

Limited support for the “abundant centre” hypothesis in birds along a tropical elevational gradient: implications for the fate of lowland tropical species in a warmer future

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Abstract

Aim: Since Darwin, ecologists have assumed that species tend to be abundant in the centre of their geographic distributions and rare at their range edges. We test two predictions of this abundant centre hypothesis: (a) that species are common in the centre of their range and rare at the edges and (b) that empirical distributions along environmental gradients are well described by symmetric bell-shaped curves.

Location: A reef-to-ridgetop elevational gradient in the Yopno–Urawa–Som Conservation Area (YUS CA) on the Huon Peninsula in Papua New Guinea.

Taxon: Birds.

Methods: We use mist net capture rates to quantify species' abundances as a function of range position, then fit a series of models with different shapes, including symmetric curves, to species' empirical abundance distributions.

Results: Species peak abundances were located near species' low elevation range edges, high elevation range edges and everywhere in between. Real abundance distributions were fit well by symmetric curves in fewer than half of the species we analysed. Most lowland species have high abundances at their low elevation margin near sea level.

Main conclusions: We find only limited support for the abundant centre hypothesis. Most lowland species appear to currently occupy a “truncated” realized niche, suggesting that they will be able to persist at low elevations even as temperatures increase and that lowland biotic attrition is unlikely. In addition to analyses, we present (a) a full species list for the 256 species recorded thus far within the YUS CA, with elevational limits for all forest species and (b) the raw data from our extensive mist net surveys. This information provides valuable baseline data that can be used by future biodiversity scientists to evaluate the changes in the YUS avifauna and will be generally useful to biodiversity scientists studying tropical elevational gradients.

KEYWORDS

abundance distribution, abundant centre hypothesis, biogeography, biotic attrition, elevational gradient, gradient analysis, truncated niche

1 | INTRODUCTION

All species on the Earth have range limits and are thus found only within certain geographic bounds. However, species are not uniformly abundant within the regions where they live. Since Darwin, biologists have assumed that species should generally be most common in the centre of their geographic distribution and relatively rare at their range margins (Brown, 1984; Brown, Mehlman, & Stevens, 1995; Darwin, 1859; Whittaker, 1967). This idea—the expectation that species' abundance distributions are statistically well described by symmetric bell-shaped curves—is termed the “abundant centre” hypothesis (Sagarin & Gaines, 2002a). Bell-shaped abundance distributions are thought to arise because environmental conditions are optimal in the centre of the population's range, and that population density is highest in these optimal conditions. Away from the range centre, conditions deteriorate, with concomitant declines in population density, until abundance drops to zero at the range limit (Brown, 1984). While other abundance distributions (e.g. flat, monotonic, plateau-shaped or skewed) may occur in nature (Austin, 2002; Oksanen & Minchin, 2002), bell-shaped abundance distributions are often assumed to predominate and have even been called “a general biogeographic rule” (Hengeveld & Haeck, 1982). However, this confidence may be misplaced: for example, a synthesis found that only 39% of 145 separate tests supported the abundant centre hypothesis (Sagarin & Gaines, 2002a), a result echoed by other recent studies (e.g., Dallas, Decker, & Hastings, 2017; Fuller, Harcourt, & Parks, 2009; Murphy, VanDerWal, & Lovett-Doust, 2006).

Whether or not the abundant centre hypothesis typically describes real-world abundance distributions along environmental gradients is not a trifling curiosity. Instead, the assumption that populations are most abundant at the centre of their range and rare near their range limits underlies many ecological ideas (reviewed in Sagarin, Gaines, & Gaylord, 2006). For this paper, we focus on one such application: predicting where lowland species will live along elevational gradients in a warmer future. Consider a species that inhabits equatorial lowland forests from sea level to 1,000 m. Climate envelope models are typically used to predict where species will live in a warmer future; such models are based primarily on temperature. These models assume that the climate at sea level approximates the warmest conditions this species can tolerate, and also that the climate at 1,000 m is the coolest conditions suitable for this species. Thus, as temperatures warm, the naïve prediction from climate envelope models is that this species will shift upslope to track its preferred climatic conditions at both its warm (sea level) and cool (1,000 m) range limits. If this is indeed the typical response of lowland taxa to warming, then lowland tropical environments near sea level will slowly decline in species richness as taxa shift upslope, a process termed “lowland biotic attrition” (Colwell, Brehm, Cardelus, Gilman, & Longino, 2008). However, while this scenario might be accurate if our focal species is most abundant at its range core and rare at its range

limits, as predicted by the abundant centre hypothesis, an alternative possibility is that the species is instead common at present near sea level (i.e. at its warm range limit). Such an abundance distribution would suggest instead that the species could tolerate environmental conditions more extreme (i.e. hotter) than those present at its warm range limit, but that such conditions simply do not yet exist. This idea is termed the “truncated niche” hypothesis (Feeley & Silman, 2010) and leads to the opposite prediction—that our focal species would persist at sea level even as temperatures increase. And if most lowland species inhabit such “truncated niches,” then species richness may remain high in tropical lowland forests even in a warmer future. Thus, assessing whether or not the abundant centre hypothesis typically holds for tropical lowland species can provide guidance on whether or not we should expect lowland biotic attrition in tropical lowland forests, which are the most biodiverse terrestrial regions on the Earth (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000).

