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# Negative range size–abundance relationships in Indo-Pacific bird communities

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The positive relationship between range size and abundance is one of the best-documented patterns in macroecology, but a growing number of studies from isolated tropical areas have reported negative or neutral relationships. It has been hypothesized that the combination of geographic isolation and environmental stability create selection pressures that favor narrowly specialized species, which could drive these non-positive relationships. To test this idea, we measured the range size–abundance relationships of eleven bird communities in mature and degraded forest on four islands in the Indo-Pacific, namely Flores in the Lesser Sundas, Seram in the Moluccas, and the New Caledonian islands of Grande Terre and Lifou. Local abundance data was gathered through extensive and methodologically consistent surveying, and regressed against global range size using linear mixed effect models. The relationship between range size and abundance was significantly negative across all combined mature and degraded forest communities. As negative relationships were found in degraded forest with little environmental stability, we conclude that the abundance of small-ranged species on the study islands cannot be ascribed to narrow specialization. Rather, cross-habitat community comparisons indicate that locally abundant endemic and near-endemic species adapted to a broad spectrum of local environmental conditions cause the observed negative relationships. We suspect that geographic isolation facilitates the evolution of species that are simultaneously broad-niched, small-ranged, and abundant, as water barriers limit the range expansions that would typically accompany species' attainment of high local population densities. The consistently negative relationships found across Indo-Pacific islands represent a striking deviation from the positive range size–abundance relationship 'rule', and future studies should seek to determine whether the patterns detected here extend to geographically isolated mainland environments.

Macroecological studies have consistently reported a positive correlation between the range size of animals and their local abundance within communities (Brown 1984, 1995, Gaston 1996, Gaston and Blackburn 2000). The pervasiveness of this observation has led some to argue that a positive range size–abundance relationship may warrant status as an ecological 'rule' (Gaston and Blackburn 2003), and numerous hypotheses have been put forward to explain it (reviewed by Borregaard and Rahbek 2010). However, much of the evidence for a general positive range size–abundance relationship is drawn from research on bird communities in temperate Europe and North America (see, for example, Gaston and Lawton 1990, Gaston and Blackburn 2000, Blackburn et al. 2006). In recent years, a growing number of studies from tropical and subtropical regions have revealed neutral or negative relationships, calling the generality of range size–abundance relationships into question. Examples include birds in the Cameroon highlands (Reif et al. 2006, Nana et al. 2014), birds in the Canary Islands (Carrascal et al. 2008), fishes and corals in the Indo-Pacific (Hughes et al. 2014), and vertebrates in the Australian Wet Tropics (Isaac et al. 2009, Williams et al. 2009).

This apparent discrepancy may reflect fundamental differences in spatial structure between communities in isolated tropical areas and those in temperate zones. Hypotheses to explain positive range size–abundance relationships have focused on the ability of generalist species to appropriate resources, which allows them to simultaneously expand their ranges and dominate local communities (Brown 1984). The combination of geographic isolation with the high environmental stability of the tropics, however, may create conditions that reward narrow specialization in terms of resource and habitat use: long-term and annual climatic stability result in fairly constant environmental selection pressures, and at the same time low dispersal rates and community turnover mean that interspecific competition is relatively unchanging (Connell and Orians 1964, Fjeldså 1999, García-Moreno and Fjeldså 2000, Fjeldså et al. 2012). Positive relationships may then be absent where stable selection pressures favor species with strong local adaptations and concomitant small range sizes.

The forests of non-land bridge tropical islands are ideal systems to test whether narrow specialization by species in geographically isolated and stable environments causes negative range size–abundance relationships. Tropical islands show remarkable long-term environmental stability because they rarely experience extreme weather events, are buffered against glacial cycles by marine currents, and have low

species turnover (Cronk 1997). The water bodies surrounding them present obvious barriers to dispersal and colonization. Thus, primary forest bird communities on these islands have evolved in conditions of extreme stability and isolation. Niche specialization theory would predict that these forests should be dominated by endemic species that are narrowly adapted to specific local environmental conditions, resulting in high abundances of small-ranged species and negative range size–abundance relationships. At the same time, however, much of the forest cover on the world's tropical islands has suffered anthropogenic disturbance and modification, and has therefore lost the element of environmental stability in recent times. If niche specialization drives range size–abundance relationships, these degraded habitats should be dominated by the more widespread, generalistic members of regional species pools that have broad habitat tolerances, resulting in the typical positive relationship. Comparing the direction of the range size–abundance relationships of bird communities in primary and degraded forest should therefore shed light on the mechanisms driving these relationships.

