BIODIVERSITY RESEARCH

Habitat fragmentation and the species–area relationship: a focus on total species richness obscures the impact of habitat loss on habitat specialists

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ABSTRACT

Aim The species–area relationship (SAR) is widely used in conservation science to predict the number of species likely to go extinct as a result of habitat loss. Often, studies employing the SAR use total species richness as the dependent variable. However, this overlooks the fact that habitat specialists and generalists differ in their susceptibility to habitat loss. We undertook a synthetic review of 23 habitat island datasets for birds to determine the impact of habitat generalists on the SAR.

Location Global.

Methods We sourced 19 habitat island datasets from the literature and combined these data with four of our own empirically gathered datasets. For each dataset, we classified all bird species as either forest habitat specialists or generalists. We then fitted the power SAR model (log–log and nonlinear forms) to the specialists, generalists and all species for each dataset and compared the resulting model parameters. We compared differences in the rate of change in richness with area between specialists and generalists using the first derivative of a multimodel SAR.

Results We found that the slope of the power model was steeper for habitat specialists in the majority of datasets, and this difference was significant in 15 and 16 of the 23 datasets, for the nonlinear and log–log forms of the power model, respectively. Comparison of the multimodel SAR curve derivatives revealed further differences in the rate of change in species richness with area between subsets.

Main conclusions The z values of both forms of the power model of the specialists' SARs were generally larger, often considerably so, than the values used in most SAR studies predicting extinctions from habitat loss. Thus, studies that have used z values derived from SAR studies using total richness may be underestimating the impact of habitat loss on specialist species, which are likely to be those of greatest conservation concern.

Keywords

conservation biogeography, fragmentation, habitat generalists, habitat loss, habitat specialists, species–area relationship, woodland birds.

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INTRODUCTION

The increase in the number of species with the area sampled is one of the oldest and most reported patterns in ecology (e.g. Arrhenius, 1921; Rosenzweig, 1995; Lomolino, 2000;

Whittaker & Fernández-Palacios, 2007). Various types of species–area relationship (hereafter SAR) have been documented for multiple taxa and been found to hold at a variety of spatial scales (Drakare *et al.*, 2006; Whittaker & Fernández-Palacios, 2007; Dengler, 2009). SARs have been widely used in

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biodiversity conservation to aid the design of protected areas (e.g. Diamond, 1975), the setting of conservation targets (Desmet & Cowling, 2004), and to predict extinctions resulting from habitat loss and fragmentation (e.g. Brooks *et al.*, 1997; Magura *et al.*, 2001; Drakare *et al.*, 2006; He & Hubbell, 2011). As the anthropogenic fragmentation and destruction of natural habitats is regarded as the primary causal factor driving the decline in global biodiversity (Wilcove, 1987; Whittaker & Fernández-Palacios, 2007), the development of the SAR as a predictive tool is of particular importance within conservation biogeography.

Herein, we are concerned with type IV SARs *sensu* Scheiner (2003), also known as island species–area relationships or ISARs (Whittaker & Fernández-Palacios, 2007), which document the number of species within each isolate versus the area of each isolate. The majority of ISAR studies – including those concerning habitat fragmentation – use the total number of species recorded in the isolate as the dependent variable. A focus on total richness may be suboptimal as it ignores the fact that some species are more susceptible to fragmentation than others because they differ in their ecological traits, habitat dependency and resilience to disturbance (Whitcomb *et al.*, 1981; Humphreys & Kitchener, 1982; Howe, 1984; Henle *et al.*, 2004; Ewers & Didham, 2007). Viewing a fragmented landscape as a simplified binary of patches of natural habitat surrounded by a matrix of anthropogenic habitat, species can be dichotomized as habitat specialists and habitat generalists. Specialists are those species acutely dependent on resources located in the patches and tend to be species of conservation concern (Lövei *et al.*, 2006). Other species recorded in habitat fragments persist and utilize resources in the surrounding matrix and are, therefore, less dependent on the area of the patch ('habitat generalists'; e.g. Brotons *et al.*, 2003; Magura *et al.*, 2008; Ruiz-Gutiérrez *et al.*, 2010; Fahrig, 2013).

While the fragmentation of natural habitat often leads to the extirpation of habitat specialists, it can also result in an influx of generalist species, which acts to conceal the decline of the specialists. Hence, as the patch core : edge ratio declines with decreasing patch size, the ratio of generalist to specialist species is likely to increase (Humphreys & Kitchener, 1982; Magura *et al.*, 2001). If habitat generalists are less dependent on habitat area, it follows that their inclusion in ISAR or other SAR calculations must affect the resulting model parameters (cf. the species accumulation curve analyses of Cook *et al.*, 2002). Thus, it has been suggested (e.g. Magura *et al.*, 2001; Bommarco *et al.*, 2010) that analyses should be based on subsets of species classified according to their level of specialization.

If the depression of the ISAR slope (z value) through the inclusion of generalists is a general pattern, it implies that the impacts of fragmentation are likely to be more deleterious than predicted by models based on total richness. Despite these implications, there have been few studies to date that have empirically investigated the impact of habitat generalists on ISAR parameters (but see Magura *et al.*, 2001,

2008; Watling & Donnelly, 2008; Bommarco *et al.*, 2010; Banks-Leite *et al.*, 2012), and we are unaware of any synthetic analysis of multiple datasets to determine the effect of generalist species on ISAR parameters.

