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Diversity and Distributions

BIODIVERSITY RESEARCH

Rapid deforestation threatens mid-elevational endemic birds but climate change is most important at higher elevations

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ABSTRACT

Aim Deforestation and climate change are two of the most serious threats to tropical birds. Here, we combine fine-scale climatic and dynamic land cover models to forecast species vulnerability in rain forest habitats.

Location Sulawesi, Indonesia.

Methods We sampled bird communities on four mountains across three seasons in Lore Lindu National Park, Sulawesi, Indonesia (a globally important hotspot of avian endemism), to characterize relationships between elevation and abundance. Deforestation from 2000 to 2010 was quantified, and predictors of deforestation were identified. Future forest area was projected under two land use change scenarios – one assuming current deforestation rates and another assuming a 50% reduction in deforestation. A digital elevation model and an adiabatic lapse rate were used to create a fine-scale map of temperature in the national park. Then, the effects of climate change were projected by fitting statistical models of species abundance as a function of current temperature and forecasting future abundance based on warming from low- and high-emissions climate change.

Results The national park lost 11.8% of its forest from 2000 to 2010. Model-based projections indicate that high-elevation species (white-eared myza *Myza sarasinorum* and Sulawesi leaf-warbler *Phylloscopus sarasinorum*) might be buffered from deforestation because their ranges are isolated from human settlement, but these species may face steep population declines from climate change (by as much as 61%). The middle-elevation sulphur-bellied whistler *Pachycephala sulfuriventer* is predicted to undergo minor declines from climate change (8–11% reduction), while deforestation is predicted to cause larger declines of 13–19%.

Main conclusions The biological richness and rapid deforestation now occurring inside the national park emphasize the need for increased enforcement, while our modelling suggests that climate change is most threatening to high-elevation endemics. These findings are likely applicable to other highland tropical sites where deforestation is encroaching from below and climate change is stressing high-elevation species from above.

Keywords

Climate change, endemism, habitat loss, Indonesia, *Myza sarasinorum*, *Pachycephala sulfuriventer*, *Phylloscopus sarasinorum*, protected area, Southeast Asia, tropics.

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INTRODUCTION

Tropical mountain ranges are critical centres of avian endemism, with about 10% of the world's bird species being restricted to tropical highlands (>500-m elevation; Harris *et al.*, 2011). Steep slopes and high elevations reduce the pressure of anthropogenic habitat degradation and other threats such as hunting on many of these species, resulting in most highland tropical birds being considered of 'least concern' (Sekercioglu *et al.*, 2008; BirdLife International, 2013). Rapid habitat loss means that the bulk of IUCN-listed species in tropical regions are found in the lowlands, close to the concentration of human activity (e.g. Brooks *et al.*, 1997). While highland species have been buffered from habitat loss in the past, the recent growth of human populations and the demands of economic development have put increasing pressure on higher-elevation habitats (Soh *et al.*, 2006). In coming decades, climate change also threatens to reduce the habitat available for montane species (La Sorte & Jetz, 2010; Noske, 2010), with many highland tropical species facing climate-change-induced range shifts combined with habitat contraction (Pounds *et al.*, 2005; Peh, 2007; Forero-Medina *et al.*, 2011a,b; Harris *et al.*, 2012; Sekercioglu *et al.*, 2012). This is a particularly serious concern for species with few adaptation options, such as mountaintop endemics and those with narrow elevational ranges (Colwell *et al.*, 2008). Worryingly, the impacts of habitat loss, climate change and other extinction drivers such as invasive species are likely to interact synergistically (Brook *et al.*, 2008).

Given this context, studies that forecast species extirpation vulnerability due to habitat loss, climate change and their interaction are urgently needed from the tropics. Two previous analyses used coarse land cover scenarios and an adiabatic lapse rate (estimate of temperature loss with increasing elevation) to estimate the vulnerability of the world's birds to climate change and habitat loss, and found that approximately 500 species (5% of the global total) may go extinct by 2100 under a mid-range warming projection by global climate models (Jetz *et al.*, 2007; Sekercioglu *et al.*, 2008). Yet few analyses have projected spatially explicit estimates of tropical deforestation (Soares-Filho *et al.*, 2006; Cannon *et al.*, 2007; Bird *et al.*, 2012; Green *et al.*, 2013; Rosa *et al.*, 2013), and fewer still have combined fine-scale land cover and climate models to produce regional projections of extirpation vulnerability (Gregory *et al.*, 2012).

Southeast Asia's combination of biological richness, varied landscapes and severe on-going anthropogenic impacts makes it a clear candidate for exploring the influence of habitat loss and climate change on tropical biodiversity. Southeast Asia has one of the highest concentrations of endemic species in the world, as a result of the region's numerous islands, tectonic history and fluctuating sea levels (Sodhi & Brook, 2006). Unfortunately, regional deforestation is so rapid that many species may lose the majority of their range in the next 20 years (Bradshaw *et al.*, 2009; Miettinen *et al.*, 2011). Within Southeast Asia, the Sulawesi region of Indonesia is of special interest because it is among the world's richest hotspots of avian endemism, with 42 species found nowhere else (Coates & Bishop, 1997). Despite this diversity, Sulawesi is ornithologically one of the least studied areas in the world, with higher elevations particularly poorly sampled, and as a result, new bird taxa are still regularly described (e.g. Madika *et al.*, 2011).

In this study, we combine new data from the field with global climate and dynamic landscape models to forecast vulnerability of endemic birds in Lore Lindu National Park, Sulawesi. Although Lore Lindu is one of the island's most biodiverse reserves, it has suffered from rapid human encroachment over the last decade (Cannon *et al.*, 2007). We used three middle- and high-elevation endemic birds as case-study species to explore the potential effects of habitat loss and climate change on Lore Lindu's birds. Given that habitat loss is pervasive at lower elevations in Sulawesi (Cannon *et al.*, 2007), and the forecasts of detrimental impacts in previous climate change studies (e.g. Colwell *et al.*, 2008), we hypothesized that: (1) habitat loss would threaten middle-elevation species more than high-elevation species; and (2) climate change would particularly threaten narrow-ranged high-elevation species.

METHODS

Study site

Lore Lindu National Park covers 2290 km^2 of Central Sulawesi and is home to approximately 78% of Sulawesi's endemic bird species (Coates & Bishop, 1997; Lee *et al.*, 2007), making it one of the island's most important protected areas (Fig. 1). The national park is under considerable pressure from an increasing human population due to migration from more populous parts of Indonesia, expansion of cacao agriculture and illegal logging (Weber *et al.*, 2007; Clough *et al.*, 2009). Most of the park lies above 1000-m elevation (Fig. S1 in Supporting Information), and 96% of the park was covered with primary forest in 2000.

Field sampling

We collected avian occurrence data on Mt. Nokilalaki (825–2365 m; S 1°15.3′, E 120° 10′), Mt. Rorekatimbu (1265–2525 m; S 1° 17′, E 120° 19′), Mt. Dali (1295–2280 m; S 1° 43′, E 120° 9′) and Mt. Rano Rano (480–1920 m; S 1° 39′, E 120° 7′) (Fig. 1). These four peaks are among the tallest mountains in Central Sulawesi and are located at opposite ends of Lore Lindu, providing broad coverage of elevations and regions of the park. Our sampling effort was representative of the distribution of elevations in the park with forested middle elevations most thoroughly sampled (Fig. S1). In Appendix S1, we list coordinates of sampling sites and notes on their land cover in 2010. Our study species are much less

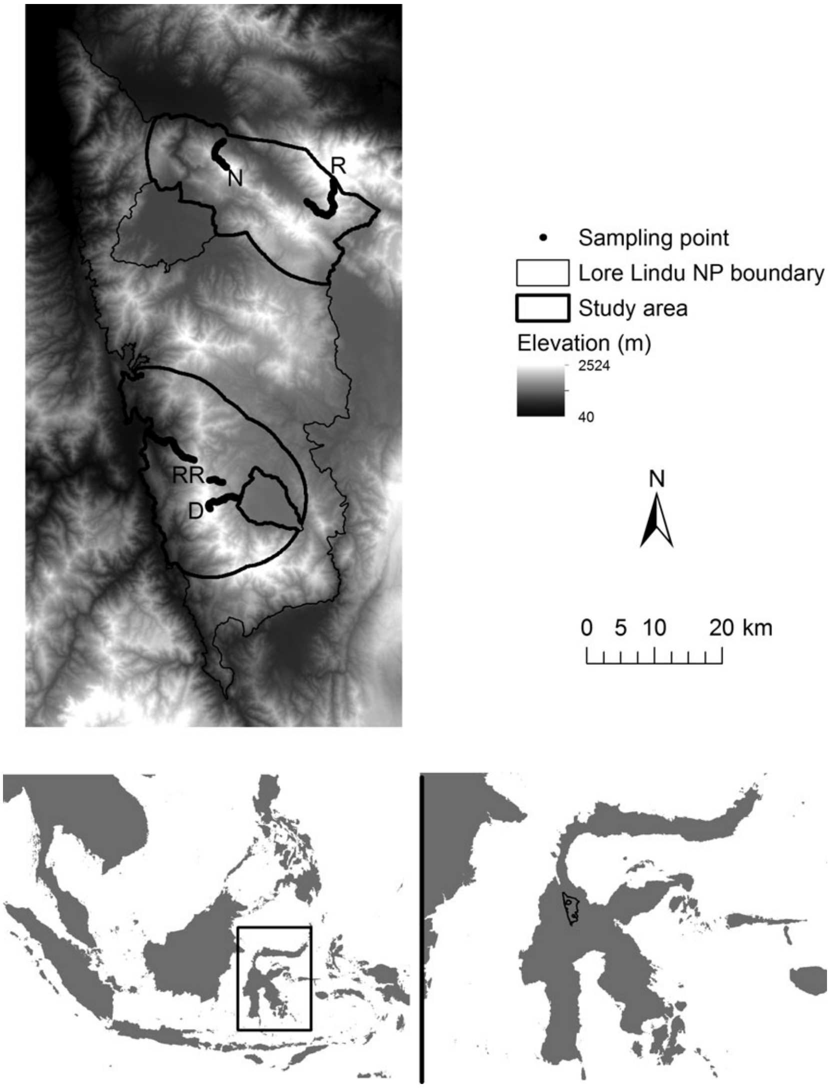


Figure 1 Location of Lore Lindu National Park and our study area and sampling sites. The two holes in the national park are annexed village areas. N indicates Mt. Nokilalaki, R indicates Mt. Rorekatimbu, D indicates Mt. Dali, and RR indicates Mt. Rano Rano.

common or absent below 1000 m, so our focus on higher elevations should not substantially impact our results.

We sampled bird communities with 10-minute duration, 50-m-radius point counts, separated by 250 horizontal metres, along elevational gradients on mountain trails and roads (Ralph *et al.*, 1995). We sampled 149 points, 126 of which were forested and within the elevational ranges of our three study species (Appendix S1). When sampling along roads (only done on parts of Mt. Rorekatimbu), we entered the forest ~ 50 m from the road to do the point counts. We controlled for seasonal variation in abundance by surveying in three seasons (September–November 2009, May–June 2010 and January–February 2011). Each point was sampled once in each season (points were visited three times in total). Co-author D.D.P., who has >10 years' experience identifying Central Sulawesi birds by sight and sound, was the primary observer in all surveys. We practiced distance estimation with audio playback and a measuring tape to make the aural 50 m estimate more accurate. A Nikon Forestry 550 laser range finder was used to check visual distance estimates.

Variability in detection may affect abundance estimates during point counts (Tingley & Beissinger, 2009). We maximized detection by only censusing birds in the morning on clear days with little wind (from dawn to 10:30). The potential for bias from differing detection probabilities along the altitudinal gradient was evaluated by converting counts to presence/absence data and modelling the probability of occupancy along the gradient in package unmarked in R v2.14.1 (Fiske & Chandler, 2011; R Development Core Team, 2011). Given that avian detectability may vary by season, we compared occupancy models that incorporated seasonal variation in detectability to those that modelled the effect of temperature on occupancy alone: Ψ(temperature)p(.),Ψ(.)p(season), Ψ(temperature)p(season), and Ψ(.)p(.). Temperature was calculated from elevation using an adiabatic lapse rate, and season was a categorical variable that represented our three sampling sessions. The Ψ(temperature)p(season) model was top-ranked for all study species (*w*AIC of 0.54, 1.0, and 0.92 for *Myza sarasinorum*, *Phylloscopus sarasinorum* and *Pachycephala sulfuriventer*, respectively). This occupancy relationship was compared with probability of presence from a binomial model that related temperature to presence/absence. We postulated that if occupancy (which explicitly accounts for detection probability) and probability of presence were similarly related to temperature, then there was no systematic bias stemming from low detection probability (Tingley & Beissinger, 2009).

Case-study species

For case-study species, we selected three locally common endemic birds that differed in their altitudinal habitat preferences: middle-elevation *Pachycephala sulfuriventer* (sulphur-bellied whistler), high-elevation *Phylloscopus sarasinorum* (Sulawesi leaf-warbler) and mountaintop *Myza sarasinorum* (white-eared myza) (Fig. 2; see Supporting Information for more natural history information). We refer to the mountaintop *Myza sarasinorum* and high-elevation *Phylloscopus sarasinorum* collectively as 'high-elevation' species. The three species were chosen, in part, because they are rarely or never seen in non-forest habitats in Lore Lindu (our data; Sodhi *et al.*, 2005; Maas *et al.*, 2009).

