

Island species–area relationships and species accumulation curves are not equivalent

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3

4 **Island species–area relationships and species–accumulation curves are not**
5 **equivalent: an analysis of habitat island datasets**

6

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28 **Running header: Island species–area relationships and species accumulation curves**

29

30 **Word count:** abstract: 286 words; main text = 5118 words; 2 Tables; 5 Figures; 42
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32 **Abstract**

33 **Aim** The relationship between species number and area is of fundamental importance within
34 macroecology and conservation science. Yet, the implications of different means of
35 quantitative depiction of the relationship remain contentious. We set out (i) to establish the
36 variation in form of the relationship between two distinct methods applied to the same habitat
37 island datasets, (ii) to explore the relevance of several key dataset properties for variation in
38 parameters of these relationships, and (iii) to assess implications for applications of the
39 resulting models.

40 **Locations** Global

41 **Methods** Through literature search we compiled 97 habitat island datasets. For each we
42 analysed the form of the island species–area relationship (ISAR) and several versions of
43 species accumulation curve (SAC), giving priority to a randomized form (Ran-SAC). Having
44 established the validity of the power model, we compared the slopes (z-values) between the
45 ISAR and the SAC for each dataset. We used boosted regression tree and simulation analyses
46 to investigate the effect of nestedness and other variables in driving observed differences in z
47 values between ISARs and SACs.

48 **Results** The Ran-SAC was steeper than the ISAR in 77% of datasets. The differences were
49 primarily driven by the degree of nestedness, although other variables (e.g. number of islands
50 in a dataset) were also important. The ISAR was often a poor predictor of archipelago species
51 richness.

52 **Main conclusions** Slopes of the ISAR and SAC for the same data set can vary substantially,
53 revealing their non-equivalence, with implications for applications of species–area curve
54 parameters in conservation science. For example, the ISAR was a poor predictor of

55 archipelagic richness in datasets with a low degree of nestedness. Caution should be
56 employed when using the ISAR for extrapolation and prediction purposes in habitat island
57 systems.

58 **Keywords** Boosted regression trees, conservation biogeography, fragmentation, habitat
59 islands, island biogeography, island species–area relationship, macroecology, nestedness,
60 species–accumulation curve, species–area relationship

61 **INTRODUCTION**

62 The increase in number of species with area is one of the few laws of ecology (Scheiner,
63 2003). While those working with species–area curves have long recognised different forms of
64 curve, confusion in terminology and usage has persisted (for use herein see Table 1), as
65 evidenced by an exchange of papers in this journal disputing the number of fundamental
66 types of relationship and the key distinctions between them (Scheiner, 2003, 2004; Gray et
67 al., 2004a,b). In their contributions, Gray et al. (2004a,b) argued that the most important
68 distinction was between species accumulation curves (SACs), which present cumulative
69 counts of increased species number with sampling area, and island-type species–area
70 relationships (herein termed ISARs) in which the function fitted is based on how many
71 species are found in each sampled area (or island). By virtue of their mode of construction,
72 SACs (which can be constructed in several distinct ways; see Appendix S1) must be rising
73 functions, whereas in principle an ISAR can have a negative slope: a large island may have
74 fewer species than a smaller one (Scheiner, 2003), suggesting the possibility that SAC and
75 ISAR form may vary substantially. However, in the island literature and in its application in
76 conservation science, it is sometimes assumed that SAC form and ISAR form are directly
77 comparable (as noted by Ulrich & Buscko, 2007, p. 55). Two classic illustrations of this are

78 to be found in the seminal works of MacArthur and Wilson (1967) and Rosenzweig (1995,
79 2003).

80 MacArthur and Wilson (1967) in their Figure 3 provide two data series, one a
81 cumulative species–area curve of contiguous sampling areas on mainland New Guinea, and
82 the other a set of points representing the richness of each island in the region. They comment
83 (p10) that “[t]he line and the cluster of points illustrate the principle that the increase in
84 number of species with area is more rapid in the case of isolated islands or archipelagos than
85 in expanding sample areas on a single land mass.” Similarly, Rosenzweig notes (1995, p10)
86 in developing the three-scales of species–area relationship model on which his reconciliation
87 ecology (2003) is largely based, that if scattered areas (or islands) are used to construct a
88 species–area curve, this will produce a steeper slope (higher z -value) than if using contiguous
89 sub-plots: moreover, the greatest disparity occurs between the richness estimated for the
90 smallest areas, while with increasing area of sample units, what we term the SAC and ISAR
91 converge towards the regional richness value. Rosenzweig (1995, p19) poses the question as
92 to whether the difference in z -values might be a consequence of the different mode of
93 construction of the two forms of function, but having provided a single demonstration of
94 similarity of values he goes on to state (p19) that “The data suggest that we do not have a
95 problem here.” The question of equivalence of SACs and ISARs is not trivial: if we assume
96 that the different mode of construction of SACs and ISARs is of no great consequence, it
97 follows that we can, for example, base projections of the consequences of habitat loss on
98 comparisons of z -values for contiguous habitat (assessed by SAC models) with z -values for
99 islands or habitat islands (assessed by ISARs). That this might be a dangerous assumption has
100 previously been argued by several authors (e.g. Ulrich & Buszko, 2007; Whittaker &
101 Fernández-Palacios, 2007; Hui, 2008; Dengler, 2009), while the significance of how SACs
102 are constructed for projections of species extinctions has also seen lively recent debate (e.g.

103 He & Hubbell, 2011, 2013; Axelsen *et al.*, 2013), revealing that our understanding of the
104 behaviour of different forms of species–area curve remains incomplete.

105 Our purpose herein is to advance understanding of the empirical differences between
106 SAC and ISAR data structures by means of a systematic comparison for a large set of habitat
107 island datasets. Specifically, we use a randomization procedure to construct a Scheiner type
108 IIIb curve (termed Ran-SAC, Table 1), and compare the z -values with a Scheiner type IV
109 curve (the ISAR) based on fits using the power model to test the hypothesis that they are non-
110 equivalent. Strictly speaking, our Ran-SAC is a variant of a Scheiner type IIIb curve as,
111 although the Ran-SAC is constructed using mean richness obtained by randomisation, the
112 observational units are habitat islands of varying area rather than non-contiguous plots of
113 equal size. However, despite this difference our Ran-SAC is still clearly a SAC, allowing us
114 to compare SAC and ISAR data structures. Next, we explore the relevance of several key
115 dataset properties for variation in parameters of these relationships, testing the hypothesis that
116 compositional nestedness (see Table 1) will be a significant determinant of variation in z
117 (slope), such that in anti-nested systems (Table 1) the Ran-SAC will be steeper than the ISAR
118 and as the degree of nestedness increases this situation will gradually reverse. While it has
119 long been appreciated that the form of species–area curves from non-contiguous samples is a
120 consequence of both alpha (local) and beta (differentiation) diversity, this is to our
121 knowledge, the first systematic attempt to quantify the interrelationship between ISAR and
122 SAC form and system nestedness across a series of habitat islands.

