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RESEARCH ARTICLE

On the edge: habitat restoration priorities for three critically endangered bird species on Sangihe, Indonesia

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Remnant forests on the small Wallacean island of Sangihe north of Sulawesi hold the entire ranges of more critically endangered (CR) bird species than any other comparable area on earth. We develop habitat association models for three of these CR species to identify critical habitat features as well as areas where habitat falls slightly short of suitability, and to determine whether another area of forest away from the largest block might be suitable as an insurance site for a translocated population. Hopes for all three species appear almost totally pinned to forest within a 13 km^2 area of the Sahendaruman crater, with virtually no near-suitable habitat away from this site. There is, however, little overlap in habitats between one CR species and the other two: cerulean flycatcher *Eutrichomyias rowleyi* is associated with mature streamside forest with full canopy cover, lianas, and mid-level growth, while Sangihe whistler *Coracornis sanghirensis* and Sangihe golden bulbul *Hypsipetes platenae* are restricted to ridgetop forest with full canopy cover and large trees. We pinpoint small areas (around 5 km^2) of forest in the crater that are already suitable or can be made so with habitat management, and these are absolute priorities for conservation action. We show how habitat characteristics identified within models might be enhanced, and how features, especially certain tree species, can be used as indicators of future habitat improvement.

Key words: bird, critically endangered, forest, habitat restoration, Indonesia

Implications for Practice

- Hopes for three key critically endangered bird species on Sangihe island lie within just a 13 km^2 area of the Sahendaruman crater.
- There are, within the crater, some areas of habitat that could, at reasonable cost, be practically managed to make them more suitable for the key species.
- Work with local communities is key to maintaining and restoring habitat for the three species within the crater, but creating suitable habitat in other parts of the island is probably out of reach for the near future.

Introduction

The high levels of extinction and endangerment of species endemic to oceanic islands are well documented (e.g. Johnson & Stattersfield 1990; Szabo et al. 2012). The vulnerability of insular biota is related to multiple factors, including anthropogenic habitat destruction, human persecution, invasive exotic species, the evolutionary defencelessness of insular species, and natural effects relating to small range sizes and populations (Manne et al. 1999; Wood et al. 2017). Importantly, small populations of species restricted to remnant habitat likely incur an "extinction debt," meaning that they are doomed to die out unless their habitats are restored, and their populations increased (Tilman et al. 1994; Triantis et al. 2010).

The most striking avian example of where such an extinction debt is likely to occur involves Sangihe, a volcanic Indonesian island (461 km^2; a quarter the size of Mauritius or Maui) hosting some 140,000 people (>300/km^2) in the Celebes Sea between Sulawesi (Indonesia) and Mindanao (Philippines). More than 99% of Sangihe's original forest was estimated to have been converted to agriculture or lost through natural disasters, including several eruptions of Gunung Awu (1,340 m), over the past few centuries (Whitten et al. 1987; Riley & Wardill 2001; Riley 2002*a*), leaving tiny fragments of original habitat within which small-scale conversion is

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continuing (Bashari et al. 2016). No evidence exists that in the process of forest conversion any bird species were lost that might have constrained the populations of those that remain; other than an insectivorous owl, the avian predators on the island are migrants that occupy open country (White & Bruce 1986; Riley 2002*a*).

Of 10 bird species endemic to the island, four—Sangihe whistler *Coracornis sanghirensis*, cerulean flycatcher *Eutrichomyias rowleyi*, Sangihe golden bulbul *Hypsipetes platenae*, and Sangihe white-eye *Zosterops nehrkorni*—are entirely confined to remnant natural forest, judged recently to cover a mere 8 km^2, on a single mountain, Gunung Sahendaruman (Bashari et al. 2016; del Hoyo & Collar 2016; BirdLife International 2021*a*) and consequently categorized as critically endangered (BirdLife International 2021*a*). The altitudinal range, forest stratum occupied and broad diet of the four species are: Sangihe whistler 575–1,000 m, mid- to upper strata, invertivore; cerulean flycatcher 475–650 m, mid-strata, invertivore; Sangihe golden bulbul less than 1,000 m, low strata to canopy, omnivore; and Sangihe white-eye 750–920 m, subcanopy, omnivore (Rozendaal & Lambert 1999; Rasmussen et al. 2000; Riley 2002*a*). Primary forest at Sahendaruman also holds a very rarely recorded population of the critically endangered Talaud bear cuscus *Ailurops melanotis* (Riley 2002*b*; R.W. Martin 2015, personal observation; Flannery & Helgen 2016; Repi et al. 2020) and, while widespread on Sangihe, both endemic mammal species (the Endangered Sangihe tarsier *Tarsius sangirensis* [Shekelle & Salim 2009; Shekelle 2020] and least concern Sanghir squirrel *Prosciurillus rosenbergi* [Chiozza 2016]) occur at their highest densities in primary forest in the crater (Riley 2002*b*).

Populations of the whistler, flycatcher, bulbul, and white-eye have been estimated at, respectively, 92–255 (Burung Indonesia 2007), 34–150 (Bashari et al. 2016), 30–150 (BirdLife International 2021*b*), and less than 50 mature individuals (BirdLife International 2021*c*). There is logarithmic scaling of time to extinction with population size (Fagan & Holmes 2006), and within vertebrate populations a benchmark of viability is around 100 mature individuals (IUCN Standards and Petitions Committee 2022). The numbers of these Sangihe forest endemic birds are therefore likely to be too low to persist into the 22nd century and beyond, and represent an immediate and extreme challenge to 21st century conservation to devise and implement measures that will pay off the extinction debt in sufficient time.

