



The species–area relationship in ant ecology

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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 multimodel 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 higher 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 nonnative species on the SAR.

KEYWORDS

ants, biodiversity, fragmentation, invasive species, island biogeography, islands, species–area relationship



1 | 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 SAR (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) (Equation 1),

$$S = cA^z \quad (1)$$

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) is linearized by logarithmic transformations of S and A (see 2) z is the slope of the resulting log-log relationship, and c represents the intercept (Equation 2) (Scheiner, 2003):

$$\log(S) = \log(c) + z\log(A) \quad (2)$$

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 centre 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 analysed 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 analysed.

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 endemism. Ant island endemism is known to vary greatly across the globe (0%–96% endemism) 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 nonnative ants (Espadaler & Bernal, 2003; Rica et al., 2005; Wetterer & O'Hara, 2002). The resulting presence of nonnative 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 (a) reviewing the ant ISAR literature in order to identify significant data gaps and (b) 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?

2 | MATERIALS AND METHODS

2.1 | 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 available: species richness per island, total species richness of all islands, island/fragment area size, z -value of the SAR, standardized errors of the slope coefficient, R^2 values from the log-log power model, locality of island/fragment, types of island/fragment, island/fragment area ranges (m^2), biogeographic realm, latitude, longitude, climate, percentage of nonnative ants, and isolation (distance to the nearest continent for true island datasets) (Table 1). Percentages of nonnative ants were limited to 25 datasets that provided full species checklists or explicitly stated nonnative ant richness in the publication. If a given true island dataset was composed of both oceanic and continental islands, then the dataset was assigned the island type comprising the majority. If full datasets from publications were not available, the corresponding author(s) of the study were contacted for access to the original