Modelling abundance

We characterized the current relationship between temperature and abundance and forecast the potential effects of climate change on bird abundance. Temperature alone is a strong climatic driver of bird distributions in humid tropical regions (e.g. Shoo *et al.*, 2005a; Forero-Medina *et al.*, 2011b). We modelled temperature as a function of elevation using an adiabatic lapse rate conversion. This is because temperature is strongly correlated with elevation on tropical mountains (Smith & Young, 1987; Bush *et al.*, 2004), changing rapidly over small horizontal distances (Raxworthy *et al.*, 2008), and because fine-scale spatial climate layers for Sulawesi are highly uncertain or unavailable at resolutions below that of global climate models (Hijmans *et al.*, 2005). We used a locally measured lapse rate (6.1°C lost per 1000-m elevation gained) to convert a fine-scale digital elevation model (30 arc seconds, srtm.csi.cgiar.org) into an average annual temperature layer of the same resolution. This was carried out by relating temperature from a lowland weather station to elevation via the lapse rate (see Appendix S2 for details).

We then used statistical models to relate temperature to abundance. We first converted bird abundance estimates from birds per 0.79 ha (the area encompassed by 50-m point count circles) to birds per 0.85 ha (30-arc-second cell in

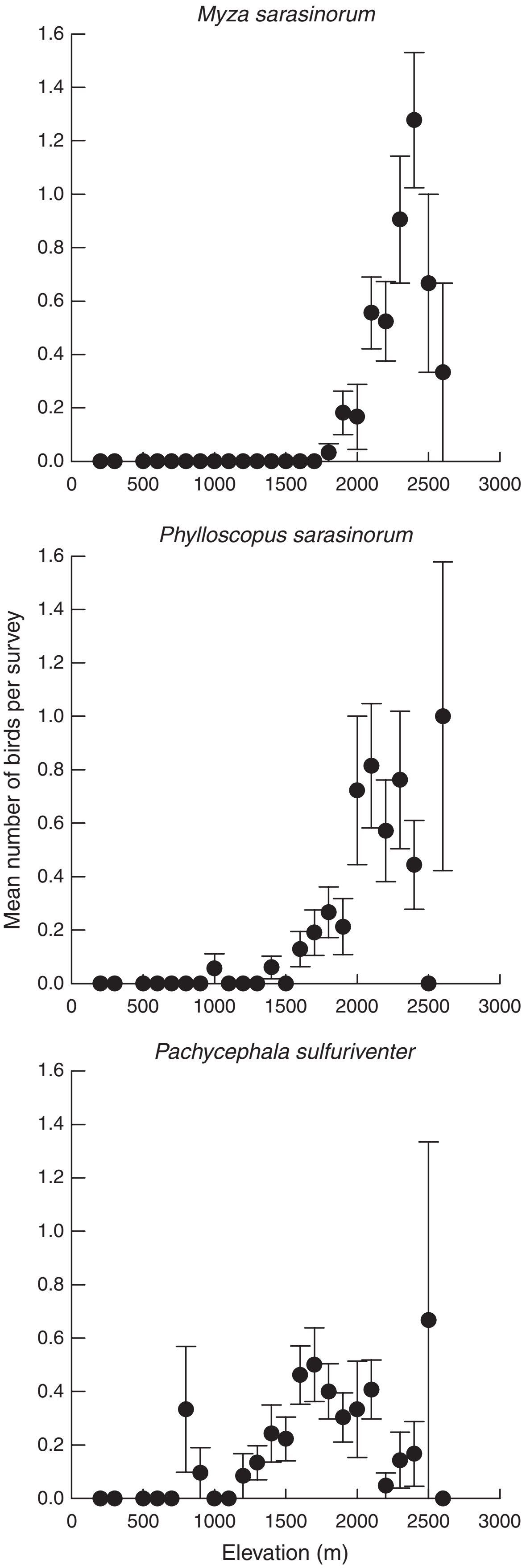


Figure 2 Abundance distributions of study species along elevational gradients on four mountains in Central Sulawesi. Average abundance per point count from three sampling sessions ± standard errors are shown. Data from all sample points are shown including point count surveys where the species was not recorded.

central Sulawesi). Given the strong dependence of the study species on forest habitats, we set cells without forest as unsuitable. For the response variable, we considered using the mean of the counts from the three sampling sessions or the sum of the counts. We chose to use the sum of the counts because 47–75% of the counts were zero, depending on study species, and rounded means would cause a strong downwards bias in abundance estimates. For example, birds were frequently recorded singly in only one sampling session, which gives a mean abundance of 0.33, which rounds to zero. Nonetheless, the sum of the counts should be viewed as an upward estimate of abundance. We analysed the zero-inflated data using a two-step hurdle modelling approach. Firstly, we modelled the probability of presence, assuming a binomial distribution and therefore defining suitable habitats where this probability is non-null. Then, we modelled the abundance in suitable habitats only, using a truncated Poisson distribution (Potts & Elith, 2006; Jackman, 2011). Hurdle models often out-perform other zero-inflated regression approaches based on integrated distributions (Potts & Elith, 2006; Zeileis *et al.*, 2008) and are relatively straightforward to interpret. For each species, we compared linear and second-order polynomial parameterizations for temperature to test for nonlinear (e.g. mid-range optimal) relationships between temperature and abundance that are to be expected in elevational species distributions (McCain, 2009). Aspect (compass direction) was also evaluated as a predictor of bird abundance. Models were built using the pscl package (Jackman, 2011), and model comparison was carried out in a maximum-likelihood multimodel inference framework (Burnham & Andersen, 2002).

Unlike previous lapse-rate-climate-change studies, we evaluated the performance of the presence/absence component of our hurdle models by calculating mean prediction error (leave-one-out cross-validation), kappa statistics and the area under the received operating characteristic curve, using the PresenceAbsence package (Freeman & Moisen, 2008). We converted from probability of presence to binary presence/absence using the maximized the sum of sensitivity and specificity as the threshold (Jiménez-Valverde & Lobo, 2007).

Population size indices and climate-change projections

We used the *abundance ~ temperature* relationships from the hurdle models of each species (Fig. S2) to generate representative measures of current population size in our 'study area' – portions of the national park that lay within 10 km of our sampling sites (93,908 ha, approximately 42% of the park; Fig. 1). We did this by taking the sum of the predicted abundance in each forested cell in the study area (see deforestation projections below). The resulting population size indices are more informative than range area metrics that assume cells of equal carrying capacity because *abundance ~ range area* relationships are typically nonlinear (Shoo *et al.*, 2005a; Fordham *et al.*, 2012a). In this study, we report population size indices as well as range area (all suitable cells) results. By modelling cell-based abundance directly, we did not need to make the unrealistic assumption of uniform abundance inside an elevational bin (Shoo *et al.*, 2005a,b; Gasner *et al.*, 2010).

To project the effects of climate change on future population size, we overlaid coarse climate projections on the fine-scale temperature layer for each year from 2010 to 2050. The climate projections are mean annual temperature layers, downscaled to 0.5°, that were generated by combining climate anomalies from an ensemble of regionally skilful global climate models using MAGICC/SCENGEN (Fordham *et al.*, 2012b, 2013) and a gridded temperature dataset that was chosen because no digital elevation model was used in its preparation (CRU 3.1 TS; http://badc.nerc.ac.uk/home/index.html). Climate layers were generated for policy (low) and reference (high) emissions scenarios, which are similar to the Representative Concentration Pathway scenarios of RCP6 and RCP2.5, respectively (Van Vuuren *et al.*, 2011) (see Appendix S2 for details). We modelled the effects of global warming by recalculating the population size indices using the parameterizations of the original hurdle models, but based on the new temperature values in each cell for each year of projection. Our approach assumes full dispersal and that the *abundance ~ temperature* relationship remains the same as observed today (Shoo *et al.*, 2005a; Gasner *et al.*, 2010).

Deforestation projections

We measured deforestation and modelled the effects of future deforestation on our case-study species. We used a raster land cover dataset that was derived from MODIS imagery and created to monitor deforestation in Southeast Asia for this analysis (Miettinen *et al.*, 2011). The relevant land cover categories for Lore Lindu are lowland (sea level to 750 m), lower montane (750–1500 m) and upper montane (1500 m +) forest (we collapsed these as 'forest'), plantation/regrowth (mostly degraded forest and secondary vegetation in Lore Lindu), and mosaic and open (collapsed as 'agriculture').

The first step was to measure deforestation by comparing forest cover in the national park in 2000 and 2010. Then, following Gregory *et al.* (2012), we used random forest models to relate observed land use change to five spatial variables: elevation, slope, distance from the park boundary, distance from roads and distance from villages (see Appendix S2 for details). We used the model to project the amount of forest cover remaining in the park by 2050 based on two scenarios: (1) a scenario that maintained deforestation at the current rate and (2) a scenario that assumed increased enforcement and (arbitrarily) cut the deforestation rate by half. To simulate the loss of easily logged sites in this mountainous national park, the current rate scenario modelled a 50% decline in the rate of deforestation once 20% of the park's forest had been converted. We chose not to project beyond the year 2050 because of high uncertainty about forest management in the far future.

RESULTS

Predictors of abundance

Phylloscopus sarasinorum and *Myza sarasinorum* preferred higher elevations and had narrower ranges compared with *Pachycephala sulfuriventer* (Fig. 2). The high-elevation species also tended to be more common than *Pachycephala sulfuriventer* (Fig. 2). The linear parameterization of temperature was the best predictor of *Myza sarasinorum* abundance, while the second-degree quadratic function of temperature was the best predictor for the other two species (Table 1). There was no support for aspect as a predictor of abundance for any of the study species (Table 1). The fitted binomial components of the hurdle models matched the patterns of occupancy (Fig. S3), suggesting that there was no systematic bias from low detection probability. Our combination of fitted hurdle-abundance models and the temperature layer created with the lapse rate suggests our study area could currently support approximately 14,000, 40,000, and 70,000 individuals of *Myza sarasinorum*, *Phylloscopus sarasinorum* and *Pachycephala sulfuriventer*, respectively (Table S1). The model validation methods found 24.5% prediction error, kappa = 0.81 ± 0.06, and AUC = 0.97 for *Myza sarasinorum*; 43.9% prediction error, kappa = 0.52 ± 0.08, and AUC = 0.82 for *Phylloscopus sarasinorum*; and 47.9% prediction error; kappa = 0.42 ± 0.08, and AUC = 0.74 for *Pachycephala sulfuriventer* (Fig. S4).

Deforestation and climate change

Our analysis indicates that Lore Lindu National Park was deforested extremely rapidly from 2000 to 2010 (11.8% cleared), which was faster than Sulawesi as a whole (10.8%; Miettinen *et al.*, 2011) (Table 2). The most important predictors of deforestation were elevation, slope and distance from roads (Fig. S5), with lower rates at higher elevations, in steeper areas, and further from roads. Our land use-change models predict that widespread deforestation of the national park may occur in the coming decades (34–40% of the park deforested by 2050), even if the deforestation rate is cut by half (Table 2; Fig. 3). Similarities in predicted forest loss between the two scenarios were the result of both scenarios quickly reaching 20% deforestation, and the deforestation rate consequently being halved (to simulate the loss of easily logged areas). Deforestation in the study area was slightly greater than in the national park. This difference probably resulted because the heavily impacted valley between Mts. Nokilalaki and Rorekatimbu takes up a disproportionate amount of the study area compared with the national park as a whole (Fig. 3; Table 2).

The climate models predicted 0.7–0.9°C of warming in the region by 2050 for low- and high-emissions scenarios, respectively. This predicted warming is forecast to cause up to a 47% decline in range area for the mountaintop *Myza sarasinorum*, while deforestation will only invoke minor declines of <4% (Fig. 4; Table S1). Projected climate change also had much larger impacts on population size of *Myza*

Table 1 Table of hurdle model results for abundance of three case-study montane tropical bird species in Sulawesi, Indonesia. Temp stands for temperature (continuous predictor). Aspect is the cardinal direction faced from the point count (4 nominal categories)

Species	Model	% DE	Evidence ratio	ΔAIC$_c$	w_i	df
Myza sarasinorum	Temp	37.9		0	0.789	4
	Temp + temp^2	38.3	4.1	2.8	0.194	6
	Temp + aspect	39.5	52.4	7.9	0.015	10
	Temp + temp^2 + aspect	39.6	344.3	11.7	0.002	12
	Null	0	>10,000	89.3	0	2
	Aspect	4.4	>10,000	90.3	0	8
Phylloscopus sarasinorum	Temp + temp^2	19.9		0	0.918	6
	Temp + temp^2 + aspect	22.1	12.5	5.0	0.074	12
	Temp	15.6	116.8	9.5	0.008	4
	Temp + aspect	17.5	2522.1	15.7	0	10
	Null	0	>10,000	54.8	0	2
	Aspect	2.7	>10,000	58.4	0	8
Pachycephala sulfuriventer	Temp + temp^2	6.4		0	0.956	6
	Temp + temp^2 + aspect	8.1	24.1	6.4	0.040	12
	Null	0	531.8	12.6	0.002	2
	Temp	1.2	551.9	12.6	0.002	4
	Temp + aspect	4.3	1519.4	14.7	0.001	10
	Aspect	2.6	3473.4	16.3	0	8

df indicates the degrees of freedom; ΔAIC$_c$ shows the difference between the model AIC$_c$ (Akaike's Information Criterion corrected for small sample sizes) and the minimum AIC$_c$ in the set of models; AIC$_c$ weights (w_i) show the relative likelihood of model *i*; %DE is percentage deviance explained by the model; an evidence ratio ($w_{top\ model}$ / w_i) of 5 indicates that the top-ranked model is 5 times better supported by the data than the reference model.

