



How important is passive sampling to explain species-area relationships? A global synthesis

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Abstract

Context The species-area relationship (SAR) is one of the main patterns in Ecology, but its underlying causes are still under debate. The random placement hypothesis (RPH) is the simplest one to explain the SAR: larger areas passively sample more individuals and, consequently, more species. However, it is still unclear the degree to which this null hypothesis is supported for different taxa and locations globally.

Objectives We performed the first global synthesis on the RPH to investigate which variables mediate variation in the degree of support of this hypothesis across taxa and regions.

Methods We conducted a review of the global literature and estimated the degree of support of the RPH. The degree of support (effect size) was inferred through the coefficient of determination of the relationship between observed (empirical) and predicted (according to the RPH) species richness. We analyzed the relationship between this effect size metric and different geographic and ecological factors.

Results About 31% of the studies explicitly considered the RPH. From these, only 14% tested the RPH

in a total of 52 independent case studies. About 42% of these case studies confirmed the RPH. The degree of support was significantly higher for plants than animals, and increased consistently with latitude for animals.

Conclusions Passive sampling is important to determine SARs, especially for animals at higher latitudes and plants. Further tests of the RPH, which is still scarcely explored in the literature, are vital to understanding the stochastic and ecological processes underlying the SAR and to advancing Landscape Ecology.

Keywords Area-effect · Habitat patches · Null models · Passive sampling · Random placement model · Species richness

Introduction

The classic relationship between the number of species and the area of a given habitat patch is one of the most general and well-known patterns in Ecology (Arrhenius 1921; Gaston and Blackburn 2000; Tjørve et al. 2021a). Such species-area relationship (SAR) is at the center of many efforts to understand the distribution of biological diversity in space (Tjørve and Turner 2009) and time (Rosenzweig 1998). Indeed, the SAR has been used to describe the structure of biological communities (Cain 1938), to estimate species richness and diversity (Arrhenius 1921; Plotkin

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et al. 2000), to quantify species loss caused by habitat loss (Pimm and Askins 1995; Brooks et al. 1997; Harrison and Bruna 1999), and to design strategies for biodiversity conservation (Picton 1979; Fattorini 2021). Although SARs have been well-documented for diverse taxa and regions, the most likely underlying causes of this pattern are still under debate (Ewers and Didham 2006; Prevedello et al. 2016; Tjorve et al. 2021b).

Several hypotheses based on different ecological processes have been proposed to explain why larger areas support more species (Blakely and Didham 2010; Didham et al. 2011; Tjorve et al. 2021b). The habitat diversity hypothesis (Williams 1943), for example, states that larger areas contain a greater variety of available habitats, and therefore are able to support more species than smaller areas. The equilibrium hypothesis from island biogeography theory (MacArthur and Wilson 1967) assumes that larger islands support larger populations, which are consequently less prone to extinction (“area per se hypothesis”). On its turn, the intermediate disturbance hypothesis (Mcguinness 1984a) assumes that small areas are more vulnerable than large areas to phenomena such as storms, tornadoes and landslides, which cause local extinctions and reduce species richness.

The exact shape of the SAR may also be affected by different ecological processes. Interspecific interactions, such as competition and mutualism, may affect patterns of co-occurrence of different species, decreasing or increasing species richness on a given habitat patch (Drakare et al. 2006). Variation in the degree of intraspecific aggregation across species or patches of different sizes may also affect the shape of the SAR (Bidwell et al. 2014). On one hand, individuals may show an aggregated pattern in larger islands due to a greater availability of resources, which sustains more abundant local populations and decreases the probabilities of extinction (the resource concentration hypothesis; Connor et al. 2000; Matthews et al. 2015). On the other hand, smaller islands may harbor a higher density of individuals due to reduced competition (the density compensation hypothesis; Connor et al. 2000) or reduced isolation (if several small islands are present in the archipelago, reducing inter-island distances; Fahrig 2017), which favors rescue effects (Hanski and Ovaskainen 2000).