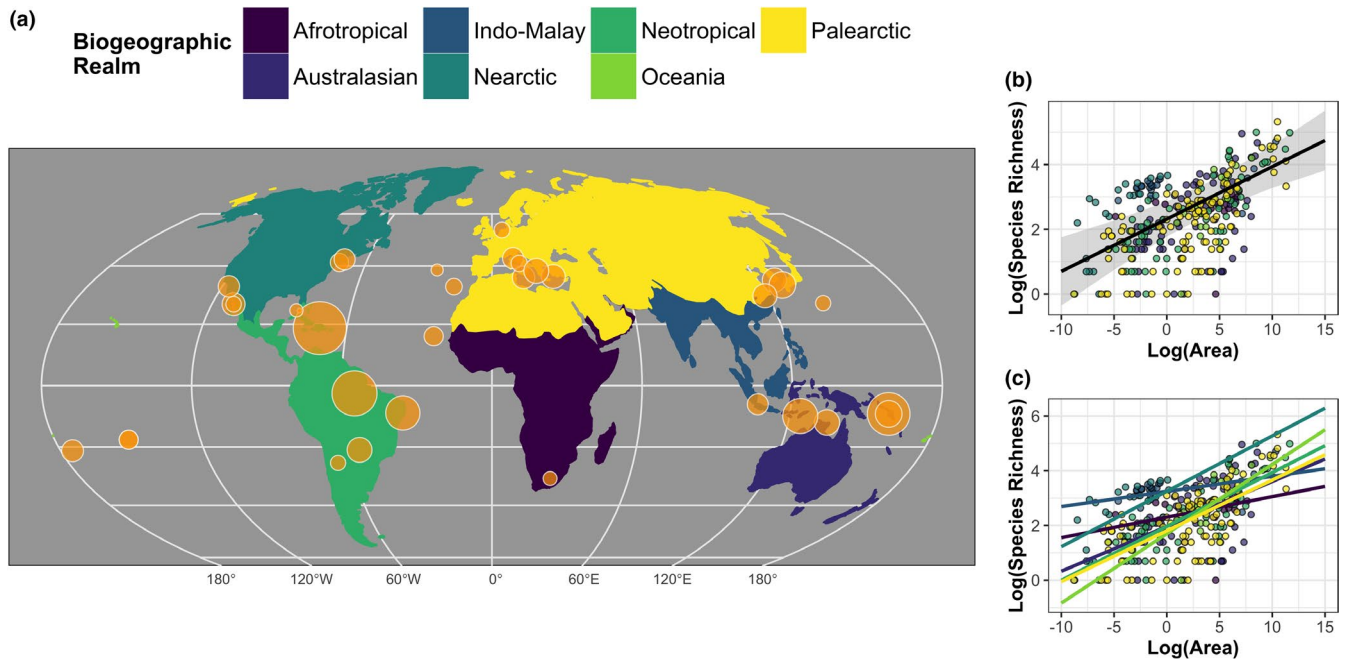


FIGURE 1 (a) A global map showcasing the variety of datasets used in modeling ant species richness as a function of area across all biogeographical realms. Size of each circle represents species richness from each individual study/dataset. Biogeographical realms are represented by different colours with the same colour 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 colour coded by biogeographic realm. (c) Random effects (coloured-lines) from the same linear-mixed effect model from (b). Points represent the data colour coded by biogeographic realm. Natural logarithms are used and the area unit is km^2 . Map uses Mollweide projection

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
Nonnative ant percentage	Calculated as the species richness of nonnative ants divided by total species richness for each dataset

raw data. Supporting Information includes both datasets and a list of literature citations.

2.2 | Species-area slopes and intercepts

Whenever possible, z -values were recalculated using a study's raw data (natural logs were used). Island/fragment areas and species

richness values from the studies were used to calculate the z -value using the log-log form of the power model (Equation 2) with ordinary least squares (OLS) regression. However, if raw data were unavailable then the reported z -value was used. In total, 30 out of 41 z -values were recalculated. For nonrecalculated z -values, only z -values of the log-log model was used, as the majority of the data collected from the literature utilized that model form. We used a paired t -test to assess the robustness of recalculated z -values compared



to reported z -values (8 paired values). However, we also undertook multi-model analyses of competing SAR models to discern the best-fitting SAR model (outlined below). None of the studies contained zero values; as such, no added constants were necessary for log-transformations. If island/fragment areas were not provided, data were recovered from online sources or manually calculated using the Google Earth engine. ISARs fitted with log-log axes have intercepts that are not independent of the units in which area is measured. In order to mitigate this issue, c -values were recalculated after standardizing area across datasets to the same units (km^2), which resulted in 30 comparable intercepts.

2.3 | Abiotic data

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

2.4 | Final datasets for analysis

As stated above, two datasets were collated for the analyses: Dataset 1 was used to assess the best fitting model for ant ISARs using a multi-model inference approach, the c and z -values of 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: $\text{Log}_{10}(\text{Maximum Area}/\text{Minimum Area})$), 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.

2.5 | Analysis

2.5.1 | 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 nonlinear 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 nonlinear 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 analysed. 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 piecewise SEM 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 recalculated 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).

2.5.2 | Dataset 2

Dataset 2 was comprised of 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 $\log(SR) \sim \log(\text{Area})$ form) slope coefficient. Natural logs were used to calculate both $\log(SR)$ and $\log(\text{Area})$. 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 analysed 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 $\log(\text{Area})$.

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" (Lüdtke, 2018) and "ggplot2" (Wickham, 2009). Pseudo R^2 values (marginal and conditional

