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No evidence for a positive correlation between abundance and range size in birds along a New Guinean elevational gradient

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ABSTRACT

A general pattern in biogeography is that species with high local abundances tend to have large geographic ranges, while species with low local abundances have small ranges. However, many tropical biotas do not show positive abundance–range–size correlations, potentially because ecological stability in the tropics promotes specialisation or because density compensation permits some higher-elevation species to be both abundant and small-ranged. I explored these ideas by studying the abundance–range–size correlation for 37 species of small-bodied understory New Guinean birds that live along a reef-to-ridgetop elevational gradient. Abundance (capture rates) is not related to range size (elevational breadth) in this dataset. In fact, when conducting phylogenetic regressions, abundance is significantly *negatively* related to range size. Because species' abundances do not systematically vary as a function of elevational zone, this pattern is not due to density compensation. Instead, elevational specialisation appears to explain the abundance–range–size correlation, interspecific competition being an important driver of elevational specialisation. If specialised taxa are sometimes able to achieve high local abundances compared to broader-ranged taxa, specialisation may break any consistent association between abundance and range size. Further studies are necessary to test the generality of this explanation.

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Introduction

Species that have larger geographic ranges are often more abundant within their range compared to species with smaller geographic distributions (Brown 1984; Lawton 1993). This relationship is typically strong. For example, Pearson's r , measuring the correlation between local abundance and geographic range size, averaged ~ 0.5 in >50 studies reviewed by Gaston (1996). The strength and near-ubiquity of the positive relationship between abundance and range size suggests the tantalising possibility that a common mechanism explains this pattern. Nevertheless, a large number of competing explanations have been proposed (reviewed by Borregaard and Rahbek 2010), which can be grouped into four general categories (Ferenc *et al.* 2016): (1) artefacts due to incomplete sampling (rare species are inherently more difficult to survey adequately than are common species); (2) niche breadth (species that can use a wider range of resources are both more common locally and have larger ranges); (3) vital rates (species with faster population growth may be both more common locally and may have larger ranges); and (4) dispersal (species

with higher dispersal will tend to have larger ranges and may have higher local abundances). Of these, the niche breadth mechanism is perhaps the most commonly invoked as it proposes the intuitively appealing idea that broad ecological niches allow species to be both locally abundant and occupy a wide range of environmental conditions, while species with narrow niches are rare and inhabit small distributions (Brown 1984; Lawton 1993). Although the abundance–range–size correlation is a more general pattern than many other eco-geographical patterns termed 'rules' or 'laws' (Gaston and Blackburn 2003), there is still variation in abundance–range–size correlations among studies, including occasional reports of negative correlations (e.g. Nana *et al.* 2014). This variation offers the opportunity to study the covariates that may explain why studies investigating the abundance–range–size correlation differ in their findings.

One intriguing idea is that the abundance–range–size correlation varies as a function of latitude. While the correlation is consistently strong and positive in the temperate zone (Gaston 1996), a number of recent studies of tropical montane taxa report that abundance is uncorrelated with (or negatively correlated to) range

size (Reif *et al.* 2006; Williams *et al.* 2009; Hughes *et al.* 2014; Nana *et al.* 2014; Reeve *et al.* 2016; Ferenc *et al.* 2016; but see Theuerkauf *et al.* 2017). There are several non-mutually exclusive explanations for why tropical taxa may have different abundance–range-size correlations than temperate-zone taxa (reviewed in Ferenc *et al.* 2016). First, methodological factors may be important. Most studies of tropical taxa come from mountains, and a negative abundance–range-size correlation could simply result from the fact that small-ranged endemic taxa tend to be high-elevation species. These endemic taxa may be locally common, but have small total ranges when range size is measured as species' total geographic range (Ferenc *et al.* 2016; Wen *et al.* 2018). Second, long-term eco-climatic stability may have permitted species to evolve ecological specialisation to a narrow range of environmental conditions, with specialists potentially able to achieve higher local abundances compared to less specialised taxa (Fjeldså *et al.* 2012). Third, high-elevation tropical species may live within small ranges but exhibit high local abundances due to density compensation, as species richness typically declines with increasing elevation (MacArthur 1972). Fourth, negative abundance–range-size patterns arise when most species with small ranges are also relatively abundant; it is possible that rare species with small ranges seldom persist over evolutionary time and hence are not observed at present (an 'extinction filter'; Williams *et al.* 2009).