Between 10 February and 7 May 2015, we undertook fieldwork in Sangihe's remaining forest fragments to identify the precise habitat requirements of these four critically endangered birds (the white-eye proving so elusive that no data could be obtained on it). We had three objectives:

(1) To determine the extent of suitable habitat for the key species within Gunung Sahendaruman and identify areas in which near-suitable habitat could be managed to improve their value to the birds.
(2) To understand the key features of habitat that could realistically be managed to increase overall carrying capacity for each of the key species.
(3) To ascertain whether there are areas away from Gunung Sahendaruman with suitable or near-suitable habitat that might represent areas to which birds could be translocated to create insurance populations.

Methods

The survey sought to establish a network of relatively closely spaced sampling points across the extent of potential habitat, which is concentrated in three main areas: Gunungs Sahendaruman, Awu and Otomata (Fig. 1). Given the restriction of the critically endangered species to Sahendaruman, the majority of survey transects (42 of 57) were located around the crater there. Almost all the eastern flank of Gunung Awu has been converted to coconut plantations or remains bare from the effects of volcanic eruptions in 1996 and 2008 (Global Volcanism Program 2013), but the western flanks retain some forest and 13 transects were placed there. A final two transects were located on the much smaller Gunung Otomata, which retains small mature secondary forest patches within the boundaries of a "protection forest."

Bird Presence Data

A point count method (Bibby et al. 1998) was used to survey the endemic birds of Sangihe, supplemented by additional encounters between points, which were established every 150 m along transects, to provide a dataset of occupied and unoccupied locations. Each point count lasted 5 minutes and all counts were audio-recorded for confirmation of uncertain identification and for documentation. A species was included as present if it was recorded within a 50-m radius of a point (Euclidean distance calculated in ArcGIS 10; ESRI 2011). Transect routes were planned to sample as much as possible of the remaining habitat within the Sahendaruman Crater, given its extreme terrain, ensuring access to each valley and ridge, and to incorporate sections of ridge slope.

Data were also obtained from previous surveys of Sahendaruman completed in 2009 and 2014 (Rosyadi 2009; Bashari & Fauzan 2014). This compilation increased the sample size for the rarest species by allowing us to disproportionately survey likely occupied areas (de Lima et al. 2017). As the present study's aims were to predict the relative suitability of areas which do not support the species at present, the use of these earlier records to achieve a reasonable maximum presence dataset was considered appropriate.

Habitat Variables

A series of topographic, floristic, and vegetation structure variables were chosen to characterize a reasonable proportion of each of the target species' niche space while minimizing collinearity (Lee & Marsden 2008). Each variable was assessed within a 10-m radius of the point count location. A restricted subset of each variable class was then identified for each species based on the previously published information on the species, and experience from the field.

When less than 15 m, distance to permanent running water was measured; when more, it was either estimated in the field

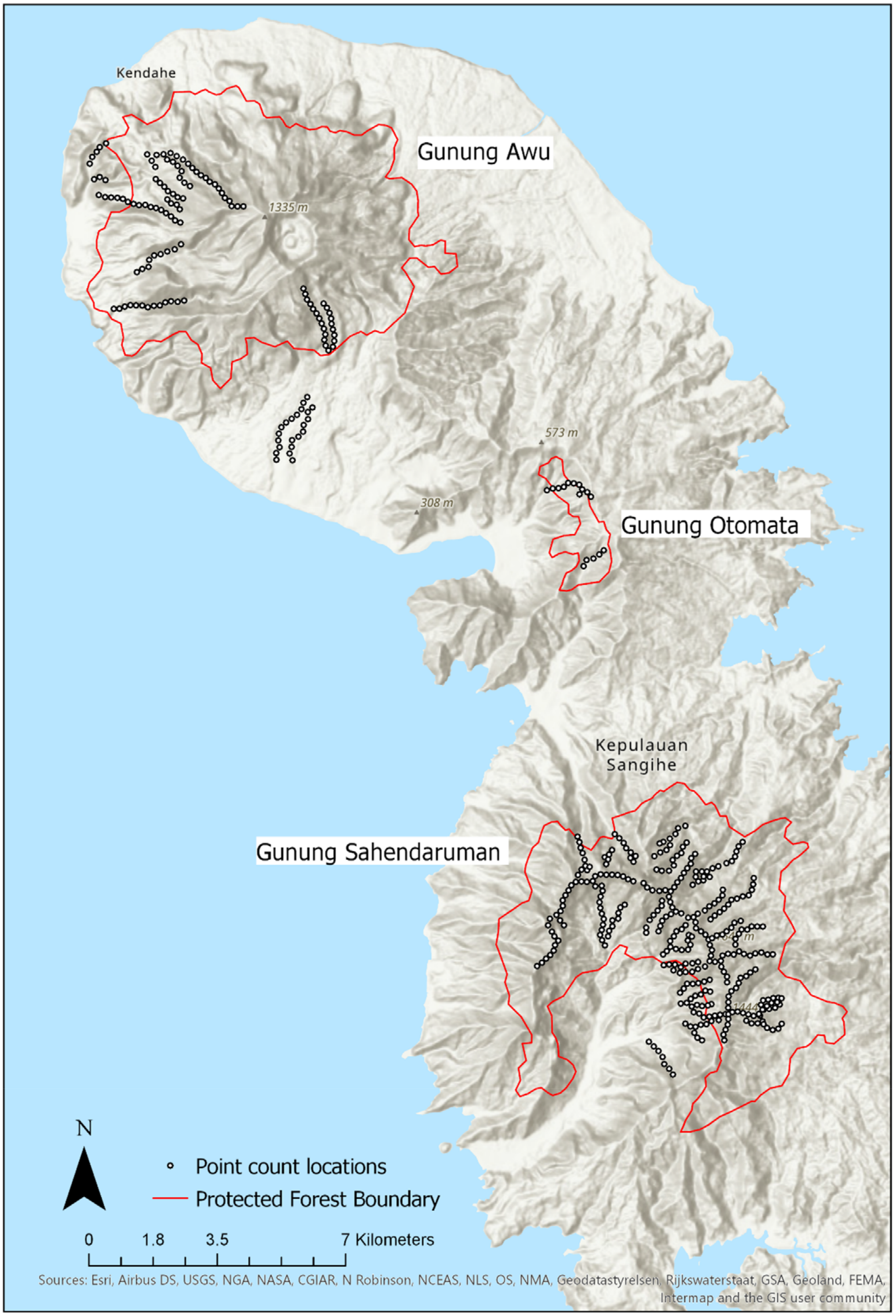


Figure 1. Location of survey points on Sangihe, showing the boundaries of the three protection forests (solid black line). Each point survey location (circles) is displayed; these are 200 m apart on walked transects.

