

An overhaul of the species–area approach for predicting biodiversity loss: incorporating matrix and edge effects

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Summary

1. Species–area (SA) models have often been used to predict biodiversity loss resulting from habitat loss. This application of SA models hinges on two fundamental assumptions: the resultant landscape matrix is inhospitable to the taxa of interest; and edge effects do not factor into extinction risks. Despite growing consensus that these assumptions are unrealistic, the SA approach continues to be used in assessments of biodiversity decline and conservation planning.

2. We propose an overhaul of the SA approach by accounting for taxon-specific responses to landscape-specific matrix quality and deleterious effects of habitat edges. We pitted nine variants of an improved SA model (calibrated for edge and/or matrix) against two variants of the conventional model (calibrated with island or continental z values) to predict species extinction and endangerment in 15 tropical biodiversity hotspots.

3. The matrix-calibrated SA model received the highest Akaike's Information Criterion weight (birds: 66.8%; mammals: 63.3%), which reflects the weight of evidence in support of it being the most parsimonious model given the set of candidate models and data considered. Additionally, the matrix-calibrated (MC) model produced species extinction predictions that were the most accurate and least biased.

4. The second best model (for both birds and mammals) was one that simultaneously corrected for matrix and edge effects.

5. The conventional SA model (particularly when calibrated with an island z value) performed worse than the matrix-calibrated and/or edge-corrected models.

6. *Synthesis and applications.* Our results suggest that accounting for the landscape matrix *per se* is a sufficient and significant improvement to the SA approach in terms of assessing species extinction risks from land-use change. More importantly, given that the MC model was also the most parsimonious model (in that it requires only one additional model parameter than the conventional SA model), it could prove to be a cost-effective heuristic tool for conservation scientists and decision makers to accurately evaluate extinction risks resulting from land-use decisions. We argue that, henceforth, the MC model, which takes account of both the extent of deforestation and quality of the resultant matrix, should replace the conventional SA model for predicting biodiversity loss.

Key-words: agriculture, biodiversity crisis, countryside biogeography, equilibrium theory, forest regeneration, power model, reconciliation ecology, succession, win–win ecology

Introduction

The power model has been used to describe species–area (SA) relationships in island archipelagos, as well as ‘habitat islands’ in terrestrial systems (Arrhenius 1920; MacArthur & Wilson

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1967; Simberloff & Abele 1976; Rosenzweig 1995; Tjørve 2003; Dengler 2009). It has also been applied to predict biodiversity losses resulting from land-use change (Pimm *et al.* 1995; Brooks & Balmford 1996; Brooks, Pimm & Collar 1997; Brooks *et al.* 2002; Brook, Sodhi & Ng 2003). The power model (henceforth referred to as SA model) is expressed as:

$$S = c \cdot A^z, \quad \text{eqn 1}$$

where S and A represent species number and habitat area, respectively; c is a taxon- and region-specific constant and z reflects the rate of change in species number as area changes (Rosenzweig 1995). When the SA model is used to predict change in biodiversity resulting from change in forest area (from A_{org} to A_{new}), the expected species number (S_{new}) can be expressed as a proportion of the original species number (S_{org}):

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

This application of the SA model is based on two fundamental assumptions: (i) the resultant landscape matrix is analogous to an ocean and, hence, completely inhospitable to the taxon of interest, and (ii) fragmentation effects, particularly edge effects, do not factor into extinction risks. The first assumption is violated where land-use change results in a landscape mosaic of different habitat types with varying degrees of suitability and permeability for the taxon (Gascon *et al.* 1999; Daily, Ehrlich & Sanchez-Azofeifa 2001; Ricketts 2001; Perfecto & Vandermeer 2002; Jules & Shahani 2003; Umetsu, Metzger & Pardini 2008). The second assumption is breached when edge effects degrade the quality of the habitat fragments near habitat margins, especially where fragment edge-to-area ratio is high (Simberloff & Abele 1976; Gilbert 1980; Murcia 1995; Laurance 2008). Since edge effects have been implicated in the degradation of forests in particular, we present our model in the context of tropical forest ecosystems, although the model can also be more generally applied.

Incorporation of matrix effects

Koh & Ghazoul (2010a) proposed a modification to the SA model that incorporates matrix effects by partitioning the slope (z value) of SA relationships into two components: γ , a constant that reflects the rate of change in species number per unit area on true island archipelagos, and σ , an area-weighted average of taxon-specific responses to matrix components. The matrix-calibrated (MC) model is expressed as:

$$\frac{S_{\text{new}}}{S_{\text{org}}} = \left(\frac{A_{\text{new}}}{A_{\text{org}}} \right)^{\gamma \cdot \sum_{i=1}^N p_i \cdot \sigma_i}, \quad \text{eqn 3}$$

where p represents the proportional area of the i th matrix component relative to the total area of the matrix, and N represents the total number of matrix components. The MC model outperformed four other candidate models – including the conventional SA model (eqn 2) calibrated with either island (0.35) or continental (0.22) z values – in terms of accurately predicting the extinction and endangerment of forest bird species in 20

biodiversity hotspots (Koh & Ghazoul 2010a). Here, we propose a further refinement of their model by also incorporating edge effects.