Although forests of tropical islands represent an excellent model for investigating exceptions to the positive range-size abundance relationship, they have been largely ignored in this context, probably because collecting good abundance data from natural habitats of such locations is often challenging. For this study, we performed extensive and methodologically consistent sampling of local bird communities over four tropical islands in the Indo-Pacific: Flores in the Lesser Sundas, Seram in the Moluccas, and the New Caledonian islands of Grande Terre and Lifou. We predict that the isolation and environmental stability of these islands will cause a negative relationship between interspecific abundance and global range size, but predict a positive relationship in human-shaped mosaic habitat, where the environmental stability that theoretically rewards narrow specialization is compromised.

## Methods

### Study areas

The four islands chosen for this study, Flores (8°S, 119–123°E), Seram (2–3°S, 127–130°E), Grande Terre (20–22°S, 164–167°E), and Lifou (20–21°S, 167°E), span over 5000 km of the tropical Indo-Pacific (Fig. 1), and vary widely in geological origin, degree of isolation, ecological community composition, and elevational span. All study islands support distinctive, endemic-rich resident avifaunas (Coates and Bishop 1997, Stattersfield et al. 1998, Spaggiari et al. 2007), though globally and regionally widespread species are also present in all communities. There was little overlap in the species recorded during surveys between the three main archipelagos covered. Surface area is similar across the three largest islands (16 000–18 000 km$^2$), with data from the significantly smaller Lifou (ca 1000 km$^2$) providing contrast.

Flores (maximum elevation 2370 m) is a young volcanic island, with a topography shaped by continual volcanic activity since its emergence from the sea. It is the least isolated of the study islands, and has been connected to nearby islands in the Inner Banda Arc by land bridges during glacial periods (Monk et al. 1997, Voris 2000). Seram (3027 m) is the product of complex tectonic interaction processes such as slab rollback (Pownall et al. 2013). It is, along with its small satellite islands, well separated from large surrounding islands by broad expanses of deep water. The New Caledonian islands of Grande Terre and Lifou are by far the most isolated of the study group. Grande Terre (1628 m) is a continental fragment of Gondwana that split off from Australia ca 80 Mya; its biota may contain some ancient relictual elements (Heads 2011), despite its near-total submersion for 20 Mya in the Paleocene and Eocene (Grandcolas et al. 2008). Lifou (104 m) is a raised coral atoll belonging to the Loyalty Islands group, separated from the Grande Terre by the deep Loyalty Basin. Although the avifauna is similar to Grande Terre's, it is sufficiently isolated from that island and its neighbors in the Loyalties to support two endemic birds.

Seven study plots in homogeneous patches of mature tropical forest (Fig. 2) were chosen on the four islands: two each on Flores, Seram, and Grande Terre, and one on Lifou. The designation 'mature' is used here, as it was often not possible to confidently distinguish primary growth from old secondary growth, and because truly undisturbed forest is virtually absent on Grande Terre. To test whether community dominance by small-ranged species can be attributed to narrow specialization to stable environments, an additional four sites were chosen in human-modified mosaic habitats with significantly reduced natural tree cover (Fig. 2;