123 **MATERIALS AND METHODS**

124 **Data collection, formatting and species–area curve construction**

125 Datasets were sourced via a comprehensive search of the literature following steps and
126 criteria for evaluating suitability set out (in Appendix S2; see also Matthews, 2015). For each

127 selected dataset we recorded: geographic location, taxon, habitat island type (forested or non-
128 forested), latitude and longitude of the study extent (for some datasets this was an estimate as
129 the data were not presented in the source papers), range of species richness and island sizes,
130 and a classification of the predominant matrix type (as per Appendix S2).

131 For each dataset we constructed (i) the standard ISAR using the raw island area and
132 richness values, (ii) several forms of species accumulation curve (SAC), using different rules
133 for combining islands into the sequence, namely small–large, large–small, poor–rich, rich–
134 poor, random (Table S1). Except where stated, we present results for the smoothed random
135 form of SAC (Ran-SAC) on the grounds that this is now standard practice for constructing
136 such curves (e.g. Ugland *et al.*, 2003)(But see Fig. S1 in Appendix S1 for exemplification of
137 the variation in form that can be observed using the full set of SAC rules). The Ran-SAC was
138 constructed using a simple bootstrap procedure, randomly selecting the order of island
139 addition into the SAC at each iteration. For example, for the second data point (i.e. two
140 islands) of the SAC of a dataset, we randomly selected two islands, noting down the
141 combined area and combined richness of this pair. We repeated this 5000 times, and used the
142 mean of the 5000 x and y values as the data point representing two islands in the analysis.

143 Our aim was to compare the form of the ISAR with that of Ran-SAC, for the same
144 dataset. The simplest way to do this is to compare the z values of the power model ($S = cA^z$)
145 fitted to both sets of data. We focus principally on z as this parameter has attracted far more
146 attention and application than has c (e.g. Rosenzweig, 1995; Tjørve & Tjørve, 2008; Triantis
147 *et al.*, 2012). However, this method is arguably only appropriate if the power model provides
148 a reasonably good fit to both sets of data. Thus, we devised a set of criteria to select suitable
149 datasets for analysis. First, we fitted the power (non-linear) model to the two different data
150 types for each dataset using non-linear regression and the ‘mmSAR’ R package (Guilhaumon

151 *et al.*, 2010), and recorded the two parameters (c , z), the R^2 , and whether the z value was
152 significantly different from zero. A dataset was deemed satisfactory according to this process
153 if the z value of the power model was significant for both the SAC and ISAR structures, and
154 the R^2 was ≥ 0.5 in both cases. This threshold was chosen arbitrarily to eliminate datasets in
155 which the power model explained only a small amount of variation in the SAR. Second,
156 while the observed shape of the power (non-linear) model is generally convex, we wished to
157 determine whether a model with a different shape provided a better fit to our data. Thus, we
158 fitted a set of 20 ISAR models (including the power model) to the ISAR and SAC data from
159 each dataset using a modified version of the fitting algorithm within the mmSAR R package
160 (see Triantis *et al.*, 2012; Matthews *et al.*, 2015b). We considered the model with the lowest
161 Akaike's information criterion corrected for small sample size (AIC_c), as providing the best
162 fit (Burnham & Anderson, 2002). AIC_c weights were computed for each model fit. Because
163 of the non-nullity constraint on the denominator of the formula, AIC_c could not be calculated
164 for datasets with fewer than seven islands and thus these datasets were discarded as were
165 models with inadequate fits (e.g. due to non-normal residuals; cf. Triantis *et al.*, 2012). We
166 then determined the observed shape of the best model fit (convex, sigmoid or linear)
167 according to the algorithm outlined in Triantis *et al.* (2012; and see Appendix S3). For each
168 dataset, if the observed shape of either of the best model fits (i.e. to the ISAR and SAC data)
169 was linear or sigmoid (a check was made for linear power model fits and none were
170 observed), the dataset was discarded as the inclusion of z values from these fits may bias our
171 comparisons. In sum, to be classified as satisfactory, both the ISAR and SAC forms of each
172 dataset needed to have: (a) significant z values from the power model fits, (b) R^2 values ≥ 0.5
173 from the power model fits, and (c) observed convex fits, when considering the best model
174 from a set of twenty competing models.

175 For these satisfactory datasets, the difference between the Ran-SAC z value and the
176 ISAR z value ($zDif$; Table 1) was used as our response variable. We also re-ran our analyses
177 using the $zDif$ values from all datasets (i.e. those deemed satisfactory and unsatisfactory).

178 **Relative influence of the explanatory variables**

179 To determine factors potentially accounting for between-dataset differences in $zDif$, we fitted
180 a boosted regression trees model (BRT; Table 1) using the functions provided in Elith *et al.*
181 (2008). In contrast to traditional regression, for which inference is drawn from a single best
182 model, BRT combines a large number of tree models in order to increase predictive
183 performance (Elith *et al.*, 2008). Recent work has shown that using weight of evidence values
184 (Burnham & Anderson, 2002) within a linear modelling framework to determine the relative
185 importance of predictor variables is flawed (Galipaud *et al.*, 2014). BRT offers a useful
186 intuitive and robust alternative (see: Elith *et al.*, 2008).

187 In the BRT analysis, $zDif$ was used as the response variable and the dataset
188 characteristics listed above were used as predictor variables. As a further predictor variable,
189 we also calculated the degree of nestedness in each dataset using the NODF metric (Almeida-
190 Neto *et al.*, 2008), implemented in the ‘vegan’ R package (Oksanen *et al.*, 2013). NODF was
191 calculated using the maximally packed matrix. Sites containing zero species were removed
192 prior to calculation, as by definition such sites have zero nestedness, and act to depress the
193 NODF value for the full set of sites (see Matthews *et al.*, 2015a). Cross-validation
194 functionality was used to determine the optimum number of trees. We experimented with
195 varying tree complexity, learning rate and bag fraction parameter values in order to minimise
196 the minimum predictive errors, selecting final values of 5 (tree complexity), 0.001 (learning
197 rate; 0.01 when using all datasets) and 0.5 (bag fraction). These values resulted in an optimal
198 number of 7050 fixed trees using only the satisfactory datasets, and 4500 trees when all

199 datasets were used. The error structure was considered to be Gaussian. No outliers were
200 removed when running the BRT analysis using the satisfactory datasets, but two outliers had
201 to be removed when using all datasets to induce normality in z Dif. The predictive power of
202 the model was assessed through cross-validation, whereby the fitted model was tested on
203 withheld portions of the data (10 subsets were used).

