



Ecological generalism and resilience of tropical island mammals to logging: A 23 year test

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Abstract

Tropical forest disturbance is a key driver of global biodiversity decline. On continents, the effects of logging are greatest on endemic species, presumably because disturbance is more likely to cover narrower distributions (the “cookie cutter” model). Islands hold disproportionate biodiversity, and are subject to accelerating biotic homogenization, where specialist endemics are lost while generalists persist. We tested responses of tropical island mammals to logging at multiple spatial scales, using a long-term experimental test in a Pacific archipelago. The most widely distributed ecological generalists did not decline after logging, and we detected no overall changes in relative abundance or species diversity. However, endemics with small ranges did decline in response to logging. The least mobile and most range-restricted species declined even at the smallest spatial scale, supporting the cookie cutter model for sedentary species, and suggesting that habitat change due to selective logging is contributing to biotic homogenization on islands.

KEYWORDS

disturbance, extinction, Melanesia, niche, Pacific, resilience, specialization

1 | INTRODUCTION

Historic and impending vertebrate extinctions are concentrated in tropical forests and on islands (Ricketts et al., 2005). More than a decade of high profile reviews warn that forest disturbance and loss will trigger catastrophic species declines (Bradshaw, Sodhi, & Brook, 2009; Lewis, Edwards, & Galbraith, 2015; Nepstad et al., 1999). Even logging without clear-felling kills or damages a high proportion of trees, allowing sunlight to dry leaf litter and understorey vegetation, changing availability of water and food for rainforest species (Nepstad et al., 1999). Rates of rainforest disturbance are exceptionally high on continental Asia and large islands such as Borneo. Industrial logging on smaller tropical islands has a lower profile but

is a source of income for many developing island nations with rapidly growing human populations, and logging is occurring at unsustainable rates in the Pacific (Wenger et al., 2018). Human population growth also increases hunting pressure on vulnerable species; particularly larger-bodied vertebrates (Fisher & Owens, 2004).

Evolution on islands produces endemic ecological specialists (Losos & Ricklefs, 2009) that are often restricted to small areas, making them particularly vulnerable to disturbance (Fisher & Owens, 2004). However, islands are most likely to be colonized by adaptable generalists, so archipelagoes can have high proportions of species with these traits, especially among newer lineages (MacArthur, Diamond, & Karr, 1972; Mayr & Diamond, 2001; Wright, 1980). Disturbance of primary forests can negatively affect specialists that are adapted to relatively homogenous landscapes and can benefit generalist species that exploit heterogeneous ones

This article is dedicated to the memory of Benjamin Kaniotolu and Adrian Ghele.

(Kerbirou, Le Viol, Jiguet, & Devictor, 2009; Marvier, Kareiva, & Neubert, 2004). Laurance et al. (2002) suggested that many birds and bats are relatively resilient to forest disturbance, because their mobility allows gap-tolerant species to traverse the matrix of regrowth and cultivated land between forest remnants. However, this advantage to mobile taxa may not apply to movements across the more hostile matrix of ocean for island taxa.

Few field experiments have tested the responses of specialist and generalist species to logging with a direct pre- and postlogging comparison. Instead, nearly all tests use a snapshot space-for-time approach to compare species occurrence in different-aged stands. However, such space-for-time tests cannot differentiate the logging treatment from inherent differences between sites, or reveal effects of changing conditions such as increasing human populations or changing hunting pressure. Long-term replicated, controlled experiments testing how species respond to timber extraction have been limited to selective logging in developed countries on continental land masses (Laurance & Laurance, 1996).

Here we use long-term longitudinal data and an experimental approach comparing times before and after widespread logging at multiple spatial scales, to test species resilience to habitat disturbance on a tropical archipelago. We investigated communities of Pteropodidae (flying foxes and blossom bats), a species-rich family that is widespread and ecologically important in the tropics (Banack, 1998; Cox & Elmqvist, 2000; Lavery, Olds, Seddon, & Leung, 2016). Pteropodids show large variation in geographic range size, island endemism, mobility, body size, and level of endangerment (indicated by their IUCN Red List status). We tested if these traits predicted population decline in response to intensive logging in tropical island mammal communities over 23 years. We hypothesized that generalist species are less likely to be negatively affected by logging than ecological specialists, that endemics with smaller distributions were more likely to decline, and that larger-bodied species would be more likely to decline.

2 | MATERIALS AND METHODS

Our sites were in Solomon Islands, a Pacific archipelago that is a biodiversity hotspot—the East Melanesian Islands (EMI; Mittermeier et al., 2004). Logging by commercial companies is selective, and legislatively constrained to elevations below 400 m a.s.l. However, there is frequent illegal logging by companies above 400 m. Timber is transported via cleared tracks to the coast for export by sea as whole logs (Furusawa, Pahari, Umezaki, & Ohtsuka, 2004; Katovai, Edwards, & Laurance, 2015). Harvest intensity is extremely high (often reaching 30 trees per hectare), leaving behind residual stands of damaged or killed immature trees, and landscapes abandoned to natural regeneration (Dauvergne, 2001; Kabutaulaka, 2005; Katovai et al., 2015).

Prior to the 1960s, primary forests covered more than 76% of the land area of Solomon Islands (Whitmore, 1966, 1969). Much of this has now been converted to secondary forest by logging and an estimated 10.7% of primary forests remain in the EMI (Sloan, Jenkins, Joppa, Gaveau, & Laurance, 2014). Commercial logging began to

escalate to unsustainable levels from the early 1990s. On one of our study islands (Kolombangara), Katovai, Burley, and Mayfield (2012) showed that functional diversity of forests logged 18 years prior resembled primary forest, but community composition still had not converged with unlogged forests even after 50 years (Katovai, Sirikolo, Srinivasan, Edwards, & Laurance, 2016). Our sampling was conducted before (1992) and after (2014–2015) the occurrence of widespread logging. At our smaller chosen spatial scales this provided us with a before-after-control-impact design of sites that were unlogged or logged once during the study period.