Here, we test whether the abundant centre hypothesis accurately describes the patterns of abundance in forest birds along an elevational gradient in New Guinea. There is a long history of biologists investigating elevational distributions in tropical taxa to test ecological and evolutionary theories (e.g. for New Guinean birds see Beehler, 1981; Diamond, 1973, 1986; Freeman, 2015). Temperature is the dominant abiotic variable that varies along tropical mountain slopes, where temperature declines linearly with increasing elevation. Thus, the environmental gradient along tropical mountain slopes is essentially one-dimensional—the dominant environmental gradient is simply the elevational gradient. This facilitates the analysis of abundance patterns compared to, for example, analyses across expanses of latitude and longitude where the relevant environmental variation is multidimensional (Sagarin & Gaines, 2002b). Nevertheless, we are not aware of previous tests of the abundant centre hypothesis in tropical montane taxa. We use a dataset of extensive mist net surveys conducted at 25 sites along a reef-to-ridgetop elevational gradient in the YUS Conservation Area (YUS CA, named after the Yopno, Urawa and Som Rivers) to investigate abundance distributions of New Guinean forest birds. We use this dataset to test the two key predictions of the abundant centre hypothesis—that (a) species are relatively abundant in the centre of their elevational distribution and rare at their range margins and (b) symmetric bell-shaped curves provide good fits to species' abundance distributions along the elevational gradient. Finally, we test the competing predictions of the lowland biotic attrition hypothesis (that lowland species' relative abundances are low near sea level) versus the truncated niche hypothesis (that lowland species relative abundances are high near sea level). New Guinean birds are rapidly shifting upslope associated with recent climate change (Freeman & Class Freeman, 2014a). Therefore, determining whether lowland biotic attrition is likely to occur as temperatures continue to rise is an important step in predicting the fate of the lowland New Guinean avifauna.



2 | MATERIALS AND METHODS

2.1 | Study site and survey methods

The YUS CA is located in the Saruwaged Range on the Huon Peninsula in Morobe Province, Papua New Guinea (between approximately 05°45′–06°20′S and 146°30′–147°00′E). Mist net surveys were conducted along an elevational gradient of primary forest stretching from the lowlands near the reef-fringed ocean at 143 m to the ridgetop at 2,936 m. The coastal strip below ~130 m has been cleared by fire and is a grassy plain dotted with small patches of isolated forest. The 143 m site is thus the lowest elevation forest along the YUS CA elevational gradient—we consider the site to approximate sea-level conditions. The 2,936 m site is located at a local ridgetop; fieldworkers were unable to survey higher elevation forests due to difficulty of access (treeline is at ~3,500 m). Fieldworkers conducted 25 extensive mist netting surveys along this reef-to-ridgetop transect between 2010 and 2012 (see Freeman, Class, Mandeville, Tomassi, & Beehler, 2013 for details, including coordinates for each mist net survey). Briefly, mist netting surveys were conducted along the 1 km trails that followed an elevational contour and typically consisted of 36 12-m nets arrayed over 600 m of the 1 km trail and opened for 2.5 days. As we deployed so many mist nets, our survey effort at each site was high (~1,000 mist net hours/site). As a consequence, we captured a sufficiently large number (~200) of individuals to satisfactorily characterize the understory bird community at each site (see Supporting Information Table S4). In addition to mist net surveys, which are most effective for understory and midstorey species, fieldworkers surveyed the entire forest avifauna present in YUS and determined forest species' elevational limits by recording ad lib observations over 15 person-months of fieldwork (various fieldworkers) and by conducting audial censuses (BMB). We present a complete species list with elevational limits in Supporting Information Table S5, and use these data to plot species richness along the YUS elevational gradient for the 216 forest species for which we determined species' elevational limits (Figure 1).

In sum, these 25 mist net surveys conducted between 2010 and 2012 along a ~3,000 m elevational gradient captured ~5,000 individuals from 139 species (raw capture data with mist netting survey effort is provided in Supporting Information Table S4). Capture rates varied by a factor of five along the elevational gradient and generally increased with elevation—capture rates were very low at the lowest elevations (<300 m), and the highest capture rates were near the top of the transect at ~2,800 m (Supporting Information Figure S1). We surveyed each site once, with the exception of the 2,150 m site that was surveyed in both 2010 and 2011. These two surveys were conducted by different teams of fieldworkers and thus offer an opportunity to investigate the effects of different years and different fieldworkers on capture rates. Capture rates within species were highly correlated at the 2,150 m site between years ($r = 0.89$, $t_{32} = 10.99$, $p \ll 0.001$; see Supporting Information Table S4), and most common species had similar capture rates between years (Supporting Information Figure S2). This tight correlation gives us

confidence that our method of combining data from different years and different teams of fieldworkers is appropriate. In all analyses in this manuscript, we use data from the 2,150 m site from the 2010 survey only.

Here, we use capture rates from this dataset to test the predictions of the abundant centre hypothesis. For our principal analysis, we restricted our analysis to 17 species (see Table 1) that met four criteria: (a) they are common understory or midstorey species for which mist nets are a reasonable method to survey abundance, (b) they had wide enough elevational distributions that they were captured at 10 or more survey sites, and (c) their entire elevational distribution fell within the extent of the survey (i.e. we did not include species found at the 2,936 m site, as these taxa likely would also occur at still higher elevations that we were unable to survey). This last provision is necessary because testing the abundant centre hypothesis requires sampling across the entire range of a species' distribution.

Estimating abundance using mist net capture rates has been criticized (e.g. Remsen & Good, 1996). Our analyses investigate the patterns of abundance within species along the elevational gradient. We thus use “relative abundance” to mean the capture rate of the species at a given elevation relative to its highest capture rate at any elevation within its range. This definition differs from common usage wherein “relative abundance” means how abundant a species is relative to other species. We believe that our use of mist net capture rates to estimate species' relative abundances within their elevational distributions is appropriate because this approach only requires one assumption—that there is no bias among elevations in capture rates within species. This assumption may not hold if capture rates increase at high elevations where mist nets cover a greater proportion of the forest strata because trees are small in stature. However, this scenario does not apply to the YUS CA, where high-elevation forests are surprisingly tall, at least within the high elevations we surveyed (canopy heights are >30 m up to ~3,000 m; Venter et al., 2017). As high-elevation forests in the YUS CA are so tall, the very high capture rates at some high-elevation sites (Supporting Information Figure S1) is not a methodological artefact of elevational changes in forest height. Instead, the densities of understory and midstorey birds are likely particularly high at ~2,800 m and other high elevation sites.