Incorporation of edge effects

We define edge effects as deleterious effects on a forest fragment mediated by biophysical interactions near the interface between forest and matrix. In the context of our SA model, the specific edge effect is a reduction in the area of forest perceived by the taxon as habitable (Laurance & Yensen 1991). Our model therefore seeks to determine the effective size of remaining forests in the landscape by accounting for the edge-affected areas within each forest fragment. With recent advances in remote sensing technology, particularly in terms of spatial resolution of satellite images and the processing power of geographical information systems (Kerr & Ostrovsky 2003; Turner *et al.* 2003; Buchanan *et al.* 2008), it is increasingly feasible to acquire spatial data on the physical characteristics of land use and land cover in fragmented landscapes at relatively high resolution. Indeed, our model specifically makes use of such data to account for edge effects. To maximize the applicability of our approach, we present two variants of our edge-corrected SA model that trade-off between data requirement and prediction accuracy: (i) a landscape-specific model that produces more accurate predictions of biodiversity loss insofar as reliable spatial data on forest fragments are available, and (ii) a generic, simplifying model that produces approximate predictions when such spatial data are lacking. These edge-corrected models build upon our previous model (Koh & Ghazoul 2010b), in that they are also calibrated for the landscape matrix.

LANDSCAPE-SPECIFIC MODEL

We define edge-penetration distance as the perpendicular distance from edge margin to forest interior along which a taxon perceives an edge effect. Often, a taxon's sensitivity to an edge declines linearly or nonlinearly as a function of distance from the edge margin (Murcia 1995). Edge effects could also peak at intermediate distances, but for simplicity, we assume edge effects to decline monotonically. Thus, for a given edge-penetration distance, the total edge-affected forest area in the landscape can be expressed as:

$$A_{\text{edge}} = \delta \cdot \sum_{j=1}^M \beta_j, \quad \text{eqn 4}$$

where β_j represents the edge-affected area of the j th forest fragment, M represents the total number of fragments and δ represents the declining function of the edge effect as perceived by the taxon (e.g. $\delta = 0.5$, if edge effect declines linearly with distance from forest margin; or $0 < \delta < 0.5$ or $0.5 > \delta > 1$, depending on the shape of a nonlinear declining function). Following this, we can derive a landscape-specific edge-corrected model (that is also calibrated for the matrix) as:

$$\frac{S_{\text{new}}}{S_{\text{org}}} = \left(\frac{A_{\text{new}} - A_{\text{edge}}}{A_{\text{org}}} \right)^{\gamma \cdot \sum_{i=1}^N p_i \cdot \sigma_i} \quad \text{or} \quad \text{eqn 5}$$

$$\frac{S_{\text{new}}}{S_{\text{org}}} = \left(\frac{A_{\text{new}} - \delta \cdot \sum_{j=1}^M \beta_j}{A_{\text{org}}} \right)^{\gamma \cdot \sum_{i=1}^N p_i \cdot \sigma_i}.$$

GENERIC MODEL

If the original forest is broken up into κ number of fragments, the average area of each fragment would be:

$$\bar{A}_{\text{new}} = \frac{A_{\text{new}}}{\kappa}. \quad \text{eqn 6}$$

Under the simplifying assumption that each fragment is approximately circular in shape, its average radius, \bar{R} , would be $\sqrt{A_{\text{new}}/\pi}$ or $\sqrt{A_{\text{new}}/(\pi \cdot \kappa)}$. For a given edge-penetration distance, ε , the average edge-affected area of a fragment would be equivalent to the area of an annulus (corrected for the declining function of edge effect, δ), which can be expressed as:

$$\bar{A}_{\text{edge}} = \begin{cases} \pi \cdot \varepsilon \cdot (2 \cdot \sqrt{A_{\text{new}}/(\pi \cdot \kappa)} - \varepsilon) \cdot \delta & \text{for } (\varepsilon \leq \bar{R}) \\ \bar{A}_{\text{new}} & \text{for } (\varepsilon > \bar{R}) \end{cases}. \quad \text{eqn 7}$$