Herein, we undertake a synthetic review of habitat island datasets for forest birds to determine the impact of habitat generalists on the ISAR. For each dataset, we classify species as either habitat generalists or specialists based on their level of forest dependency. We then use two analytical approaches to determine the impact of habitat generalists on the ISAR in these datasets. First, we focus on the power SAR model (Arrhenius, 1921) as this is the most widely used model in conservation studies (Rosenzweig, 1995). The majority of studies utilize the linear (i.e. log–log) version of the power model (e.g. Watling & Donnelly, 2008). However, given modern advances in computing, we can also fit the (intrinsically superior) nonlinear version of the power model, which is particularly useful as the two versions result in different parameter estimates (Triantis *et al.*, 2012). Thus, we use both versions to ensure that our results are relevant to as broad a range of studies as possible. We fit both versions of the model to the specialist and generalist species separately, for each dataset, and compare the parameter estimates using various methods. Second, we fit a set of eight candidate ISAR models and generate a weighted multimodel ISAR curve for the specialists and generalists separately, from which we compare the rates of change in species richness with area for each dataset. We focus on birds because the strongest evidence of the negative impacts of habitat fragmentation has come from studies on bird populations in forest fragments (Robinson & Sherry, 2012). Birds are also a well-studied taxon, possessing traits that enable them to be accurately classified in regard to habitat specialization.

METHODS

Data acquisition and species classification

Relevant studies were identified via an extensive search of the databases 'ISI Web of Science' and 'Scopus' between May 2011 and June 2013. A wide range of search strings were used, involving rearranging and amalgamating the phrases 'habitat fragmentation', 'species–area relationships' and 'birds'. Each potential dataset was reviewed to ascertain that the following conditions were met:

1. A minimum of five forested habitat fragments had been sampled.
2. Each fragment conformed to Watson's (2002) definition of a true habitat island, that is, an area of natural habitat (in this case forest) surrounded by a matrix of a contrasting land use type.
3. The area of each fragment was presented.
4. The studies included a full inventory of the bird species in each fragment.
5. The dataset did not overlap with that from any other study that had been accepted for analysis.

In addition to the above, four fragmented landscapes in Europe (France, Spain, Norway and the UK) were sampled by TJM and the resulting datasets added to the analysis. In each of these landscapes, around 40 forest fragments of varying area (see Appendix S1 in Supporting Information for details) were sampled using 10 min point counts of 50-m radius. All birds seen or heard were recorded. Counts took place from dawn to 10:00 h during April–July in 2012 and 2013. Each fragment was sampled three times, with the time of sampling randomized in each instance.

To determine the habitat specialization level, T.J.M. and H.E.W.C.-J. classified each species independently based on a large amount of material sourced from the ornithological and wider ecological literature (a full list of the references and key terms used in the literature searches is provided in Appendix S1). We then compared our independent classifications and undertook further investigation (including obtaining additional opinions from various senior ornithologists) to classify species on which we initially disagreed. Species were classified based on their level of habitat specialization in regard to the habitat island type in each particular study (i.e. classification was not based on any metric of sensitivity to patch area). This classification was determined using a selection of information regarding species' traits and information on where the species had previously been recorded.

Data analysis

Power model

Three versions of each dataset were created: area–specialist species richness (herein 'SAR$_{sp}$'), area–generalist species richness (herein 'SAR$_g$') and area–total species richness (herein 'SAR$_t$'). Firstly, we fitted the linear version of the power function (log–log model) of Arrhenius (1921) to each version of the datasets, after log-transforming both variables, using linear regression:

$$\mathrm{Log}S = \mathrm{Log}c + z\mathrm{Log}A \tag{1}$$

where S = species richness, A = area, and z and c are fitted constants. All fragment areas were converted to hectares to permit comparison of the c parameter (Rosenzweig, 1995). All logarithmic transformations were to the base ten. As log (0) is non-defined, $\log(x + 0.1)$ was applied for the transformation of species richness in each case. We then fitted the nonlinear power model to each version of the datasets using nonlinear regression and the 'mmSAR' R package (Guilhaumon *et al.*, 2010):

$$S = c.A^z \tag{2}$$

To determine ISAR significance for the power models, the slope (z) of the observed regression line was tested in each case against a null hypothesis of the slope being equal to zero ($P < 0.05$). To determine whether the parameters (z and c)

of the log–log power model significantly differed between different versions of each dataset, ANCOVA was used to compare the regression lines of SAR$_{sp}$ and SAR$_g$. As SAR$_{sp}$ and SAR$_g$ are not independent of SAR$_t$, we could only compare the regression lines of SAR$_{sp}$ and SAR$_g$ using the ANCOVA model. A critical value of $P < 0.05$ was used. In addition, we calculated the effect size (Cohen's D) for each dataset using the ANCOVA F score and the 'compute.es' R package (Del Re, 2010). We then calculated the pooled effect size (d+) using the weighted mean of the individual effect sizes, where the weights represented the inverse of the variance of the individual effect sizes (Hedges & Olkin, 1985). A Z score and P value were generated to determine whether d+ was significantly different from zero.

Using ANCOVA is not possible for nonlinear models. Thus, to compare the z values of the nonlinear power model between specialists and generalists, we generated 95% confidence intervals for each parameter value and the z values were said to differ if the confidence intervals did not overlap (cf. Gaston *et al.*, 2006).

Multimodel inference

While the power model is the most frequently used ISAR model, it should not be assumed that it provides a better fit than competitor SAR models *a priori* (although for real islands, a recent synthetic analysis shows that it is the best performing model overall; Triantis *et al.*, 2012). Thus, we fitted a set of eight SAR models (power, exponential, negative exponential, Monod, logistic, ratio, Weibull-3 and Lomolino) to the SAR$_{sp}$ and SAR$_g$ versions of each dataset using nonlinear regression and the mmSAR R package. Models were compared using Akaike's information criterion corrected for small sample size (AIC$_c$; Burnham & Anderson, 2002). Models with the lowest AIC$_c$ value were considered to provide the best fit, and all models within ΔAIC$_c < 2$ of the best model were considered to have similar support (Burnham & Anderson, 2002).