2.2 | Statistical analysis

We tested two predictions of the abundant centre hypothesis. At its most basic, this hypothesis predicts that species are most abundant in the centre of their distributions and relatively rare at their range limits. To test whether this is indeed the case, we plotted relative abundances for the 17 common species that were captured at 10 or more sites and visually assessed whether field data generally conformed to the predicted distribution. Second, we analysed the species' distributions using a set of statistical models. We fit the set of five Huisman–Olff–Fresco (HOF) models to each of these 17 species to determine which model best fit species' real abundance

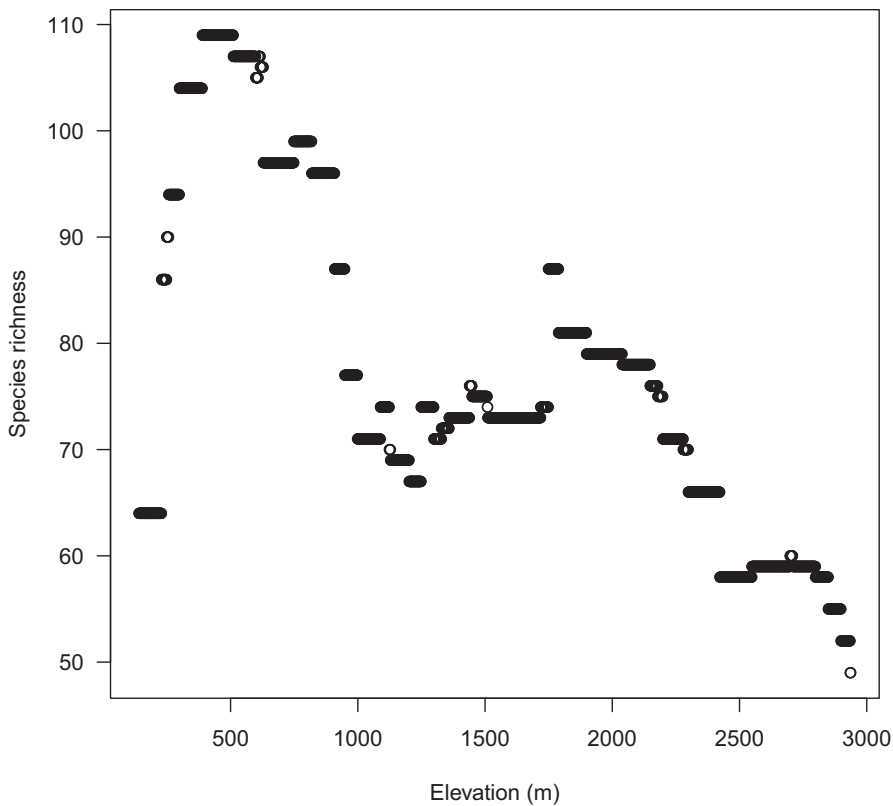


FIGURE 1 Species richness of forest birds along the elevational gradient in the YUS CA (for raw data, see Supporting Information Table S5). Species richness peaks at ~500 m and then declines, with a secondary peak at ~1,800 m. Humans have cleared the coastal plain, which may explain why species richness below 300 m is markedly low

distributions along the YUS elevational gradient. These five HOF models are hierarchical and, from simplest to most complex, define flat, monotonic, plateau, symmetric and skewed (either left or right skewed) abundance responses along the environmental gradient of interest (in our case, elevation). We conducted all analyses using the R software (R Development Core Team, 2017) and fit models following the equations described by Oksanen and Minchin (2002) using the “nlsm” function from the ‘Minpack.lm’ package (Elzhov, Mullen, Spiess, & Bolker, 2016). We then used Bayesian Information Criteria (BIC) to select the best fitting model for each species. Analyzing only the best fitting model can be misleading when multiple models have similarly good fits. Thus, we considered models within $\Delta 2$ BIC of the top model to be reasonably good model fits. We then plotted model predictions to visualize the shape of best fit models (e.g. to evaluate whether best fit symmetric models really fit symmetric curves to the data). We were unable to fit the complete set of HOF models for two species out of the 17 we investigated (skewed models did not resolve for *Cicinnurus magnificus* and *Symposiachrus axillaris*). Thus, we were able to assess which model (flat, monotonic, plateau, symmetric or skewed) best described species’ abundance distribution for 15 species (out of 17; see Table 1).

Next, we quantified lowland species’ relative abundances near sea level. We considered species captured at the 143 m survey site to be “lowland” species and calculated the relative abundances at the 143 m survey site for a total of 16 common species (Table 2; note that eight of these species were captured at 10 or more sites and thus also included in the analyses above, the others were captured at four or more sites and only included in this second, lowland

analysis). As described above, there is little forest below this site in the YUS CA; the coastal plain has largely been converted to a grassy expanse. We use this simple analysis to provide a crude evaluation of whether lowland species are likely to persist in the lowest forested elevations in the YUS CA as species shift upslope associated with temperature increases. We assume that species with low relative abundances at 143 m may be limited by the warm conditions near sea level (or other abiotic or biotic aspects of lowland forests, see Discussion for consideration of how factors other than temperature determine species’ elevational range limits). If so, these taxa are likely to shift upslope at their low elevation range limit such that they will disappear from forests near sea level within the YUS CA as temperatures increase. In contrast, we suggest that species with high-relative abundances at 143 m are likely to persist at this site even as temperatures rise.

