sloping terrain typical of Karimui's elevation elsewhere in New Guinea. None of the 25 lowland forest species anomalously present at Karimui was recorded at Okasa (Table 2, column 1).

The second respect in which Karimui's avifauna is anomalous for its elevation is the converse of the first: the absence or rarity at Karimui of 16 hill forest species abundant at Karimui's elevation elsewhere in New Guinea, such as *Seicercus poliocephalus*, Grey-green Scrubwren *Sericornis arfakianus* and White-eyed Robin *Pachycephalopsis poliosoma* (Table 3). Of those 16 hill forest species, nine were unrecorded at Karimui; three were recorded just as 1–4 immature individuals; and four were recorded just as 1–4 adults. But 14 of the 16 hill forest species were encountered as soon as JD started up Mt. Karimui's steep slopes into zones 1–2 of his mountain surveys; and 13 of the 16 were recorded at Okasa (Table 3).

The third and most striking evidence for the effect of slope on elevational distributions of bird species at Karimui is the discontinuous elevational ranges of three species characteristic of sloping hill forests: Fairy Lorikeet *Charmosyna pulchella*, Black Fantail *Rhipidura atra* and *Pachycephalopsis poliosoma*. These species were common on Mt. Karimui's lower slopes just above the basin floor (1,220–1,448 m), disappeared or became rare when JD descended to the latter (1,110 m), and reappeared when JD crossed the basin's mountain ring and descended again to sloping terrain at lower elevations (610–985 m). Probably there were many other hill forest species that shared these discontinuous distributions but which JD did not observe, because he only walked quickly through the 610–985-m zone en route to and from a 600-m site, and the three species that he did observe are especially vocal and abundant.

Of New Guinea's *c.*190 upland bird species and superspecies, *c.*80 are members of pairs, trios, quartets or quintets of congeners that replace each other with elevation (Diamond 1972, Freeman & Class Freeman 2014). In seven cases the anomalous features of Karimui's avifauna just discussed result in Karimui supporting the lowland member of an elevational sequence, rather than (five cases) or in addition to (two cases) the higher-elevation member of the sequence prevalent at Karimui's elevation elsewhere in New Guinea. These cases are: Red-flanked Lorikeet *Charmosyna placentis*, Yellow-billed Kingfisher *Syma torotoro*, Pale-

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TABLE 2
Lowland forest species anomalously present in the flat montane Karimui Basin. These 25 species characteristic of New Guinea lowland forest are absent or uncommon at Karimui's elevation (1,110 m) over most of New Guinea, where the terrain is normally sloping, often steeply, but they are present, mostly in abundance, at Karimui, where the terrain (exceptionally for that elevation in New Guinea) is flat.

		1. At Okasa?	**2. Mt. K zone 1?**	**3. Mt. K zone 2?**
Stephan's Emerald Dove	*Chalcophaps stephani*	–	–	–
Wompoo Fruit Dove	*Megaloprepia magnifica*	–	✓	–
Dwarf Fruit Dove	*Ptilinopus nainus*	–	–	–
Red-necked Crake	*Rallina tricolor*	–	–	–
Greater Black Coucal	*Centropus menbeki*	–	✓	–
Eastern Koel	*Eudynamys orientalis*	–	–	–
Pacific Baza	*Aviceda subcristata*	–	✓	–
Yellow-billed Kingfisher	*Syma torotoro*	–	–	–
Red-flanked Lorikeet	*Charmosyna placentis*	–	✓	✓
Large Fig Parrot	*Psittaculirostris desmarestii*	–	✓	–
Orange-breasted Fig Parrot	*Cyclopsitta gulielmitertii*	–	–	–
Red-cheeked Parrot	*Geoffroyus geoffroyi*	–	–	–
White-eared Catbird	*Ailuroedus buccoides*	–	–	–
Ruby-throated Myzomela	*Myzomela eques*	–	–	–
Plain Honeyeater	*Pycnopygius ixoides*	–	–	–
Pale-billed Scrubwren	*Sericornis spilodera*	–	✓	✓
Boyer's Cuckooshrike	*Coracina boyeri*	–	–	–
Golden Cuckooshrike	*Campochaera sloetii*	–	–	–
Rusty Shrikethrush	*Pseudorectes ferrugineus*	–	–	–
Southern Variable Pitohui	*Pitohui uropygialis*	–	–	–
Sooty Thicket Fantail	*Rhipidura threnothorax*	–	–	–
King Bird of Paradise	*Cicinnurus regius*	–	–	–
Golden Monarch	*Carterornis chrysomela*	–	✓	–
Olive Flyrobin	*Kempiella flavovirescens*	–	–	–
Banded Yellow Robin	*Gennaeodryas placens*	–	–	–

Column 1: present at Okasa? A site near Karimui and at similar elevation, but with sloping terrain typical of that elevation in New Guinea.

Column 2: present on Mt. Karimui's slopes rising steeply from the flat Karimui Basin, in JD's lowest survey zone (zone 1) starting only 110 m above the basin floor?

Column 3: present on Mt. Karimui's steep slopes, in JD's next-lowest survey zone (zone 2) starting only 231 m above the basin floor?

Note that, of these 25 lowland forest species anomalously present in the flat Karimui Basin, none is present at Okasa, only seven in zone 1, and just two in zone 2.

billed Scrubwren *Sericornis spilodera*, Olive Flyrobin *Kempiella flavovirescens* and White-eared Catbird *Ailuroedus buccoides* present, instead of the expected Fairy Lorikeet *Charmosyna pulchella*, Mountain Kingfisher *Syma megarhyncha*, *Sericornis arfakianus*, Yellow-legged Flyrobin *Kempiella griseoceps* and Black-eared Catbird *Ailuroedus melanotis* respectively; and

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TABLE 3

Hill forest species anomalously absent or rare in the flat montane Karimui Basin. These 16 characteristic species of New Guinea hill forest are widespread and common at Karimui's elevation (1,110 m) over most of New Guinea, where the terrain is normally sloping, often steeply. But they are absent, or rare, or present only as occasional immatures ('imm.') at Karimui, where the terrain (exceptionally for that elevation in New Guinea) is flat (column 1). Columns 2–4: as columns 1–3 of Table 2. Note: of these 16 hill forest species anomalously absent in the flat Karimui Basin, most are present in the sloping terrain of Okasa at the same elevation as Karimui, and in Mt. Karimui's zones 1 and 2 above the Karimui Basin.

