

A Matrix-Calibrated Species-Area Model for Predicting Biodiversity Losses Due to Land-Use Change

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Abstract: Application of island biogeography theory to prediction of species extinctions resulting from habitat loss is based on the assumption that the transformed landscape matrix is completely inhospitable to the taxa considered, despite evidence demonstrating the nontrivial influence of matrix on populations within habitat remnants. The island biogeography paradigm therefore needs refining to account for specific responses of taxa to the area of habitat “islands” and to the quality of the surrounding matrix. We incorporated matrix effects into island theory by partitioning the slope (z value) of species–area relationships into two components: γ , a constant, and σ , a measure of taxon-specific responses to each component of a heterogeneous matrix. We used our matrix-calibrated model to predict extinction and endangerment of bird species resulting from land-use change in 20 biodiversity hotspots and compared these predictions with observed numbers of extinct and threatened bird species. We repeated this analysis with the conventional species–area model and the countryside species–area model, considering alternative z values of 0.35 (island) or 0.22 (continental). We evaluated the relative strength of support for each of the five candidate models with Akaike’s information criterion (AIC). The matrix-calibrated model had the highest AIC weight ($w_i = 89.21\%$), which means the weight of evidence in support of this model was the optimal model given the set of candidate models and the data. In addition to being a valuable heuristic tool for assessing extinction risk, our matrix-calibrated model also allows quantitative assessment of biodiversity benefits (and trade-offs) of land-management options in human-dominated landscapes. Given that processes of secondary regeneration have become more widespread across tropical regions and are predicted to increase, our matrix-calibrated model will be increasingly appropriate for practical conservation in tropical landscapes.

Keywords: agriculture, biodiversity crisis, countryside biogeography, equilibrium theory, forest regeneration, power model, reconciliation ecology, secondary succession

Un Modelo Especies-Área Calibrado para la Matriz para Predecir las Pérdidas de Biodiversidad Debido a Cambios en el Uso de Suelo

Resumen. La aplicación de la teoría de biogeografía de islas a la predicción de extinciones de especies como resultado de la pérdida de hábitat se basa en el supuesto de que la matriz de paisaje transformado es inhóspito para los taxa considerados, no obstante la evidencia que demuestra la influencia no trivial de la matriz sobre las poblaciones en los remanentes de hábitat. Por lo tanto, el paradigma de la biogeografía de islas requiere refinación para explicar las respuestas específicas de los taxa al área de las “islas” de hábitat y a la calidad de la matriz circundante. Incorporamos los efectos de la matriz en la teoría de islas dividiendo la pendiente (valor z) de las relaciones especies-área en dos componentes: γ , una constante, y σ , una medida de las respuestas específicas del taxón a cada componente de una matriz heterogénea. Utilizamos nuestro modelo

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Paper submitted May 22, 2009; revised manuscript accepted October 27, 2009.

calibrado para la matriz para predecir la extinción y estatus de riesgo de especies de aves como resultado del cambio en el uso de suelo en 20 sitios de importancia para la biodiversidad y comparamos estas predicciones con el número observado de especies de aves extintas y amenazadas. Repetimos este análisis con el modelo especies-área convencional y el modelo especies-área rural, considerando valores alternativos de z de 0.35 (isla) o 0.22 (continental). Evaluamos la solidez relativa del soporte de cada uno de los cinco modelos con el criterio de información Akaike (AIC). El modelo calibrado para la matriz tuvo el mayor AIC ($w_i = 89.21\%$), lo que significa que el peso de la evidencia que soporta este modelo fue el modelo óptimo dado el conjunto de modelos candidatos y los datos. Además de ser una herramienta heurística valiosa para evaluar el riesgo de extinción, nuestro modelo calibrado para la matriz también permite una evaluación cuantitativa de los beneficios para la biodiversidad de las opciones de manejo de suelo en paisajes dominados por la actividad humana. Debido que los procesos de regeneración secundaria se han extendido en las regiones tropicales y que se espera que incrementen, nuestro modelo calibrado para la matriz cada vez será más apropiado para la conservación en paisajes tropicales.