3 | RESULTS

We conducted extensive fieldwork over multiple years to document 256 species of birds that occur between sea level and ~3,000 m along the YUS CA elevational gradient. We believe that this accounting of the local avifauna is nearly complete, as we added <5 species to this list in 2012, the final year of our fieldwork. We determined elevational limits for 216 species of forest birds of the total of 256 species recorded along the YUS Transect—some species were too rare to determine their elevational limits, while others were migrants or found only in grassy habitats (see Supporting Information

TABLE 1 Summary data for the 17 common species that we used to statistically analyse the shape of their abundance distribution along the elevational gradient. For each species, we provide the total number of mist netted individuals, the number of sites where they were captured, their elevational limits and elevation of peak abundance, the shape of the best fit HOF model (flat, monotonic, plateau, symmetric or skewed), and also any additional models that had strong support (within 2 BIC of the top model)

Species	Number of individuals mist netted	Number of sites	Low elevation limit (m)	High elevation limit (m)	Elevational breadth	Elevation of peak abundance	Scaled elevation of peak abundance	Best fit HOF models (plus models within $\Delta 2$ BIC)
<i>Gallicolumba beccarii</i>	37	13	390	2850	2460	2710	0.94	Monotonic
<i>Ailuroedus buccoides</i>	39	10	143	910	767	390	0.32	Flat
<i>Crateroscelis murina</i>	84	13	143	1660	1517	750	0.4	Symmetric (skewed)
<i>Chaetorhynchus papuensis</i>	43	14	303	2150	1847	1000	0.38	Flat (symmetric)
<i>Rhipidura atra</i>	171	15	610	2710	2100	1790	0.56	Symmetric (skewed)
<i>Symposiachrus guttula</i>	159	11	143	1000	857	610	0.54	Symmetric (but not peak abundance at centre)
<i>Symposiachrus axillaris</i>	35	12	750	2280	1530	1360	0.4	Models did not converge, see text
<i>Rhagologus leucostigma</i>	31	10	1090	2850	1760	1790	0.4	Flat
<i>Colluricincla megarhyncha</i>	186	15	143	1790	1647	750	0.37	Skewed
<i>Pitohui dicrous</i>	65	13	143	1660	1517	303	0.11	Plateau (monotonic)
<i>Melanocharis nigra</i>	166	11	230	1090	860	1000	0.9	Flat (plateau, monotonic, symmetric (but not rare at margins))
<i>Toxorhamphus novaeguineae</i>	68	10	143	910	767	303	0.21	Flat (monotonic)
<i>Toxorhamphus poliopterus</i>	265	15	610	2420	1810	1000	0.22	Skewed
<i>Oedistoma iliolophus</i>	153	14	230	1790	1560	1360	0.72	Symmetric
<i>Melilestes megarhynchus</i>	84	13	143	1790	1647	1000	0.52	Symmetric
<i>Xanthotis flaviventer</i>	22	10	143	1000	857	910	0.89	Monotonic (flat)
<i>Cicinnurus magnificus</i>	41	11	258	1360	1102	303	0.04	Models did not converge, see text

Table S5). Species richness along the YUS Transect peaks at ~500 m in the lowlands and declines at higher elevations, with a secondary peak at ~1,800 m (Figure 1). We present this summary of species richness patterns along the YUS Transect because it may be of interest to readers but reiterate that our primary motivation in this paper is to use mist netting data to describe the patterns of abundance *within* common species.

We found little support for the prediction of the abundant centre hypothesis that species should be common in the centre of their

elevational distribution and rare at their elevational range limits (Figure 2a). Instead, commonly mist netted species with wide elevational ranges in the YUS CA show a diversity of abundance distributions. There are species that reach peak abundance at their low elevation limit, their high elevation limit, and everywhere in between (Figure 2b). Similarly, low relative abundances occurred at all range positions and were common even within the centre of species' elevational distributions (Table 1; Figure 2b). The abundant centre hypothesis also predicts that species' abundance distributions are

TABLE 2 Summary data for the 16 common lowland species that we used to analyse the lowland biotic attrition versus truncated niche hypotheses. For each species, we provide the total number of mist netted individuals, the number of sites where they were captured, their elevational limits and elevation of peak abundance, and their relative abundance at the lowest elevation sampled site (the 143 m site)

Species	Number of individuals mist netted	Low elevation limit (m)	High elevation limit (m)	Elevation of peak abundance	Scaled elevation of peak abundance	Relative abundance at 143 m site
<i>Pitta sordida</i>	19	143	610	258	0.25	0.72
<i>Crateroscelis murina</i>	84	143	1660	750	0.4	0.06
<i>Rhipidura leucothorax</i>	16	143	610	143	0	1
<i>Symposiachrus guttula</i>	159	143	1000	610	0.54	0.19
<i>Symposiachrus manadensis</i>	25	143	618	390	0.52	0.36
<i>Arses insularis</i>	14	143	618	230	0.18	0.55
<i>Myiagra alecto</i>	12	143	610	230	0.19	0.22
<i>Poecilodryas hypoleuca</i>	29	143	750	143	0	1
<i>Colluricincla megarhyncha</i>	186	143	1790	750	0.37	0.21
<i>Pitohui kirhocephalus</i>	22	143	750	143	0	1
<i>Pitohui dicrous</i>	65	143	1660	303	0.11	0.79
<i>Toxorhamphus novaeguineae</i>	68	143	910	303	0.21	0.59
<i>Melilestes megarhynchus</i>	84	143	1790	1000	0.52	0.04
<i>Xanthotis flaviventer</i>	22	143	1000	910	0.89	0.17
<i>Cininnurus regius</i>	17	143	610	143	0	1

well fitted by symmetric curves. However, only 33% (5 out of 15) of species had abundance distributions that were best fit by symmetric curves (Table 1; Figure 3), and one of these species' (*Symposiachrus guttula*) fitted "symmetric" curve actually had a peak abundance near the lower range edge (Supporting Information Figure S6). Flat abundance distributions ($N = 5$) were equally common as the best fit model, and species' abundance distributions were also best fit by monotonic ($N = 2$), plateau ($N = 1$) and skewed ($N = 2$) models (Figure 3). Visual inspection of the abundance distributions for the two species that were not included in this analysis (due to failure of skewed models to converge; *Cininnurus magnificus* and *Symposiachrus axillaris*) suggests that they are likely best fit by skewed models (Supporting Information Figure S6). In several cases, multiple models provided similarly good fits (within $\Delta 2$ BIC of the top-ranked model). Pertinent to the abundant centre hypothesis, there were an additional three species for which the symmetric model was not the top model but was within $\Delta 2$ BIC of the top model (Table 1). However, in one of these species—*Melanocharis nigra*—the "symmetric" fit did not decline to low abundance at the range edges (Supporting Information Figure S6). Finally, we consider the possibility that our results are artefacts of random chance when analyzing small samples. We designed our analysis to minimize such problems by only including commonly captured taxa, and further note that sample size appears to be unrelated to our results. For example, our most commonly mist netted species (*Toxorhamphus poliopterus*, see Table 1) was most common near its lower range limit and had an abundance distribution that was best fit by a skewed curve. Thus, we believe that our results reflect biological reality rather than an artefact of sampling.