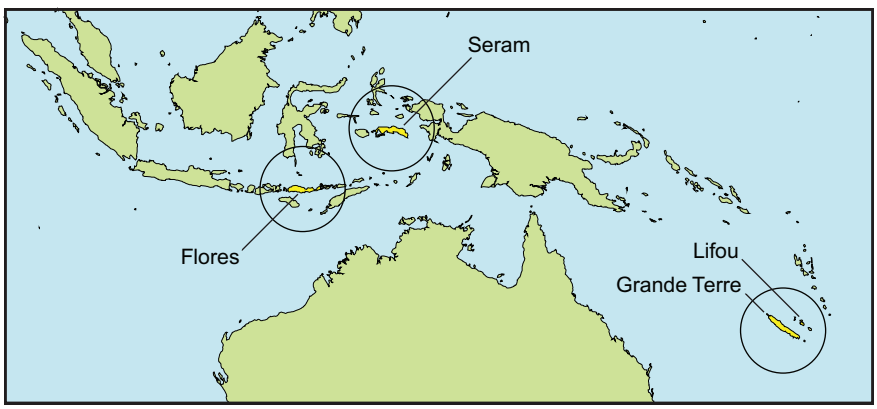


Figure 1. Map of the study region.

Figure 2. Mature and degraded forest plots. Left: mature forest in Manusela National Park (high plot), Seram (photo: Pierre-Henri Fabre). Right: degraded forest in Galang, Flores (photo: Andrew H. Reeve).

see Supplementary material Appendix 1, Table A1 for individual site details). These degraded forest plots, two on Flores and two on Grande Terre, corresponded with nearby mature forest plots on the respective islands. Degraded forest plots on Grande Terre had existed in a disturbed state for several decades, and this is strongly suspected for the degraded forest plots on Flores as well. This is probably long enough to mitigate the effect of lagged responses by local birds to the habitat change, though estimating the time needed for particular communities to reach equilibrium following disturbance is not straightforward (Ewers and Didham 2006). Vegetation surveys were performed across all sites (see below); canopy cover was measured at 60–90% among mature forest sites and 0–30% among degraded forest sites (Supplementary material Appendix 1, Table A2). An effort was made to keep the plots on a given island within a narrow altitudinal range to improve comparability, and all were located well inland. Plots were generally square-shaped, and measured from 1–1.5 km$^2$, except for a single 0.8 km$^2$ plot on Lifou. This size corresponds approximately with the area used by birds that join mixed feeding flocks in the tropics (Poulsen 1996). Fieldwork was carried out at the end of the dry season in southwestern Flores (September and October 2011), during the rainy season in the central Seram highlands (February 2012), and during the transition from the warm to cool seasons in central and southern Grande Terre and northern Lifou (April and May 2012).

## Bird sampling

All bird surveys were carried out by Andrew Reeve using a variation of the 'random walk' method (Fjeldså 1999), which is specifically tailored for work in dense tropical forest environments characterized by rugged terrain, poor access and a of lack good trails. The method entails walking slowly, and as randomly as possible through a plot, recording all individual birds seen or heard within a 50 m radius. Surveys were conducted in the mornings from dawn, and in the afternoons until dusk, with a pause at midday to coincide with the period of diminished bird activity. Censusing work was suspended during heavy rain. Between 26.5 and 42.1 h per plot were devoted to these surveys (Table 1), which was adequate to record virtually all species resident

Table 1. Results of bird surveys from plots on Flores, Seram, Grande Terre, and Lifou. Only the subset of observations fitting the criteria summarized in the Methods section is included.

| Study site | Island | Species recorded | Individuals recorded | Survey effort (h) |
|---|---|---|---|---|
| Sisok Forest | Flores | 25 | 388 | 28.8 |
| Mbeliling Forest Reserve | Flores | 37 | 872 | 42.1 |
| Galang | Flores | 39 | 1526 | 36.5 |
| Lamung | Flores | 44 | 1222 | 31.0 |
| Manusela National Park (low) | Seram | 30 | 308 | 30.5 |
| Manusela National Park (high) | Seram | 25 | 829 | 26.5 |
| Parc Provincial de la Rivière Bleue | Grande Terre | 24 | 716 | 33.5 |
| Parc Provincial des Grandes Fougères | Grande Terre | 29 | 918 | 30.0 |
| Farino | Grande Terre | 33 | 1329 | 30.6 |
| Bois du Sud | Grande Terre | 20 | 739 | 35.7 |
| Wetr | Lifou | 16 | 1243 | 30.1 |

within a plot in these relatively species-poor island communities. Bird observations were not compiled into sub-lists, as is sometimes done in conjunction with the 'random walk' method, as sub-listing renders the data unsuitable for many statistical analyses (MacLeod et al. 2011). Using unmodified counts of individuals solves this problem, and produces datasets that closely match the per-species abundance percentages obtained using traditional point counts (Fjeldså 1999).

