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The species–area relationship in ant ecology

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

Running title: Species-area relationships in ant ecology

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

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

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

Abstract

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

Location: Islands around the world

Taxon: Ants (Hymenoptera: Formicidae)

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

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

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

Key words

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

Introduction

The Theory of Island Biogeography (MacArthur & Wilson, 1967), a foundational framework for ecology and biogeography, was motivated in part by consideration of the species–area relationship (SAR). This relationship was first noted by Forster (1778) and brought to light by 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),

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

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):

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

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

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

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

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

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

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

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

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

Methods

Data Collection

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

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

Analysis

Dataset 1

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

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

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

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

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

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

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

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

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

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

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

Dataset 2

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

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

All mixed-effects models were run using the lme4 package (Bates et al., 2015). Visualization of fixed and random effects were conducted using the 'R' packages "ggeffects" (Lüdecke, 2018) and "ggplot2" (Wickham, 2009). Pseudo-R^2 values (Marginal and conditional R^2) were calculated using the "MuMin" package (Barton, 2019). AIC_c values were calculated using the package "bbmle" (Bolker & R Development Core Team, 2020).

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

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

Results

Dataset 1

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

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

Mainland islands had the highest variance in log–log power model *z*-values (Figure 2C). The number of islands or fragments used to generate a slope value from a study ranged from 3 to 81. The range in difference in order of magnitude between the smallest and largest island areas was 0.70 to 6.17. The minimum *z*-value was 0.04, the maximum was 0.89, and the average was 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 ±
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*

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

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

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

Discussion

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

Dataset 1: Mainland vs. Insular Systems

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

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

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

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

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

Dataset 1: Climatic drivers of the ISAR

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

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

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

Gaps in the ant species–area relationship

Sampling gaps and data deficiencies

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

Incorporation of habitat diversity & other variables

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

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

Conclusions

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

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

Data Availability Statement

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

References

Andersen, A. N., Kohout, R. J., & Trainor, C. R. (2013). Biogeography of timor and surrounding wallacean islands: Endemism in ants of the genus polyrhachis fr. Smith. *Diversity*, *5*(1), 139–148. https://doi.org/10.3390/d5010139

Arrhenius, O. (1920a). *Öcologisher Studien in den Stockholmer Scären*. University of Stolkholm, Stockholm.

Arrhenius, O. (1920b). Yta och arter. I. *Svensk Botansik Tidsskrift*, *14*, 327–329.

Arrhenius, O. (1921). Species and area. *Journal of Ecology*, *9*, 95–99.

Badano, E. I., Regidor, H. A., Núñez, H. A., Acosta, R., & Gianoli, E. (2005). Species richness and structure of ant communities in a dynamic archipelago: Effects of island area and age. *Journal of Biogeography*, *32*(2), 221–227. https://doi.org/10.1111/j.1365-2699.2004.01174.x

Baroni-Urbani, C. (1968). Studi sulla mirmecofauna d'Italia. IV. La fauna mirmecologica delle isole Maltesi ed il suo significato ecologico e biogeografico. *Ann. Mus. Civ. Stor. Nat. "Giacomo Doria," 77*, 408–559.

Baroni-Urbani, C. (1971). Studien zur Ameisenfauna Italiens XI. Die Ameisen des Toskanischen Archipels. Betrachtungen zur Herkunft der Inselfaunen. *Rev. Suisse Zool.*, *7*(78), 1037–

1067.
Baroni-Urbani, C. (1974). Studi sulla mirmecofauna d'Italia. XII. Le Isole Pontine. *Fragm. Entomol.*, *9*, 225–252.
Baroni-Urbani, C. (1976). Le formiche dell'arcipelago della Galita (Tunisia). *Redia*, *59*, 207–223.
Barton, K. (2019). *MuMIn: Multi-Model Inference. R apakcage version 1.43.6*.
Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01.
Bolker, B., & R Development Core Team. (2020). *bbmle: Tools for General Maximum Likelihood Estimation.* https://cran.r-project.org/package=bbmle
Bolton, B. (2020). *An online catalog of the ants of the world.* https://antcat.org
Boomsma, J. J., Mabelis, A. A., Verbeek, M. G. M., & Los, E. C. (1987). Insular Biogeography and Distribution Ecology of Ants on the Frisian Islands. *Journal of Biogeography*, *14*(1), 21. https://doi.org/10.2307/2844784
Borowiec, L., & Salata, S. (2018a). Notes on ants (Hymenoptera: Formicidae) of Samos Island, Greece. *Annals of the Upper Silesian Museum, Entomology*, *27*(003), 1–13.
Borowiec, L., & Salata, S. (2018b). Notes on ants (Hymenoptera: Formicidae) of Zakynthos Island, Greece. *Annals of the Upper Silesian Museum, Entomology*, *27*(004), 1–13.
Boulton, A. M., & Ward, P. S. (2002). Ants. In T. J. Case, M. L. Cody, & E. Exequiel (Eds.), *Island Biogeography of the Sea of Cortez* (pp. 112–126). Oxford University Press.
Burns, K. C., Paul Mchardy, R., & Pledger, S. (2009). The small-island effect: Fact or artefact? *Ecography*, *32*(2), 269–276. https://doi.org/10.1111/j.1600-0587.2008.05565.x
Chase, J. M., Gooriah, L., May, F., Ryberg, W. A., Schuler, M. S., Craven, D., & Knight, T. M. (2019). A framework for disentangling ecological mechanisms underlying the island species-area relationship. *Frontiers of Biogeography*, *11*(1), 0–17. https://doi.org/10.21425/F5FBG40844
Choi, B. M., Ogata, K., & Terayama, M. (1993). Comparative studies of ant faunas of Korea and Japan I. Faunal comparison among islands of Southern Korea and Northern Kyushu, Japan. *Bulletin of the Biogeographic Society of Japan*, *48*(1), 37–49.
Clark, A. T., Rykken, J. J., & Farrell, B. D. (2011). The effects of biogeography on ant diversity and activity on the Boston Harbor islands, Massachusetts, U.S.A. *PLoS ONE*, *6*(11). https://doi.org/10.1371/journal.pone.0028045
Cole, B. J. (1983). Assembly of mangrove ant communities: Patterns of geographical distribution. *Journal of Animal Ecology*, *52*(2), 339–347.
Collingwood, C. (1993). A comparative study of the ant fauna of five Greek islands. *Biologia Gallo-Hellenica*, *20*, 191–197.
Connor, E. F., & McCoy, E. D. (1979). The statistics and biology of the species-area relationship. *The American Naturalist*, *113*(6), 791–833.
Cuissi, R. G., Lasmar, C. J., Moretti, T. S., Schmidt, F. A., Fernandes, W. D., Falleiros, A. B., Schoereder, J. H., & Ribas, C. R. (2015). Ant community in natural fragments of the Brazilian wetland: species–area relation and isolation. *Journal of Insect Conservation*, *19*(3), 531–537. https://doi.org/10.1007/s10841-015-9774-5
Dean, W. R. J., & Bond, W. J. (1990). Evidence for rapid faunal changes on islands in a man-made lake. *Oecologia*, *83*(3), 388–391. https://doi.org/10.1007/BF00317565
Drakare, S., Lennon, J. J., & Hillebrand, H. (2006). The imprint of the geographical,