		1. At Karimui?	**2. At Okasa?**	**3. Mt. K zone 1?**	**4. Mt. K zone 2?**
Mountain Kingfisher	*Syma megarhyncha*	—	—	—	—
Fairy Lorikeet	*Charmosyna pulchella*	—	—	—	✓
Black-eared Catbird	*Ailuroedus melanotis*	—	✓	—	✓
Ornate Melidectes	*Melidectes torquatus*	rare	✓	—	✓
Grey-green Scrubwren	*Sericornis arfakianus*	—	✓	—	✓
Mottled Berryhunter	*Rhagologus leucostigma*	rare	✓	—	✓
Sclater's Whistler	*Pachycephala soror*	imm.	✓	✓	✓
Black Fantail	*Rhipidura atra*	—	✓	✓	✓
Trumpet Manucode	*Phonygammus keraudrenii*	imm.	✓	✓	✓
Lawes's Parotia	*Parotia lawesii*	—	✓	✓	✓
Superb Bird of Paradise	*Lophorina superba*	—	✓	✓	✓
Fantailed Monarch	*Symposiachrus axillaris*	imm.	✓	✓	✓
White-eyed Robin	*Pachycephalopsis poliosoma*	rare	✓	✓	✓
Yellow-legged Flyrobin	*Kempiella griseoceps*	—	✓	—	—
White-faced Robin	*Tregellasia leucops*	rare	✓	✓	✓
Island Leaf Warbler	*Seicercus poliocephalus*	—	—	—	✓

Red-cheeked Parrot *Geoffroyus geoffroyi* and Southern Variable Pitohui *Pitohui uropygialis* present in addition to the expected Blue-collared Parrot *Geoffroyus simplex* and Hooded Pitohui *Pitohui dichrous*, respectively.

A likely explanation for these effects of slope on bird distributions at Karimui is that it controls drainage and hence forest composition and structure. This interpretation could be tested by comparing bird communities at other pairs or sets of New Guinea sites similar in elevation but differing markedly in slope. If our interpretation is correct, then differences in slope are likely to be a major cause of local variation in species elevational ranges, with Karimui's large flat expanse making it an extreme example of a phenomenon widespread in milder form.

The Massenerhebung effect

There is an extensive worldwide literature on elevational differences not only in species elevational ranges, but also in habitats and climate, among different mountains within the same geographic area. Initially described for the Alps and other European mountains, these differences have been subsequently recognised for tropical mountains as well (Troll 1948, Richards 1952, Howard 1968, Grubb 1971, Whitmore 1990, Foster 2001, Bruijnzeel *et al*. 2010). The effect is cited most often by its original German name Massenerhebungeffekt (= 'mass elevation effect'), or less often recently by the English name 'Merriam effect'. The

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main pattern is that comparable habitat zones and species elevational ranges tend to be at higher elevations on large high mountains far from the sea than on small coastal mountains or isolated mountains. While explanations of the effect are still incomplete, contributing factors include lower limits of mountain cloud caps near the thermally stable ocean than inland, and also differences in exposure to wind. We shall now provide three sets of examples for New Guinea birds.

Comparisons of one species on many mountains.—Table 4 lists elevational ceilings and floors that we determined for *Seicercus poliocephalus* on 13 New Guinea mountains. This warbler offers three advantages: it is widely distributed in New Guinea; it is abundant and sings frequently and distinctively, lending itself to accurate determination of its elevational range; and it has no New Guinea congener, whose presence or absence might have affected the species' elevational range and thereby confounded the interpretation.

Four of these 13 mountains are high peaks (2,560–4,770 m) of New Guinea's Central Range at a mean distance of 177 km (90–250 km) from the coast. The other nine peaks are lower peaks (mostly 1,400–2,218 m, plus one of 2,954 m) of New Guinea's outlying ranges (eight peaks) and of the former outlier Yapen Island (once part of the New Guinea mainland during Pleistocene times of low sea level, now a separate island) (see Fig. 1 of Diamond & Bishop 2021b). These nine outlying peaks lie at a mean distance of only 19 km (4–50 km) from the coast. Of the transects that we studied on these nine outliers, four were on the coastal watershed directly exposed to ocean winds; two transects were on the inland-facing watershed, wind-protected because they faced directly inland and away from the coast;

TABLE 4

Elevational range of Island Leaf Warbler *Seicercus poliocephalus* on 13 New Guinea mountains. Elevational ranges were measured either by JD & KDB, or by JD (six and seven mountains, respectively). Sources: Diamond (1972), Beehler *et al*. (2012), Diamond & Bishop (2015, 2020, 2021a), and our unpubl. observations. Fourth column: four of these mountains belong to New Guinea's Central Range, whilst the others are among the outliers depicted in Fig. 1 of Diamond & Bishop (2021b). (NCR = North Coastal Range.) Fifth column: approximate distance of the transect from the coast. Sixth column: of the transects studied on outliers, four ('coastal') lie in the coastal watershed facing the coast, two ('inland') in the inland watershed facing the inland lowlands, and three ('interior') lie within the outlier surrounded by mountainous terrain of the outlier itself. Note that the elevational range of this warbler varies greatly among transects, as depicted in Fig. 1. This variation exemplifies the Massenerhebung effect, discussed in the text.