The pteropodid bats comprise some 46 genera and almost 200 species of fruit and nectar-eating flying foxes and blossom bats (Giannini, 2019). Their center of diversity is in the western Pacific region and adjacent SE Asian archipelagoes. Pteropodids show high endemism on small islands (Almeida, Giannini, DeSalle, & Simmons, 2011). Twenty-five species of pteropodid dominate the mammal fauna of Solomon Islands, as abundant keystone pollinators and seed dispersers (Banack, 1998; Cox & Elmqvist, 2000; Lavery et al., 2016). These are all forest-dwelling species. Five belong to the Solomon Islands endemic genus *Pteralopex* (monkey-faced bats, which are each restricted to single islands or small island chains and are all threatened). Two are in the EMI endemic genus *Melonycteris* (nectarivorous blossom bats). Of genera that extend beyond the EMI, there are five species of *Pteropus* and two *Nyctimene* that are endemic to single or closely adjacent islands, and a Solomon Islands endemic *Dobsonia*. Remaining species belong to the genera *Pteropus*, *Nyctimene*, *Rousettus*, and *Macroglossus* and are more widespread in Papua New Guinea, Asia, and/or Australia.

2.1 | Home range estimates of pteropodids and choice of spatial scales

We intensively sampled at eight sites on three of the main islands in the Western Province island chain in 1992 (Fisher & Tasker, 1997) and in 2014–2015, at the same net locations at each site in both periods, at the same times of year (Figure 1; Table 1; Data S1). We calculated the proportion of forest logged between these two times at each site at multiple spatial scales: 3; 30; 300; 3,000; and 30,000 ha areas around each site (area of logged forest divided by the total forest area at each of the given spatial scales). We chose these scales based on known home range estimates and dispersal movements from telemetry studies, in Melanesian pteropodids and related species in the same genera: *Melonycteris melanops* (39–61 g, 2.3 ha; Bonaccorso & Winkelmann, 2005); *Syconycteris australis* (15–21 g, 2.7–13.6 ha; Winkelmann, Bonaccorso, & Strickler, 2000); *Dobsonia minor* (74–102 g, 5.1 ha; Bonaccorso, Winkelmann, & Dumont, 2002); *Macroglossus minimus* (15.4 g, 5.8 ha; Winkelmann & Bonaccorso, 2003); *Pteropus dasymallus* (295–568 g, 52.5 ha; Nakamoto, Kinjo, & Izawa, 2012); *Pteropus niger* (550–800 g, 31,072 ha female–74,633 ha male; Oleksy et al., 2019); *Pteropus rufus* (650–1,100 g, 5,191 ha; Oleksy, Racey, & Jones, 2015); *Pteropus vampyrus* (<1,100 g, 11.6–25 ha restricted movement phases, and

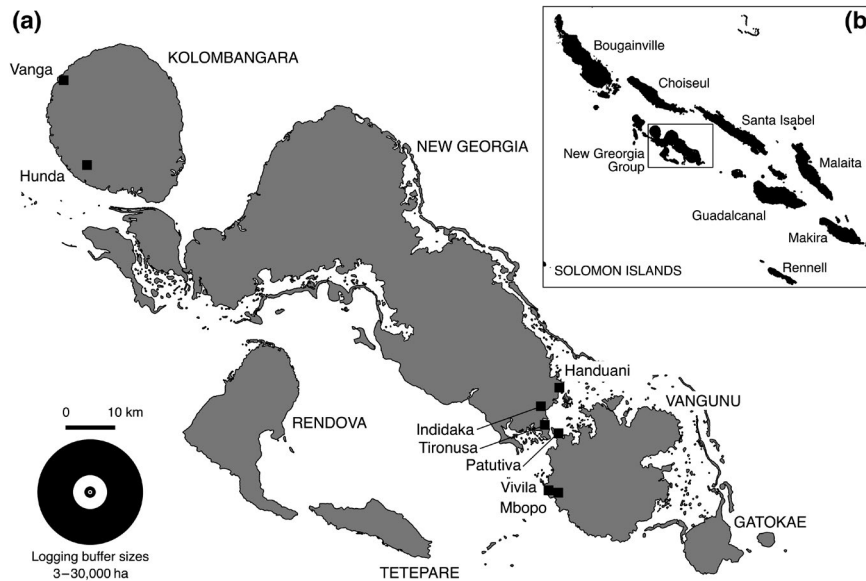


FIGURE 1 Location of study sites (a) in Western Province; and (b) in the Solomon Islands Archipelago. Solid black squares indicate sites surveyed in 1992 and 2014–2015. Concentric circles in the bottom left of the figure are to scale and indicate areas of 3, 30, 300, 3,000, and 30,000 ha, for which the proportion of logged and unlogged vegetation were calculated surrounding each survey site. The logging history of our three study islands differs: Kolombangara was almost entirely logged below 400 m a.s.l. in the 1960s–1980s (including our sites), New Georgia was almost entirely logged below 400 m a.s.l. in the 1990s–2000s, and Vangunu was partially logged in the 1990s–2000s

TABLE 1 Primary forest disturbance due to logging between 1992 and 2015 in 3, 30, 300, 3,000, and 30,000 ha areas around each sampling site. Logging commenced on Kolombangara in 1965, on New Georgia in c. 1993, and on Vangunu in c. 1995. Logged/unlogged forest calculations were derived for each site from forest cover maps (Hansen et al., 2013) with SPOT 5 and Landsat 7 imagery analysis (Sinclair Knight Merz, 2012) and cross-referenced with Google Earth images dated: 1. August 2, 2013; 2. November 4, 2014; 3. October 29, 2014; and 4–8. November 4, 2014

Island	Site name	% Primary forest disturbance between 1992 and 2015				
		3 ha	30 ha	300 ha	3,000 ha	30,000 ha
Kolombangara	Vanga ¹	81	71	40	23	15
New Georgia	Tironusa ²	80	65	58	80	79
New Georgia	Handuani ³	100	82	46	65	61
Vangunu	Patutiva ⁴	100	100	100	98	71
New Georgia	Indidaka ⁵	31	42	91	61	66
Kolombangara	Hunda ⁶	0	27	45	79	34
Vangunu	Mbopo ⁷	0	0	13	54	59
Vangunu	Vivila ⁸	0	0	5	42	96

891.2 ha continual movement phases; Gumal, 1999); and *P. vampyrus* (6,400,000–12,800,000 ha; Epstein et al., 2009). Our spatial scales for analysis encompass this range of variation across species of similar body size as our study species (Data S1).

The reasons for each site being logged or left intact depended on social context and land ownership and were unrelated to environmental characteristics. To map logged and primary forests in 1992 and 2014, we combined forest cover maps (Hansen et al., 2013) with SPOT 5 and Landsat 7 imagery analysis (Sinclair Knight Merz, 2012) and cross-referenced with Google Earth imagery at a 500 m scale. Logged forests (especially logging tracks) were clearly discernable from Google Earth imagery and forest cover maps (Hansen et al., 2013). We delineated polygons of logged secondary and unlogged

primary forests in QGIS (QGIS Development Team, 2009), further cross-referenced these with additional deforestation data (Katovai et al., 2012, 2015, 2016; Whitmore, 1989), and ground-truthed the extent of 2014 logging during field surveys. The proportion of logged forests in the defined areas around each site (excluding oceans) was calculated in QGIS (QGIS Development Team, 2009).