204 The relative influence of the predictor variables was again calculated using the
205 functions in Elith *et al.* (2008), which weigh the number of times a predictor is chosen for
206 splitting by the squared improvement to the model due to each split. Partial dependence plots
207 were also used to assess and visualize the effect of a predictor after accounting for the effects
208 of all other model predictors (Elith *et al.*, 2008). In partial dependence plots the y-axis shows
209 the effect of a predictor variable on the response variable after accounting for the effects of
210 the other model predictors (i.e. the marginal effect of the predictor).

211 **Simulation analyses**

212 As the BRT analyses revealed NODF to be the most important variable (see Results), we
213 undertook a simulation analysis to further examine the relevance of nestedness for the
214 difference between the z values of the two forms of dataset. First, we simulated a set of six
215 islands with area and species richness values conforming roughly to a convex ISAR (area= 1,
216 5, 10, 15, 20, and 30; containing 10, 12, 14, 16, 17 & 18 species respectively; herein ‘Sim1’).
217 We fitted the power model (non-linear) to the ISAR-structured form of Sim1 and recorded
218 the model parameters. We then simulated a perfectly nested (i.e. NODF=100)
219 presence/absence matrix using the data characteristics of Sim1 (i.e. island number and species
220 richness) and used this matrix to construct the SL (small–large) SAC (see Appendix S1),
221 fitting the power model to the resulting curve. We used the SL-SAC in this analysis, as
222 constructing the Ran-SAC for this many matrices would have been computationally

223 intensive. We then altered the presence/absence matrix (without changing the area and
224 richness values) to change the degree of matrix nestedness, by randomly shuffling the
225 presences along the sites (i.e. matrix rows) using the “commsimulator” function in the vegan
226 R package and discarding any matrix which had already been simulated. The total number of
227 species in the species pool (i.e. the total number of possible columns in the presence-matrix)
228 was set to 40, and we allowed gamma diversity to change between matrices, while the alpha
229 diversity of each island remained constant. This permitted us to create matrices with
230 substantially different levels of nestedness. However, as this meant that the number of
231 columns (total number of species) varied between matrices we used the NODF-by-rows value
232 as our measure of nestedness. For each accepted matrix, we constructed the SAC curve and
233 fitted the power model. We started the random shuffling from different starting points (i.e.
234 different initial presence–absence matrices), used a variety of community simulation
235 algorithms (i.e. R0, R1 and R2) and repeated this process iteratively for 12,000 runs, to cover
236 a wide range of NODF values. We then examined $zDif$ values for each iteration, plotting $zDif$
237 as a function of nestedness.

238 **Determining the degree of deviation of the archipelagic point**

239 To determine whether the archipelagic point (‘regional richness’) of a dataset deviated from
240 the ISAR of the constituent islands, we followed the method and nomenclature outlined by
241 Santos *et al.* (2010). We also use ‘archipelagic point’ to refer to the total area and richness of
242 the corresponding set of habitat islands (i.e. the archipelago). For each dataset, we fit the
243 power (log–log; base 10) SAR model to the ISAR structure and derived the fitted values of
244 the model for each island (‘SIpred’). The log–log version of the power model was used in this
245 analysis as it was the model used by Santos *et al.* (2010) and thus allowed us to compare our
246 results with theirs. Also following Santos *et al.* (2010), we added 0.01 to each species
247 richness value to avoid zero values, although we acknowledge that other constants could also

248 be used. We then calculated the archipelagic point as the cumulative total area of all habitat
249 islands in the dataset plotted against the cumulative species richness total ('SAobs'); and
250 predicted the number of species in the archipelagic point ('SApred') using the ISAR model of
251 the constituent islands. We followed Santos *et al.* (2010) and calculated the archipelagic
252 residual ('ArcRes'; Table 1) as the absolute difference between $\log(\text{SAobs})$ and SApred,
253 standardised by $\log(\text{SAobs})$ (see Appendix S3 for details). We noted whether the ISAR over-
254 or under- predicted richness in the archipelagic point for each dataset. This ArcRes
255 methodology represents a simple metric with which to describe how well the ISAR predicts
256 the archipelagic richness.

257 To determine if any dataset characteristics (above) could explain variation in ArcRes
258 between datasets we repeated our BRT analyses (learning rate of 0.01) using ArcRes as the
259 response variable. We only used ArcRes values from datasets in which the power (log-log)
260 provided a significant fit (cf. Santos *et al.*, 2010). Nine outlying points required removing to
261 induce normality, as there was a long left-hand tail in the distribution of ArcRes values. The
262 optimal number of fixed trees was 2200. All analyses and simulations were conducted in R
263 (version 3.1.1.; R Development Core Team, 2014). A significance level of 0.05 was
264 employed in all analyses.

265 **RESULTS**

266 We screened over 1000 published articles, of which 97 were deemed suitable for analysis
267 (Table S2 in Appendix S2): 69 vertebrate, 20 invertebrate and 8 plant datasets. For the
268 majority of both the ISAR and Ran-SAC datasets the observed best-fitting model shape was
269 convex (for the ISARs the mean $wAIC_c$ of convex model fits = 0.86, linear = 0.09, sigmoid =
270 0.09; for Ran-SAC the equivalent results were, convex = 0.99, linear = 0.00, sigmoid = 0.02).
271 The power model was within the set of six best models (i.e. was ranked as one of the top six

272 models according to AIC_c) for 67 of the ISAR datasets, and nine of the Ran-SAC datasets.

273 According to our three additional dataset acceptance criteria, 50 datasets were deemed

274 satisfactory for the $zDif$ analyses.

275 *Differences in the z value of ISARs and Ran-SACs*

276 Considering only the 50 satisfactory datasets, the Ran-SAC z was greater than the ISAR z for

277 32 (e.g. see Fig. 1) and was smaller for the remaining 18 cases. The power model explained a

278 larger amount of variance for the Ran-SAC (mean $R^2 = 0.97$) than for the ISAR (mean $R^2 =$

279 0.76); although this result is easily explained by the smoothing process involved in

280 calculating the Ran-SAC values. Considering all 97 datasets, the Ran-SAC z value was larger

281 in 75 cases. The z and c values are provided in Table S3 in Appendix S4, as are values from

282 the power model fitted to the other SAC data structures (e.g. the Small-Large SAC).

283 *Boosted regression tree results*

284 When $zDif$ values from satisfactory datasets were used as the response variable, NODF was

285 the most important explanatory variable (relative influence value of 24.6; see Table 2). Both

286 the minimum number of species and the number of islands also had relatively high influence

287 values (Table 2, Fig. 2a, b). In terms of the overall predictive performance of the model, the

288 mean coefficient of the correlation between the observed and predicted response values was

289 0.63 when based on the cross-validation data. Results were qualitatively similar when

290 considering $zDif$ values from all datasets (mean correlation coefficient = 0.68).