Mountain	**Summit (m)**	**Elevational range (m)**	**Central Range?**	**Distance from coast (km)**	**Watershed**
Mt. Mandala	4,700	1,683–1,991	yes	250	
Mt. Albert-Edward	3,990	1,851–2,152	yes	90	
Arfak	2,954	1,207–1,728	no	20	interior
Mt. Sisa	2,689	1,866–2,100	yes	240	
Mt. Karimui	2,560	1,311–1,860	yes	130	
Foja	2,218	951–1,409	no	50	coastal
Cyclops	2,160	1,091–1,677	no	10	inland
Wandammen	2,075	1,000–1,387	no	4	coastal
NCR (Mt. Menawa)	1,886	808–1,372	no	40	inland
Adelberts	1,675	1,250–1,655	no	30	interior
Kumawa	1,654	366–1,219	no	5	coastal
Yapen	1,430	675–1,195	no	10	interior
Fakfak	1,400	552–1,261	no	6	coastal

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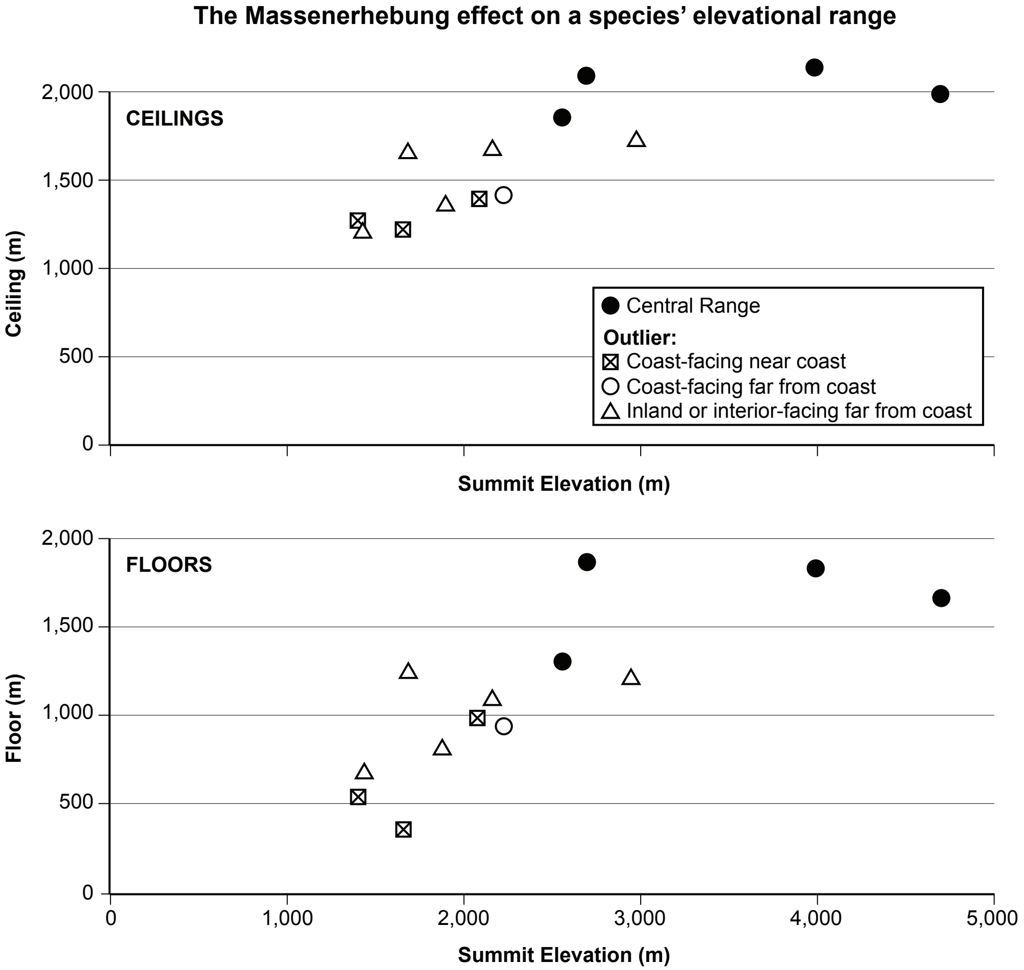

Figure 1. Example of the Massenerhebung effect: variation in the elevational ceiling and floor of the Island Leaf Warbler *Seicercus poliocephalus* on New Guinea mountains. Note that the warbler's ceiling (upper graph) and floor (lower graph) are higher on Central Range peaks than on outlier peaks; that they tend to be higher on higher peaks (summit elevation, abscissa); that they tend to be higher on inland-facing or interior-facing outlier transects than on coast-facing outlier transects; and that they tend to be higher on outlier transects further from the coast than on outlier transects nearer the coast. Data from Table 4.

and three were inside the interior of an outlier, also wind-protected because they were not directly exposed either to ocean wind or to the inland lowlands.

Table 4 and Fig. 1 show that the warbler's floor varies among mountains from 366 to 1,866 m, and its ceiling from 1,195 to 2,152 m. Both the floor and ceiling are higher on all four Central Range peaks than on any of the nine outliers (mean floor and ceiling 1,678 and 2,026 m, respectively, vs. only 878 and 1,434 m, respectively). Among the nine outliers, floors and ceilings are related to three factors: summit elevation, transect distance from the coast, and transect orientation. As for elevation, both floors and ceilings are higher on the four highest outliers (elevation ≥2,075 m: floors 951–1,207 m, ceilings 1,387–2,152 m) than on four of the five lowest outliers (elevations ≤1,886 m: floors 366–808 m, ceilings 1,195–1,372 m). (The exception is the Adelberts, which are only 1,675 m high, but whose transect faces the Adelberts' interior, and which lie further from the coast than most of the other outliers, and which consequently have a higher floor and ceiling than expected by

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their elevation alone.) As for distance from the coast, the three outliers closest to the coast (4–6 km) have on average lower floors and ceilings (639 and 1,289 m, respectively) than the six outliers 10–50 km from the coast (floors and ceilings 997 and 1,506 m, respectively). As for orientation, the four coastal-facing transects have on average lower floors and ceilings (717 and 1,319 m, respectively) than the five inland- or interior-facing transects (floors and ceilings 1,006 and 1,525 m, respectively). With three independent variables (elevation, distance and orientation), we would need a sample size larger than the nine outliers to apportion quantitively the relative effects of these three variables on floors and ceilings.

