

The species–area relationship in ant ecology

Ohyama, Leo; Holt, Robert D.; Matthews, Tom; Lucky, Andrea

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1 Strapline: The ant species–area relationship
2 The species–area relationship in ant ecology

3
4 *Running title:* Species-area relationships in ant ecology

5
6 Leo Ohyama^{1,2*}, Robert D. Holt³, Thomas J. Matthews^{4,5}, Andrea Lucky¹

7
8 *Corresponding Author, leoohyama12@gmail.com

9
10 ¹ *University of Florida, Entomology and Nematology Department, 1881 Natural Area Drive,*
11 *Gainesville, Florida, USA, 32611*

12
13 ² *University of Florida, Biodiversity Institute, 432 Newell Drive, Gainesville, Florida, USA,*
14 *32611*

15
16 ³ *University of Florida, Department of Biology, 876 Newell Drive, Gainesville, Florida, USA,*
17 *32611*

18
19 ⁴ *GEES (School of Geography, Earth and Environmental Sciences) and Birmingham Institute of*
20 *Forest Research, University of Birmingham, Birmingham, B15 2TT*

21
22 ⁵ *CE3C – Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity*
23 *Group and Universidade. dos Açores – Depto de Ciências Agrária e Engenharia do Ambiente,*
24 *PT-9700-042, Angra do Heroísmo, Açores, Portugal.*

25
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36
37 *Author contributions*

38 LO conceived the idea, LO collected the data, LO and RDH were responsible for the
39 development of the idea, LO and TJM analyzed the data, LO wrote the manuscript with input
40 from RDH, TJM, and AL.

41
42 *Statement of significance*

43 Understanding why the number of species in a given area increases across space is crucial to
44 determining the current and future states of biodiversity. We review and analyze data from the
45 literature on the ants, one of the best-studied invertebrate ecosystem engineers in insular systems.
46 We find that ant diversity scales faster across space in mainland versus insular systems. We also

47 find that precipitation and areas with unique evolutionary histories (e.g. the Neotropics)
48 influence the rate at which diversity scales across space. Finally, we identify knowledge gaps and
49 solutions, extendable to other taxa, to better understand the scaling of biodiversity.

50

51 **Abstract**

52 Aim: The positive relationship between species richness and area – the species–area relationship
53 (SAR) – is a key principle in ecology. Previous studies show large variation in the SAR across
54 taxa, collectively indicating the necessity of a taxon-focused approach to accurately evaluate
55 biodiversity scaling patterns. Ants are ideal for this given their global distribution, and role in
56 ecosystem functioning. Using data from insular ant communities, this study quantified and
57 investigated various attributes of ant SARs and reviewed the SAR literature for ant faunas,
58 world-wide, to identify specific areas for improvement.

59

60 Location: Islands around the world

61

62 Taxon: Ants (Hymenoptera: Formicidae)

63

64 Methods: We aggregated data on species richness and island characteristics from previous
65 studies on ant SARs to evaluate effects of climate, biogeographic realm and latitude on slope
66 values from these studies. A multi-model inference approach was used to determine the form of
67 the different SARs, and whether there were any differences between mainland and insular SARs.
68 We also assessed differences between mainland and insular SAR slopes and intercepts. To seek a
69 general slope coefficient for ants, we used a mixed-effect model. Finally, we tested for potential
70 thresholds in the global insular SAR using piecewise regression models.

71

72 Results: There was a negative relationship between SAR slopes and precipitation in both
73 mainland and insular SARs, while SAR slopes and intercept values were lower and higher,
74 respectively, in mainland compared to insular systems. Strong evidence of thresholds emerged in
75 the global insular SAR. Finally, a general slope of 0.16 was observed for insular systems, which
76 is lower than found in previous studies.

77

78 Main conclusions: A taxon-focused approach proves to showcase unexpected patterns in the
79 SAR. Ant diversity increases faster across area in mainland areas compared to true islands. The
80 influences of climate and biogeographic realms on the ant SAR warrant deeper study. Our
81 review highlights knowledge gaps in the ant SAR that also extend to other taxa, such as the
82 effects of non-native species on the SAR.

83

84 **Key words**

85 Ants, Biodiversity, Fragmentation, Invasive species, Islands, Island biogeography, Species–area
86 relationship

87

88 **Introduction**

89 The Theory of Island Biogeography (MacArthur & Wilson, 1967), a foundational framework for
90 ecology and biogeography, was motivated in part by consideration of the species–area
91 relationship (SAR). This relationship was first noted by Forster (1778) and brought to light by
92 Wallace (1914), and has played a central role in biogeography up to the present (Matthews et al.,

2020, *In Press*). A SAR describes the tendency for species richness to increase with increasing area (Mittelbach & McGill, 2019) and is one of the few patterns in ecology that has been called a general “law” (Lomolino, 2000; Whittaker & Fernandez-Palacios, 2007). SARs have been instrumental in the field of conservation biogeography (Whittaker et al., 2005), including in the design of nature reserves, extinction forecasting, and gauging the effects of habitat fragmentation (Halley et al., 2014; Suarez et al., 1998; Whittaker & Fernandez-Palacios, 2007).

In this study, we focus on the island species–area relationship (hereafter referred to as the ISAR), which utilizes distinct islands or distinctly bounded patches within larger regions (Matthews et al., 2016; Rosenzweig, 1995; Scheiner, 2003). ISARs in both mainland and insular systems were investigated to better understand how biodiversity changes across different-sized independent areas and in relation to various environmental and biogeographical conditions. Here, we define insular ISARs as those that focus on species richness and areas of true islands, landforms completely surrounded by water. We define mainland ISARs as those that focus on “islands” (i.e. habitat islands) found within the boundaries of continents, such as discrete patches created by geomorphological processes (e.g., outcrops of granite or patches of serpentine), or by anthropogenic processes of habitat destruction and habitat fragmentation.

Most often, the ISAR is fit with a power function (Arrhenius, 1920b)(eq 1.1),

$$S = cA^z \quad (1.1)$$

where S is species richness, A is area, and c and z are fitted constants. Different mathematical models with different forms for describing ISARs have been proposed, and in some cases these other forms (e.g. linear, sigmoidal) provide a better fit to the ISAR than does the convex power law (Scheiner, 2003; Even Tjørve, 2003). When expression (1.1) is linearized by logarithmic transformations of S and A (see (1.2.)) z is the slope of the resulting log-log relationship, and c represents the intercept (eq 1.2) (Scheiner, 2003):

$$\log(S) = \log(c) + z\log(A) \quad (1.2)$$

The meaning of z (called the z -value hereafter) holds a place of great interest as it captures the scaling of species richness with increasing area (Arrhenius, 1920a; Kylin, 1923). The z -value has been observed to approach unity when the spatial areas under consideration are considerably larger than entire species’ ranges (Mittelbach & McGill, 2019), as seen in the tri-phasic ISAR where, at large provincial scales, the z -value increases compared to smaller scales (Rosenzweig, 1995; Shmida & Wilson, 1985). The intercept $\log(c)$ (called the c -value hereafter) represents the species richness of an island of unit area and can be influenced by the study taxon and biogeographic region (MacArthur & Wilson, 1967). It has also been used to indicate the biotic richness of an insular system and hence the degree of island impoverishment (Whittaker & Fernandez-Palacios, 2007).

There are several proposed explanations for the ISAR. Three of the more well-developed hypotheses center on habitat diversity, sampling effects, and colonization-extinction dynamics. The *habitat diversity hypothesis* assumes that habitat variety increases as area increases, resulting in greater niche space and species richness (Lack, 1976; Williams, 1964). The *sampling effect* posits that larger areas include more individuals than smaller areas, hence representing a larger ‘sample’, in effect drawn from a regional species pool (Arrhenius, 1921; Connor & McCoy, 1979). Finally, the *colonization and extinction dynamics hypothesis* posits that a homogenous

139 area's increasing size supports larger populations with lower chance of extinction and higher
140 chance of colonization (MacArthur & Wilson, 1967; Mittelbach & McGill, 2019).

141 One challenge to exploring the mechanisms underpinning ISARs is that multiple taxon
142 groups are often analyzed together. By contrast, using a single-taxon (e.g. mammals, birds, frogs,
143 or ants) approach to evaluating ISARs removes known variation in ISAR form and z -values due
144 to taxon effects (Nilsson et al., 1988). Previous studies have found that the z -value of the ISAR
145 can vary between systems, across climatic (Kalmar & Currie, 2007) and latitudinal gradients
146 (Drakare et al., 2006), and by island type (Matthews et al., 2016). These studies document wide
147 variation in the ISAR, possibly resulting from multiple mechanisms that vary depending upon
148 environmental context and ecologically heterogeneous taxa. Differences in z -values by taxa are
149 widespread. For example, a study of ISARs in a mixture of both oceanic and continental islands
150 in the Lesser Antilles found birds to have a z -value of 0.21, bats 0.23, butterflies 0.27, and
151 reptiles and amphibians 0.17 (Ricklefs & Lovette, 1999). Even within lower taxa such as
152 invertebrates, differences in both c and z -values are observed. For example, in the Mediterranean
153 islands centipedes, isopods, and tenebrionid beetles range in z -values (0.24-0.31, 0.20-0.26, 0.27,
154 respectively) and c -values (0.24,-0.31, 0.59-0.80, 0.61-0.94) (Fattorini et al., 2017). Taxon-based
155 differences in both z and c values are likely to be influenced by each taxon's traits such as
156 dispersal capacity or life history strategies. This is observed in butterflies where higher z -values
157 are associated with butterflies with smaller ranges and lower reproductive potential (Franzen et
158 al., 2012). Therefore, an ideal taxon for studying ISARs would be a geographically widespread,
159 taxonomically resolved, species-rich group, with a wide range of well-defined traits and
160 ecosystem roles (e.g. granivores, predators, omnivores) that can be separately analyzed.