Table 2 Land cover percentages from 2000 and 2010, and projected changes to 2050 based on halved and current deforestation rates, across the 40-year projection period. The study area is the portion of the national park within 10 km of sampling points

Land cover	2000	2010	2050 halved deforestation rate	2050 current deforestation rate
Lore Lindu National Park				
Forest	95.6	83.8	65.9	59.0
Plantation/regrowth	3.1	10.9	27.4	33.7
Agriculture (open/mosaic)	1.2	5.4	6.7	7.3
Study area				
Forest	95.8	78.8	64.7	58.8
Plantation/regrowth	3.1	12.6	26.0	31.3
Agriculture (open/mosaic)	1.0	8.6	9.3	9.8

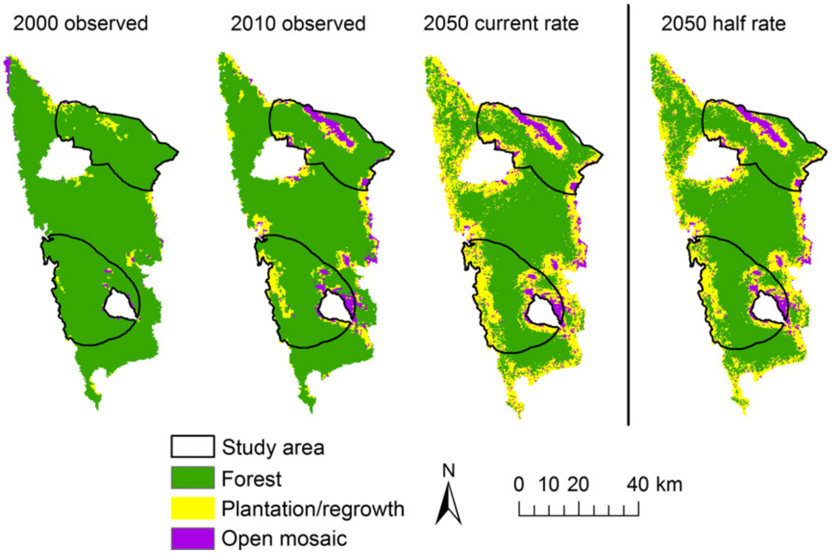


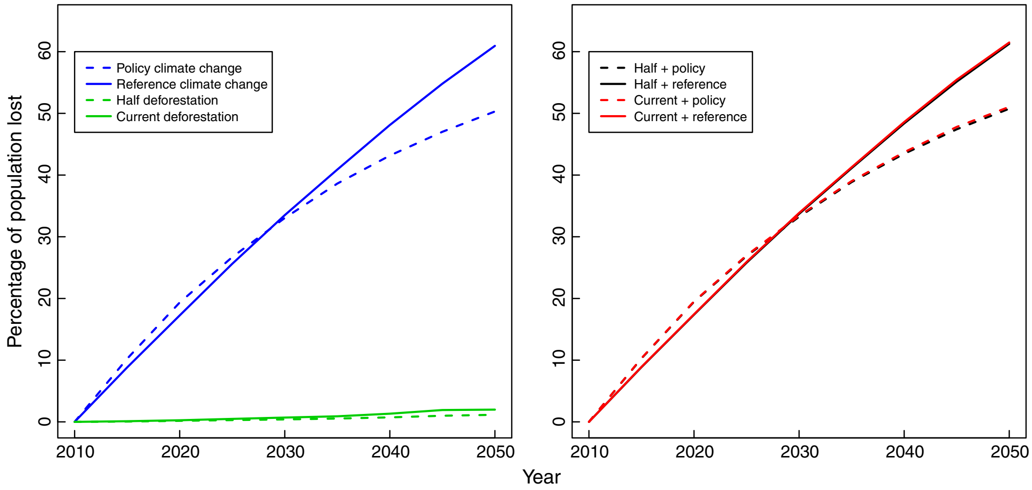
Figure 3 Observed (2000–2010) and projected (2030–2050) land cover change in Lore Lindu National Park. Observed data come from Miettinen *et al.* (2011). Land cover-change models were built by relating forest change from 2000 to 2010 to landscape variables and projecting to 2050 based on the current deforestation rate as well as half the current rate, assuming increased enforcement. The two white sections in the park are annexed village areas. The black outlines show the study area.

sarasinorum (50–61% declines) compared with deforestation (1–2% declines). In the high-elevation *Phylloscopus sarasinorum*, predicted climate change and deforestation caused comparable declines in range area (up to 18% and 15% respectively), but climate change had a much larger impact on population size (up to a 39% decline compared with a 7% decline from deforestation). In contrast to the high-elevation species, in the middle-elevation *Pachycephala sulfuriventer*, deforestation caused larger declines in range area compared with climate change (up to 24% vs. 5%), and larger declines in population size (up to 19% and 11%, respectively). When climate change and deforestation are combined, loss of range area and population size are amplified, resulting in 19–42% declines in area and 19–62% declines in population size across species (Fig. 4; Table S1). In the combined scenarios, population size declines were at least 13% greater than range area declines in the two high-elevation species, while differences between range area and population size declines were negligible for *Pachycephala sulfuriventer* (Fig. 4). Halving the deforestation rate did not appreciably improve outcomes; all differences in population declines between the two scenarios were <6%.

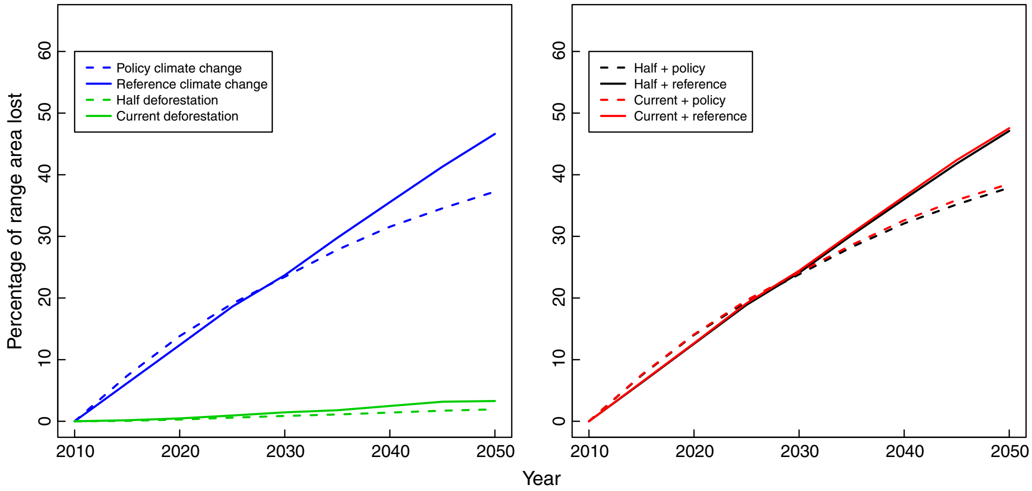
DISCUSSION

Our results suggest that climate change will have a greater impact on high-elevation species, whereas deforestation will be more important for middle-elevation *Pachycephala sulfuriventer*. In high-elevation species, climate change, but not deforestation, caused population size declines to exceed range area declines in our analysis. This is because the high-elevation species are most common at higher elevations, where habitable areas are projected to shrink disproportionately from climate change compared with deforestation. In contrast, large extents of high-elevation species' habitat at lower elevations are predicted to be lost from deforestation, but the effect on population size is minimized because the species are less common at these elevations. Differences between range area and population size predictions were less marked for the middle-elevation *Pachycephala sulfuriventer* because of the species' more uniform abundance across elevations. The mismatches between range area and population size declines we observed underscore the need for caution when projecting extinction risk based on range area predictions alone (Shoo *et al.*, 2005a; Fordham *et al.*, 2012a).

(a) ***Myza sarasinorum*** **percentage population lost**



(b) ***Myza sarasinorum*** **percentage range area lost**



(c) ***Phylloscopus sarasinorum*** **percentage population lost**

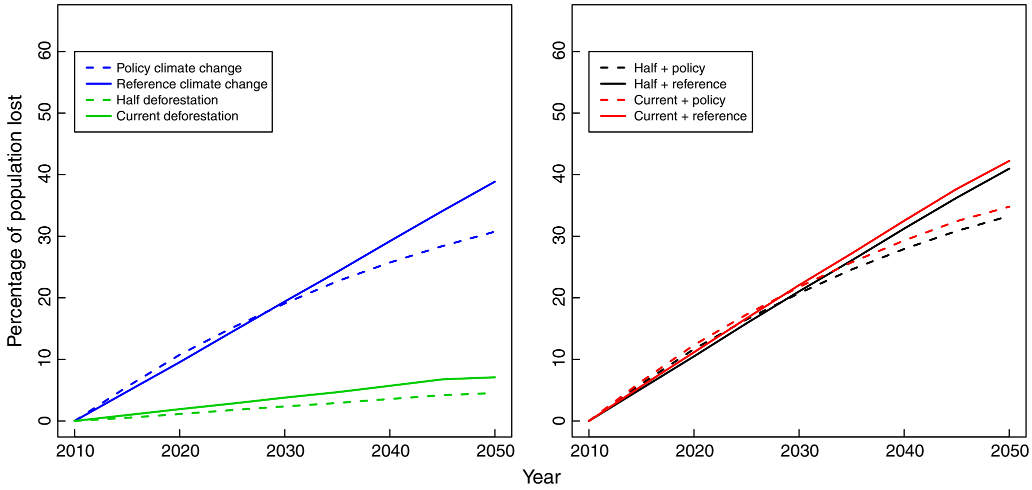
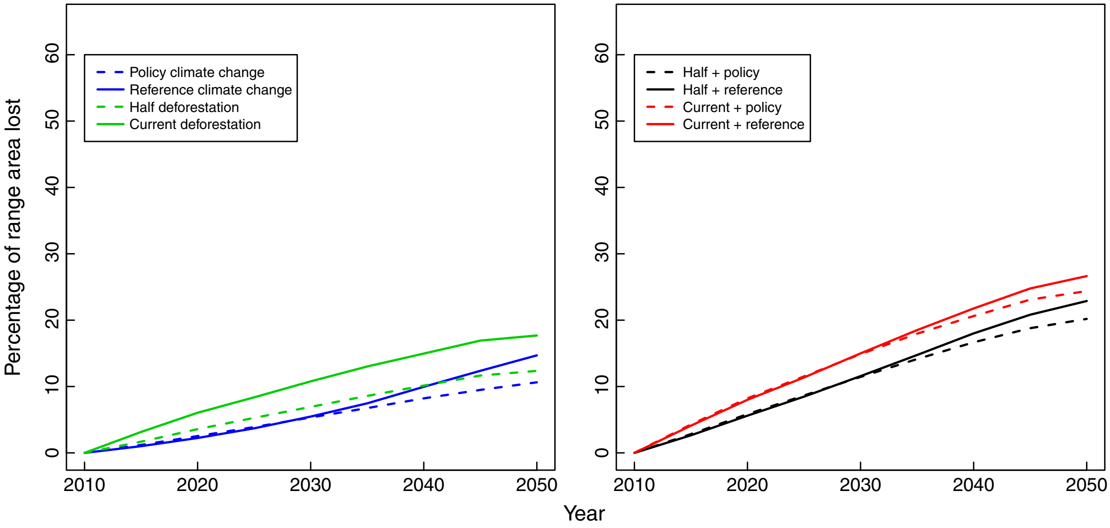
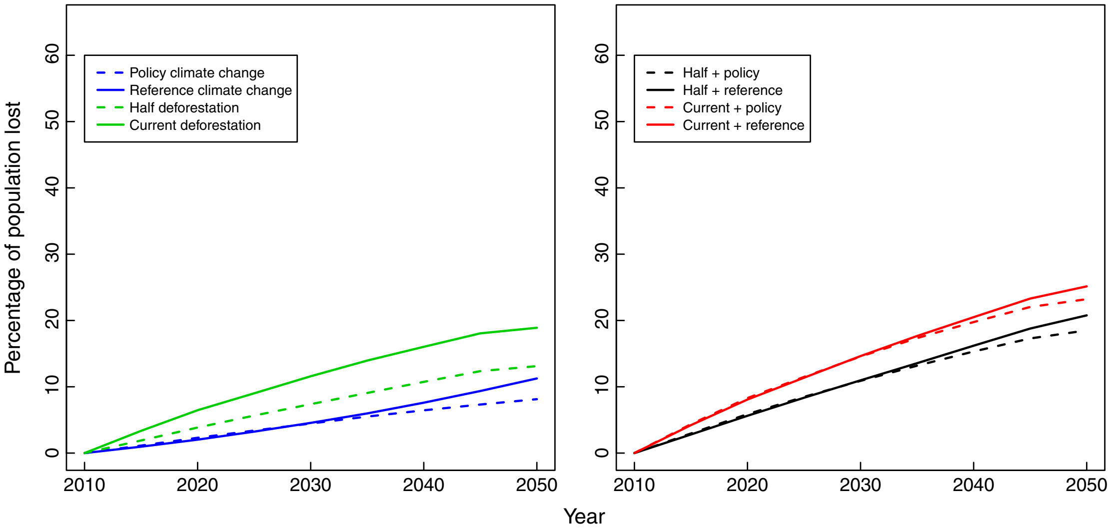


Figure 4 Projected percentage population and range area declines from climate change and deforestation for a (a–b) mountaintop species, *Myza sarasinorum*, (c–d) high-elevation species, *Phylloscopus sarasinorum*, and (e–f) middle-elevation species, *Pachycephala sulfuriventer*. The three study species are birds that are endemic to Sulawesi, Indonesia. The policy scenario models emissions mitigation; reference indicates high-emissions climate change; current indicates the current deforestation rate; half indicates reducing the current deforestation rate by half.