Palabras Clave: agricultura, biogeografía rural, crisis de biodiversidad, ecología de reconciliación, modelo de poder, regeneración de bosques, sucesión secundaria, teoría del equilibrio

Introduction

Globally, habitat loss, fragmentation, and degradation continue to threaten the long-term persistence of terrestrial ecosystems and biodiversity (Sodhi et al. 2004; Bradshaw et al. 2009), undermine ecosystem services and human well-being (Diaz et al. 2006; Dobson et al. 2006), and exacerbate dangerous climate change (Houghton 2005; Gullison et al. 2007). The most direct and visible consequence of habitat perturbation arguably is the extinction of populations and species. Thus, current research is focused on understanding the patterns and processes of species extinction to predict future biodiversity scenarios and guide conservation actions (Brook et al. 2008). Island biogeography theory (MacArthur & Wilson 1967) and metapopulation dynamics (Hanski 1998) are key theoretical frameworks underpinning most ecological and conservation studies on species extinction (Ricketts 2001). In particular, the power model (Arrhenius 1920)—one of several alternative models used to describe species-area relationships (Tjørve 2003; Dengler 2009)—has been applied widely to predict biodiversity losses resulting from deforestation in terrestrial systems (e.g., Brooks et al. 1997; Brooks et al. 2002; Brook et al. 2003). The power model is expressed as

$$S = c \cdot A^z, \quad (1)$$

where S and A are the number of species and area of habitat, respectively; c is a constant that depends on the taxon and region; and z , another constant, indicates the rate of change in the number of species per unit area (Rosenzweig 1995). When a habitat shrinks from an original size (A_{org}) to a current size (A_{new}), one can derive from Eq. 1 the expected number of species (S_{new}) as a proportion of the original number of species (S_{org}):

$$\frac{S_{\text{new}}}{S_{\text{org}}} = \left(\frac{A_{\text{new}}}{A_{\text{org}}} \right)^z. \quad (2)$$

Some researchers question the relevance of applying island theory to real-world situations, particularly for understanding the effects of deforestation and habitat fragmentation (e.g., Simberloff & Abele 1976; Gilbert 1980; Laurance 2008). Confounding factors that could limit applicability of island theory include nonrandom habitat conversion, edge effects, community-level changes, interspecies interactions, and differential responses of species to the matrix (Laurance 2008). Matrix effects, notably, have received increasing research attention. Empirical studies demonstrate that land-use change typically results in a matrix that comprises a mosaic of habitat types with variable degrees of suitability and permeability for different taxa (e.g., Ricketts 2001; Revilla et al. 2004; Umetsu et al. 2008).

Although most researchers acknowledge the importance of the matrix (Ricketts 2001), the species-area approach of assessing extinction risk is still based on a binary landscape of either habitat (e.g., an old-growth forest remnant) or nonhabitat (e.g., farmland). Recently two conceptually similar methods have been proposed to reconcile the island biogeography paradigm with the heterogeneous nature of the landscape matrix. They are both based on building and combining species-area models for subgroups of taxa that presumably respond differently to different landscape components (Tjørve 2002; Pereira & Daily 2006). These methods advance understanding of how taxa might respond to the matrix. But they still rely on an arbitrary definition of the slope (z value) of species-area relationships, and slope has a strong influence on extinction predictions (Rosenzweig 1995; Laurance 2008). Of course, the fact that a model is sensitive to z values does not lessen the utility of the model for predicting species' extinctions as long as the model's z value is appropriately calibrated for every system considered.

We propose an alternative approach to incorporate matrix effects into island theory by calibrating the z value of the power model (Eq. 1) on the basis of taxon-specific responses to each component of a heterogeneous

landscape. The rationale behind our approach is as follows: between two alternative landscape matrices that differ in terms of suitability and permeability to a taxon, the more hospitable matrix (e.g., diverse agroforestry) alleviates extinction pressure from habitat loss and lowers the slope of species–area relationships more than the more hostile matrix (e.g., intensive monoculture plantations). This hypothesis is supported by two recent empirical observations. Cook et al. (2002) experimentally investigated the effects of patch size and isolation on plant species richness in 106 habitat patches ranging in size from 32 m² to 5000 m². They reported that patch size and isolation significantly affected species richness of only those species that could not survive in the matrix; species that thrived in the matrix were unaffected by these island effects. In a meta-analysis, Watling and Donnelly (2006) investigated whether *z* values consistently differed across matrix types and taxa in 148 studies sampled from the primary literature. They concluded that for all taxonomic groups considered (i.e., invertebrates, amphibians, reptiles, birds, nonvolant mammals, and bats), *z* values were significantly lower in the least hostile matrix, agriculture, compared with the other matrix types of desert, urban area, and water.