The 'random walk' method was chosen because it permits the observer a high degree of flexibility during census work in difficult terrain, and is more time-efficient than point counts, which exclude all records made between observation points. A drawback is that walking speed is variable to some degree; however, a concentrated effort was made to maintain a consistently slow, steady pace of approximately 0.5 km $h^{-1}$ across all sites. At this pace it was possible to move quietly while recording nearly all birds that were active in the area. Counting only from within a narrow 50 m radius, where all bird species have similar detectability, helps solve the problem of varying conspicuousness between species (Reif et al. 2006). In two plots, Sisok Forest on Flores and Manusela N. P. (high) on Seram, exceedingly steep terrain made strictly random walking impossible, and here survey routes largely followed ridgelines (in the former) or narrow footpaths (in the latter). Potential problems that could arise due to the flexibility of the 'random walk' method were minimized in this study due to the fact that a single worker conducted all the surveys. This provided a degree of consistency with regard to variables such as walking pace, detection ability and identification skill.

## Vegetation sampling

Vegetation was measured in all study sites to quantify the structural differences between mature and degraded forest plots. Visual estimates of plant cover were made within a 20 m radius around census points. Vegetation layers were defined as ground cover (up to 20 cm off the ground), herbacious layer (up to 1 m off the ground), scrub layer (1–3 m), small understorey trees (5–10 m), and canopy (everything above 10 m). The proportion of the ground covered by the vertical projection of each layer was estimated to the nearest ten percent (Jennings et al. 1999).

Vegetation structure was calculated differently for mature and disturbed plots. In mature forest plots, ten census points were chosen at random across the site, and measurements from each vegetation layer were averaged. In degraded forest plots, a different approach was necessary due to the high structural heterogeneity of the plant cover. Four or five predominant vegetation categories were defined for each site (e.g. pasture, dense ferns, naiouli scrub, etc.), with all habitat within a given plot being categorized, and census points were chosen within habitat patches representative of these categories. Satellite imagery was used to measure the percent coverage of respective vegetation categories in each plot. These measurements were used to weight data from the census points, which yielded vegetation structure estimates for individual degraded forest study plots. Results are given in Supplementary material Appendix 1, Table A2).

## Data analyses

For the statistical analyses, observations of nocturnal, introduced, and non-breeding migrant species were eliminated, as well as birds that were recorded flying above canopy-level. Swifts (family Apodidae) were also eliminated because they are aerial species that only indirectly utilized the terrestrial habitats surveyed, and because the counting criteria used were not adequate to gauge their abundance consistently across sites. Each species' abundance is defined as the number of individuals recorded per hour of surveying, calculated by dividing the number of total observations of that species per study plot by the total number of hours spent surveying there. In this study, a species' range size is defined as the extent of its global breeding range, measured in $1° \times 1°$ grid cells (Rahbek et al. 2012), and following IOC taxonomy (Gill and Donsker 2014).

We used linear mixed models to analyze the range size–abundance relationship across the 11 study plots, employing the 'lmer' function in the lme4 package (Bates et al. 2013) in R (R Development Core Team). Range size and abundance measurements were log transformed to improve normality. Abundance was used as the response variable, which is often done by convention, though this does not reflect a consensus that range size controls abundance (Komonen et al. 2013). In addition to 'range size' and 'abundance', 'habitat' (two levels: 'mature' and 'degraded') was included as a third fixed effect. Random effects were 'island' and 'plot'. The most parsimonious structure of random and fixed effects was found following the protocol of Bunnefeld and Phillimore (2012). First, the optimal random effects structure was determined by testing which of several different combinations yielded the lowest Akaike information criterion corrected for small sample size (AICc). Each configuration of 'plot' nested within 'island', 'island' singly and 'plot' singly was allowed to affect the slope ('random slope'), intercept ('random intercept'), or both slope and intercept of the 'range size–abundance' interaction. Having defined the optimal random effects structure, the 'dredge' function in the MuMIn package (Bartoń 2013) was used to find the most parsimonious combination of the three fixed effects. The effect of 'habitat' on the relationship slope was measured at this stage. Different model configurations were ranked according to AICc. P-values for the mixed models were obtained using the lmerTest package (Kuznetsova et al. 2014).