Despite the potential influence of such ecological processes on species richness, SARs may also be

produced by simple stochastic processes (Tjorve et al. 2021b), especially random placement (or “passive sampling”; Arrhenius 1921; Coleman 1981; Prevedello et al. 2016). The random placement hypothesis (RPH) explains SARs as a simple consequence of a passive sampling phenomenon, rather than ecological processes (Coleman 1981; Coleman et al. 1982). According to the RPH, habitat patches function as “targets” that passively accumulate individuals: larger patches accumulate more individuals and, consequently, more species than smaller patches. Despite the fact that the RPH dates back to the 1920’s (Arrhenius 1921), this hypothesis was largely ignored in the species-area literature until the seminal papers of Coleman (1981) and Coleman et al. (1982) (Gotelli and Graves 1996). Because it is basically based only on probabilistic processes, the RPH may serve as a null hypothesis for SAR studies (Coleman et al. 1982; Gotelli and Graves 1996; Bidwell et al. 2014). Therefore, explicit comparisons of observed vs predicted (by the RPH) species richness could reveal the relative importance of probabilistic and ecological factors on observed SARs (Gotelli and Graves 1996).

Despite the simplicity and potential importance of the RPH, it is still unclear how frequently this hypothesis has been explicitly considered and tested in the literature. Previous individual studies have already highlighted the scarcity of explicit RPH studies testing this hypothesis (Mcguinness 1984b; Fattorini 2007). In addition, there is still no global assessment of the support of explicit RPH tests in explaining SARs for different taxa, in different types of islands and in different regions across the globe. Such knowledge gaps are of special concern considering that the SAR is one of the most important patterns in Ecology, and that appropriate tests of null hypotheses are essential to understand the ecological processes underlying such patterns (Gotelli and Graves 1996; Sutherland et al. 2013; Prevedello et al. 2016; Tjorve et al. 2021b).

Here, we performed the first global synthesis on the RPH to investigate which variables mediate variation in the degree of support of this hypothesis across taxa (animals versus plants), habitat types (islands versus habitat patches), and regions of the world (latitude). First, we test the hypothesis that the RPH has greater support for plants than animals, for two reasons. Plant dispersal is more passive and, therefore, more likely to reflect simple stochastic processes

(Condit et al. 2002; Latimer et al. 2005). Additionally, the traditional Coleman's model may have limited applicability for most vagile animals, as it assumes that each individual occupies a single point in space, ignoring area requirements (home range), which vary among species and affect individual's placement in landscapes (Prevedello et al. 2016).

Secondly, we test two alternative hypotheses: i) the RPH has less support at lower latitudes (tropical areas), assuming that biological diversity is higher and biological interactions are stronger at tropical regions (e.g. Hilldebrand 2004; Roslin et al. 2017), thus making ecological (deterministic) processes more important than simple probabilistic processes; or ii) conversely, stochastic processes are stronger in tropical areas due to weaker environmental filters (e.g. lower climatic variability), and, therefore, result in a higher support for the RPH in tropical areas (Hubbell 2001).

Finally, we also test two alternative hypotheses regarding habitat types: i) the RPH is more supported in insular landscapes (where the matrix is inhospitable) than continental landscapes, since the random placement model does not consider the use of the matrix (Coleman et al. 1982); or ii) conversely, the effects of habitat type will be negligible when islands are far apart, as dispersal would be limited for both insular and continental landscapes, making random placement unimportant. To test all the previous hypotheses regarding taxa, latitude and habitat types, we moved beyond the classic binary classification of the RPH ("confirmed" or "rejected" the RPH), by using a quantitative metric, which allows quantifying the degree of support of the RPH in explicit tests across different case studies.