Matrix-Calibrated Model

We propose that the *z* value of the power model (and more generally, the slope of species–area relationships) can be partitioned into two components: γ , a constant, and σ , a measure of the sensitivity of the taxon to the transformed habitat (quantified as the proportional decrease in the number of species [$0 < \sigma < 1$]):

$$z = \gamma \cdot \sigma. \tag{3}$$

Substituting Eq. 3 into Eq. 2 yields

$$\frac{S_{\text{new}}}{S_{\text{org}}} = \left(\frac{A_{\text{new}}}{A_{\text{org}}} \right)^{\gamma \cdot \sigma}. \tag{4}$$

Equation 4 implies that the expected level of species extinction and endangerment depends on the extent of habitat loss and on the sensitivity of the taxon to the matrix (Fig. 1). In an extreme scenario, where rising sea levels drive the formation of land-bridge islands, the ocean becomes the matrix, which presumably represents a completely inhospitable habitat for the taxon ($\sigma = 1$). In this case, Eq. 4 reduces to the classical island biogeography model (Eq. 2):

$$\frac{S_{\text{new}}}{S_{\text{org}}} = \left(\frac{A_{\text{new}}}{A_{\text{org}}} \right)^{\gamma}.$$

From this scenario (ocean as matrix), one can infer that γ is equivalent to the observed *z* value of the taxon in true island archipelagos. In an alternative scenario, where

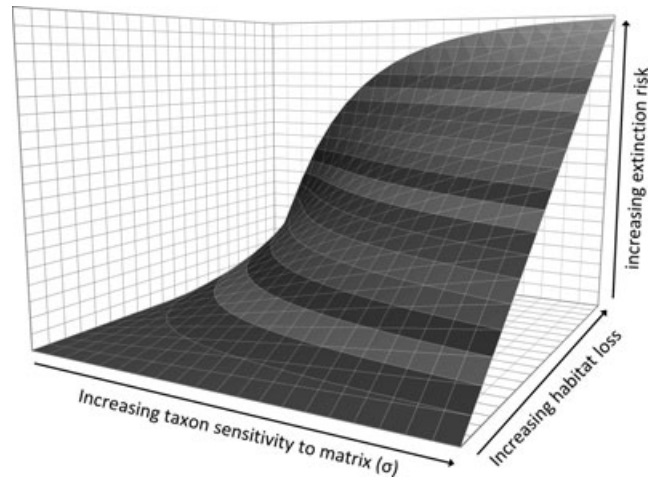


Figure 1. The matrix-calibrated model (Eq. 6), illustrating the functional relationships between species extinction risk ($1 - \frac{S_{\text{new}}}{S_{\text{org}}}$), extent of habitat loss ($1 - \frac{A_{\text{new}}}{A_{\text{org}}}$), and sensitivity of taxon to the matrix (σ) (S_{org} , original number of species; S_{new} , expected number of species; A_{org} , original habitat size; A_{new} , current habitat size; $\gamma = 1$ for this illustrative purpose).

land-use change results in no (or negligible) change in habitat quality for the taxon ($\sigma = 0$) (e.g., when part of an intact forest is managed for the harvesting of nontimber forest products), Eq. 4 reduces to

$$\frac{S_{\text{new}}}{S_{\text{org}}} = \left(\frac{A_{\text{new}}}{A_{\text{org}}} \right)^0 = 1,$$

which implies that even though $A_{\text{new}} < A_{\text{org}}$, this form of land-use change results in no expected change in the number of species (i.e., no change in extinction risk). Nevertheless, if the managed forest declines in habitat quality over time, for example, owing to the encroachment of agriculture or other development pressures, taxon sensitivity (σ) to this habitat would increase, leading to biodiversity losses.