291 As predicted, further analysis revealed that in highly nested systems the z values for

292 ISARs were greater than those for Ran-SACs, and the reverse for systems with little nesting

293 (see Fig. 2a and Fig. 3a). In addition, the z value of the Ran-SAC was significantly related to

294 the NODF value (Fig. 3b), whereas there was no relationship between the z of the ISAR and
295 NODF (Fig. 3c).

296 *Nestedness simulations*

297 The simulation analyses revealed further evidence for the importance of nestedness in
298 explaining the difference in z value between ISARs and SACs. In the case of Sim1, when the
299 system was anti-nested (low NODF values), the z value of the SL-SAC was greater than that
300 of the ISAR. As the degree of nestedness was increased, the difference in z values declined
301 until the ISAR z exceeded that of the SL-SAC (Fig. 4a). Figure 4b illustrates this effect for
302 two SL-SAC curves, constructed from the most nested and anti-nested Sim1 iterations,
303 respectively (we used the SL-SAC curve type as the area range of the ISAR and SAC are
304 similar, making the plot easier to interpret).

305 *The fit of the archipelagic data point*

306 Considering only datasets in which the power (log–log) model provided a significant fit
307 ($n=73$), the archipelagic point deviated substantially (following the rule of thumb used by
308 Santos *et al.*, 2010) from the prediction of the constituent ISAR in 14 datasets (see Fig. 5 for
309 an example of both scenarios). The ISAR under-predicted the archipelagic richness in 45
310 cases (Table S3 in Appendix S4). Considering 64 datasets (the 75 significant fits minus the
311 nine outliers), when ArcRes was used as a response variable in a BRT analysis, NODF was
312 the variable with the highest relative influence value (Table 2). The number of species and
313 the minimum number of species in a dataset were also important variables (Table 2). The
314 mean coefficient of the correlation between the observed and predicted response values was
315 0.35.

316

317 **DISCUSSION**

318 To evaluate the impact of confounding ISAR and SACs in SAR analyses and syntheses and
319 to understand their differing emergent properties we compared the z values of ISAR and Ran-
320 SAC curves using a large compilation of habitat island datasets. Constructing SACs from
321 island data has previously been attempted (e.g. Quinn & Harrison, 1988; Rosenzweig, 1995;
322 Fischer & Lindenmayer, 2002), although previous studies have largely focused on small-
323 large and large-small SACs. We decided to focus on a Ran-SAC as it represents an average
324 of the various SAC construction permutations (see Appendix S1) and thus seems a sensible
325 choice if only one type of SAC is to be used in comparative analyses. As noted by previous
326 authors (e.g. Ulrich & Buszko, 2007), critical tests of how different types of SAR affect
327 model shape and parameters are lacking. We found that the z values and form of the ISAR
328 and SAC curves varied considerably within datasets, and that this variation was primarily
329 explicable as a function of the degree of nestedness in the archipelago. We also observed that
330 the ISAR was often a poor predictor of SAobs, demonstrating the dangers of extrapolating
331 the ISAR, for example, to predict the richness of an archipelago of fragments.

332 **Why are SACs generally steeper than ISARs?**

333 In accordance with our first hypothesis we found considerable differences between the z
334 values of ISARs and SACs (e.g. Figs 1 and S1). Hence, our results illustrate that different
335 inferences might be drawn depending on which data structure is used in an analysis (and see
336 Ulrich & Buszko, 2007, for an analysis based on a different SAC type). Consistent with our
337 second hypothesis, the difference in the z values of SACs and ISARs is best explained by
338 variation in compositional nestedness, a pattern which is to be expected as a function of the
339 procedures used in constructing the two types of curves (Gray *et al.*, 2004a, b); a fact
340 highlighted by both empirical and simulation analyses (Figs 2, 4).

341 A number of factors have been argued to underpin the z value of SACs, through an
342 effect on species overlap and/or nestedness (e.g. Quinn & Harrison, 1988; Chase & Knight,
343 2013). Two of these factors are particularly relevant to habitat island systems. First, a large
344 species pool means that, all else being equal, there is a smaller probability that the same
345 species will succeed in occupying each island, and thus species overlap between islands is
346 reduced. Furthermore, if islands within an archipelago (of real or habitat islands) draw
347 species from different species pools the likelihood is that species overlap across all islands
348 will be reduced (Whittaker & Fernández-Palacios, 2007). Second, habitat islands are
349 generally disturbed systems, and disturbance usually has a disproportionate effect in smaller
350 islands (Whittaker & Fernández-Palacios, 2007). This means that matrix and generalist
351 species are relatively over-represented in smaller fragments (Matthews *et al.* 2014b), again
352 resulting in reduced overlap. In previous work we have shown that the relatively high
353 incidence of generalist species in smaller fragments reduces the slope of a multimodel ISAR
354 curve for a number of habitat island datasets (Matthews *et al.*, 2014b). This reduction in
355 ISAR slope coupled with the reduced species overlap across islands provides one explanation
356 for the many positive $zDif$ values (Ran-SAC steeper than ISAR) observed.

357 Our analyses indicated that other variables are also important, independent of
358 nestedness (Table 2), with the minimum number of species (Min.) on an island in a dataset
359 being the second most influential variable explaining variation in $zDif$ (Table 2). The partial
360 dependence plot of this variable (Fig. 2b) indicates that low Min. values have a negative
361 effect on $zDif$; in this case, in many datasets with low Min. values the ISAR is steeper than
362 the Ran-SAC (i.e. $zDif$ is negative). Interestingly, the maximum number of species and the
363 total number of species in the archipelago had low relative influence values (Table 2). It is
364 possible that this finding could be due to an indirect effect of additional variables not

365 included in our analyses that are correlated with Min. Further research is needed to fully
366 explore the implications of these results.

367 Landscape context variables (e.g. the habitat matrix, and island type) were relatively
368 unimportant (Table 2). This is surprising as the habitat matrix is considered to be important in
369 determining differences in z value between ISARs and SACs due to the influence of matrix
370 properties on species turnover (see Crist & Veech, 2006). The lack of an effect of these
371 variables is likely due, at least in part, to the coarse matrix and island type classifications
372 utilised in our analyses.

373 **Interpreting variation in ArcRes**

374 Using the simple descriptive metric adopted by Santos *et al.* (2010) we found that the
375 archipelagic point deviated substantially from the ISAR prediction in 19% of datasets with a
376 significant ISAR, compared to 12% in Santos *et al.*'s analyses of true island datasets.