Materials and methods

Data compilation

We performed a comprehensive literature search using Web of Science, to search for all SAR studies published after the first formal proposal and empirical test of the RPH in the literature (see Figure S1 in Appendix S1; Coleman 1981; Coleman et al. 1982). We used the following three searching terms: "species-area relationship", "area effect", and "species-area relation". This search was conducted considering

the titles, keywords and abstracts of articles published between 1983 and 2018. We refined the search only for journals related to Biology, Ecology, Geography, Environmental Sciences and Oceanography. Subsequently, we conducted a second separate search to obtain studies that explicitly considered the RPH as a potential explanation for the SAR, which requires using some sort of random placement model that produces "predicted" species richness values and compares them to the empirically observed richness values. Considering that the study of Coleman et al. (1982) is broadly acknowledged as the first robust and explicit test of the RPH, we searched for all studies that cited this seminal work. From this second set of studies, we analyzed all studies that used some type of random placement model to explicitly test the RPH (e.g. Coleman et al. 1982; Tjorve et al. 2008; Guadagnin et al. 2009; Bidwell et al. 2014).

The vast majority of studies used the traditional Coleman's (1981) model for randomizations, whereas few studies used some modified version of the traditional model, for example an individual-based model (Guadagnin et al. 2009) or algorithms for randomizing grid occupancy data (Tjorve et al. 2008). All species richness data, both observed and estimated by a random placement model, were extracted from the original studies (Figure S1). For studies that reported data for more than one taxonomic group (e.g. mammals, reptiles, plants), we assumed that each group represented a separate empirical test (hereafter referred to as a "case study") of the RPH. The potential non-independence of case studies from the same study (paper) was considered in the analysis (see "Data analysis").

Degree of support of the RPH

To calculate the degree of support of the RPH, we first extracted for each case study data on species richness, both observed and predicted by a random placement model. We extracted data directly from tables or plots of case studies using the R package metaDigitise (Pick et al. 2019). Then, for each case study, we performed a linear regression between the observed and predicted richness values obtained in the previous step, and extracted the coefficient of determination (R^2) (for examples, see Figure S2). We used R^2 as our metric of effect size, which measures the degree of support of the RPH for each case study (Table S1

in Appendix S1). The R^2 indicates how much of the variance in the observed values is predictable from the RPH, while other components like the slope (b) and the intercept (a) describe, respectively, the model's consistency and bias of the linear regression model (Smith and Rose 1995; Piñeiro et al. 2008). In a perfect match between observed and predicted richness, the observed data is perfectly predicted by the RPH, which would result in a $R^2 = 1$ (Prevedello et al. 2016). In this study, the pairwise correlations between R^2 , b and a were relatively low (only significant correlation: R^2 vs b , $r = 0.49$; $p < 0.001$). This metric was successfully validated by comparing R^2 values between case studies that “confirmed” versus “rejected” the RPH (see “Data analysis”). Therefore, we calculated R^2 for all case studies of the RPH, and used this metric as the dependent variable in subsequent statistical analyses (Figure S1).

Independent variables

To assess which variables determine variation in RPH's degree of support (effect size, R^2) across case studies, we extracted four explanatory variables from each: major taxon, geographic region, and the habitat type and size variation of the studied patches (Table S2). These four variables are directly related to at least one of the two axes of the SAR (species richness and area) and, therefore, may impact the effect size. Major taxon was simply “flora” or “fauna”, as more refined taxonomic classifications would result in relatively small sample sizes for some groups. This coarse classification allows differentiating organisms that disperse passively from those that actively move for dispersal and habitat selection (Brown and Lomolino 1998; Aduse-Poku et al. 2018).

The geographic region was assessed using the absolute latitude (in degrees), where each case study was conducted. The type of patch studied was classified as “island”, when patches were surrounded by water such as oceans, rivers, or lakes, or as “habitat patch”, when they were embedded within continental terrestrial habitats (e.g. fragmented forests). Therefore, landscapes composed of oceanic islands, rocks in rivers, reservoir islands (dams), or lakes were classified as islands. Landscapes composed of forest fragments, forest clearings, or ponds (for frogs) were classified as habitat patches.