In most real-world situations, land-use change results in a mosaic of several habitat types of varying quality for the taxon. To account for this, one can incorporate an area-weighted average of the taxon’s response to each component of this heterogeneous transformed landscape into the exponent described by Eq. 3 which becomes:

$$z = \gamma \cdot \sum_i^n p_i \sigma_i, \tag{5}$$

where *p* is the proportional area of the *i*th habitat type relative to the total converted land area (matrix), and *n* represents the total number of habitat types. Substituting Eq. 5 into Eq. 2 yields our calibrated species–area model

Table 1. Observed and predicted percentage of extinct and threatened endemic bird species in 20 biodiversity hotspots.^a

Biodiversity hotspot	Observed ^b	Predicted bird extinction and endangerment (% total known endemic species) ^c				matrix-calibrated
		conventional _{continental-z}	conventional _{island-z}	countryside _{continental-z}	countryside _{island-z}	
Atlantic Forest	38.5	42.5 (+)	58.5 (+)	14.4 (-)	21.6 (-)	36.9 (-)
Caribbean Islands	29.0	39.7 (+)	55.3 (+)	11.6 (-)	17.6 (-)	30.7 (+)
Cerrado	58.8	28.6 (-)	41.5 (-)	12.0 (-)	18.3 (-)	25.3 (-)
Coastal Forests of Eastern Africa	18.2	39.7 (+)	55.3 (+)	10.4 (-)	15.8 (-)	28.5 (+)
Eastern Afromontane	33.0	39.1 (+)	54.6 (+)	10.7 (-)	16.3 (-)	28.7 (-)
East Melanesian Islands	22.1	23.3 (+)	34.4 (+)	10.9 (-)	16.6 (-)	21.1 (-)
Guinean Forests of West Africa	41.3	34.1 (-)	48.5 (+)	10.7 (-)	16.3 (-)	26.1 (-)
Horn of Africa	37.5	48.3 (+)	65.0 (+)	8.0 (-)	12.3 (-)	27.3 (-)
Indo-Burma	28.1	48.3 (+)	65.0 (+)	12.8 (-)	19.3 (-)	38.4 (+)
Madagascar & Indian Ocean Islands	31.5	39.7 (+)	55.3 (+)	7.3 (-)	11.3 (-)	21.6 (-)
Madrean Pine-Oak Woodlands	31.8	29.8 (-)	43.1 (+)	6.5 (-)	10.0 (-)	16.1 (-)
Mesoamerica	15.4	29.8 (+)	43.1 (+)	8.2 (-)	12.6 (-)	19.7 (+)
New Caledonia	30.4	25.0 (-)	36.8 (+)	9.4 (-)	14.5 (-)	19.9 (-)
Philippines	30.1	44.3 (+)	60.6 (+)	16.0 (-)	23.9 (-)	40.2 (+)
Polynesia-Micronesia	56.4	28.9 (-)	41.9 (-)	16.5 (-)	24.5 (-)	30.3 (-)
Sundaland	30.3	44.8 (+)	61.2 (+)	11.9 (-)	18.1 (-)	34.5 (+)
Tropical Andes	19.0	26.3 (+)	38.4 (+)	6.1 (-)	9.4 (-)	14.1 (-)
Tumbes-Chocó-Magdalena	19.1	26.9 (+)	39.3 (+)	8.0 (-)	12.2 (-)	18.1 (-)
Wallacea	18.7	34.1 (+)	48.5 (+)	13.4 (-)	20.2 (+)	30.1 (+)
Western Ghats and Sri Lanka	28.6	27.6 (-)	40.2 (+)	9.4 (-)	14.5 (-)	21.0 (-)

^a Extinct and threatened species are those classified as vulnerable, endangered, critically endangered, or extinct (IUCN 2008).

^b Observed percentage of extinct and threatened species in each biodiversity hotspot is based on latest estimates by IUCN (2008) and Conservation International (2008).

^c Predictions of species extinction and endangerment are based on the conventional species-area model assuming a z value of either 0.22 (conventional_{continental-z}) or 0.35 (conventional_{island-z}), the countryside species-area model assuming a z value of either 0.22 (countryside_{continental-z}) or 0.35 (countryside_{island-z}), or the matrix-calibrated model. For the countryside and matrix-calibrated species-area models, we performed Monte Carlo simulations (10,000 runs) to account for variability in taxon sensitivity to each transformed land-use type and calculated a mean predicted value and its associated variance (not presented here) for each biodiversity hotspot (+, overestimate; -, underestimate).