Next, we found limited support for the lowland biotic attrition hypothesis. Here, we focus on species' relative abundances near sea level rather than the shape of their abundance distribution. This is because the lowland biotic attrition hypothesis predicts that lowland species are scarce near sea level and more common at higher elevations, such that sea level conditions represent the edge of the species' climatic envelope. This logic leads to the projection that lowland species will gradually disappear from the lowest elevations as they shift upslope in response to climate change (Figure 4a). Instead, our results are more consistent with the truncated niche hypothesis that predicts lowland species remain relatively common at the warm limit of the elevational gradient (Figure 4b). We found that half of the common species (8 of 16) found at the lowest surveyed site along the YUS CA elevational gradient had relative abundances at this site of at least 0.5, and nearly all (14 of 16 species) had relative abundances of at least 0.15 (Table 2, Figure 4c). Thus, of the 16 lowland species we analysed, eight are common at the 143 m site, consistent with the truncated niche hypothesis, six are uncommon and do not clearly support either hypothesis, and two are rare, consistent with the lowland biotic attrition hypothesis.

4 | DISCUSSION

We found limited support for the abundant centre hypothesis in our investigation of abundance distributions along the YUS elevational gradient. While some species are indeed abundant in the middle of their distribution and rare at their edges, many others are not. For example, there were several species that reached peak relative

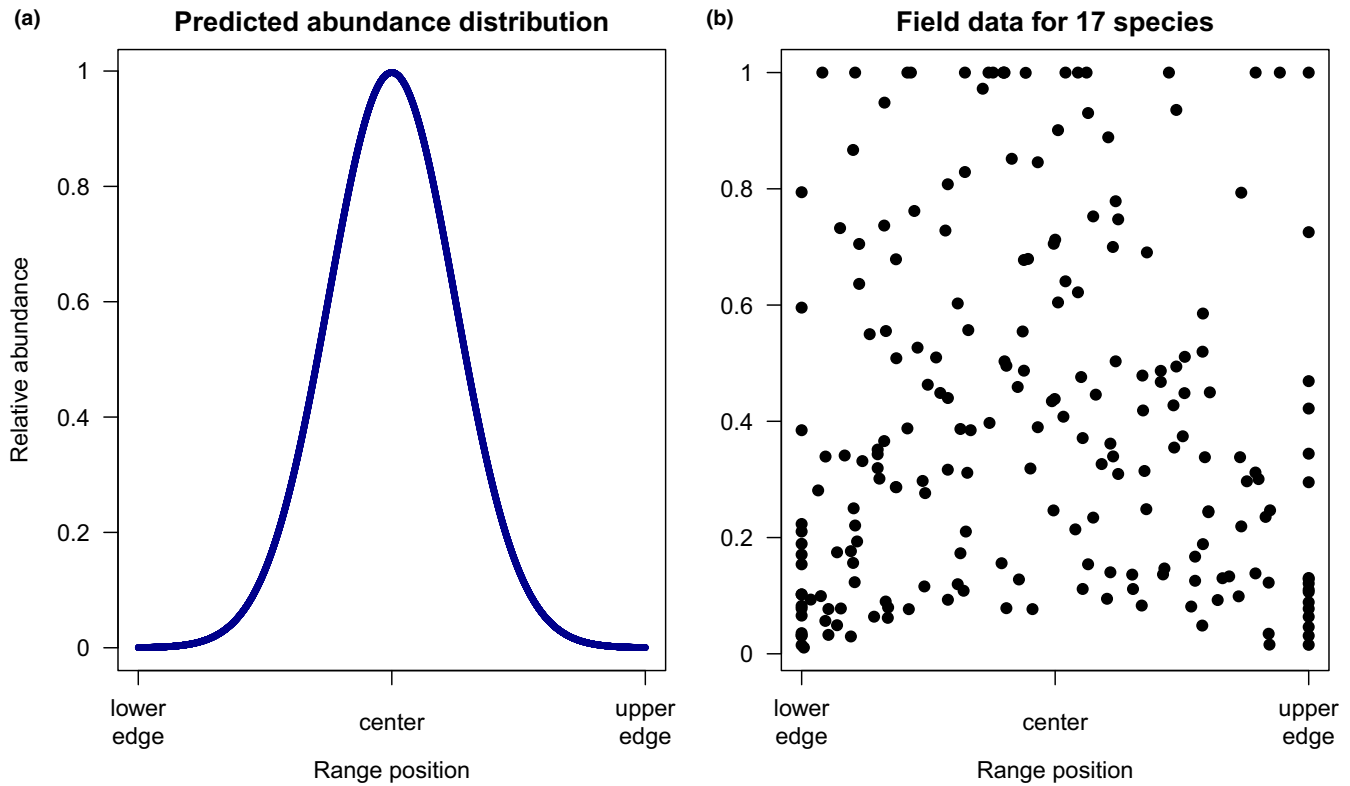


FIGURE 2 The abundant centre hypothesis predicts that species are relatively abundant in the centre of their distribution but rare at their range edges (a). Relative abundances from mist netting data of 17 common species with wide elevational distributions in the YUS CA in Papua New Guinea reveals a diversity of patterns (b). There are species with peak relative abundances at their lower range edge, their upper range edge and everywhere in between, and many examples where species are relatively rare in the centre of their ranges. Thus, birds do not generally inhabit abundant centre distributions along the YUS elevational gradient