or calculated later using the relative distance from other points with estimated or measured values in ArcGIS 10 (ESRI 2011). Distance to water was log transformed and was not included in the models for the whistler and bulbul as the large distance from their ridgetop habitat rendered the predictor uninformative. Slope was measured using an inverted clinometer at five random positions within each plot, and an absolute mean slope derived for each plot, giving an overall "steepness" score for each,

Table 1. Details of presence and absence points for modeling of each of the three CR species on Sangihe and habitat predictors used in models.

	Species		
Attribute/predictor	*CF*	*SW*	*SGB*
Presence points (this study)	20	19	16
Presence points (2014)	6	5	6
Presence points (2009)	1	4	6
Altitudinal cropping (m)	475–650	>660	>620
Number of absence points	153	153	147
Distance to water	x		
Slope	x	x	x
Canopy cover	x	x	x
Mid-level cover	x	x	x
Low-level cover	x	x	x
Ground cover	x	x	x
Canopy height	x	x	x
Largest trees mean girth	x		
Proportion large trees		x	x
Crop score	x		
Lianas	x		
Gingers		x	x
Areca	x	x	x
Tree pandanus		x	x
Ground pandanus			x
Tompioliu		x	x

regardless of slope direction. Altitude was estimated from a 30 m resolution digital elevation model based on GPS recordings from the field.

Within each 10 m radius plot, percentage vegetation cover at four strata was estimated by eye: (1) canopy cover (>15 m above the ground, as viewed directly upwards, excluding emergents); (2) mid-level (vegetation below the canopy, but >5 m above the ground); (3) low-level (vegetation 1–5 m above the ground); and (4) ground cover (<1 m). A canopy height variable was measured by taking the mean height of the second to fifth tallest trees within plots (the tallest tree was excluded to reduce the effect of emergents). The girths-at-breast-height of the 10 largest trees within the 10-m radius plot were measured. From these, we calculated the mean of the two largest-girthed trees (to identify points dominated by one or two very large trees). The proportion of large trees was the proportion of the 10 trees measured which had DBH greater than 0.6 m.

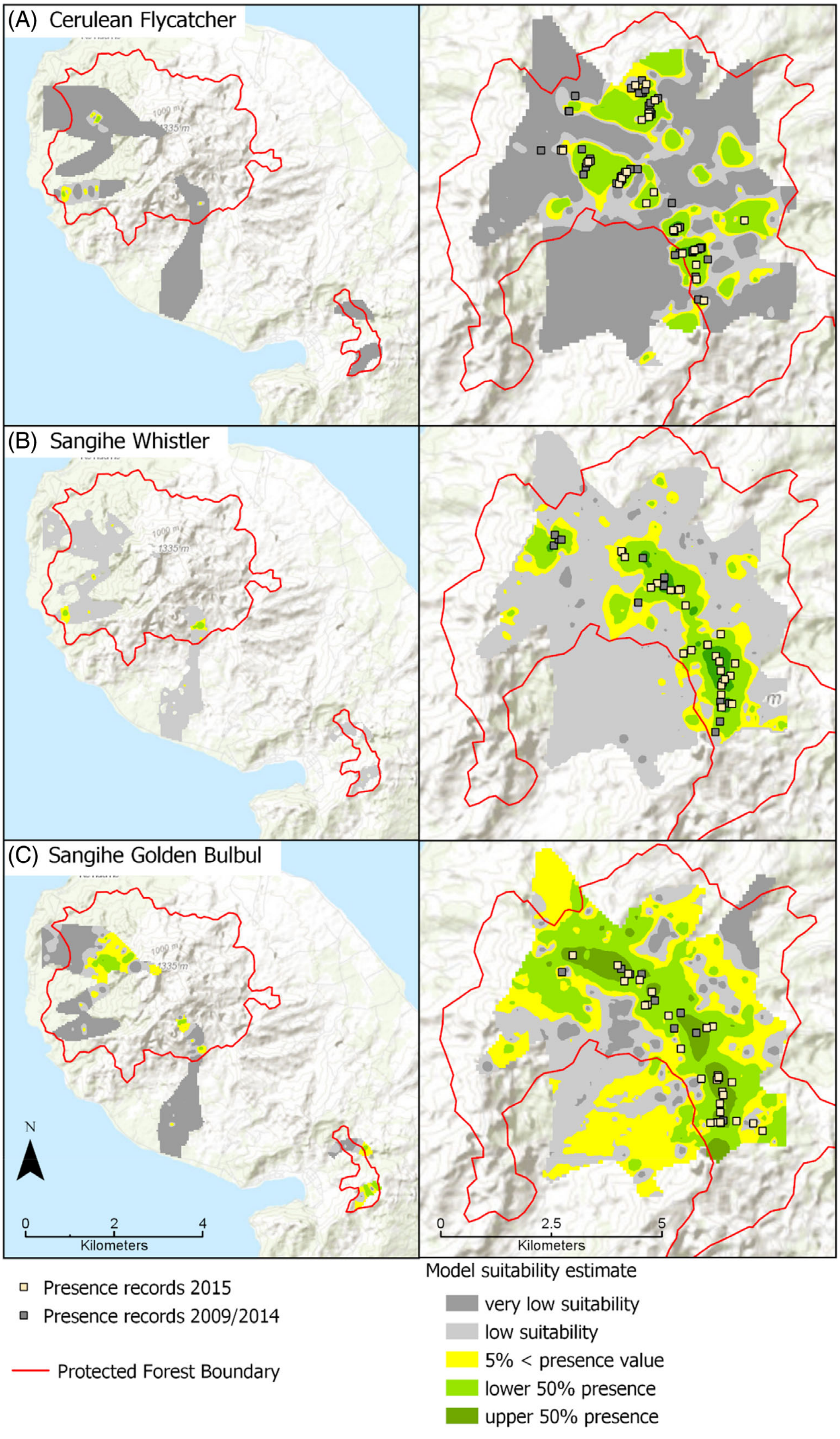
An experienced Sangihe guide made identifications of the 10 largest-girthed trees. These local-name identifications were cross-referenced with names assigned to specimens collected during the Action Sampiri expedition (D. Hicks unpublished data), and with Holthuis and Lam's (1942) detailed investigation of the flora of the neighboring island of Talaud, which shares many names with Sangihe. For those trees remaining unnamed, further works associating local names with species groups/genera were consulted to produce an identification at least to family level and in most cases to genus. To identify associations of each CR species with tree species, we used random forests (package "*caret*" in R; Kuhn et al. 2016; R Core Team 2017), with presence of the CR species as the dependent variable and a presence/absence dataset of all trees found at 15 or more points. K-fold cross-validation with 10-folds and three repeats was used to evaluate the relative importance of each predictor variable, and the top five most "important" trees were retained for use in subsequent modeling.