We used the 'multi-SAR' function in the mmSAR package to generate a multimodel SAR curve for each version of the datasets by weighting the predicted values of the eight aforementioned SAR models based on the Akaike weights of the individual models (Guilhaumon *et al.*, 2010). To compare the multimodel SAR curves between SAR$_{sp}$ and SAR$_g$ for each dataset, we calculated the first derivative of the multimodel SAR curves (i.e. the rate of change in species richness with respect to area; cf. Diouf *et al.*, 2009) and plotted the derivative as a function of island area (i.e. we constructed a growth rate curve). This was performed separately for each dataset, and examination of the relative position of the specialist and generalist curves in these plots allowed us to infer differences in the rate of change in species richness with area between specialists and generalists. As a further test we subtracted the generalist curve from the specialist curve: unless the curves cross, a positive result indicates that the specialist curve is steeper.

Specialist : generalist ratio

Following previous workers (e.g. Humphreys & Kitchener, 1982; Sfenthourakis & Triantis, 2009), we calculated the ratio of specialist to generalist species (herein 'S : G') in each habitat island and plotted this against island area for each study system. We also conducted boundary tests using EcoSim (Gotelli & Entsminger, 2001) for each ratio plot to determine whether any corners of the plots contained fewer data points than expected by chance. Both the 'number of points' and 'sum of squares' boundary test methods were used. With the exception of the boundary tests, all analyses were conducted in R (version 3.0.0.; R Development Core Team, 2013).

RESULTS

More than 250 published articles were screened, from which 19 datasets were deemed suitable for analysis (see Appendix S1 for details). Grouping these with our own four sampled datasets resulted in 23 datasets in total. All datasets comprised forested habitat islands surrounded by a matrix of contrasting habitat. In the majority of cases the matrix comprised agricultural land uses.

Power (log–log)

For 16 of the 23 (70%) datasets, the slopes of the linear regression lines significantly differed between SAR_g and SAR_{sp} (Table 1), with the slopes (z values) being steeper for SAR_{sp} ISARs in each case (Table 1, see Fig. 1 for example). Indeed, with the exception of system 22, which failed to provide a significant ISAR for SAR_{sp}, SAR_g or SAR_t, all z values were higher for SAR_{sp} than SAR_g. For six of the seven datasets in which the slopes did not significantly differ, the intercepts were significantly different (results not presented). Only for system 10 did both the slopes and intercepts of the specialist and generalist ISARs not differ significantly. The effect size results followed the ANCOVA results, that is, the datasets with significant values of Cohen's D were the same datasets in which the ANCOVA results were significant (individual Cohen's D values are given in Table 1). The pooled effect size (d+) was 0.53 (CIs: 0.39–0.66; $Z = 7.5$, $P \leq 0.0001$), which indicates a medium to large effect size.

Table 1 Model fit and ANCOVA results for the 23 bird habitat island datasets. The z value of the power SAR function (log–log) model along with the P value corresponding to the significance of the z value in parentheses is presented. The z value is given for the model parameters calculated using all species and specialist and generalist species separately. For each dataset, the F statistic and corresponding P value of the ANCOVA model with species richness as the dependent variable, island area as the covariate and species type (i.e. generalist or specialist) as the two level factor is also given. Cohen's D effect size metric is also given in each case (calculated using the ANCOVA F statistic). All ANCOVA and Cohen's D P values significant at the 0.05 level are highlighted in bold.

