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# The Countryside Species-Area Relationship Is a Valid Alternative to the Matrix-Calibrated Species-Area Model

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| Abstract: | |
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# The Countryside Species-Area Relationship Is a Valid Alternative to the Matrix-Calibrated Species-Area Model

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 (Wright 2010; Pereira et al. 2010; de Baan et al. 2013). Species-area relationships have been one of the main models used to develop such projections, but they have been recently criticized for overestimating extinctions (He & Hubbell 2011). One problem is that classic projections assume that all natural habitats converted to human-dominated habitats, such as agriculture and forestry, become completely hostile to biodiversity. However, there has been a growing recognition that many species are not constrained to native habitat fragments, and that the matrix habitats can play an important role in the conservation of biodiversity (Prugh et al. 2008; Karp et al. 2012). Recently a comparison of two models that incorporate the wider landscape context, the countryside SAR (Pereira & Daily 2006) and the matrix-calibrated SAR (Koh & Ghazoul 2010), has been done by Koh and Ghazoul (2010). Here we show that 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 landscapes. The richness of each functional group $S_i$ is given by

$$S_i = c_i \left( \sum_{j=1}^{m} h_{ij} A_j \right)^{z_i} \tag{1}$$

where $h_{ij}$ 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 species-area relationship. The affinities $h_{ij}$ can be interpreted as the proportion of area of habitat $j$ that is usable by functional group $i$, so that $0 \leq h_{ij} \leq 1$.

Consider now a landscape that was originally covered by native habitat only, which we name habitat 1. Assuming a single functional group (i.e. dropping the subscript $i$ in Eq. 1), the proportion of species remaining after habitat conversion is

$$\frac{S^{new}}{S^{org}} = \left( \frac{\sum_j h_j A_j^{new}}{h_1 A_1^{org}} \right)^{z} \tag{2}$$

where $A_1^{org}$ is the original area of native habitat, $A_j^{new}$ is the area of habitat $j$ after conversion, $S^{new}$ is the new number of species in the landscape, and $S^{org}$ is the original number of species. Note that the original area of native habitat equals the sum of the new areas of all habitats, $A_1^{org} = \sum_j A_j^{new}$. Furthermore, we assume that species have maximum affinity for the native habitat, $h_1 = 1$.

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

$$\frac{S^{new}}{S^{org}} = \left( \frac{A_1^{new}}{A_1^{org}} \right)^{z \cdot \sum_{j=2}^{m} p_j \sigma_j} \tag{3}$$

where $p_j$ is the proportional area of habitat $j$ relative to the total converted area (the 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.

In order to compare the performance of different species-area models in projecting species extinctions, Koh and Ghazoul (2010) look at birds in 20 biodiversity hotspots in the world. For each hotspot they estimate the proportion of native habitat remaining and the proportion that has been converted into each of three human-dominated habitats: disturbed forest, agricultural land and urban area. They estimate extinctions as all endemic bird species to each hotspot that have been classified as extinct, critically endangered, endangered or vulnerable by IUCN, assuming that threatened species would become extinct in the future when species richness would reach an equilibrium with the amount of available habitat. Next they estimate the sensitivities $\sigma_j$ and affinities $h_j$ using a database of studies of how many species disappear locally when natural habitat is converted to each of the human-dominated habitats.

For the countryside SAR, the affinity for habitat $k$ can be derived from such database using Eq. (2),

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

where we assume 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 conversion as Eq. (3) always tends to zero when $A_1^{new} \rightarrow 0$. Instead Koh and Ghazoul (2010) assume:

$$\frac{S^{new}}{S^{org}} = 1 - \sigma_k \tag{5}$$

This shows that affinities and sensitivities are related as ${h_k}^z = 1 - \sigma_k$. Unfortunately, in their paper, Koh and Ghazoul (2010) calculate the affinities simply as $h_k = 1 - \sigma_k$, ignoring the exponent $z$. Using this incorrect calculation of affinities they find that the best projections of endemic bird extinctions are made by the matrix model, followed by the classic SAR, and that the countryside SAR has the worst performance. We have recalculated the projections of extinction rates using the data from Koh and Ghazoul (2010) and the same z-value (0.35), but the correct estimate of habitat affinities. We found that the countryside SAR outperforms both the matrix-calibrated SAR and the classic SAR in this dataset (Table 1, Figure 1).