(hereafter, matrix-calibrated model) expressed as

$$\frac{S_{\text{new}}}{S_{\text{org}}} = \left(\frac{A_{\text{new}}}{A_{\text{org}}} \right)^{\gamma \cdot \sum_i p_i \sigma_i} \quad (6)$$

We tested our model on 20 biodiversity hotspots in the tropics (Table 1), which represent geographic regions that each contain at least 0.5% of the world’s flora and have already lost over 70% of their original habitat (Myers et al. 2000). The focus of research attention on biodiversity hotspots over the past decade has produced a considerable amount of biodiversity and biophysical data (Conservation International 2008). Thus, these hotspots are ideal test sites for our matrix-calibrated model. We used our model to predict species extinction and endan-

germent resulting from land-use change in each hotspot. We then compared these predictions with observed numbers of extinct and threatened species (i.e., classified as “vulnerable,” “endangered,” “critically endangered,” or “extinct”; IUCN [International Union for Conservation of Nature] 2008). We included extant species threatened with extinction to account for extinction debts (lag effects) that might take decades or centuries to unfold (Tilman et al. 1994; Brooks et al. 1999). (Henceforth, *extinction* refers to both extinction and endangerment, and extinct species include both extinct and threatened species.)

We repeated our analysis with the conventional species-area model (Eq. 2; henceforth, referred to as conventional model) and the countryside species-area

model proposed by Pereira and Daily (2006) (henceforth, referred to as countryside model), which is expressed as

$$\frac{S_{\text{new}}}{S_{\text{org}}} = \left(\frac{\sum_i^n b_i A_i}{A_{\text{org}}} \right)^z,$$

where b is the affinity of a species to the i th habitat type (proportion of habitat that can be used by a taxon; for this study we let $b = 1 - \sigma$). Finally, we assessed which set of model predictions (conventional, countryside, or matrix calibrated) most accurately reflects the observed number of extinct species in these hotspots.

Methods

As with previous studies (e.g., Pimm & Askins 1995; Brooks et al. 2002), we restricted our analysis to species endemic to each hotspot (i.e., not occurring elsewhere; Conservation International 2008). We focused only on birds because they are well studied in terms of their sensitivity to different forms of land-use change in the tropics (e.g., Sodhi et al. 2009) and data on their conservation status are most reliable, updated, and readily available from Conservation International (2008) and IUCN (2008). A species qualifies for listing as vulnerable, endangered, or critically endangered on the IUCN Red List if it meets any of a range of quantitative criteria, including habitat loss (i.e., decrease in area of occupancy; IUCN 2001). To address the issue of circularity that might arise from the use of the IUCN Red List to verify extinction predictions made based on habitat loss, we excluded all species red listed by the IUCN solely on the basis of criteria A1c, A2c, and B2a-c. These criteria are based entirely on species' habitat decline. Out of a total of 2664 species of endemic birds occurring in the 20 biodiversity hotspots considered, only two species were thus excluded: Restinga Antwren (*Formicivora littoralis*) and Black-capped Petrel (*Pterodroma hasitata*).

We calculated area for the following land-use classes occurring in each biodiversity hotspot on the basis of land-cover data from Conservation International (2008) and the European Space Agency (ESA) (2008): original vegetation extent, vegetation remaining, disturbed forest, agricultural land, and urban area (see Supporting Information). In addition, on the basis of data compiled by Watling and Donnelly (2006), we calculated mean slope of species-area relationships of birds on land-bridge archipelagos and used this value, $z = 0.35$ (SE 0.06, $n = 6$), as the γ value in the matrix-calibrated model and as the z value in the conventional and countryside models. Continental habitat islands typically have lower species-area slopes than true island archipelagos (Rosenzweig 1995). Therefore, we also calculated a continental species-area slope for birds ($z = 0.22$ [SE 0.02], $n = 17$; Watling & Donnelly 2006).