Tropical elevational gradients are excellent systems in which to test the predictions of these explanations for the correlation between abundance and range size. Thorough sampling along a mountain slope permits measuring abundance and range size at the same spatial scale, and hence avoids difficulties that arise when comparing abundances measured at smaller spatial scales to range sizes measured at larger spatial scales (Ferenc *et al.* 2016; Wen *et al.* 2018). The specialisation idea does not make any obvious a priori predictions, but empirical data may be helpful to distinguishing between two different but not mutually exclusive drivers of specialisation – tropical montane species may inhabit narrow ranges either because they are thermal specialists with narrow fundamental niches (Janzen 1967), or because they are restricted to narrow distributions by competition with close relatives. If species have broad fundamental niches but are restricted to narrow realised niches by competition then the prediction is that most narrow-ranged species should have close relatives that live in different elevational zones, while this is not expected if thermal specialisation alone explains narrow ranges. In contrast, the density compensation hypothesis makes a clear prediction that can

be directly addressed: species richness should decrease at high elevations, and high-elevation species should be more common than low-elevation species. Last, it is not possible to directly test the extinction filter idea, but observing many species with small ranges and low abundances would cast doubt on this explanation. In this paper, I test these predictions using a dataset of the relationship between abundance and range size of New Guinean birds that inhabit primary forest along a reef-to-ridgetop elevational gradient.

Materials and methods

Study site and survey methods

The YUS Conservation Area (YUS CA, named after the Yopno, Urawa and Som Rivers) 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). From 2009 to 2012, a team of fieldworkers conducted extensive surveys of the avifauna along a trail that climbs through primary forest from near the reef-fringed coastline to ~3000 m (the YUS Transect; see Freeman *et al.* 2013 for survey details). The habitat at the bottom of this transect (below ~130 m) is open grassland, the result of a long history of anthropogenic fire. Fieldworkers were not able to access high-elevation forest above ~3000 m (the treeline is at ~3500 m). Thus, fieldworkers were able to survey the avifauna along an elevational gradient that stretched from 143 to 2936 m. Along this transect, fieldworkers: (1) conducted extensive mist-net surveys at 25 elevations, spaced roughly every 150 m in elevation along the transect, and (2) recorded ad lib observations during 15+ person-months of fieldwork where a primary goal was to determine species' elevational range limits. In addition, B. M. Beehler, an expert on New Guinean birds, conducted audial censuses along the gradient to better determine species' elevational limits. In sum, fieldworkers detected 256 species of birds. Because only four new species were detected during the final year of fieldwork, this is likely a nearly complete accounting of the resident avifauna along the YUS Transect. In addition to this species list, fieldworkers recorded species' elevational limits for 216 species of forest-dwelling birds that were encountered on >5 occasions (see Table S5 in Freeman and Beehler 2018 for a full species list with elevational limits).

Here, I use an extensive dataset of ~5000 mist-net captures to estimate the abundance of species that are well sampled by mist nets. Each mist net survey consisted of setting a large number of mist nets (typically 36 mist nets, each 12 m long) along trails that followed

the elevational contour at each site (see Freeman *et al.* 2013 for more details). Nets were 3 m in height, and their lower edge was set on the ground to capture species that walk on the ground. Fieldworkers operated nets for 2.5 days per site, resulting in an effort of ~1000 mist-net hours per site. Consequently, fieldworkers captured ~200 unique individuals per site, sufficient to characterise for each site both which understory species were present and also their relative abundances (see Table S4 in Freeman and Beehler 2018 for complete raw data of species captured/site and survey effort). Captured individuals were weighed, measured and released; fieldworkers clipped the ends of one or two outer rectrices in order to identify recaptured individuals. Recaptured individuals were not counted for this study.