There might be other datasets where the matrix-calibrated SAR outperforms the countryside SAR, and 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 habitat cover or species composition is not known. Recently, two studies have shown 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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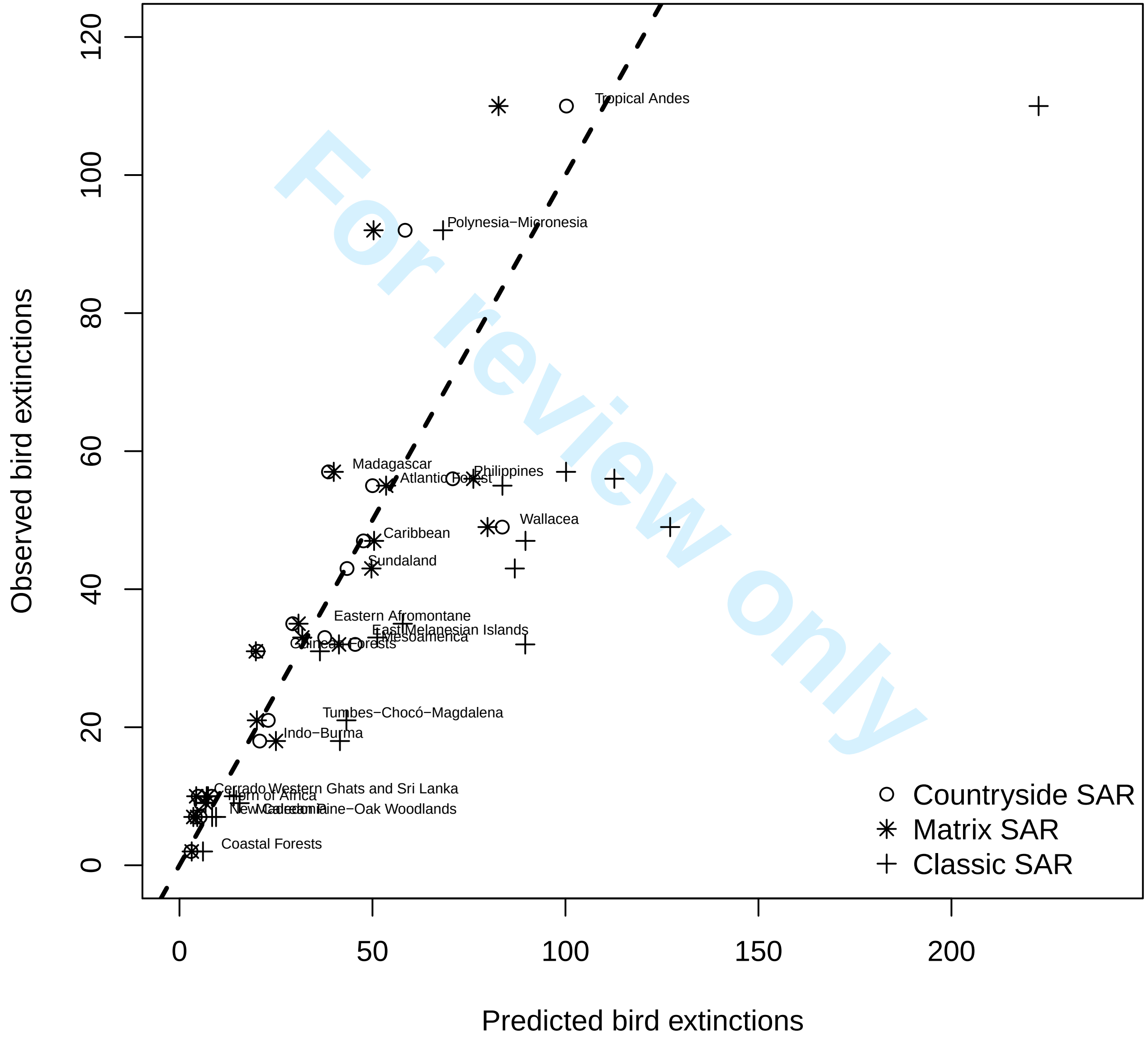
**Table 1. Comparison of the classic SAR, countryside SAR and matrix-calibrated SAR in predicting extinct or threatened endemic bird species in 20 biodiversity hotspots (z=0.35). Modified from Koh and Ghazoul (2010).**

| Model | $\sum\varepsilon^2$ | AIC | $w_i$ (%) | Evidence ratio |
|---|---|---|---|---|
| Countryside SAR | 3417.2 | 46,7 | 77,4 | 1,00 |
| Matrix-calibrated SAR | 4535.1 | 49,1 | 22,6 | 3,42 |
| Classic SAR | 34320.6 | 66,7 | 0,0 | 22446 |

**Figure 1. Comparison of observed and predicted number of extinct and threatened endemic bird species in 20 biodiversity hotspots. Modified from Koh and Ghazoul (2010).**


Observed bird extinctions
Predicted bird extinctions
0
20
40
60
80
100
120
0
50
100
150
200
Tropical Andes
Polynesia−Micronesia
Madagascar
Atlantic Forest
Philippines
Wallacea
Caribbean
Sundaland
Eastern Afromontane
East Melanesian Islands
Mesoamerica
Guinean Forests
Tumbes−Chocó−Magdalena
Indo−Burma
Cerrado
Western Ghats and Sri Lanka
Horn of Africa
New Caledonia
Madrean Pine−Oak Woodlands
Coastal Forests
Countryside SAR
Matrix SAR
Classic SAR