2.2 | Mist net surveys

We surveyed bats using black 75 denier, 38 mm mesh nylon mist nets (12 m in length × 2.6 m in height; M. Nakamori & Co., Ltd.). We configured two to four nets individually in the forest understory and

subcanopy, on wooden poles up to 10 m, or suspended on ropes up to 20 m above the ground. We placed nets on ridgelines, spanning watercourses, or natural forest gaps to maximize captures. Detailed field notes, landowner knowledge, and marked sites on topographic maps from the original survey allowed us to return to the exact locations where nets were erected in 1992 for repeat sampling in 2014/2015. Surveys commenced at dusk and we checked nets throughout the night until they were closed shortly after dawn. We calculated survey effort as square meter mist net hours (net-m²/hr): thus one 12 × 2.6 m net deployed for 1 hr gave an effort of 31.2 net-m²/hr.

2.3 | Data analysis

To test how the spatial scale of logging affected species capture rates, accounting for island size and logging history (Figure 1), we used linear mixed effect models in the *nlme* package (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017) in R (R Core Team, 2016), to analyze eight sites that were sampled at both times (1992 and 2014/2015). Fixed predictor variables were the proportion of area logged at each of the five spatial scales, the island on which the site was located, and island area. Site was included as a random term. We applied likelihood ratio tests to models that included and omitted fixed variables, to test whether logging treatments had effects that differed from zero. We addressed the potential for spatial autocorrelation of our sites by fitting models with a spatial correlation structure. Using the package *effects* (Fox & Hong, 2009) in R we converted parameter estimates into condition mean and confidence interval estimates for species models. We tested for changes in species diversity between the two survey periods using Simpson's index.

3 | RESULTS

At the smaller scales of 3 and 30 ha, some sites were entirely logged between 1992 and 2014/2015, and some were entirely intact at both times (Table 1). At spatial scales above 300 ha, all sites were affected by commercial logging in the study period, that is, there were some logged areas within 1–2 km of every trapping site in 2014

and 2015. This means that our sampling included before (1992), after (2014/2015), treatment (logged), and control (unlogged) sites at spatial scales <300 ha, but at scales of >3,000 ha there were no unlogged or minimally logged controls in the “after” category (Table 1).

We captured 893 individuals of nine species; two were restricted-range island endemic species that belong to EMI endemic genera (New Georgia monkey-faced bat *Pteralopex taki* and Fardoulis's blossom bat *Melonycteris fardoulisi*), and seven more widespread species in other genera (Figure 2; Data S1). Total capture rates per 1,000 net-m²/hr for each site were 27.8 ± 6.4 SE in 1992 and 18.7 ± 4.6 SE in 2014/2015. Overall captures per site at the 3 ha scale (relative abundance) and species diversity (Simpson's index) did not differ significantly between the two survey periods (abundance: $t_{(7)} = 1.24$, $p = .26$; diversity: $t_{(7)} = 0.63$, $p = .55$).

In agreement with our predictions, island endemism at the genus and species level and small geographic range size predicted poor resilience to commercial logging in Solomon Islands pteropodids. Island size was not an important predictor. Increased logging decreased capture rates of two restricted-range endemics at different spatial scales (Figure 3). Captures of the Solomon Islands endemic Fardoulis's blossom bat *M. fardoulisi* decreased by a mean of $75.6 \pm 5.6\%$, with the proportion of logged forest at the 30,000 ha scale associated with decline ($X_{(4)} = 10.6$, $p < .05$; Figure 3). Decline was greatest among females. In 1992 there were 1.6 females per male, in 2014/2015 there were 0.43 females per male. We caught the Western Province endemic New Georgia monkey-faced bat (*P. taki*) at fewer sites in 1992 than 2014/2015. In 1992 we captured this species at four of the eight sites, and in 2014/2015 at seven of the eight sites, including six individuals on Kolombangara Island where the species had been presumed extinct (Fisher & Tasker, 1997). However, our overall captures of this species declined by a third in the two decades of the study. We caught 27 (1.17 per 1,000 net-m²/hr) in 1992 and 18 individuals in 2014/2015 (1.03 per 1,000 net-m²/hr). The proportion of logged forest at the 30 ha scale ($X_{(4)} = 9.7$, $p < .05$) was associated with the decline in this species (Figure 3).

Contrary to the expectation that larger-bodied mammals are most likely to decline under pressure from expanding human populations, captures of the second largest pteropodid (the 200 g Admiralty flying fox *Pteropus admirallatum solomonis*) increased after logging.

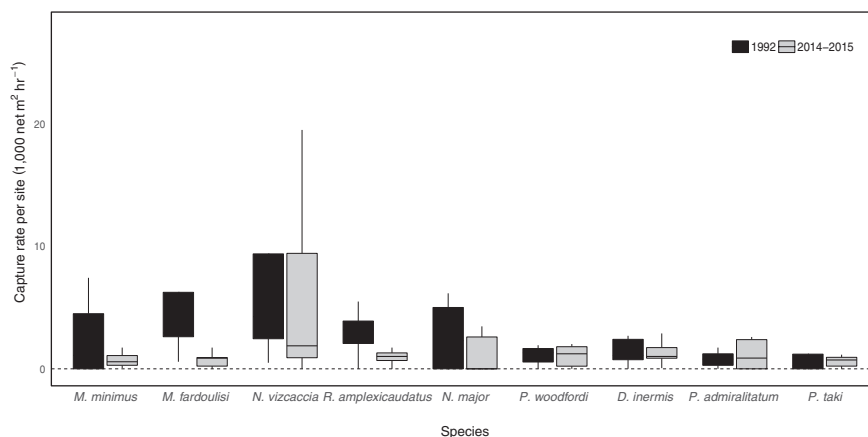


FIGURE 2 Box plot depicting capture rates (per 1,000 net-m²/hr) of nine species of pteropodid in 1992 and 2014–2015. Data are total captures of each species per site across eight repeated sampling sites. Capture rates (without consideration of logging extent) varied between years for one species (*Melonycteris fardoulisi*; $t_{(7)} = 2.44$, $p = .04$)