873 evolutionary and ecological context on species-area relationships. *Ecology Letters*, *9*(2),
874 215–227. https://doi.org/10.1111/j.1461-0248.2005.00848.x
875 Economo, E. P., Janda, M., Guénard, B., & Sarnat, E. (2017). Assembling a species–area curve
876 through colonization, speciation and human-mediated introduction. *Journal of*
877 *Biogeography*, *44*(5), 1088–1097. https://doi.org/10.1111/jbi.12884
878 Economo, E. P., & Sarnat, E. M. (2012). Revisiting the ants of melanesia and the taxon cycle:
879 Historical and human-mediated invasions of a tropical archipelago. *American Naturalist*,
880 *180*(1), 1–16. https://doi.org/10.1086/665996
881 Espadaler, X., & Bernal, V. (2003). Exotic ants in the Canary Islands (Hymenoptera,
882 Formicidae). *Vieraea: Folia Scientarum Biologicarum Canariensium*, *31*(31), 1–8.
883 Ewers, R. M., Didham, R. K., Pearse, W. D., Lefebvre, V., Rosa, I. M. D., Carreiras, J. M. B.,
884 Lucas, R. M., & Reuman, D. C. (2013). Using landscape history to predict biodiversity
885 patterns in fragmented landscapes. *Ecology Letters*, *16*(10), 1221–1233.
886 https://doi.org/10.1111/ele.12160
887 Fattorini, S., Borges, P. A. V., Dapporto, L., & Strona, G. (2017). What can the parameters of the
888 species–area relationship (SAR) tell us? Insights from Mediterranean islands. *Journal of*
889 *Biogeography*, *44*(5), 1018–1028. https://doi.org/10.1111/jbi.12874
890 Fick, S. E., & Hijmans, R. J. (2017). New 1-km spatial resolution climate surfaces for global
891 land areas. *International Journal of Climatology*, *37*(12), 4302–4315.
892 Flantua, S. G. A., Payne, D., Borregaard, M. K., Beierkuhnlein, C., Steinbauer, M. J., Dullinger,
893 S., Essl, F., Irl, S. D. H., Kienle, D., Kreft, H., Lenzner, B., Norder, S. J., Rijsdijk, K. F.,
894 Rumpf, S. B., Weigelt, P., & Field, R. (2020). Snapshot isolation and isolation history
895 challenge the analogy between mountains and islands used to understand endemism. *Global*
896 *Ecology and Biogeography*, *29*(10), 1651–1673. https://doi.org/10.1111/geb.13155
897 Forster, J. R. (1778). *Observations made during a voyage round the world*. Printed for G.
898 Robinson, London.
899 Fournier, A., Penone, C., Pennino, M. G., & Courchamp, F. (2019). Predicting future invaders
900 and future invasions. *Proceedings of the National Academy of Sciences of the United States*
901 *of America*, *116*(16), 7905–7910. https://doi.org/10.1073/pnas.1803456116
902 Franzen, M., Schweiger, O., & Betzholtz, P.-E. (2012). Species-area relationships are controlled
903 by species traits. *PloS One*, *7*(5), e37359. https://doi.org/10.1371/Citation
904 Gibb, H., Stoklosa, J., Warton, D. I., Brown, A. M., Andrew, N. R., & Cunningham, S. A.
905 (2015). Does morphology predict trophic position and habitat use of ant species and
906 assemblages? *Oecologia*, *177*(2), 519–531. https://doi.org/10.1007/s00442-014-3101-9
907 Goldstein, E. L. (1975). Island biogeography of ants. *Evolution*, *29*(4), 750–762.
908 Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T.
909 E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R.
910 M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C.
911 R., … Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's
912 ecosystems. *Science Advances*, *1*(2), e1500052–e1500052.
913 https://doi.org/10.1126/sciadv.1500052
914 Hakala, S. M., Seppa, P., & Helantera, H. (2019). Evolution of dispersal in ants (Hymenoptera:
915 Formicidae): a review on the dispersal strategies of sessile superogranisms. *Myrmecological*
916 *News*, *29*, 35–55. https://doi.org/10.25849/myrmecol.news
917 Halley, J. M., Sgardeli, V., & Triantis, K. A. (2014). Extinction debt and the species-area
918 relationship: A neutral perspective. *Global Ecology and Biogeography*, *23*(1), 113–123.