Estimating relative abundance using mist-net capture rates can be problematic. This is because, even if species are equivalent in true abundance, they will vary in the probability they will be captured (reviewed in Remsen and Good 1996). Most obviously, canopy species do not fly near ground level, and mist-net data thus cannot be used to evaluate the abundance of taxa that do not regularly use the understory strata where the nets are located. Another major concern is that capture rates will be higher in some habitats than others. For example, capture rates will typically be higher in small-statured forest because mist nets cover a greater proportion of the forest strata. Despite these and other concerns, mist nets can be effective tools to estimate abundance for understory birds, including in tropical forests (e.g. Blake and Loiselle 2001). Canopy heights along the entirety of the YUS Transect are >30 m, including at the highest-elevation forests at ~3000 m (Venter *et al.* 2017). Hence, bias that results from comparing abundance among sites that differ in forest stature does not appear to apply to the dataset I analyse here.

Given these concerns, I analysed the link between abundance (capture rates) and elevational breadth only for species that (1) regularly use understory strata, and (2) have body masses less than 50 g. I excluded larger species from analyses because larger species are less likely to be captured in mist nets (and more likely to escape), biasing abundance metrics based on capture rates for these taxa. For each of 37 species that met these criteria, I calculated elevational breadth (upper elevation limit – lower elevation limit), and local abundance (average capture rate within its elevational distribution). Different approaches to quantifying abundance were tightly correlated with average capture rate. For example, the average capture rate of a species within its elevational distribution was tightly correlated

with its capture rate at the elevation where it was most common ($r = 0.92$). I therefore used average capture rate within a species' elevational distribution as my metric of abundance for this study.

Statistical analysis

I used both correlations and regression models to statistically test the prediction that species with broader elevational distributions are more abundant than species with narrower elevational distributions. All analyses were conducted using R software (R Development Core Team 2017). First, I calculated the correlation (Pearson's r) between these two metrics, and tested the significance of this correlation using the 'cor.test' function. Second, I fit an ordinary least squares (OLS) linear model with abundance as the response variable and elevational breadth as the predictor variable. For this and all subsequent regression models I used the log of both variables to improve normality of residuals. While using range size as the predictor of abundance is a common approach in studies that investigate abundance–range-size correlations, it is not obvious which variable is dependent and which independent, and both variables are measured with error. In this situation, major axis regression models are preferable to OLS models. I therefore fit a major axis regression model using the 'lmodel2' package (Legendre 2018). The general prediction that species with larger distributions are more abundant does not depend on species' evolutionary relationships. However, a related but distinct prediction is that evolutionary transitions towards larger elevational range sizes are associated with evolutionary transitions towards higher abundances. This prediction is explicitly evolutionary. To test this possibility, I fit phylogenetic generalised least squares (PGLS) regression models in the 'ape' package (Paradis *et al.* 2004) using a maximum clade credibility phylogenetic tree (Hackett backbone; all species) downloaded from bird-tree.org (Jetz *et al.* 2012). Last, the density compensation hypothesis predicts that high-elevation species are more abundant. I tested the prediction by testing the significance of the correlation between species' mean elevation and their abundance.

Results

I found little evidence that abundance is related to range size when considering 37 species of small-bodied understory birds found along the reef-to-ridgetop YUS Transect. The correlation between abundance and elevational breadth was positive but small ($r = 0.10$), and not significant ($t_{35} = 0.61$, $p = 0.55$).