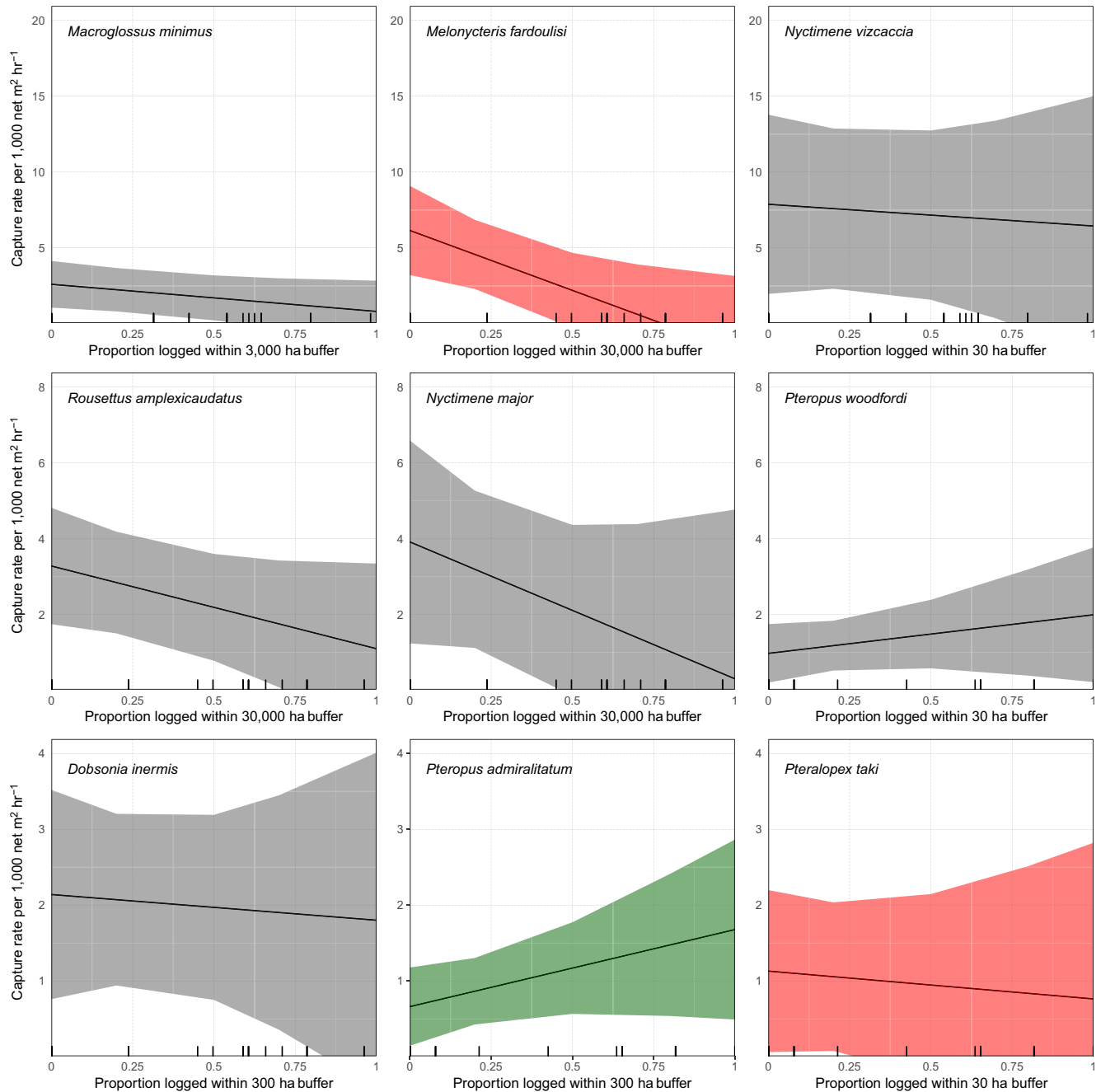


FIGURE 3 Effects of logging on capture rates of the nine species of pteropodid bats. Y-axis values are condition mean estimates for species linear mixed effects models. Confidence intervals (95%) are shaded in light gray for best-fit models of species for which capture rates were unaffected by logging at any scale, green for models where capture rates increased and red for models where capture rates decreased

In 1992 we captured 0.62 individuals per 1,000 net-m²/hr, and in 2014/2015 this doubled to 1.23 individuals per 1,000 net-m²/hr. Logging at the 30, 300, and 3,000 ha scales were associated with increases in this species ($X_{(4)} = 11.6$, $p = .02$; Figure 3; Data S1).

4 | DISCUSSION

In agreement with global comparative studies of extinction risk in mammals and other taxa (Fisher & Blomberg, 2011; Fisher & Owens,

2004; Purvis, Agapow, Gittleman, & Mace, 2000), island endemics were the most vulnerable to decline from habitat disturbance. We found that on a 20–25 year time scale, detrimental effects of logging were apparent only in the two species that are endemic at both the genus and species level, and which had the smallest ranges (New Georgia monkey-faced bat *P. taki*, range ~6,000 km² on three islands in Solomon Islands, and Fardoulis's blossom bat *M. fardoulisi*, range ~20,000 km² on eight islands in Solomon Islands (Bonaccorso, Helgen, & Hamilton, 2008). The other pteropodid species were more widespread and did not decline, and none of the species recorded in 1992

were absent in 2014/2015. Captures of one widespread generalist (Admiralty flying fox *P. admiralitatum solomonis*, range ~80,000 km²) increased in the same time period.

Endemism may be associated with high extinction risk because narrow-range endemics are ecological specialists, which are particularly disadvantaged by disturbance to the advantage of generalists (the biotic homogenization model; Harrison, 1993; McKinney & Lockwood, 1999; Olden & Rooney, 2006). Under this model, specialist ecology, life history, and behavior predispose island endemics to extinction at a landscape scale (Loehle & Eschenbach, 2011). Increased disturbance results in the replacement of many specialists with few widespread generalists.

Pimm, Russell, Gittleman, and Brooks (1995) proposed the "cookie cutter" model to explain why small-range endemics are particularly vulnerable to extinction. As increasingly larger areas of primary forest are altered, there is a greater likelihood that the crucial habitat or entire distribution of endemic species will be affected. Under this model, life history, ecological specialization, and behavior do not make island biotas intrinsically more vulnerable than mainland ones. Rather, a higher proportion of island species have endangering traits of small range and high endemism, because isolation promotes speciation on islands.