377 Consistent with our findings for slope differences (i.e. $zDif$; above), NODF had the largest
378 effect on ArcRes (Table 2), while the ISAR more frequently under-predicted than over-
379 predicted the richness of the archipelagic point (Fig. 5a). A role for nestedness in under-
380 prediction of system richness may reflect the fact that habitat islands often contain a large
381 number of singletons (i.e. species that are only sampled in one habitat island in a dataset and
382 whose presence reduces the nestedness of the full data matrix) as a result of factors such as
383 source–sink dynamics and transient species that may be using suitable, but unsampled
384 patches of habitat within the study area, thus enabling their persistence despite low
385 frequencies in the dataset. A recent meta-analysis, using many of the same datasets, has
386 shown that contrary to earlier work, the majority of habitat island systems described in the
387 literature have low levels of nestedness, and indeed that significant anti-nestedness is more
388 common than significant nestedness (Matthews *et al.*, 2015a). Taken together, these findings

389 bring into question the extrapolation of ISARs (see also Fig. 1b) and certain other species–
390 area curves of similar or composite construction: a common applied use of the ISAR (cf.
391 Whittaker *et al.*, 2005; Ulrich & Buszko, 2007; Hui, 2008).

392 **Implications and conclusions**

393 The choice of species–area curve construction and method of analysis are important
394 considerations when using the SAR for applied purposes (Whittaker *et al.*, 2005; Ulrich &
395 Buszko, 2007; Halley *et al.*, 2013; Matthews *et al.*, 2015b), but conservation biogeographic
396 studies are often unclear about the type of SAR employed and indeed, terminology is
397 inconsistent and disputed across the literature (see e.g. Scheiner, 2003, 2004; Gray *et al.*,
398 2004a, b; Whittaker & Fernández-Palacios, 2007). Our analyses have provided empirical
399 proof that ISAR and SAC are not equivalent and may differ substantially in fitted parameters
400 (contrary to assumptions in e.g. MacArthur & Wilson, 1967, p10; Rosenzweig, 2005, p19).
401 This distinction has not always been recognised and greater attention should therefore be paid
402 to explicitly identifying the type of species–area curve and method of fit used in future
403 ecological analyses (see also Scheiner, 2003; Ulrich & Buszko, 2007). The present analysis
404 does not argue in favour of one specific species–area function being universally preferable;
405 rather, the choice depends on the aim of study and the data available. For example, SACs are
406 arguably more useful than ISARs for assessing the contribution of different sized islands to a
407 protected area network (Fischer & Lindenmayer, 2002; Watson *et al.*, 2009).

408 Based on the self-similar scaling properties of the power model, Tjørve & Tjørve
409 (2008; see also Harte *et al.*, 1999) used a form of SAC to show mathematically that the
410 proportional overlap between two areas of the same size can be plotted as a function of z : as z
411 increases, the degree of species overlap decreases. For example, a z of 0.58 equates to 50% of
412 the species being shared between the two areas (Tjørve & Tjørve, 2008). Our results provide

413 an empirical illustration of this point (e.g. Fig. 3b) and indicate that (a) the SAC is often
414 steeper than the ISAR when the curves are constructed using habitat island data, and (b) the z
415 value of the ISAR only becomes consistently steeper than the z of the SAC when the data are
416 highly nested i.e., the NODF value is approximately 70 or above (e.g. Fig. 3a & Fig. 4b).

417 It is also evident that for a number of habitat island systems the ISAR is a poor
418 predictor of the overall number of species in an archipelago (e.g. Fig. 5a). Thus, caution
419 should be employed when using the ISAR for extrapolation purposes in fragmented systems,
420 particularly when species overlap is thought to be low (Crist & Veech, 2006). The SAC is
421 likely to provide more accurate results in such contexts as it incorporates information on the
422 degree of nestedness/overlap in the region (Quinn & Harrison, 1988; Hui, 2008). It is already
423 acknowledged that the choice of sampling design is an important consideration in SAR
424 studies, and our results provide more evidence for those who have recently argued for a more
425 consistent SAR theory applicable to general SAR sampling designs (e.g. Whittaker *et al.*,
426 2005; He & Hubbell, 2013).

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534

535 **SUPPORTING INFORMATION**

536 **Appendix S1** The different types of species–area relationship

537 **Appendix S2** Source paper information

538 **Appendix S3** Expanded study methods

539 **Appendix S4** Supplementary results

540

541 **BIOSKETCHES**

542 **Tom Matthews** is a research associate at the University of Oxford. He is interested in the
543 study of macroecological patterns in habitat islands, and the application of island theory to
544 fragmented landscapes.

545 Author contributions: T.J.M., K.A.T. and R.J.W. conceived the ideas; T.J.M. collected the
546 data; T.J.M. ran the analyses; and T.J.M. and R.J.W. wrote the paper with a significant
547 contribution from K.A.T, M.K.B., F.R. and F.G. All authors discussed the results and
548 commented on the manuscript.

549

550 **Appendix 1 - Data sources**

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- 765

766 **TABLES**767 **Table 1** A glossary of the terms used in this study.

Abbreviation	Full term	Definition
.....	Species–area curve/relationship	Here used as general terms for the relationship between sample area and species richness/number.
ISAR	Island species–area relationship	Whereby the number of species occurring within each of a set of islands is analysed as a function of the area of each island. Equivalent to Scheiner (2003) type IV curves.
SAC	Species accumulation curve	Plots of increasing cumulative species number with increasing sampling effort/area
SL SAC	Small-Large SAC	The order of island incorporation into the SAC starts with the smallest island and increases up to the largest.
Ran-SAC	Random SAC	The order of island accumulation when constructing the SAC is random.
z		The slope parameter of the power SAR model.
$zDif$		The difference between the SAC z value and the ISAR z value.
BRT	Boosted regression tree analysis	A regression method which combines a large number of tree models.
Nestedness	The situation in which depauperate island faunas constitute proper subsets of the species in richer islands (see Matthews <i>et al.</i> , 2015a). In the current study, we are interested in species nestedness between isolates.
Anti-nestedness	A dataset which is significantly less nested than expected by chance (Matthews <i>et al.</i> , 2015a).
NODF	Nestedness metric based on overlap and decreasing fill	A nestedness metric based on the twin properties of standardized differences in row and column fills and the overlap of presences in two adjacent columns.
ArcRes	Archipelagic residual	The standardised absolute difference between the observed number of species across all islands in a dataset, and the number of species predicted by the log–log power model (log transformed).