| Dataset	z (P value)			ANCOVA		
	All species	Specialists	Generalists	F value	P value	Cohen's D (P)
1	0.04 (0.08)	0.09 (0.00)	−0.07 (0.04)	18.17	**0.00**	1.63 (< **0.001**)
2	0.31 (0.00)	0.38 (0.00)	0.20 (0.00)	14.59	**0.00**	1.08 (< **0.001**)
3	0.13 (0.00)	0.31 (0.00)	0.08 (0.04)	11.67	**0.00**	1.24 (**0.01**)
4	0.68 (0.00)	0.95 (0.00)	0.61 (0.00)	11.43	**0.00**	0.28 (< **0.001**)
5	0.17 (0.00)	0.32 (0.00)	0.03 (0.26)	23.54	**0.00**	1.45 (< **0.001**)
6	0.20 (0.00)	0.58 (0.00)	0.18 (0.00)	5.34	**0.03**	0.62 (**0.03**)
7	0.68 (0.00)	0.63 (0.00)	0.62 (0.00)	0.01	0.91	0.03 (0.92)
8	0.18 (0.02)	0.36 (0.00)	0.11 (0.11)	10.62	**0.01**	1.21 (**0.02**)
9	0.11 (0.04)	0.26 (0.09)	0.08 (0.20)	1.34	0.26	0.44 (0.26)
10	0.08 (0.00)	0.09 (0.00)	0.06 (0.02)	1.23	0.28	0.32 (0.28)
11	0.15 (0.00)	0.18 (0.00)	0.13 (0.00)	1.90	0.19	0.48 (0.2)
12	0.20 (0.00)	0.29 (0.00)	0.14 (0.00)	7.81	**0.02**	0.35 (**0.04**)
13	0.25 (0.00)	0.53 (0.00)	0.20 (0.00)	9.02	**0.00**	0.47 (< **0.001**)
14	0.36 (0.00)	0.60 (0.00)	0.33 (0.00)	9.69	**0.00**	0.45 (< **0.001**)
15	0.19 (0.00)	0.58 (0.00)	0.17 (0.00)	9.52	**0.00**	0.45 (< **0.001**)
16	0.29 (0.00)	0.61 (0.00)	0.25 (0.00)	9.55	**0.00**	0.52 (< **0.001**)
17	0.20 (0.00)	0.58 (0.02)	0.17 (0.01)	3.96	**0.05**	0.59 (**0.05**)
18	0.21 (0.04)	0.38 (0.01)	0.06 (0.58)	9.67	**0.02**	1.42 (**0.04**)
19	0.62 (0.00)	0.96 (0.00)	0.55 (0.00)	7.15	**0.01**	0.44 (**0.01**)
20	0.21 (0.00)	0.32 (0.00)	0.14 (0.00)	4.96	**0.03**	0.52 (**0.04**)
21	0.07 (0.02)	0.09 (0.00)	0.06 (0.06)	0.60	0.45	0.21 (0.45)
22	0.03 (0.08)	0.02 (0.26)	0.04 (0.06)	0.78	0.39	0.32 (0.4)
23	0.12 (0.00)	0.17 (0.00)	0.09 (0.02)	2.83	0.11	0.2 (0.12)
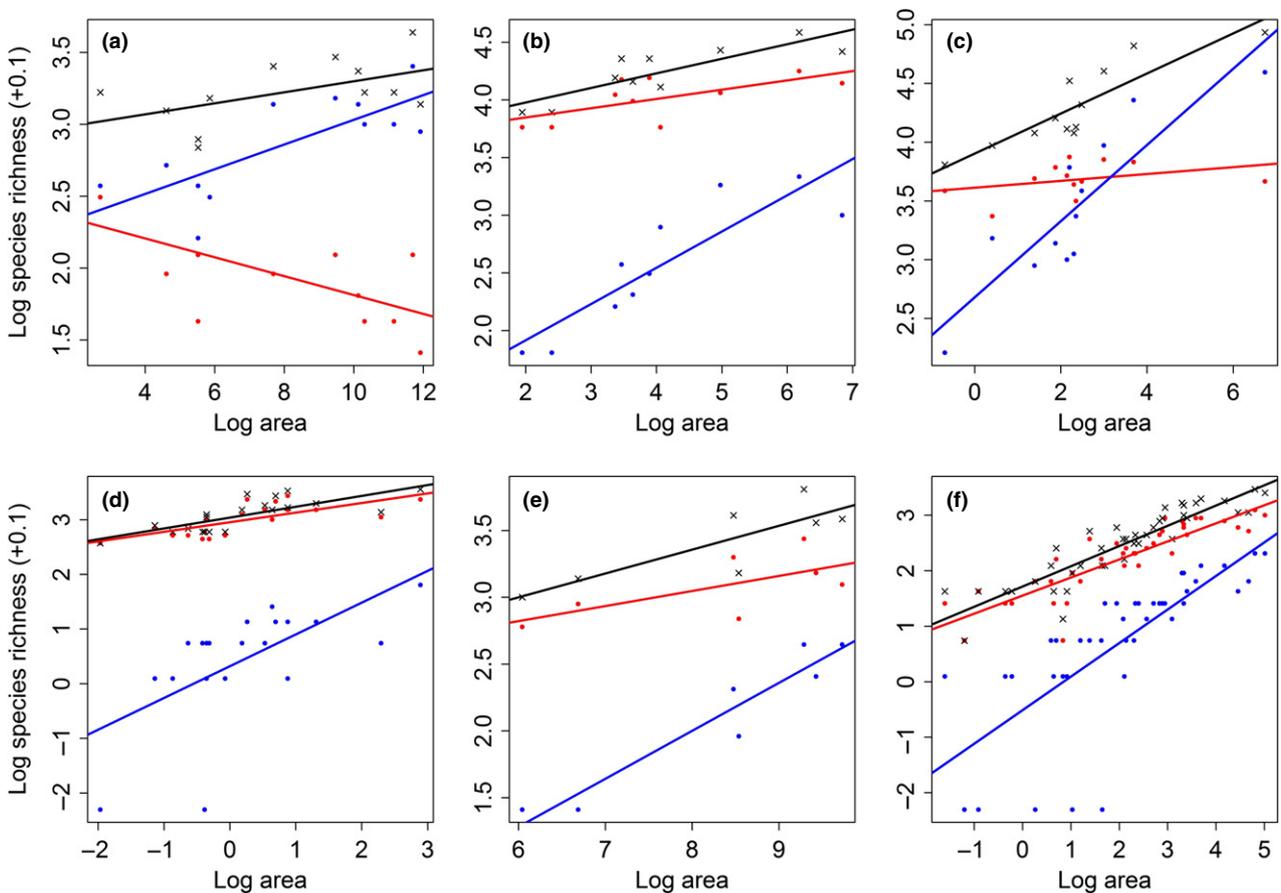
Figure 1 Selection of plots of type IV SARs *sensu* Scheiner (2003) (here termed ISARs) using log–log power models, for six bird datasets. In each plot, the data points (symbols) and linear regression best fit lines (solid lines) for all species (black crosses and line), specialists (blue dots and line) and generalists (red dots and line) are presented. In two instances, the slope of the regression line for the generalist species was not significantly different from zero (c & e); in all other instances, the slope of the regression line was significantly different from zero (i.e. $P < 0.05$). The sources of the datasets are as follows: (a) Anciães & Marini (2000), (b) Castelletta *et al.* (2005), (c) dos Anjos & Boçon (1999), (d) Ford (1987), (e) Gillespie & Walter (2001) and (f) this study – Norway. See Appendix S1 for full details on each of the datasets. All areas are in hectares (log transformed to the base ten).

Power (Nonlinear)

While the parameter values generated from the nonlinear power model (Table 2 & Table S2 in Appendix S2) differed from those generated by the log–log model (compare Table 1 with Table 2), the overall results were qualitatively similar. For 15 (65%) datasets, the z value of the SAR_{sp} was greater than that of the SAR_g and the confidence intervals did not overlap (Table 2). For the remaining datasets, the z value of the SAR_{sp} was larger, but the confidence intervals did overlap.