Our results support the biotic homogenization model because the narrowest range endemics, which declined due to logging, have specialist ecologies. New Georgia monkey-faced bat abundance declined as a result of logging at the local site scale (30 ha). *P. taki* was the least commonly captured bat in both survey periods, consistent with the general rule that population density and local distribution are correlated with geographic range size across species (Gaston, Blackburn, & Lawton, 1997). Slatyer, Hirst, and Sexton (2013) argued that broader niches cause ecological generalists to be both more widespread and more locally abundant throughout their ranges than specialists.

The decline of the New Georgia monkey-faced bat is consistent with the mechanism of progressive alteration of habitat proposed by Pimm et al. (1995). The decline in response to logging at the 30 ha scale appears to represent a genuine reduction in carrying capacity in the vicinity of netting locations in logged areas, because radio tracking has shown that this species is highly sedentary (Fisher & Tasker, 1997). The New Georgia monkey-faced bat depends on large tree hollows provided by lowland primary forests and historic village sites in primary forest areas, in emergent strangler figs (*Ficus* spp.) and canopy level ngali trees (*Canarium indicum*), because it roosts communally in cavities and is relatively large bodied (Fisher & Tasker, 1997).

Fardoulis's blossom bat was strongly affected by logging at the landscape scale of 30,000 ha, indicating it is more sensitive to disturbance than *P. taki*. This possibly relates to species-specific impacts of logging on forest resources, such as a widespread loss of important flowering species for *Melonycteris* versus less intensive losses of noncommercial strangler figs for *Pteralopex*. *M. fardoulisi* apparently specializes on nectar and the sexes appear to further specialize on different foraging habitats, and thus potentially different food

species (Flannery, 1995). Decline in a species with specialist dietary ecology and ecological divergence between sexes is consistent with biotic homogenization, in which specialists are disadvantaged by habitat disturbance at a landscape scale. Moreover, morphological distinctiveness and >6% genetic divergence between the subspecies endemic to our three study islands (*M. fardoulisi mengermani*) and the other subspecies suggest that this may in fact be a distinct species with a geographic range area similar to that of *P. taki* (Pulvers & Colgan, 2007). The decline of *M. fardoulisi* in 23 years was much more severe in females, implying that logging is particularly affecting an important aspect of females' natural history, and thus there may be an accelerating decline from a shortage of females in the future.

Residual stands of immature trees typically remain after harvesting in the study area, and within 18 years these can form secondary forest in which the overall density of plants with bat-dispersed seeds is similar to unlogged forests (Katovai et al., 2012, 2016). However, tree species composition of secondary forest differs from that of primary forest. This may disadvantage dietary specialists in the long term (because they may be less capable of switching from scarcer food sources impacted by logging), while food abundance for generalists is maintained in the decades after disturbance as fruiting pioneer species regenerate (Bowman, Woinarski, Sands, Wells, & McShane, 1990; Katovai et al., 2016; Meijaard & Sheil, 2008).

Species that did not decline during the study have broader roosting habitat, diets, and foraging habitat (Flannery, 1995). The Admiralty flying fox *P. admiralitatum solomonis* apparently benefitted from logging at local to regional scales of 30, 300, and 3,000 ha: captures in 2014/2015 were double that of 1992. This and other relatively large-bodied *Pteropus* species at our sites are mobile ecological generalists (Breed, Field, Smith, Edmonston, & Meers, 2010; Data S1) and readily exploit disturbed environments such as village gardens and cyclone-damaged forests (McNab, 1994; McNab & Bonaccorso, 2001). Ecological generalists may change their behavior in fragmented landscapes. Increased captures of the Admiralty flying fox at the local scales over which this species readily travels may reflect attraction to disturbed sites.

Generalists such as the Admiralty flying fox may also be advantaged because species richness is lower on these islands than on continents. On depauperate islands, individual species can expand into vacant niches occupied by specialists on mainlands, so greater generalism evolves on archipelagos, and this makes species more resilient to disturbance. For example, 29 of 52 mainland New Guinea birds that colonized one island expanded habitat or altitudinal range, changed vertical foraging ranges, or became more numerous in their preferred habitat than on the mainland (Diamond, 1970). Thus, fewer generalists can fill island niches that are occupied by more specialists in equivalent mainland forests (MacArthur et al., 1972; Mayr & Diamond, 2001; Wright, 1980). If the mechanism of increasing ecological generalism in mobile species applies to bats as well as birds, this may also explain why seven widespread pteropodids were resilient to logging at all spatial scales in this study.

If high human population growth in the study period had resulted in increased hunting, and this was the cause of declines in flying foxes,

we expected to see declines in the largest bodied, group roosting species, because these are targeted by human hunters (Fisher & Owens, 2004; Lavery & Fasi, 2017). However, large and conspicuous species (*P. admiraltatum solomonis*, *P. woodfordi*, and *Dobsonia inermis*), did not decline during the study period. A small, solitary species that is not hunted (*M. fardoulisi*) declined strongly. This suggests that hunting is not the explanation for the observed declines.

In a global meta-analysis addressing responses of abundance, richness, structure, and demography, Gibson et al. (2011) concluded that selective logging was the least harmful form of disturbance, and that mammals, particularly bats, were least affected by the conversion of primary forest to secondary forest. However, differential responses of narrow-range and island endemic, specialist and threatened species may not be captured in this broad approach. Our results agree with the findings of several space-for-time studies in the continental neotropics, where dietary and roost specialist bats were absent from logged sites on scales of 3–4,000 ha (Estrada & Coates-Estrada, 2002; Faria, 2006; Schulze, Seavy, & Whitacre, 2000) resulting in lower species richness of logged secondary forests. For example, 15–40 year old secondary forests in continental French Guiana (Brosset, Charles-Dominique, Cockie, Cosson, & Masson, 1996) and Brazil (Faria, 2006) had between one-third and two-thirds of the species diversity of primary forests. In the Neotropics, bat abundance was higher in areas close to mature forest (Falcão, Espírito-Santo, Fernandes, & Paglia, 2018), and deforestation resulted in losses of closely related species that were forest specialists (Frank, Frishkoff, Mendenhall, Daily, & Hadly, 2017). Logging in tropical forests has also resulted in severe reductions in bird species richness from all forest strata, presumably because high proportions of species are late-successional forest specialists (LaManna & Martin, 2016). The secondary forests in our study had been left to naturally regenerate. At scales below 3,000 ha, regrowth patches were adjacent to primary forest, so primary forest could serve as a source of colonizers (provided that colonizing species are resilient to fragmentation at this scale; Gibson et al., 2011). Further logging is likely to reduce the availability of emigrants from primary forest, and the value of regrowth for threatened species (Edwards et al., 2011). While Edwards et al. (2011) argued that repeatedly logged forest has conservation value, as it retained most species of birds, our results suggest that endemic and threatened specialist species will be disproportionately lost, even from relatively resilient taxa.