161 According to these criteria, ants provide an ideal and important taxon to use for exploring
162 ISARs. With over 13,800 species distributed globally, ants are one of the world's most dominant
163 arthropod groups (Bolton, 2020; Hölldobler & Wilson, 1990). They are also one of the most
164 well-sampled invertebrates in insular systems. Their diversity is immense but well-studied;
165 authoritative taxonomic keys and identification materials permit accurate species identification
166 even in remote areas of the world. Ant trait variation has been well studied and defined (Gibb et
167 al., 2015; Sosiak & Barden, 2020), allowing for the opportunity to disentangle variation in the
168 SAR due to trait diversity. Ants also have the ability to structure entire ecosystems (Lach et al.,
169 2010) and can make up to 15-20% of terrestrial animal biomass (Schultz, 2000). Importantly,
170 ants show high levels of island endemism. Ant island endemism is known to vary greatly
171 across the globe (0% to 96% endemism) and has been linked to the size, location, and isolation
172 of islands (Morrison, 2016). For example, over 70% (187 total species) of the ant fauna of the
173 island of Fiji is endemic (Sarnat & Economo, 2012), while in contrast, very few species are
174 endemic to the Bahamas (Morrison, 2003).

175 Based on the extensive literature on ant biogeography, a number of observations on ant
176 ISARs can be made. First, studies of biogeographical histories (Choi et al., 1993; Ranta et al.,
177 1983; Trainor & Andersen, 2010) and speciation processes on islands illustrate the variability of
178 the ant ISAR across the globe (Economo et al., 2017; Economo & Sarnat, 2012; Wilson, 1961).
179 Second, habitat diversity exerts a persistent and significant influence (Boomsma et al., 1987;
180 Goldstein, 1975; Torres & Snelling, 1997;. Wilson, 1961) as does elevation on insular (Morrison,
181 1997) or mainland (Sanders, 2002) ant diversity. Third, while dispersal is known to be an
182 important driver of ISAR form (MacArthur & Wilson, 1967), its effect is less well studied in ants
183 compared to other taxa. Fourth, and linked to the third point, anthropogenic transport breaks
184 down natural barriers which has resulted in the colonization of many remote islands by non-

185 native ants (Espadaler & Bernal, 2003; Rica et al., 2005; Wetterer & O'Hara, 2002). The
186 resulting presence of non-native ants on many islands (Espadaler & Bernal, 2003; Rica et al.,
187 2005; Wetterer & O'Hara, 2002) can directly influence the ISAR (Wilson & Taylor, 1967).

188 Based on this previous literature, we can make certain predictions of how ant ISARs may
189 differ based on a series of extrinsic variables. Research across both vertebrates and invertebrates
190 show that mainland SARs often have lower z -values and higher c -values compared to insular
191 systems (Matthews et al., 2016). This is attributed to the greater isolation of insular systems.
192 Given an ant's ability to take advantage of human-assisted dispersal (Pyšek et al., 2017) and to
193 establish in impoverished areas we expect more similar patterns in z and c -values between
194 mainland and insular systems than for other taxa. Ant ISARs are also heavily influenced by
195 habitat structure and diversity (Goldstein, 1975; Morrison, 2016). As such, we expect habitat
196 diversity to be a bigger driver of ant richness than area per se. Therefore, we expect certain
197 climatic variables that track habitat diversity to negatively affect the rate of which ant diversity
198 increases with area. Finally, competitive interactions (Wilson & Taylor, 1967) and microhabitat
199 diversity (Goldstein, 1975; Torres & Snelling, 1997) could constrain the species richness of ants
200 on small islands, while processes such as speciation are more likely to influence diversity on
201 larger islands (Economio et al., 2017; Economio & Sarnat, 2012; Wilson, 1961). The shift in
202 importance of these different mechanisms of island community assembly along the area gradient
203 could result in points of inflection in the ant ISAR. While ant ISARs have been well investigated,
204 no research has synthesized all known information on ant ISARs and doing so would help
205 highlight consistent findings and identify knowledge gaps.

206 This study aims to provide a general synthesis of ant ISARs by i) reviewing the ant ISAR
207 literature in order to identify significant data gaps, and ii) quantifying global patterns of ant
208 ISARs through the synthetic analysis of mainland and insular ant ISAR studies. We summarized
209 and compared ant ISAR c -values and z -values across multiple datasets to derive results that can
210 be compared to previous research on ISARs. Specifically, we answered the questions: (1) how do
211 insular and mainland c -values and z -values differ for ants? (2) do climatic variables or isolation
212 influence the z -value of the ISAR for ants? (3) are z -values associated with latitude? (4) are there
213 thresholds in ant ISARs? and (5) is there a general z -value for ants when accounting for variables
214 such as biogeographic realm?

215

216

217 **Methods**

218

219 *Data Collection*

220 We acquired species-level datasets on ants from published articles, primarily species checklists,
221 insular or mainland studies of the ISAR, and island biogeography studies. These data were used
222 to create two 'datasets' (datasets 1 and 2) that formed the basis of the analyses. Dataset 1 was
223 constructed to assess the ant ISAR at the archipelago level which permits the analyses of z and c
224 values. Dataset 2 was constructed to include all individual islands from all datasets to seek
225 general patterns of the ant ISAR. For dataset 1 (see below), a total of 36 studies and 41 datasets
226 were collected (Figure 1A). While dataset 2 comprised a total of 44 studies and 51 datasets.
227 Datasets were recovered using the Web of Science repository, FORMIS (A Master Bibliography
228 of Ant Literature, USDA), scanning of supplementary data of review papers assessing the SAR
229 in multiple taxa (Drakare et al., 2006; Matthews et al., 2016), and unpublished manuscripts
230 (James Wetterer, pers comm.). The following variables were collected from each dataset when

231 available: species richness per island, total species richness of all islands, island/fragment area
232 size, z -value of the SAR, standardized errors of the slope coefficient, R^2 values from the log–log
233 power model, locality of island/fragment, types of island/fragment, island/fragment area ranges
234 (m^2), biogeographic realm, latitude, longitude, climate, percentage of non-native ants, and
235 isolation (distance to the nearest continent for true island datasets) (Table 1). Percentages of non-
236 native ants were limited to 25 datasets that provided full species checklists or explicitly stated
237 non-native ant richness in the publication. If a given true island dataset was comprised of both
238 oceanic and continental islands, then the dataset was assigned the island type comprising the
239 majority. If full datasets from publications were not available, the corresponding author(s) of the
240 study were contacted for access to the original raw data. The supplementary material (Appendix
241 2 and 3) includes both datasets and a list of literature citations.

242

243 *Species-Area Slopes and Intercepts*

244 Whenever possible, z -values were recalculated using a study's raw data (natural logs were used).
245 Island/fragment areas and species richness values from the studies were used to calculate the z -
246 value using the log–log form of the power model (equation 1.2) with ordinary least squares
247 (OLS) regression. However, if raw data were unavailable then the reported z -value was used. In
248 total, 30 out of 41 z -values were recalculated. For non-recalculated z -values, only z -values of the
249 log–log model was used, as the majority of the data collected from the literature utilized that
250 model form. We used a paired t-test to assess the robustness of recalculated z -values compared to
251 reported z -values (8 paired values). However, we also undertook multi-model analyses of
252 competing SAR models to discern the best-fitting SAR model (outlined below). None of the
253 studies contained zero values; as such, no added constants were necessary for log-
254 transformations. If island/fragment areas were not provided, data were recovered from online
255 sources or manually calculated using the Google Earth engine. ISARs fitted with log–log axes
256 have intercepts that are not independent of the units in which area is measured. In order to
257 mitigate this issue, c -values were recalculated after standardizing area across datasets to the same
258 units (1-km^2), which resulted in 30 comparable intercepts.

259

260 *Abiotic data*

261 Climate data, including mean annual temperature (MAT) and mean annual precipitation (MAP),
262 were extracted from coordinates of study locations using the Worldclim database (1 km^2
263 resolution) (Fick & Hijmans, 2017). If climate data were unavailable at specific coordinates then
264 data were collected using island climate data from Weigelt et al. (2013). For studies that spanned
265 islands across large latitudinal or longitudinal gradients (e.g. New Guinea to the Hawaiian
266 Islands), an averaged value of the MAT and MAP from the individual study islands available
267 from Weigelt et al. (2013) was assigned. This approach was considered more accurate than
268 choosing coordinates at a midpoint and extracting the MAP/MAT using the Worldclim database.
269 Isolation for the true islands was calculated by measuring the distance of the island closest to a
270 continent from a dataset. Not all studies included island location or names and therefore isolation
271 values were limited to 29 datasets.

272

273 *Final Datasets for Analysis*

274 As stated above, two datasets were collated for the analyses: Dataset 1 was used to assess the
275 best fitting model for ant ISARs using a multi-model inference approach, the c and z -values of
276 each study, and the effects of isolation and climate on z -values. Dataset 2 was used to calculate a

277 general z -value from all islands and evaluate the potential for thresholds or points of inflection in
278 the ant ISAR. Dataset 1 included c and z -values for each study, isolation, biogeographic realm,
279 difference in order of magnitude in island area range per study (calculated as: $\text{Log}_{10}(\text{Maximum}$
280 $\text{Area} / \text{Minimum Area})$), general latitude and longitude, MAP, MAT, standard errors of the
281 slope, R^2 of the log-log model, and ISAR type. The ISAR type variable specifies whether the
282 study was done on the mainland or in an insular system (true islands). Dataset 2 focused on
283 individual islands and included data from each island in studies that provided areas and species
284 richness values for each island. Dataset 2 included studies not in dataset 1 as some studies only
285 inventoried ants on a single island. If any duplicate islands appeared in dataset 2 (multiple
286 studies sampling the same island) then the most recent study and values were used. Variables
287 included with this dataset were: island area, species richness, SAR type, and biogeographic realm
288 of the island.

289

290 *Analysis*

291

292 **Dataset 1**

293 Dataset 1 comprised 41 datasets and their z -values. Only datasets with positive z -values were
294 considered. Four formats of dataset 1 were used for four different questions. The first format of
295 dataset 1 included the individual islands areas and species richness values. This format was used
296 to assess the robustness of the power model in fitting the datasets, and to determine whether
297 other model forms better represent ant ISARs. The second format used each dataset's z -value and
298 abiotic data to determine differences between mainland and insular ISARs, as well as the effects
299 of abiotic variables on z -values. The third format used only true island (insular) studies with
300 isolation values to assess the effects of isolation on z -values. The final format used only the
301 datasets where c -values were recalculated using the same measurement units (km^2). This dataset
302 was used to determine potential differences in c -values between mainland and insular studies.