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771 **Table 2** The relative contributions (%) of predictor variables for boosted regression tree
772 models developed using cross-validation. The model was fitted using two different response
773 variables: z Dif (number of datasets = 50; 7050 fixed trees), and ArcRes (number of datasets =
774 66; 2300 fixed trees). z Dif is the difference between the z value of the SAC and the z value of
775 the ISAR, for each dataset. ArcRes is the standardised difference between the cumulative
776 species richness total of the archipelago and the predicted the number of species in the
777 archipelagic point using the ISAR model of the constituent islands. A set of dataset
778 characteristics were used as the predictor variables (see Materials and Methods): Min =
779 minimum, Max = maximum, No = number of, Ar. = area, Isl. = island, Sp. = species. The
780 nestedness of the archipelago was measured using the NODF metric (maximally packed
781 matrix). Island type was a categorical variable indicating whether a dataset was a forested or
782 a non-forest island, and taxon was a categorical variable indicating whether a dataset was a
783 plant, vertebrate or invertebrate dataset. Matrix was a variable indicating the permeability of
784 the surrounding matrix type. Variables are ordered by their relative influence (Rel. influence)
785 in each case.

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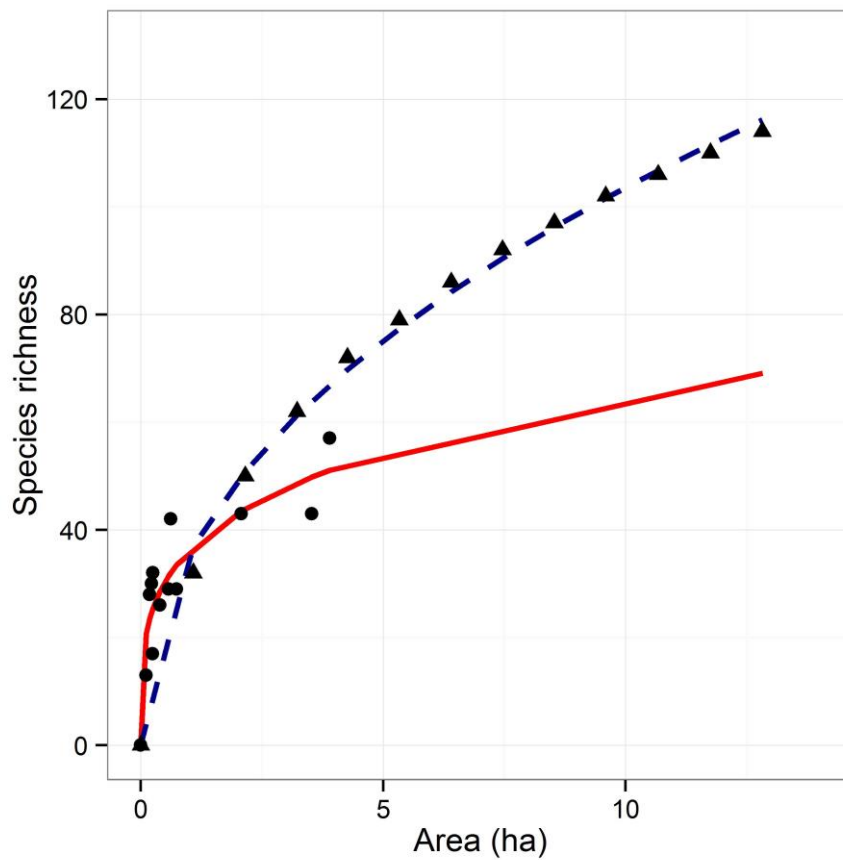
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z Dif		ArcRes	
Variable	Rel. Influence	Variable	Rel. Influence
NODF	24.61	NODF	30.11
Min. Sp.	17.94	No. Sp.	16.62
No. Isl.	17.12	Min. Sp.	13.60
Ar. Ratio	13.15	Ar. Ratio	8.00
Max Ar.	9.80	Latitude	7.15
Longitude	4.53	Longitude	6.33
Latitude	4.52	Max Ar.	5.31
No. Sp.	2.78	Max Sp.	3.44
Max Sp.	2.14	No. Isl.	3.40
Matrix	1.43	Taxon	2.20
Min. Ar.	0.99	Min. Ar.	2.06
Isl. Type	0.88	Isl. Type	0.92
Taxon	0.11	Matrix	0.86

803 **FIGURES**

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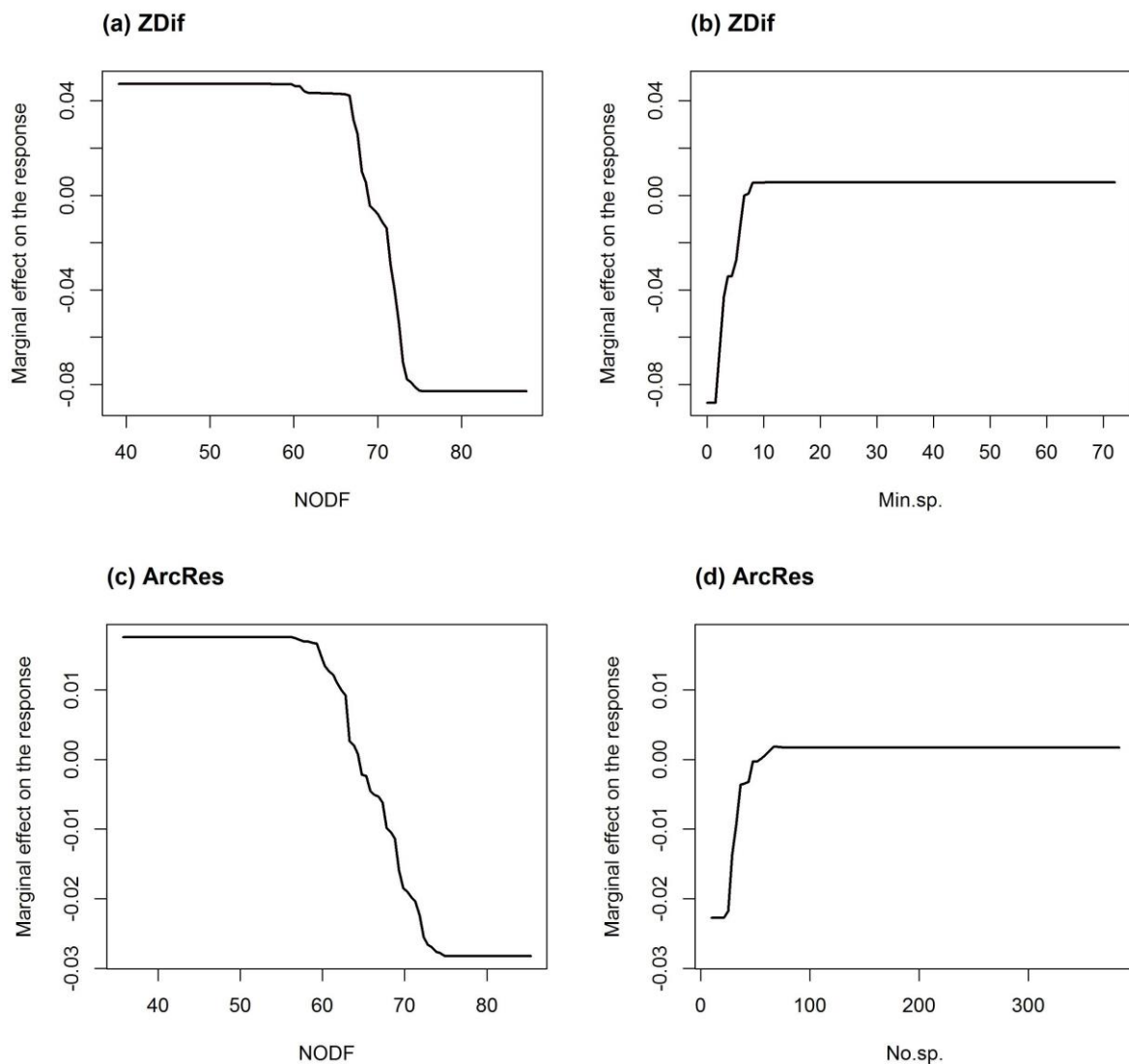
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806 **Figure 1** Power model fits constructed from the same habitat island dataset: Gavish *et al.*
807 (2012; invertebrates in a study system from Israel; number of islands = 12; number of species
808 = 114). The fits of the power model (non-linear) to the ISAR data (solid circles; solid line =
809 fit of the model) and the Ran SAC data (solid triangles; dashed line) are shown. For the ISAR
810 model fit, the power model has been extrapolated to the total cumulative area of all habitat
811 islands in the system using the parameters derived from model fitting process. The z values of
812 the models are 0.25 for the ISAR model, and 0.46 for the SAC model.