(d) ***Phylloscopus sarasinorum*** **percentage range area lost**



(e) ***Pachycephala sulfuriventer*** **percentage population lost**



(f) ***Pachycephala sulfuriventer*** **percentage range area lost**

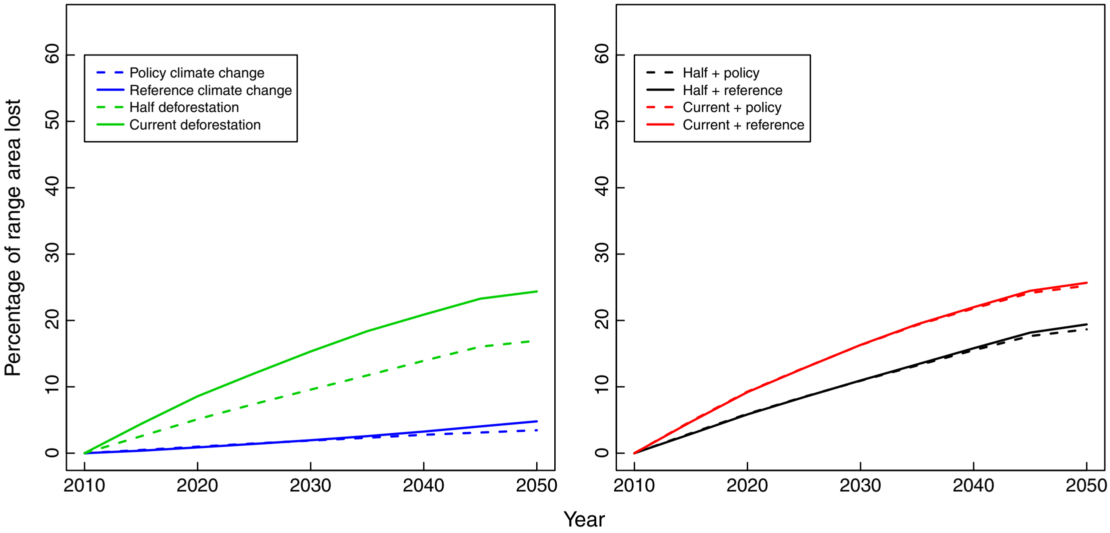


Figure 4 Continued

The results indicate that management strategies should be tailored to species based on their elevational distributions, with greater emphasis placed on climate adaptation strategies for high-elevation species and reducing deforestation for middle-elevation species. Our results agree with other studies that suggest highland tropical endemic birds (most of which are currently considered of 'least concern' in the IUCN Red List) are threatened with extinction in the medium term (Williams *et al.*, 2003; Shoo *et al.*, 2005a; Sekercioglu *et al.*, 2008; Gasner *et al.*, 2010; La Sorte & Jetz, 2010).

From 2000 to 2010, Sulawesi lost approximately 11% of its forest, and 12% of Lore Lindu National Park (which hosts 78% of the island's endemic bird species) was cleared. This deforestation rate is among the fastest of any Indonesian protected area so far reported (Linkie *et al.*, 2004; Gaveau *et al.*, 2009). Our projections indicate approximately 40% of the park will be deforested by 2050 even if the deforestation rate is cut by half. Such large-scale deforestation will cause substantial declines in forest-dependent birds that are endemic to Sulawesi (Sodhi *et al.*, 2005; Maas *et al.*, 2009). Most deforestation in the region leads to permanent conversion, so substantial regeneration should not be expected (Clough *et al.*, 2009). It should be a priority of the Indonesian government and the conservation community to work towards halting deforestation inside the national park, especially in the particularly sensitive mid-elevational regions that are most vulnerable to the synergy of direct habitat loss from clearing and indirect climate-related shifts (see Forero-Medina *et al.*, 2011a). Maintaining large forested protected areas, such as Lore Lindu, will likely give species critical scope to respond to climate change (Beale *et al.*, 2013).

Our lapse-rate modelling approach could under- or over-estimate the impacts of climate change on tropical birds. Our approach could over-estimate declines if species shift slower than predicted by the lapse rate. Studies have documented moths, reptiles, amphibians and birds shifting upwards more slowly than the lapse rate (Raxworthy *et al.*, 2008; Chen *et al.*, 2009; Forero-Medina *et al.*, 2011b), but other (lower resolution) studies from Asia had mixed results, with some birds shifting faster than predicted (Peh, 2007; Harris *et al.*, 2012). We believe our estimates of potential climate-change impacts are conservative (at least for the high-emissions scenario) because we limited our forecasts to 2050 and because nonlinear increases in species endangerment from each degree of warming (because of range contraction) were predicted in a previous global study (Sekercioglu *et al.*, 2008).

Our approach made several other assumptions that should be considered as caveats when interpreting our results. When modelling population changes from climate change, we assumed (due to absence of alternatives) full dispersal and that the current *abundance ~ temperature* relationship was maintained over time (Shoo *et al.*, 2005a; Gasner *et al.*, 2010), despite future climate-induced shifts in range attributes and suitability. In addition, we were only able to test two predictors of species abundance (temperature and aspect). In the current situation, temperature explains 6–38% of the variation in abundance and 11–64% in presence/absence depending on study species. Our population indices should be considered upper estimates of true population size because the sum of the counts was the response variable; still, this should not strongly affect the percentage changes in population size (Fig. 4). We were also unable to consider species interactions, which are important determinants of species ranges (Jankowski *et al.*, 2010, 2013; Gifford & Kozak, 2011). *Myza sarasinorum* likely competes with its elevational replacement species *Myza celebensis* at lower elevations (see Supporting Information). In addition, we could not model vegetation shifts (or lack thereof) from climate change (Feeley & Silman, 2010), or incorporate explicitly the potential synergistic feedbacks between threats, both of which can be important drivers of species distributions. It is also possible that our study species respond to shorter and mossier trees, which are correlated with elevation. In addition, all land cover change inference was based on a comparison between two time periods (2000 and 2010) because no other years were available.

If rapid deforestation continues inside of Sulawesi's Lore Lindu National Park, endemic species will have much less scope to adapt to the stresses of climate change. Management efforts should therefore account for the differential pressures of deforestation and climate change on middle- and high-elevation species. Our results provide important new field data and forecasts to reinforce previous studies that suggested highland tropical birds are threatened with substantial population declines from climate change. Our study demonstrates how models can be linked to predict the relative impacts of fine-scale habitat loss and climate change on population status in poorly known tropical regions.

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REFERENCES

Beale, C.M., Baker, N.E., Brewer, M.J. & Lennon, J.J. (2013) Protected area networks and savannah bird biodiversity in the face of climate change and land degradation. *Ecology Letters*, **16**, 1061–1068.

Bird, J.P., Buchanan, G.M., Lees, A.C., Clay, R.P., Develey, P.F., Yépez, I. & Butchart, S.H. (2012) Integrating spatially explicit habitat projections into extinction risk assessments: a reassessment of Amazonian avifauna incorporating projected deforestation. *Diversity and Distributions*, **18**, 273–281.

BirdLife International (2013) *BirdLife International data zone*. Available at: http://www.birdlife.org/datazone.html (accessed 1 January 2013).

Bradshaw, C.J.A., Sodhi, N.S. & Brook, B.W. (2009) Tropical turmoil: a biodiversity tragedy in progress. *Frontiers in Ecology and the Environment*, **7**, 79–87.

Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, **23**, 453–460.

Brooks, T.M., Pimm, S.L. & Collar, N.J. (1997) Deforestation predicts the number of threatened birds in insular southeast Asia. *Conservation Biology*, **11**, 382–394.

Burnham, K.P. & Andersen, D.R. (2002) *Model selection and multimodel inference*, 2nd edn. Springer, New York.

Bush, M.B., Silman, M.R. & Urrego, D.H. (2004) 48,000 years of climate and forest change in a biodiversity hot spot. *Science*, **303**, 827–829.

Cannon, C.H., Summers, M., Harting, J.R. & Kessler, P.J.A. (2007) Developing conservation priorities based on forest type, condition, and threats in a poorly known ecoregion: Sulawesi, Indonesia. *Biotropica*, **39**, 747–759.

Chen, I.C., Shiu, H.-J., Benedick, S., Holloway, J.D., Chey, V.K., Barlow, H.S., Hill, J.K. & Thomas, C.D. (2009) Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences USA*, **106**, 1479–1483.

Clough, Y., Faust, H. & Tscharntke, T. (2009) Cacao boom and bust: sustainability of agroforests and opportunities for biodiversity conservation. *Conservation Letters*, **2**, 197–205.

Coates, B.J. & Bishop, K.D. (1997) *A guide to the birds of Wallacea*. Dove publications, Alderly, Qld, Australia.

Colwell, R.K., Brehm, G., Cardelus, C.L., Gilman, A.C. & Longino, J.T. (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, **322**, 258–261.

Feeley, K.J. & Silman, M.R. (2010) Land-use and climate change effects on population size and extinction risk of Andean plants. *Global Change Biology*, **16**, 3215–3222.

Fiske, I. & Chandler, R. (2011) Unmarked: an R Package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, **43**, 1–23.

Fordham, D.A., Akçakaya, H.R., Araújo, M.B., Elith, J., Keith, D., Pearson, R., Auld, T.D., Mellin, C., Morgan, J.W., Regan, T.J., Tozer, M., Watts, M.J., White, M., Wintle, B., Yates, C. & Brook, B.W. (2012a) Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global warming? *Global Change Biology*, **18**, 1357–1371.

Fordham, D.A., Wigley, T.M.L., Watts, M.J. & Brook, B.W. (2012b) Strengthening forecasts of climate change impacts with multi-model ensemble averaged projections using MAGICC/SCENGEN 5.3. *Ecography*, **35**, 4–8.

Fordham, D.A., Akçakaya, H.R., Araújo, M.B., Keith, D.A. & Brook, B.W. (2013) Tools for integrating range change, extinction risk and climate change information into conservation management. *Ecography*, **36**, 956–964.

Forero-Medina, G., Joppa, L. & Pimm, S.L. (2011a) Constraints to species' elevational range shifts as climate changes. *Conservation Biology*, **25**, 163–171.

Forero-Medina, G., Terborgh, J., Socolar, S.J. & Pimm, S.L. (2011b) Elevational ranges of birds on a tropical montane gradient lag behind warming temperatures. *PLoS ONE*, **6**, e28535.

Freeman, E.A. & Moisen, G. (2008) PresenceAbsence: an R package for presence-absence model analysis. *Journal of Statistical Software*, **23**, 1–31.

Gasner, M.R., Jankowski, J.E., Ciecka, A.L., Kyle, K.O. & Rabenold, K.N. (2010) Projecting the local impacts of climate change on a Central American montane avian community. *Biological Conservation*, **143**, 1250–1258.

Gaveau, D.L.A., Epting, J., Lyne, O., Linkie, M., Kumara, I., Kanninen, M. & Leader-Williams, N. (2009) Evaluating whether protected areas reduce tropical deforestation in Sumatra. *Journal of Biogeography*, **36**, 2165–2175.

Gifford, M.E. & Kozak, K.H. (2011) Islands in the sky or squeezed at the top? Ecological causes of elevational range limits in montane salamanders. *Ecography*, **35**, 193–203.

Green, J.M.H., Larrosa, C., Burgess, N.D., Balmford, A., Johnston, A., Mbilinyi, B.P., Platts, P.J. & Coad, L. (2013) Deforestation in an African biodiversity hotspot: extent, variation and the effectiveness of protected areas. *Biological Conservation*, **164**, 62–72.

Gregory, S.D., Brook, B.W., Goossens, B., Ancrenaz, M., Alfred, R., Ambu, L.N. & Fordham, D.A. (2012) Long-term field data and climate-habitat models show that orangutan persistence depends on effective forest management and greenhouse gas mitigation. *PLoS ONE*, **7**, e43846.

Harris, J.B.C., Sekercioglu, C.H., Sodhi, N.S., Fordham, D.A., Paton, D.C. & Brook, B.W. (2011) The tropical frontier in avian climate impact research. *Ibis*, **153**, 877–882.

Harris, J.B.C., Yong, D.L., Sheldon, F.H., Boyce, A.J., Eaton, J.A., Bernard, H., Biun, A., Langevin, A., Martin, T.E. & Wei, D. (2012) Using diverse data sources to detect elevational range changes of birds on Mt. Kinabalu, Malaysian Borneo. *Raffles Bulletin of Zoology*, **25**, 189–239.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Jackman, S. (2011) *pscl: classes and methods for R developed in the Political Science Computational Laboratory*. Stanford University, Stanford, CA. Version 1.04.1.

Jankowski, J.E., Robinson, S.K. & Levey, D.J. (2010) Squeezed at the top: interspecific aggression may constrain elevational ranges in tropical birds. *Ecology*, **91**, 1877–1884.

Jankowski, J.E., Londoño, G.A., Robinson, S.K. & Chappell, M.A. (2013) Exploring the role of physiology and biotic interactions in determining elevational ranges of tropical animals. *Ecography*, **36**, 1–12.

Jetz, W., Wilcove, D.S. & Dobson, A.P. (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, **5**, 1211–1219.

Jiménez-Valverde, A. & Lobo, J.M. (2007) Threshold criteria for conversion of probability of species presence to either-or presence-absence. *Acta Oecologica*, **31**, 361–369.

La Sorte, F.A. & Jetz, W. (2010) Projected range contractions of montane biodiversity under global warming. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 3401–3410.

Lee, T.M., Sodhi, N.S. & Prawiradilaga, D.M. (2007) The importance of protected areas for the forest and endemic avifauna of Sulawesi (Indonesia). *Ecological Applications*, **17**, 1727–1741.