We also considered a methodological variable, “size variation”, which is a measure of variation in the size (area) of habitat patches (either “islands” or “habitat patches”) in each landscape of each case study. This variable was calculated as the ratio between the size of the largest and the smallest patch in each case study. A landscape with a large variation in the size of their patches had a greater value for this variable. We expected that higher ratios should favor the confirmation of RPH, as the variation in patch size is the only predictive variable explicitly considered by the RPH to calculate the expected numbers of individuals and species in a patch (Coleman et al. 1982). For example, for two landscapes A and B, in which the smallest and largest patches are 0.01 – 1.00 km² and 0.15 – 4.00 km², would have a size variation of 100.00 and 26.67, respectively. Landscape/archipelago extent and mean patch sizes could also potentially impact the degree of support of the RPH, but were unavailable for most studies.

Data analysis

To validate our effect size metric (R^2), we first compared its values between case studies that “confirmed” versus “rejected” this hypothesis, based on the binary classification originally stated in the researched studies. Most studies used Coleman's original rule, considering that the RPH is corroborated when 2/3 of the observed points are within ± 1 standard error of the estimated richness. However, some studies tested the RPH with some form of comparison tests between estimated and observed data, based e.g. on R^2 values, slopes or sum of squared residuals. If the effect size metric is suitable to measure the degree of support of the RPH, its values must be higher for studies that originally concluded that this hypothesis was corroborated (“confirmed”). To perform this validation test, we built a generalized linear mixed model (GLMM), using R^2 as the dependent variable, and the binary outcome of the case study (confirmed vs rejected) as the independent variable (fixed effect). We included random intercepts for each case study, to control the potential non-independence of tests from the same study (random effect). We used a beta error distribution and a logit link function, as R^2 values ranged continuously from 0 to 1 (Crawley 2013).

To determine which factors drive variation in effect sizes (R^2 values) across case studies, we built

a second GLMM, using R^2 as the dependent variable, and taxon, geographic region, patch type, and variation in patch size (log-transformed) as independent variables (fixed effects; Figure S1). We did not include interactions in the model due to absence of clear hypotheses and the relatively reduced number of case studies ($N = 53$). Again, we included random intercepts for each case study to control for non-independence, with beta error distribution, and a logit link function. We also tested separately the other two components of the linear regression between observed and predicted data, intercept and slope. All analyses were run in R version 4.2.0 (R Core Team 2022), using R base functions and the package “glmmTMB” to perform the GLMM (Brooks et al. 2017), “DHARMA” to analyze the residuals (Hartig 2022), “piecewiseSEM” to calculate the pseudo- R^2 , marginal and conditional effects (Lefcheck 2016), and the “sjPlot” and “ggplot2” to plot results (Wickham 2016; Lüdtke et al. 2022).

Results

Literature overview

We found 798 published articles on the SAR. Among these, 252 studies cited the seminal study of the RPH by Coleman et al. (1982). Two of these articles were not accessible (Johnson 1986; Paszkowski and Tonn 2000) and were excluded from further analyses. Thus, according to our criteria, the RPH was considered in 31% of the studies that evaluated the SAR. Only 14% (35 of the 250 studies) that cited Coleman et al. (1982) applied some model to actually test the RPH explicitly. From these 35 studies, 30 reported the data needed to compare observed vs predicted species richness, resulting in a total of 53 case studies. An outlier case study (Yamaura et al. 2016; with plants) was excluded from the analysis because its model included an imperfect detection for predicted plant species richness, resulting in an overestimation of 400-fold high richness than observed. The case study of these authors with animals, on its turn, did not have this correction for imperfect detection, so it was maintained in our analysis. Therefore, we only considered 52 case studies. About 42% of these case studies confirmed the RPH considering the binary

classification, whereas 58% rejected it (see Table S1 in Appendix S1).

Factors explaining variation in the degree of support of the RPH

The values for the degree of support were significantly higher ($\chi^2 = 28.44$, $df = 1$, $p < 0.0001$) for case studies that confirmed the RPH (R^2 mean = 0.90, $sd = 0.15$, $n = 22$) compared to case studies that rejected this hypothesis (R^2 mean = 0.57, $sd = 0.25$, $n = 30$). Therefore, the effect size metric (R^2) was validated as a valid effect size measure of the relative degree of support of the RPH across case studies.

