Ecologically flexible endemics dominate Indo-Pacific bird communities

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Abstract

Reeve et al. (2016, *Ecography*, **39**, 990-997) found that ecologically flexible endemics dominate Indo-Pacific bird communities. This negative relationship between local abundance and global range size contrasts strongly with the positive range size-abundance relationship "rule," which would predict community dominance by globally widespread species. Theuerkauf et al. (2017, *Journal of Biogeography*, **44**, 2161–2163) provide new data from New Caledonia which they claim invalidate our study. They find positive relationships between local abundance and local range size, which they attribute to endemic species having narrower habitat niches than globally widespread species. We reanalysed their data using global range sizes, corroborating the pattern we originally reported: negative relationships between local abundance and global range size, driven by a subset of adaptable endemic species. We stress the importance of being explicit about the scale of ecological mechanisms, and ensuring that the scale of analysis matches the scale of interpretation.

In Reeve, Borregaard, and Fjeldså (2016) we reported negative range size-abundance relationships in bird communities across four islands in the Indo-Pacific. Negative relationships between global range size and local abundance were found both in mature and degraded forest. These relationships were driven by endemic and near-endemic species that persist in high abundances in moderately degraded habitat. Theuerkauf, Chartendrault, Desmoulins, Barré, and Gula (2017) present an analysis of their own dataset from New Caledonia which they claim invalidates our findings. They estimated abundances and extrapolated island-wide species occupancies using point count data (Barré, Villard, Manceau, Monimeau, & Ménard, 2006; Legault, Chartendrault, Theuerkauf, Rouys, & Barré, 2011) from a variety of habitats across the islands of Grande Terre and Lifou (where we also sampled), as well as Île des Pins. They found positive relationships between these estimates of local abundance and local range size. They ascribe this to endemic species having narrower habitat niches than globally widespread species, based on simple qualitative habitat assessments for 15 New Caledonian birds.

Theuerkauf et al. (2017) claim that our study is flawed on four points: (a) that the negative range size abundance relationships we detected are not real; (b) that we misunderstood the dynamics between globally widespread and endemic species that drive the relationship; (c) that our sampling effort was "very small" and (d) that we overlook that abundance may be lower near range edges, constituting a "methodological error." None of these critiques stand up to further examination. Below, we address each point in turn.

The first and main criticism by Theuerkauf et al. (2017) is based on the superficial disagreement between the negative range size-abundance relationships we reported and the positive relationships they found. These results are not actually contradictory. The discrepancy is due to the use of different range size scales (local vs. global). We reanalysed their abundance data, substituting global range sizes (Rahbek, Hansen, & Fjeldså, 2012) for their local range size estimates, to allow useful comparison with our own local abundance vs. global range size study. Theuerkauf et al. (2017) use two separate methods to estimate abundance: (a) mean number of species observations per point only at points where the respective species was recorded; and (b) mean number of species observations per point across all points. We point out that there is broad consensus in the literature that comparing mean abundance as derived by the second method to site occupancy is not ecologically informative in the context of range size-abundance relationships. It essentially correlates the mean of a zero-inflated distribution with the number of non-zeros, and thus using this method is quite unusual (Gaston & Lawton, 1990; Webb, Freckleton, & Gaston, 2012). Regardless, reanalysis of their large dataset (81,388 individual birds counted across 4,208 points over 1,000+ survey hours) yielded results that are essentially the same as ours. Relationships are negative across all three islands; weakly so on Grande Terre, and significantly on Île des Pins and Lifou (Figure 1, Table 1).

Thus, Theuerkauf et al.'s new data support our original finding that ecologically flexible endemics dominate Indo-Pacific bird communities. These are typified by species such as New Caledonian Myzomela *Myzomela caledonica* and Green-backed White-eye *Zosterops xanthochroa*, globally rare birds that are widespread and abundant within their tiny ranges. Such species are "broad-niched" in the sense that they are common across a range of naturally occurring local habitat types, and are tolerant of moderate anthropogenic disturbance. Theuerkauf et al. (2017), in their second point of critique, argue that "endemic species have narrower habitat niches than wide-range species," implying that we claimed the opposite. We did not, and pointed out, as they do, that endemics are typically replaced by widespread species in open and heavily degraded habitats. However, in the natural and semi-natural habitat focused on by both studies, endemic species are generally more common and widespread.

Specific criticisms by Theuerkauf et al. (2017) regarding our study methodology carry little weight given the consistency of

