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Loss of forest intactness elevates global extinction risk in birds

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Abstract

Only around a third of the world's remaining forest cover survives in the form of Intact Forest Landscapes (IFL), and that proportion is declining. Loss of intactness could impact on biodiversity in many ways but the relationship between intactness and extinction risk has not been quantified. We created Extent of Suitable Habitat (ESH) maps for all the world's forest-dependent birds and intersected them with an independently derived IFL layer. We also estimate the proportion of the total global range-rarity of forest-dependent birds that is captured by IFL. The majority of forest-dependent bird species are now confined largely or entirely to be degraded, disturbed, or fragmented (non-IFL) forests. Furthermore, only 22.5% of global hotspots of range-rarity for forest-dependent birds are found within intact forests. We find a very strong positive relationship between the global extinction risk of forest-dependent birds and the proportion of forest within their ESH that is no longer intact. This effect was independent of overall range size and phylogeny. There was also a tendency for extinction risk to be higher in species that lost more intactness in their forest ESHs between 2000 and 2016. Restoring intactness to forest landscapes will reduce global extinction risk in forest-dependent birds.

Introduction

The world's pristine environments are being eroded at an unprecedented rate (Watson *et al.*, 2016). In the forest environment, this loss is reflected not only in conversion of forests to other land cover types but also to fragmentation and disturbance within remaining forest tracts. Loss of forest in intact landscapes has a higher impact on vertebrate biodiversity than equivalent losses in already degraded landscapes (Betts *et al.*, 2017), and fragmentation can have pervasive impacts on biota that extend well beyond the newly-created forest edges (Pfeifer *et al.*, 2017). Fragmentation can be scale dependent, and so is difficult to quantify. Intact Forest Landscapes (IFL) have been defined as unbroken expanses of natural ecosystems within the forest zone of at least 500 km^2 in area, a minimum width of 10 km (measured as the diameter of a circle that could be entirely inscribed within the boundaries of the territory), and a minimum corridor/appendage width of 2 km, and which have no remotely detected signs of human activity (Greenpeace International 2006, Potapov *et al.*, 2008, 2009, 2017). Only around a third of the world's remaining forests, and a fifth of the world's tropical forests, are considered to meet this definition of IFL (Potapov *et al.*, 2017), yet IFL are disproportionately important in terms of capturing important biodiversity, carbon sequestration and storage, water provision, indigenous culture and the maintenance of human health (Watson *et al.*, 2018).

The area of IFL is declining as forests become increasingly fragmented, disturbed and opened up by roads (Heino *et al.*, 2015; Kleinschroth *et al.*, 2017; Potapov *et al.*, 2017); between 2000 and 2013, 7.2% of global IFL was lost (Potapov *et al.*, 2017) and in parts of the world, such as the Congo Basin, this rate of loss is expected to accelerate (Zhuravleva *et al.*, 2013). This is likely to have a negative impact on species requiring undisturbed forest landscapes. However, the relationship between the loss of intactness and global extinction risk remains unquantified. We therefore assess whether the proportion forest that remains intact within the distributions of all the world's forest-dependent birds predicts their global extinction risk, as measured by their IUCN Red List categories, and whether loss of forest intactness since 2000 predicts their extinction risk. The null hypotheses being tested were therefore that the extinction risk of forest-dependent birds is independent of the intactness of the forest they occupy, and to the loss of this intactness. We also quantify the proportion of summed global range-rarity (an index of range restriction; see Materials and methods) of all forest-dependent birds that remains in intact forest landscapes, and identify areas where high range-rarity intersects areas of low forest intactness. This analysis thereby aims to improve our understanding of the vulnerability of forest-dependent birds to loss of forest intactness and to identify important areas for the restoration of intactness.