From eqns 6 and 7, we can derive a generic edge-corrected (and matrix-calibrated) model as:

$$\frac{S_{\text{new}}}{S_{\text{org}}} = \left(\frac{(\bar{A}_{\text{new}} - \bar{A}_{\text{edge}}) \cdot \kappa}{A_{\text{org}}} \right)^{\gamma \cdot \sum_{i=1}^N p_i \cdot \sigma_i} \quad \text{or}$$

$$\frac{S_{\text{new}}}{S_{\text{org}}} = \left(\frac{\left(\frac{A_{\text{new}}}{\kappa} - \pi \cdot \varepsilon \cdot (2 \cdot \sqrt{A_{\text{new}}/(\pi \cdot \kappa)} - \varepsilon) \cdot \delta \right) \cdot \kappa}{A_{\text{org}}} \right)^{\gamma \cdot \sum_{i=1}^N p_i \cdot \sigma_i}. \quad \text{eqn 8}$$

In cases where the taxon is not sensitive to edge effects ($\delta = 0$), both the landscape-specific (eqn 5) and generic (eqn 8) edge-corrected models reduce to the matrix-calibrated SA model (eqn 3).

We assessed the relative weight of evidence in support of nine variants of an improved SA model (calibrated for edge and/or matrix) and two variants of the conventional model (calibrated with island or continental z values) for predicting species extinction and endangerment for birds and mammals in 15 tropical biodiversity hotspots.

Materials and methods

Biodiversity hotspots represent geographical 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). We tested our models on 15 biodiversity hotspots in the tropics that vary in terms of the extent of deforestation and severity of forest fragmentation (Table 1 and Table S1, Supporting information). We pitted four variants of the landscape-specific edge-corrected model (eqn 5), which varied in terms of edge-penetration distance ($EC_{\text{LS}(50\text{m})}$, $EC_{\text{LS}(100\text{m})}$, $EC_{\text{LS}(200\text{m})}$ and $EC_{\text{LS}(400\text{m})}$) and four variants of the generic edge-corrected model (eqn 8; $EC_{\text{gen}(50\text{m})}$, $EC_{\text{gen}(100\text{m})}$, $EC_{\text{gen}(200\text{m})}$ and $EC_{\text{gen}(400\text{m})}$) against the MC model (eqn 3) and two variants (in terms of z values) of the

conventional SA model (eqn 2; $SAR_{\text{continent}}$ and SAR_{island} ; see Tables 1 and 2). The edge-penetration distances we considered (50–400 m) span the range of values reported by previous studies (Laurance 1991; Laurance & Yensen 1991; Murcia 1995), and we assumed the edge effects to decline linearly with distance from forest margin (i.e. $\delta = 0.5$). We used each model to predict species extinction and endangerment resulting from historical land-use change in each hotspot, and compared these predictions with the observed numbers of extinct and threatened species in the latest species red list published by the International Union for Conservation of Nature (IUCN; i.e. classified as 'vulnerable', 'endangered', 'critically endangered', 'extinct in the wild' or 'extinct'; Table S2, Supporting information; IUCN 2008). We included threatened species in our analyses to account for 'extinction debts' (because of lag effects) that we assume to be attributable to historical land-use change (Tilman *et al.* 1994; Brooks, Pimm & Oyugi 1999). (Henceforth, 'extinction' refers also to endangerment, and 'extinct species' include threatened species.)

LAND-USE AND LAND-COVER DATA

We restricted our analysis to tropical moist and dry forest ecoregions within each hotspot (i.e. biomes 1 and 2, *sensu* Olson *et al.* 2001). Ecoregions are biogeographical units that emphasize the importance of endemic genera, distinct species assemblages and the influence of geological history on species distributions (Olson *et al.* 2001); and are commonly used in the study of broad-scale patterns of species richness and endemism (e.g. Lee & Jetz 2008). We aggregated ecoregions into biodiversity hotspots because hotspots offer a more sizable pool of total known species for generating predictions of extinction risk (Table S2, Supporting information). We evaluated historical land-use change in each hotspot based on the GlobCover Land Cover Version 2.2 data set produced by the European Space Agency (ESA 2008). GlobCover is derived from a time series of composite satellite images (December 2004 to June 2006), obtained from the Medium Resolution Imaging Spectrometer sensor on board the ESA's Environmental Satellite (ENVISAT). This data set comprises 23 main land-cover classes at *c.* 300 m resolution. We based our analysis on the ENVISAT data set because it is the global data set with the highest spatial resolution that met all of the following criteria: (i) it encompasses all 15 biodiversity hotspots in the tropics where the models were tested; (ii) it adequately distinguishes among the various land-cover classes, from which we could extract information on matrix composition and quality; and (iii) it is freely and readily accessible online. We calculated the area for the following five aggregated land-cover classes within each hotspot: (i) primary forest [aggregating GlobCover land-cover classes of closed deciduous, evergreen or mosaic forests, and closed to open forests on permanently or regularly flooded soil (fresh, brackish or saline water)]; (ii) secondary forest or regrowth [closed to open deciduous or evergreen forests, and closed to open vegetation on regularly flooded soil (fresh, brackish or saline water)]; (iii) degraded vegetation (sparse, herbaceous or mosaic shrubland or grassland, and mosaic cropland); (iv) agricultural land (irrigated or rainfed croplands); and (v) bare areas (urban or bare areas). We calculated the number of primary forest fragments in each biodiversity hotspot based on the primary forest land-cover class. We entered this number as the variable, κ , in the generic edge-corrected model (eqn 8). Within each primary forest fragment, we also created inner buffer zones at 50, 100, 200 and 400 m away from the fragment edge to calculate edge-affected areas at these edge-penetration distances. These areas were entered as the variable, β , in the landscape-specific edge-corrected model (eqn 5). All spatial analyses were performed using ArcGIS Desktop 9.3.1 (ESRI, Redlands, CA, USA).