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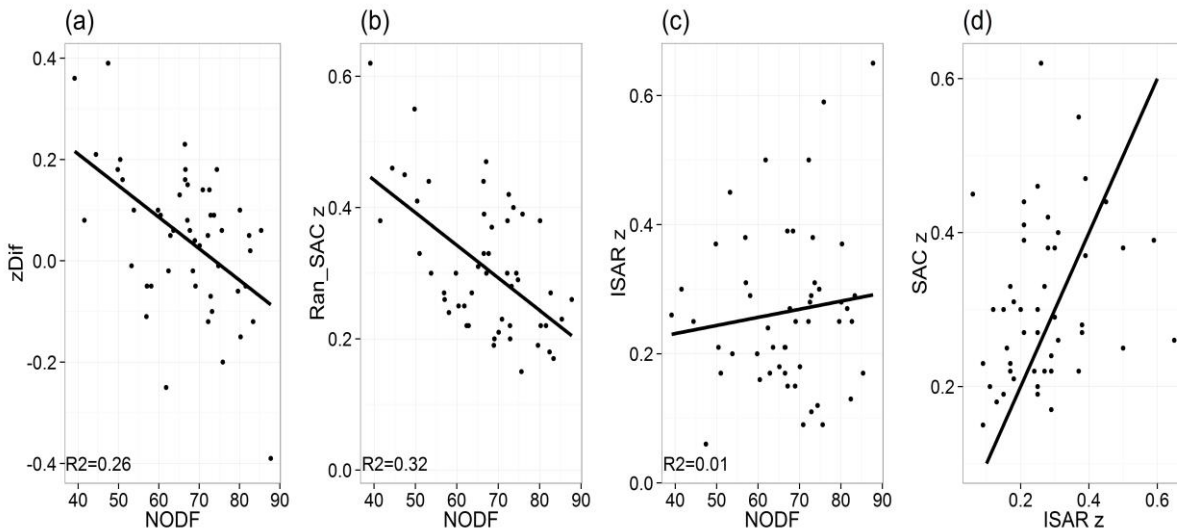


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817 **Figure 2** Partial dependence plots for two of the most influential variables in two boosted
 818 regression tree (BRT) models. The response variable was $zDif$ (a-b; the difference between
 819 the z value of the SAC and the z value of the ISAR, for each dataset), and in the second
 820 model the response was $ArcRes$ (c-d; the standardised difference between the cumulative
 821 species richness total of the archipelago and the predicted the number of species in the
 822 archipelagic point using the ISAR model of the constituent islands). Only $zDif$ values from
 823 satisfactory datasets were used ($n = 50$) in (a) and (b), and only $ArcRes$ values from datasets
 824 in which the fit of the power (log–log) model was significant ($n = 73$, reduced to 64 after
 825 removing nine outliers) were used in (c) and (d). The two predictor variables in the first
 826 model are (a) nestedness (NODF; for the relative contributions of each variable see Table 2)
 827 and (b) the minimum number of species in a dataset (Min. sp.). The two predictor variables in
 828 the second model are (c) nestedness (NODF), and (d) the number of species in a dataset (No.
 829 sp.). The y-axis shows the effect of a predictor variable (x-axis) on the response variable after

830 accounting for the effects of the other model predictors (i.e. the marginal effect of the
 831 predictor). The y-axis represents the effect of the predictor on the response, and is not an
 832 indicator of the value of the response at a given value of the predictor. A positive y-value
 833 indicates that at the given x-value, the effect (based on the model) on the y-value (the
 834 response) is positive, and *vice versa*. The ends of the curves represent areas of the plotting
 835 space with fewer data points and are relatively uninformative.

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838 **Figure 3** The relationship between nestedness (measured by the NODF metric) and (a) zDif
 839 (the difference between the Ran SAC z value and the ISAR z value, (b) the SAC z value, and
 840 (c) the ISAR z value. Only z values from the satisfactory datasets (n=50) were used to
 841 construct the plots. In each plot, the solid line represents the best line of a linear regression
 842 model, and the R^2 of this fit is given on each plot. The z value was significant in each plot
 843 apart from (c), which is shown for illustrative value only. Increasing NODF value indicates
 844 an increasing degree of nestedness, according to this metric. (d) The z value of the power
 845 model fitted using ISAR structured data plotted against z values derived using randomly
 846 constructed SAC data. The solid line in (d) represents a 1:1 fit line; points below the line
 847 represent datasets in which the ISAR z value was larger than the SAC z value, and vice versa.
 848 The z values in all plots relate to the non-linear power SAR model.