To determine the sensitivity (i.e., the σ value in Eq. 6) of birds to each transformed land-use type, we used data compiled by Sodhi et al. (2009) to calculate mean percent decrease in bird species richness when a pristine habitat is converted to either a disturbed forest ($\sigma = 0.25$ [SE 0.03], $n = 42$) or agricultural land ($\sigma = 0.68$ [SE 0.05], $n = 17$; Supporting Information). We assumed urban areas are completely inhospitable to birds ($\sigma = 1$). We performed a Monte Carlo simulation to account for variability in taxon sensitivity to the land-use types of disturbed forest and agricultural land. In 10,000 runs, we generated a random σ value derived from the mean and standard deviation of the calculated σ value and by assuming a normal distribution. We entered the randomized σ value to the matrix-calibrated model to calculate the mean number (and 95% confidence interval) of species extinction resulting from land-use change in each biodiversity hotspot.

Finally, we used the conventional and countryside models to estimate species extinction in each hotspot, considering alternative slopes of 0.35 (island z value) or 0.22 (continental z value). We evaluated relative strength of support for each of the following five candidate models with the Akaike's information criterion (AIC; Burnham & Anderson 1998): conventional model with continental z value (conventional_{continental-z}), conventional model with island z value (conventional_{island-z}), countryside model with continental z value (countryside_{continental-z}), countryside model with island z value (countryside_{island-z}), and the matrix-calibrated model.

Results

Across all biodiversity hotspots considered, the observed percentage of extinct bird species ranged from 15.4% in Mesoamerica to 58.8% in the Cerrado (Table 1). Of the five models considered, the matrix-calibrated model had the highest AIC weight ($w_i = 89.21\%$), which reflects the weight of evidence in support of this model being the optimal model given the set of candidate models and the data considered (Table 2). The matrix-calibrated model was 13.5 times more strongly supported by the data than the next-best model, conventional_{continental-z} ($w_i = 6.61\%$). Both countryside models—countryside_{island-z} ($w_i = 3.89\%$) and countryside_{continental-z} ($w_i = 0.28\%$)—performed more poorly than either the matrix-calibrated or conventional_{continental-z} models. The conventional_{island-z} model performed the worst ($w_i = 0.01\%$).

The matrix-calibrated model produced prediction errors that were more evenly distributed (seven overestimates and 13 underestimates) than in the other four models (Table 1; Fig. 2). The conventional_{continental-z} model overestimated species extinction for 14 out of

Table 2. Candidate models for predicting extinct or threatened endemic bird species in 20 biodiversity hotspots.*

Candidate model	$\sum \varepsilon^2$	AIC	w_i (%)	Evidence ratio
Matrix calibrated	4592.7	49.2	89.21	1
Conventional _{continental-z}	8363.5	54.4	6.61	13.5
Countryside _{island-z}	9447.2	55.5	3.89	22.9
Countryside _{continental-z}	17,384.5	60.8	0.28	324.1
Conventional _{island-z}	34,320.6	66.7	0.01	6215.7

*See Table 1 for explanation of candidate models ($\sum \varepsilon^2$, sum of differences between predicted and observed values of extinction risk in 20 biodiversity hotspots; AIC, Akaike's information criterion; w_i , Akaike weight, defined as the weight of evidence in support of a candidate model; evidence ratio, ratio of Akaike weights between the optimal model and each candidate model). The AIC is calculated as, $AIC = n \log(\frac{\sum \varepsilon^2}{n}) + 2K$, where $n = 20$ biodiversity hotspots and K (number of parameters) is 1 (Burnham & Anderson 1998).

the 20 hotspots (the most extreme values being Tropical Andes, Wallacea, and the Philippines) and underestimated extinction for six hotspots, including the Cerado and Polynesia-Micronesia (Table 1; Fig. 2). The conventional_{island-z} model overestimated species extinction for 18 hotspots, whereas both countryside models produced extinction predictions that were mostly underestimates (Table 1).

Discussion

Biodiversity hotspots largely encompass developing nations that typically have limited conservation expertise and resources (Sodhi et al. 2004; Bradshaw et al. 2009). Given these challenges, heuristic tools are particularly useful for conservation scientists and decision makers to accurately and rapidly assess the consequences of land-use decisions for biodiversity. To this end the

species-area approach has been adopted widely by ecologists because the underlying island theory is elegant and intuitive. Nevertheless, this approach is limited by its simplicity; specifically it does not account for quality of the matrix. Our approach of calibrating the species-area model retains the heuristic property of the conventional model, but also includes a more realistic calibration that is based on extent and habitat quality of transformed land uses as perceived by the taxon. Our matrix-calibrated model performed considerably better than the conventional and countryside models in predicting biodiversity losses. In addition, although we removed species listed primarily on the basis of habitat area to avoid circularity, a similar analysis with the entire data set generated nearly identical conclusions, which implies that our matrix-calibrated method can be applied broadly in conservation practice.