Additionally, we performed standard linear regression of (log-log) range size against abundance for each individual study plot; regression lines were fitted through the resulting plots, and the significance of the relationships tested using the Pearson correlation coefficient. Finally, we determined the degree to which small-ranged species abundant in mature forest declined following habitat degradation. These community comparisons could only be usefully made in mature-degraded plot pairs where the original habitat cover was similar, so the pairs from central Grande Terre (P. P. Grandes Fougères and Farino) and southern Grande Terre (P. P. Rivière Bleu and Bois du Sud) were compared separately, while all Flores plots could be compared together. Species were considered 'small-ranged' and 'abundant' if they had a range size smaller than 50 $1° \times 1°$ grid cells, and occurred

Table 2. AICc values for the five most parsimonious random effects structures, with abundance as the response variable and range size and habitat as fixed effects. An X indicates the inclusion of a variable in the model; a blank space its exclusion.

| Random intercept | | Random slope | | |
|---|---|---|---|---|
| Island | Plot | Island | Plot | AICc |
| | X | | | 1189.45 |
| X | | | | 1190.80 |
| X | X | | | 1191.54 |
| X | | X | | 1192.82 |
| | | X | | 1192.82 |

in the top half of a given plot's species abundance ranking (for the two Grande Terre plot pairs), or occurred in the top halves of the species abundance rankings of both mature forest plots (for Flores). The percentage of these species that remained in the upper halves of the species abundance rankings in corresponding degraded plots was then calculated.

## Results

Observations across all study plots of 10 090 individual birds representing 141 different species fit the criteria for inclusion in this analysis. A plot-by-plot summary of surveying results can be found in Table 1.

In the 'lmer' model, the random effects structure with the lowest AICc included only 'plot' (with random intercept), although including only 'island' (with random intercept) increased the AICc by just 1.346 points (Table 2). Nesting 'island' in 'plot', and allowing for random slope and combinations of random slope and random intercept worsened model performance. The best model found with the 'dredge' function included only 'range size' and 'abundance' as fixed effects. However, two other model configurations obtained similar AICc weights and AICc scores within two points of the best model (Table 3), and thus have substantial support (Burnham and Anderson 2002). The slope of the relationship between 'range size' and 'abundance' was found to be significantly negative ($p < .05$) in all of the three best-performing 'lmer' models (Table 4). The slope is significantly negative in both mature and degraded plots (model 3); it is more strongly negative in mature than in degraded plots, but not significantly so ($p = 0.287$). Model 2 shows a slightly higher relationship intercept in degraded plots, which is not significant ($p = 0.304$). This reflects a weak pattern of higher bird densities and larger average range sizes in these plots. The variation explained by the random effect is very low (2.9% in model 1; 2.6% in model 2; 2.7% in model 3).

Plotting range size vs abundance for individual study plots shows that this relationship is negative across all plots, although with a high degree of scatter amongst the datapoints (Fig. 3). The Pearson correlation coefficient was significant in P. P. Grandes Fougères, Grande Terre ($p = 0.001$), but was insignificant in all other individual sites ($p > 0.05$). The percentage of abundant, small-ranged species in mature plots that also had higher-than-median abundance rankings in corresponding degraded plots was as follows: 84.6% (11 of 13 species) in the P. P. Grandes Fougères-Farino plot pair; 72.7% (8 of 11 species) in the P. P. Rivière Bleu-Bois du Sud plot pair; and 75.0% (6 of 8 species) in the four Flores plots).