303 To assess the robustness of the power model, a multi-model inference approach was
304 executed utilizing 20 different ISAR models (including the power model in its non-linear form)
305 using the "sars" R package (Matthews et al., 2019) and following the approach outlined in
306 Matthews et al. (2016) and Triantis et al. (2012). The 20 models represented a range of ISAR
307 forms including linear, convex, and sigmoidal. During maintenance of the 'sars' package while
308 preparing these analyses, it was discovered that the He & Legendre logistic model and the mmf
309 model were equivalent (see also Williams et al., 2009). Thus, as an alternative to the mmf model,
310 we used the standard logistic model (see Tjørve, 2003). Models were fitted to each study's
311 distinct dataset and compared using AIC_c (Akaike's Information Criterion corrected for small
312 sample sizes). The models were fitted twice to each dataset (areas were all first converted to
313 km^2): once when implementing model residuals validation checks (for normality using a
314 Lilliefors test, and homogeneity of variance using a Pearson's correlation of the squared
315 residuals with the area values) and once with no checks. For the former, if a model failed one or
316 both of the two checks it was removed from the model comparison for that dataset (see Matthews
317 et al., 2019). When fitting models, we used a grid search procedure (setting the `grid_search`
318 argument to 'exhaustive' in the `sar_average` function) to test a large number of starting parameter
319 values (5000 combinations for each model) in the non-linear regression optimization algorithm;
320 this increases the likelihood that optimum parameter estimates are found.

321 The performance of individual models across datasets was calculated by comparing the
322 mean AIC_c weight and the mean rank (i.e. a model's rank in the model comparison for each

323 dataset) (Triantis et al., 2012). When model residuals tests were used, the mean rank and weight
324 of a model across datasets were calculated after removing the cases where the model did not pass
325 the tests. It was necessary to remove datasets with fewer than seven observations, the minimum
326 number required to calculate AIC_c for models with four parameters. This resulted in 25 datasets
327 being analyzed. All models were fitted using untransformed data.

328 To assess differences between the z -values of insular and mainland datasets a generalized
329 linear model (GLM) with a Gamma (link = log) error distribution was run using the z -values as
330 the response variable, and study type as a predictor. The Gamma distribution was chosen as z -
331 values were not normally distributed and error distributions used for skewed data such as the
332 Poisson or negative binomial assume a discrete error distribution. In addition, because mainland
333 islands were smaller than the majority of true islands across the dataset, a secondary model (with
334 the same specifications) including a covariate of mean area of the datasets was run with a
335 reduced dataset of 30 observations (Number of data sets with a mean area). Model assumptions
336 were checked using residual diagnostic plots.

337 To assesses the potential effects of climate or latitude on z -values, GLMs with a Gamma
338 (link = log) error distribution were used. Two model structures were used to incorporate two
339 different covariates. The first model used the order of magnitude in island size range per dataset
340 as a covariate, as potential variation in slope values corresponding to different ranges in areas
341 among different datasets should be considered (Martin, 1981). We included interaction terms
342 between the covariate and climate variables because of the non-linearity that is observed in how
343 biodiversity increases across space (Keil & Chase, 2019). As such, the effect of climatic factors
344 on the rate at which species richness increases with area is not constant across scales. Seven of
345 the 41 datasets had no island area ranges (only z -values were provided with no island area data),
346 and as such the final modeling dataset here used a total sample size of 35.

347 The second model structure utilized the SAR type (insular or mainland) as a covariate, as
348 z -values were observed to significantly vary by this category. Models used with this structure
349 had a sample size of 41 as all datasets had a specified SAR type. With this model structure,
350 interactions between the covariate and climate variables were not included because the effects of
351 climate were presumed to be the same in mainland and insular systems. Both covariates could
352 not be used in the same model because the low sample size would have resulted in lower
353 statistical power and an increased risk of model overfitting. Mixed-effect models were not used
354 because the low sample size resulted in singularity in the models.

355 Other predictors in the two model structures included MAP, MAT, latitude, and
356 biogeographical realm. Models never included MAP and MAT variables together due to
357 collinearity. Specific model structures are detailed in Table 3. The maximum number of
358 predictors allowed in a model was three to avoid overfitting. All models were assessed using
359 generalized variance inflation factors (VIFs), with a particular focus on models with both
360 biogeographical realm and climate variables. All continuous variables were scaled (to a mean of
361 zero and unit variance) prior to running models. Model comparison was conducted using AIC_c
362 for each set of models corresponding to the two different covariates. Pseudo- R^2 values were
363 calculated using the piecewiseSEM package in R.

364 Isolation values were measured for 29 insular datasets. To assess the impacts of isolation
365 on z -values, a GLM with a Gamma (link = log) error distribution was used. Thirty of the 41
366 datasets had re-calculated c -values. OLS regression was used to test for differences in these c -
367 values between insular and mainland studies. The Gamma distribution was not implemented
368 because it does not accommodate negative values. Data were not transformed because c -values

369 were already on a log-scale. Similar to the second GLM used to account for mean area when
370 assessing differences between the z -values of insular and mainland datasets, a second model was
371 run on c -values with a covariate of mean area per c -value dataset. To verify that all model
372 assumptions were met, model residuals were evaluated for normality and homogeneity of
373 variance.

374 Finally, we re-ran models with datasets that contained 10 or more islands. This was done
375 in an effort to reduce the impact of datasets that did not survey enough islands and to offer a
376 potentially more biologically meaningful perspective on c and z -values. All analyses were
377 implemented in R (version 4.0.0) (R Development Core Team, 2018).

378

379 ***Dataset 2***

380 Dataset 2 comprised all individual islands with area and species richness values. This dataset
381 permitted us to provide broad assessments of ISARs, utilizing information from singleton islands
382 not themselves part of an explicit SAR study. Linear mixed-effect models were used to seek a
383 general power model (based on the $\log(\text{SR}) \sim \log(\text{Area})$ form) slope coefficient. Natural logs
384 were used to calculate both $\log(\text{SR})$ and $\log(\text{Area})$. Not all studies provided island-specific data,
385 but a total of 481 islands (both mainland and true islands) with species richness observations
386 were collected. There was a distinct difference in species richness and area between mainland
387 islands and true islands (Figure 2B); the two types of island are also likely affected, to different
388 degrees, by different biogeographical processes (e.g. dispersal, speciation). Furthermore,
389 mainland islands spanned a distinctly smaller area gradient compared to true islands. Therefore,
390 dataset 2 was further divided into mainland ($n = 161$) and true island ($n = 320$) subsets, which
391 were analyzed separately with two different mixed-effect models. In both models, log species
392 richness was assessed as a function of log area with biogeographic realm used as a random
393 effect.

394 The model implemented with the mainland subset failed to meet model assumptions
395 based on visual diagnostics of residuals and therefore results and discussion of this model are not
396 included in this study. Failure to meet assumptions was likely due to an absence of a linear trend
397 between $\log(\text{SR})$ and $\log(\text{Area})$.

398 All mixed-effects models were run using the lme4 package (Bates et al., 2015).
399 Visualization of fixed and random effects were conducted using the ‘R’ packages “ggeffects”
400 (Lüdtke, 2018) and “ggplot2” (Wickham, 2009). Pseudo- R^2 values (Marginal and conditional
401 R^2) were calculated using the “MuMin” package (Barton, 2019). AIC_c values were calculated
402 using the package “bbmle” (Bolker & R Development Core Team, 2020).

403 In a separate analysis, threshold models were fitted to the insular and mainland subsets to
404 identify any potential points of inflection in their ISARs. We fitted two piecewise models (the
405 continuous and left-horizontal one-threshold models) using new functionality in the “sars” R
406 package (Matthews & Rigal, 2021). Both models have two segments. The continuous model
407 allows both segments to vary in slope, while the left-horizontal model assumes the first segment
408 to have a slope of zero, which is characteristic of the classic small island-effect (MacArthur &
409 Wilson, 1967; Whitehead & Jones, 1969), where there is a lack of relationship between area and
410 richness on smaller islands. The models were fitted in both log–log space (area and richness log
411 transformed; natural logarithms) and semi–log space (area log transformed) as the choice of log-
412 transformation has been found to influence the fit of threshold models (Burns et al., 2009;
413 Matthews et al., 2014). In both cases, the two threshold models were compared (using AIC_c)
414 with a linear model (i.e. either the logarithmic or power SAR models depending on

415 transformation) and an intercept-only null model. Following Matthews et al. (2014), we
416 checked for influential observations in the threshold model fits using Cook's distance and a
417 threshold of one. Threshold models were not fit to individual datasets (i.e. those in dataset 1) due
418 to the smaller sample sizes involved. Finally, to determine whether the observed piecewise
419 relationships were driven by biome effects, we fitted a mixed-effects piecewise regression model
420 using functions written by the author of the 'segmented' R package (Muggeo, 2016; Muggeo et
421 al., 2014). For ease, we focused on the continuous one-threshold model (semi-log transformation)
422 for the insular subset. Log-transformed area was the fixed effect, and biogeographic realm was
423 used as a random effect. We fitted two variants of this model: i) a model with just a random
424 intercept for biogeographic realm, and ii) a model with both a random intercept and a random
425 breakpoint for biogeographic realm. An identity regression model for the changepoint was used
426 (Muggeo, 2016). As we were interested in the random effects and were not comparing models,
427 we fitted the models using restricted maximum likelihood.

428

429 **Results**

430

431 *Dataset 1*

432 Of the 41 total datasets examined for this study, z and c values were recalculated for 30 of them.
433 Of the 11 remaining datasets, all reported z -values (log-log power model slopes) in their
434 associated papers, none reported standard errors of z -values, and 7 reported R^2 values and c -
435 values (not used for analyses). The paired t-test showed no significant differences between
436 recalculated and reported z -values. In total, 30 datasets were from insular systems and 11 were
437 from mainland systems. The majority of the mainland datasets (7 of 11 datasets) were from
438 fragments due to anthropogenic activities. The biogeographical realm with the most studies was
439 the Palearctic (13) and the realm with the fewest was the Afrotropics (2) (Table 2, Figure 2A).
440 Non-native ant percentage ranged from 0 to 87% and the average percentage of non-native ants
441 in mainland and insular datasets was 2.82% and 29.90% respectively. Continental and oceanic
442 island datasets had an average non-native percentage of 18.7% and 34.6% respectively. The
443 biogeographical realms with the highest non-native ant percentage in mainland and insular
444 systems were the Palearctic (5%, one dataset) and Oceania (average 51%, 3 datasets)
445 respectively.