https://doi.org/10.1111/geb.12098
Hölldobler, B., & Wilson, E. O. (1990). *The Ants*. Harvard University Press.
Holway, D. A., Lach, L., Suarez, A. V., Tsutsui, N. D., & Case, T. J. (2002). The causes and consequences of ant invasions. *Annual Review of Ecology and Systematics*, *33*(Redford 1987), 181–233. https://doi.org/10.1146/annurev.ecolsys.33.010802.150444
Jenkins, D. G., & Quintana-Ascencio, P. F. (2020). A solution to minimum sample size for regressions. *PLoS ONE*, *15*(2), 1–15. https://doi.org/10.1371/journal.pone.0229345
Kalmar, A., & Currie, D. J. (2007). A unified model of avian species richness on islands and continents. *Ecology*, *88*(5), 1309–1321. https://doi.org/10.1890/06-1368
Keil, P., & Chase, J. M. (2019). Global patterns and drivers of tree diversity integrated across a continuum of spatial grains. *Nature Ecology and Evolution*, *3*(3), 390–399. https://doi.org/10.1038/s41559-019-0799-0
Kylin, H. (1923). Växtsociologiska randanmärkningar. *Botaniska Notiser*, 1161–1234.
Lach, L., Parr, C., & Abbott, K. (2010). *Ant Ecology*. Oxford University Press.
Lack, D. (1976). *Island Biology Ilustrated by the Land Birds of Jamaica*. University of California Press.
Leal, I. R., Filgueiras, B. K. C., Gomes, J. P., Iannuzzi, L., & Andersen, A. N. (2012). Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest. *Biodiversity and Conservation*, *21*(7), 1687–1701. https://doi.org/10.1007/s10531-012-0271-9
Legakis, A. (2011). Annotated list of the ants (Hymenoptera, Formicidae) of Greece. *Hellenic Zoological Archives*, *7*, 1–55.
Lomolino, M. V. (2000). Ecology's most general, yet protean pattern: The species-area relationship. *Journal of Biogeography*, *27*(1), 17–26. https://doi.org/10.1046/j.1365-2699.2000.00377.x
Losos, J. B., & Schluter, D. (2000). Analysis of an evolutionary species-area relationship. *Nature*, *408*(6814), 847–850. https://doi.org/10.1038/35048558
Lüdecke, D. (2018). ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. *Journal of Open Source Software*, *3*(26), 772.
MacArthur, R. H., & Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton Univeristy Press.
Martin, T. E. (1981). Species-area slopes and coefficients: A caution on their interpretation. *The American Naturalist*, *118*(6), 823–837.
Matthews, T. J., Guilhaumon, F., Triantis, K. A., Borregaard, M. K., & Whittaker, R. J. (2016). On the form of species–area relationships in habitat islands and true islands. *Global Ecology and Biogeography*, *25*(7), 847–858. https://doi.org/10.1111/geb.12269
Matthews, T. J., & Rigal, F. (2021). Thresholds and the species–area relationship: a set of functions for fitting, evaluating and plotting a range of commonly used piecewise models in R. *Frontiers of Biogeography*, *0*(0), 0–9. https://doi.org/10.21425/f5fbg49404
Matthews, T. J., Steinbauer, M. J., Tzirkalli, E., Triantis, K. A., & Whittaker, R. J. (2014). Thresholds and the species-area relationship: A synthetic analysis of habitat island datasets. *Journal of Biogeography*, *41*(5), 1018–1028. https://doi.org/10.1111/jbi.12286
Matthews, T. J., Triantis, K. A., & Whittaker, R. J. (Eds.). (2020). *The Species–Area Relationship: Theory and Application*. Cambridge University Press.
Matthews, T. J., Triantis, K. A., Whittaker, R. J., & Guilhaumon, F. (2019). sars: an R package for fitting, evaluating and comparing species–area relationship models. *Ecography*, *42*(8),

1446–1455. https://doi.org/10.1111/ecog.04271
Menozzi, C. (1936). Nuovi contributi alla conoscenza della fauna delle Isole italiane dell'Egeo. VI. Hymenoptera - Formicidae. *Bollettino Del Laboratorio Di Zoologia Generale e Agraria Della Reale Scuola Superiore d'Agricoltura. Portici*, *29*, 261–311.
Mittelbach, G. G., & McGill, B. J. (2019). Patterns of biological diversity. In *Community Ecology* (2nd ed., pp. 11–36). Oxford University Press.
Morrison, L. W. (1997). Polynesian ant (Hymenoptera: Formicidae) species richness and distribution: A regional survey. *Acta Oecologica*, *18*(6), 685–695. https://doi.org/10.1016/S1146-609X(97)80051-3
Morrison, Lloyd W. (2003). A review of Bahamian ant (Hymenoptera: Formicidae) biogeography. *Journal of Biogeography*, *25*, 561–571. https://doi.org/10.1016/B978-0-323-60984-5.00062-7
Morrison, Lloyd W. (2016). The ecology of ants (Hymenoptera: Formicidae) on islands. *Myrmecological News*, *23*(September), 1–14.
Muggeo, V. M. (2016). *Segmented mixed models with random changepoints in R. R Working Paper.*
Muggeo, V. M., Atkins, D. C., Gallop, R. J., & Dimidjian, S. (2014). Segmented mixed models with random changepoints: a maximum likelihood approach with application to treatment for depression study. *Statistical Modelling*, *14*, 293–313.
Mühlenberg, A. M., Leipold, D., Mader, H. J., & Steinhauer, B. (2016). Island ecology of arthropods. II. Niches and relative abundances of Seychelles Ants (Formicidae) in different habitats. *Oecologia*, *29*(2), 135–144.
Nilsson, S. G., Bengtsson, J. A. N., & Ast, S. (1988). Habitat diversity or area per se? Species richness of woody plants, Carabid beetles, and land snails on islands. *Journal of Animal Ecology*, *57*(2), 685–704.
Poldi, B., Mei, M., & Rigato, F. (1995). Hymenoptera Formicidae. *Checklist Delle Specie Della Fauna Italiana*, *102*, 1–10.
Primack, R. B., Miller-Rushing, A. J., Corlett, R. T., Devictor, V., Johns, D. M., Loyola, R., Maas, B., Pakeman, R. J., & Pejchar, L. (2018). Biodiversity gains? The debate on changes in local- vs global-scale species richness. *Biological Conservation*, *219*, A1–A3. https://doi.org/10.1016/j.biocon.2017.12.023
Pyšek, P., Blackburn, T. M., García-Berthou, E., Perglová, I., & Rabitsch, W. (2017). Displacement and local extinction of native and endemic species. In *Impact of biological invasions on ecosystem services* (pp. 157–175). Springer.
R Development Core Team. (2018). *R: A language and environment for statistical computing* (3.4.1).
Ranta, E., Vepsalainen, K., As, S., Haila, Y., Pisarski, B., & Tiainen, J. (1983). Island biogeography of ants (Hymenoptera, Formicidae) in four Fennoscandian archipelagoes. *Acta Entomologica Fennica*, *42*(August 2014), 64.
Rica, C., Solomon, S. E., & Mikheyev, A. S. (2005). The ant (Hymenoptera : Formicidae) fauna of Cocos Island, Costa Rica. *Florida Entomologist*, *88*(4), 415–423.
Ricklefs, R. E., & Lovette, I. J. (1999). The roles of island area per se and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology*, *68*(6), 1142–1160. https://doi.org/10.1046/j.1365-2656.1999.00358.x
Rizali, A., Lohman, D. J., Buchori, D., Prasetyo, L. B., Triwidodo, H., Bos, M. M., Yamane, S., & Schulze, C. H. (2010). Ant communities on small tropical islands: Effects of island size