The degree of support of the RPH (R^2) was significantly affected by the taxon studied and the latitude where the case study was conducted (Table 1). Type of patch and size variation in patch area had no significant effects on R^2 (Table 1). Together, these four variables explained 86% of the variation in R^2 across case studies. This degree of support was about 2 times as higher for plants than animals and increased consistently with latitude for animals (Figure 1). Additional tests for plants and animals confirmed that this latitudinal effect occurred only for animals (Table S3). The additional tests for the intercept and

TABLE 1 Factors affecting the degree of support of the random placement hypothesis (RPH) across case studies, as measured by the effect size metric (R^2)

Independent variables	χ^2	df	P
Taxon	43.61	1	< 0.001
Latitude	5.91	1	0.02
Type of patch	0.32	1	0.57
Size variation	1.22	1	0.27

Results from a generalized linear mixed model (GLMM), R^2 is a dependent variable, and four independent variables (fixed effects) considered: Taxon (Flora vs Fauna), Latitude (absolute latitude, in degrees), Type of patch (Habitat patch vs Island) and size variation in patch area (ratio between the size of the largest and the smallest patch). The model used a beta error distribution and a logit link function. Data from 52 case studies obtained in 30 studies published between 1983–2018 and that tested RPH. The identification of studies (Author ID) was the random effect. Statistically significant variables ($P < 0.05$) are highlighted in bold. Random effects: Intercept standard deviation = 0.25; Residual standard deviation = 0.50; Marginal $R^2 = 0.86$; Conditional $R^2 = 0.99$

Statistically significant variables ($P < 0.05$) are highlighted in bold

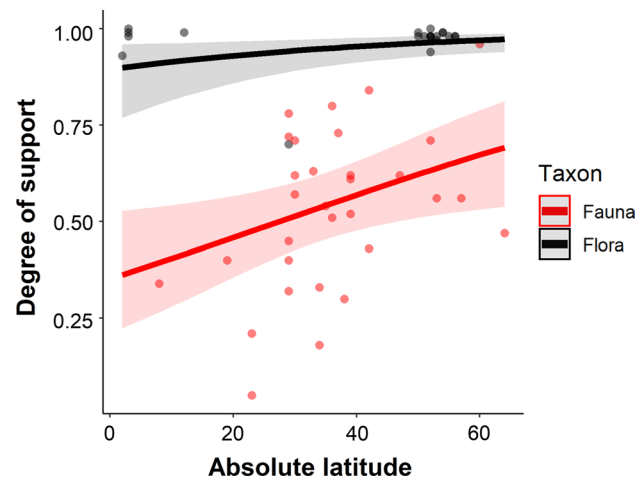


Fig. 1 Relationship between the degree of support (effect size, R^2) of the random placement hypothesis (RPH) and the taxon (animals in red, plants in black) and latitude. The R^2 values represent predicted values by generalized linear mixed model (GLMM), estimated for each taxon and latitude by keeping constant the other explanatory variables (type of patch and

size variation). Data from 52 case studies of the RPH obtained from 30 studies published between 1983–2018. The variables taxon, latitude, type, and size variation of habitat patches were the fixed effects of the GLMM, while the study ID was considered a random effect

slope of the linear regression indicated only a Taxon effect for the slope (Table S4).

Discussion

Literature overview

Null models have been extensively used in ecological studies for more than 40 years and are currently considered consolidated analytical tools (Colwell and Lees 2000; Gotelli and Graves 1996; Gotelli 2000, 2001). Even so, our results show that relatively few studies have explicitly tested the RPH as a potential explanation for observed SARs. This means that most studies on the SAR evaluated in our study either did not attempt to determine the causes of this pattern or did not explicitly consider that the relationship may reflect simple probabilistic processes (Coleman et al. 1982; Prevedello et al. 2016). This result is surprising, giving the simplicity and plausibility of the RPH as the proper null expectation for SARs. The low explicit consideration of the RPH may partially reflect the difficulty in obtaining a complete census of individuals in a studied community (Connor and Mccoy 1979; Gotelli and Graves 1996; Tjorve et al. 2021a), a requirement for testing the RPH according