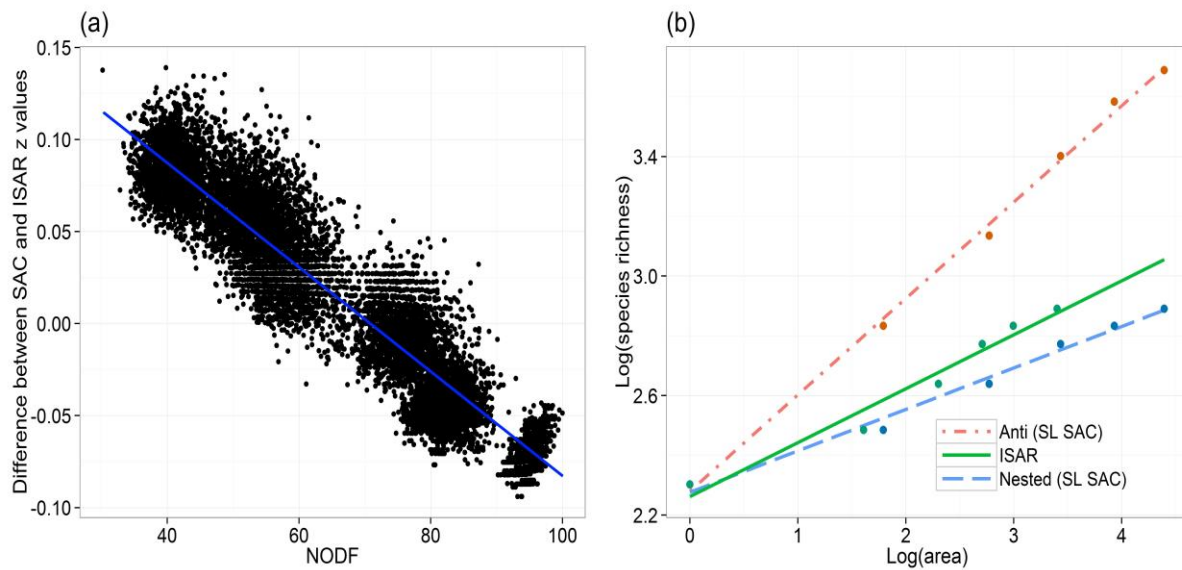
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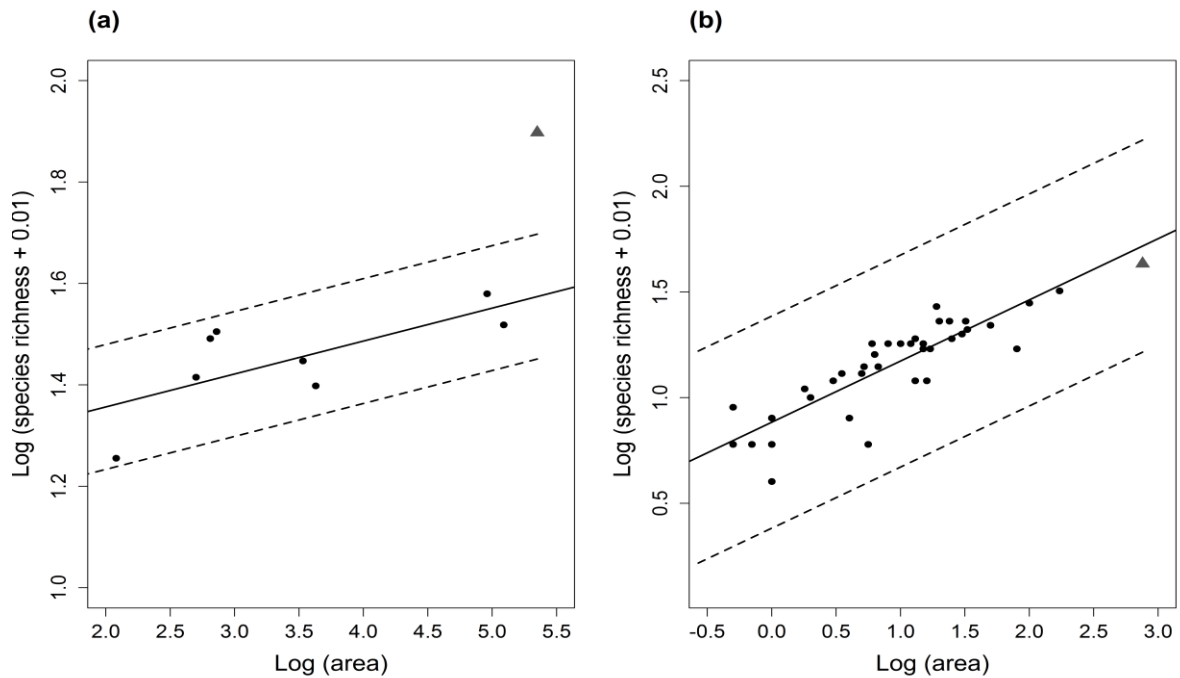
856 **Figure 4** The relationship between nestedness and the variation in z values of ISARs and
 857 small-large (SL; the order of island incorporation into the SAC starts with the smallest island
 858 and increases up to the largest; see Appendix S1) constructed SACs. For (a), a perfectly
 859 nested presence/absence matrix for a set of six islands of varying area was simulated (area of
 860 each island = 1, 5, 10, 15, 20 & 30; species richness of each island = 10, 12, 14, 16, 17 & 18).
 861 First, the power model (non-linear) was fitted to the data matrix in ISAR form, and the z
 862 value recorded. The SL SAC was then constructed using the same data matrix and, again the
 863 power model was fitted. The presence/absence matrix was then rearranged to change the level
 864 of nestedness, with the constraint that the species richness of each island was kept constant
 865 (i.e. the ISAR remained unchanged), although the overall number of species in the
 866 archipelago was allowed to vary; the power model was then fitted to both the ISAR and SAC
 867 constructed using this new data matrix. This process was repeated iteratively along a gradient
 868 of NODF (by rows, i.e. sites) values. A total of 12,000 matrix permutations were simulated.
 869 The best fit linear regression line (solid line) through these points (dots) is also shown. (b)
 870 The power (log–log) model, fitted to ISAR structured data (solid line, $z = 0.18$), and to SL
 871 SAC structured data using the same simulated island data as for (a). The fit of SL SAC curves
 872 to two matrix permutations are shown: a perfectly nested set of isolates (dashed line, $z = 0.14$),
 873 and a perfectly anti-nested set of isolates (dashed and dotted line, $z = 0.32$).

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881 **Figure 5** The island species–area relationship (power log–log model) for two habitat island
 882 datasets: (a) Benedick *et al.* (2006; invertvertebrates in Malaysia; number of islands = 8), and (b)
 883 this study (birds in the UK; number of islands = 37). The dots represent individual habitat
 884 islands and the fit of the power (log–log) model is indicated by the solid line. In both plots
 885 the archipelagic point, calculated as the total cumulative area and species richness of all
 886 habitat islands in the dataset, and is illustrated as a triangle. The intervals defined by the
 887 maximum residual criterion are shown as the dashed line: this criterion relates only to the
 888 difference between the ISAR prediction and the archipelagic point, the dashed lines have then
 889 just been continued down the y-axis. If the archipelagic point lies outside these bounds (e.g.
 890 (a)) it is said to deviate from the prediction of the ISAR calculated using the constituent
 891 habitat islands; and *vice versa* (e.g. b; cf. Santos *et al.*, 2010).