and isolation are obscured by habitat disturbance and “tramp” ant species. *Journal of Biogeography*, *37*(2), 229–236. https://doi.org/10.1111/j.1365-2699.2009.02194.x
Rosenzweig, M. L. (1995). *Species Diversity in Space and Time*. Cambridge University Press.
Sanders, N. J. (2002). Elevational gradients in ant species richness: Area, geometry, and Rapoport’s rule. *Ecography*, *25*(1), 25–32. https://doi.org/10.1034/j.1600-0587.2002.250104.x
Sarnat, E., Blanchard, B., Guénard, B., Fasi, J., & Economo, E. (2013). Checklist of the ants (Hymenoptera, Formicidae) of the Solomon Islands and a new survey of Makira Island. *ZooKeys*, *257*, 47–88. https://doi.org/10.3897/zookeys.257.4156
Sarnat, E. M., & Economo, E. P. (2012). *Ants of Fiji*. University of California Press.
Scheiner, S. M. (2003). Six types of species-area curves. *Global Ecology and Biogeography*, *12*(6), 441–447. https://doi.org/10.1046/j.1466-822X.2003.00061.x
Schoereder, J. H., Galbiati, C., Ribas, C. R., Sobrinho, T. G., Sperber, C. F., DeSouza, O., & Lopes-Andrade, C. (2004). Should we use proportional sampling for species-area studies? *Journal of Biogeography*, *31*(8), 1219–1226. https://doi.org/10.1111/j.1365-2699.2004.01113.x
Schultz, T. R. (2000). In search of ant ancestors. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(26), 14028–14029. https://doi.org/10.1073/pnas.011513798
Shmida, A., & Wilson, M. V. (1985). Biological determinants of species diversity. *Journal of Biogeography*, *12*(1), 1–20.
Sosiak, C. E., & Barden, P. (2020). Multidimensional trait morphology predicts ecology across ant lineages. *Functional Ecology*, *October 2020*, 139–152. https://doi.org/10.1111/1365-2435.13697
Storch, D. (2016). The theory of the nested species–area relationship: geometric foundations of biodiversity scaling. *Journal of Vegetation Science*, *27*(5), 880–891. https://doi.org/10.1111/jvs.12428
Storch, D., Evans, K. L., & Gaston, K. J. (2005). The species-area-energy relationship. *Ecology Letters*, *8*(5), 487–492. https://doi.org/10.1111/j.1461-0248.2005.00740.x
Suarez, A. V., Bolger, D. T., & Case, T. J. (1998). Effects of fragmentation and invasion on native ant communities in coastal southern California. *Ecology*, *79*(6), 2041–2056. https://doi.org/10.1890/0012-9658(1998)079[2041:EOFAIO]2.0.CO;2
Sugiura, S. (2010). Species interactions-area relationships: Biological invasions and network structure in relation to island area. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1689), 1807–1815. https://doi.org/10.1098/rspb.2009.2086
Terayama, M. (1992). Structure of ant communities in East Asia I. Regional differences and species richness. *Bulletin of the Biogeographic Society of Japan*, *41*, 1–31.
Tjørve, E. (2003). Shapes and functions of species–area curves: a review of possible models. *Journal of Biogeography*, *30*, 827–835.
Tjørve, Even. (2003). Shapes and functions of species-area curves: A review of possible models. *Journal of Biogeography*, *30*(6), 827–835. https://doi.org/10.1046/j.1365-2699.2003.00877.x
Torres, J. A., & Snelling, R. R. (1997). Biogeography of Puerto Rican ants: A Non-equilibrium case? *Biodiversity and Conservation*, *6*(8), 1103–1121. https://doi.org/10.1023/A:1018332117719
Trainor, C. R., & Andersen, A. N. (2010). The ant fauna of Timor and neighbouring islands:

Potential bridges between the disjunct faunas of South East Asia and Australia. *Australian Journal of Zoology*, *58*(3), 133–144. https://doi.org/10.1071/ZO09113

Triantis, K A, Mylonas, M., Lika, K., Natural, K. V., & Museum, H. (2003). A model for the species – area – habitat relationship. *Journal of Biogeography*, *30*, 19–27.

Triantis, Kostas A, Guilhaumon, F., & Whittaker, R. J. (2012). The island species-area relationship: Biology and statistics. *Journal of Biogeography*, *39*(2), 215–231. https://doi.org/10.1111/j.1365-2699.2011.02652.x

Tschinkel, W. R., & King, J. R. (2017). Ant community and habitat limit colony establishment by the fire ant, Solenopsis invicta. *Functional Ecology*, *31*(4), 955–964. https://doi.org/10.1111/1365-2435.12794

Vasconcelos, H. L., Vilhena, J. M. S., Magnusson, W. E., & Albernaz, A. L. K. M. (2006). Long-term effects of forest fragmentation on Amazonian ant communities. *Journal of Biogeography*, *33*(8), 1348–1356. https://doi.org/10.1111/j.1365-2699.2006.01516.x

Wallace, A. R. (1914). *The World of life: a manifestation of creative power, directive mind and ultimate purposeNo Title*. Chapman and Hall.