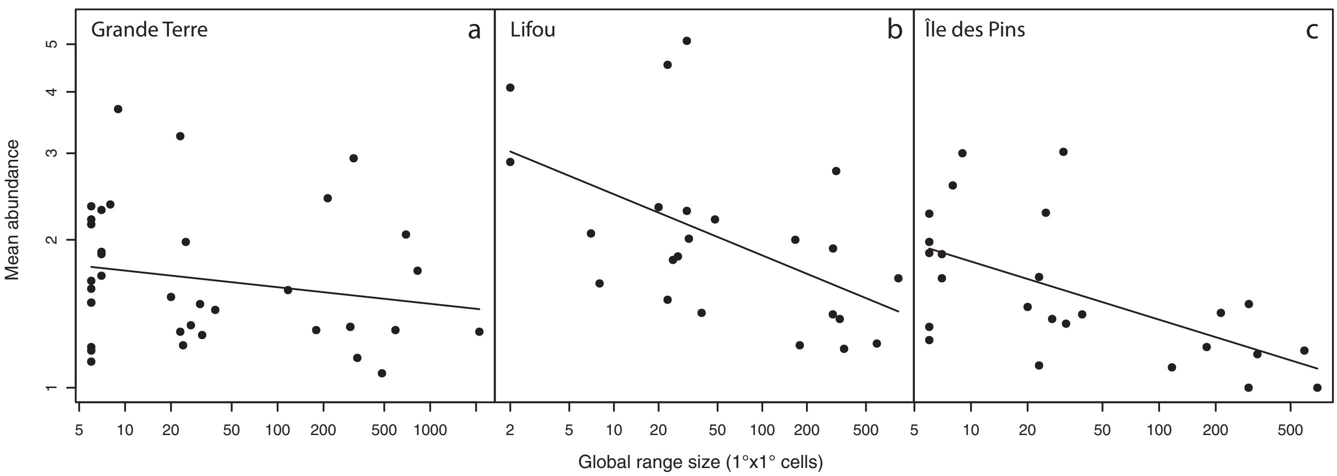

FIGURE 1 Interspecific range size-abundance relationships of birds on the New Caledonian islands of Grande Terre (a), Lifou (b), and Île des Pins (c). Regression lines illustrate relationship slopes. Mean abundance: abundance within range on individual islands (Theuerkauf et al. (2017). Global range size in 1° × 1° grid cells, from Rahbek et al. (2012)

TABLE 1 Pearson correlation coefficients of New Caledonian bird abundances from Theuerkauf et al. (2017) vs. global range size. See text and Theuerkauf et al. (2017) for details on the two methods of abundance estimation. Global range size from Rahbek et al. (2012). Both variables log-transformed

	Avg abundance (within range)			Avg abundance		
	r	d.f.	*p*	*r*	d.f.	*p*
Grande Terre	−0.202	35	0.230	−0.220	35	0.191
Lifou	−0.530	21	0.009	−0.643	21	0.001
Île des Pins	−0.597	23	0.002	−0.506	23	0.010

results under the same analyses. Still, we would like to comment on their third critique: that our bird sampling was "very small," which they speculate skewed the direction of range size-abundance relationships. Our purpose-built dataset comprises 10,090 bird identifications from 355 survey hours across 11 plots on four islands—an effort well within the norm for this kind of analysis (e.g. Reif et al., 2006). Even taken at face value their claim is a surprising one, as there is no well-known mechanism that would cause incomplete sampling to lead to negative range size-abundance relationships. With regard to relationships with local occupancy, it is well established both theoretically (Bock & Ricklefs, 1983) and empirically (Selmi & Boulinier, 2004) that incomplete sampling will lead to spuriously positive occupancy-abundance relationships. Moreover, Theuerkauf et al. (2017) justify their accusation with an invalid comparison between their list of 36 species recorded in the 90 km^2 Parc Provincial de la Rivière Bleue on Grande Terre, against our data record of 24 species recorded within 1 km^2 of mature forest within the reserve. Our list included nearly all expected forest birds, including the elusive, low-density species (Kagu *Rhynochetos jubatus*, Crow Honeyeater *Gymnomyza aubryana*, etc.). A Chao 1 estimate (Chao, 1984) indicates the detection of 86% of focal species present in the plot. The species count from Theuerkauf et al. (2017) inevitably includes non-forest species absent from our carefully delimited mature forest plot.

Finally, Theuerkauf et al. (2017) contend that our use of global range sizes is a "methodological error," because species might have lower abundances near the edge of their geographical ranges, and presumably, large-ranged species are more likely to be near their range edge in the study region. This mechanism, known as the range position hypothesis, has been tested extensively in the literature with little empirical support; importantly, the underlying assumption that species are most common at the centre of their range is at best questionable (Dallas, Decker, & Hastings, 2017). The critique that we should have overlooked this mechanism is the more surprising as we discuss it explicitly in the discussion section of Reeve et al. (2016). To reiterate: if species are rare at range margins due to imperfect adaptations to local conditions, this is in fact broadly consistent with the mechanisms discussed in Reeve et al. (2016).

In conclusion, Reeve et al. (2016) found negative relationships between local abundance and global range size in New Caledonian birds, while Theuerkauf et al. (2017) found positive relationships between local abundance and local range size. Reanalysis of Theuerkauf et al.'s data, correcting for scale, reveals negative relationships that corroborate the results of our original study. The superficial disagreement between relationship slopes highlights the potential scale-dependent variability in range size-abundance relationships (see e.g. Borregaard & Rahbek, 2010). Examination of individual biological communities at a variety of geographical scales may be helpful for identifying the underlying drivers of range size-abundance relationships—but only with the careful consideration of ecological mechanisms within this multi-scale framework.

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Keywords

abundance, bird, endemism, Indo-Pacific, New Caledonia, range size

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