Similarly, the relationship was positive but not significant in both OLS linear regression (slope \pm standard error = 0.16 ± 0.22 , $p = 0.47$, adj $r^2 = -0.014$; see Figure 1) and major axis regression models (slope = 4.91; 95% confidence interval for slope = $0.99 - 2.44$, p from permutation test = 0.24, adj r^2 of model = 0.014). Hence, there is no statistical evidence that species with broader elevational distributions are more abundant in this dataset. This lack of a relationship is evident when examining the raw data. For example, the species with the highest abundance along the YUS Transect – the Bicoloured Mouse-warbler (*Sericornis nigrorufa*) – was found in an extremely narrow (240 m) elevational distribution. While this example is extreme, four of the six most abundant species had elevational distributions less than 1000 m in elevational breadth. In contrast to the non-phylogenetic regressions described above, the relationship between abundance and elevational breadth was significantly negative in a phylogenetic regression (lambda = 1; slope \pm standard error = -0.40 ± 0.13 , $p = 0.0053$; see Figure 1). This result indicates that evolutionary transitions towards *smaller* elevational ranges are significantly associated with greater abundance in this dataset. Stated another way, when a pair of closely related species is found along the YUS Transect and differs in elevational breadth, it is the species with a narrower elevational zone that tends to be more abundant. Last, I found little evidence to support the density compensation hypothesis – species'

mean elevation and abundance are positively correlated ($r = 0.13$), but this correlation is not significant ($t_{35} = 0.75$, $p = 0.46$).

Discussion

The widespread pattern that abundance is positively correlated with geographic range size does not apply to New Guinean birds distributed along an elevational gradient. Although species in this dataset varied considerably in both abundance and elevational range size, these metrics were unrelated in an OLS regression model and were significantly *negatively* related when analysed using phylogenetic regression. There are few previous examples of datasets that report either non-significant or negative abundance–range-size relationships from the temperate zone (Gaston 1996; Päävinen *et al.* 2005), but several studies have reported non-significant or negative abundance–range-size relationships from the tropics, both in birds (Reif *et al.* 2006; Nana *et al.* 2014; Ferenc *et al.* 2016; Reeve *et al.* 2016; but see Theuerkauf *et al.* 2017) and more broadly in other taxonomic groups (Isaac *et al.* 2009; Williams *et al.* 2009; Hughes *et al.* 2014). My results fit with this growing literature, raising the intriguing possibility that abundance–range-size relationships may be different in the tropics (at least on tropical mountains) compared to the temperate zone.

I first consider the possibility that my results are a consequence of methodological choices. Both