Table 4. Coefficients of the fixed effects for the three most parsimonious linear mixed models between range size and abundance with plot as a random intercept random effect (Table 3). DF, denominator degrees of freedom.

| Parameter | Estimate | SE | DF | *t* | p |
|---|---|---|---|---|---|
| Model 1 | | | | | |
| Intercept | –0.287 | 0.209 | 81 | –1.37 | 0.174 |
| Slope | –0.217 | 0.046 | 305 | –4.68 | 0.000 |
| Model 2 | | | | | |
| Intercept (degraded forest) | –0.114 | 0.262 | 31 | –0.43 | 0.275 |
| Intercept (mature forest) | –0.366 | 0.219 | 42 | –1.67 | 0.102 |
| Slope | –0.223 | 0.047 | 309 | –4.77 | 0.000 |
| Model 3 | | | | | |
| Intercept (degraded forest) | –0.338 | 0.336 | 65 | –1.01 | 0.319 |
| Intercept (mature forest) | –0.204 | 0.267 | 87 | –0.77 | 0.446 |
| Slope (degraded forest) | –0.168 | 0.069 | 263 | –2.43 | 0.016 |
| Slope (mature forest) | –0.268 | 0.063 | 317 | –4.24 | 0.000 |

## Discussion

A consistent and statistically significant negative relationship between range size and abundance was found across all combined study plots on Flores, Seram, Grande Terre, and Lifou. Bird communities on these islands are dominated by small-ranged species, with more marginal representation from widespread taxa. This result contrasts dramatically with the typical positive range size–abundance relationship (Brown 1984, 1995, Gaston 1996, Gaston and Blackburn 2000).

While the relationship is negative across mature forest plots, as expected, it is also negative across all plots containing degraded forest (Fig. 3), which is opposite to our prediction. We hypothesized that simultaneous conditions of geographic isolation and environmental stability reward narrow specialization, but this does not appear to be the mechanism causing the negative range size–abundance relationships on the study islands; small-ranged species continued to dominate communities even when the element of environmental stability was compromised.

Table 3. AICc values, ΔAICc, and AICc weight for the three most parsimonious fixed effects structures, with plot as a random intercept random effect. An X indicates the inclusion of a variable in the model; a blank space its exclusion.

| Model | Intercept | Range size | Habitat | Range size: habitat | AICc | ΔAICc | AICc weight |
|---|---|---|---|---|---|---|---|
| 1 | X | X | | | 1176.6 | 0.00 | 0.45 |
| 2 | X | X | X | | 1177.2 | 0.61 | 0.33 |
| 3 | X | X | X | X | 1178.1 | 1.48 | 0.22 |