Weigelt, P., Jetz, W., & Kreft, H. (2013). Bioclimatic and physical characterization of the world's islands. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(38), 15307–15312. https://doi.org/10.1073/pnas.1306309110

Wetterer, J. K. (2002). Ants of Tonga. *Pacific Science*, *56*(2), 125–135. https://doi.org/10.1353/psc.2002.0019

Wetterer, J. K. (2006). Ants (Hymenoptera: Formicidae) of Niue, Polynesia. *Pacific Science*, *60*, 413–416.

Wetterer, J. K., Espadaler, X., Wetterer, A. L., Aguin-Pombo, D., & Franquinho-Aguiar, A. M. (2007). Ants (Hymenoptera: Formicidae) of the Madeiran archipelago. *Sociobiology*, *49*(3), 265–297.

Wetterer, J. K., Espadaler, X., Wetterer, A. L., & Cabral, S. G. M. (2004). Native and exotic ants of the Azores (Hymenoptera: Formicidae). *Sociobiology*, *44*(1), 1–20.

Wetterer, J. K., & O'Hara, B. C. (2002). Ants (Hymenoptera: Formicidae) of the Dry Tortugas, the outermost Florida Keys. *Florida Entomologist*, *85*(2), 303–307. https://doi.org/10.1653/0015-4040(2002)085[0303:ahfotd]2.0.co;2

Whitehead, D. R., & Jones, C. E. (1969). Small Islands and the Equilibrium Theory of Insular Biogeography. *Evolution*, *23*(1), 171. https://doi.org/10.2307/2406492

Whittaker, R. J., Araújo, M. B., Jepson, P., Ladle, R. J., Watson, J. E. M., & Willis, K. J. (2005). Conservation biogeography: Assessment and prospect. *Diversity and Distributions*, *11*(1), 3–23. https://doi.org/10.1111/j.1366-9516.2005.00143.x

Whittaker, R. J., & Fernandez-Palacios, J. (2007). *Island Biogeography: Ecology, Evolution, and Conservation*. Oxford University Press.

Whittaker, R. J., Triantis, K. A., & Ladle, R. J. (2008). A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, *35*(6), 977–994. https://doi.org/10.1111/j.1365-2699.2008.01892.x

Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag.

Williams, C. B. (1964). *Patterns in the balance of nature*. Academic Press.

Williams, M. R., Lamont, B. B., & Henstridge, J. D. (2009). Species–area functions revisited. *Journal of Biogeography*, *36*, 1994–2004.

Wilson, E. (1961). The nature of the taxon cycle in the Melanesian ant fauna. *The American Naturalist*, *95*(882), 169–193.

Wilson, E. O. (2005). Early ant plagues in the New World. *Nature*, *433*(7021), E1. https://doi.org/10.1038/nature03256

Wilson, Edward O. (1988). The Biogeography of the West Indian Ants (Hymenoptera:Formicidae). In *Zoogeography of Carribean Insects* (pp. 214–230).

Wilson, Edward O., & Taylor, R. W. (1967). An estimate of the potential evolutionary increase in species density in the Polynesian ant fauna. *Evolution*, *21*(1), 1. https://doi.org/10.2307/2406735

Woinarski, J. C. ., Reichel, H., & Andersen, A. N. (1998). The distribution of ants on the Wessel and English Company Islands, in the seasonal tropics of Australia's Northern Territory. *Australian Journal of Zoology*, *46*, 557–578.

Yan, H., Liang, C., Li, Z., Liu, Z., Miao, B., He, C., & Sheng, L. (2015). Impact of precipitation patterns on biomass and species richness of annuals in a dry steppe. *PLoS ONE*, *10*(4), 1–14. https://doi.org/10.1371/journal.pone.0125300

Zhao, Y., Dunn, R. R., Zhou, H., Si, X., & Ding, P. (2020). Island area, not isolation, drives taxonomic, phylogenetic and functional diversity of ants on land-bridge islands. *Journal of Biogeography*, *August 2019*, 1–11. https://doi.org/10.1111/jbi.13860

Zhu, H., Wang, D., Wang, L., Fang, J., Sun, W., & Ren, B. (2014). Effects of altered precipitation on insect community composition and structure in a meadow steppe. *Ecological Entomology*, *39*(4), 453–461. https://doi.org/10.1111/een.12120

Biosketches

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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Figures