Various potential indicator plant/plant groups were identified, namely, lianas; ginger; *Areca* palm; tree pandanus; ground pandanus; tree ferns; and a flowering high-altitude plant known as "tompioliu." Each was scored at each point using an estimated abundance measure, with 5 for dominant (>50% of all vegetation within the 10-m radius), 4 for abundant (30–50%), 3 for frequent (10–30%), 2 for occasional (5–10%), and 1 for rare (<5%). In addition to these single-taxon measures, we calculated a total crop score for each point, derived from the abundance of both tree crops (clove *Syzygium aromaticum*, nutmeg *Myristica fragrans*, coconut *Cocos nucifera*, banana *Musa* sp., durian *Durio zibethinus*, mango *Mangifera indica*, langsat *Lansium domesticum*) and field crops (e.g. cassava *Manihot esculenta*).

Modeling

Generalized linear models (GLM) with a binomial error distribution and logit link function were used to investigate the relationship between each CR bird species and a series of habitat variables (R Core Team 2017). Models were fitted using only data collected in and around Sahendaruman ($n = 327$ points). We chose to exclude plots (all negative) from other areas. While none of the species has been recorded away from Sahendaruman in the past 20 years despite targeted search effort, there is a single report of the flycatcher in December 1978 from Gunung Awu (White & Bruce 1986), suggesting that relatively recent extinctions may have occurred, quite possibly through the impacts of volcanic eruptions. The absence of these species may not therefore reflect currently unsuitable habitat. Models were used to estimate the probability of occurrence at each of the surveyed points across the island ($n = 468$) with the aim of assessing the present similarity (and assumed potential suitability) of sites outside their current, highly restricted, elevational limits. For the prediction to be unconstrained by a minimum elevation, a restricted set of points was used from within those sampled at Sahendaruman based on the known elevational range, with a buffer of 40 vertical meters to account for uncertainty.

The "dredge" function in package "MuMIn" (Barton 2016) was used to rank models from the initial candidate set, with variables not present within two AICc units of the "best" model removed and the process repeated for the restricted subset of variables. This final candidate set of models was used to generate model-averaged values in order to predict probabilities of occurrence across the full extent of the surveyed area of the island (Burnham & Anderson 2002). A "full average" of the candidate set was employed, as this emphasizes the predictors that have the strongest effect on the response variable (Grueber et al. 2011). Model accuracy was assessed using area under the curve (AUC) of the receiver operating characteristic: discriminatory ability was considered good above values of 0.7 (Burnham & Anderson 2002). Model-averaged logistic



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regression coefficients and both unconditional standard errors and standard errors conditional on the best model were then extracted; the former are considered more accurate estimates of coefficient precision, as variance due to model uncertainty is included (Burnham & Anderson 2002). The "*predict*" function in the "*stats*" package of "R" (R Core Team 2017) was then used to obtain predicted probabilities of occurrence for each of the 468 points sampled across the island based on the model-averaged values. To visualize the results, inverse distance-weighted interpolation was used in ArcGIS 10 (ESRI 2011) to create an "occurrence" likelihood surface for each species based on weighted averages of probabilities at neighboring points. Suitable habitat for each species was defined as areas/plots where the predicted occurrence value was the same or greater than that at the lowest confirmed presence location, after excluding outliers. Potential restoration habitat was defined as the area predicted to have values within 5% of that at the lowest confirmed presence location. The area currently occupied by each species was separately estimated from the extent of suitable habitat within the known elevational range which held confirmed presence records: areas with no confirmed records since 2009 were excluded. Table 1 shows the number of survey points used for analysis, altitudinal ranges, and the habitat predictors used in the models for each species.

Results

Random forest analysis of tree morphospecies identified five, three, and three that were likely associated with presence of the flycatcher, whistler and bulbul, respectively. The local names for these were linked to the following tree species (Table S1); (flycatcher) *Dendrocnide* aff. *Amplissima/microstigma*, *Adinadra* cf. *celebica*, *Endocomia macrocoma*, *Scolopia spinosa*, and *Saurauia* cf. *tristyla/nudiflora*; (whistler) *Litsea* spp., *Schuurmansia henningsii*, and *Elaeocarpus teysmannii*; and (bulbul) *Litsea* spp., *Zanthoxylum integrifoliolum*, and *Sterculia* cf. *insularis/*cf. *oblongata*.