Linkie, M., Smith, R.J. & Leader-Williams, N. (2004) Mapping and predicting deforestation patterns in the lowlands of Sumatra. *Biodiversity and Conservation*, **13**, 1809–1818.

Maas, B., Putra, D.D., Waltert, M., Clough, Y., Tscharntke, T. & Schulze, C.H. (2009) Six years of habitat modification in a tropical rainforest margin of Indonesia do not affect bird diversity but endemic forest species. *Biological Conservation*, **142**, 2665–2671.

Madika, B., Putra, D.D., Harris, J.B.C., Yong, D.L., Mallo, F.N., Rahman, A., Prawiradilaga, D.M. & Rasmussen, P.C. (2011) An undescribed *Ninox* hawk owl from the highlands of Central Sulawesi, Indonesia? *Bulletin of the British Ornithologists' Club*, **131**, 94–102.

McCain, C.M. (2009) Global analysis of bird elevational diversity. *Global Ecology and Biogeography*, **18**, 346–360.

Miettinen, J., Shi, C. & Liew, S.C. (2011) Deforestation rates in insular Southeast Asia between 2000 and 2010. *Global Change Biology*, **17**, 2261–2270.

Noske, R.A. (2010) Potential impacts of climate change on the birds of Indonesia. *Proceedings of the International German Alumni Summer School Program. Impact of climate change on biodiversity: does nature conservation need new strategies?* (ed. by J. Slowik, M. Pangau-Adam and K. Barua), pp. 23–37. Cuvillier Verlag, Göttingen, Germany.

Peh, K.S.H. (2007) Potential effects of climate change on elevational distributions of tropical birds in Southeast Asia. *Condor*, **109**, 437–441.

Potts, J.M. & Elith, J. (2006) Comparing species abundance models. *Ecological Modelling*, **199**, 153–163.

Pounds, J.A., Fogden, M.P.L. & Masters, K.L. (2005) Responses of natural communities to climate change in a highland tropical forest. *Climate change and biodiversity* (ed. by T. Lovejoy and L. Hannah), pp. 70–74. Yale University Press, New Haven, CT.

R Development Core Team (2011) *R: a language and environment for statistical computing. Version 2.14.1.* R Foundation for Statistical Computing, Vienna.

Ralph, C.J., Sauer, J.R. & Droege, S. (1995) *Monitoring bird populations by point counts*. US Forest Service General Technical Report PSW-GTR-149. USDA, Forest Service, Pacific Southwest Research Station, Albany, CA.

Raxworthy, C.J., Pearson, R.G., Rabibisoa, N., Rakotondrazafy, A.M., Ramanamanjato, J.B., Raselimanana, A.P., Wu, S., Nussbaum, R.A. & Stone, D.A. (2008) Extinction vulnerability of tropical montane endemism from warming and upslope displacement: a preliminary appraisal for the highest massif in Madagascar. *Global Change Biology*, **14**, 1703–1720.

Rosa, I.M., Purves, D., Souza, C. Jr & Ewers, R.M. (2013) Predictive modelling of contagious deforestation in the Brazilian Amazon. *PLoS ONE*, **8**, e77231.

Sekercioglu, C.H., Schneider, S.H., Fay, J.P. & Loarie, S.R. (2008) Climate change, elevational range shifts, and bird extinctions. *Conservation Biology*, **22**, 140–150.

Sekercioglu, C.H., Primack, R.B. & Wormworth, J. (2012) The effects of climate change on tropical birds. *Biological Conservation*, **148**, 1–18.

Shoo, L.P., Williams, S.E. & Hero, J.M. (2005a) Potential decoupling of trends in distribution area and population size of species with climate change. *Global Change Biology*, **11**, 1469–1476.

Shoo, L.P., Williams, S.E. & Hero, J.M. (2005b) Climate warming and the rainforest birds of the Australian Wet Tropics: using abundance data as a sensitive predictor of change in total population size. *Biological Conservation*, **125**, 335–343.

Smith, A.P. & Young, T.P. (1987) Tropical alpine plant ecology. *Annual Review of Ecology and Systematics*, **18**, 137–158.

Soares-Filho, B.S., Nepstad, D.C., Curran, L.M., Cerqueira, G.C., Garcia, R.A., Ramos, C.A., Voll, E., McDonald, A., Lefebvre, P. & Schlesinger, P. (2006) Modelling conservation in the Amazon basin. *Nature*, **440**, 520–523.

Sodhi, N.S. & Brook, B.W. (2006) *Southeast Asian biodiversity in crisis*. Cambridge University Press, London, UK.

Sodhi, N.S., Koh, L.P., Prawiradilaga, D.M., Darjono, Tinulele, I., Putra, D.D. & Tan, T.H.T. (2005) Land use and conservation value for forest birds in Central Sulawesi (Indonesia). *Biological Conservation*, **122**, 547–558.

Soh, M.C.K., Sodhi, N.S. & Lim, S.L.H. (2006) High sensitivity of montane bird communities to habitat disturbance in Peninsular Malaysia. *Biological Conservation*, **129**, 149–166.

Tingley, M.W. & Beissinger, S.R. (2009) Detecting range shifts from historical species occurrences: new perspectives on old data. *Trends in Ecology & Evolution*, **24**, 625–633.

Van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G.C., Kram, T., Krey, V. & Lamarque, J.-F. (2011) The representative concentration pathways: an overview. *Climatic Change*, **109**, 5–31.

Weber, R., Faust, H., Schippers, B., Shohibuddin, M., Mamar, S., Sutarto, E. & Kreisel, W. (2007) Migration and ethnicity as cultural driving forces of land use change in the rainforest margin of Central Sulawesi, Indonesia. *The stability of tropical rainforest margins: linking ecological, economic and social constraints of land use and conservation* (ed. by T. Tscharntke, C. Leuschner, E. Guhardja and M. Zeller), pp. 415–434. Springer Verlag, Berlin.

Williams, S.E., Bolitho, E.E. & Fox, S. (2003) Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 1887–1892.

Zeileis, A., Kleiber, C. & Jackman, S. (2008) Regression models for count data in R. *Journal of Statistical Software*, **27**, 1–25.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Coordinates, elevation and land cover of the point counts.

Appendix S2 Detailed methods.

Figure S1 Histograms of elevation, forest cover and sampling effort within the study area.

Figure S2 Relationships between temperature and abundance from fitted hurdle models for each study species.

Figure S3 Plots comparing probability of occupancy to probability of presence from the binomial component of hurdle models for the study species.

Figure S4 Plots of receiver operating characteristic curves showing predictive ability of the binomial part of hurdle models the study species.

Figure S5 Variable importance plots from random forest models that predicted deforestation in the study area.

Table S1 Projected reductions in the population size index and range area for the study species under climate and land use change scenarios.

Table S2 Land cover classification errors in Miettinen *et al.*'s (2011) dataset at our 149 sampling points.

BIOSKETCH

The authors are part of the Global Change Ecology group at the University of Adelaide. Research in the group addresses the effects of global change on biodiversity.

Author contributions: J.B.C.H., N.S.S., D.A.F., B.W.B. and D.M.P. conceived the ideas; D.D.P. and J.B.C.H. collected the data; J.B.C.H., S.D.G. and D.W. analysed the data; all authors wrote the paper.

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Supporting Information

Appendix S1. Point count coordinates, elevation, and land-cover. Forested points inside the elevational ranges of the study species (Coates & Bishop, 1997; n = 126) were used in the analysis (shown in bold). We present these data to promote re-surveys.

Point	Easting	Northing	Elevation (m)	Field notes on land-cover	Correct classification in Miettinen *et al.*'s (2011) dataset
Pakuli 1	829494	9863670	174	mixed agriculture	open/mosaic
Pakuli 2	829748	9863606	204	scrubby secondary growth with bamboo	open/mosaic
Pakuli 3	830009	9863596	292	disturbed secondary forest with some tall trees	plantation/regrowth
Pakuli 4	830160	9863389	417	cacao patch surrounded by tall secondary forest	open/mosaic
Pakuli 5	830230	9863136	502	edge of tall secondary forest above cacao	forest
Pakuli 6	830378	9862921	618	tall secondary forest with some agrofrestry	forest
Pakuli 7	830639	9862897	786	primary forest	forest
Dali 1	184023	9811929	1659	riparian, wet, tall forest like at Danau Tambing	forest
Dali 2	183794	9811837	1681	riparian, wet, tall forest like at Danau Tambing	forest
Dali 3	183555	9811717	1713	riparian, wet, tall forest like at Danau Tambing	forest
Dali 4	183328	9811629	1772	forest, foot of drier ridge	forest
Dali 5	183084	9811707	1884	forest, drier ridge, low elevation	forest
Dali 6	182864	9811811	1959	forest, drier ridge, low	forest

				elevation	
Dali 7	182653	9811655	1996	many oaks, higher elevation, still on ridge	forest
Dali 8	182419	9811555	2077	many oaks, higher elevation, still on ridge	forest
Dali 9	182218	9811412	2200	high mountain forest, very mossy	forest
Dali 10	182145	9811164	2229	high mountain forest, very mossy	forest
Dali 11	182202	9810915	2228	high mountain forest, very mossy	forest
Dali 12	182322	9810689	2245	high mountain forest, very mossy	forest
Dali 13	184220	9812093	1632	forest, foot of drier ridge	forest
Dali 14	184477	9812073	1689	forest, foot of drier ridge with much leaf litter	forest
Dali 15	184623	9812272	1650	forest, foot of drier ridge with much leaf litter	forest
Dali 16	184853	9812398	1626	last primary forest point before entering disturbed area	forest
Dali 17	185098	9812440	1597	tall secondary forest	forest
Dali 18	185352	9812486	1567	tall secondary forest	forest
Dali 19	185596	9812535	1532	tall secondary forest	forest
Dali 20	185836	9812437	1483	tall secondary forest	forest
Dali 21	186080	9812335	1433	tall secondary forest	forest
Dali 22	186338	9812345	1357	edge of field (grassy)	open/mosaic
Dali 23	186563	9812220	1350	in forest patch surrounded by field	forest
Dali 24[1]	186826	9812217	1357	grass	open/mosaic
Dali 25	187080	9812179	1350	grass	open/mosaic
Dali 26	187327	9812098	1348	grass	open/mosaic
Dali 27	187582	9812036	1327	grass	open/mosaic
Dali 28	187838	9812011	1295	grass	open/mosaic

Nokilalaki 1	184603	9866234	823	cacao	open/mosaic
Nokilalaki 2	184372	9866133	854	mixed agriculture	open/mosaic
Nokilalaki 3	184183	9865973	886	mixed agriculture	open/mosaic
Nokilalaki 4	184114	9865733	915	mixed agriculture	open/mosaic
Nokilalaki 5	184102	9865485	943	mixed agriculture, a few remnant trees in riparian corridor	open/mosaic
Nokilalaki 6	184158	9865244	973	mixed agriculture	open/mosaic
Nokilalaki 7	184235	9865006	1003	mixed agricuture and grass	open/mosaic
Nokilalaki 8	184256	9864757	1032	second growth (small patch)	plantation/regrowth
Nokilalaki 9	184037	9864644	1063	primary forest next to edge	forest
Nokilalaki 10	183897	9864424	1110	forest	forest
Nokilalaki 11	183656	9864340	1178	forest	forest
Nokilalaki 12	183476	9864187	1210	forest	forest
Nokilalaki 13	183338	9863999	1277	forest	forest
Nokilalaki 14	183233	9863780	1378	forest	forest
Nokilalaki 15	183117	9863563	1486	forest	forest
Nokilalaki 16	183063	9863314	1544	forest	forest
Nokilalaki 17	182975	9863083	1611	forest	forest
Nokilalaki 18	182966	9862831	1674	forest	forest
Nokilalaki 19	183047	9862597	1736	forest	forest
Nokilalaki 20	183060	9862354	1835	forest	forest
Nokilalaki 21	183306	9862303	1915	forest	forest
Nokilalaki 22	183540	9862213	2024	forest	forest
Nokilalaki 23	183685	9862014	2060	forest	forest
Nokilalaki 24	183873	9861849	2052	forest	forest
Nokilalaki 25	184087	9861723	2171	forest	forest
Nokilalaki 26	184199	9861502	2215	forest	forest
Nokilalaki 27	184353	9861304	2278	forest	forest
Nokilalaki 28	184524	9861124	2340	forest	forest

Nokilalaki 29	184722	9860969	2362	forest	forest
Rorekatimbu 1	199662	9853794	1695	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 2	199683	9854041	1761	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 3	199939	9854082	1803	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 4	200115	9854272	1855	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 5	200349	9854366	1883	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 6	200471	9854581	1921	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 7	200430	9854828	1984	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 8	200483	9855076	2027	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 9	200696	9855221	2040	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 10	200597	9855449	2038	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 11	200487	9855675	2072	tall secondary forest along trail with older	forest

				forest off trail	
Rorekatimbu 12	200349	9855887	2055	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 13	200226	9856114	2108	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 14	200111	9856345	2140	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 15	200223	9856565	2160	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 16	200229	9856816	2158	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 17	200363	9857029	2170	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 18	200519	9857229	2224	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 19	200664	9857430	2245	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 20	200643	9857713	2311	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 21	200614	9857967	2366	mossy primary forest	forest
Rorekatimbu 22	200546	9858202	2369	mossy primary forest	forest
Rorekatimbu	200568	9858455	2399	mossy primary forest	forest