A large range in z values was observed for SAR_t, SAR_{sp} and SAR_g for both the log–log and nonlinear versions of the power model (Fig. 2). Across all studies, the z values of SAR_{sp} and SAR_g differed significantly according to a Welch's two sample t-test for both the log–log model ($t = 3.34$, $P \leq 0.001$) and the nonlinear model ($t = 4.21$, $P \leq 0.001$). The c parameter was lower for SAR_{sp} compared with SAR_g and SAR_t, for all 23 systems, for

both forms of the model, and the difference in c values between SAR_{sp} and SAR_g was significant for both models (log–log: $t = -4.86$, $P \leq 0.001$; nonlinear: $t = -3.72$, $P \leq 0.001$).

Multimodel inference

The power model (nonlinear) was selected as the best model or was within $\Delta < 2AIC_c$ of the best model, for 15 SAR_g datasets and 14 SAR_{sp} datasets (Table S3 in Appendix S2). For the remaining datasets, a variety of the other candidate models provided the best fit (Table S3). Analysis of the derivative plots and subtraction results indicated that the rate of change in richness with area was greater for specialists than generalists for 15 of the 23 datasets (see Fig. 3 for example; all plots presented in Fig. S1 in Appendix S2). In one dataset (plot k in Fig. S1), the curves were almost identical, and in the remaining six, the generalists' curve was steeper. In terms of overlap with the

Table 2 z parameter of the nonlinear power SAR model and associated lower (LCI) and upper (UCI) 95% confidence intervals for the 23 bird habitat island datasets. The z value is given for the model parameters calculated using specialist and generalist species separately. For each dataset, the z values were said to be significantly different between generalists and specialists if the confidence intervals for the z parameter did not overlap. Specialist z values that are significantly larger than generalist z values are highlighted in bold.

	Generalists			Specialists		
Dataset	z	LCI	UCI	z	LCI	UCI
1	−0.07 (1.00)	−0.14	−0.01	**0.08 (0.01)**	0.03	0.14
2	0.18 (0.00)	0.12	0.22	**0.29 (0.00)**	0.23	0.36
3	0.07 (0.04)	0.00	0.14	**0.29 (0.01)**	0.16	0.44
4	0.47 (0.00)	0.42	0.51	**0.58 (0.00)**	0.52	0.66
5	0.02 (0.32)	−0.03	0.07	**0.25 (0.00)**	0.17	0.34
6	0.15 (0.00)	0.07	0.21	**0.36 (0.00)**	0.22	0.53
7	0.16 (0.00)	0.08	0.23	**0.39 (0.00)**	0.24	0.54
8	0.11 (0.16)	−0.02	0.22	**0.38 (0.01)**	0.24	0.54
9	0.11 (0.13)	−0.03	0.27	0.16 (0.28)	−0.08	0.47
10	0.06 (0.02)	0.01	0.11	0.09 (0.00)	0.05	0.14
11	0.12 (0.00)	0.07	0.17	0.15 (0.00)	0.10	0.20
12	0.15 (0.00)	0.09	0.17	**0.32 (0.01)**	0.21	0.52
13	0.24 (0.00)	0.18	0.30	**0.45 (0.00)**	0.35	0.54
14	0.28 (0.00)	0.23	0.33	**0.43 (0.00)**	0.36	0.52
15	0.22 (0.00)	0.16	0.28	**0.44 (0.00)**	0.30	0.60
16	0.21 (0.00)	0.16	0.27	**0.42 (0.00)**	0.32	0.52
17	0.16 (0.02)	0.04	0.29	0.3 (0.04)	0.05	0.58
18	0.04 (0.64)	−0.24	0.32	0.35 (0.01)	0.16	0.58
19	0.35 (0.00)	0.32	0.38	**0.43 (0.00)**	0.40	0.43
20	0.14 (0.00)	0.09	0.17	**0.24 (0.00)**	0.21	0.33
21	0.07 (0.07)	−0.01	0.15	0.08 (0.01)	0.03	0.13
22	0.05 (0.05)	0.00	0.09	0.02 (0.26)	−0.02	0.06
23	0.1 (0.00)	0.05	0.15	0.17 (0.00)	0.11	0.24

power model results, in three datasets with a significant ANCOVA result, the rate of change in richness with area for specialists was less than for generalists; and for four datasets with a non-significant ANCOVA result, the specialists' derivative curve was steeper.

Specialist : generalist ratio

Inspection of the plots of S : G against island area indicates that in the majority of cases, S : G increases with island area but in a nonlinear fashion, that is, after a certain island area, the relationship tends to flatten out (see Fig. 4 for example; all plots are presented in Fig. S2 in Appendix S2). The boundary tests revealed no significant results when using the 'number of points method' for any quadrant of the plots and only one marginally significant result for the lower right quadrant ($P = 0.05$; dataset 14) when using the 'sum of squares' method (results not presented). Thus, in all but one case, there were no regions of the ratio plots that were unusually empty.
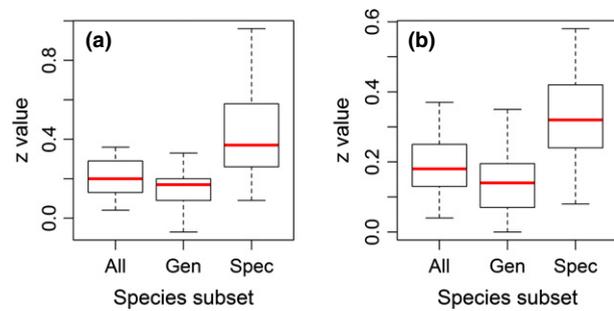

Figure 2 Box plots displaying the z values of the power model (log–log) (a) and the nonlinear power model (b). Only z values from significant ISARs are used to generate the plots. z values are presented for the model fitted using all species in the dataset (all) and using generalist (Gen) and specialist (Spec) species separately. See Table 1 and Table S3 for the individual z values for both models.