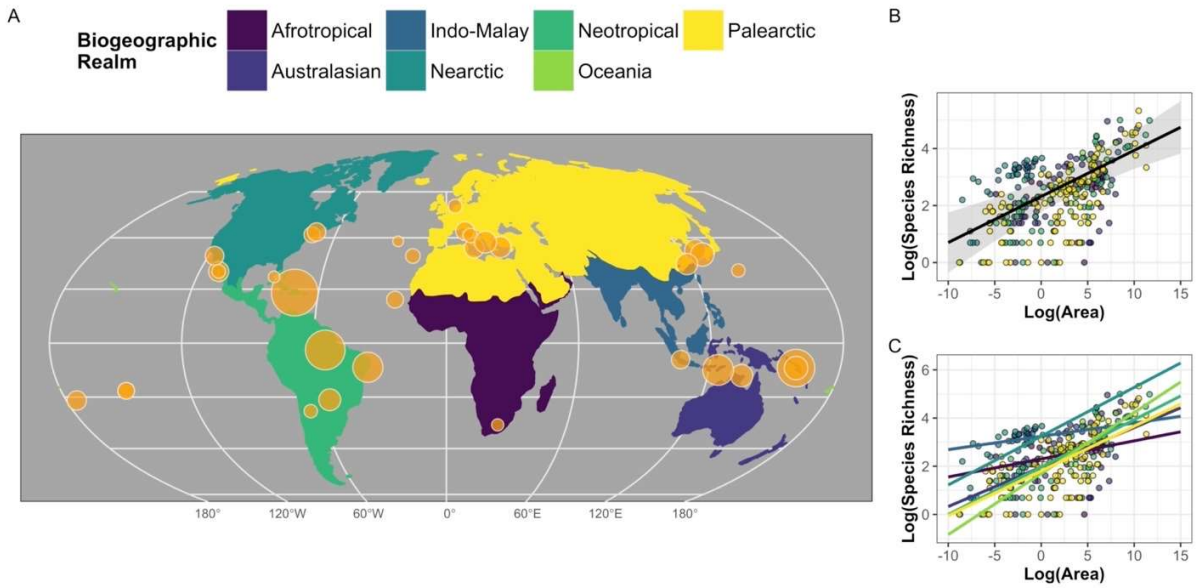

Figure 1. (A) A global map showcasing the variety of datasets used in modeling ant species richness as a function of area across all biogeographical realms. Size of each circle represents species richness from each individual study/dataset. Biogeographical realms are represented by different colors with the same color scheme applied to (B) and (C). Both (B) and (C) show the fixed and random effects of a linear mixed-effect model for only true islands. (B) Fixed effect (solid black line) of area on species richness from the linear mixed-effect model predicting log species richness as a function of log area with a random slope for biogeographical realm. Grey shading represents the 95% confidence intervals of the fixed effect. Points represent the data color coded by biogeographic realm. (C) Random effects (colored-lines) from the same linear-mixed effect model from (B). Points represent the data color coded by biogeographic realm. Natural logarithms are used and the area unit is km^2. Map uses Mollweide projection.

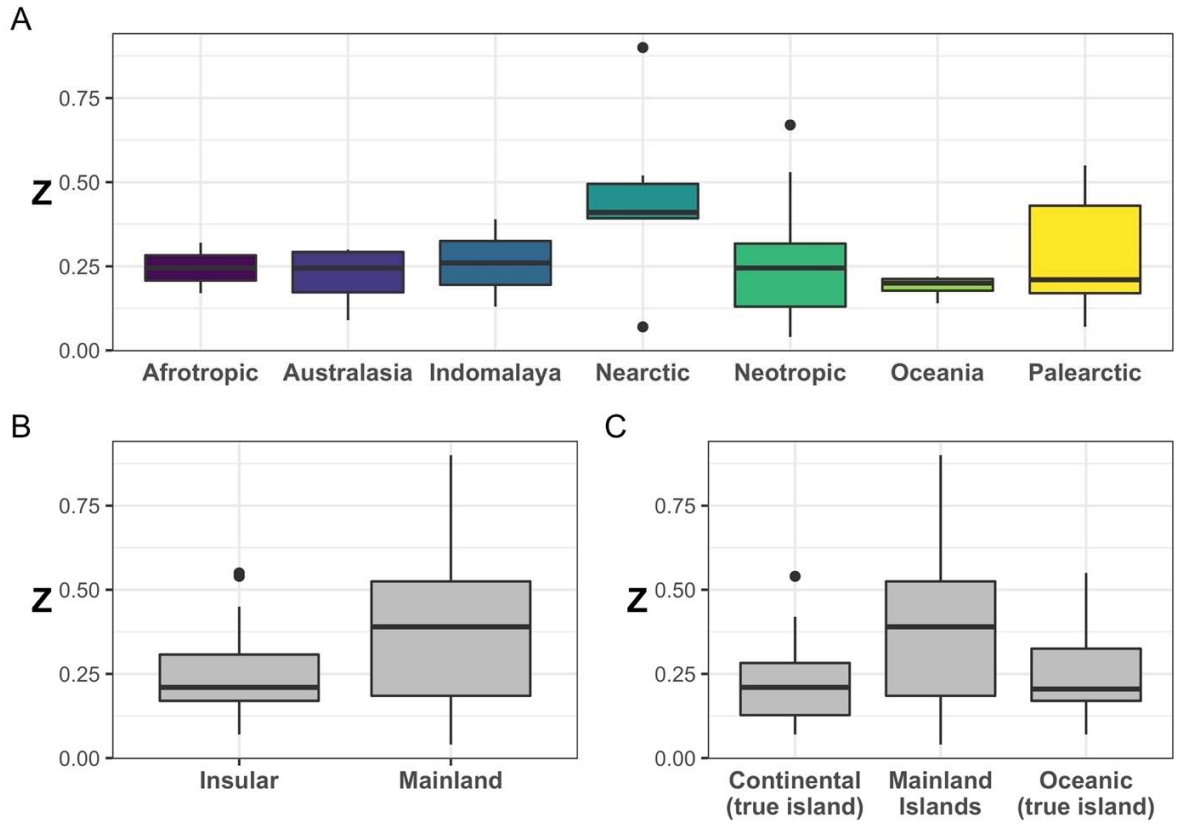

Figure 2. Boxplots showing the distribution of slope values (Z) across studies (n = 41) for ants across all biogeographic realms. (A) Boxplots of z by biogeographic realms. (B) Boxplots of z by insular or mainland studies. (C) Boxplots of z-values by the types of islands in the study.