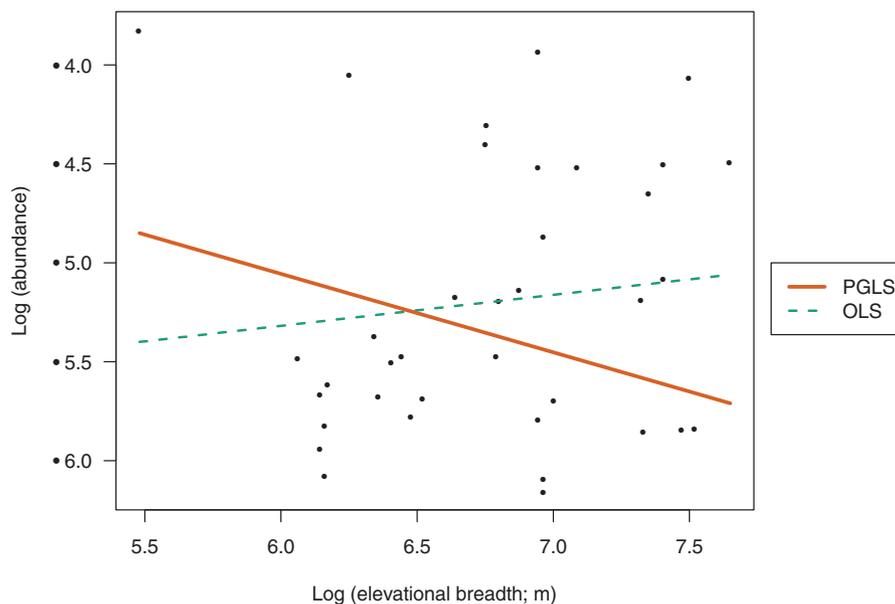


Figure 1. The relationship between abundance and elevational range size for 37 species of small-bodied, understorey forest birds, plotted on log scales. Predictions from ordinary least squares (OLS) and phylogenetic generalised least squares (PGLS) regressions are plotted. Only the PGLS regression has a slope significantly different from zero; the model prediction for the PGLS regression is therefore plotted with a solid line.

abundance and range size can be measured in many different ways, and different methodologies can lead to different results (Lawton 1993; Gaston 1996; Borregaard and Rahbek 2010). Perhaps the most important consideration is the spatial scale at which abundance and range size are measured. In this study, I measured both variables at the same spatial scale, avoiding the problem of comparing abundances measured at local scales with range sizes measured at continental scales. Measuring range size as elevational breadth is not a standard approach, and hence caution is warranted when making comparisons with other studies that measured range size in units of area. However, studies measuring range size as elevational breadth have reported tight positive relationships between abundance and range size (Wen *et al.* 2018), indicating that measuring range size in this way is unlikely to bias abundance–range-size correlations in and of itself. However, using elevational breadth to measure range size of taxa along elevational gradients offers the twin advantages of matching the spatial scale of abundance data and avoiding complications of using area-based metrics. This is because mountains are often shaped like pyramids (but see Elsen and Tingley 2015) such that high elevations typically have less available area compared with lower elevations. Hence, I anticipate that similar analyses will become more common in the literature. I further note that my results depend on my metrics of abundance and range size, both of which are measured with error that I was unable to quantify. For example, sampling effort in determining species' elevational distributions was biased towards sites where mist-net surveys were conducted, and I was unable to measure temporal variation in local abundance at sites, as surveys were conducted once per site (with the exception of one site surveyed in 2 years: reassuringly, species' abundances between years at this site were tightly correlated; Freeman and Beehler 2018). These issues should add noise but not bias to my results.

I show that abundance is unrelated (or is negatively linked) to range size along the YUS Transect, but there is little evidence that density compensation explains this pattern. Species richness does decline at high elevation along the YUS Transect, while capture rates are consistent across the elevational gradient (and in fact are highest at high elevations; Freeman and Beehler 2018). These observations are consistent with the idea that density compensation at high elevations leads to elevated abundances of high-elevation taxa living in species-poor forests. However, in this paper I restrict

analyses to small-bodied understory species, and species richness of these taxa is actually highest at higher elevations along the YUS Transect (Freeman and Beehler 2018). As a consequence, small-bodied understory species' abundances are statistically unrelated to their mean elevation. This differs from the situation for birds on Mt. Cameroon, where fieldworkers surveyed the entire avifauna and found that density compensation was a strong explanation for why abundance–range-size relationships differed among elevational zones (low vs. middle vs. upper; Ferenc *et al.* 2016). Efforts that use multiple survey techniques to measure abundance (e.g. mist nets to survey small-bodied understory birds and also point counts to survey the entire avifauna) would be necessary to evaluate whether these different approaches lead to different results when quantifying abundance–range-size correlations.

