



# Countryside Species–Area Relationship as a Valid Alternative to the Matrix-Calibrated Species–Area Model

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Land-use change remains a major driver of biodiversity loss, and projecting extinction rates for different scenarios of habitat conversion is a key concern in conservation research (Pereira et al. 2010; Wright 2010; de Baan et al. 2013). Species–area relationships (SARs) have been one of the main models used to develop such projections, but they have been criticized recently for overestimating extinctions (He & Hubbell 2011). One problem is that classic projections are based on the assumption that all natural areas converted to human-dominated areas, such as agriculture and forestry, become completely hostile to biodiversity (Pereira et al. 2012). However, there is a growing recognition that many species are not constrained to fragments of their native habitat and that the matrix can play an important role in the conservation of biodiversity (Prugh et al. 2008; Karp et al. 2012). Recently a comparison of 2 models that incorporate the wider landscape context, the countryside SAR (Pereira & Daily 2006) and the matrix-calibrated SAR was conducted by Koh and Ghazoul (2010). Here we show that the results of that comparison are incorrect and that in contrast with their results, the countryside SAR outperforms both the matrix-calibrated SAR and classic SAR projections in projecting tropical bird extinctions.

The countryside SAR classifies species into functional groups with particular affinities for different habitats in

the landscape. The richness of each functional group  $S_i$  is given by

$$S_i = c_i \left( \sum_{j=1}^m b_{ij} A_j \right)^{z_i}, \quad (1)$$

where  $b_{ij}$  is the affinity of functional group  $i$  to habitat  $j$ ,  $A_j$  is the area of habitat  $j$  in the landscape,  $m$  is the number of habitat types, and  $c_i$  and  $z_i$  are the usual parameters of the classic SAR. Affinity can be interpreted as the proportion of area of habitat  $j$  that is usable by functional group  $i$ , so that  $0 \leq b_{ij} \leq 1$ .

Consider a completely native landscape where habitat conversion takes place. Assuming there is a single functional group (i.e., dropping the subscript  $i$  in Eq. 1), the proportion of species remaining after habitat conversion is

$$\frac{S^{\text{new}}}{S^{\text{org}}} = \left( \frac{\sum_j b_j A_j^{\text{new}}}{b_1 A_1^{\text{org}}} \right)^z, \quad (2)$$

where  $A_1^{\text{org}}$  is the original area of the native habitat,  $A_j^{\text{new}}$  is the area of habitat  $j$  after conversion,  $S^{\text{new}}$  is the new number of species in the landscape, and  $S^{\text{org}}$  is the original number of species. The original area of native habitat equals the sum of the new areas of all habitats,  $A_1^{\text{org}} = \sum_j A_j^{\text{new}}$ . Furthermore, we assume that species have maximum affinity for the native habitat,  $b_1 = 1$ .

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**Table 1.** Goodness of fit of the classic species–area relationship (SAR), countryside SAR, and matrix-calibrated SAR projections of bird extinctions in 20 biodiversity hotspots ( $z = 0.35$ ).<sup>a</sup>

Model	$\sum \varepsilon^2$	AIC	w (%)	Evidence ratio
Countryside SAR	3,417.2	46.7	77.4	1.00
Matrix-calibrated SAR	4,535.1	49.1	22.6	3.42
Classic SAR	34,320.6	66.7	0.0	22,446

<sup>a</sup>Modified from Koh and Ghazoul (2010). The  $\sum \varepsilon^2$  is the sum of the squares of the differences between projected extinctions and observed number of extinct and threatened species; AIC is the Akaike’s information criterion calculated as  $AIC = n \log \left( \frac{\sum \varepsilon^2}{n} \right) + 2K$ , where  $n = 20$  biodiversity hotspots and  $K$  (number of parameters) is 1;  $w$  is the Akaike weight  $(e^{-\Delta AIC/2} / \sum_i e^{-\Delta AIC_i/2})$  where  $\Delta AIC$  is the difference between the AIC of that model and the best model; and evidence ratio is the ratio between the Akaike weight of the best model and that model.