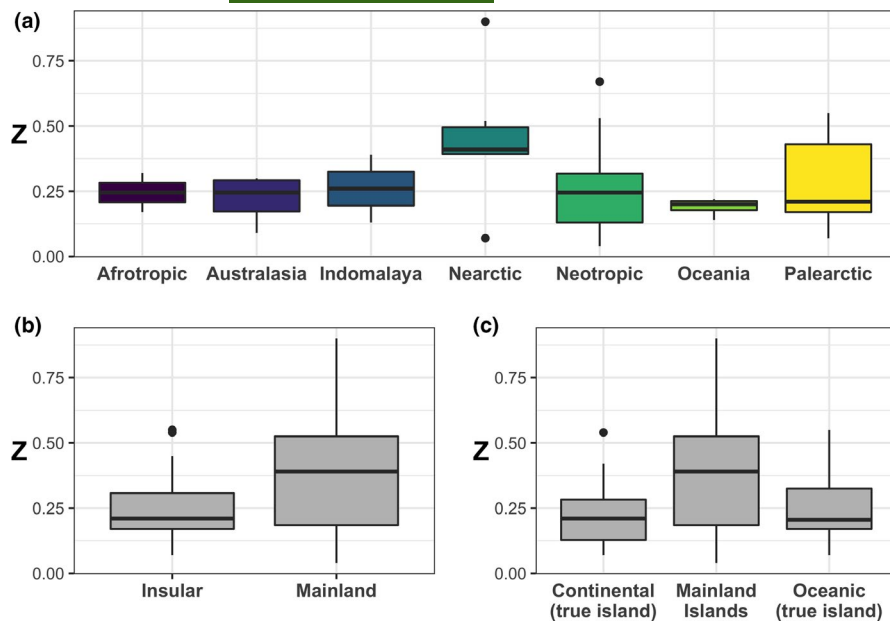


FIGURE 2 Boxplots showing the distribution of slope values (Z) across studies ($n = 41$) for ants across all biogeographic realms. (a) Boxplots of z -values by biogeographic realms. (b) Boxplots of z -values by insular or mainland studies. (c) Boxplots of z -values by the types of islands in the study

R^2) were calculated using the “MuMin” package (Barton, 2019). AIC_c values were calculated using the package “bbmle” (Bolker, 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 intercept-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 continuous 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: (a) a model with just a random intercept for biogeographic realm and (b) 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.

3 | RESULTS

3.1 | 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). Nonnative ant percentage ranged from 0% to 87% and the average percentage of nonnative ants in mainland and insular datasets was 2.82% and 29.90% respectively. Continental and oceanic island datasets had an average nonnative percentage of 18.7% and 34.6% respectively. The biogeographical realms with the highest nonnative 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 Figure S1). 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 (Figure S1). It was the second-ranked model according to mean rank (behind the Kobayashi



TABLE 2 A summary table showing the number of datasets used in dataset 1, by biogeographic realm, species–area relationship type, island type, and citation

Biogeographic realm	Number and Citation	Species-area relationship type	No. of datasets	Island type	No. of datasets
Afrotropic	2 (1)	Insular	1	Continental:	0
				Mainland Islands:	1
Australasia	4 (2)	Mainland	1	Oceanic:	1
		Insular	4	Continental:	2
				Mainland Islands:	0
Indomalaya	2 (3)	Mainland	0	Oceanic:	2
		Insular	2	Continental:	1
Nearctic	6 (5)			Mainland Islands:	0
		Mainland	0	Oceanic:	1
		Insular	2	Continental:	2
Neotropic	10 (6)			Mainland Islands:	4
		Mainland	4	Oceanic:	0
		Insular	5	Continental:	3
Oceania	4 (7)			Mainland Islands:	5
		Mainland	5	Oceanic:	2
		Insular	4	Continental:	0
Palearctic	13 (8)			Mainland Islands:	0
		Mainland	0	Oceanic:	4
		Insular	12	Continental:	5
Total:	41			Mainland Islands:	1
		Mainland	1	Oceanic:	7
		Total Insular:	30	Total Continental:	13
		Total Mainland:	11	Total Mainland Islands:	11
				Total Mixed:	0
				Total Oceanic:	17

Citations: 1. (Dean & Bond, 1990, Wetterer et al., *unpublished*), 2. (Sarnat et al., 2013; 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; Wilson, 1988) 7. (Morrison, 1997; Wetterer, 2002; 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, 2018a, 2018b; Legakis, 2011; Mühlenberg et al., 2016; Poldi et al., 1995; Terayama, 1992; Wetterer, 2006, Wetterer, *unpublished*)

Second column indicates specific citation by number-code in parentheses. Datasets focused on only single islands used in dataset 2 are cited at the bottom but not listed in the table.

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

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) ($n = 41$), assessing slope values (z) as a function of abiotic variables based on AIC_c (Akaike Information Criterion with correction for small sample sizes) rankings

	ΔAIC_c	Weight (w_i)	Pseudo R^2
Model with island order of magnitude range (OMR) covariate			
$z \sim$ 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			
$z \sim$ 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

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 pseudo R^2 .

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

Seven models were run to assess the effects of climate and latitude on z -values while accounting for ISAR type (Table 3). The most

plausible model based on AIC_c was one that evaluated z -values as a function of the additive effects of ISAR type (covariate) and MAP (Pseudo- $R^2 = 0.18$). There was a nonsignificant effect from the covariate but a significant effect of MAP on z -values (-0.26 ± 0.09).