The abundance–range-size correlation I document is related to patterns of elevational specialisation in the YUS avifauna. The YUS Transect encompasses primary forest that stretches from near sea level to ~3000 m, without any barriers to dispersal. Thus, the observation that forest-dwelling species typically live in only ~1000 m of this expanse constitutes evidence that New Guinean birds are indeed elevational specialists (for 216 species, the mean and median elevational breadths are 1004 and 877 m; Figure 2), as is generally true for tropical montane species (Janzen 1967; Cadena *et al.* 2012). However, there is still wide variation in elevational range sizes within the YUS Transect avifauna. Hence, greater overall specialisation in the tropics cannot in and of itself break a positive abundance–range-size relationship that is widely observed in the temperate zone, and often attributed to attributes of species that affect both abundance and occupancy (e.g. niche breadth, population growth rate and dispersal abilities). Instead, specialisation in tropical mountains impacts abundance–range-size relationships when more specialised species are able to achieve higher abundances compared to less specialised species.

Multiple lines of evidence support the idea that elevational specialisation in the YUS avifauna is due to narrow realised niches rather than narrow fundamental niches. Although tropical montane birds' thermal tolerances have been little studied, available data from New Guinea (Freeman 2016; Freeman *et al.* 2016) and the tropical Andes (Londoño *et al.* 2015) do not support the hypothesis that tropical montane birds' thermal physiologies are specialised to narrow ranges of temperatures such that they have narrow fundamental niches, at least for adult birds. In contrast, distributional patterns are consistent with the idea that