446 When no residual checks were used, the power model was the best overall model across
447 datasets, according to both mean model rank and mean AIC_c weight (see Fig. S1 in Appendix 1).
448 The model provided the best fit (lowest AIC_c) to 11 of 25 datasets and was ranked in the top five
449 for 20. When model validation was implemented, the power model rank shifted slightly (Fig.
450 S1). It was the second-ranked model according to mean rank (behind the Kobayashi model; also
451 a convex non-asymptotic model) but was still the top-ranked model according to mean AIC_c
452 weight. With model validation, the power model provided the best fit to eight datasets and was
453 ranked in the top five for 15; for seven datasets it did not pass validation checks. Overall, these
454 results indicate that power model represents a generally robust model for characterizing ant
455 ISARs and allow us to confidently analyze power model z -values across our datasets.

456 Mainland islands had the highest variance in log-log power model z -values (Figure 2C).
457 The number of islands or fragments used to generate a slope value from a study ranged from 3 to
458 81. The range in difference in order of magnitude between the smallest and largest island areas
459 was 0.70 to 6.17. The minimum z -value was 0.04, the maximum was 0.89, and the average was
460 0.28. z -values varied by biogeographic realm and by ISAR type (insular or mainland). The mean

461 z -value for mainland studies (0.38 ± 0.08) was significantly higher than insular studies ($0.25 \pm$
462 0.02). This was verified with a GLM (effect size of mainland studies relative to insular studies:
463 0.43 ± 0.20 , $p < 0.05$, Pseudo- $R^2 = 0.07$). The second GLM run on the reduced dataset showed
464 no significant effects from either covariate (mean area) or SAR type on z -values. While the
465 covariate of mean area did not significantly impact z -values, its inclusion reduced the available
466 degrees of freedom. This coupled with the reduction of observations for this model (11 less
467 observations) resulted in lower statistical power to potentially detect a difference between
468 mainland and insular z -values.

469 Nine competing GLMs, including a null model, were fitted to evaluate effects of climate
470 and latitude on z -values while accounting for the order of magnitude in island area range.
471 Latitude effects were not observed in any of the models. The most plausible model based on
472 AIC_c was a model evaluating z -values as a function of the additive effects of order of magnitude
473 in island area (covariate) and MAP (Pseudo- $R^2 = 0.11$). The covariate had a non-significant
474 effect, but MAP had a significant negative effect on z -values (-0.24 ± 0.11). It's important to
475 note that the second ranked model (a model with only the covariate as the predictor) was within a
476 ΔAIC_c of 2 suggesting that both models were commensurate with one another. While the second
477 ranked model had one less parameter, the top-ranked model was still designated as most
478 plausible given the higher pseudo- R^2 . However, we still exercised caution when interpreting this
479 model.

480 Seven models were run to assess the effects of climate and latitude on z -values while
481 accounting for ISAR type (Table 3). The most plausible model based on AIC_c was one that
482 evaluated z -values as a function of the additive effects of ISAR type (covariate) and MAP
483 (Pseudo- $R^2 = 0.18$). There was a non-significant effect from the covariate but a significant effect
484 of MAP on z -values (-0.26 ± 0.09).

485 Mainland ISARs had significantly higher c -values compared to insular ISARs (effect size
486 of mainland studies relative to insular studies: 2.71 ± 0.66 , $p < 0.05$, Adjusted- $R^2 = 0.35$).
487 Average c -values for mainland and insular ISARs were 4.55 ± 0.86 and 1.44 ± 0.26 ,
488 respectively. The second model that accounted for mean area when assessing differences
489 between insular and mainland datasets showed a significant effect of the covariate but no
490 significant effect of SAR type. Across biogeographical realms that had both insular and mainland
491 ISAR types (Afrotropics, Nearctic, Neotropic, Palearctic), c -values were lower in mainland
492 systems only in the Nearctic (see Table S1 in Appendix 1). Finally, no significant effects of
493 isolation on z -values were observed.

494 Models re-run on datasets with 10 or more islands showed no difference between
495 mainland and insular z -values and no effect of isolation on z -values. There was a significant
496 difference between mainland and insular c -values with mainland c -values being on average
497 higher than insular c -values (effect size of mainland studies relative to insular studies: 3.07 ± 0.9 ,
498 $p < 0.05$, Adjusted- $R^2 = 0.43$). AIC_c rankings of GLMs assessing the effect of climate and
499 latitude with two different covariates showed the top ranked models both included a significant
500 and negative effect of MAT on z -values. However, both models were within a ΔAIC_c of 2 of the
501 null models (z -slope ~ 1). As such these models are not discussed further but their model outputs
502 and AIC_c rankings have been made available in the supplementary materials (see Tables S2-S4
503 in Appendix 1).

504
505 *Dataset 2*

506 Of the 481 islands in dataset 2, 161 were mainland islands, and 320 were true islands. True
507 islands types were made up of 160 oceanic and 160 continental islands. The linear-mixed effect
508 model evaluating the ISAR for insular data showed a significant effect of area on species
509 richness (model coefficient: 0.16 ± 0.03) (Figures 1B & 1C). Based on marginal and conditional
510 R^2 values, area explained 29% of the variation in species richness. However, when including the
511 random effects of biogeographic realm, the model explained 60% of the variation (difference =
512 31%). The lowest random intercepts were from Oceania and the Palearctic while the highest
513 intercepts were from Indomalaya and the Afrotropics (Figure 1C). The steepest random slopes
514 were found in the Nearctic and Oceania while the lowest random slopes were in the Indomalaya
515 and Afrotropics.

516 Based on AIC_c , when using both the log–log and semi-log transformations, the two
517 threshold models both provided a better fit to the global insular dataset than the linear (log–log
518 power and logarithmic model, respectively) and intercept-only null models (Table 4), with the
519 continuous one-threshold model providing the best fit in both cases. The R^2 value of the best
520 threshold model for the insular dataset ranged from 0.36 to 0.54, depending on the
521 transformation. Figure 5 shows the best threshold model fits to the insular dataset, using both the
522 log–log and semi-log transformations. There was one threshold model fit (left-horizontal model
523 fit to the insular data in semi-log space) with a Cook’s distance greater than one. However, we
524 left the data point in as it was only slightly greater than one (1.09) and removing it did not
525 change the overall results or general model fit. More generally, the insular semi-log threshold
526 model fits should be viewed tentatively as their residuals deviated from normality and/or plots of
527 the fitted values against the residuals tended to show that the magnitude of the residuals was not
528 constant along the fitted values. For the global mainland dataset, the continuous one-threshold
529 model provided the best fit to the log–log data, while the left-horizontal model provided the best
530 fit to the semi-log data (Appendix 1 Table S5). However, the mainland threshold model fits were
531 harder to interpret, with the R^2 value of the best threshold model ranging between 0.20 and 0.23,
532 some of the model residuals deviating from normality and exhibiting heteroscedasticity, and the
533 relationships seemingly driven by biome effects (see Figure S2). As such, these model fits are
534 not discussed further.

535 The mixed-effects piecewise models fitted to the insular subset revealed that the
536 population estimate (i.e., the fixed effect piecewise relationship) provided a good rough
537 approximation for all the biogeographic realms except for the Nearctic, and to a lesser extent the
538 Afrotropics (the plots of these model fits are provided in Figure S3-S4 in Appendix 1). In the
539 case of the Nearctic, the lack of an obvious threshold relationship was likely due to the limited
540 range in island area, that is, there were no islands near or above the breakpoint value(s) observed
541 for the other biogeographic realms (Fig. S3). For the model where the breakpoint varied by
542 biogeographic realm, the standard deviation of the random breakpoint was 2.6 (on the log-scale).
543 This variation was affected by the value for the Nearctic realm, where the breakpoint is much
544 lower and is likely a statistical artefact (again due to the lack of large islands in our dataset for
545 this realm). In addition, the random breakpoints for the Afrotropics and Indomalaya were
546 considerably larger than the population estimate (Fig. S4). Overall, these results indicate that,
547 although the intercept and the exact breakpoint value do vary to a degree between realms, the
548 observed threshold relationship in the insular ISAR is not simply driven by islands from one or
549 two realms.

550
551

552 **Discussion**

553 Studies of the ISAR in ants extend over the past 60 years, spanning all biogeographical realms,
554 except Antarctica. Here, we demonstrate that the scaling of ant species richness with area can
555 differ between mainland and insular systems, and along precipitation gradients. We also show
556 that incorporating biogeographical realm types into analyses provides a better explanation of this
557 scaling pattern than does area alone, suggesting a macroevolutionary perspective on species–area
558 relationships.

559

560 *Dataset 1: Mainland vs. Insular Systems*

561 We found that z -values, the rate at which log species richness increases with log area, vary
562 widely across studies of ant communities, highlighting the extent of variation in the z -value of
563 the ISAR within a single taxonomic group. An intriguing finding from our analyses is the
564 significant difference in average z -values between mainland and insular systems, a result which
565 contrasts with results of an extensive meta-analysis which did not detect differences in z -values
566 (Drakare et al. 2006). Whereas past studies reported steeper z -values in insular systems than in
567 mainland systems (MacArthur & Wilson, 1967; Matthews et al., 2016; Triantis et al., 2012;
568 Whittaker & Fernandez-Palacios, 2007), in this study mainland ant ISARs have *steeper* z -values
569 compared to insular systems (Figure 2B). While area effects can influence z -values given that the
570 majority of mainland islands were smaller than true islands in our data, we found a lack of
571 significant effect of mean area as a covariate, when analyzing a reduced dataset. Higher z -values
572 in mainland systems may reflect a biological pattern or could be explained by sampling bias in
573 our dataset, as a higher proportion of mainland studies (50%) were conducted in the Neotropics,
574 a biogeographical realm considered to include the world's highest ant diversity (Hölldobler &
575 Wilson, 1990). If species geographical ranges are typically smaller in species rich faunas, one
576 would expect richness to tend to increase more strongly with area, for studies that span much of
577 biogeographical provinces. However, mainland datasets in our study only focused on habitat
578 patches or fragments where dispersal is likely not as limited as in insular systems (Storch, 2016),
579 and this range size effect would not likely be evident at small spatial scales.