to the classical Coleman's (1981) model. However, modified versions of this model also allow testing the RPH even with incomplete censuses (e.g. Tsao 2000; Tjorve et al. 2008; Guadagnin et al. 2009; Bidwell et al. 2014), offering a great potential for the application of the RPH in future studies. A more likely explanation for the relatively small number of studies that explicitly considered the RPH is a general tendency in the SAR literature to emphasize more the detection and description of this pattern than its underlying processes (Ewers and Didham 2006; Prevedello et al. 2016; Tjorve et al. 2021b). Moreover, there is also the possibility that, as a null model, researchers avoid using the RPH under the statement that it would not represent a real empirical scenario, as it presents no structure or it is entirely random (Roughgarden 1983).

In fact, null models also present a controversial history, possibly because they are generally misunderstood (Gotelli 2001): they *do* incorporate considerable structure from existing data, rather than assume that every aspect of a given system is random (Strong 1980; Gotelli 2000). Null models are pattern-generating models that exclude a mechanism of interest (e.g. a given deterministic process), and allow for randomization tests of ecological and biogeographic data (Strong 1980; Gotelli

and Graves 1996; Gotelli 2000, 2001). Therefore, null models should be viewed as reference points, to which alternative and more complex hypotheses should be contrasted. This is clearly the case of the RPH, which predicts the occurrence of SARs due to passive sampling only, even in the absence of extinction, disturbance and habitat heterogeneity, for example. It is likewise important to mention that passive sampling is also considered a real stochastic process, along with random dispersal, population fluctuations, disturbance events and stochastic extinction (see Figure 4.3 in Tjorve et al. 2021b). In his Neutral Theory, Hubbell (2001) stated, for example, that ecological drift and random dispersal would contribute to differences in the structure of communities of islands. Therefore, the RPH should be then understood not only as the expectation from which a ‘deviation’ would be detected in empirical SARs, but likewise a true mechanism that is always present (Tjorve et al. 2021b).

Thus, it is not surprising that almost half of the case studies that explicitly tested the RPH confirmed it. Ecologists must therefore increasingly acknowledge that stochastic processes can also govern, at least in part, many observed SARs (Gotelli and Graves 1996; Bidwell et al. 2014; Prevedello et al. 2016; Tjorve et al. 2021b). On the other hand, as observed among the case studies that refuted the RPH, several deterministic processes can also govern SARs in addition to stochastic processes, such as species abundance distribution derived from niche partition processes (Matthews et al. 2015, Tjorve et al. 2021b), intra and interspecific interactions (Elmberg et al. 1994; Baldi and Kisbenedek 1999), habitat diversity (Douglas and Lake 1994; Guadagnin et al. 2009), niche differentiation (Wang et al. 2008), dispersal and immigration (Plotkin et al. 2000; Kadoya et al. 2004; Murgui 2007), disturbances (Mcguinness 1984b), reproduction and recruitment (Peake and Quinn 1993), and historical conditions (Fattorini 2007). Therefore, future studies should attempt to understand the relative importance of stochastic (quantified by null models, such as an area- or individual-based model) and deterministic processes on the structure and composition of communities, for a better understanding of the causes of the SAR (Sutherland et al. 2013; Aduse-Poku et al. 2018; Gooriah et al. 2021).