Koh and Ghazoul (2010) proposed instead the matrix-calibrated SAR, which gives the proportion of species remaining as

$$\frac{S^{new}}{S^{org}} = \left( \frac{A_1^{new}}{A_1^{org}} \right)^{z \sum_{j=1}^m p_j \sigma_j}, \quad (3)$$

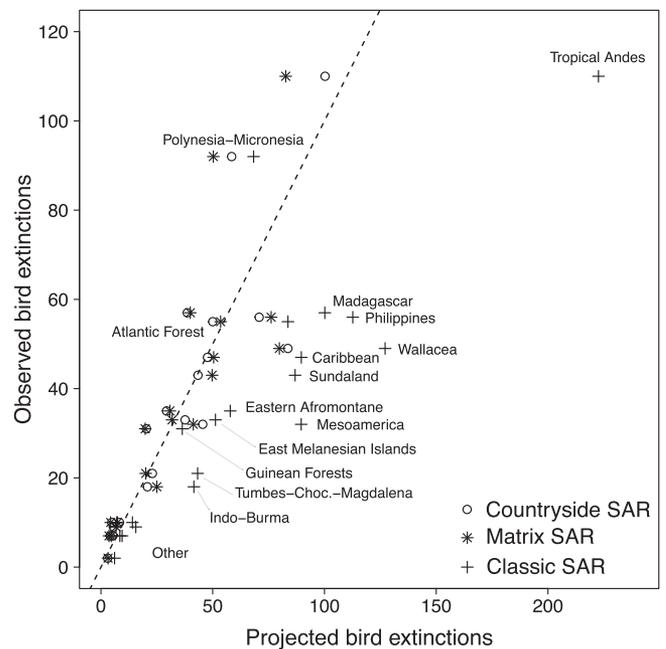
where  $p_j$  is the proportional area of habitat  $j$  relative to the total converted area (area of the matrix),  $p_j = \frac{A_j^{new}}{A_1^{org} - A_1^{new}}$ , and  $\sigma_j$  is the sensitivity of the taxon to the transformed habitat ( $\sigma_1 = 0$ ).

To compare the performance of different species-area models in projecting species extinctions, Koh and Ghazoul examined birds in 20 biodiversity hotspots in the world. For each hotspot they estimated the proportion of native habitat remaining and the proportion converted to disturbed forest, agricultural land, and urban area. For each hotspot, they estimated the number of species extinct or threatened with extinction as all endemic bird species in each hotspot classified as extinct, critically endangered, endangered, or vulnerable by the IUCN. Threatened species are included because they are expected to become extinct when species richness reaches an equilibrium with the amount of remaining habitat. Next they estimated sensitivities,  $\sigma_j$ , and affinities,  $h_j$ , through the use of a database of studies of how many species disappear locally when natural habitat is converted to each type of human-dominated landscape.

For the countryside SAR, the affinity for habitat  $k$  can be derived from such a database with Eq. 2,

$$\frac{S^{new}}{S^{org}} = \left( \frac{h_k A_k^{new}}{A_1^{org}} \right)^z = h_k^z, \quad (4)$$

if one assumes full habitat conversion ( $A_1^{new} = 0$  and  $A_k^{new} = A_1^{org}$ ). For the matrix-calibrated SAR, it is not possible to derive such an expression for full habitat conver-



**Figure 1.** Comparison of observed and projected number of extinct and threatened endemic bird species in 20 biodiversity hotspots (dashed line, perfect fit between projections and observations). Modified from Koh and Ghazoul (2010).

sion because Eq. 3 always tends to zero when  $A_1^{new} \rightarrow 0$ . Instead Koh and Ghazoul assumed:

$$\frac{S^{new}}{S^{org}} = 1 - \sigma_k. \quad (5)$$

This shows that affinities and sensitivities are related because  $h_k^z = 1 - \sigma_k$ . Unfortunately, Koh and Ghazoul calculated the affinities simply as  $h_k = 1 - \sigma_k$  and ignored the exponent  $z$ . Using this incorrect calculation of affinities they found that the best projections of endemic bird extinctions are with the matrix model, followed by the classic SAR, and that the countryside SAR has the worst performance. We recalculated the projections of extinction rates with the data from Koh and Ghazoul, the  $z$  value they used (0.35), and the correct estimate of habitat affinities. We found that the countryside SAR outperformed both the matrix-calibrated SAR and the classic SAR in this data set (Table 1, Fig. 1).

There might be other data sets where the matrix-calibrated SAR outperforms the countryside SAR; more research is needed to compare the different SAR models. The countryside SAR is particularly suitable to describe diversity patterns in multi-habitat landscapes even when the original cover or species composition is not known. The results of 2 recent studies show that the performance of the countryside SAR is better than the classic SAR in describing bird (Guilherme & Pereira 2013) and plant (Proenca & Pereira 2013) diversity in such landscapes.

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