Table 1. Observed and predicted number of extinct and threatened species of (a) birds and (b) mammals in 15 tropical biodiversity hotspots*

Biodiversity hotspot	Predicted†											
	Observed‡	SAR _{continent}	SAR _{island}	MC	EC _{LS(50m)}	EC _{LS(100m)}	EC _{LS(200m)}	EC _{LS(400m)}	EC _{gen(50m)}	EC _{gen(100m)}	EC _{gen(200m)}	EC _{gen(400m)}
(a) Atlantic Forest	29	45 (±16)	62 (±19)	28 (±16)	29 (±16)	30 (±17)	31 (±18)	32 (±18)	29 (±16)	30 (±17)	32 (±18)	34 (±19)
Caribbean	15	22 (±8)	30 (±9)	13 (±8)	13 (±8)	14 (±8)	15 (±9)	15 (±9)	13 (±8)	14 (±8)	15 (±9)	16 (±9)
Coastal Forests of Eastern Africa	4	2 (±1)	3 (±1)	1 (±1)	1 (±1)	1 (±1)	1 (±1)	2 (±1)	1 (±1)	1 (±1)	1 (±1)	2 (±1)
East Melanesian Islands	29	77 (±25)	99 (±27)	43 (±27)	44 (±27)	44 (±28)	44 (±28)	45 (±28)	44 (±27)	44 (±27)	45 (±28)	46 (±28)
Guinean Forests of West Africa	20	35 (±11)	46 (±13)	19 (±13)	20 (±13)	20 (±14)	21 (±14)	21 (±14)	20 (±13)	20 (±14)	21 (±14)	22 (±15)
Indo-Burma	10	25 (±8)	33 (±10)	15 (±9)	15 (±9)	16 (±9)	16 (±9)	17 (±9)	15 (±9)	16 (±9)	17 (±9)	17 (±10)
Madagascar and the Indian Ocean Islands	33	25 (±9)	36 (±12)	17 (±10)	17 (±11)	18 (±11)	19 (±12)	20 (±12)	17 (±11)	18 (±11)	19 (±12)	21 (±13)
Mesoamerica	18	46 (±17)	66 (±22)	23 (±17)	24 (±17)	25 (±17)	25 (±18)	26 (±19)	25 (±18)	26 (±18)	28 (±19)	31 (±21)
New Caledonia	6	12 (±4)	15 (±4)	6 (±4)	6 (±4)	7 (±4)	7 (±5)	7 (±5)	6 (±4)	7 (±4)	7 (±5)	20 (±0)
Philippines	14	70 (±21)	86 (±22)	44 (±24)	45 (±24)	45 (±24)	46 (±24)	47 (±25)	45 (±24)	46 (±24)	47 (±24)	48 (±25)
Sundaland	17	33 (±11)	44 (±13)	17 (±12)	17 (±12)	17 (±12)	17 (±12)	17 (±12)	17 (±12)	17 (±12)	17 (±12)	18 (±12)
Tropical Andes	69	159 (±53)	209 (±59)	73 (±64)	75 (±66)	77 (±67)	79 (±69)	81 (±71)	75 (±65)	77 (±67)	80 (±70)	84 (±73)
Tumbes-Choco-Magdalena	12	44 (±15)	58 (±16)	24 (±16)	25 (±16)	25 (±17)	26 (±17)	27 (±18)	25 (±16)	25 (±17)	26 (±17)	28 (±18)