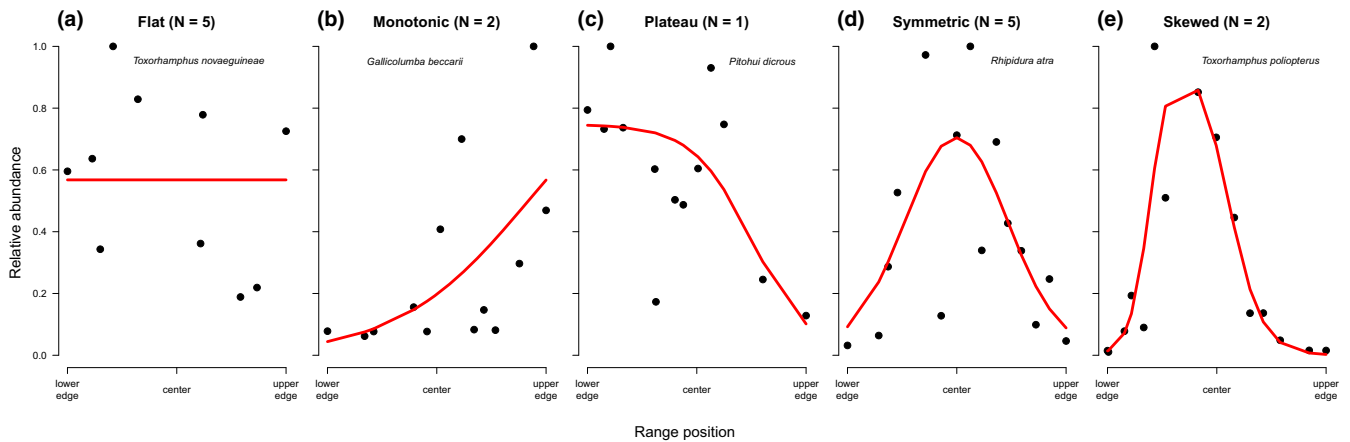


FIGURE 3 We fit a hierarchical set of five Huisman–Olf–Fresco (HOF) models for 15 common species with wide elevational distribution in the YUS CA to statistically assess support for different abundance distributions. From simplest to most complex, these models define flat, monotonic, plateau, symmetric and skewed abundance responses along the gradient of interest. We found examples where each model type was the best model for species in the YUS CA (a–e); the best fit model was a symmetric curve (as predicted by the abundant centre hypothesis) in only 5 of 15 cases (d)

abundance near their range limits, including some of the most common taxa (e.g. *Toxorhamphus poliopterus*), and many others that had similar relative abundances throughout the entirety of their elevational distributions. The abundant centre hypothesis predicts that

symmetric bell-shaped curves provide good fits to real abundance data, but a symmetric model was the best fit model in only 5 of 15 species for which we were able to fit the full array of five models (flat, monotonic, plateau, symmetric and skewed). There were a

further three species for which the symmetric model received high-statistical support during model comparison. However, on visual inspection, the best fit or highly supported symmetric models for these species actually approximated normal bell-shaped curves in only six out of eight species. Thus, using the most lenient criteria possible, only 40% (6 of 15) of the species we investigated are consistent with the predictions of the abundant centre hypothesis, a similar result to the 39% of cases consistent with the abundant centre hypothesis found in a larger review (Sagarin & Gaines, 2002a).

There are many factors that could explain why species do not exhibit abundant centre distributions (reviewed in Sagarin et al., 2006). First, species may actually inhabit abundant centre distributions, but this pattern may be difficult to detect due to human land use changes, temporal variation or incorrect identification of the environmental gradient used for analysis. It is clear, for example, that human-caused land use changes can alter species' abundances and thus their abundance distributions. Our study took place along an elevational gradient of contiguous primary forest in a remote mountain range, and thus this criticism is unlikely to apply to our results. We note that the avifauna of our lowest elevation site likely has been altered by its proximity to the anthropogenic coastal grassland. If so, this would likely reduce forest species' abundances and bias us

towards finding low abundances at lowland species' low elevation range edge (biasing our analysis towards finding abundant centre distributions). We, therefore, conclude that land use is unlikely to confound our results. Similarly, we argue that our analyses are relatively robust to noise from random sampling and temporal variation because we only considered common species mist netted at 10 or more sites, and because capture rates were tightly correlated at the one site that was surveyed in two different years. Moreover, while elevational migration is indeed common in many New Guinean frugivores and nectarivores (Diamond, 1972; Freeman & Class Freeman, 2014b), the species we analysed are mainly insectivores that defend year-round territories. Finally, we argue that defining species' abundance distributions along the elevational gradient is appropriate. The entire YUS elevational gradient is humid, precipitation is uniformly high and temperature is the dominant abiotic variable that varies between sites. Although there could be additional abiotic variables that are not correlated with elevation (e.g. consistency of cloud cover), we think it is likely that this elevational gradient is an appropriate one-dimensional environmental gradient over which to analyse the shape of abundance distributions.