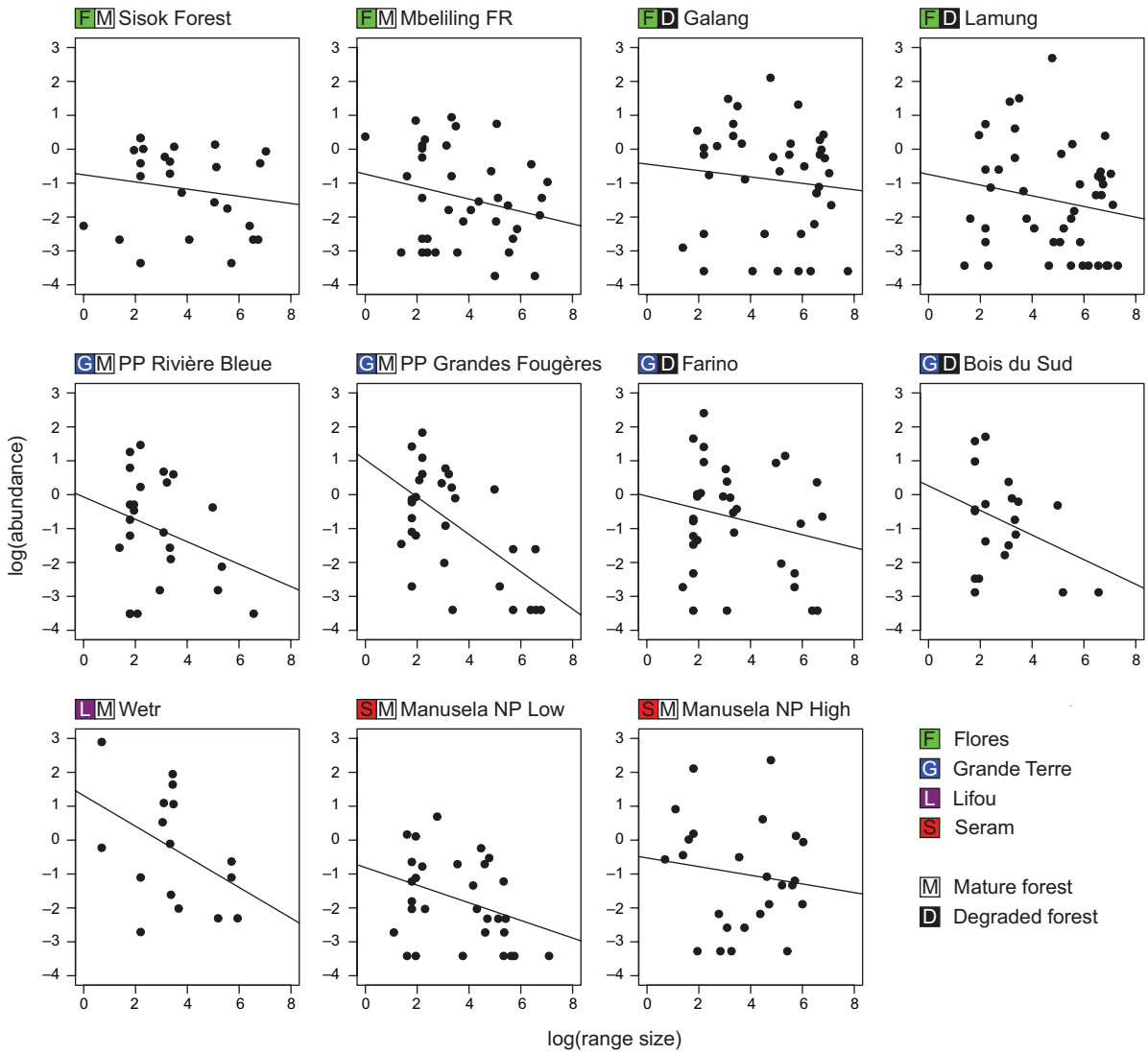


Figure 3. Interspecific range size–abundance relationships of individual Indo-Pacific island bird communities. Regression lines illustrate relationship slopes; note, however, that linear mixed effects models 1 and 2 indicate that slopes among all plots are statistically indistinguishable; model 3 indicates that slopes are statistically indistinguishable within the respective mature and degraded habitat plot groups. Abundance and range size are measured as described in the Methods section, and log-transformed.

The cross-habitat community assemblage comparisons suggest a different explanation for the negative relationship. Most of the small-ranged species that dominated mature plots were also abundant in corresponding degraded plots. On Flores, these were small-ranged (but not strictly endemic) species, and on Grande Terre, a mix of strict and near-endemics. The persistence of these species following forest degradation indicates that they have broad rather than narrow habitat niches. This presents an apparent contradiction: large niche-breadth seems to be rewarded on these islands, but so too does strong adaptation to local environmental conditions, as implied by the fact that endemic and near-endemic birds occur at higher densities than widespread species. Most probably, the explanation for this can be traced back to natural habitat disturbance events such as volcanic eruptions, fires, and particularly landslides along steep terrain (Dykes 2002), all of which can affect habitat composition on islands with otherwise stable environmental conditions. It appears that the small-ranged species dominating both mature and degraded habitats have adapted to exploit the entire naturally occurring spectrum of intact and fragmented forest, and so do not disappear from plots where humans have essentially mimicked these natural disturbance processes. Thus, they are simultaneously broad-niched and well-adapted to local conditions.

Following this interpretation, habitat modified to the point that it bears little resemblance to naturally occurring local environments would no longer be expected to confer any advantage to small-ranged species, and these would mostly disappear. Observations made in such habitat outside of formal surveys support this idea. Certain habitat modifications in the degraded study plots, such as the planting of non-native crops, are dissimilar to those resulting from natural disturbance processes, and this may explain why the negative range size–abundance relationship is marginally weaker here than in mature plots, as indicated in model 3.