DISCUSSION

Generalist species mask the decline in specialists following habitat loss

The ISAR is an important conservation tool and is often used to predict the number of extinctions resulting from the loss of native habitat (see Fattorini & Borges, 2012). However, when calculating the ISAR total species richness is often used, which amalgamates habitat specialists and generalists into a single sample. We amassed 23 habitat island datasets for forest birds and classified all species into generalists and specialists. We found that in 15 and 16 cases, the slope of the specialists' ISAR was significantly steeper than the generalists' ISAR, for the nonlinear and log–log versions of the power model, respectively. Analysis of the multimodel derivative plots also reveals differences in the rate of change in species richness with area between subsets.

In predictive ISAR studies, it is often the case that a set z value derived from the literature is used, such as the canonical value (Preston, 1962) of approximately 0.25 (e.g. Brooks et al., 1997). However, our results show that the z value of SAR_{sp} was greater than 0.25 in 17 (74%) of the datasets when the log–log model was used, and in 14 (61%) of the datasets using the nonlinear model (Tables 1 and 2). In fact, the mean z value for SAR_{sp} was considerably larger than 0.25 for both models (Fig. 4). As specialists are largely the species that are at risk of extinction due to habitat loss (Howe, 1984), it seems unwise to assume a z value lower than the average for such species. These differences are not trivial. For example, consider a hypothetical 100-ha patch of habitat containing 350 species, which is reduced in area by 50%. Using the backward version of the power model (see Brooks et al., 1997; Whittaker & Matthews, 2014) with a traditional z value of 0.25, results in 56 predicted patch extinctions, while a z value of 0.95 (the highest we recorded) results in 170 predicted patch extinctions. This issue can be further exemplified by that the fact that in one dataset, the ISAR
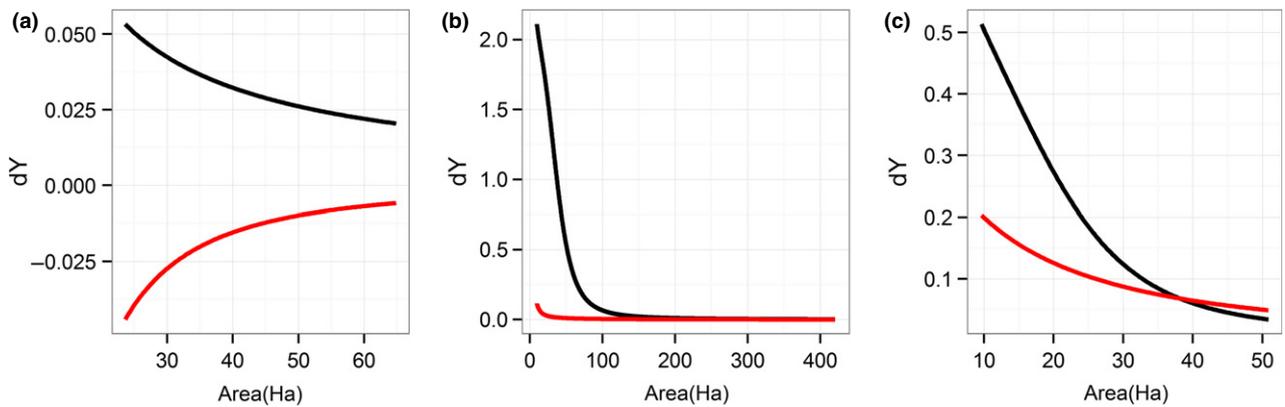
Figure 3 Selection of derivative plots for three bird habitat–island datasets. In each plot the curves represent the first derivative of the multimodel SAR curve (dY) plotted against island area, for both specialists (black line) and generalists (red line). Thus, the curves represent the change in the slope of the multimodel SAR curve with increasing area. The plots have been truncated at the right-hand side to improve presentation. The sources of the datasets are as follows: (a) Anciães & Marini (2000), (b) dos Anjos & Boçon (1999) and (c) this study – Norway. See Appendix S1 for full details for each of the datasets.
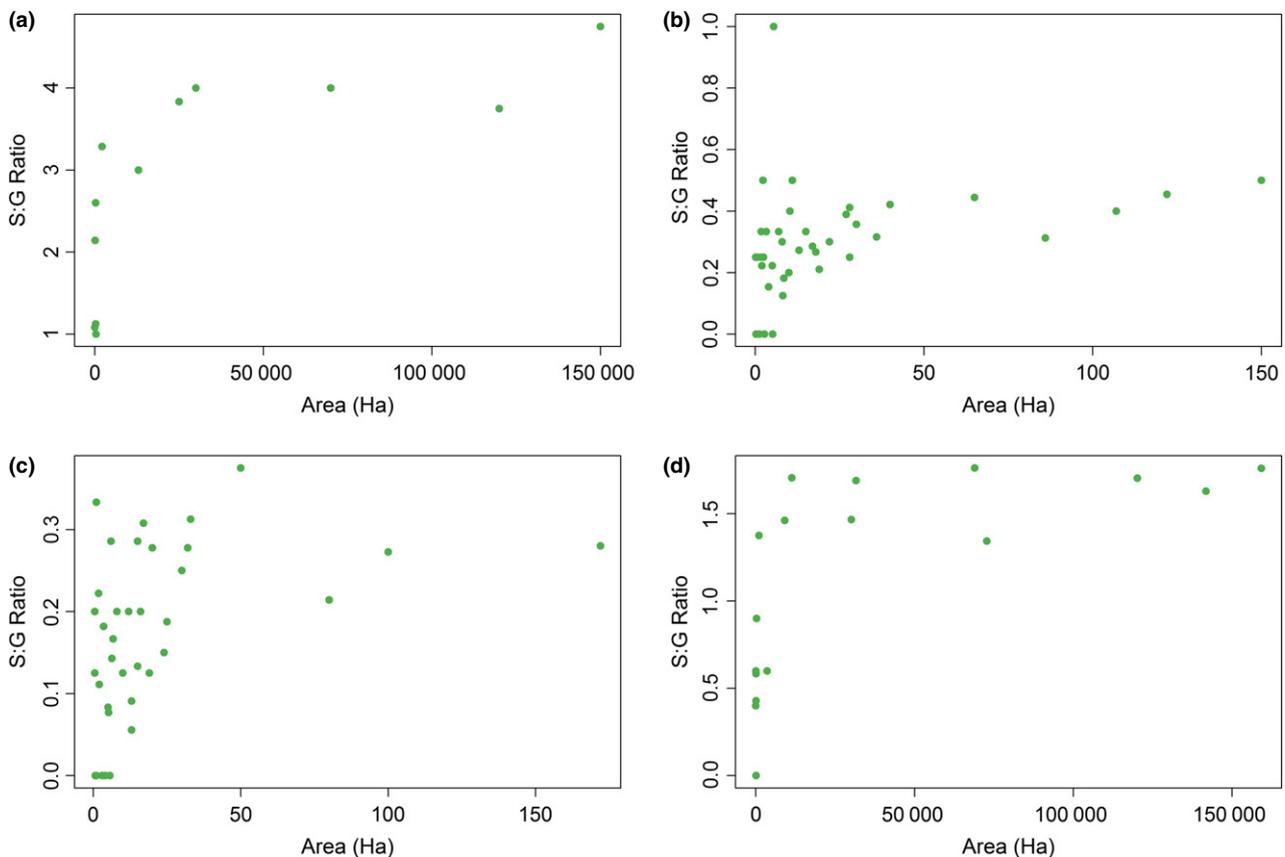
Figure 4 Selection of plots in which the ratio of specialist species to generalist species (S : G) against habitat island area is plotted for a selection of bird datasets. The sources of the datasets are as follows: (a) Anciães & Marini (2000), (b) this study – Norway, (c) this study – UK and (d) Watson (2003). See Table S1 in Appendix S1 for full dataset information. Each of the plots illustrates the threshold pattern whereby over small areas the ratio of specialist to generalists increases rapidly, but after a point the relationship flattens.