We suggest that our results should be taken at face value, and that New Guinean birds may often occupy abundance distributions

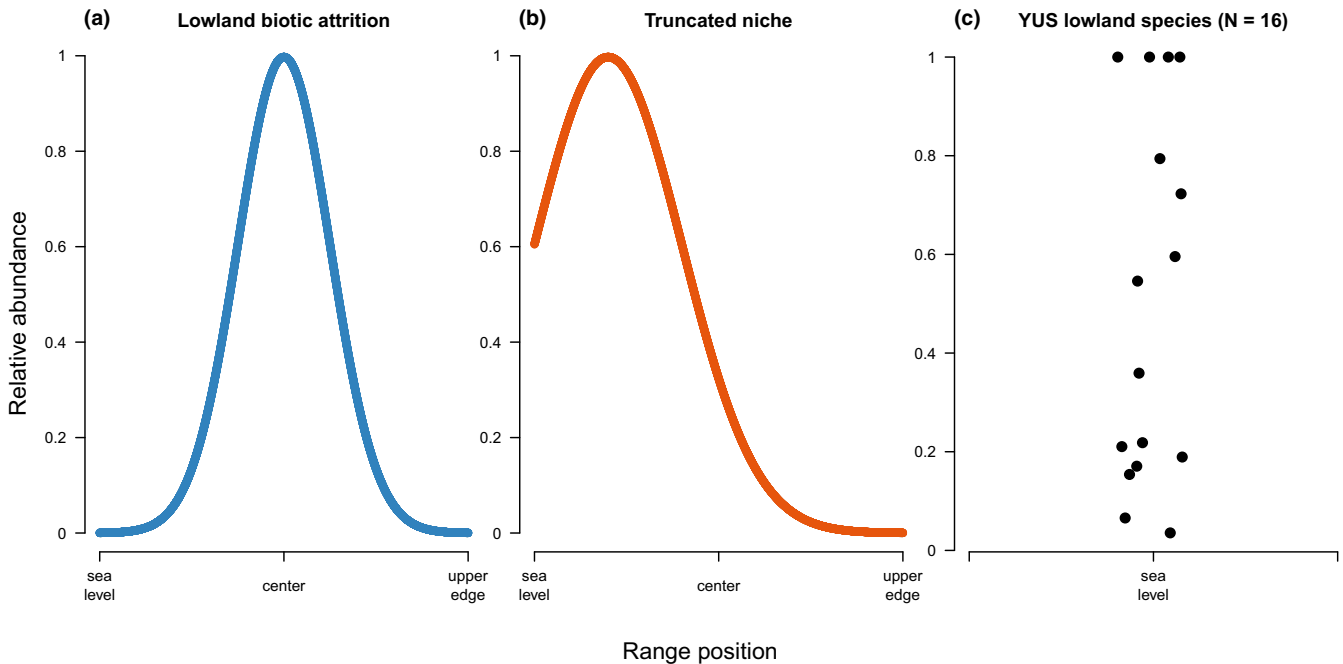


FIGURE 4 Most tropical species are shifting their distributions upslope due to climate change. However, an unanswered question is whether lowland species will shift upslope at their warm range limit (i.e. at sea level). If lowland species have low-relative abundance at sea level, they may indeed be likely to shift upwards at their warm range limit, leading to a decline in species richness at the lowest elevations (lowland biotic attrition, (a)). If lowland species are instead relatively abundant at sea level, their realized niche may be “truncated” such that they will persist at sea level as temperatures rise (b). For illustration purposes, we plot a smooth curve in (b), but note that a variety of abundance distributions (flat, monotonic, plateau, skewed, etc.) are consistent with the truncated niche hypothesis so long as relative abundance remains relatively high at sea level. The lowest elevation forest we surveyed in the YUS CA was located at 143 m—the coastal plain has been burned and consists of grass. We, therefore, consider this site to approximate “sea level” conditions along the YUS gradient. The majority of 16 lowland species found at 143 m are relatively common at this site—eight species have relative abundances >0.5 and 14 have relative abundances >0.15 (c). This suggests that most (but not all) lowland species in the YUS CA inhabit “truncated niches” and are likely to persist near sea level in the face of continued climate change



along elevational gradients that are not symmetric, bell-shaped curves. One interesting idea is that, even with a smooth underlying environmental gradient, biotic interactions may dramatically alter species' abundance distributions. For example, Diamond (1972) showed that two congeneric New Guinean understory birds that replace one another along the elevational gradient (*Crateroscelis murina* and *C. robusta*) reached peak abundance at their shared range margin; an "abundant edge" pattern that strongly suggests interspecific competition limits the distributions of these species of elevational replacements. We did not find this pattern for this particular species pair along the YUS gradient, perhaps because a third species (*C. nigrorufa*) is found in the YUS CA, where it is abundant in a narrow swath of middle elevations between lowland *murina* and montane *robusta* (*C. nigrorufa* was not present on Diamond's mountain). However, we found other examples where pairs of elevational replacements reach peak abundance near their shared range border; for example, the lowland *Toxorhamphus novaeguineae* occupies a uniform distribution (Figure 3a) while the upper elevation *T. poliopterus* is most common just above the range of *T. novaeguineae* (Figure 3a, see also raw data in Supporting Information Table S4). More generally, closely related species that replace one another along the elevational gradient are common in tropical montane avifauna (Freeman, 2017). Interspecific competition is one hypothesis that may explain the current maintenance of such distributions (Freeman, Class Freeman, & Hochachka, 2016; Jankowski, Robinson, & Levey, 2010; Terborgh & Weske, 1975), but it is difficult to rigorously test this idea. We suggest that quantitative analyses of abundance distributions of elevational replacements offer a promising avenue to test the interspecific competition hypothesis—this hypothesis predicts that species are relatively common at their shared range borders and can be rejected if species are instead relatively rare at their shared range border.

4.1 | Abundance distributions, climate change, and the fate of lowland species

Although data are sparse, montane New Guinean birds seem to be generally shifting their distributions upslope associated with recent temperature increases (Freeman & Class Freeman, 2014a; we are not aware of similar data for lowland New Guinean avifauna or indeed lowland species of any taxa from any tropical site). Upslope shifts driven by climate change can alter the patterns of species richness along elevational gradients—for example, species richness at single montane sites may increase as lower elevation species shift upslope. However, a major unanswered question is what happens to lowland communities. After all, at the bottom of tropical mountains, there are no species that can colonize from still hotter regions. If lowland species shift upslope at their low elevation boundary, a likely consequence will be that lowland communities decline in species richness, a process termed lowland biotic attrition (Colwell et al., 2008). Alternately, lowland species may be able to persist in place as temperatures warm if they are able to survive in conditions warmer than the warmest environment that currently exists (Feeley &

Silman, 2010). We suggest that relative abundances can help determine which of these two fates are most probable for particular taxa—lowland species that are rare at the bottom of the mountain may be sensitive to hot lowland environments such that they are likely to shift upslope in response to continued temperature increases, while if they are instead relatively common, they may be likely to persist in the lowlands even as temperatures continue to rise.