580 Another possible reason for higher z -values in mainland systems is the differences in ant
581 dispersal success and propagule pressure between mainland and insular systems. Insular systems
582 often have higher levels of isolation for longer periods of time. As a result, when compared to
583 true islands, mainland islands often hold a larger portion of the regional species pool (Flantua et
584 al., 2020). Furthermore, ant species that successfully disperse and colonize insular systems are
585 usually generalists and are likely to be excellent dispersers (Morrison, 2016). Insular studies
586 often gauge dispersal possibilities of ants based on isolation distance between sampled islands
587 (Woinarski et al., 1998); other studies view dispersal to be a hidden variable that cannot be
588 quantified accurately (Badano et al., 2005). While one study showed that increasing isolation
589 actually led to higher aboveground ant species richness in naturally fragmented landscapes
590 (Cuissi et al., 2015), this relationship was not observed with arboreal ants, suggesting that
591 isolation may affect ants in various strata differently. Moreover, natural dispersal may be
592 irrelevant in some insular systems where human colonization of islands has led to human-
593 assisted dispersal of ants and dominance of local ant communities by introduced species
594 (Holway et al., 2002; Pyšek et al., 2017; Wilson & Taylor, 1967). Although dispersal is likely a
595 key element underlying ISARs, the sparse literature on dispersal effects on ISARs points to the
596 difficulty in quantifying this factor (Hakala et al., 2019). Clearly, more sampling in mainland

597 islands across different biogeographical realms is needed to fully understand the observed
598 differences between mainland and insular slopes.

599 We observed lower c -values in insular systems than mainland systems indicating higher
600 degrees of island impoverishment or lower biotic richness in local communities on true islands
601 (Whittaker & Fernandez-Palacios, 2007). This was also observed in datasets with only 10 or
602 more islands. When accounting for mean area of the islands per dataset, mean area significantly
603 affected c -values while differences between mainland and insular studies became statistically
604 negligible. This suggests that area differences between mainland and true islands contributes to
605 differences in c -values. Island impoverishment levels likely impact the colonization process of
606 insular ants compared to ant dispersal which often relies on the capitalization of habitat resources
607 (Morrison, 2016). For example, impoverished true islands may have less habitat heterogeneity or
608 food resources specifically for ants due to lower plant biotic richness which can result in a lower
609 likelihood of successful colonization, less opportunity for speciation or higher extinction rate.
610 Identifying the causal underpinnings of the differences in c (local richness) and z (spatial scaling
611 of richness) between continental and insular systems is an important challenge for future work.

612 Higher z and c -values found with the mostly anthropogenically created mainland
613 fragments from this study potentially opens exciting avenues of future research, such as the
614 effect of fragment age on the mainland ISAR. Such research could develop a continental analog
615 of the general dynamic model of island equilibrium theory (Whittaker et al., 2008), which links
616 the temporal development of volcanic islands to the equilibrium theory of island biogeography.
617 Previous research has already utilized landscape histories (e.g., how a landscape becomes
618 fragmented over time) to develop models capable of predicting species extinctions and
619 biodiversity in fragmented landscapes (Ewers et al., 2013). However, we still lack a general
620 framework for understanding how fragment age affects different biodiversity properties. Any
621 framework would need to account for extinction debts, especially those in smaller fragments, and
622 the quality of habitats within different-sized fragments. Differences in how gradual
623 fragmentation versus pulse fragmentation events influence biodiversity patterns, similar to the
624 differences observed between continental and oceanic islands, could also be incorporated.
625 Perhaps, the integration of these different phenomena into a single framework could lead to the
626 development of a general dynamic model of anthropogenic landscapes.

627
628 *Dataset 1: Climatic drivers of the ISAR*

629 Another clear result from this study is the finding that higher precipitation levels lead to a
630 significant decrease in z -values. This was observed from the results of generalized linear models
631 that predicted z -values as a function of a covariate (either ISAR type or order of magnitude
632 island range) and precipitation (Figure 3). Precipitation is known to influence aboveground plant
633 biomass, habitat diversity (e.g., more vegetation strata and litter with increasing precipitation),
634 and net primary productivity (NPP) (Yan et al., 2015; Zhu et al., 2014). Considering
635 precipitation as a proxy for NPP, our results are similar to those reported in Storch et al. (2005),
636 who identified a negative relationship between productivity and the ISAR z -value. Lower R^2
637 values are present at higher levels of precipitation (see Figure 4), illustrating that area effects
638 explain less of the variation in ant species richness as precipitation increases. Our results also
639 agree with other studies on insular ants that show the effect of habitat diversity as being as
640 important as area when predicting species richness (Goldstein, 1975; Torres & Snelling, 1997).

641 One mechanism through which increased precipitation could weaken area effects would
642 be a boost in overall abundance, per species, which could lower extinction rates or heighten

643 colonization rates in habitat patches or islands. Another mechanism would be that increased
644 precipitation can yield a higher diversity of microhabitats for ants at a local scale; the diversity
645 and available biomass of plants is crucial, providing a diversity of resources through both plant-
646 ant interactions and heterogeneity in the range of suitable nesting sites (Hölldobler & Wilson,
647 1990; Lach et al., 2010). Unraveling the effects of precipitation on both macro- and microhabitat
648 diversity in insular systems that vary in spatial areas will help us understand the scales at which
649 abiotic conditions significantly impact biodiversity.

650 Morrison (2016) indicated that isolation may provide only weak effects on ant species
651 richness at small scales but may be more important at larger ones. This would be logical as
652 dispersal distance among habitat islands in a continental setting is likely modest compared to the
653 distances relevant to (most) oceanic islands. While our analyses show that isolation had no
654 significant effect on the z -value despite isolation distances spanning from 0.348 to 4,820
655 kilometers, isolation cannot be discounted as an important component to ant community
656 assembly in all true island systems. Further discussion on the potentially weakening effects of
657 isolation as a barrier to dispersal in ants are provided later in this discussion.

658 Overall, two clear results emerged from the analyses of dataset 1. First, z -values of
659 mainland ISARs appear to be significantly *higher* than insular ISARs. Second, increases in
660 precipitation lead to *lower* z -values in ant ISARs. Therefore, the extent of area effects on ant
661 ISARs is dependent on both abiotic conditions and whether or not one is considering ‘true’
662 islands, or habitat islands (influences that have been noted in previous studies, e.g. Drakare et al.,
663 2006; Kalmar & Currie, 2007).

664 *Dataset 2: A general species–area relationship in ants*

665 To arrive at a global-scale z -value for ants, we implemented a linear mixed-effect model with
666 320 true islands and their respective ant species richness and found a global and general z -value
667 of 0.16 for ants. This value is lower than what is expected from general ISARs observed in other
668 taxa, especially in true islands at regional scales (Rosenzweig, 1995). However, the random
669 slopes for the 7 biogeographical realms ranged from 0.06 (Indomalaya) to 0.25 (Oceania). This
670 variation in random slopes across realms and the improvement of explanatory power when
671 accounting for biogeographical realms as a random effect, implies that the ant ISAR is not
672 constant, but varies according to different realms (Figure 1C). Differences between
673 biogeographic realms are expected to influence the ant ISAR as each realm has a unique
674 geological and evolutionary history with different aged ant faunas and historical pattern of
675 speciation, which could lead to different ISAR patterns (Choi et al., 1993; Ranta et al., 1983;
676 Trainor & Andersen, 2010). The low random slope in the Afrotropics may be an artifact of small
677 sample size as only 15 of the 320 islands come from this realm (this realm has relatively few true
678 islands), while lower random intercepts for Oceania and the Palearctic suggest systematically
679 lower alpha diversity in those regions. In Figure 2, the outlier among realms is Oceania, which
680 has considerably steeper ISARs than the other realms. In the Nearctic, all islands that were
681 sampled were continental islands ($n = 23$) while 57% of islands ($n = 65$) in the Neotropics were
682 oceanic islands but both realms held similar random slope values (Nearctic 0.20, Neotropics
683 0.19). However, the majority of islands from the Neotropics come from areas close to the
684 northern limits of this realm (e.g. Sea of Cortez, West Indies) which may explain the similarity in
685 slope values.

686
687 In regard to the threshold in the global true island ISAR (Fig. 5), the threshold (excluding
688 the left-horizontal model in log–log space) was identified at roughly 133–163 km². The mixed-

689 effects piecewise model fit revealed that the observed threshold did vary between biogeographic
690 realms (e.g., being larger for Indomalaya), but, with the exception of the Nearctic and possibly
691 the Afrotropics, the general pattern was consistent. This finding does not mean such a threshold
692 does not exist for Nearctic islands, but simply that our data did not include a wide enough range
693 of island areas to test this proposition. These thresholds, or points of inflection, can indicate
694 specific spatial scales at which species richness accumulates at different rates across areas,
695 reflecting processes such as the “small-island effect” (MacArthur and Wilson 1967; a
696 distinctiveness of habitats on small islands, e.g. edge effects in habitat fragments). The high
697 threshold observed for insular systems here could indicate an important role for speciation in
698 driving ant diversity on large true islands. Speciation events can strongly influence the ISAR in
699 larger true islands compared to smaller-sized island systems in ants (Economio et al., 2017;
700 Economio & Sarnat, 2012; Wilson, 1961). Speciation rates are positively correlated with island
701 area and, above a certain threshold, in-situ speciation can be a richer source of new species
702 within an island than establishment from colonizing species (Losos & Schluter, 2000).
703 Speciation in natural true insular systems likely affects ant ISAR patterns because eco-
704 evolutionary specialization in colonizing generalists can lead to in situ speciation, a pattern
705 consistent with the taxon cycle hypothesis (Economio & Sarnat, 2012; Wilson, 1961). These
706 speciation events within island systems can yield high levels of endemism in ants, levels that in
707 some cases are higher than those observed in birds or vascular plants (Andersen et al., 2013).