These conclusions must be considered in view of the following caveats. First, we did not exclude species on the IUCN Red List (classified as extinct or threatened) for reasons other than habitat loss (e.g., overexploitation), as some studies have done (e.g., Brooks et al. 2002). Instead, we assumed that the red-listing of a species is always ultimately attributable to land-use change. This assumption is supported by considerable evidence that overexploitation in tropical forests is facilitated by increased accessibility that accompanies forest clearance (Nepstad et al. 2001; Laurance et al. 2002). Second, given that the conventional approach consistently overestimated extinction, it could be construed as being more precautionary than the matrix-calibrated method because there is less likelihood of underestimating biodiversity losses. Erring on the side of caution may be desirable from a strict conservationist perspective, but our matrix-calibrated estimation of extinction, being more realistic, would provide more objective guidance to conservation policy.

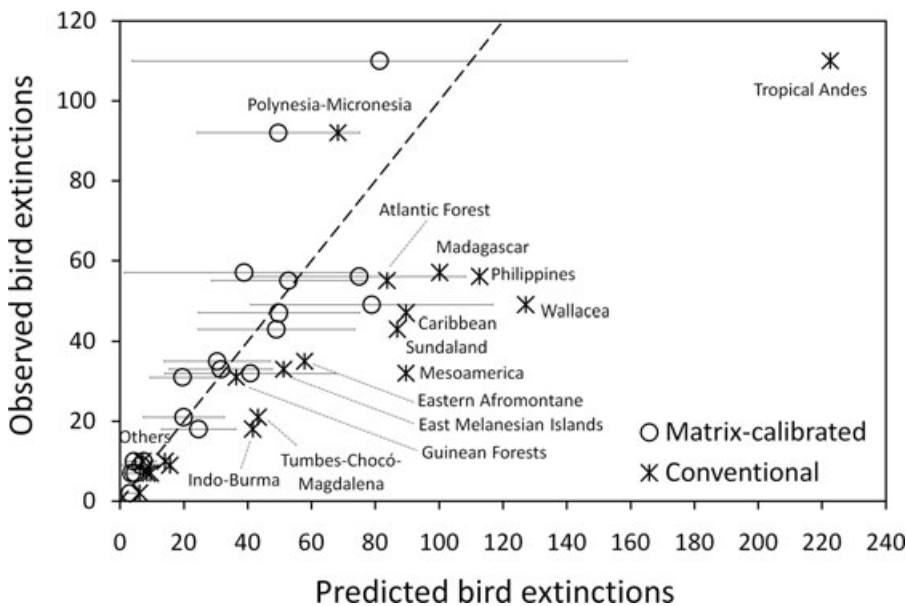


Figure 2. Comparisons of observed and predicted numbers of extinct and threatened endemic bird species in 20 biodiversity hotspots. Predicted values are based on either the conventional species-area model (Eq. 2), assuming a continental z value of 0.22 or the matrix-calibrated species-area model (Eq. 6). For the matrix-calibrated model, we plotted the mean of predicted values with error bars representing 95% confidence intervals. Dashed line reflects perfect match in predicted and observed values.