Our findings show strong parallels with the few other studies that have examined the range size–abundance relationship in isolated tropical areas. Jones et al. (2001) found that the local abundance of birds on the Wallacean islands of Buru and Sumba increased along with degree of taxon endemicity, and was negatively correlated with number of islands occupied in Wallacea, indicating a negative relationship between abundance and range size. Tolerance of habitat degradation was positively correlated with degree of endemism (on Buru), or with degree of subspecific representation across Wallacea (on Sumba). In a study on the effects of logging, Marsden (1998) found that endemic birds on Seram were generally resilient to habitat disturbance. Reif et al. (2006) discovered no relationship between abundance and range size in the Cameroon highlands, attributing this to the environment's island-like properties. They found that endemic and non-endemic montane bird species had relatively broad niches, with widespread species occupying a small subset of the habitats there despite being broad-niched globally. The results from these different studies support the idea that small-ranged species broadly adapted to local environmental conditions cause negative relationships, and hint at the pervasiveness of this pattern across similar environments.

The dominance of broad-niched endemics and near-endemics in Indo-Pacific bird communities is likely a product of the geographic isolation of these islands. Carrascal et al. (2008) cited the inhibition of normal population dynamics processes as a likely cause of non-significant range size–abundance relationships among birds in the Canary Islands, as dispersal barriers limit the range expansions that would typically accompany species' attainment of high local population densities. This is a convincing explanation for the patterns found on our study islands: the large niche-breadth of the small-ranged species here indicates that they would be capable of expanding their ranges by colonizing similar nearby habitats, were these not made inaccessible by water barriers. Note that our results do not allow us to predict whether a backdrop of climatic stability is needed for negative relationships to occur in isolated communities, because we do not test the climatic niche of the birds sampled.

The apparent role of geographic isolation in causing negative relationships may clarify the mechanisms underlying the more general range size–abundance relationship, which is typically positive in continental and temperate areas. Our study finds a strong link between the local abundance of species and their ability to exploit a wide variety of local resources, supporting the widely-cited 'resource use' hypothesis (Brown 1984). According to this hypothesis, the wide niche of these locally abundant species should allow them to also attain larger ranges; our study indicates that the mechanism requires relatively free dispersal that is not limited by barriers. However, another possibility is that adaptations to local conditions make small-ranged species competitively dominant across a wide range of habitats, so that they are able to sustain high abundances upon their home islands. This possibility for local specialization and interspecific competition to affect distribution–abundance relationships is not very well discussed in the literature, although the potential has been pointed out by some authors (Holt et al. 2002). However, these conjectures cannot be tested with our results, as we do not quantify the niche breadth of the bird species sampled. Another widely cited (but poorly empirically supported; Borregaard and Rahbek 2010) explanation for positive distribution–abundance relationships is the 'range position' hypothesis. This hypothesis states that species that have their range centers close to the study area might have denser patterns of occupancy and higher local abundances. If the most widespread species all have range centers in continental areas far from the studied archipelagos, this mechanism could also theoretically cause the observed negative pattern. Note that this would require species to be less abundant along their range margins, e.g. as a consequence of poor adaptation to local conditions, and thus this hypothesis does not necessarily contradict the other mechanisms discussed here.

Our study shows negative range size–abundance relationships for bird communities on oceanic Indo-Pacific islands, caused by small-ranged species that have adapted to exploit a broad spectrum of local environmental conditions. The pattern observed here raises the possibility that negative range size–abundance relationships may also characterize isolated continental areas with high levels of endemism. In places such as tropical mountain ranges, habitat and climate boundaries may interact with interspecific competition to hinder dispersal, in much the same way as water barriers hinder dispersal in islands. This is expected to lead to a similar pattern, with high densities of locally-adapted endemics centered within a small area, and lower densities of widespread species. With studies from sites in the Cameroon highlands reporting non-positive relationships (Reif et al. 2006, Nana et al. 2014), and other studies from African highland areas reporting high abundances of endemic species (Fjeldså 1999, Ryan et al. 1999, Sekercioğlu and Riley 2005, Fjeldså et al. 2010, 2012), tropical mountain ranges are a promising focal point for further investigation of the range size–abundance relationship.

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Supplementary material (Appendix ECOG-01622 at <www.ecography.org/appendix/ecog-01622>). Appendix 1.