Wallacea	28	162 (±47)	197 (±49)	97 (±56)	99 (±56)	99 (±57)	101 (±57)	102 (±58)	99 (±56)	100 (±57)	102 (±57)	105 (±59)
Western Ghats and Sri Lanka	8	13 (±5)	18 (±5)	6 (±5)	6 (±5)	7 (±5)	7 (±5)	7 (±6)	6 (±5)	7 (±5)	7 (±5)	7 (±6)
(b) Atlantic Forest	5	5 (±2)	5 (±1)	3 (±1)	3 (±1)	3 (±1)	3 (±1)	3 (±1)	3 (±1)	3 (±1)	3 (±1)	3 (±1)
Caribbean	3	2 (±1)	2 (±0)	1 (±0)	1 (±0)	1 (±0)	1 (±0)	1 (±0)	1 (±0)	1 (±0)	1 (±0)	2 (±0)
Coastal Forests of Eastern Africa	5	1 (±1)	2 (±0)	1 (±0)	1 (±0)	1 (±0)	1 (±0)	1 (±0)	1 (±0)	1 (±0)	1 (±0)	1 (±0)
East Melanesian Islands	17	22 (±8)	25 (±3)	12 (±4)	12 (±4)	12 (±4)	13 (±4)	13 (±4)	12 (±4)	12 (±4)	13 (±4)	13 (±4)
Guinean Forests of West Africa	18	29 (±11)	33 (±4)	16 (±6)	17 (±6)	17 (±6)	17 (±6)	18 (±6)	17 (±6)	17 (±6)	18 (±6)	19 (±6)
Indo-Burma	10	25 (±10)	29 (±3)	14 (±5)	14 (±5)	14 (±5)	15 (±5)	15 (±5)	14 (±5)	14 (±5)	15 (±5)	16 (±5)
Madagascar and the Indian Ocean Islands	26	28 (±12)	32 (±5)	18 (±6)	19 (±6)	20 (±6)	21 (±6)	22 (±7)	19 (±6)	20 (±6)	21 (±6)	23 (±7)
Mesoamerica	11	13 (±6)	15 (±2)	7 (±3)	7 (±3)	7 (±3)	7 (±3)	7 (±3)	7 (±3)	7 (±3)	8 (±3)	9 (±3)
New Caledonia	3	4 (±1)	4 (±0)	2 (±1)	2 (±1)	2 (±1)	2 (±1)	2 (±1)	2 (±1)	2 (±1)	2 (±1)	6 (±0)
Philippines	13	46 (±17)	52 (±5)	28 (±9)	28 (±9)	28 (±9)	29 (±9)	30 (±9)	28 (±9)	28 (±9)	29 (±9)	30 (±9)
Sundaland	32	45 (±18)	52 (±6)	21 (±9)	22 (±9)	22 (±9)	22 (±9)	22 (±9)	22 (±9)	22 (±9)	22 (±9)	23 (±10)
Tropical Andes	3	11 (±4)	12 (±1)	5 (±2)	5 (±2)	5 (±2)	5 (±3)	6 (±3)	5 (±2)	5 (±3)	5 (±3)	6 (±3)
Tumbes-Choco-Magdalena	1	3 (±0)	3 (±0)	1 (±1)	1 (±1)	2 (±1)	2 (±1)	2 (±1)	1 (±1)	1 (±1)	2 (±1)	2 (±1)
Wallacea	38	80 (±29)	91 (±8)	47 (±16)	47 (±16)	48 (±16)	49 (±16)	49 (±16)	47 (±16)	48 (±16)	49 (±16)	51 (±17)
Western Ghats and Sri Lanka	6	8 (±3)	9 (±1)	3 (±2)	3 (±2)	3 (±2)	3 (±2)	4 (±2)	3 (±2)	3 (±2)	3 (±2)	4 (±2)