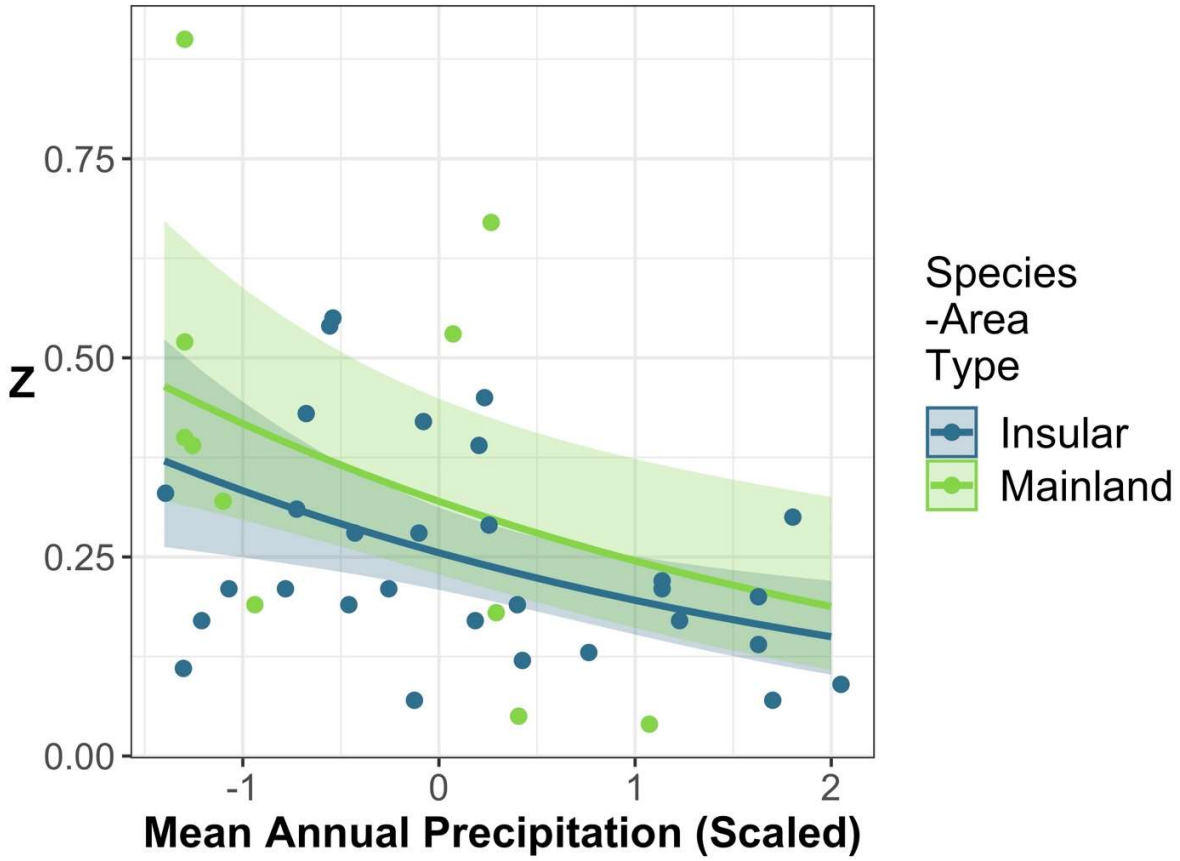

Figure 3. Predictions of the most plausible model of ant *z*-values across all biogeographical realms when accounting for the covariate ISAR type (insular or mainland studies). The y-axis represents slope values (Z) and the x-axis represents mean annual precipitation (scaled). Lines represent model predictions.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

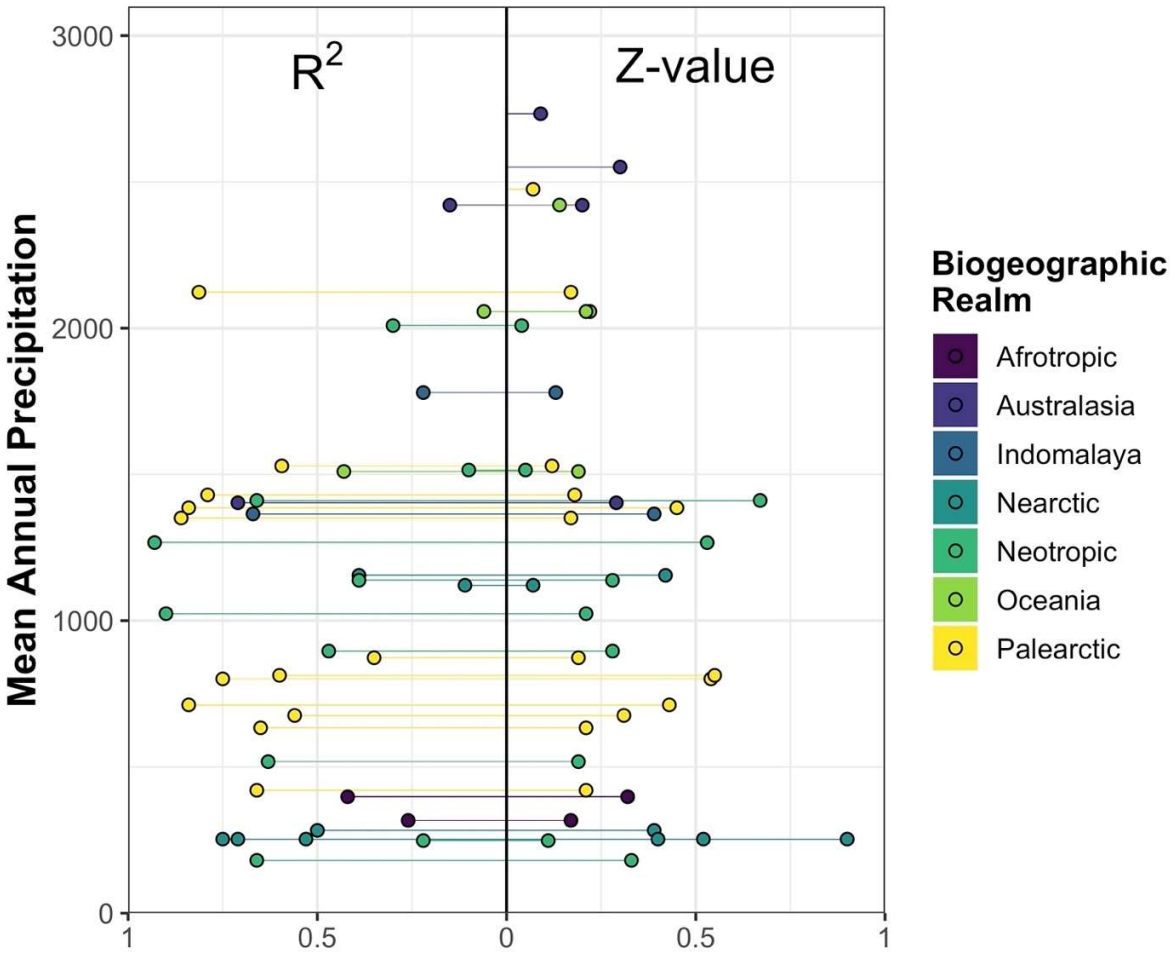

Figure 4. Plot showing both R^2 values and slope values (Z) of ant studies across all biogeographical realms (both mainland and insular) used in the analysis. The y-axis represents precipitation (in mm). The x-axis represents both R^2 values and *z*-values from 0 to 1 going in both left and right directions. Colors represent the biogeographic realm of the study.