Materials and methods

Deriving ESH maps for forest-dependent birds

We define forest-dependent species as those whose listed habitat(s) as defined by the IUCN Habitat Classification Scheme (http://www.iucnredlist.org/technical-documents/classification-schemes/habitats-classification-scheme-ver3) include only those grouped under the level 1 classification 'Forest & Woodland'. This includes both tropical and temperate species. Extent of Suitable Habitat (ESH), also referred to as Extent of Potentially Suitable Habitat or Area of Habitat, refers to the parts of a species' broad range that contain potentially suitable ecological conditions, most frequently measured in terms of major land cover type and altitude (e.g. Beresford *et al.*, 2011; Rondinini *et al.*, 2011; IUCN 2016). We developed ESH maps for all the world's forest dependent birds by first rasterizing their breeding range polygons (from BirdLife International & Handbook of the Birds of the World 2017) to a 900-m resolution. We then created a map of the world's forest cover in 2000 by dissolving tree cover data from Hansen *et al.* (2003), and created an altitude layer from the Shuttle Radar Topography Mission (SRTM) (USGS 2005) to the same 900-m resolution. Finally, for each species' breeding range, we used Python scripts to exclude cells which were not classified as forest in 2000 or which fell outside the species' altitudinal limits (Fig. S1). The remaining maps therefore depict the extent of forest cover in 2000 at suitable altitudes within the breeding range of each forest-dependent species. Because we included only forest-dependent species, all ESHs comprised exclusively forest, but the proportion comprising IFL and non-IFL forest differed between species. For the very small number of species (n = 10) whose ESH was zero due to an error in the coding of their altitudinal limits, we substituted an ESH map based solely on forest cover. The ranges of a small number of extant species are not sufficiently known to map, and these were excluded.

Range-rarity map for forest-dependent birds

We created a global range-rarity layer for all forest-dependent birds following the methods of (Buchanan, Donald & Butchart, 2011). For each forest-dependent species, the number of cells within its forest ESH was summed and each cell was allocated a value equivalent to the reciprocal of the sum (1/n, where n is the number of cells in the species' ESH). The values across all species were then summed for each cell (Σ1/n) to derive a range-rarity score. Thus, species with a large ESH contributed a small value to each cell within their ESH, whereas species with a small ESH contributed larger values. The cell sums are therefore a product of the number of species whose ESH includes the cell and the number of other cells each species' ESH includes. In practice, the final score is determined largely by the latter metric; cells with high scores are those that contain species with small ESHs, and the scores therefore approximate to an index of range-restriction (Buchanan *et al.*, 2011). We intersected the range-rarity layer with the IFL layer to calculate the proportion of summed global range-rarity that falls within intact forests. Because range-rarity scores are very heavily skewed (Buchanan *et al.*, 2011), we also identified the 10% of cells with the highest values of range-rarity and assessed the proportion of these falling inside and outside intact forests.

Intersecting ESH maps with IFL layers

We intersected ESH maps of all birds with the IFL layers of Potapov *et al.* (2017), which provides estimates of global IFL cover in 2000, 2013 and 2016 (although we only used data from 2000 to 2016). These are derived from the same high-resolution satellite imagery of forest cover that we used to create our ESH maps, so the two layers were spatially aligned. For each species we calculated the proportion of ESH cells for each species that were classified as (1) non-intact forest in 2000, (2) intact forest in 2000 but whose intactness had been lost by 2016 and (3) intact forest in both 2000 and 2016. Since ESH was already constrained to include only cells forested in 2000, the sum of these three classes of cell equaled the total number of cells in each species' ESH.

Modelling IFL and extinction risk of forest-dependent birds

We assessed the relationship between the proportion of a forest-dependent species' ESH that falls within IFL and its global IUCN Red List category of extinction risk by modelling Red List category as an ordered 5-level factor (ranked in the order Least Concern < Near Threatened < Vulnerable < Endangered < Critically Endangered). We did this using ordinal logistic regression in the form of cumulative link mixed models, fitted with the 'clmm' function in the R package 'ordinal' (Christensen, 2018). These models quantify the probability of a species' Red List category falling into higher classes of extinction risk with increasing or decreasing values of the fitted covariates. The proportion of the ESH falling within IFL in 2000 was fitted as a covariate to assess whether more threatened species had a smaller proportion of their ranges within IFL than less threatened species). Because this might not be independent of species' range sizes (randomly distributed small ranges might be expected under some assumptions to be less likely to intersect with IFL than randomly-distributed large ranges), and because range size itself is unlikely to be independent of Red List status, we also fitted the breeding range size (log-transformed) of the species as another covariate. As Red List category and responses to loss of forest intactness may not be phylogenetically independent, we assessed three competing models; a model with the two covariates only, a model with the two covariates and taxonomic order as a random effect, and a model with the two covariates and family nested within order as a random effect. Taxonomy followed Handbook of the Birds of the World and BirdLife International

(2017), which is the taxonomy that underpins the IUCN Red List for birds. The three starting models were therefore:

1) Red List category = ESH/IFL + log(range size)
2) Red List category = ESH/IFL + log(range size) + (order)
3) Red List category = ESH/IFL + log(range size) + (order/family)

where 'ESH/IFL' is the proportion of the species' ESH that falls within IFL, '(order)' is a random effect of taxonomic order, and '(order/family)' is the random effect of family nested within order.