*Extinct and threatened species are those classified as vulnerable, endangered, critically endangered, or extinct in the wild or extinct.

†Based on IUCN (2008) (see 'Materials and methods').

‡Based on the conventional species-area model using either continental (SAR_{continent}) or island (SAR_{island}) z values, the matrix-calibrated model (MC), or either the landscape-specific (EC_{LS}) or generic (EC_{gen}) edge-corrected species-area model (numeric subscripts in parentheses represent assumed edge-penetration distances). Numbers in parentheses indicate standard deviation from Monte Carlo simulations.

Table 2. Candidate species–area models for predicting extinction and endangerment of (a) birds and (b) mammals*

Rank	Candidate model	SS	<i>K</i>	AIC _c	<i>w_i</i> (%)	Evidence ratio
(a)						
1	MC	6399.0	3	47.63	66.8	1.0
2	EC _{LS(50m)}	6663.9	4	51.71	8.7	7.7
3	EC _{LS(100m)}	6855.9	4	51.90	7.9	8.4
4	EC _{LS(200m)}	7170.9	4	52.19	6.8	9.8
5	EC _{LS(400m)}	7604.6	4	52.57	5.6	11.8
6	SAR _{continent}	34424.6	2	55.41	1.4	48.9
7	EC _{gen(50m)}	6680.6	5	56.40	0.8	80.1
8	EC _{gen(100m)}	6935.9	5	56.64	0.7	90.5
9	EC _{gen(200m)}	7456.2	5	57.11	0.6	114.5
10	EC _{gen(400m)}	8434.2	5	57.92	0.4	171.0
11	SAR _{island}	65942.3	2	59.65	0.2	406.3
(b)						
1	MC	559.9	3	31.76	63.3	1.0
2	EC _{LS(50m)}	565.8	4	35.65	9.1	7.0
3	EC _{LS(100m)}	573.7	4	35.74	8.7	7.3
4	EC _{LS(200m)}	588.2	4	35.90	8.0	7.9
5	EC _{LS(400m)}	611.8	4	36.16	7.0	9.0
6	EC _{gen(50m)}	566.6	5	40.32	0.9	72.3
7	SAR _{continent}	3431.2	2	40.39	0.8	74.8
8	EC _{gen(100m)}	576.9	5	40.44	0.8	76.7
9	EC _{gen(200m)}	603.7	5	40.74	0.7	88.9
10	EC _{gen(400m)}	656.7	5	41.29	0.5	117.0
11	SAR _{island}	5592.5	2	43.57	0.2	367.0

*See Table 1 for definitions of model abbreviations. SS, sum of squares of deviations of predicted values from observed values of species extinction and endangerment; *K*, number of model parameters, which may include z , γ , σ , δ , ϵ and the error term; AIC_c, Akaike's Information Criterion corrected for small sample sizes; w_i , Akaike weight of evidence in support of a candidate model; evidence ratio, ratio of Akaike weights between the optimal model and each candidate model.

BIODIVERSITY DATA

We restricted our analysis to avian and mammalian species occurring in, and endemic to, the tropical moist and dry forest ecoregions within each hotspot (1554 avian and 601 mammalian species; Table S2, Supporting information; WWF 2006). To address the issue of circularity that might arise from the use of the IUCN red list to verify extinction predictions made based upon habitat loss (i.e. decrease in area of occupancy) (IUCN 2001), we excluded all threatened species red-listed solely for the criteria A1c, A2c and B2a–c that are based entirely on species' habitat decline (representing *c.* 9% of the species pool). We included species classified as 'data deficient' (IUCN 2008) in the pool of known species in each hotspot but deemed these species not to be under threat of extinction.

Based on data compiled by Watling & Donnelly (2006), and following Koh & Ghazoul (2010a), we calculated the mean slope of SA relationships in land-bridge archipelagos for birds [0.35 ± 0.15 (SD)] and mammals (0.28 ± 0.05), and used these values as the γ value in the matrix-calibrated (eqn 3) and edge-corrected models (eqns 5 and 8), and as the island z value in the conventional SA model (eqn 2). Using the same data set (Watling & Donnelly 2006), we also calculated the mean slope of SA relationships in terrestrial habitat islands and used these as continental z values for the conventional model (birds: 0.22 ± 0.1 ; mammals: 0.25 ± 0.13). Previous applications of the conventional SA model to predict species losses employed model

exponents that typically ranged between island and continental z values (e.g. Brook, Sodhi & Ng 2003).

Based on an unpublished pan-tropical data set of biodiversity studies compiled by N.S.S. and T.M.L. ($n = 186$ for birds, $n = 22$ for mammals; data available from the authors upon request), we calculated – separately for birds and mammals – the mean percentage change in species richness when a primary forest is converted to each of the four disturbed land-cover classes in the landscape matrix (e.g. regrowth). These values indicate the sensitivity of each taxon to each matrix component (i.e. the σ value in eqns 3, 5 and 8). We assumed bare areas to be completely inhospitable to any taxon ($\sigma = 1$). The geographical coverage of the sensitivity data used in this study supersedes that used in Koh & Ghazoul (2010a), which was restricted to tropical Southeast Asia.

COMPUTER SIMULATION AND MODEL SELECTION

We performed Monte Carlo simulations to account for variability in both the slope of SA relationships and taxon sensitivity to each land-cover class. For a total of 100 000 simulation runs, we entered randomized γ and σ values – derived from their mean and standard deviation (assuming normal distribution of errors; see 'Biodiversity data') – to each of the 11 candidate SA models to calculate the mean number (and SD) of species extinction in each biodiversity hotspot. Variability in γ and σ values, although accounted for in our analyses, would not be expected to affect the relative performance of the 11 candidate models. Instead, models were differentiated based on their formulation (eqn 2 vs. eqn 5 vs. eqn 8), the z values used (island or continental, for the conventional model variants) or the assumed edge-penetration distances (for edge-corrected model variants). We used the Akaike's Information Criterion corrected for small sample sizes (AIC_c) to assign relative strengths of evidence to each model (Burnham & Anderson 1998). This model selection approach identifies the most parsimonious model by taking account of the trade-off between model complexity (number of model parameters) and prediction accuracy (Burnham & Anderson 2004).