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

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

3.2 | 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) (Figure 1b,c). 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,



TABLE 4 Threshold models comparison summary

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

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

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 (Table S5). However, the mainland threshold model fits were harder to interpret, with the R² 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 Figures S3 and S4). 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 (Figure 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 (Figure 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.

4 | 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 SARs.

4.1 | Dataset 1: Mainland versus 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 analysing 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 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.

4.2 | 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

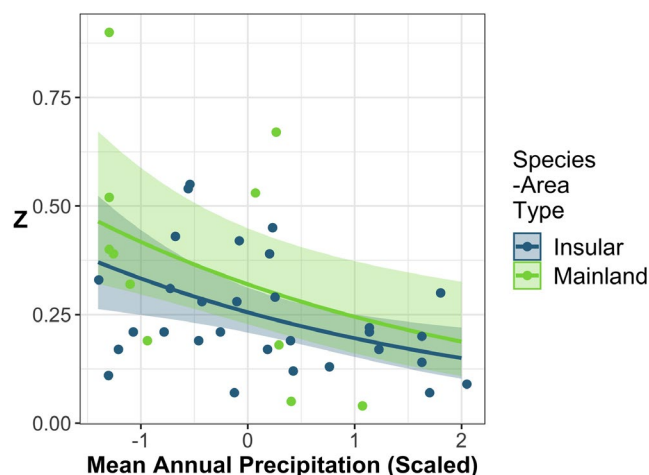
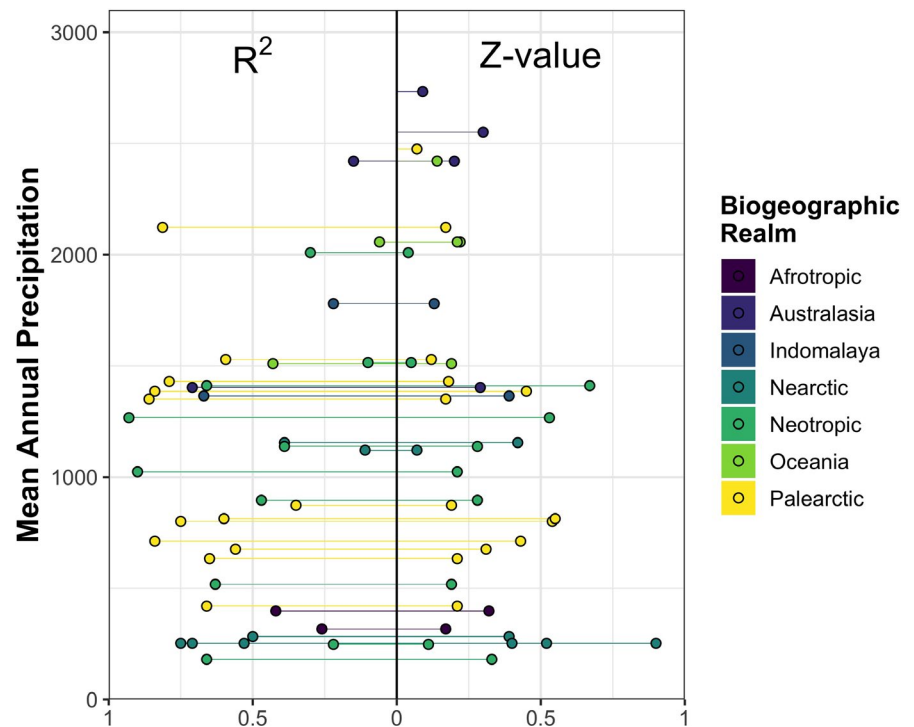
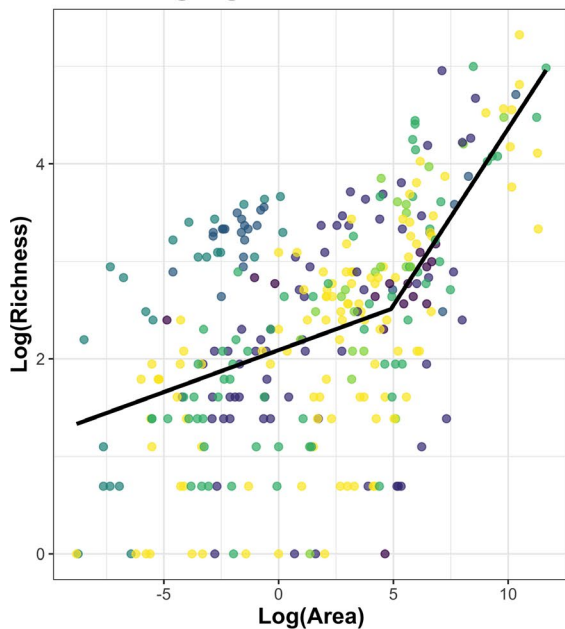