These three models were compared using the 'ANOVA' command in R (R Core Team, 2016). Once the best-supported combination of random effects was identified, the relative contribution of each of the two covariates was assessed by fitting models with both covariates and with each covariate individually, and comparing their ΔAICc scores and model weights (Burnham & Anderson, 2002).

To assess the relationship between extinction risk and loss of IFL between 2000 and 2016, we ran a further set of models that was limited to the subset of species that had non-zero sums of IFL within their ESH in the year 2000, since loss could not be estimated for species that already had zero IFL cover in the first year. The same modelling rationale was applied to this reduced set of species, including tests to find the most appropriate random effects structure, with the difference that proportional loss of IFL between 2000 and 2016 was fitted as a third covariate.

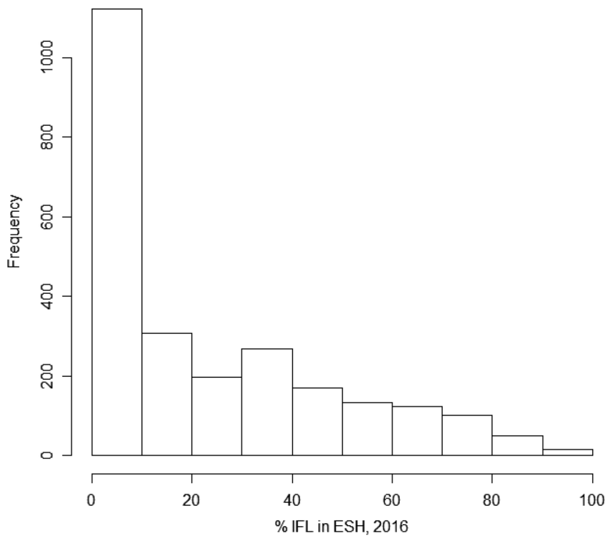

Figure 1 Histogram of percentage of forest extent of suitable habitat (ESH) that comprised intact forest (IFL) in the distributions of 2488 forest-dependent bird species in 2016.

Results

In total, 2488 extant species for which range maps were available were coded only to forest habitat classes and hence were classed as being forest-dependent (a list of the species included in the analyses is available from the authors on request). This represents around 22.5% of all the world's extant bird species.

Intact forest landscape (IFL) within species' extents of suitable habitat (ESH)

IFL formed only a small proportion of the ESH of most forest-dependent birds. The average percentage of IFL within the ESH of forest-dependent species was 25.8% in 2000, falling to 23.1% in 2016, but the distribution was heavily skewed, with only 17% of species in 2016 having over 50% of their ESH in IFL (Fig. 1). There were significant differences between species assemblages in different biogeographic realms in the extent to which their forest ESH contained IFL, and the extent to which IFL was lost from their ESH between 2000 and 2016; species in Australasia and the Neotropics had a higher proportion of their ESH captured by IFL than those in other realms, and those in the Nearctic and Palearctic lost the highest proportion of IFL from their ESH between 2000 and 2016 (Fig. 2).