Results

PREDICTION BIAS

Both variants of the conventional SA model tended to overestimate species extinctions for both birds and mammals (overestimating extinctions for 12–14 hotspots), with the most extreme values being Tropical Andes and Wallacea for birds, and Wallacea and the Philippines for mammals (Table 1; Fig. 1). In contrast, the MC model produced prediction errors that were more evenly distributed (8 overestimates and 7 underestimates for birds; 5 overestimates and 10 underestimates for mammals). The edge-corrected models tended to slightly overestimate extinctions for birds (overestimating extinctions for 9–12 hotspots, depending on model variant), and underestimate extinctions for mammals (underestimating extinctions for 8–10 hotspots).

PREDICTION ACCURACY

For both birds and mammals, the MC model produced the most accurate predictions of species extinction among candidate models (i.e. having the lowest sum of squares of deviations

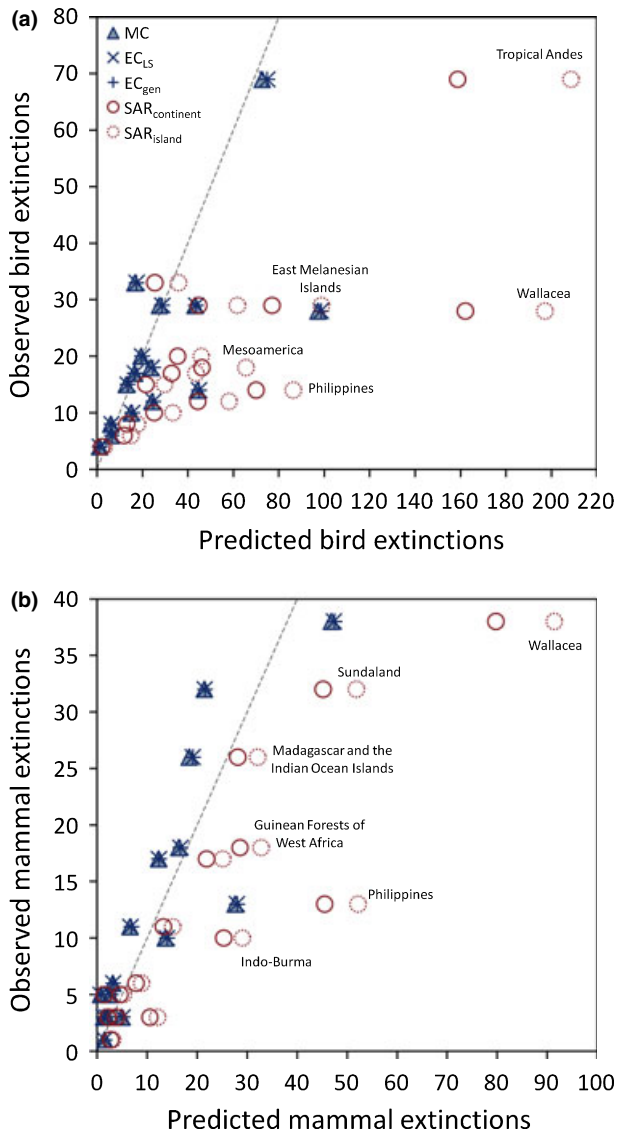


Fig. 1. Observed and predicted number of extinct and threatened species of (a) birds and (b) mammals in 15 tropical biodiversity hotspots, based on the conventional species-area model calibrated with either a continental ($SAR_{continent}$) or island (SAR_{island}) z value, the matrix-calibrated model (MC), or the landscape specific (EC_{LS}) or generic (EC_{gen}) edge-corrected models (at 50 m edge-penetration distance). Dashed line reflects perfect match in predicted and observed values.

from the observed values), whereas the conventional SA models produced the least accurate predictions (Table 2). The conventional SA model calibrated with island z value performed the worst for both taxa. Among the edge-corrected models, model accuracy decreased as the assumed value of edge-penetration distance increased; and landscape-specific variants generally produced more accurate predictions than the generic variants of the edge-corrected model (Tables 1 and 2).