Taxon and latitude mediate the degree of support of the RPH

The degree of support of the RPH was higher for plants than animals, confirming our first hypothesis. This result suggests that stochastic processes are more important in shaping SARs in plants than animals. In fact, much evidence supports that random processes are especially important for sessile organisms (Hubbell 2001; Condit et al. 2002; Latimer et al. 2005). In previous studies with animal communities, random processes seemed to be especially important only when researchers analyzed separately the microhabitats belonging to extremes of an environmental gradient, reducing environmental variation and the effects of active dispersal and habitat selection (Ellwood et al. 2009; Aduse-Poku et al. 2018). The higher support of the RPH for plants may reflect the fact that animals select habitats and actively disperse, whereas plants do not actively choose where to recruit and settle because their dispersal is passive, depending on seed dispersal vectors (Brown and Lomolino 1998; Aduse-Poku et al. 2018). Our results thus may reinforce the importance of the dispersal mode (active or passive) in structuring biological communities across patches. However, the higher support of the RPH for plants may also reflect the assumption of Coleman’s model that each individual occupies a point in space, rather than an area. This assumption is met for plants, which may occupy all patches as assumed by passive sampling, whereas vagile animals may only occur in patches larger than individual home ranges, causing deviation from passive sampling (Prevedello et al. 2016). It is also important to note that the taxon effect for the Flora group is very dependent on one study, Tjorve et al. (2008). This study used 15 different high-latitude datasets to assess the effects of species abundances and spatial distribution on the SAR shape, using grid occupancy data. The authors adapted the Coleman model to their grid system (see model 3 in Tjorve et al. 2008), which resulted in a predicted richness similar to the observed one, resulting in a cluster of high R^2 values (Figure 1).

The degree of support of the RPH also increased consistently with latitude for animals, suggesting that stochastic (probabilistic) processes are indeed especially important in explaining SARs at higher latitudes for this group (Figure 1). This pattern may reflect the influence of latitudinal gradients of energy

and diversity on the ecological and random processes that structure animal communities. The reduction in species richness towards the poles is well documented, leading to a smaller number of species and trophic levels at higher latitudes (Wallace 1878; Gaston and Blackburn 2000; Liang et al. 2022), potentially reducing the magnitude of ecological interactions and deterministic processes compared to tropical environments (Schemske et al. 2009; Roslin et al. 2017; Pontarp et al. 2019). Indeed, an increase in the number of dominant deterministic processes that govern biodiversity patterns towards lower latitudinal levels has been suggested recently (Liang et al. 2022). In addition, low-latitude species may be more sensitive to extinction by deterministic processes like habitat loss, fragmentation and edge effects, due to a low historical exposure to disturbances (i.e., forest loss and climatic instabilities such as glaciers and fires) compared to high-latitude species (Betts et al. 2017; Willmer et al. 2022). Finally, habitat diversity could be less important in shaping SARs at higher latitudes, if habitats would be more homogeneous in temperate/boreal regions compared to tropical regions. In fact, environmental homogeneity is considered an important factor to explain the low biological diversity in temperate forests in opposition to tropical habitats (Myers et al. 2013), which, in turn, present higher habitat diversity and spatial niche partition (Srivastava and Lawton 1998; Pontarp et al. 2019). Interestingly, there was no latitudinal gradient in the degree of support of the RPH for plants, which was high regardless of latitude (see Fig. 1). This absence of latitudinal effect may reflect the utmost importance of stochastic process for structuring plant communities, as discussed in the previous paragraph.

Conclusions

Despite disregarding the myriad of ecological factors that can affect species richness, the RPH explains a large fraction of observed SARs, especially for animals at higher latitudes, and plants. Despite its simplicity and potential usefulness, however, this hypothesis is still rarely considered explicitly in the literature on the SAR. This is worrisome, as a large part of the analyzed literature did not explicitly acknowledge that stochastic processes are always present to some degree, and sometimes can explain reasonably well

one of the most general and interesting patterns in Ecology, the SAR. The explicit consideration and test of the RPH in future studies, either alone or in combination with additional hypotheses based on different ecological factors, can advance substantially the comprehension of the processes that affect community structure across different areas.

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Author contributions Marco Aurélio Ferreira da Silva and Jayme Augusto Prevedello contributed to the conception and design of the study. Material preparation, data collection and analysis were performed by Marco Aurélio Ferreira da Silva and Clarice Braúna Mendes. The first draft of the manuscript was written by Marco Aurélio Ferreira da Silva, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability All data generated or analysed during this study are included in this published article and its supplementary information files. All artwork has been made using Microsoft Power Point and Paint softwares.

Declarations

Competing interests The authors declare no competing interests.

Competing interests: The authors have no relevant financial or non-financial interests to disclose.

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