23					
Rorekatimbu 24	200638	9858697	2485	mossy primary forest	forest
Rorekatimbu 25	200486	9858895	2512	mossy primary forest	forest
Rorekatimbu 26	199420	9853870	1671	tall old forest, probably secondary	forest
Rorekatimbu 27	199219	9854033	1632	forest	forest
Rorekatimbu 28	198959	9854013	1585	forest	forest
Rorekatimbu 29	198799	9854204	1564	scrubby forest	plantation/regrowth
Rorekatimbu 30	198554	9854277	1539	secondary scrub, younger than R29	plantation/regrowth
Rorekatimbu 31	198272	9854222	1531	forest	forest
Rorekatimbu 32	198059	9854410	1535	forest	forest
Rorekatimbu 33	197953	9854644	1494	tall secondary forest	forest
Rorekatimbu 34	197789	9854842	1458	tall secondary forest, forest in better shape than at R20 and R30	forest
Rorekatimbu 35	197605	9855051	1430	slightly more disturbed than R34	forest
Rorekatimbu 36	197491	9855285	1361	tall secondary forest	forest
Rorekatimbu 37	197285	9855443	1343	tall secondary forest	forest
Rorekatimbu 38	197050	9855551	1309	tall secondary forest	forest
Rorekatimbu 39	196822	9855674	1296	disturbed secondary forest	plantation/regrowth

Rorekatimbu 40	196636	9855891	1264	secondary, next to first farmer's field	plantation/regrowth
Rano Rano 1	184505	9814624	1498	tall forest like at Danau Tambing, but lower elevation	forest
Rano Rano 2	184238	9814575	1503	tall forest like at Danau Tambing, but lower elevation	forest
Rano Rano 3	183977	9814585	1581	ridge forest	forest
Rano Rano 4	183721	9814629	1618	ridge forest	forest
Rano Rano 5	183486	9814742	1646	forest	forest
Rano Rano 6	183294	9814914	1715	forest	forest
Rano Rano 7	183054	9815020	1771	forest	forest
Rano Rano 8	182790	9814963	1844	forest	forest
Rano Rano 9	182538	9814907	1894	forest	forest
Rano Rano 10	182280	9814878	1919	forest	forest
Rano Rano 16	179997	9817864	1898	forest	forest
Rano Rano 17	179765	9817963	1892	forest	forest
Rano Rano 18	179511	9818012	1860	forest	forest
Rano Rano 19	179273	9818114	1812	forest	forest
Rano Rano 20	179036	9818213	1764	taller, more tropical forest	forest
Rano Rano 21	178790	9818153	1749	forest	forest
Rano Rano 22	178544	9818229	1722	forest	forest
Rano Rano 23	178330	9818369	1709	forest	forest

Rano Rano 24	178161	9818569	1620	forest	forest
Rano Rano 25	177971	9818749	1570	forest	forest
Rano Rano 26	177791	9818918	1516	forest	forest
Rano Rano 27	177593	9819091	1459	forest	forest
Rano Rano 28	177410	9819272	1403	secondary forest, edge of regenerating field	plantation/regrowth
Rano Rano 29	177269	9819487	1354	forest	forest
Rano Rano 30	177170	9819721	1282	return to primary forest	forest
Rano Rano 31	177065	9819953	1283	forest	forest
Rano Rano 32	176971	9820191	1252	forest	forest
Rano Rano 33	176887	9820438	1206	forest	forest
Rano Rano 34	173323	9821909	480	bamboo, scrubby woodland above river	open/mosaic
Rano Rano 35	173449	9821678	616	young secondary forest	open/mosaic
Rano Rano 36	173688	9821560	684	secondary forest	plantation/regrowth
Rano Rano 37	173867	9821377	716	a field	open/mosaic
Rano Rano 38	174075	9821218	768	0.18 km from RR 39 to RR 38 lightly disturbed primary forest	forest
Rano Rano 39	174268	9821046	838	primary forest	forest
Rano Rano 40	174464	9820878	874	becoming disturbed, but still tall forest; rattan trails	forest

Rano Rano 41	174694	9820755	876	primary forest nearby; some rattan collection	forest
Rano Rano 42	174944	9820684	884	primary forest with bamboo (continues until RR 41)	forest
Rano Rano 43	175194	9820614	917	scruby area near forest	plantation/regrowth
Rano Rano 44	175400	9820445	979	primary forest	forest
Rano Rano 45	175658	9820423	993	primary forest	forest
Rano Rano 46	175798	9820644	1034	primary forest	forest
Rano Rano 47	176023	9820778	1042	forest	forest
Rano Rano 48	176283	9820802	1108	forest	forest
Rano Rano 49	176544	9820765	1159	forest	forest
Rano Rano 50	176702	9820588	1220	forest	forest

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[1] Points Dali 24-28, Rorekatimbu 21-25 are outside of the national park.

Appendix S2. Supplementary Methods

Details on study species

Myza sarasinorum (white-eared myza) is a medium-sized honeyeater that inhabits montane forest and mossy elfin forest (1700–2800 m), especially on ridges, where it feeds on nectar and gleans insects from the understory to the canopy (Coates & Bishop, 1997; Higgins *et al.*, 2008). *M. sarasinorum* is replaced by the smaller, less conspicuous, *M. celebensis* (dark-eared myza) at lower altitudes. M. sarasinorum is a pugnacious defender of flowers (Coates & Bishop, 1997); we postulate that M. celebensis would be subordinate to M. sarasinorum. *Phylloscopus sarasinorum* (Sulawesi leaf-warbler) inhabits the midstory and canopy of montane forest where it gleans and hover-gleans small arthropods, often in association with mixed-species foraging flocks (Coates & Bishop, 1997; Alström *et al.*, 2006). *Phylloscopus sarasinorum* is found from 600 to 3500 m. There are no other resident *Phylloscopus* on Sulawesi. *Pachycephala sulfuriventer* (sulphur-bellied whistler), is found in upland forest where it forages for insects along branches and tree trunks from the understory to the canopy (Coates & Bishop, 1997; Boles, 2007). *P. sulfuriventer* is found from sea level to 2500 m, mainly above 800 m. There are no other *Pachycephala* on Sulawesi. *Coracornis raveni* (maroon-backed whistler) is an inconspicuous inhabitant of the lower levels of montane forest from 1500–2300 m. There is no information on potential competitive interactions between *C. raveni* and *P. sulfuriventer*. None of the study species' nests have been described, and none are threatened with extinction (Alström *et al.*, 2006; Boles, 2007; Higgins *et al.*, 2008; BirdLife International, 2013).

Abundance models

We used the Poisson component of the hurdle abundance model for each species to check for overdispersion. The residual deviance divided by the degrees of freedom from the top-ranked Poisson model for each species was close to one (0.6–1.3 for the three study species). This indicated our data were not substantially overdispersed (Crawley, 2007), and Poisson errors were supported over negative binomial (Potts & Elith, 2006).

Land-cover change modeling

Miettinen *et al.* (2012) classified land-cover in Southeast Asia in 2000 and 2010 at a 250 m resolution. We evaluated the accuracy of the land-cover data in our study areas by comparing the land-cover type we observed at each bird sampling point to the layer classification. We found the layer had 87% accuracy along our 149 points, which is similar to the overall accuracy across the region (85%; Miettinen *et al.*, 2012; Table S2).

In the land-cover projections, deforestation represented the permanent conversion of forest to degraded (plantation/regrowth) or cleared (open/mosaic) land. We did not model forest regeneration because conversion is usually permanent in Central Sulawesi (Weber *et al.*, 2007; Clough *et al.*, 2009). Deforestation was modeled as an annual transition matrix, projected as a discrete-transition Markov Chain (Takada *et al.*, 2010). To identify which raster cells would be changed at each time step, and to which class they would change, we used 2010 land-cover prediction probabilities from random forest models relating land-cover change to the spatial variables mentioned above (Liaw & Wiener, 2002; Hijmans & van Etten, 2012). The models assigned each cell a probability of class membership in each land-cover class calculated as the proportion of iterations in which they were assigned to that class. A cell’s predicted 2010 land-cover class is that which has the highest probability of class membership. We calculated each cell's vulnerability to change as the maximum probability of membership to any other land-cover class (Eastman *et al.*, 1995). For each time step, the land-cover change model calculated how many and which raster cells to change, based on the deforestation projections and cell vulnerabilities, and then altered their land-cover class to that with the second highest probability of class membership.

Lowland temperature, adiabatic lapse rate, and climate modeling

The closest lowland weather station with the most complete recent observations was the GHCN Gorontalo station (ID number 50397048000, 0.52° N, 123.07° E, elevation 2 m, http://www.ncdc.noaa.gov/ghcnm/v3.php station). We calculated annual mean temperature from 2007–2010 at the station.

The best temperature records for Lore Lindu National Park come from two meteorological research stations. We calculated the lapse rate by relating temperate to elevation at the 417 m elevation Gimpu meteorological station (c. 1.6° S, 120.1°E; mean annual temperature from 2002–2006; Schwendenmann *et al.*, 2010), and the 1,400 m elevation Bariri meteorological tower (c. 1.7° S, 120.3°E; mean annual temperature from six months of measurements in 2011–2012). This calculation resulted in a lapse rate of 6.1°C of temperature loss per 1000 m of elevation gained. This estimate is similar to lapse rates calculated globally that range from 5–6°C (Sarmiento, 1986; Smith & Young, 1987; Kitayama, 1992; Gaffen *et al.*, 2000; Bush *et al.*, 2004) and lapse rates calculated in Sulawesi from shorter temperature records (7 °C on Mt. Rantemario from approximately five days of measurements (Whitten *et al.*, 2002, pers. comm.) and ~ 6.8 °C in the Mt. Nokilalaki region from two months of measurements (Musser, 1982)).

We modelled the effect of climate change on abundance for each year from 2010–2050 according to two emissions scenarios: a no-climate-policy reference scenario (no greenhouse gas emission stabilization; MiniCAM Ref.) and a corresponding policy (stabilization) scenario (MiniCAM, Level 1) designed to stabilize at an equivalent CO_2 concentration of 450 ppm (Clarke *et al.*, 2007; Wigley *et al.*, 2009). Seven regionally skillful Atmosphere-Ocean General Circulation Models (BCCRBCM2, CCCMA–31, CSIR0–30, GFDLCM20, MIROCMED, CCSM–30 and UKHADGEM) were used to generate an annual time series of multi-model averaged climate projections using MAGICC/SCENGEN (Fordham *et al.*, 2012). These were downscaled to a grid cell resolution of 0.5° (approximately 50 km) using the “change factor” method, where the low-resolution multi-model averaged predicted change in temperature was added directly to a higher resolution baseline observed climatology − an interpolated temperature dataset that was developed without the support of a digital elevation model (CRU 3.1 TS; http://badc.nerc.ac.uk/home/index.html).

Supplementary Figures

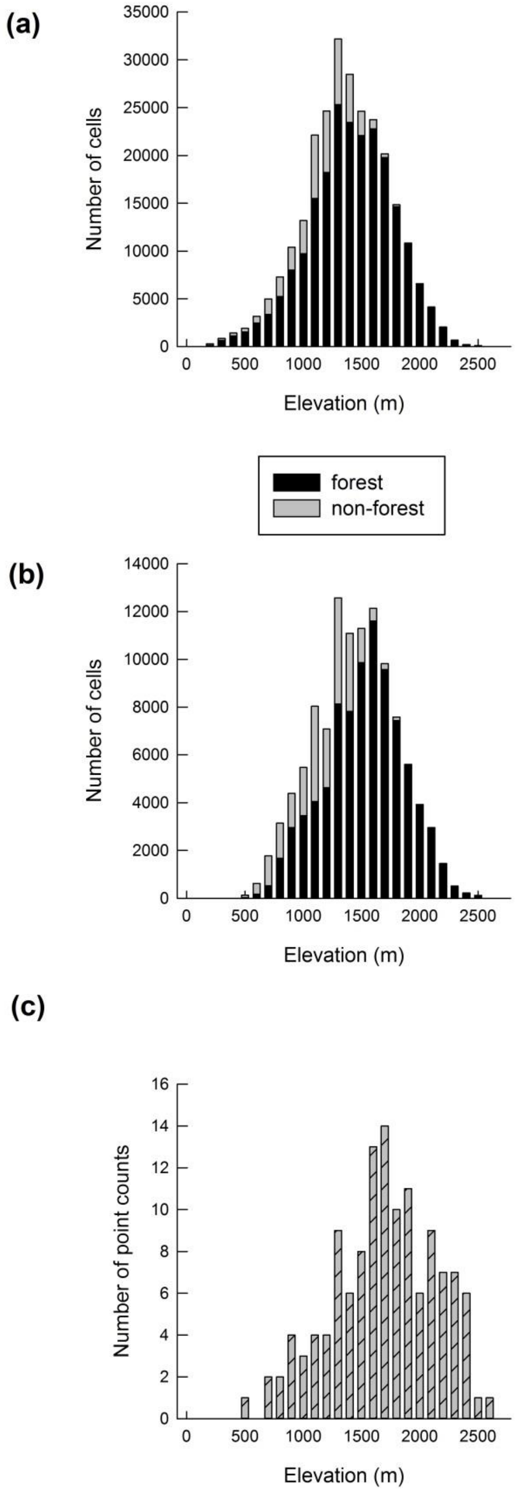
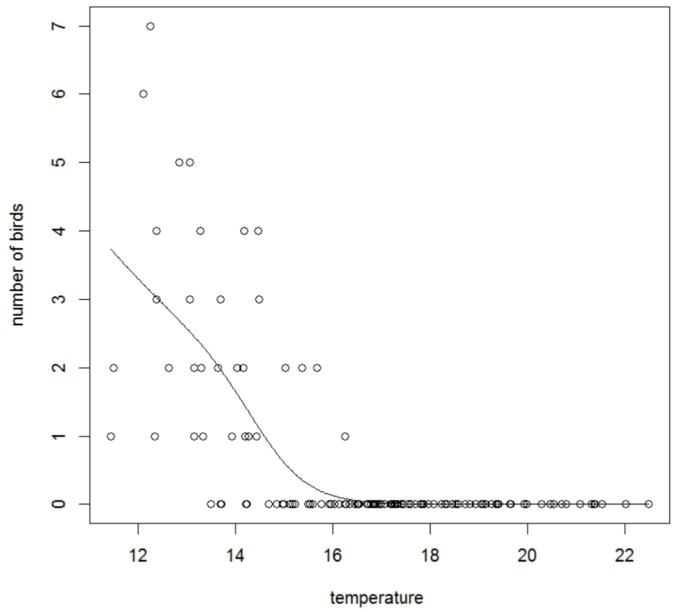