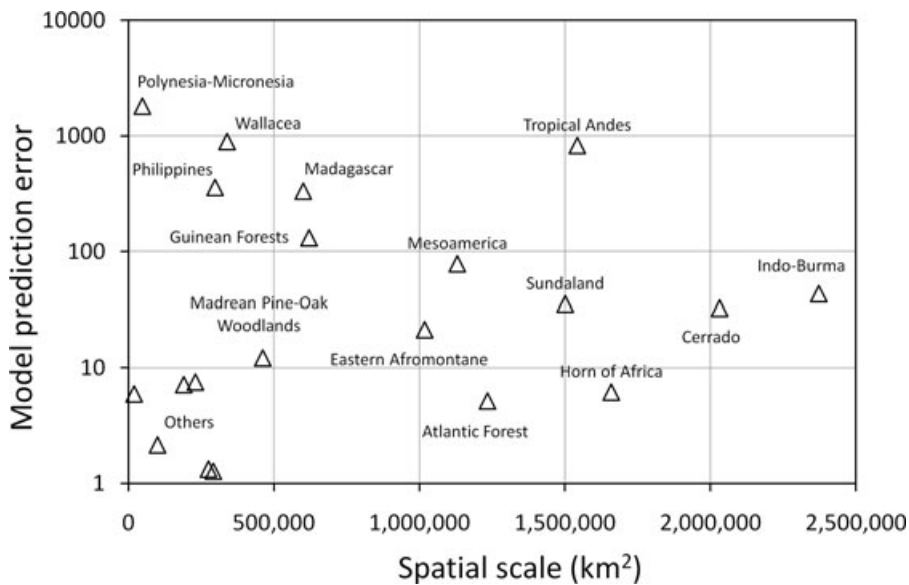


Figure 3. Plot of spatial scale and error of predictions from the matrix-calibrated model for 20 biodiversity hotspots. The spatial scale of analysis ranged from 18,972 km² (New Caledonia hotspot) to 2,373,057 km² (Indo-Burma hotspot). Model prediction errors were calculated as the square of the difference between predicted and observed number of threatened or extinct endemic bird species.

Third, our analysis is necessarily crude because we have treated birds as a single homogeneous group, whereas birds may differ in their response to the matrix by taxonomic or functional subgroups. Although current information does not permit more detailed analysis, our method provides the means to undertake such analyses as the information becomes available. Fourth, we assumed the σ values we used—which were extracted from a tropical Asian data set (Sodhi et al. 2009)—are applicable to other tropical regions. To the best of our knowledge, a pan-tropical data set of σ values has not been compiled, but extracting them from the literature would have required effort beyond that available for this analysis. Finally, although we cannot be certain our model predictions will remain robust at spatial scales beyond what we considered, there was no discernible effect of spatial scale on model prediction errors, at least within the range of spatial scales we considered (i.e., from 18,972 km² [New Caledonia hotspot] to 2,373,057 km² [Indo-Burma hotspot]; Fig. 3).

In addition to being a valuable tool for assessing extinction risk, our calibrated species-area model also has important implications for land management in human-dominated landscapes. First, for a given amount of unavoidable deforestation in a landscape undergoing development, our model suggests that extinction risk could be minimized by improving the habitat quality of the matrix for the taxon of interest (i.e., by lowering the σ value in Eq. 6). More importantly, the model enables a quantitative assessment of the biodiversity benefits (and trade-offs) of such mitigation measures. Second, for a landscape that has experienced historical land-use change, biodiversity could be enhanced by improving the habitat quality of the matrix (i.e., $\frac{S_{\text{new}}}{S_{\text{org}}}$ can be >1 when $\sigma < 0$). In the context of tropical forests, this could be achieved by al-

lowing farmland to regenerate to secondary forests or by facilitating the succession of young secondary forests to old-growth forests. For example, the natural regeneration of abandoned pasture and coffee plantations in Puerto Rico produced secondary forests with similar structure and species diversity compared with the island's mature forests (Zimmerman et al. 2007). Such processes of regeneration are widespread across tropical regions (Chazdon 2008) and are predicted to increase over coming decades (Wright & Muller-Landau 2006), which indicates our calibrated model will be increasingly appropriate for practical conservation in future tropical landscapes.

Acknowledgments

We thank W.R. Turner, J.I. Watling, N.S. Sodhi, T.M. Lee, C.J.A. Bradshaw, and B.W. Brook for helpful discussions. We thank T. Donovan and two anonymous reviewers for useful suggestions. This study was inspired by a question posed by D.S. Wilcove, to which the answer is, converting 1 acre of Borneo's primary forest to oil palm is roughly as bad for biodiversity as selectively logging 2.5 acres of the forest. L.P.K. was supported by an ETH (Eidgenössische Technische Hochschule) Fellowship and the Swiss National Science Foundation.

Supporting Information

Data used in the analysis (Appendices S1 and S2) are available as part of the on-line article. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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