708

709 *Gaps in the ant species–area relationship*

710

711 ***Sampling gaps and data deficiencies***

712 The rich history of research in ant biodiversity has resulted in a significant body of species-level
713 data on ant communities. Our analyses of these data clearly illustrate that different island
714 systems exhibit different species–area relationships. However, as Figure 1A illustrates, the
715 studies are unevenly distributed across the globe, with scant studies from Africa and tropical
716 mainland Asia. These gaps highlight the regions of the world from which additional ant
717 biodiversity data would be especially valuable. It would be valuable to expand the range of
718 studies in anthropogenically generated islands (resulting from habitat fragmentation). Especially
719 now that forests in particular are becoming increasingly fragmented around the globe, creating
720 multiple new continental ‘islands’ (Haddad et al., 2015) for examination of species-area
721 relationships.

722

723 ***Incorporation of habitat diversity & other variables***

724 Future research aiming to understand the drivers of variation in the ant ISAR will need to
725 incorporate variables beyond area, a point extensively discussed in the literature (Chase et al.,
726 2019; Triantis et al., 2003; Whittaker & Fernandez-Palacios, 2007). One clear way forward with
727 ants is to consider variables such as habitat diversity in the context of competing hypotheses. It is
728 unarguable that habitat diversity is an influential factor affecting ant ISARs (Torres & Snelling,
729 1997; Wilson, 1961) and, in some cases, habitat diversity measures have been incorporated as
730 covariates within the log-log ISAR model (e.g. as variables quantifying soil clay content)
731 (Goldstein, 1975). Future investigations of ant ISARs should use ISAR models that implement
732 habitat diversity, such as the choros model, which utilizes habitat diversity indices within the
733 power function by multiplying a habitat diversity index with area. This model has led to a better
734 fit of the ISAR when compared with conventional models (Triantis et al., 2003). Moreover, our

735 finding that higher precipitation leads to a shallower ISAR (see also Storch et al. 2005) suggests
736 broad-scale ecosystem drivers of the spatial scaling of species richness, a pattern that warrants a
737 clear mechanistic interpretation.

738

739 *Sample size*

740 The average number of islands used per study from this paper in insular and mainland systems
741 was 16 and 15 respectively. However, recent work indicates that a minimum of sample size of 25
742 is often necessary to identify significant trends of variation when there is high variance in the
743 data (Jenkins & Quintana-Ascencio, 2020). That same study reported that 79% of 217 island
744 biogeography studies constructed species–area curves with fewer than 25 observations. While
745 acquiring insular data can be difficult, it is important that future studies aim to sample enough
746 islands to reach a minimum sample size that can effectively quantify the ISAR. Although this
747 can be problematic in studies of true archipelagos that contain few islands (i.e. the small sample
748 size is intrinsic to the system, not a sampling issue), it should not be a problem in continental
749 regions, where anthropogenic habitat fragmentation is creating an abundance of fragments
750 varying greatly in area and isolation.

751

752 *Impacts of non-native ants on the SAR*

753 Our ability to understand and predict the effects of non-native species on the ISAR is limited by
754 a paucity of knowledge of the interactions between non-native and native ants within insular
755 systems. However, observational evidence does exist of specific non-native and invasive ants,
756 called “plague ants”, completely displacing native ant populations in insular systems (Morrison,
757 2016; Wilson, 2005). Multiple studies have previously demonstrated that slope values of SARs
758 can be different when native or non-native status of species are taken into account (Rica et al.,
759 2005; Wilson & Taylor, 1967). Well-sampled areas like the Florida keys show specific non-
760 native species as being dominant on certain islands while native species remain dominant on
761 others (Wetterer & O’Hara, 2002). Such systems raise questions as to why certain islands may be
762 more susceptible to the establishment of non-native ants and how non-native ants influence the
763 ISAR both empirically and theoretically.

764 In our study, we show that non-native ants can comprise anywhere from 0% (Boomsma
765 et al., 1987; Dean & Bond, 1990; Leal et al., 2012; Vasconcelos et al., 2006) to 87% (Sugiura,
766 2010) of the ant fauna. We also observed higher percentages of non-native ants in insular
767 systems compared to mainland systems, likely as a result of human-assisted dispersal often
768 favoring non-native species with generalist tendencies (Morrison, 2016). Generalist ant species
769 often have traits such as a broad range of nesting habitats (Fournier et al., 2019) that aid in
770 surviving human-assisted dispersal and subsequent island colonization. In fact, Rizali et al.
771 (2010) clearly shows that non-native species track human settlements on the islands of West
772 Java, Indonesia. Human-assisted dispersal allows species to move over much greater distances
773 than feasible by natural dispersal, resulting in colonization of more remote islands (often distant
774 oceanic islands) which may have impoverished native faunas. This is reflected in our data where
775 we observe almost double the non-native ant percentage in oceanic islands compared to
776 continental islands. While many ants can produce thousands of reproductive alates for dispersal,
777 the chance of any one successful colonization is extremely low. For example, Levins et al.
778 (1973) estimated the rate of successful colonization by queen ants to islands near Puerto Rico to
779 be ~4%. In terrestrial mainland systems, the red-imported fire ant is reported to have queen
780 survival rates as low as 0.5% in field conditions (Tschinkel & King, 2017). However, this may

781 be offset by higher propagule pressure from human-assisted dispersal. Ultimately, a better
782 understanding of the trade-offs in ant dispersal and colonization will shed more light on the
783 effects of non-native ants on the SAR.

784

785 *Conclusions*

786 Our study presents exciting and unexpected results of analyses on ISARs for ants and offers the
787 most definitive evidence to date that ant communities on mainland islands tend to have steeper
788 relationships, with diversity increasing more rapidly over area, than do true islands. We also
789 demonstrate that precipitation is a major factor influencing ISAR z -values, leading to a
790 weakening of area effects on the scaling of biodiversity in localities with likely high primary
791 productivity and/or habitat diversity. Further research is needed to broaden our understanding of
792 the ISAR in ants. Based on a review of ~60 years of literature we have identified major gaps in
793 ISAR knowledge as it pertains to ants, highlighted priority areas for future research and
794 suggested approaches to fill these gaps of knowledge. Immediate areas of potential improvement
795 lie in further developing testable models based on habitat diversity hypotheses and further efforts
796 into better understanding the trade-offs in dispersal and colonization in ants.

797 While our study focuses on ants, the implications and suggestions from this study extend
798 well beyond a single taxon. This is especially important at a time where human impacts on
799 biodiversity patterns from local to global scales show conflicting trends in the scientific literature
800 (Primack et al., 2018). The remaining pockets of biodiversity in minimally disturbed systems are
801 rapidly disappearing. Therefore, now more than ever, there is a need to further understand the
802 scaling properties of biodiversity. Research conducted on taxonomically well-resolved and
803 globally distributed organisms, like ants, can provide this much needed and time-sensitive
804 information.

805

806 **Data Availability Statement**

807 Datasets 1 and 2 which were used for all formal analyses from this study are available in the
808 supplementary materials (Appendix 2 and 3).

809

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1125 **Biosketches**

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Leo Ohyama is a PhD candidate and Biodiversity Institute Fellow at the University of Florida with main interests in macroecology, biogeography, and ant ecology. He has previously worked with ants at local community scales through running large-scale field studies.