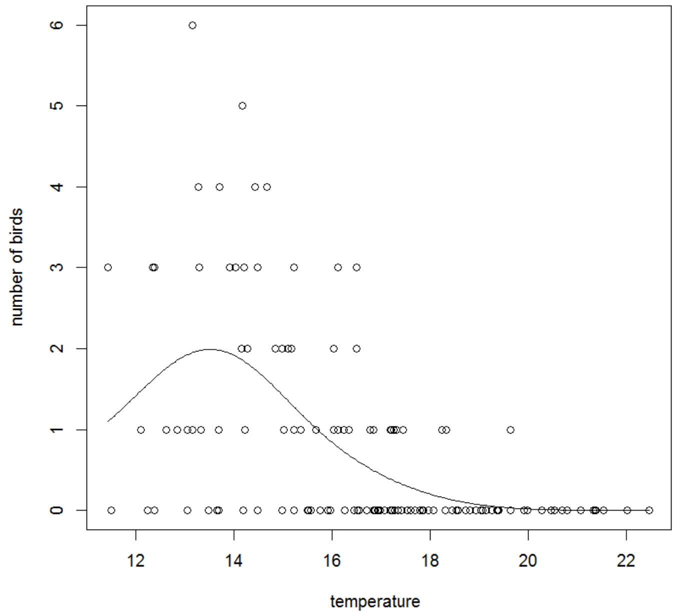
Figure S1. Elevation and 2010 forest cover of (a) Lore Lindu National Park and (b) the study area (within 10 km of sampling points). Cells are approximately 0.85 ha; forest cover data come from Miettinen *et al.* (2011). (c) Sampling effort by elevation within the study area (one sampling session; hatched bars).

(a)



number of birds
0
1
2
3
4
5
6
7
12
14
16
18
20
22
temperature

(b)



number of birds
0
1
2
3
4
5
6
12
14
16
18
20
22
temperature

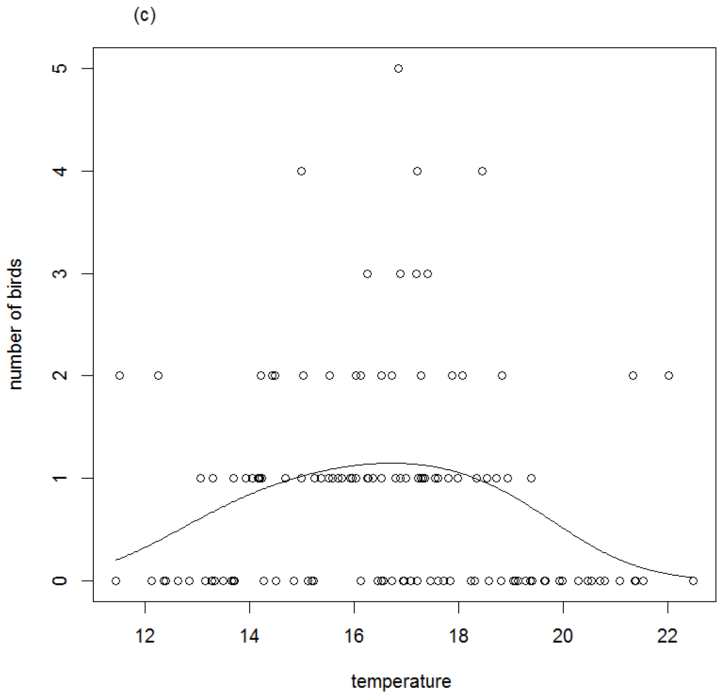
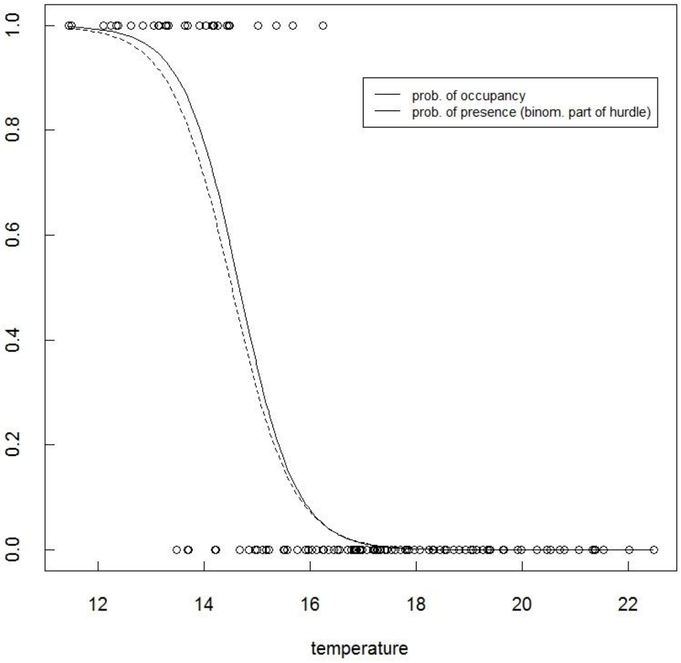
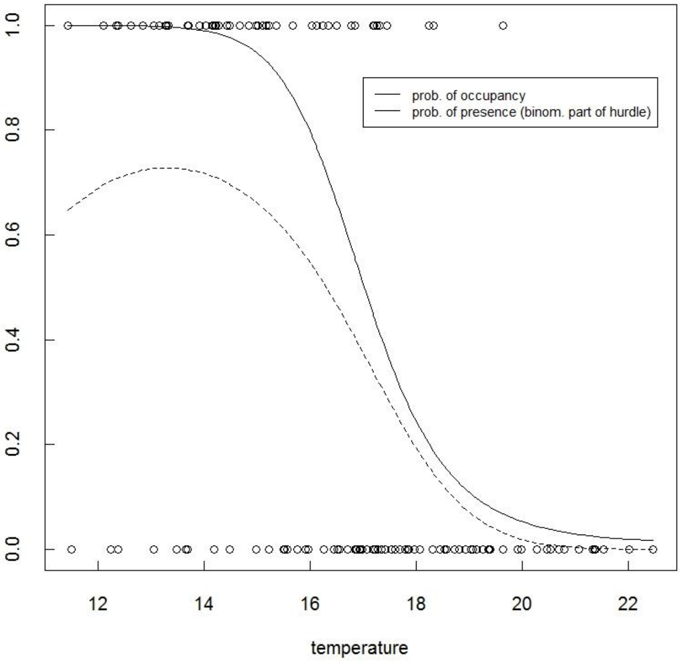


Fig. S2. Relationships between temperature and abundance from fitted hurdle models. (a) *Myza sarasinorum*, (b) *Phylloscopus sarasinorum*, (c) *Pachycephala sulfuriventer*. The linear parameterization of temperature was the best predictor of *Myza sarasinorum* abundance, while the second degree quadratic function of temperature was the best predictor for the other two species.

(a)


0.0
0.2
0.4
0.6
0.8
1.0
12
14
16
18
20
22
temperature
prob. of occupancy
prob. of presence (binom. part of hurdle)

(b)


0.0
0.2
0.4
0.6
0.8
1.0
12
14
16
18
20
22
temperature
prob. of occupancy
prob. of presence (binom. part of hurdle)

(c)

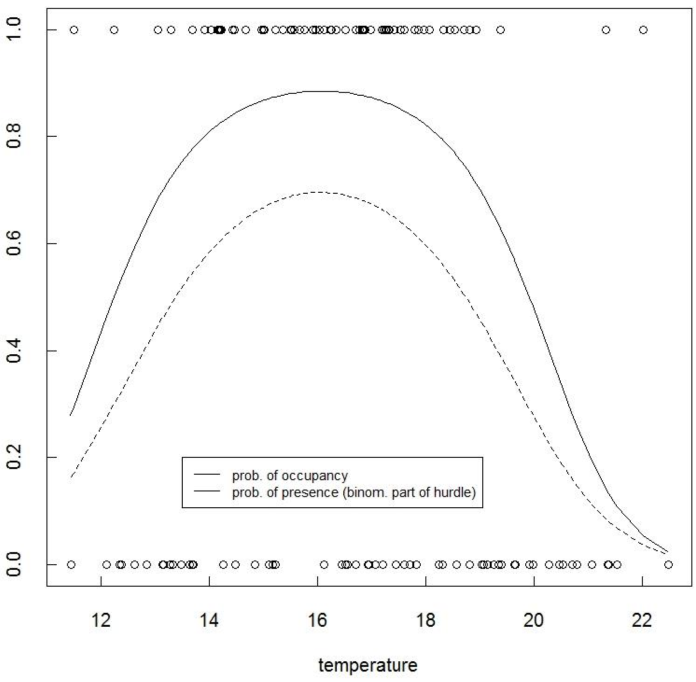
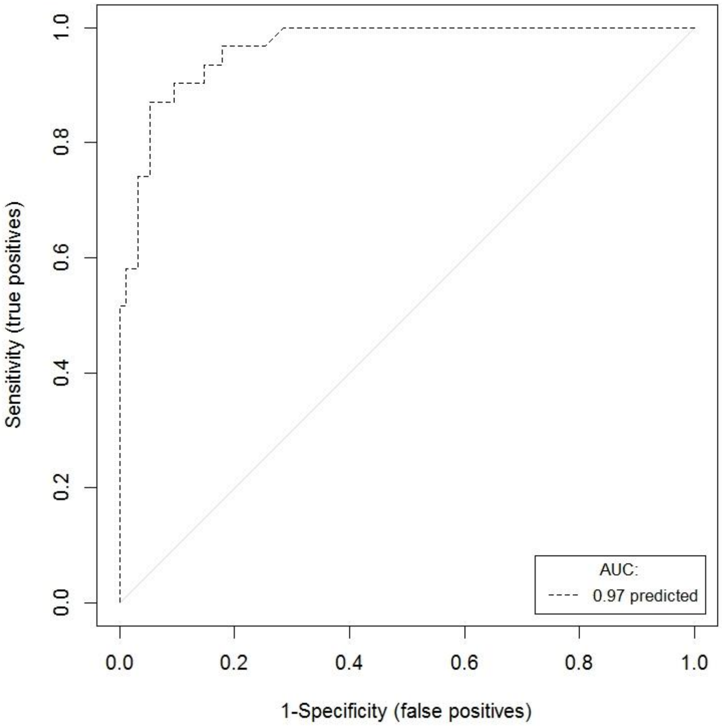


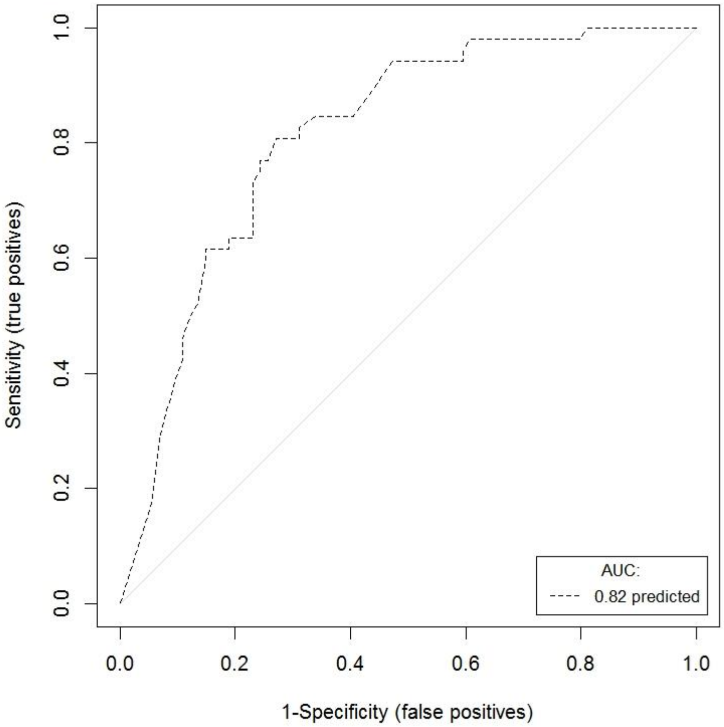
Figure S3. Plots comparing probability of occupancy (from occupancy models from three sampling sessions) to probability of presence from the binomial component of hurdle models. (a) *Myza sarasinorum*, (b) *Phylloscopus sarasinorum*, (c) *Pachycephala sulfuriventer*.