Thus, Table 4 and Fig. 1 illustrate for one New Guinea species the main pattern that we mentioned above for the Massenerhebung effect worldwide: that '…species elevational ranges tend to be at higher elevations on large high mountains far from the sea than on small coastal mountains or isolated mountains.'

Comparison of coastal- and inland-facing transects in the same mountain range.—In two cases we can illustrate the Massenerhebung effect by comparing two transects within the same outlier: a coastal-facing transect, compared to an inland- or interior-facing transect. One such involves the Kumawa Mts. (Diamond & Bishop 2015), where JD's 1983 North Kumawa coastal transect rose directly from the coast to an elevation of 938 m at 5 km inland, while JD & KDB's Central Kumawa inland transect descended to 1,025 m in the mountains' interior 14 km inland and separated from the coast by many higher ridges. Three vocal, common or abundant, easily detected species were present at or above 1,025 m on the interior transect but had elevational ceilings below 938 m on the coastal one: Great Cuckoo-Dove *Reinwardtoena reinwardti*, Little Shrikethrush *Colluricincla megarhyncha* and Northern Fantail *Rhipidura rufiventris*, with ceilings at 742, 876 and 671 m, respectively.

Our other comparison involves the Foja Mts. (Beehler *et al*. 2012), where JD's 1979 coastal transect peaked at 1,408 m and his 1981 inland-facing transect descended to 1,015 m. Three common species—*Charmosyna pulchella*, Red-breasted Pygmy Parrot *Micropsitta bruijnii* and Tropical Scrubwren *Sericornis beccarii*—had much higher elevational floors on the inland-facing transect than on the coastal one (1,442 vs. 610 m, 1,244 vs. 692 m, and 1,244 vs. 610 m, respectively). Conversely, there was no species with a well-established higher floor or ceiling on the coastal transect than on the inland-facing transect.

Each of these two comparisons of coastal vs. inland or interior transects within the same mountain range provides only limited tests of the Massenerhebung effect, because the two transects compared were at substantially different elevations. The transect locations were chosen for other reasons: accessibility, and to sample different elevations. To test specifically for the Massenerhebung effect, one would instead seek a coastal transect paired with an inland or interior transect spanning the same elevations, and one would perform repeated surveys to control for seasonal variation.

Differences in species elevational ranges between the Foja Mts. and Van Rees Mts.—Two of the outliers, Foja and Van Rees, offer a convenient comparison because they are close to each other (see Figs. 1–2 of Diamond & Bishop 2021b), and the Van Rees upland avifauna is virtually a subset of the Foja upland avifauna, but the Foja Mts. are almost twice as high as the Van Rees Mts. (2,218 vs. 1,262 m), and more than twice as far from the coast (50 vs. 20 km). Hence the Massenerhebung effect should lead to higher elevational ceilings and floors in the Foja Mts. than in the Van Rees Mts. The following paragraphs, to be summarised in Table 6, will confirm this. Ceilings and floors were measured by JD for a Foja coastal transect in 1979 and a Foja inland transect in 1981 (Diamond 1982, Beehler *et al*. 2012), and by JD & KDB for a Van Rees inland transect mostly in 1994, plus some observations at lower elevations in four earlier years (Diamond & Bishop 2021b). We shall compare in turn the elevational

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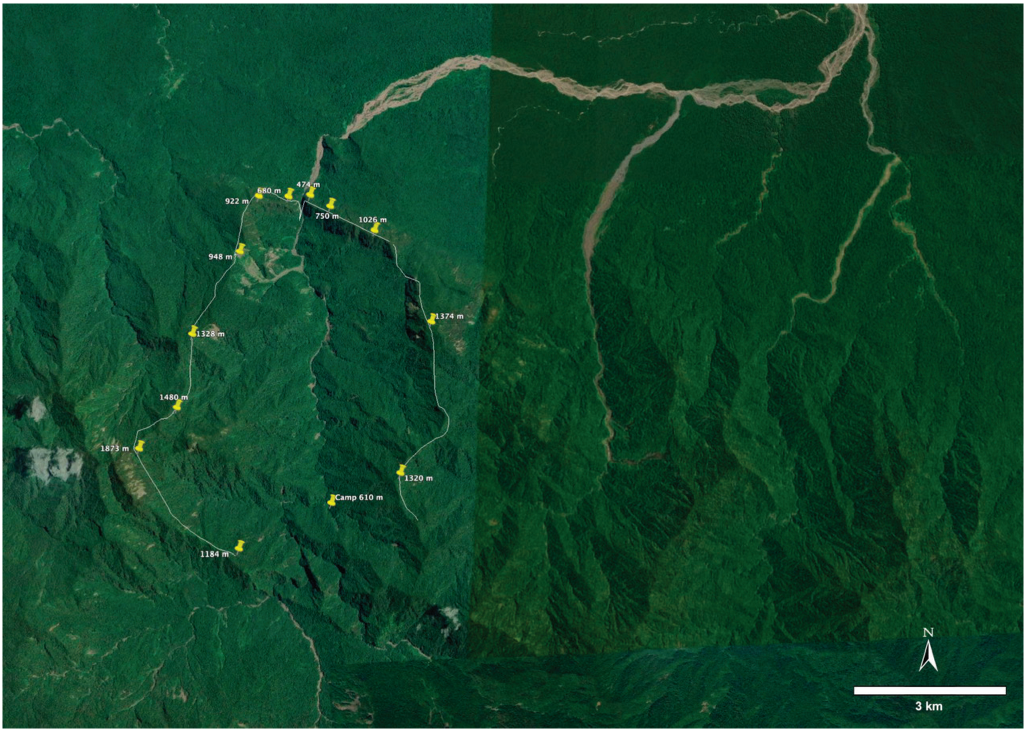

Figure 2. Google Earth view of the environment of Diamond's 1979 Foja coastal transect. Visible are the narrow north-flowing stream on which Diamond's camp was sited; the western and eastern ridges flanking the valley in which the stream lies; at the bottom of the field of view, the ridges south of Diamond's camp, rising towards the Foja summits; the near-vertical east / west barrier ridge constituting the northern flank of the basin, and pierced by the stream; and, at the top, New Guinea's lowland coastal plain beyond the east / west ridge, and in which the stream flows in a braided gravel bed. A line traces the crest of the western, eastern and northern ridges, with numbers denoting elevation readings in metres. Diamond's camp in the basin, labelled 610 m, was at 02°45′S, 138°63′E.

ceilings of shared upland species, the floors of shared upland species, and the ceilings of shared lowland species between the two outliers.