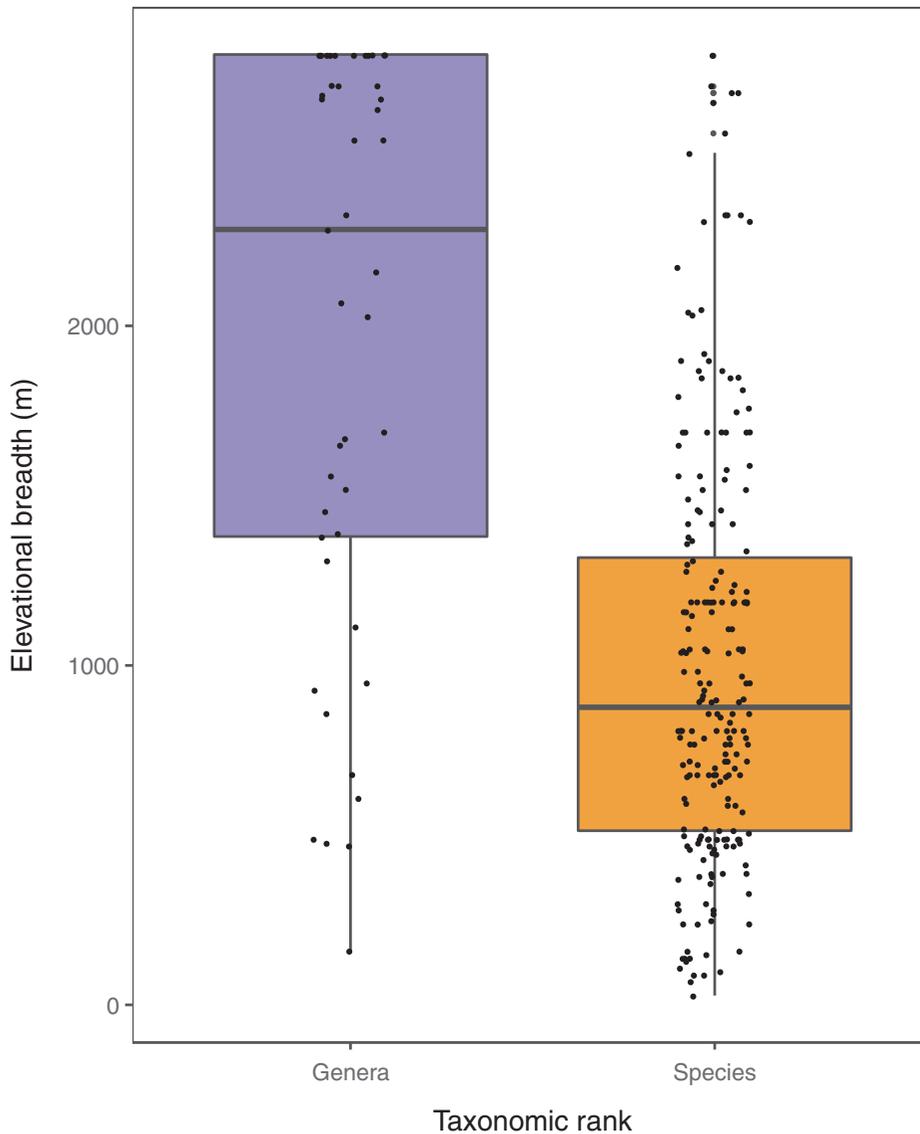


Figure 2. Elevational range sizes for both genera (with at least two species; $N = 45$) and species ($N = 216$) found along the YUS Transect.

interspecific competition limits New Guinean birds to occupying narrow realised niches. For example, ‘elevational replacements’ – wherein closely related species live in largely non-overlapping elevational zones – are pervasive within the YUS avifauna (Freeman *et al.* 2013) and more broadly in New Guinea (Diamond 1973, 1986; Beehler 1981; Freeman and Class Freeman 2014; Freeman 2015). For example, the Bicoloured Mouse-Warbler is the most common understorey bird along the YUS Transect but lives only within a ~250 m elevational band, possibly because of competition with ecologically similar congeneric species. The Bicoloured Mouse-Warbler was recently discovered to be a *Sericornis* (rather than a *Crateroscelis*; Marki *et al.* 2017; Norman *et al.* 2018), and related congeneric species live both above and

below the Bicoloured Mouse-Warbler along the YUS Transect, potentially preventing the Bicoloured Mouse-Warbler from expanding its elevational distribution. The Bicoloured Mouse-Warbler is an extreme example of elevational specialisation, but exemplifies the pattern that while species are elevational specialists along the YUS Transect, genera are elevational generalists (for 45 genera with two or more species, the mean and median elevational breadths of the genus are 1971 m and 2184 m; Figure 2). While it must be true that genera have a broader range of trait values than their constituent species, the idea of phylogenetic niche conservatism, which is widespread in the literature (Wiens *et al.* 2010), predicts that closely related species will tend to have very similar climatic niches (and hence elevational ranges). If so, the elevational breadth of genera should

be only slightly larger than that of individual species. This expectation is not met for birds along the YUS Transect, demonstrating that evolutionary constraints on elevational distributions in the New Guinean avifauna are weak. Hence, available data are most consistent with the interpretation that stable eco-climatic conditions set the stage for competition to drive the evolution of elevational specialist taxa, and that these taxa, by virtue of their specialisation, are often able to achieve reasonably high local abundances within their narrow ranges. Last, I note that species' ability to persist over long periods of time is likely to shape current patterns of distribution and abundance – in particular, species with very small elevational ranges may be likely to have high extinction rates if they are rare.

In this paper I have shown that local abundance of forest bird species along a New Guinean elevational gradient is not positively related to the breadth of their elevational distribution. Indeed, when examined in a phylogenetic context, this relationship is negative. My results add to a growing list of tropical studies that fail to exhibit positive abundance–range-size correlations. This apparent pattern may indicate that the relationship between abundance and range size is qualitatively different in the tropics vs. the temperate zone. Alternatively, this apparent pattern may simply indicate differences between mountain and lowland regions – most tropical studies come from montane regions while most temperate-zone studies come from either lowland regions or from large regions that are predominantly lowlands. A comparative study that uses the same methodology to measure abundance–range-size correlations in both montane and lowland biotas across a wide latitudinal expanse would be helpful to shed light on these issues. I encourage biologists with similar datasets of species' abundances along tropical elevational gradients to investigate abundance–range-size correlations; many such relationships will need to be quantified to test whether the patterns demonstrated by New Guinean birds in this study – and my proposed explanation – apply more generally to other taxa along other mountain slopes.

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