(a)



Sensitivity (true positives)
1-Specificity (false positives)
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.2
0.4
0.6
0.8
1.0
AUC:
0.97 predicted

(b)



Sensitivity (true positives)
1-Specificity (false positives)
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.2
0.4
0.6
0.8
1.0
AUC:
0.82 predicted

(c)

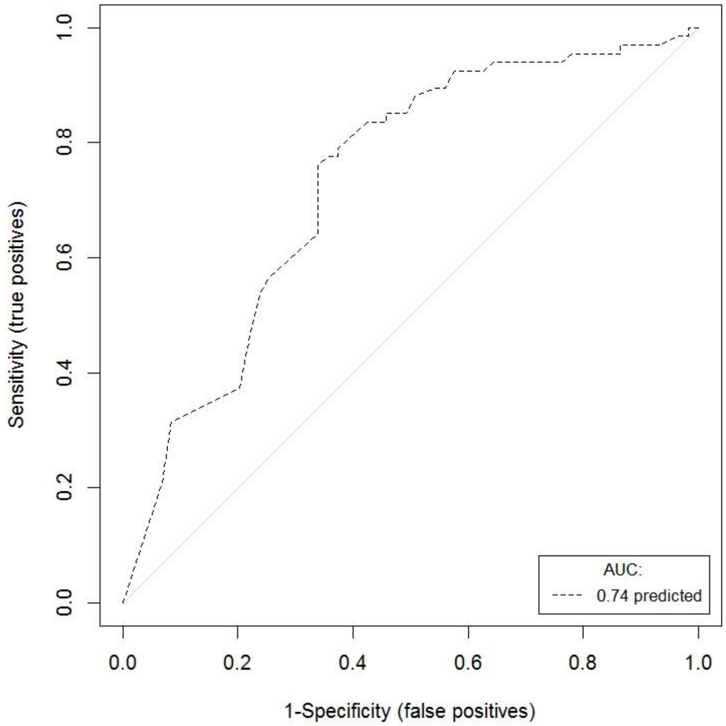


Figure S4. Plots of receiver operating characteristic curves showing predictive ability of the binomial part of hurdle models for (A) *Myza sarasinorum*, (B) *Phylloscopus sarasinorum*, (C) *Pachycephala sulfuriventer* at different discrimination thresholds. The gray line shows a random prediction where the model is unable to distinguish between occupied and unoccupied sites. The area under the receiver operating characteristic curve (AUC) is given.

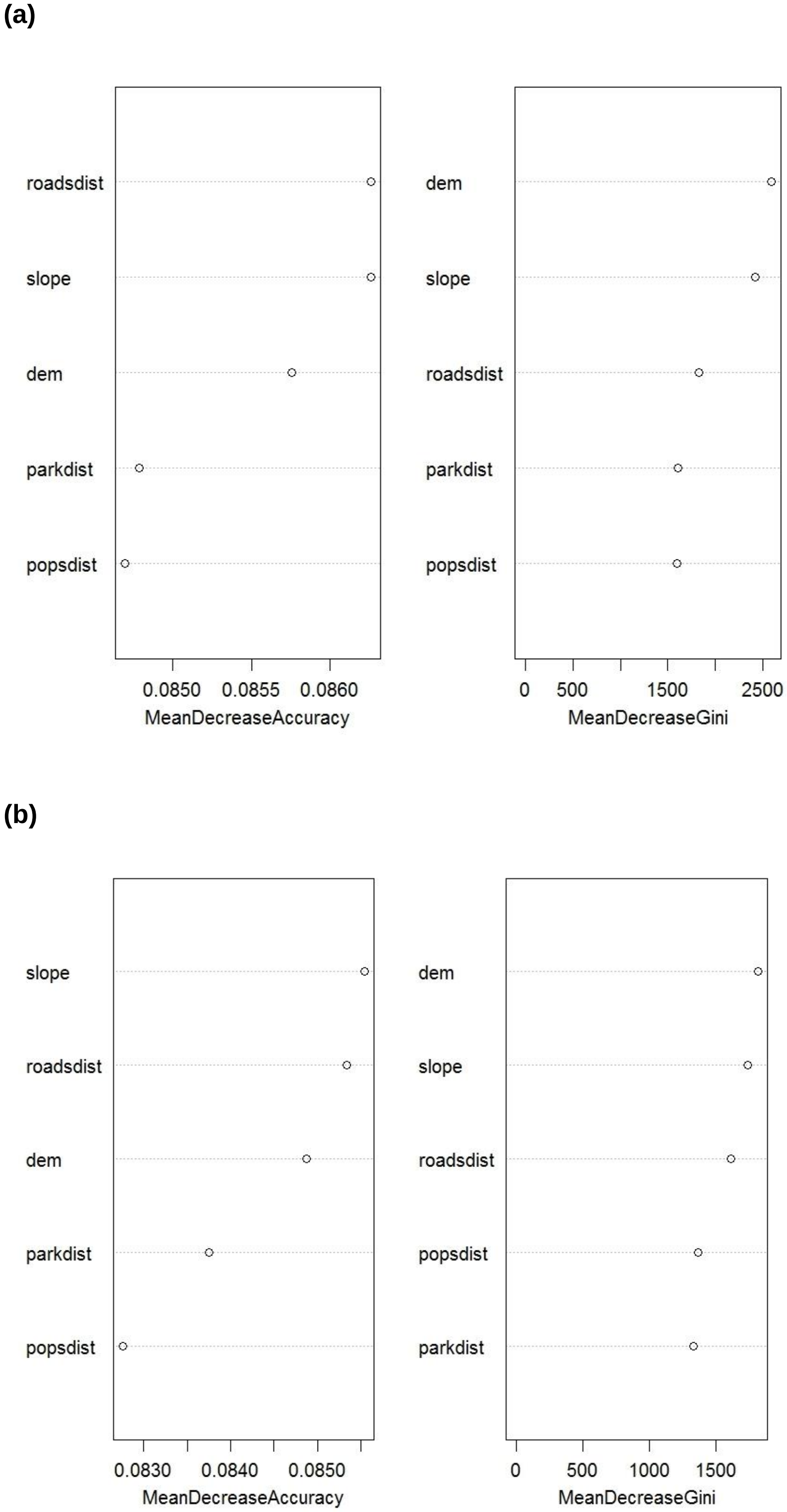


Figure S5. Variable importance plots from random forest models that predicted deforestation at (A) the current rate of deforestation and (B) half the current rate. The most important variables are displayed at the top of the plot. dem stands for elevation, roadsdist stands for distance from roads, popsdist stands for distance from villages, parkdist stands for distance from park boundary. Mean decrease accuracy measures how much the inclusion of a predictor in the model reduces classification error, while mean decrease Gini measures the role a predictor variable plays in partitioning the data into defined classes. See Liaw and Wiener (2002) for more details.

Supplementary Tables

Table S1. Projected reductions in the population size index (number of birds in the study area) and range area (hectares) by 2050 for the three study species under climate and land-use change scenarios.

		climate change		deforestation		climate change + deforestation			
Species	baseline (2010)	policy	reference	half rate	current rate	half + policy	half + reference	current + policy	current + reference
Population size (number of birds)									
Myza sarasinorum	13,917	6,917	5,437	13,757	13,641	6,855	5,391	6,813	5,360
Phylloscopus sarasinorum	38,486	26,637	23,517	36,732	35,751	25,654	22,704	25,080	22,222
Pachycephala sulfuriventer	71,179	65,392	63,168	61,846	57,728	58,011	56,394	54,657	53,280
Habitat area (hectares)									
Myza sarasinorum	17,648	11,071	9,420	17,306	17,067	10,960	9,334	10,850	9,256
Phylloscopus sarasinorum	60,558	54,118	51,660	53,076	49,846	48,330	46,699	45,795	44,426
Pachycephala sulfuriventer	72,026	69,539	68,573	59,816	54,476	58,585	58,050	53,845	53,532

Table S2. Land-cover classification errors in Miettinen *et al.*'s (2011) dataset at our 149 sampling points. There were 19 errors (87% accuracy).

Type of error	classified as forest; should have been non-forest	classified as non-forest; should have been forest	classified as agriculture; should have been regrowth	classified as regrowth; should have been agriculture
Number of point counts	7	9	1	2

References

Alström, P., Aymí, R., Clement, P., Dyrcz, A., Gargallo, G., Hawkins, A. F. A., Madge, S. C., Pearson, D. J. & Svensson, L. (2006) Family Silviidae (old world warblers). *Handbook of the birds of the world. Volume 11: old world flycatchers to old world warblers*. (ed. by J. del Hoyo, A. Elliot and D. A. Christie), pp. 492–712. Lynx Edicions, Barcelona, Spain.

BirdLife International (2013) *BirdLife International data zone*. Available at: http://www.birdlife.org/datazone.html (accessed 1 January 2013).

Boles, W. E. 2007. Family Pachycephalidae (whistlers). *Handbook of the birds of the world. Volume 12: picathartes to tits and chickadees*. (ed. by J. del Hoyo, A. Elliot and D. A. Christie), pp. 374–437. Lynx Edicions, Barcelona, Spain.

Bush, M. B., Silman, M. R. & Urrego, D. H. (2004) 48,000 years of climate and forest change in a biodiversity hot spot. *Science*, **303**, 827–829.

Clarke, L. E., Edmonds, J. A., Jacoby, H. D., Pitcher, H., Reilly, J. M. & Richels, R. (2007) *Scenarios of greenhouse gas emissions and atmospheric concentrations. A report by the climate change science program and the subcommittee on global change research.* Washington, DC.

Clough, Y., Faust, H. & Tscharntke, T. (2009) Cacao boom and bust: sustainability of agroforests and opportunities for biodiversity conservation. *Conservation Letters*, **2**, 197–205.

Coates, B. J. & Bishop, K. D. (1997) *A guide to the birds of Wallacea.* Alderly, QLD, Australia, Dove publications.

Crawley, M. J. (2007) *The R book.* Chichester, Wiley.

Eastman, J., Jin, W., Kyem, P. & Toledano, J. (1995) Raster procedures for multi-criteria/multi-objective decisions. *Photogrammetric Engineering and Remote Sensing*, **61**, 539–547.

Fordham, D. A., Wigley, T. M. L. & Brook, B. W. (2012) Multi-model climate projections for biodiversity risk assessments. *Ecological Applications*, **32**, 3317–3331.

Fordham, D. A., Wigley, T. M. L., Watts, M. J. & Brook, B. W. (2012) Strengthening forecasts of climate change impacts with multi-model ensemble averaged projections using MAGICC/SCENGEN 5.3. *Ecography*, **35**, 4–8.

Gaffen, D. J., Santer, B. D., Boyle, J. S., Christy, J. R., Graham, N. E. & Ross, R. J. (2000) Multidecadal changes in the vertical temperature structure of the tropical troposphere. *Science*, **287**, 1242.

Higgins, P. J., Christidis, L. and Ford, H. A. (2008) Family Melaphagidae (honeyeaters). *Handbook of the birds of the world. Volume 13: penduline-tits to shrikes.* (ed. by J. del Hoyo, A. Elliot and D. A. Christie), pp. 498–691. Lynx Edicions, Barcelona, Spain.

Hijmans, R. J. & van Etten, J. (2012) *raster: geographic analysis and modeling with raster data*. R package. Version 1.9–82. Available at: http://CRAN.R-project.org/package=raster.

Kitayama, K. (1992) An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio*, **102**, 149–171.

Liaw, A. & Wiener, M. (2002) Classification and regression by randomForest. *R News*, **2**, 18–22.

Miettinen, J., Shi, C. & Liew, S. C. (2011) Deforestation rates in insular Southeast Asia between 2000 and 2010. *Global Change Biology*, **17**, 2261–2270.

Miettinen, J., Shi, C., Tan, W. J., Chin, S. & Liew, S. C. (2012) 2010 land cover map of insular Southeast Asia in 250-m spatial resolution. *Remote Sensing Letters*, **3**, 11–20.

Musser, G. G. (1982) *Crunomys* and the small-bodied shrew rats native to the Philippine Islands and Sulawesi (Celebes). *Bulletin of the American Museum of Natural History*, **174**, 1–95.

Potts, J. M. & Elith, J. (2006) Comparing species abundance models. *Ecological Modelling*, **199**, 153–163.

Sarmiento, G. (1986) Ecologically crucial features of climate in high tropical mountains. *High altitude tropical biogeography*. (ed. by F. Vuilleumier and M. Monasterio), pp. 11–45. Oxford University Press, Oxford, UK.

Schwendenmann, L., Veldkamp, E., Moser, G., Hölscher, D., Köhler, M., Clough, Y., Anas, I., Djajakirana, G., Erasmi, S., Hertel, D., Leitner, D., Leuschner, C., Michalzik, B., Propastin, P., Tjoa, A., Tscharntke, T. & van Straaten, O. (2010) Effects of an experimental drought on the functioning of a cacao agroforestry system, Sulawesi, Indonesia. *Global Change Biology*, **16**, 1515–1530.

Smith, A. P. & Young, T. P. (1987) Tropical alpine plant ecology. *Annual Review of Ecology and Systematics*, **18**, 137–158.

Takada, T., Miyamoto, A. & Hasegawa, S. (2010) Derivation of a yearly transition probability matrix for land-use dynamics and its applications. *Landscape Ecology*, **25**, 561–572.

Weber, R., Faust, H., Schippers, B., Shohibuddin, M., Mamar, S., Sutarto, E. & Kreisel, W. (2007) Migration and ethnicity as cultural driving forces of land use change in the rainforest margin of Central Sulawesi, Indonesia. *The stability of tropical rainforest margins: linking ecological, economic and social constraints of land use and conservation.* (ed. by T. Tscharntke, C. Leuschner, E. Guhardja and M. Zeller), pp. 415–434. Springer Verlag, Berlin.

Whitten, T., Henderson, G. S. & Mustafa, M. (2002) *The ecology of Sulawesi. The ecology of Indonesia series, vol. 4.* Hong Kong, Periplus Editions.

Wigley, T. M. L., Clarke, L. E., Edmonds, J. A., Jacoby, H. D., Paltsev, S., Pitcher, H., Reilly, J. M., Richels, R., Sarofim, M. C. & Smith, S. J. (2009) Uncertainties in climate stabilization. *Climatic Change*, **97**, 85–121.