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DATA AVAILABILITY STATEMENT

The vegetation data that support the findings of this study are openly available from Global Forest Change at <https://earthenginepartners.appspot.com/science-2013-global-forest>, <http://doi.org/10.1126/science.1244693>, and Solomon Islands Ministry of Forestry & Research <http://mofr.gov.sb/foris/reports.do>. Bat capture data are available from the corresponding author upon reasonable request.

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REFERENCES

- Almeida, F. C., Giannini, N. P., DeSalle, R., & Simmons, N. B. (2011). Evolutionary relationships of the old world fruit bats (Chiroptera, Pteropodidae): Another star phylogeny? *BMC Evolutionary Biology*, 11(1), 281. <https://doi.org/10.1186/1471-2148-11-281>
- Banack, S. A. (1998). Diet selection and resource use by flying foxes (genus *Pteropus*). *Ecology*, 79(6), 1949–1967. <https://doi.org/10.2307/176701>
- Bonaccorso, F., Helgen, K., & Hamilton, S. (2008). *Melonycteris fardoulisi*. The IUCN red list of threatened species 2008: e.T13141A3413281. <https://doi.org/10.2305/IUCN.UK.2008.RLTS.T13141A3413281.en>
- Bonaccorso, F. J., & Winkelmann, J. R. (2005). Home range, territoriality, and flight time budgets in the black-bellied fruit bat, *Melonycteris melanops* (Pteropodidae). *Journal of Mammalogy*, 86(5), 931–936. [https://doi.org/10.1644/1545-1542\(2005\)86%5B931:HRTAF T%5D2.0.CO;2](https://doi.org/10.1644/1545-1542(2005)86%5B931:HRTAF T%5D2.0.CO;2)
- Bonaccorso, F. J., Winkelmann, J. R., Dumont, E. R., & Thibault, K. (2002). Home range of *Dobsonia minor* (Pteropodidae): A solitary, foliage-roosting fruit bat in Papua New Guinea. *Biotropica*, 34(1), 127–135. <https://doi.org/10.1111/j.1744-7429.2002.tb00248.x>
- Bowman, D., Woinarski, J., Sands, D., Wells, A., & McShane, V. (1990). Slash-and-burn agriculture in the wet coastal lowlands of Papua New Guinea: Response of birds, butterflies and reptiles. *Journal of Biogeography*, 17, 227–239. <https://doi.org/10.2307/2845121>
- Bradshaw, C. J., Sodhi, N. S., & Brook, B. W. (2009). Tropical turmoil: A biodiversity tragedy in progress. *Frontiers in Ecology and the Environment*, 7(2), 79–87. <https://doi.org/10.1890/070193>
- Breed, A. C., Field, H. E., Smith, C. S., Edmonston, J., & Meers, J. (2010). Bats without borders: Long-distance movements and implications for disease risk management. *EcoHealth*, 7(2), 204–212. <https://doi.org/10.1007/s10393-010-0332-z>
- Brosset, A., Charles-Dominique, P., Cockie, A., Cosson, J., & Masson, D. (1996). Bat communities and deforestation in French Guiana. *Canadian Journal of Zoology*, 74, 1974–1982. <https://doi.org/10.1139/z96-224>
- Cox, P. A., & Elmqvist, T. (2000). Pollinator extinction in the Pacific Islands. *Pacific Conservation Biology*, 14(5), 1237–1239. <https://doi.org/10.1046/j.1523-1739.2000.00017.x>
- Dauvergne, P. (2001). *Loggers and degradation in the Asia Pacific: Corporations and environmental management*. Cambridge: Cambridge University Press.
- Diamond, J. M. (1970). Ecological consequences of island colonization by southwest Pacific birds, II. The effect of species diversity on total population density. *Proceedings of the National Academy of Sciences of the United States of America*, 67(4), 1715–1721. <https://doi.org/10.1073/pnas.67.4.1715>