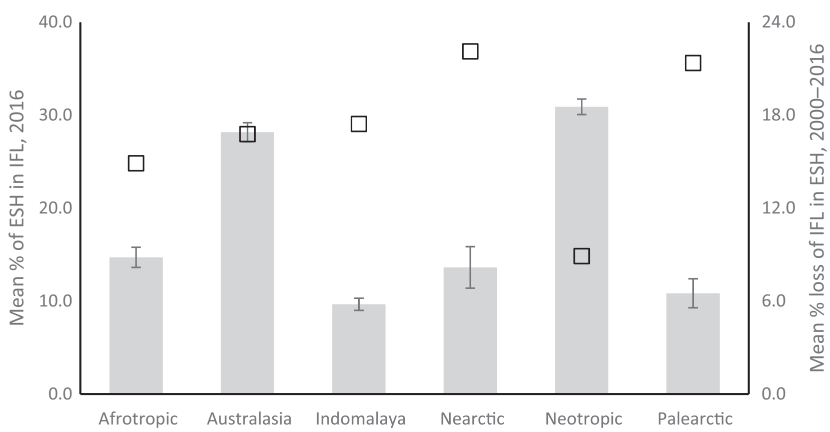

Figure 2 Mean percentage of ESH made up by intact forest (IFL) in the distributions of 2488 forest-dependent bird species in 2016, by biogeographic realm. The squares shows the mean percentage loss of IFL from species' ESH between 2000 and 2016 for the subset of species (n = 1968) that had some IFL in their ESH in 2000.

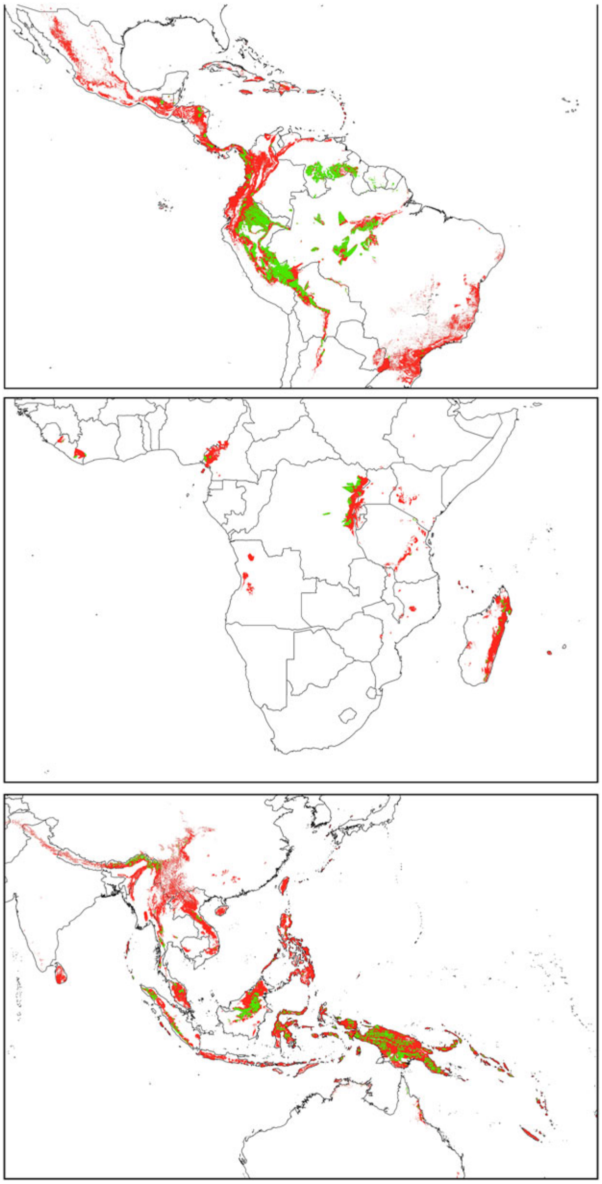

Figure 3 Distribution of the highest 10% of cells of global range-rarity for forest-dependent birds, which between them capture 76% of total global range-rarity, shaded according to whether they intersect intact forest landscapes (green) or whether they occur in fragmented, disturbed or degraded forests (red). Although the analysis covered all the world's forest, both temperate and tropical, only the tropical regions shown in the figure contained areas of high range-rarity.

Intact Forest Landscapes and range-rarity of forest-dependent birds

In 2016, 76.3% of the total global sum of range rarity of forest-dependent birds, and 77.5% of the 10% of cells with the highest values of range-rarity, fell in fragmented, disturbed or degraded (non-IFL) forests. Extensive areas of high (top 10% of cells) range-rarity falling outside IFL included the northern Andes and the Atlantic Forest in South America, the montane forests of Mesoamerica, the Cameroonian Highland forests, Albertine Rift and Eastern Arc of Africa, Madagascar's eastern forests, Sri Lanka's forests, and much of the remaining forest in south-east Asia, Sundaland, Wallacea and New Guinea (Fig. 3).