(log–log) of generalists is in fact negative (Fig. 1a). Closer inspection of the species in this dataset reveals there to be a small number of species in the smaller patches, that are primarily matrix specialist species (e.g. *Thraupis sayaca*) and whose incidence declines with increasing area, contributing to the observed negative ISAR.

We are not the first to report z values for habitat islands exceeding the commonly used 0.25 value. Whereas some studies have argued that standard SARs always overestimate the number of extinctions (e.g. He & Hubbell, 2011), a number of studies have argued that they usually underestimate extinctions (Brooks et al., 2011; Fattorini & Borges, 2012). Such differences of view may reflect factors such as the analytical approach taken, opinions on delayed extinctions (i.e. extinction debt; Triantis et al., 2010; Tanentzap et al., 2012) or the effects of fragmentation that generally accompany habitat loss (Fattorini & Borges, 2012). We caution, however, that in their analysis of 465 'real' island datasets, Triantis et al. (2012) observe strong scale dependency of the z value, which tends to decline with increasing range of island areas. Given that only four of our datasets have a maximum island size > 1000 ha, two of which have z values lower than 0.25, it would be unwise to assume that the distribution of z values reported in Table 1 is representative of larger scales of application (e.g. the analyses of Brooks et al., 1997). However, it is worth bearing in mind that the majority of habitat island datasets contain relatively small islands in relation to oceanic island datasets. These observations point to the need for further work to establish appropriate z values for applications involving extinction risk estimates for habitat specialists and specifically for potential scale (range of area and range of isolation) sensitivity of ISAR parameters for habitat island systems.

Interpreting patterns in the c parameter of the power model is even less straightforward than for the z parameter (Gould, 1979; Whittaker & Fernández-Palacios, 2007). One commonly accepted interpretation is that c represents a measure of the carrying capacity of the system, that is, the species richness present at one unit of area (Gould, 1979; Rosenzweig, 1995). Thus, as the c value of specialists was always lower than for generalists, our results indicate that one unit area of habitat island forest can support fewer specialist species than generalist species. This is consistent with previous studies that have reported that, in general, habitat specialists require more patch resources than generalists to complete their life history (see Henle et al., 2004) and that generalists are less reliant on patch resources as they are more able to utilize resources in the surrounding matrix (Brotons et al., 2003). This pattern in c values again implies that habitat specialists are more sensitive to habitat loss than habitat generalists; combining the two sets of species acts to average out the parameter value in the aggregate.

The good performance of the power model for the majority of datasets is reassuring, given that it is the most widely used ISAR model (see also Triantis et al., 2012). However, with the exception of the logistic model, every ISAR model was selected as the best model for at least one version of a dataset (Table S3), thus emphasizing the potential relevance of considering multiple models in ISAR analyses. In this regard, our method of comparing the derivative curves is a practical and robust way of combining an assemblage deconstruction approach with multimodel inference, which

is independent of species richness, and we recommend its use in future studies of this nature (see also Diouf et al., 2009).

This is not the first study to advocate the use of a dependent variable other than total species richness when using the ISAR or other SARs for conservation purposes (e.g. Humphreys & Kitchener, 1982; Azeria et al., 2007; Watling & Donnelly, 2008; Bommarco et al., 2010). For example, a number of studies have advised using only endemic species and the related endemic–area relationship ('EAR'; e.g. He & Hubbell, 2011; Tanentzap et al., 2012), and others have shown differences in ISARs between native and introduced species (Magura et al., 2008). However, this is, to our knowledge, the first study to use multiple datasets to quantify how subdivision into generalists and specialists alters the parameters of ISARs, parameters which in turn are often used to guide conservation efforts (but see Bommarco et al., 2010; Banks-Leite et al., 2012 for examples using data from individual systems).