Table 5 compares elevational ceilings of upland species shared between Foja and Van Rees, for those species for which the floors can be determined with confidence. (We define upland species as those largely confined to sloping elevated terrain, and absent from the flat lowlands at or near sea level: Diamond & Bishop 2015, 2020, 2021a.) Of the 37 upland species of Van Rees, we could not analyse four because they are absent in Foja; we could not analyse four others, because we had too few observations in Foja, Van Rees, or both to permit defining the ceilings with confidence; and we could not analyse nine others, because their Van Rees ceiling was 'truncated' (i.e., we observed the species right up to our Van Rees summit of 1,206 m or within 50 vertical metres of it, so that our highest observation did not necessarily represent a species ceiling above which lay further terrain in which the species was certainly absent).

That leaves 20 upland species for analysis. A potentially confounding factor, discussed earlier, is that elevational distributions tend to be higher on inland-facing slopes than on coastal slopes. All of our Van Rees observations were on the inland-facing slope. Fourteen of the 20 Foja ceilings listed in Table 5 are from JD's inland-facing Foja transect, directly comparable to the Van Rees inland-facing transect. The other six Foja ceilings are from JD's coastal Foja transect, either because the species was not encountered on the inland-facing

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TABLE 5

Ceilings of upland species: Foja vs. Van Rees. For upland species present in both Foja and Van Rees, and for which elevational ceilings could be determined with confidence, this table gives the ceilings in each range. The right-hand column (Δ) is the Foja ceiling minus the Van Rees ceiling. Most ceilings are considerably higher in Foja than Van Rees, as predicted under the Massenerhebung effect. See text for discussion.

		Ceiling (in m)		
		Foja	**Van Rees**	**Δ**
Dwarf Cassowary	*Casuarius bennetti*	1,829	1,146	+683
Black-billed Cuckoo-Dove	*Macropygia nigrirostris*	1,912	1,119	+793
Pheasant Pigeon	*Otidiphaps nobilis*	1,670	1,079	+591
Claret-breasted Fruit Dove	*Ptilinopus viridis*	1,500	1,079	+421
Papuan Mountain Pigeon	*Gymnophaps albertisii*	2,040	1,067	+973
White-eared Bronze Cuckoo	*Chalcites meyerii*	1,238	1,034	+204
New Guinea Vulturine Parrot	*Psittrichas fulgidus*	1,637	1,049	+588
Blue-collared Parrot	*Geoffroyus simplex*	1,921	143	+1,778
Black-eared Catbird	*Ailuroedus melanotis*	1,113	1,146	-33
Mountain Meliphaga	*Meliphaga orientalis*	1,244	1,049	+195
White-eared Meliphaga	*Meliphaga montana*	1,020	1,206	-186
Obscure Honeyeater	*Caligavis obscura*	884	1,003	-119
Stout-billed Cuckooshrike	*Coracina caeruleogrisea*	1,384	1,098	+286
Piping Bellbird	*Ornorectes cristatus*	1,113	1,127	-14
Rusty Whistler	*Pachycephala hyperythra*	1,281	1,128	+153
Drongo Fantail	*Chaetorhynchus papuensis*	1,311	1,073	+238
Trumpet Manucode	*Phonygammus keraudrenii*	1,378	366	+1,012
Green-backed Robin	*Pachycephalopsis hattamensis*	1,238	1,070	+168
Papuan Scrub Robin	*Drymodes beccarii*	1,198	1,067	+131
White-rumped Robin	*Peneothello bimaculata*	762	884	-122

one (five cases) or because the species had a lower ceiling there than on the coastal transect (one case). As we shall see in the next paragraph, the inclusion of records from the Foja coastal transect strengthens rather than confounds our conclusions.

Table 5 shows that, of the 20 species ceilings compared, 15 have considerably higher ceilings (by 131 to 1,778 m, mean 548 m) in Foja than in Van Rees; only three species have slightly higher ceilings in Van Rees (by only 119, 122 and 186 m); and for two species the ceilings are the same (within 14 or 33 m). This is as expected for the Massenerhebung effect, because Foja is considerably higher than Van Rees and lies considerably further from the coast. The difference that the Massenerhebung effect causes between Foja and Van Rees is probably even greater than Table 5 shows, because six of the 20 Foja ceilings in Table 5 are from Foja's coastal transect. Table 4, and the three examples that we gave in the preceding section to compare Foja's coastal and inland-facing transects, suggest that some of the six species would have had even higher Foja ceilings if we had been able to measure them on the Foja inland-facing transect.

We similarly compared elevational floors of upland species and elevational ceilings of lowland species shared between Foja and Van Rees, for those species for which the floors could be determined with confidence. (It is meaningless to compare floors of lowland

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TABLE 6

Species ceilings and floors: Foja vs. Van Rees. For species present both in Foja and Van Rees, and whose elevational ceilings and / or floors could be ascertained, we compared the ceilings of upland species, the floors of upland species, and the ceilings of lowland species between the two ranges. For each of those three elevational limits, the table gives the number of species (no. species) for which the limit is higher in Foja by ≥100 m, the number for which the limit is higher in Van Rees by ≥100 m, and the number for which the limit is about the same (i.e., differs by less than 100 m between the two ranges). Numbers in parentheses (Δ in m) are the mean differences (in m) between the two ranges. Note that, for each limit, many more species have that limit at a higher elevation in Foja than Van Rees, and that the average difference is much greater for species with a higher limit in Foja than for species with a higher limit in Van Rees—exemplifying the Massenerhebung effect. See text for discussion.