Intact forest landscapes and extinction risk in forest-dependent birds

As extinction risk increased there was a clear decline in the mean proportion of forest within the ESH of forest-dependent birds that remains intact, and an increase in the percentage of species whose ESH comprised entirely non-intact forest in 2016 (Fig. 4). This pattern was confirmed by the results of cumulative link mixed models. Of the three starting models (no random effects, Order as a random effect, or Family nested within Order as a random effect), the best supported was that with Family nested within Order as a random effect (ANOVA, $P < 0.0001$), reflecting the known non-random distribution of extinction risk across taxonomic groups. Subsequent removal of each covariate from this model indicated that by far the best supported model was that containing both range size and the proportion of the forest ESH comprising intact forest, each of which therefore had independent explanatory power (Table 1a). The coefficients for both covariates were negative, indicating that the probability of a species being listed in a higher class of extinction risk increased with smaller global range size and with a smaller proportion of intact forest remaining within their forest ESH.

In models fitted to only the sample of forest-dependent species that had at least some IFL in their ESHs in 2000 ($n = 1968$), to which loss of IFL between 2000 and 2016 was fitted as a third covariate, the best-supported combination of random effects was again that of Family nested within Order. The highest-ranking model was that containing all three covariates, the directions of the coefficients indicating that high extinction risk was associated with small range size, with low intersection with IFL and with higher rates of IFL loss between 2000 and 2016. However, a model without the covariate relating to loss of IFL also received some support but with half the model weight (ΔAICc = 1.04; Table 1b).

Discussion

We show that the majority of the world's forest-dependent birds, and most hotspots of global range-rarity, now occupy fragmented, disturbed or degraded (non-intact) forests. Our results therefore support those of a recent analysis that concluded that protecting only undisturbed parts of the world is likely to be insufficient to conserve global biodiversity (Pimm, Jenkins & Li, 2018). Furthermore, we found a clear relationship between the global extinction risk of forest-dependent birds and the degree to which their forest habitats have been fragmented or disturbed and are therefore no longer in an intact state. This effect is independent of species' range size and of the known phylogenetic non-independence of extinction risk. We also found a weaker effect of

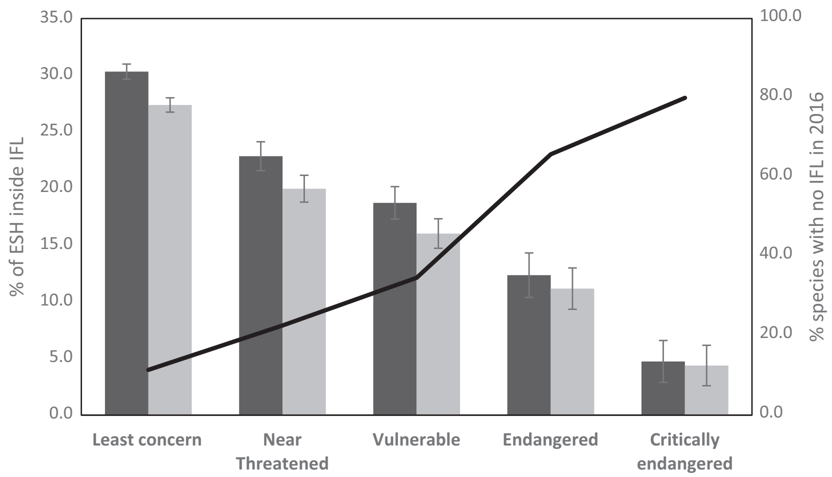

Figure 4 Bars show the mean percentage of ESH of forest-dependent bird species, broken down by increasing global IUCN Red List category of extinction risk, that comprises intact forest landscapes (IFL) by increasing IUCN Red List category (± 1 se). In each case, the dark grey bars show the value in 2000, the pale grey bars show the value in 2016. The line shows the percentage of species in each Red List category that had no IFL within their forest ESH in 2016.