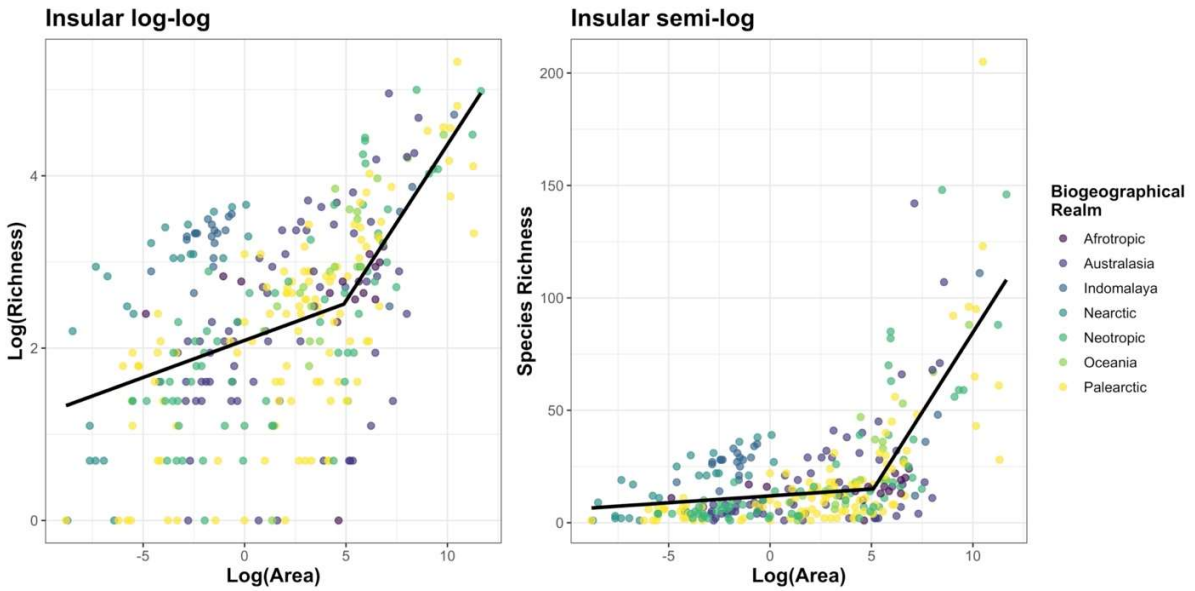

Figure 5. Plot showing the best threshold model for ants across biogeographical realms (continuous one-threshold model; black lines) fitted to dataset 2 for true islands (n = 320) in (A) log-log and (B) semi-log space. Points are coloured by biogeographic realm, and the colours are consistent across 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, Neotropic, 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

Table 2. A summary table showing the number of datasets used in datatset 1, by biogeographic realm, species–area relationship type, island type, and citation. Second column indicates specific citation by number-code in parentheses. Note datasets focused on only single 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	Continental:	0
				Mainland Islands:	1
		Mainland	1	Oceanic:	1
Australasia	4 (*2*)	Insular	4	Continental:	2

		Mainland	0	Mainland Islands:	0
				Oceanic:	2
Indomalaya	2 (*3*)	Insular	2	Continental:	1
				Mainland Islands:	0
		Mainland	0	Oceanic:	1
Nearctic	6 (*5*)	Insular	2	Continental:	2
				Mainland Islands:	4
		Mainland	4	Oceanic:	0
Neotropic	10 (*6*)	Insular	5	Continental:	3
				Mainland Islands:	5
		Mainland	5	Oceanic:	2
Oceania	4 (*7*)	Insular	4	Continental:	0
				Mainland Islands:	0
		Mainland	0	Oceanic:	4
Palearctic	13 (*8*)	Insular	12	Continental:	5
				Mainland Islands:	1
		Mainland	1	Oceanic:	7
Total:	**41**	**Total Insular:**	**30**	**Total Continental:**	**13**
				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*)

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,

AIC_c weights, and the adjusted R^2.

Model with island order of magnitude range (OMR) covariate	ΔAIC_c	Weight (w_i)	Pseudo-R^2
$z \sim$ OMR + Precipitation	0.0	0.415	0.11
$z \sim$ OMR	1.2	0.223	0.03
$z \sim$ OMR + Temperature	2.5	0.122	0.05
$z \sim$ OMR * Precipitation	2.6	0.115	0.11
$z \sim$ OMR + Latitude	3.7	0.066	0.03
$z \sim$ OMR * Temperature	4.9	0.036	0.05
Null Model	5.9	0.021	0
$z \sim$ OMR + Biogeographic realm + Precipitation	11.1	0.0016	0.26
$z \sim$ OMR + Biogeographic realm + Temperature	20.9	< 0.001	0.07
Model with ISAR type covariate	**ΔAIC_c**	**Weight (w_i)**	**Pseudo-R^2**
$z \sim$ ISAR type + Precipitation	0.0	0.631	0.18
$z \sim$ ISAR type + Temperature	2.3	0.200	0.12
$z \sim$ ISAR type	4.0	0.085	0.07
$z \sim$ ISAR type + Latitude	4.1	0.083	0.10
$z \sim$ ISAR type + Biogeographic realm + Precipitation	14.3	< 0.001	0.12
Null Model	18.3	< 0.001	0
$z \sim$ ISAR type + Biogeographic realm + Temperature	19.4	< 0.001	0.12

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 R^2 values are provided, and for the threshold models the area value (km^2) 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**	**R^2**	**Th1**
Insular: log–log			
ContOne	867.31	0.36	4.895
ZslopeOne	882.15	0.32	1.695

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