	Foja higher		**VR higher**		**Same**	
	No. species	**(Δ in m)**	**No. species**	**(Δ in m)**	**No. species**	**(Δ in m)**
upland species ceilings	15	(548)	3	(142)	2	(24)
upland species floors	10	(474)	2	(182)	4	(60)
lowland species ceilings	25	(409)	12	(238)	11	(48)

species, because these are defined as species descending to sea level.) As summarised in Table 6, for all three comparisons—ceilings and floors of upland species, and ceilings of lowland species—elevational limits are higher in Foja than in Van Rees. Even more than for upland species ceilings, these comparisons under-estimate the effect for upland species floors and for lowland species ceilings, because many more of the upland floors and lowland ceilings than upland ceilings were measured on Foja's coastal slope, rather than on Foja's inland-facing slope (which offers a better comparison for Van Rees's inland-facing slope).

Thus, for many species the Massenerhebung effect is illustrated by differences between both floors and ceilings in the lower Van Rees Mts. compared to the higher and further inland Foja Mts. This agrees with the conclusions from our tabulation for *Seicercus poliocephalus* on 13 mountains in Table 4.

Barriers to dispersal?

It remains to discuss a surprising feature of the Foja avifauna that emerged from comparison with the Van Rees avifauna, and that was not recognised in JD's previous discussion of his Foja surveys (in Beehler *et al*. 2012): the unexpected absence, on Foja's low-elevation coastal transect, of 33 lowland species encountered at similar elevations in Van Rees and on numerous other New Guinea mountains (Table 7).

JD's low-elevation Foja transect, surveyed in 1979, was in the hills on the coastal slope and ran from 610 to 1,409 m. In eight days, JD observed 113 species: 62 lowland and 51 upland species. Our Van Rees transect surveyed in 1994 was on the inland-facing slope and ran from 494 to 1,206 m. In 20 days, we observed 147 species: 109 lowland species, 35 upland species and three winter visitors. The higher number of species observed on the Van Rees transect vs. the Foja transect is probably at least partly, though perhaps not entirely, due to the facts that more days of field work were devoted to the former transect, by two observers (JD & KDB) rather than by just one (JD).

But it is still surprising that the Foja coastal transect yielded no records of 33 species recorded at the same elevations (i.e., ≥610 m) in Van Rees. That's not because those species are absent from Foja: all 33 were recorded by Beehler *et al*. (2012) at or near Kwerba at the inland foot of the Foja Mts., 29 at elevations of 73–271 m, the other four at or slightly above 350 m (Beehler *et al*. 2012 reported very few observations above 271 m on their Kwerba

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TABLE 7

Expected lowland species missing on the Foja coastal transect. List of 33 lowland species that we observed on our Van Rees transect (494–1,206 m), but that JD did not find on his 1979 Foja coastal-slope hill transect (610–1,409 m). Columns 3–4 give the species' elevational ceiling on the Kwerba transect (73–750 m) on Foja's inland slope (surveyed by Beehler *et al*. 2012), and on our Van Rees transect, respectively. None of these 33 species was observed by JD on his 1981 Foja inland-slope transect (1,015–2,040 m). The right-hand column denotes records of each species on five other mountains, surveyed by JD (three) or by JD & KDB (two) at a similar elevational range: K = Mt. Karimui in the Central Range, 610–1,113 m (Diamond 1972); A = an interior transect in the Adelbert Mts., 639–1,294 m (Diamond & Bishop 2021a); F = coastal transect in the Fakfak Mts., 600–1,208 m (Diamond & Bishop 2015); N = coastal transect in the North Kumawa Mts., 573–938 m (Diamond & Bishop 2015); and Y = coastal transect in the mountains of Yapen Island, 610–1,260 m (Diamond & Bishop 2020). Square brackets denote a different allospecies from the Van Rees and Foja allospecies of the same superspecies. Of the 33 species, one (*Heteromyias brachyurus*) lies outside the geographic range of mountains K, F, A and N, whilst nine lie outside the geographic range of Y. Thus, of the 33 lowland species not observed on the coastal Foja transect, 33 of 33, 26 of 32, 22 of 32, 20 of 32, 20 of 32, and 18 of 24 geographically 'available' species were observed in Van Rees and on K, A, F, N and Y, respectively. See text for possible reasons why these otherwise widespread species are absent on Foja's coastal transect, although present at lower elevations in Foja.