FIGURE 3 Predictions of the most plausible model of ant *z*-values across all biogeographical realms when accounting for the covariate ISAR type (insular or mainland studies). The y-axis represents slope values (*Z*) and the x-axis represents mean annual precipitation (scaled). Lines represent model 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. Colours represent the biogeographic realm of the study



(a) Insular log-log



(b) Insular semi-log

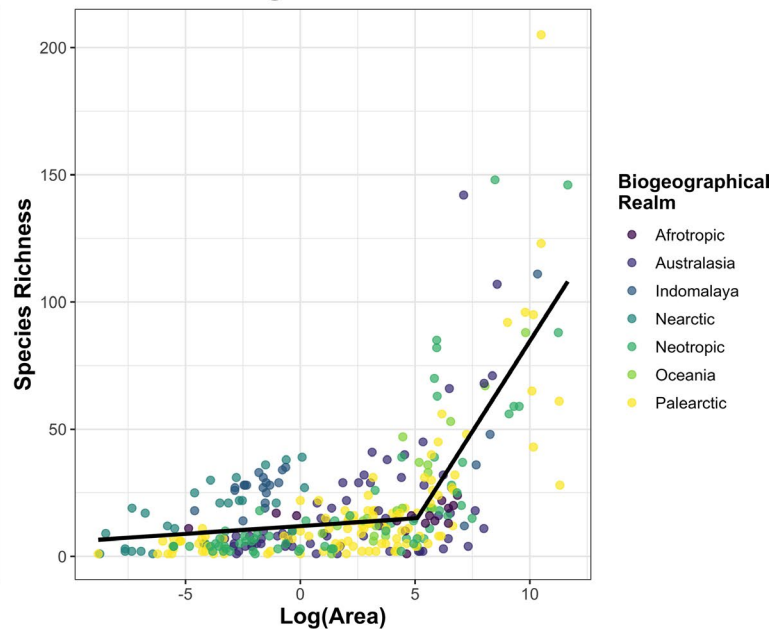


FIGURE 5 Plot showing the best threshold model for ants across biogeographical realms (continuous one-threshold model; black lines) fitted to dataset 2 for true islands ($n = 320$) in (a) log-log and (b) semi-log space. Points are coloured by biogeographic realm, and the colours are consistent across plots (i.e., the legend in (b) applies to both plots). Natural logarithms are used and the area unit is km^2

species, which could lower extinction rates or heighten colonization rates in habitat patches or islands. Another mechanism would be that increased precipitation can yield a higher diversity of microhabitats for ants at a local scale; the diversity and available biomass of plants is crucial, providing a diversity of resources through both plant-ant

interactions and heterogeneity in the range of suitable nesting sites (Hölldobler & Wilson, 1990; Lach et al., 2010). Unraveling the effects of precipitation on both macro- and microhabitat diversity in insular systems that vary in spatial areas will help us understand the scales at which abiotic conditions significantly impact biodiversity.

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

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

4.3 | Dataset 2: A general SAR in ants

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

In regard to the threshold in the global true island ISAR (Figure 5), the threshold (excluding the left-horizontal model in log–log space)

was identified at roughly 133–163 km². 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 & 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 (Economato et al., 2017; Economato & 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 (Economato & 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).

4.4 | Gaps in the ant SAR

4.4.1 | 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 SARs. 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.

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

4.4.3 | Sample size

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

4.4.4 | Impacts of nonnative ants on the SAR

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

the establishment of nonnative ants and how nonnative ants influence the ISAR both empirically and theoretically.

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

5 | 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.

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DATA AVAILABILITY STATEMENT

Datasets 1 and 2 which were used for all formal analyses from this study are available in the Supporting Information.

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BIOSKETCH

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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 analysed the data, LO wrote the manuscript with input from RDH, TJM, and AL.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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