Our primary finding that the SAR_{sp} was steeper than the SAR_g was not universal, and a number of datasets exhibited the opposite pattern. A possible explanation for this counter-intuitive result is that for these datasets, a large number of specialist species have already been extirpated from the larger habitat islands, which acts to depress the SAR_{sp} (see Bommarco et al., 2010). For example, the Castelletta et al., (2005; dataset number 3 in Table S1) dataset is of birds in forest fragments on the island of Singapore. Singapore has suffered almost complete deforestation (approximately 99.5% of native forest has been removed) and habitat degradation, which has had significant negative effects on the native avifauna (Castelletta et al., 2005). It is thus likely that the most patch area-sensitive species have already been extirpated from the system, confounding our ISAR analyses. It is also possible that other life history traits, such as body size and dispersal capability (Ewers & Didham, 2007; Bommarco et al., 2010), are more important than habitat specialization in moderating the ISAR for species in these datasets.

Ratio of specialists to generalists

The ratio of specialists to generalists (S : G) generally increases steeply with patch area before appearing to flatten out (Fig. 3). Other studies have shown that S : G increases with area (e.g. Whitcomb et al., 1981; Humphreys & Kitchener, 1982), but the flattening of the relationship has not been generally recognized. The initial increase in S : G with area results from the fact that certain species respond positively to fragmentation (i.e. edge and generalist species) and are thus more likely to be present in smaller patches (McCollin, 1993). By definition, generalists have a wider niche and less specialized resource requirements than specialists, in addition to being better able to utilize resources outside the patch (Laurance & Bierregaard, 1996). Taken together, these traits allow generalists to maintain high levels of occupancy in small patches. In contrast, specialists are

expected to have a low incidence in smaller patches as both the resource base (Dennis *et al.*, 2012) and habitat diversity (Ricklefs & Lovette, 1999) are reduced. At large patch sizes, the increased resource availability allows larger populations of specialists to coexist and out-compete the generalist species (Diamond, 1979). Thus, generalists and specialists have the opposite incidence function with respect to area, which explains the initial increase in S : G with area. The flattening of the S : G relationship could be due to two reasons. First, the relationship may simply mirror the power law ISAR curve whereby in larger patches, few species of any type are added. Second, it may be that as patch area increases richness continues to rise, but specialists and generalists are added at a constant rate. Examination of the data suggests that both processes are occurring. In certain datasets, the S : G relationship flattens as the rate of species addition decreases with area in accordance with a power law relationship, while in other datasets, richness continues to increase in larger patches, albeit at a slightly reduced rate, but specialists and generalists are added at the same rate.

Conservation implications

Our results indicate that SAR_{sp} ISARs have higher z values than do SAR_g ISARs; in the majority of cases significantly so. Analysis of multimodel derivative curves provides further evidence for differences in the rate of change in richness with area between subsets. Thus, studies that have used total species richness, or z values derived from ISAR studies using total richness, to estimate the effects of habitat loss, may in this respect be underestimating the impact of fragmentation on the loss of specialist species, which are likely to be those of greatest conservation concern. By the same token, they may be overestimating the value of small fragments. At the extreme, you could have a situation whereby following a fragmentation event, a set of newly created forest fragments undergoes complete turnover of species, replacing all the forest specialists with matrix generalist and edge species. The z value of the ISAR before and after turnover might remain relatively consistent, indicating no biodiversity loss through time and masking the loss of the forest specialists (Banks-Leite *et al.*, 2012). It is also possible that this 'masking effect' is impeding our ability to detect other ecological patterns. For instance, Krauss *et al.* (2010) found evidence of an extinction debt in grassland vascular plant specialists, but not for non-specialized species, in a study of 147 European grasslands. However, it always has to be recalled that ISARs describe merely how many species are found on average in a patch or island of a particular size and do not describe the degree of compositional overlap or beta diversity across the system. Should the distribution of species be highly nested, then it follows that there should be a close correspondence between ISAR form and species loss rates, but if the distributions are strongly non-nested, then there may be decoupling of extinction risk from ISAR form (see discussion in Whittaker & Fernández-Palacios, 2007).

In sum, a focus on total richness in ISAR studies can be misleading as the sensitivity of different species groups to habitat area shows high variability. A deconstruction approach (Marquet *et al.*, 2004), whereby the total species compliment is split into constituent subsets (e.g. based on trophic status or habitat specialization), has been advocated as a useful method for ecological and conservation oriented research, but is regularly overlooked in ISAR studies (but see Bommarco *et al.*, 2010). Our results indicate that predictions of specialist species loss following fragmentation are too moderate in the absence of a deconstruction approach. This finding is especially concerning as these are the species that are most sensitive to fragmentation. Therefore, we argue that it is essential to adopt a deconstruction approach if the ISAR is to be an effective conservation tool.

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SUPPORTING INFORMATION

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

Appendix S1 Data source paper summaries, references and species classification methodology.

Appendix S2 Supplementary results, including Tables S1, S2 and S3 and Figs S1 and S2.

Table S1 Source paper information.

Table S2 The c parameter and R^2 values of the power model for the three versions of each dataset.

Table S3 Model selection results.

Figure S1 The derivative plots for each dataset.

Figure S2 The S : G ratio plots for each dataset.

BIOSKETCHES

Tom Matthews is a doctoral student at the University of Oxford. He is interested in the study of macroecological patterns in habitat islands and the application of island theory to fragmented landscapes. His recent work has focused on the prevalence of multimodal species abundance distributions in fragmented landscapes and the use of piecewise regression to detect thresholds in the species–area relationship.

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