Table 1 Results of cumulative link mixed models of Red List extinction risk category

a. All species (n = 2488)

% IFL in 2000	Range	df	AICc	ΔAICc	weight
−0.01589	−0.6026	6	4397.7	0.00	1
	−0.6206	5	4459.2	61.49	0
−0.02359		5	5260.5	862.73	0

b. Species with >0% IFL in 2000 (n = 1968)

% IFL in 2000	Range	IFL loss	df	AICc	ΔAICc	weight
−0.012960	−0.5560	0.6537	7	3023.2	0.00	0.63
−0.013470	−0.5565		6	3024.3	1.04	0.37
	−0.5279	0.9222	6	3049.6	26.35	0
	−0.5282		5	3053.6	30.36	0
−0.007446		0.6494	6	3413.2	390.01	0
−0.008163			5	3414.3	391.09	0
		0.8871	5	3422.4	399.21	0

(a) competing models of extinction risk for all forest-dependent birds, with the percentage of their ESH that was inside IFL in 2000 and their overall range size fitted as covariates, in combination or singly. (b) competing models of extinction risk for forest-dependent birds that had at least some of their ESH inside IFL in 2000, with the percentage of their ESH that was inside IFL in 2000, their overall range size and percentage loss of IFL between 2000 and 2016 fitted as covariates, in combination or singly. In each case models are ranked by ascending AICc. All models included taxonomic Family nested within Order as a random effect.

the loss of intactness between 2000 and 2016 as a further predictor of global extinction risk in forest-dependent birds. Taken together, these results suggest that loss of forest intactness is a strong predictor of extinction risk in forest-dependent birds. They therefore add further weight to recent assessments of the very high conservation value of the world's remaining intact forests and the severe environmental impacts of their loss (Watson *et al.*, 2016, 2018).

It is possible that the relationship between global extinction risk and loss of intactness is underestimated, since species existing largely or wholly in fragmented or disturbed forests are likely to undergo further deterioration in their conservation status through the process of 'extinction debt', the time lag between fragmentation and eventual extinction (e.g. Tilman *et al.*, 1994; Kuussaari *et al.*, 2009; Hylander & Ehrlén, 2013). Furthermore, loss of intactness is also often associated with other threats, such as hunting. This process makes it likely that the conservation status of species confined entirely to fragmented or disturbed forests will continue to decline, while that of species that still have large expanses of intact forest within their ranges will decline more slowly or remain unchanged. Our equivocal finding of an additional effect of IFL loss since 2000 in determining species' extinction risk further suggests that the conservation status of forest-dependent birds will continue to decline.

The strong relationship between a species' global Red List status and the proportion of its remaining forest that is in an intact state suggests that attempts to predict changes in species' extinction risk on the basis of past or predicted deforestation (e.g. Buchanan *et al.*, 2008; Bird *et al.*, 2012; Tracewski *et al.*, 2016) could be greatly improved by integrating measures of forest intactness and changes in intactness. Furthermore, the conservation status of other, less well known, forest taxa might usefully be informed by their spatial coincidence, or otherwise, with intact forest landscapes.

The restoration of intactness is likely to reduce the extinction risk of forest-dependent species. However, there is little recognition of the importance of intactness in many major policy instruments. The International Standards of the Forest Stewardship Council (FSC) recognize intact forest landscapes as having High Conservation Value. Aichi Target 5 in the

Strategic Plan on Biodiversity (https://www.cbd.int/decision/cop/?id=12268) commits parties to at least halve the rate of loss of all natural habitats by 2020, and to significantly reduce degradation and fragmentation, but does not set explicit targets for the conservation of intact forest landscapes. Furthermore, there is no explicit recognition of the importance of forest intactness in mechanisms such as reducing emissions from deforestation and forest degradation in developing countries (REDD+), or in Performance Standard 6 of the International Finance Corporation (IFC; https://www.ifc.org/wps/wcm/connect/topics_ext_content/ifc_external_corporate_site/sustainability-at-ifc/policies-standards/performance-standards/ps6). Our results lend further weight to previous claims that the conservation of intactness in forest ecosystems is likely to be an efficient and cost-effective way to conserve biodiversity, maintain ecological integrity and bring a wide range of other environmental and societal benefits, and should therefore be an important component of global conservation strategy (Watson *et al.*, 2018). Conserving intact landscapes is likely to require holistic broad-scale policy responses, including the integration of local stakeholders and governments in the design of land management strategies as well as the creation of large protected areas (Peres, 2005; Haurez *et al.*, 2017; Chazdon, 2018).

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Illustration of how range maps were converted to ESH, first by removing all areas that were not forest in 2000, second by removing all areas outside the species' altitudinal limits.