Satisfactory models were built for the flycatcher (AUC = 0.94) and whistler (AUC = 0.88), but there was considerable uncertainty in the models for the bulbul (AUC = 0.79). Best models for the flycatcher included three structural variables—canopy cover, lianas, and mid-level cover (all positive)—and presence of the trees *S. spinosa* and *D.* aff *amplissima/microstigma* (Table S2). Best models for the whistler also included canopy cover, along with number of large trees (both positive), and presence of the indicator plant "*tompioliu*" and trees *Litsea* spp. and *S. henningsii*; absence of *Areca* palms may also have been important. Models for the bulbul were unclear, but low-level vegetative cover and "*tompioliu*" (both positive) were likely to be associated with presence, while large

Table 2. Total area of predicted suitable habitat for each species and the extent of predicted overlap.

	Area in km²		
	Cerulean Flycatcher	*Sangihe Whistler*	*Sangihe Golden Bulbul*
Cerulean Flycatcher	3.41 (64%)	0.29 (6%)	1.10 (10%)
Sangihe Whistler	0.29 (5%)	0.48 (9%)	3.89 (35%)
Sangihe Golden Bulbul	1.10 (21%)	3.89 (75%)	5.47 (50%)
All species overlap	0.51 (10%)	0.51 (10%)	0.51 (5%)
Total	5.31	5.17	10.97
	Area in km²		
	Cerulean Flycatcher	*Sangihe Whistler*	*Sangihe Golden Bulbul*
Predicted suitable habitat (km²)	5.31	5.17	10.97
Current estimated occupancy (km²)	2.45	3.09	2.95
Unoccupied suitable habitat (km²)	2.86 (54%)	2.08 (40%)	8.02 (73%)
Near-suitable habitat (km²)	2.31	3.71	10.98
Total suitable and near-suitable habitat (km²)	7.62	8.88	21.95
Near-suitable habitat not overlapping other suitable habitat (km²)	1.19	1.25	9.02
Near-suitable habitat not overlapping other near-suitable habitat (km²)	0.62	0.6	8.02
Near-suitable habitat overlapping bulbul (km²)	1.75	2.49	—

(Figure legend continued from previous page.)
Figure 2. A–C. Modeled probability of suitability for (A) cerulean flycatcher; (B) Sangihe whistler; and (C) Sangihe golden bulbul. Left panel shows Gunung Awu and Otomata, right Gunung Sahendaruman area. Occurrence probabilities are weighted averages of occurrence probabilities at each surveyed point with natural neighbor interpolation. Shading is set to minimum probability of suitability with confirmed presence: Values were 0.167 for cerulean flycatcher, 0.148 for Sangihe whistler, and 0.186 for Sangihe golden bulbul. Green colors are all areas assigned a higher occurrence probability than this minimum, divided at the 50% value. Areas within 5% below the minimum value are yellow and the remainder of the extrapolated area is gray, divided at the 50% value.