MODEL PARSIMONY

For both bird and mammal extinction predictions, the MC model received the highest AIC_c weight (birds: $w_i = 66.8\%$;

mammals: $w_i = 63.3\%$), which reflects the weight of evidence in support of this model being the most parsimonious model, given the set of candidate models and the data considered (Table 2). The MC model was approximately seven times more strongly supported by the data than the next best model ($EC_{LS(50m)}$). The conventional SA model calibrated with island z value received the lowest AIC_c weight in predictions of both bird and mammal extinctions. In general, landscape-specific variants of the edge-corrected model were more parsimonious in predicting extinctions than its generic variants; and models specifying a smaller edge-penetration distance performed better than those specifying greater distances (Table 2).

Discussion

Our method assumes that accounting for the area-adjusting effects of edge on the taxon is a sufficient and economical approach (in terms of data requirement) for predicting biodiversity losses because of land-use change. We do, however, recognize that the effects of forest fragmentation are not restricted to just the amelioration of habitable areas near forest margins but would also be influenced by metapopulation dynamics, including isolation-mediated local extinction risk and recolonization probability, the rate of migration among populations and the correlation of local extinction events (Hanski 1991, 1998; Burgman, Ferson & Akcakaya 1993; McCarthy & Lindenmayer 1999). Further model development might incorporate some of these processes by considering the spatial distribution of habitat fragments relative to the vagility of the taxa concerned. However, such development would require adding layers of complexity that might not be warranted given its likely marginal benefit.

Our results do not imply that edge effects are unimportant. Instead, they suggest that accounting for the landscape matrix *per se* is a sufficient and significant improvement to the SA approach in terms of assessing species extinction risks from land-use change. In fact, the MC model outperformed all other candidate models in terms of minimizing prediction bias and maximizing prediction accuracy. More importantly, given that the MC model was also the most parsimonious model (in that it requires only one additional model parameter, σ , than the conventional SA model), it could prove to be a cost-effective heuristic tool for conservation scientists and decision makers to accurately evaluate extinction risks resulting from land-use decisions.

Whereas the conventional SA model is used to predict extinctions based solely on the extent of deforestation, the MC model could be used to explore the consequences of land-use changes in the entire landscape. These changes include not just the amount of forest but also the quality of the resultant land uses that now comprise the matrix. Perhaps more importantly, users of the MC model could also predict potential biodiversity enhancements from improvements in the quality of the matrix with respect to the taxon of interest. This is a significant step forward in the development and application of SA models because users could potentially prescribe measures to enhance, or at least maintain, biodiversity.

Many developing countries are grappling with intensifying conflicts of land use between nature conservation and economic development (Ghazoul *et al.* 2010). The key to resolving such conflicts is the ability to evaluate trade-offs among different land-use and development options (Koh & Ghazoul 2010b). To this end, another major utility of the MC model is that conservationists can now begin to explore questions concerning trade-offs in biodiversity loss under alternative land-use scenarios. For example, the model could be used to evaluate the biodiversity consequences of converting large extents of a forested landscape to extensive but wildlife-friendly agriculture vs. converting smaller extents of the landscape to intensive production systems (Koh & Ghazoul 2010b). These practical questions, which are highly relevant to policymakers, could not have been addressed with the conventional SA model.

In our analyses, we used the highest resolution global land-use and land-cover data set available (at *c.* 300 m resolution). Inasmuch as edge effects would be even less detectable at coarser resolution data sets (which necessarily would imply simplified forest fragment features), the MC model could be generally applied to global land-cover data sets spanning the range of spatial resolution currently available, such as the Global Land Cover 2000 data set (at *c.* 1 km resolution; European Commission Joint Research Centre 2002; Hoekstra *et al.* 2005).

Of course, the MC model needs to be considered in view of several caveats, which have been discussed in detail by Koh & Ghazoul (2010a). We reiterate three of the most important ones here: (i) in testing the model, we assumed that the red-listing of a species is ultimately attributable to land-use change, an assumption supported by evidence linking other drivers of extinction, such as overhunting, to enhanced accessibility associated with deforestation (Nepstad *et al.* 2001; Laurance *et al.* 2002); (ii) the conventional SA model could be favoured by some for being more precautionary (in that it tends to overestimate extinction; Fig. 1), although we believe that the MC model, in producing less biased predictions, would provide more objective decision support to conservation and land-use policies; and (iii) the robustness of our conclusions cannot be ascertained beyond the spatial scales we considered, although we did not detect any discernible effect of hotspot extent on model prediction error for any of the 11 models we considered for either birds or mammals (Fig. S1, Supporting information).

We conclude by arguing that the conventional SA model should no longer be used to predict biodiversity losses resulting from habitat loss. Instead, the MC model, which takes account of both extent of deforestation and quality of the resultant matrix, should be used for assessing the consequences of land-use change.

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Supporting Information

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

Table S1. Summary data on land cover.

Table S2. Summary data on bird and mammal species in hotspots.

Figure S1. Relationship between spatial scale and prediction error from the matrix-calibrated model.

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