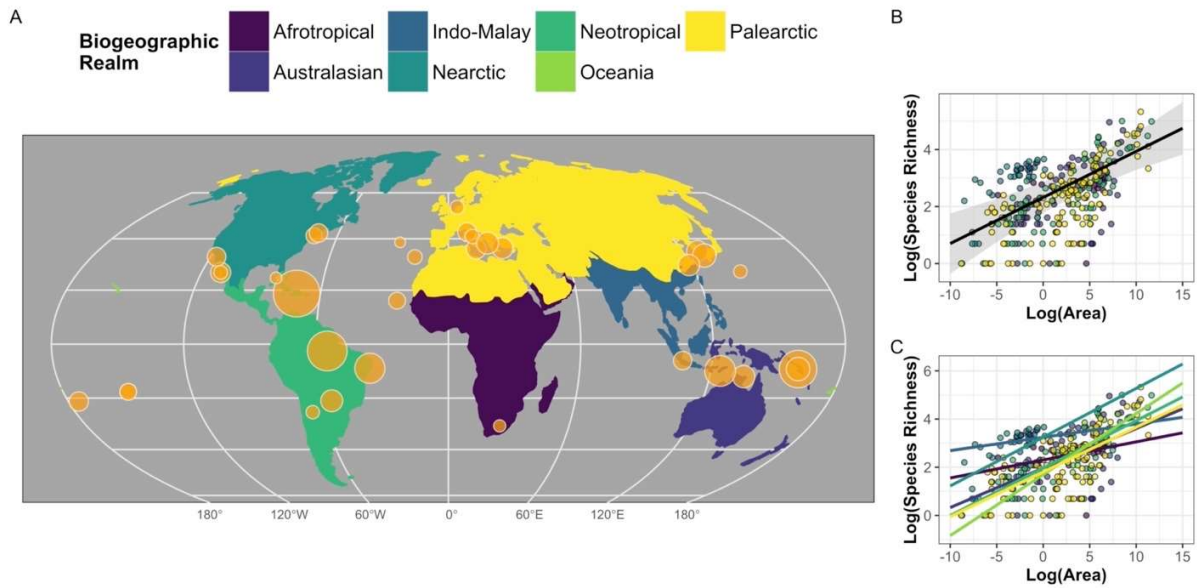
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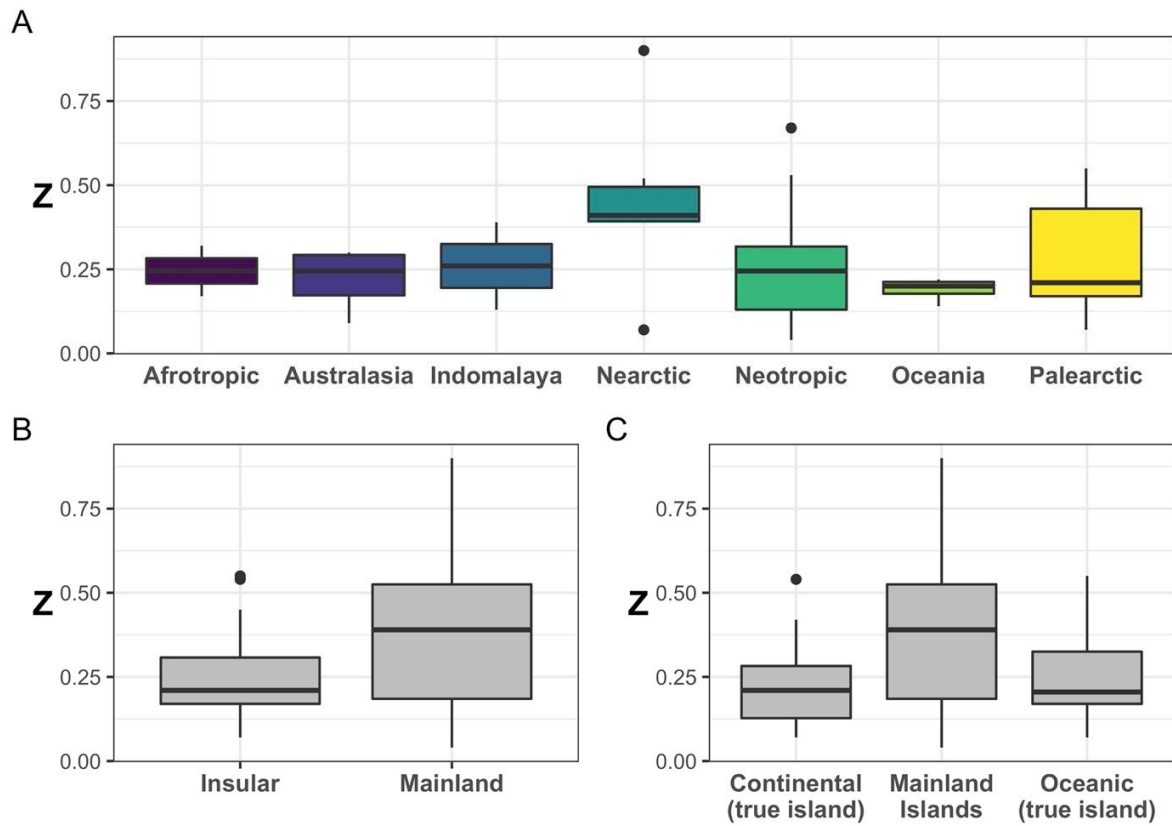
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1154 **Figures**
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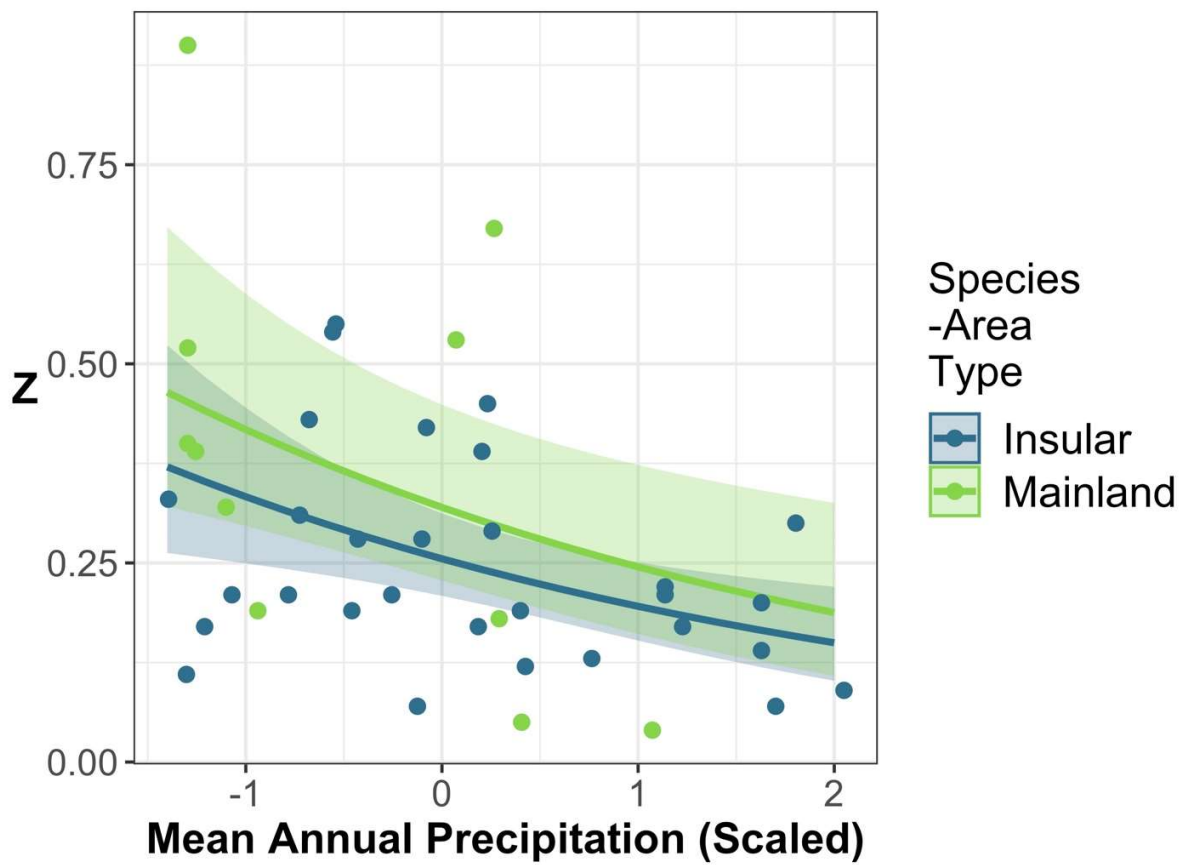


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1157 Figure 1. (A) A global map showcasing the variety of datasets used in modeling ant species
1158 richness as a function of area across all biogeographical realms. Size of each circle
1159 represents species richness from each individual study/dataset. Biogeographical realms are
1160 represented by different colors with the same color scheme applied to (B) and (C). Both (B)
1161 and (C) show the fixed and random effects of a linear mixed-effect model for only true
1162 islands. (B) Fixed effect (solid black line) of area on species richness from the linear mixed-
1163 effect model predicting log species richness as a function of log area with a random slope
1164 for biogeographical realm. Grey shading represents the 95% confidence intervals of the
1165 fixed effect. Points represent the data color coded by biogeographic realm. (C) Random
1166 effects (colored-lines) from the same linear-mixed effect model from (B). Points represent
1167 the data color coded by biogeographic realm. Natural logarithms are used and the area unit
1168 is km². Map uses Mollweide projection.
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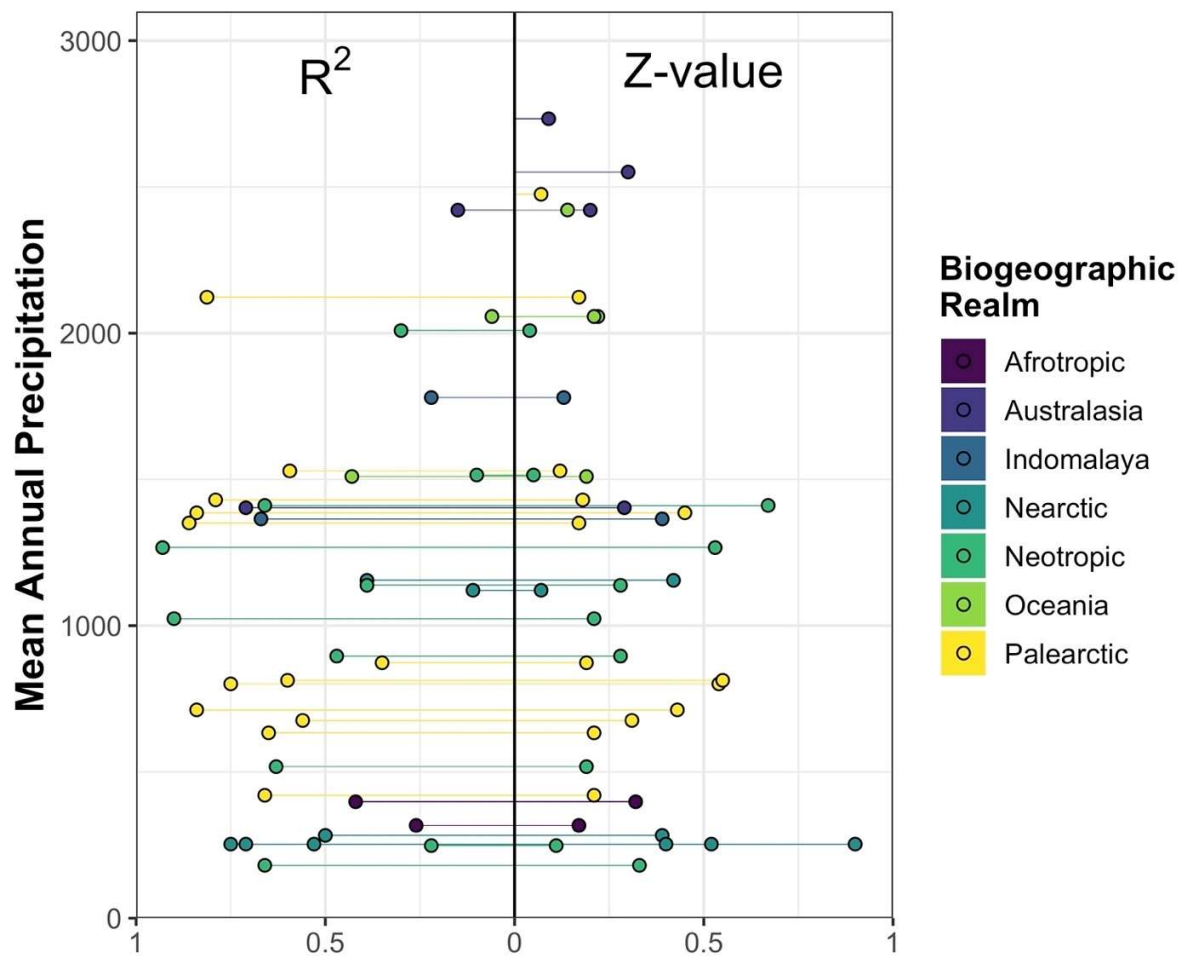
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Figure 2. Boxplots showing the distribution of slope values (Z) across studies ($n = 41$) for ants across all biogeographic realms. (A) Boxplots of z by biogeographic realms. (B) Boxplots of z by insular or mainland studies. (C) Boxplots of z -values by the types of islands in the study.