- Edwards, D. P., Larsen, T. H., Docherty, T. D. S., Ansell, F. A., Hsu, W. W., Derhé, M. A., ... Wilcove, D. S. (2011). Degraded lands worth protecting: The biological importance of Southeast Asia's repeatedly logged forests. *Proceedings of the Royal Society B: Biological Sciences*, 278, 82–90. <https://doi.org/10.1098/rspb.2010.1062>
- Epstein, J. H., Olival, K. J., Pulliam, J. R. C., Smith, C., Westrum, J., Hughes, T., ... Daszak, P. (2009). *Pteropus vampyrus*, a hunted migratory species with a multinational home-range and a need for regional management. *Journal of Applied Ecology*, 46(5), 991–1002. <https://doi.org/10.1098/rspb.1996.0075>
- Estrada, A., & Coates-Estrada, R. (2002). Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. *Biological Conservation*, 103, 237–245. [https://doi.org/10.1016/S0006-3207\(01\)00135-5](https://doi.org/10.1016/S0006-3207(01)00135-5)
- Falcão, L., Espírito-Santo, M., Fernandes, G., & Paglia, A. (2018). Effects of habitat structure, plant cover, and successional stage on the bat assemblage of a tropical dry forest at different spatial scales. *Diversity*, 10(2), 41. <https://doi.org/10.1016/j.ncon.2014.09.001>
- Faria, D. (2006). Phyllostomid bats of a fragmented landscape in the north-eastern Atlantic forest, Brazil. *Journal of Tropical Ecology*, 22(05), 531–542. <https://doi.org/10.1017/S0266467406003385>
- Fisher, D. O., & Blomberg, S. P. (2011). Correlates of rediscovery and the detectability of extinction in mammals. *Proceedings of the Royal Society B: Biological Sciences*, 278(1708), 1090–1097. <https://doi.org/10.1098/rspb.2004.2724>
- Fisher, D. O., & Owens, I. (2004). The comparative method in conservation biology. *Trends in Ecology & Evolution*, 19, 391–398. <https://doi.org/10.1016/j.tree.2004.05.004>
- Fisher, D. O., & Tasker, E. (1997). Natural history of the New Georgia monkey-faced bat *Pteralopex* sp. nov. from the Solomon Islands. *Pacific Conservation Biology*, 3, 134–142. <https://doi.org/10.1071/PC970134>
- Flannery, T. (1995). *Mammals of the South-west Pacific and Moluccan Islands*. Chatswood, NSW: Reed Books.
- Fox, J., & Hong, J. (2009). Effect displays in R for multinomial and proportional-odds logit models: Extensions to the effects package. *Journal of Statistical Software*, 32(1), 1–24.
- Frank, H. K., Frishkoff, L. O., Mendenhall, C. D., Daily, G. C., & Hadly, E. A. (2017). Phylogeny, traits, and biodiversity of a Neotropical bat assemblage: Close relatives show similar responses to local deforestation. *The American Naturalist*, 190(2), 200–212. <https://doi.org/10.5061/dryad.mb552>
- Furusawa, T., Pahari, K., Umezaki, M., & Ohtsuka, R. (2004). Impacts of selective logging on New Georgia Island, Solomon Islands evaluated using very-high-resolution satellite (IKONOS) data. *Environmental Conservation*, 31(4), 349–355. <https://doi.org/10.1017/S0376892904001638>
- Gaston, K., Blackburn, T., & Lawton, J. (1997). Interspecific abundance-range size relationships: An appraisal of mechanisms. *The Journal of Animal Ecology*, 66, 579–601. <https://doi.org/10.2307/5951>
- Giannini, N. (2019). Family Pteropodidae (old world fruit bats). In D. E. Wilson & R. A. Mittermeier (Eds.), *Handbook of the mammals of the world* (Vol. 9, pp. 16–163). Barcelona: Lynx Edicions.
- Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., ... Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478, 378–381. <https://doi.org/10.1038/nature10425>
- Gumal, M. T. (1999). Diurnal home range and roosting trees of a maternity colony of *Pteropus vampyrus natunae* (Chiroptera: Pteropodidae) in Sedilu, Sarawak. *Journal of Tropical Ecology*, 20(3), 247–258. <https://doi.org/10.1017/S0266467403001275>
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., ... Townshend, J. R. G. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, 342, 850–853. <https://doi.org/10.1126/science.1244693>
- Harrison, S. (1993). Species diversity, spatial scale, and global change. In P. Kareiva, J. Kingslover, & R. Huey (Eds.), *Biotic interactions and global change* (pp. 388–401). Sunderland, MA: Sinauer.
- Kabutaulaka, T. T. (2005). Rumble in the jungle: Land, culture and (un)sustainable logging in Solomon Islands. In A. Hooper (Ed.), *Culture and sustainable development in the Pacific* (pp. 88–97). Canberra: ANU E Press and Asia Pacific Press.
- Katovai, E., Burley, A. L., & Mayfield, M. M. (2012). Understorey plant species and functional diversity in the degraded wet tropical forests of Kolombangara Island, Solomon Islands. *Biological Conservation*, 145(1), 214–224. <https://doi.org/10.1016/j.biocon.2011.11.008>
- Katovai, E., Edwards, W., & Laurance, W. F. (2015). Dynamics of logging in Solomon Islands: The need for restoration and conservation alternatives. *Tropical Conservation Science*, 8(3), 718–731. <https://doi.org/10.1177/194008291500800309>
- Katovai, E., Sirikolo, M., Srinivasan, U., Edwards, W., & Laurance, W. F. (2016). Factors influencing tree diversity and compositional change across logged forests in the Solomon Islands. *Forest Ecology and Management*, 372(C), 53–63. <https://doi.org/10.1016/j.foreco.2016.03.052>
- Kerbiriou, C., Le Viol, I., Jiguet, F., & Devictor, V. (2009). More species, fewer specialists: 100 years of changes in community composition in an island biogeographical study. *Diversity and Distributions*, 15(4), 641–648. <https://doi.org/10.1111/j.1472-4642.2009.00569.x>
- LaManna, J. A., & Martin, T. E. (2016). Logging impacts on avian species richness and composition differ across latitudes and foraging and breeding habitat preferences. *Biological Reviews*, 92(3), 1657–1674. <https://doi.org/10.1371/journal.pone.0081358>
- Laurance, W. F., & Laurance, S. (1996). Responses of five arboreal marsupials to recent selective logging in tropical Australia. *Biotropica*, 28(3), 310–322.
- Laurance, W. F., Lovejoy, T. E., Vasconcelos, H. L., Bruna, E. M., Didham, R. K., Stouffer, P. C., ... Sampaio, E. (2002). Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology*, 16(3), 605–618. <https://doi.org/10.1046/j.1523-1739.2002.01025.x>
- Lavery, T. H., & Fasi, J. (2017). Buying through your teeth: Traditional currency and conservation of flying foxes *Pteropus* spp. in Solomon Islands. *Oryx*, 1–8. <https://doi.org/10.1017/S0030605317001004>
- Lavery, T. H., Olds, A. D., Seddon, J. M., & Leung, L. K.-P. (2016). The mammals of northern Melanesia: Speciation, ecology, and biogeography. *Mammal Review*, 46(1), 60–76. <https://doi.org/10.1111/mam.12057>
- Lewis, S. L., Edwards, D. P., & Galbraith, D. (2015). Increasing human dominance of tropical forests. *Science*, 349(6250), 827–832.
- Loehle, C., & Eschenbach, W. (2011). Historical bird and terrestrial mammal extinction rates and causes. *Diversity and Distributions*, 18(1), 84–91. <https://doi.org/10.1111/j.1472-4642.2011.00856.x>
- Losos, J. B., & Ricklefs, R. E. (2009). Adaptation and diversification on islands. *Nature*, 457(7231), 830–836. <https://doi.org/10.1038/nature07893>
- MacArthur, R. H., Diamond, J. M., & Karr, J. R. (1972). Density compensation in island faunas. *Ecology*, 53(2), 330–342. <https://doi.org/10.2307/1934090>
- Marvier, M., Kareiva, P., & Neubert, M. (2004). Habitat destruction fragmentation and disturbance promote invasion by habitat generalists in a multispecies metapopulation. *Risk Analysis*, 24, 869–878. <https://doi.org/10.1111/j.0272-4332.2004.00485.x>
- Mayr, E., & Diamond, J. (2001). *The birds of northern melanesia: Speciation, ecology & biogeography*. New York: Oxford University Press.
- McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, 14(11), 450–453. [https://doi.org/10.1016/S0169-5347\(99\)01679-1](https://doi.org/10.1016/S0169-5347(99)01679-1)
- McNab, B. (1994). Resource use and the survival of land and freshwater vertebrates on oceanic islands. *The American Naturalist*, 144, 643–660. <https://doi.org/10.1086/285698>