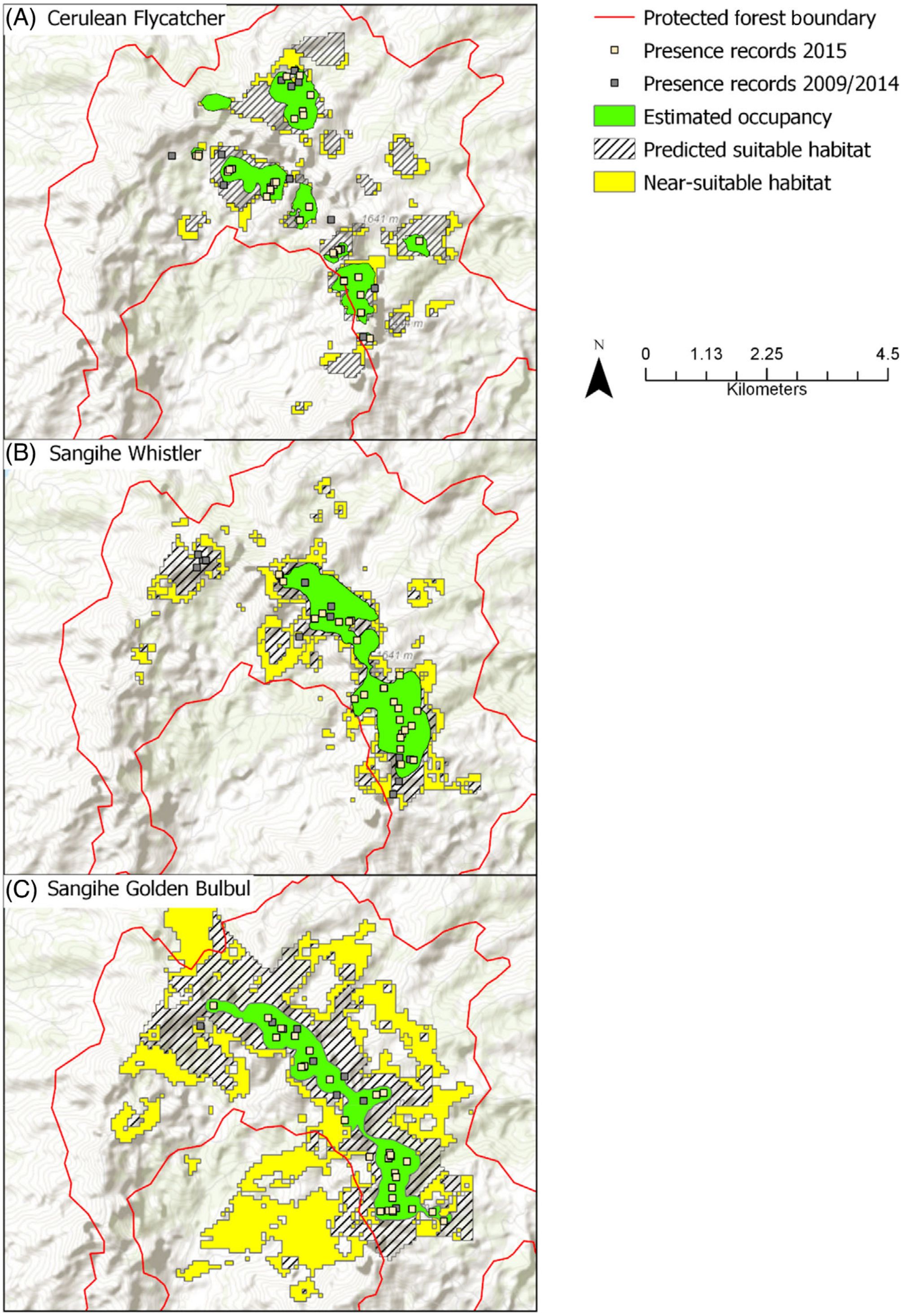

Figure 3. Estimated occupancy, predicted suitable and near-suitable habitat areas for (A) cerulean flycatcher; (B) Sangihe whistler; (C) Sangihe golden bulbul. Estimated occupancy is based on presence records and contiguous suitable habitat. Predicted suitable habitat is the additional area with occurrence probabilities exceeding that of the minimum occupied point. Near-suitable habitat is the area with estimated occurrence probabilities within 5% below the minimum presence probability.

but short trees generally, and presence of *Z. integrifoliolum* in particular, may be important.

For all three species, and especially for the flycatcher and whistler for which models were more reliable, the suitability of habitat away from the Sahendaruman crater was extremely low (Fig. 2). Mapped habitat with a suitability score equal to or greater than that of the lowest-scoring presence point totalled only 0.08 km^2 on Gunung Awu for the flycatcher and 0.15 km^2 for the whistler. For the bulbul, an area of 0.81 km^2 on Gunung Awu and 0.27 km^2 within Gunung Otomata just exceeded the minimum occurrence probability.

Within the Sahendaruman crater itself, suitable habitat was restricted and patchy. The area of habitat of greater than the minimum suitable probability was 5.31 km^2 for the flycatcher, 5.17 km^2 for the whistler and 10.97 km^2 for the bulbul (Table 2; Fig. 2). There was substantial overlap in predicted habitat between the whistler and bulbul, with 85% of whistler habitat also suitable for the bulbul. There was, however, far less overlap with flycatcher habitat: just 16% (<1 km^2) and 15% (1.6 km^2) of the whistler and bulbul habitat, respectively. In total 91% of the area suitable for the whistler was also predicted to be suitable for one or both other species. In contrast, 64% of the flycatcher's predicted habitat was suitable for that species alone.

The areas estimated to be currently occupied by each species (restricted to contiguous habitat with recent records) were considerably smaller than the predicted suitable habitat; 2.45 km^2 for the flycatcher (46% of the predicted area), 3.09 km^2 for the whistler, and 2.95 km^2 for the bulbul (Fig. 3). Areas with high restoration potential (within 0.05 of the minimum presence probability) totalled 2.31, 3.71, and 10.98 km^2 for the flycatcher, whistler, and bulbul, respectively. However, these areas overlap with predicted suitable habitat and with one another. For the flycatcher and whistler, only 1.19 km^2 (52%) and 1.25 km^2 (34%) of habitat predicted to be near-suitable did not overlap with areas predicted suitable for another species (Table 2; Fig. 3). The bulbul had 9.02 km^2 (82%) of potential restoration area predicted as currently unsuitable for the other two species. But 46% of the potential restoration area for the flycatcher and 39% of that for the whistler overlap with area predicted to be currently suitable for the bulbul. All areas of overlap occur at the upper elevation limit of the flycatcher and the lower elevation limits of the other two species.

In the potential restoration areas predicted as currently unsuitable for any species, 0.62 km^2 would be restoration for the flycatcher alone and 0.6 km^2 for the whistler alone (Table 2; Fig. 3). There is little overlap (0.1 km^2) between the restoration areas for the flycatcher and the whistler. The predicted restoration area for the bulbul alone totals 8.02 km^2, while a further 0.51 km^2 is shared with the flycatcher and 0.59 km^2 with the whistler. Consequently, excluding the bulbul restoration area almost doubles the potential restoration area for both other species.

Discussion

Sangihe holds the entire range of more critically endangered bird species than any comparably small area. The flycatcher and bulbul presumably once extended more widely across Sangihe given their lower elevational limits—e.g. the flycatcher's type locality is Tabukan on the coast (Riley & Wardill 2001)—and the likelihood that the island was once largely forested (see Introduction), and while the whistler currently exists in the best forest on the very tops of the tallest ridges on the island, it has been recorded as low as 575 m on the island in the past and the type locality is given as a village on the slopes of Gunung Awu in the north of the island (Rozendaal & Lambert 1999). The Sangihe white-eye remains an enigma, always very rare (Rasmussen et al. 2000); there was only a single in-flight record of a *Zosterops* species in our survey. All four species may represent end-of-taxon-cycle (Stage IV) relicts, derived from old colonizers of Sangihe that retreated to higher altitudes and narrower niches as subsequent colonizers competed with them (Ricklefs & Bermingham 2002; Jønsson et al. 2018). The plausibility of such an evolutionary circumstance recently increased with the discovery that the flycatcher is not a monarch (Monarchidae), as previously thought, but part of a relictual family (Lamproliidae) with one other member on New Guinea and two on Fiji (Jønsson et al. 2018). Contraction of the area occupied (Riley 2002*a*) continues, with further loss noted between surveys carried out in 2009 (Rosyadi 2009), 2014 (Bashari & Fauzen 2014), and the present survey in 2015. The only area currently close to suitable for establishing an additional population of the flycatcher, whistler, and bulbul is a small patch of disturbed forest on Gunung Awu, but this would require additional reforestation of currently unsuitable areas as well as restoring the tiny areas of low to medium suitability, and effort in this area would be permanently vulnerable to eruptions, which occur approximately every 20 years (Bani et al. 2020).