		Ceiling (m)		
		Foja inland	**Van Rees**	**Other mountains**
Victoria Crowned Pigeon	*Goura victoria*	375	799	[F] [N]
Pink-spotted Fruit Dove	*Ptilinopus perlatus*	100	921	K A F N Y
Purple-tailed Imperial Pigeon	*Ducula rufigaster*	73	1,152	K F N
Pinon's Imperial Pigeon	*Ducula pinon*	100	1,049	A F Y
Little Bronze Cuckoo	*Chalcites minutillus*	73	640	A F
White-crowned Cuckoo	*Caliechthrus leucolophus*	150	848	K A F N
Marbled Frogmouth	*Podargus ocellatus*	73	1,049	K A F N Y
Papuan Frogmouth	*Podargus papuensis*	73	1,049	K A Y
Palm Cockatoo	*Probosciger aterrimus*	271	1,049	K A F N Y
Red-flanked Lorikeet	*Charmosyna placentis*	271	854	K A F
Rainbow Lorikeet	*Trichoglossus haematodus*	271	1,049	K A F N Y
Salvadori's Fig Parrot	*Psittaculirostris salvadorii*	111	671	[K]
Eclectus Parrot	*Eclectus roratus*	271	1,104	K A F N Y
Red-cheeked Parrot	*Geoffroyus geoffroyi*	271	951	K A F N Y
Buff-faced Pygmy Parrot	*Micropsitta pusio*	73	945	A
White-eared Catbird	*Ailuroedus buccoides*	110	729	K N
Helmeted Friarbird	*Philemon buceroides*	271	902	K A N Y
Puff-backed Meliphaga	*Meliphaga aruensis*	73	1,006	K F
Mimic Meliphaga	*Meliphaga analoga*	73	732	K F N Y
Yellow-bellied Gerygone	*Gerygone chrysogaster*	111	817	K A F N Y
Black Butcherbird	*Cracticus quoyi*	73	854	K A F N
Hooded Butcherbird	*Cracticus cassicus*	73	945	K A N Y
Boyer's Cuckooshrike	*Coracina boyeri*	111	863	K A F N Y
Black-browed Triller	*Lalage atrovirens*	111	860	[K] A F
Northern Fantail	*Rhipidura rufiventris*	350	845	K A F N Y
Spangled Drongo	*Dicrurus bracteatus*	271	878	K A N Y
Twelve-wired Bird of Paradise	*Seleucidis melanoleucus*	400	610	K Y
King Bird of Paradise	*Cicinnurus regius*	111	619	
Hooded Monarch	*Symposiachrus manadensis*	271	732	
Spot-winged Monarch	*Symposiachrus guttula*	111	787	K F N
Black-chinned Robin	*Heteromyias brachyurus*	500–600	691	Y
Black-sided Robin	*Poecilodryas hypoleuca*	111	799	K A N
Black Sunbird	*Leptocoma aspasia*	271	799	K A Y

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transect). Also, JD recorded 11 of the 33 species in his brief stop at Bora Bora village in the coastal lowlands 20 km north of his Foja coastal transect, in just a few hours at the village and airstrip distant from forest. All 33 are lowland species: their elevational ceilings on the Van Rees transect all fell between 610 and 1,152 m (mean 867 m); and none was found on the Foja high-elevation inland-facing transect that JD surveyed in 1981 (1,177–2,040 m, plus four hours at 1,177–1,015 m). Why, when all of these species were present in the lowlands at Foja, and when all of them ascended to at least 610 m in Van Rees, did none reach at least 610 m on the Foja lowland transect?

Brace yourself for some complicated reasoning, as we eliminate possible mundane explanations for those 33 absences!

First: could many of the 33 species have been present but overlooked on the Foja coastal transect? About four of the 33 missing species are inconspicuous (Buff-faced Pygmy Parrot *Micropsitta pusio*), uncommon (Little Bronze Cuckoo *Chalcites minutillus*) or both. But at least half are among the commonest, or noisiest, or most conspicuous species of New Guinea hill forest. It is very unlikely that Pinon's Imperial Pigeon *Ducula pinon*, Palm Cockatoo *Probosciger aterrimus*, Rainbow Lorikeet *Trichoglossus haematodus*, Eclectus Parrot *Eclectus roratus*, Helmeted Friarbird *Philemon buceroides*, Yellow-bellied Gerygone *Gerygone chrysogaster*, Black Butcherbird *Cracticus quoyi*, Hooded Butcherbird *Cracticus cassicus* and Spangled Drongo *Dicrurus bracteatus* would have escaped JD's attention for his eight days on the Foja coastal transect if they had been present.

Some of those species are targets of hunters in inhabited areas of New Guinea. Might they have been hunted out on the Foja coastal transect, but not on the Van Rees transect? Surely not: both transects lie in very sparsely populated regions; both were remote from the nearest habitation; neither showed any signs of any past human visit; and at both transects the tameness of large mammals and birds that elsewhere in New Guinea are the favoured prey of hunters testified to their lack of experience of hunting on the transect.

Might the explanation for the absence of the 33 species on the Foja coastal transect, despite their presence at the same elevations on the Van Rees transect, involve some peculiarity of the latter, rather than a peculiarity of the Foja transect? No: their presence at elevations of 494–1,152 m on the Van Rees transect is normal for New Guinea; their absence at 610–1,409 m on the Foja coastal transect is the exception requiring explanation. Table 7's right-hand column lists records of the 33 species, in approximately the same elevational range as that of the Foja coastal transect, on five other New Guinea mountains surveyed by JD (three) or by JD & KDB together (two). Each mountain lies outside the geographic range of 1–9 of the 33 species, leaving 24–32 species to analyse. On the five mountains, 18, 20, 20, 22 and 26 of the 24–32 geographically available species were recorded. Thus, the norm at those elevations in New Guinea is the presence of most of the 'available' species among the 33, rather than the absence of all of them.

Might the absence of the 33 species on the Foja coastal transect be a consequence of the Massenerhebung effect? (Now for the most complicated paragraph of reasoning!) In theory, that would be possible if Foja ceilings were on average so much lower than Van Rees ceilings that the predicted Foja ceilings for Table 7's 33 species of our Van Rees transect missing on the 1979 Foja coastal transect were all lower than 610 m, the base of the Foja transect. In reality, Foja ceilings of lowland species are on average higher, not lower, than Van Rees ceilings (Table 6): higher by 157 m. Some Foja ceilings were on the inland-facing transect of JD's 1981 survey and the three surveys of Beehler *et al*. (2012); some were on the Foja coastal transect of JD's 1979 survey. If we restrict attention to Foja ceilings on the coastal transect (i.e., the transect whose species absences we seek to explain), then for species present on both our Van Rees transect and JD's 1979 Foja coastal transect, ceilings

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were virtually the same: on average, just 51 m higher on the former. (That is because of two opposite components of the Massenerhebung effect: Foja, being larger and higher and further inland than Van Rees, tends for that reason to have higher ceilings; but our Van Rees transect, because it is inland-facing, tends to have higher ceilings than the Foja 1979 coastal transect.) The main conclusion is that ceiling differences of lowland species shared by these two transects are much too small, and apparently (but not significantly) in the wrong direction, to explain absences of 33 other lowland species from the Foja transect.