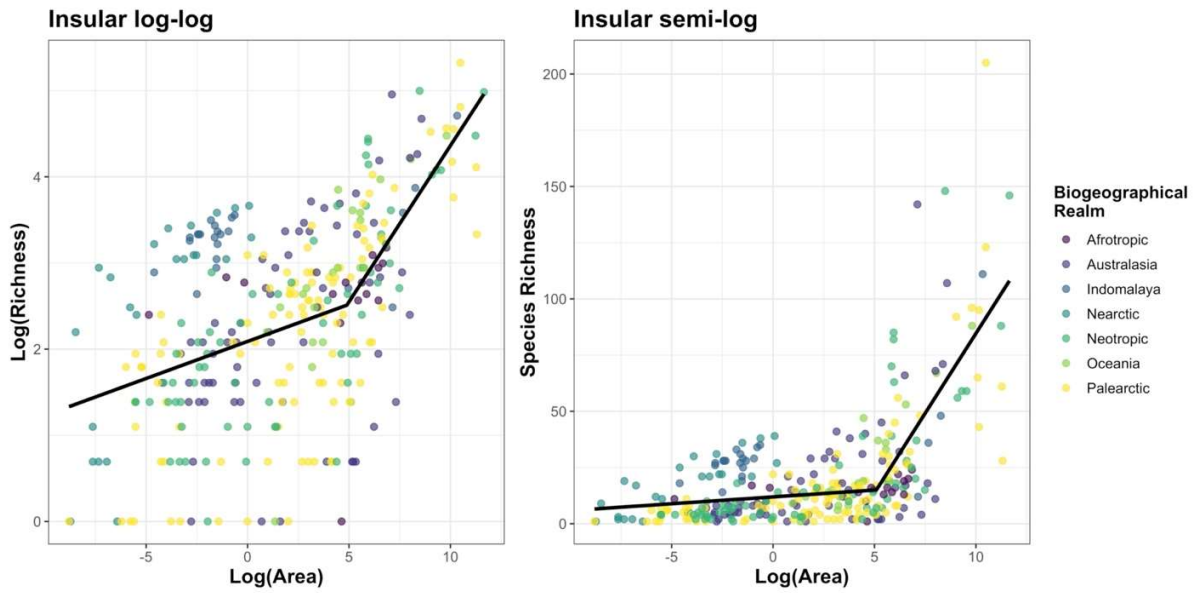


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Figure 3. Predictions of the most plausible model of ant z -values across all biogeographical realms when accounting for the covariate ISAR type (insular or mainland studies). The y-axis represents slope values (Z) and the x-axis represents mean annual precipitation (scaled). Lines represent model predictions. Shaded regions represent 95% confidence intervals. Points represent actual data. Green points and shading indicate mainland studies while blue indicates insular studies.



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 1189 Figure 4. Plot showing both R^2 values and slope values (Z) of ant studies across all
 1190 biogeographical realms (both mainland and insular) used in the analysis. The y-axis
 1191 represents precipitation (in mm). The x-axis represents both R^2 values and z -values from 0
 1192 to 1 going in both left and right directions. Colors represent the biogeographic realm of the
 1193 study.
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Figure 5. Plot showing the best threshold model for ants across biogeographical realms (continuous one-threshold model; black lines) fitted to dataset 2 for true islands ($n = 320$) in (A) log-log and (B) semi-log space. Points are coloured by biogeographic realm, and the colours are consistent across plots (i.e. the legend in (b) applies to both plots). Natural logarithms are used and the area unit is km^2 .

Tables

Table 1. All variables and a description of each, collected from studies to build the datasets used in the analyses.

Variables collected from studies	Description
Slope value (z)	Slope coefficient of the log-log species area relationship
Standard error of slope value	Error attributed to the slope coefficient estimate
Coefficient of correlation (R^2)	Amount of variation in richness explained by area
Biogeographic realm of study	Afrotropic, Australasia, Indomalaya, Nearctic, Neotropical, Oceania, Palearctic
Island types used in the study	Habitat-patches, Continental islands, Oceanic islands
Number of sampling methods	The number of unique sampling methods used in collecting ants for the study

Coordinates of study	Latitude and longitude of study. If study was done across large spatial areas, a midpoint coordinate was calculated.
Island area	Areas for islands/fragments used in the studies if disclosed
Species richness per island	Species richness values for each island/fragment if disclosed
Non-native ant percentage	Calculated as the species richness of non-native ants divided by total species richness for each dataset

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1239 Table 2. A summary table showing the number of datasets used in dataset 1, by biogeographic
1240 realm, species–area relationship type, island type, and citation. Second column indicates
1241 specific citation by number-code in parentheses. Note datasets focused on only single
1242 islands used in dataset 2 are cite at the bottom but not listed in the table.

Biogeographic Realm	Number and Citation	Species-area relationship type	# of datasets	Island type	# of datasets
Afrotropic	2 (1)	Insular	1	<u>Continental:</u>	0
				<u>Mainland Islands:</u>	1
		Mainland	1	<u>Oceanic:</u>	1
Australasia	4 (2)	Insular	4	<u>Continental:</u>	2

				<u>Mainland Islands:</u>	0
		Mainland	0	<u>Oceanic:</u>	2
Indomalaya	2 (3)	Insular	2	<u>Continental:</u>	1
		Mainland	0	<u>Mainland Islands:</u>	0
Nearctic	6 (5)	Insular	2	<u>Oceanic:</u>	1
		Mainland	4	<u>Continental:</u>	2
Neotropic	10 (6)	Insular	5	<u>Mainland Islands:</u>	5
		Mainland	5	<u>Oceanic:</u>	2
Oceania	4 (7)	Insular	4	<u>Continental:</u>	0
		Mainland	0	<u>Mainland Islands:</u>	0
Palearctic	13 (8)	Insular	12	<u>Oceanic:</u>	4
		Mainland	1	<u>Continental:</u>	5
				<u>Mainland Islands:</u>	1
				<u>Oceanic:</u>	7
		Total Insular:	30	Total Continental:	13
Total:	41			Total Mainland Islands:	11
		Total Mainland:	11	Total Mixed:	0
				Total Oceanic:	17

Citations: 1. (Dean & Bond, 1990, Wetterer et al., *unpublished*), 2. (E. Sarnat et al., 2013; E. Wilson, 1961; Woinarski et al., 1998), 3. (Rizali et al., 2010; Trainor & Andersen, 2010), 4. (Clark et al., 2011; Goldstein, 1975), 5. (Clark et al., 2011; Goldstein, 1975; Sanders, 2002; Suarez et al., 1998), 6. (Badano et al., 2005; Boulton & Ward, 2002; Cole, 1983; Cuissi et al., 2015; Leal et al., 2012; Schoereder et al., 2004; Vasconcelos et al., 2006; Wetterer & O'Hara, 2002; Edward O. Wilson, 1988) 7. (L. W. Morrison, 1997; Wetterer, 2002; Edward O. Wilson & Taylor, 1967), 8. (Baroni-Urbani, 1968, 1971, 1974; Boomsma et al., 1987; Choi et al., 1993; Collingwood, 1993; Menozzi, 1936; Sugiura, 2010; Wetterer et al., 2004, 2007; Zhao et al., 2020)

Papers with single island records used in dataset 2: (Baroni-Urbani, 1976; Borowiec & Salata, 2018b, 2018a; Legakis, 2011; Mühlenberg et al., 2016; Poldi et al., 1995; Terayama, 1992; Wetterer, 2006, Wetterer, *unpublished*)

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Table 3. A table showing the competing models under two different covariates, island range (order of magnitude) ($n = 35$) and species–area relationship type (mainland or insular) ($n = 42$), assessing slope values (z) as a function of abiotic variables based on AIC_c (Akaike Information Criterion with correction for small sample sizes) rankings. Predictor variables for each model are shown along with each model's AIC_c score, the change in AIC_c for every lower ranked model,

1250 AIC_c weights, and the adjusted R².

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Model with island order of magnitude range (OMR) covariate	ΔAIC_c	Weight (<i>w_j</i>)	Pseudo-R²
<i>z</i> ~ OMR + Precipitation	0.0	0.415	0.11
<i>z</i> ~ OMR	1.2	0.223	0.03
<i>z</i> ~ OMR + Temperature	2.5	0.122	0.05
<i>z</i> ~ OMR * Precipitation	2.6	0.115	0.11
<i>z</i> ~ OMR + Latitude	3.7	0.066	0.03
<i>z</i> ~ OMR * Temperature	4.9	0.036	0.05
Null Model	5.9	0.021	0
<i>z</i> ~ OMR + Biogeographic realm + Precipitation	11.1	0.0016	0.26
<i>z</i> ~ OMR + Biogeographic realm + Temperature	20.9	< 0.001	0.07
Model with ISAR type covariate	ΔAIC_c	Weight (<i>w_j</i>)	Pseudo-R²
<i>z</i> ~ ISAR type + Precipitation	0.0	0.631	0.18
<i>z</i> ~ ISAR type + Temperature	2.3	0.200	0.12
<i>z</i> ~ ISAR type	4.0	0.085	0.07
<i>z</i> ~ ISAR type + Latitude	4.1	0.083	0.10
<i>z</i> ~ ISAR type + Biogeographic realm + Precipitation	14.3	< 0.001	0.12
Null Model	18.3	< 0.001	0
<i>z</i> ~ ISAR type + Biogeographic realm + Temperature	19.4	< 0.001	0.12

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Table 4. Threshold models comparison summary. Results are presented for the insular global dataset, for both the log–log and semi-log transformations. For each model, the AIC_c and R² values are provided, and for the threshold models the area value (km²) where the inflexion point is located (on a log scale) is provided (Th1). For each comparison, the intercept-only model is not included to save space as it was always the worst model. ContOne is the continuous one-threshold model, and ZslopeOne the left-horizontal one-threshold model. In log–log space the linear model is the power model, and in semi-log space it is the logarithmic model.

Model	AIC_c	R²	Th1
Insular: log–log			
ContOne	867.31	0.36	4.895
ZslopeOne	882.15	0.32	1.695

Linear	889.79	0.30	NA
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Insular: semi-log			
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ContOne	2751.14	0.54	5.095
ZslopeOne	2753.08	0.54	4.995
Linear	2887.31	0.29	NA
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