Our data show that most lowland species in the YUS CA have moderate to high relative abundances at the lowest elevation forest along this elevational gradient. Thus, most species in our study site appear to currently inhabit "truncated" realized niches such that they are likely to persist as climate change creates novel and hotter conditions near sea level. Still, there are several cases of species with low relative abundance at the lowest elevation forest that may be likely to disappear from their warm range limit in the coming decades as temperatures increase. It is unclear if this result can be generalized to other taxa or other tropical lowland regions. We await similar tests that examine lowland species' relative abundance patterns along tropical elevational gradients—amassing these types of datasets will provide insight into whether or not we should generally expect lowland biotic attrition in the tropics as climate change continues.

This line of reasoning assumes that species' range limits are controlled either directly by temperature or, alternately, by other abiotic or biotic factors that are themselves so tightly correlated to temperature that it appears as if temperature controls range limits. This may be the case if tropical taxa are physiologically specialized to the narrow range of temperatures they experience at a given site (Janzen, 1967). While tropical insects appear to often be physiologically specialized to narrow temperature regimes (Deutsch et al., 2008; García-Robledo, Kuprewicz, Staines, Erwin, & Kress, 2016), available data suggest that tropical birds are not particularly thermally specialized to the temperatures they experience within the elevational zone they inhabit (Londoño, Chappell, Castañeda, Jankowski, & Robinson, 2015), including within New Guinea, where species' thermal tolerances are not correlated with the ambient temperatures they experience at different elevations (Freeman, 2016). Understanding the degree to which species' range limits may be set by other abiotic factors (e.g. precipitation) or biotic interactions (e.g. the plant species that compose their habitats or insects that are vectors of diseases) is beyond the scope of this paper, but the recent findings that tropical taxa, including birds, are shifting their distributions upslope associated with recent temperature increases (e.g. for birds, see Forero-Medina, Terborgh, Socolar, & Pimm, 2011; Freeman & Class Freeman, 2014a). This implies that temperature is an important factor controlling tropical birds' elevational range limits, but it is more likely that temperature indirectly influences bird populations' range limits by altering species interactions than by directly impacting species' thermal physiology.

Species' range limits are influenced not only by myriad abiotic and biotic factors but also by human land use. The YUS CA is a remote landscape that consists nearly entirely of primary forest. Nevertheless, the coastal plain at our study site has been heavily

influenced by anthropogenic activities, and this has likely had consequences for the bird communities residing in the lowland forests adjacent to the coastal plain. In general, bird species richness along elevational gradients is high at low elevations and declines at higher elevations (McCain, 2009; Quintero & Jetz, 2018). However, the lowest elevation forests along the YUS gradient (below 300 m) had markedly lower species richness than nearby hilly lowland forest above 300 m (Figure 1)—YUS lowland bird communities are depauperate in comparison with other New Guinean lowland forests that have been studied (Beehler, Sengo, Filardi, & Merg, 1995; Mack & Dumbacher, 2007; note that lowland forests also had by far the lowest capture rates, Supporting Information Figure S1). We think it is likely that this low species richness at low elevations in the YUS CA is partially a result of the clearing of the coastal plain. Species richness in the YUS CA peaks at ~500 m and declines at higher elevations, but there is a noticeable secondary peak at ~1,800 m. While species richness sometimes peaks at low positions along elevational gradients (McCain, 2009), the existence of a secondary diversity peak at middle-high elevations is an unusual observation. We are unable to directly address why species richness is high at ~1,800 m. This may represent a real biological pattern (e.g., there may be distinct lowland and montane avifauna), but an alternate possibility is that relatively low avian species richness between ~1,000 and ~1,500 is related to the fact that slopes in YUS tend to be extremely steep (>45°) in this zone, leading to lower abundances and decreased diversity of the general biota (Venter et al., 2017).

5 | CONCLUSION

Tropical elevational gradients are the hottest of biodiversity hotspots (Myers et al., 2000) and provide an excellent natural laboratory to investigate ecological and evolutionary hypotheses (Jankowski, Londoño, Robinson, & Chappell, 2012). Both theory and empirical data suggest that tropical species may be especially vulnerable to climate change (Freeman & Class Freeman, 2014a; Laurance et al., 2011). In this paper, we show that common birds along a New Guinean elevational gradient exhibit a diversity of abundance distributions, and that the abundant centre hypothesis applies to a minority of the species we analysed. We further show that most lowland species exhibit moderate to high relative abundances near sea level, which is consistent with the idea that tropical lowland taxa may often persist near sea level in the face of temperature increases rather than shift upslope. Empirical data are urgently needed to assess how climate change has impacted lowland biota both in New Guinea and more generally in tropical regions. Finally, the advancement of biodiversity science relies on making hard-won field data publically available. To that end, we provide (a) a full list of the 256 species of birds documented thus far along the YUS elevational gradient, including elevational limits for all forest-dwelling species (Supporting Information Table S5), and (b) the raw data from our mist netting surveys (Supporting

Information Table S4), which we believe represent the most thorough mist netting survey of a single tropical elevational gradient published to date (taxonomy follows Beehler & Pratt, 2016). This information provides valuable baseline data that can be used by future biodiversity scientists to evaluate the changes in the YUS avifauna and will be generally useful to biodiversity scientists studying tropical elevational gradients.

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DATA AVAILABILITY

All relevant data are provided in Supporting Information Tables S4 and S5.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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