- McNab, B., & Bonaccorso, F. (2001). The metabolism of New Guinean pteropodid bats. *Journal of Comparative Physiology B*, 171, 201–214. <https://doi.org/10.1007/s003600000163>
- Meijaard, E., & Sheil, D. (2008). The persistence and conservation of Borneo's mammals in lowland rain forests managed for timber: Observations, overviews and opportunities. *Ecological Research*, 23, 21–34. <https://doi.org/10.1007/s11284-007-0342-7>
- Mittermeier, R., Robles Gil, P., Hoffman, M., Pilgrim, J., Brooks, T., Mittermeier, C., ... da Fonseca, G. (2004). *Hotspots revisited*. Mexico City: CEMEX.
- Nakamoto, A., Kinjo, K., & Izawa, M. (2012). Ranging patterns and habitat use of a solitary flying fox (*Pteropus dasymallus*) on Okinawajima Island, Japan. *Acta Chiropterologica*, 14(2), 387–399. <https://doi.org/10.3161/150811012X661701>
- Nepstad, D. C., Verssimo, A., Alencar, A., Nobre, C., Lima, E., Lefebvre, P., ... Brooks, V. (1999). Large-scale impoverishment of Amazonian forests by logging and fire. *Nature*, 398, 505–508. <https://doi.org/10.1038/19066>
- Olden, J., & Rooney, T. (2006). On defining and quantifying biotic homogenization. *Global Ecology and Biogeography*, 15, 113–120. <https://doi.org/10.1111/j.1466-822X.2006.00214.x>
- Oleksy, R. Z., Ayady, C. L., Tatayah, V., Jones, C., Howey, P. W., Froidevaux, J. S. P., ... Jones, G. (2019). The movement ecology of the Mauritian flying fox (*Pteropus niger*): A long-term study using solar-powered GSM/GPS tags. *Movement Ecology*, 7, 1–12. <https://doi.org/10.1186/s40462-019-0156-6>
- Oleksy, R., Racey, P. A., & Jones, G. (2015). High-resolution GPS tracking reveals habitat selection and the potential for long-distance seed dispersal by Madagascan flying foxes *Pteropus rufus*. *Global Ecology and Conservation*, 3, 678–692. <https://doi.org/10.1016/j.gecco.2015.02.012>
- Pimm, S., Russell, G., Gittleman, J., & Brooks, T. (1995). The future of biodiversity. *Science*, 269(5222), 347–350.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2017). nlme: Linear and nonlinear mixed effects models. R package version 3.1-131.
- Pulvers, J., & Colgan, D. (2007). Molecular phylogeography of the fruit bat genus *Melonycteris* in northern Melanesia. *Journal of Biogeography*, 34(4), 713–723. <https://doi.org/10.1111/j.1365-2699.2006.01634.x>
- Purvis, A., Agapow, P.-M., Gittleman, J., & Mace, G. (2000). Non-random extinction and the loss of evolutionary history. *Science*, 288, 328–330. <https://doi.org/10.1126/science.288.5464.328>
- QGIS Development Team. (2009). *QGIS geographic information system*. Open Source Geospatial Foundation: Retrieved from <http://qgis.osgeo.org>
- R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Ricketts, T. H., Dinerstein, E., Boucher, T., Brooks, T. M., Butchart, S. H. M., Hoffmann, M., ... Wikramanayake, E. (2005). Pinpointing and preventing imminent extinctions. *Proceedings of the National Academy of Sciences of the United States of America*, 102(51), 18497–18501. <https://doi.org/10.1073/pnas.0509060102>
- Schulze, M. D., Seavy, N. E., & Whitacre, D. F. (2000). A comparison of the phyllostomid bat assemblages in undisturbed neotropical forest and in forest fragments of a slash-and-burn farming mosaic in Peten, Guatemala. *Biotropica*, 32(1), 174–184. <https://doi.org/10.1111/j.1744-7429.2000.tb00459.x>
- Sinclair Knight & Merz. (2012). *Solomon Islands national forest resources assessment: 2011 update*. Retrieved from <http://mofr.gov.sb/foris/reports.do>
- Slatyer, R., Hirst, M., & Sexton, J. (2013). Niche breadth predicts geographical range size: A general ecological pattern. *Ecology Letters*, 16, 1104–1114. <https://doi.org/10.1111/ele.12140>
- Sloan, S., Jenkins, C. N., Joppa, L. N., Gaveau, D. L. A., & Laurance, W. F. (2014). Remaining natural vegetation in the global biodiversity hotspots. *Biological Conservation*, 177(C), 12–24. <https://doi.org/10.1016/j.biocon.2014.05.027>
- Wenger, A. S., Atkinson, S., Santini, T., Falinski, K., Hutley, N., Albert, S., ... Jupiter, S. D. (2018). Predicting the impact of logging activities on soil erosion and water quality in steep, forested tropical islands. *Environmental Research Letters*, 13(4), <https://doi.org/10.1088/1748-9326/aab9eb>
- Whitmore, T. (1966). *Guide to the forests of the British Solomon Islands*. London: Oxford University Press.
- Whitmore, T. (1969). The vegetation of the Solomon Islands. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, 255(800), 259–270. <https://doi.org/10.1098/rstb.1969.0010>
- Whitmore, T. (1989). Changes over twenty-one years in the Kolombangara rain forests. *Journal of Ecology*, 77(2), 469–483. <https://doi.org/10.2307/2260763>
- Winkelman, J. R., & Bonaccorso, F. J. (2003). Home range and territoriality in the least blossom bat, *Macroglossus minimus*, Papua New Guinea. *Journal of Mammalogy*, 84(2), 561–570. <https://doi.org/10.1644/1545-1542%282003%29084%3C0561%3AHRA-TIT%3E2.0.CO%3B2>
- Winkelman, J. R., Bonaccorso, F. J., & Strickler, T. L. (2000). Home range of the southern blossom bat, *Syconycteris australis*, Papua New Guinea. *Journal of Mammalogy*, 81(2), 408–414. [https://doi.org/10.1644/1545-1542\(2000\)081<0408:HROTSB>2.0.CO;2](https://doi.org/10.1644/1545-1542(2000)081<0408:HROTSB>2.0.CO;2)
- Wright, S. J. (1980). Density compensation in island avifaunas. *Oecologia*, 45(3), 385–389. <https://doi.org/10.1007/BF00540211>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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