The protection forest around the Sahendaruman crater totals 35.9 km^2 but most of it has been converted to plantation gardens (Bashari et al. 2016); this circumstance cannot now be reversed. Nevertheless, if habitat within the Sahendaruman crater resembling locations currently occupied by our three target species could be made suitable, this could expand the potential habitat of the flycatcher by 22–33% (depending whether habitat assessed as suitable for the bulbul is included—see below) and the whistler by 24–48%. For the bulbul the difference would be even greater, resulting in a doubling of the area of suitable habitat (but see below). The area of currently suitable habitat is tiny—around 5–6 km^2 for each species, with little overlap in habitat use between the flycatcher and other two, so that the combined extent of habitat suitable for the three birds is 12.7 km^2. This is rather larger than the previously reported extent of primary forest, as we based our suitable habitat area on species occurrence data rather than forest type (Riley 2002*a*; Mamengko & Mole 2006). However, the area actually occupied by these species is much smaller, ranging from 2.45 to 3.09 km^2, with the flycatcher and whistler occupying less than 60% of the predicted suitable habitat present and the bulbul less than 30%.

Uncertainty in our estimates of area occupied is greatest for sites where a species has apparently been "lost," and a judgment must be made on whether effort has been sufficient to exclude continuing undetected presence: one such area included for the flycatcher accounts for 12% of the suitable area, while another of 10% of the suitable area was excluded for the whistler. That the bulbul appears to occupy such a small portion of the predicted suitable habitat is a strong indication that its area of suitability is overpredicted, hence the occupied area is restricted closely to the extent of records. The species was observed to produce loud, far-carrying vocalizations that may have reduced the precision of the match between sighting and the habitat variables collected, and individuals were also observed traveling moderately large distances between areas along the ridgetop, potentially reducing the value of the associations recovered, especially given the small sample size.

Such disparity between predicted and occupied areas of habitat is concerning. While in most studies this would be expected, detectability never being 100% (Kellner & Swihart 2014), here the available habitat has been repeatedly surveyed at a high spatial resolution, each time relocating a similar total of individuals in virtually identical locations. It therefore appears unlikely that the predicted suitable habitat is occupied, suggesting that factors other than habitat extent may be restricting population sizes. It is possible that each species has requirements relating to cover, food and reproduction which constrain them in ways our parameter measurements could not register. Alternatively, all three may be declining toward extinction in response to factors such as inbreeding depression, genetic drift, conservative dispersal behavior and stochastic events like skewed sex ratios and undetected pressures from alien species and diseases (Caughley 1994; Donald 2007; Bellard et al. 2017). Currently, what may work for these species is unknown, but in situ efforts such as maximizing productivity through preventing nest predation, or providing supplementary food, and/or establishing ex situ populations, as used with a suite of severely threatened landbirds on the Indian Ocean islands (Bristol et al. 2005; Safford & Jones 2008), are possible options to consider. Clearly, in such circumstances, a rapid increase in numbers is highly desirable, to reduce the risk of further genetic attenuation, but it remains vital to ensure there is habitat into which to release birds in future.

To maximize the chances of long-term survival of these three species, therefore, a fine-scaled, long-term program of forest restoration is urgently needed, guided by a parallel research initiative to identify other constraints on the species and determine what further interventions might be of most benefit to them. The flycatcher occurs in forest in steep valleys regularly disturbed by natural processes: this may explain previous occurrence records at sites classified as secondary forest (Riley & Wardill 2001; Mamengko & Mole 2006). We found that it selects forest with high canopy closure, moderate mid-level cover, and heavy liana loads, which may include areas judged to be secondary as well as primary forest by analysis based on vegetation structure and composition (Mamengko & Mole 2006). By contrast, records of the whistler have always been from ridgetops (Riley & Wardill 2001), but our models show, within these areas, positive associations with high canopy closure, large trees, and tree species most frequently found in areas judged to be primary forest, reinforcing previous reports tying the species solely to primary forest (Riley 2002*a*). The model predictions for the bulbul appear to have overestimated the area of potentially suitable habitat, and it may be restricted by habitat features we did not sample. All three species, but particularly the bulbul, merit in-depth autecological study to improve our knowledge of their needs. Logically, however, those areas deemed suitable for but apparently unoccupied by the bulbul, but which are near-suitable for the other two species, should be prioritized for targeted restoration according to the identified preferences of those latter species. The considerable overlap in habitat use between the bulbul and the whistler suggests that targeted restoration for the whistler will not render a site unusable by the bulbul.

High canopy closure can occur early in Sulawesi forest succession (Dietz et al. 2006; Cannon et al. 2007; Clark et al. 2021), suggesting that even in the absence of active restoration key locations can move rapidly toward suitability if allowed. Further simple strategies are to prioritize restoration efforts for areas adjacent to currently occupied sites and maximize connectivity between them to reverse fragmentation and extend time to extinction (Newmark et al. 2017), potentially by reducing barriers to dispersal by young birds, and to focus on those sites that have been subject to even minor recent damage or clearance. One location held the flycatcher in 2014 but not in 2015, a change attributable to logging and small-scale clearance between the two surveys; but restoration of this site should be possible if clearance ceases, and targeted restoration could accelerate this through the planting of *S. spinosa* ("*bunaro*") and *Dendrocnide* sp. ("*sahai*") saplings and the seeding of lianas into the subcanopy.

Any forest restoration effort must be based on the correct sourcing and subsequent handling of seed material (ENSCONET 2009; Pedrini et al. 2020) and this will require confirmation of the identification of the key trees given here. The method of tree identification used allowed the rapid identification of morphospecies associated with the critically endangered bird species by leveraging the detailed local botanical knowledge of local guides, and to use previous work that linked specimens from the region to local names (Holthuis & Lam 1942; D. Hicks unpublished data) but cannot give certain species identification to those morphospecies. Hence, it is essential to continue close cooperation with the local community, especially those with detailed botanical knowledge of the forest, to confirm the key species identifications. From this, work to locate seed sources, establish collecting methods and protocols and establish an ex situ seed nursery can follow (Erickson & Halford 2020; Pedrini et al. 2020).