Instead, as a hypothesis to explain the absence of those 33 lowland species from the Foja transect, we call attention to a peculiarity of its terrain that became apparent only via detailed examination of Google Earth satellite views of the region. The Foja coastal transect rises from what is in effect a sunken basin surrounded by high steep-sided ridges. JD selected the transect for his 1979 Foja survey because his helicopter was at that time not carrying equipment necessary to construct a landing pad in the 1,621-m Foja bog clearing that JD had discovered from the air, and which subsequently served as camp for his 1981 survey (and possibly also for the high-elevation surveys of Beehler *et al*. in 2005, 2007 and 2008). The site closest to high elevations at which the helicopter was able to land and to unload JD was the bank of a narrow mountain stream at 610 m, at 02°45’S, 138°63’E. That camp served as the base for his 1979 coastal transect, which sloped steeply upwards south from the bank.

Google Earth views (Fig. 2) show that JD’s camp and the transect base lie in a basin at the south end of a stream flowing due north. The basin’s west and east sides consist of steep-sided ridges rising to *c*.1,500 m and 1,375 m, respectively. The basin’s south side (JD’s coastal transect) rises steeply towards a Foja summit (*c*.2,175 m). Some 6.3 km north of JD’s camp, the stream is almost completely blocked by a remarkable east / west barrier ridge. This ridge is narrow (<50 m wide) from north to south, has near-vertical south and north faces, and extends several km east and west to join the north / south ridges forming the basin’s east and west sides. Most of the barrier ridge’s crest is at 700–1,000 m, dipping to 474 m at the stream’s exit.

As for the stream draining the basin, it flows north from JD’s campsite through an increasingly narrow V-shaped valley, until the valley’s width for the final km before the east / west barrier ridge forming the valley’s north wall is less than 20 m wide. The valley floor and the stream drop from an elevation of 610 m at JD’s camp to *c*.200 m where the stream pierces the barrier ridge via a very narrow vertical cleft 270 m high and less than 20 m wide (Fig. 3). Beyond this, the stream enters gently rolling terrain, lies in a broad braided gravel bed, within a few km reaches New Guinea’s flat north coastal plain covered in lowland rainforest at an elevation of 170 m, and flows east in meanders to join the north-flowing Tor River.

What does this topography mean for the potential dispersal routes of lowland bird species from the north coastal plain at 170 m into the basin from which JD’s coastal transect rises? Entering the basin from the west or east would require crossing steep ridges at about *c*.1,500 or 1,375 m. Entering it from the south, from lowland forests of the Mamberamo River basin, would require flying up the Foja’s south slope to the watershed at *c*.2,000 m, and descending the north slope. Entering the basin from the north would require either: ascending the near-vertical north face of the barrier ridge, most of which rises 530–830 m from the coastal plain, decreasing to a 270-m rise at the stream cleft; flying high over the coastal plain to cross the barrier ridge in the air; or flying through the stream cleft itself, which approximates to a tunnel 1 km long and <20 m wide. JD’s coastal transect did support 62 lowland species, which must have arrived by one or more of those unappealing routes. But the 33 species of Table 7 did not arrive, or else they arrived in too low numbers to

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Figure 3. Google Earth close-up view, from the south, of the east / west ridge closing to the north the basin viewed in Fig. 2. The ridge has near-vertical southern and northern faces, and is pierced by the basin's stream via a cleft only *c.*20 m wide.

establish populations. We note that only eight of those 33 are species regularly observed to fly high above the forest canopy. Most of the rest inhabit the forest interior. We would not expect *Goura* pigeons, Yellow-bellied Gerygone, King Bird of Paradise, Spot-winged Monarch *Symposiachrus guttula* or Black-sided Robin *Poecilodryas hypoleuca* to ascend high vertical cliff faces, or to fly through a long narrow tunnel over a mountain torrent. But those 33 lowland species faced no such significant obstacles in traversing the gradually sloping foothills of the Van Rees Mts. to reach our transect thereon.

Of course, this interpretation that barriers to dispersal explain the Foja coastal transect's missing 33 species is speculative. Perhaps its plausibility can be assessed by examining possible barriers to bird dispersal elsewhere in New Guinea. Such effects of barriers could prove important, for example by causing actual species ranges to be smaller than implied by the usual maps showing continuous distributions.

We are grateful to an anonymous reviewer for pointing out that our interpretation of these upland dispersal barriers limiting and impoverishing lowland species access to a lowland basin is the converse of the much more familiar phenomenon of lowland dispersal barriers limiting upland species access to mountain tops. Competitive release—i.e., expansion of elevational range in the absence of a congener—is frequently observed for those upland species that do succeed in colonising a mountain top (*cf.* our preceding section on competition). Might those lowland species that did succeed in colonising JD's Foja coastal transect also exhibit competitive release of their elevational range?

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Outlook

Obviously, our studies provide only an initial overview of variation in species elevational ranges in New Guinea. They leave much still to be done. We suggest some priorities for further studies.

Many of the transects analysed in this paper were surveyed ornithologically only once. But bird distributions may vary between seasons and years. Hence the patterns that we have described require confirmation by repeated surveys over multiple years while controlling for seasonal effects.

Are there any systematic differences between elevational ranges on the northern and southern watersheds of the Central Range?

Can one generalise about how often the presence or absence of competing species cause changes in New Guinea elevational ranges, as Terborgh (1971) and Terborgh & Weske (1975) did for Peru?

Can other effects of terrain slope on elevational ranges be recognised, besides the ones that JD noted at Karimui?

The Massenerhebung effect on elevational distributions has been studied extensively elsewhere in the world, but not in New Guinea. Our Tables 4–6 show that it is also significant for New Guinea birds. It warrants much more study in New Guinea, not only for birds but also for other animal groups and vegetational zones. The effect's explanation around the world remains debated.

Our Table 7, comparing the lowland avifauna of Diamond's 1979 Foja coastal transect with our own Van Rees transect, suggests a large effect of barriers to dispersal on species distributions. If our interpretation of that comparison is correct, such barriers are likely to be an important phenomenon elsewhere in New Guinea as well.

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