The complementary ranges of the three studied bird species cover the remaining area of intact or original forest on Sangihe, and together overlap the full extent of the known habitat of Talaud bear Cuscus on the island and the area of the highest density of the two endemic mammal species (Riley 2002*b*). Conserving and expanding habitat for the three birds is therefore expected to benefit these, and likely further species of mammals and species from other poorly studied taxonomic groups on Sangihe, by them acting as a "multi-species umbrella" (Lambeck 1997; Roberge & Angelstam 2004; Breckheimer et al. 2014). While the bear cuscus may intuitively seem like a good "umbrella" species as the largest mammal present, it occurs in only part of the intact forest, is difficult to detect and information on the species from the island is so limited that even its occurrence on Sangihe is considered unproven by some authors (Flannery & Helgen 2016; Repi et al. 2020). It does represent a suitable "flagship" species for wider public engagement with conservation at the site (Smith et al. 2012).

Climate change has the potential to overwhelm these restoration proposals, with the potential for mountaintop species to lose their climatic envelope off the top of their mountain (Williams et al. 2007; Colwell et al. 2008), a very real prospect for the three bird species restricted to the ridgetop forest (the white-eye, bulbul, and whistler). High-elevation species in Sulawesi were predicted to suffer the greatest loss of abundance due to climate change, in addition to range reduction (La Sorte & Jetz 2010; Harris et al. 2014) and Afrotropical montane species have shifted upslope by a mean of 93 m in 40 years (Neate-Clegg et al. 2021). If a similar shift is operating on Sahendaruman the area within the elevational range of the whistler and the bulbul would effectively have vanished by 2070. However, distributions of birds may be constrained more by biotic interactions than physiological tolerance (Freeman et al. 2016; Londoño et al. 2017) such that subtle habitat and resource changes may be key, and these may be most influenced by precipitation (Neate-Clegg et al. 2020). This indicates that by extending the extent of montane forest, which generates greater and more consistent volumes of precipitation, at least some portion of the impact of increased temperature on these species may be mitigated. Changes in precipitation may be extremely important in Sahendaruman, with the potential that historic forest loss around the crater may have accelerated any drying trend. During fieldwork local people indicated that the source of crater streams was now lower than in the past. All nests of the flycatcher found so far have been located above flowing water along one of these streams (H. Bashari in litt. 2015; R.W. Martin, personal observation), implying that selection that selection pressure to guard against nest predation by terrestrial predators may be strong (Collias & Collias 1984). Therefore, any reduction in the elevation of the emergence of flowing water in these streams may be an additional restriction on the suitable breeding sites of this species, although interannual variation in rainfall may have a larger impact than the underlying trend for some time.

Our study identified the biological conditions that would allow the key species the chance to increase their ranges on Sangihe. However, much the most crucial element in the endeavor to conserve all three species is the active support and engagement of the local stakeholders on and around Sahendaruman. The findings of this study can help refine current conservation actions for the area. Since 2002, Village Resource Management Agreements (VRMAs) have been developed with the adjacent communities, aiming to maintain natural forest cover and recently also to identify potential restoration areas, while ensuring community involvement in debates over resource use and boundaries. The most recent BirdLife Preventing Extinctions Programme/Burung Indonesia project on Sangihe has updated VRMAs in three villages and created new agreements in two additional villages, with all these communities subsequently seeking to formalize the agreements as village regulations (Burung Indonesia/BirdLife International Preventing Extinctions Programme, unpublished report). The benefits of forest preservation and restoration to these communities and to those further downslope and at the coast include a sustained source of forest products, a secure water supply and a reduced risk of significant landslips (e.g. Pattanayak 2004). Recent landslips within the crater that caused loss of life and severe infrastructure damage are linked by the local communities to riverbank tree clearance, leading to willingness to seek to restore forest (Burung Indonesia/BirdLife International Preventing Extinctions Programme, unpublished report). We recommend that forest restoration work commences urgently in the areas identified here and with reference to the key tree species identified. Beyond these areas, the sooner efforts to return areas to forest commence and the greater their extent the sooner additional sites may approach suitability for the key species.

The existing boundaries of the protection forest have been the source of conflict with local communities that has hindered conservation action over the past two decades. In one location on the west side of the south-eastern crater edge, above Lelipang district, habitat suitable for the flycatcher extends outside the protection forest boundary, which consequently needs urgent modification to include this area. But this is a small exception: the problem is that the boundaries as defined greatly exceed remaining suitable habitat for species dependent on intact forest on Sangihe. In fact, most of the protection forest area has long been converted to clove, nutmeg, and coconut plantations with existing land ownership rights and tenant agreements in place for generations (Burung Indonesia/BirdLife International Preventing Extinctions Programme, unpublished report). To resolve this conflict, we recommend a new participatory process to define land use zonation within the protection forest. Under a social forestry scheme provided by the Indonesian government community members with cultivation within the existing Protection Forest would be permitted to continue to manage these areas in line with principles agreed with the community and the regional Forest Management Unit, alongside regional governance structures. It is hoped this would refocus the debate onto land management for the purpose of community wellbeing including protection of biodiversity and enhancement of the ecological and environmental services provided by native forest, and away from boundary conflict.

This study both identifies areas of maximum benefit to the most threatened of Sangihe's birds and provides the basic ecological associations that could allow more targeted restoration to prevent further population reductions within the framework of the VRMAs. With the recent appearance of additional threats (e.g. mining: Berryman 2021) to this tiny, unique forest assemblage, the more that local people can become part of the solution for the threatened birds of Gunung Sahendaruman, the greater the chance must be that the solution will work.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Tree names and associated habitat. *Lehing bawi is given as the local name for multiple specimens in the data sheet prepared by D. Hicks (unpublished).

Table S2. Results from generalized linear models (GLMs) describing habitat associations of three critically endangered bird species on Sangihe.

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