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RESEARCH ARTICLE

Species range size shapes distance-decay in community similarity

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Abstract

Aim: (i) To assess the dependence between the form of the decrease in biological similarity with distance (distance-decay) and species range size and (ii) to introduce the use of a sigmoidal model, the Gompertz function, as a flexible alternative able to fit distance-decay models under a wide variety of species range sizes.

Location: Applicable worldwide.

Methods: We computed distance-decay curves from simulated communities to assess how the species range sizes shape the functional form of distance-decay patterns (i.e. negative exponential, power-law or sigmoidal [Gompertz] relationships). Simulations were performed using different sample sizes and species detection probabilities. We also used distribution data of South American mammals to explore the relationship between species range size and the distance-decay form in an empirical dataset.

Results: Our simulations showed that the power-law is the best supported model when range sizes tend to be small. An increase in range sizes leads to a negative exponential relationship, taking the shape of a sigmoidal (Gompertz) relationship with the largest range size values. Similar results have been found in the distance-decay pattern of South American mammals. Remarkably, the Gompertz function fits the data reasonably well in all scenarios.

Main conclusions: The functional form of distance-decay patterns depends on a key biogeographical attribute: species range size. This dependence makes it an interesting tool to detect biodiversity threats associated with species range expansion, such as the biotic homogenization of faunas. The Gompertz function is the mathematical model that best accommodates different frequency distributions of species range size and, thus, allows cross-taxa comparison of this biogeographical and ecological pattern.

KEYWORDS
beta diversity, biological similarity, distance-decay, Gompertz function, range size, sigmoidal relationship

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1 | INTRODUCTION

The decrease in community similarity with spatial or environmental distance, that is, distance-decay of similarity, is a general property of biological systems that has been studied for a large range of organisms, for example, archaea (Barreto et al., 2014), bacteria (Barreto et al., 2014; Milici et al., 2016), diatoms (Astorga et al., 2012; Wetzel et al., 2012), fungi (Bahram et al., 2013), plants (König et al., 2017; La Sorte et al., 2008; Nekola & White, 1999; Qian, 2009) and both invertebrate (Saito et al., 2015; Thieltges et al., 2009) and vertebrate animals (Maloney & Munguia, 2011; Qian & Ricklefs, 2012); in different environments, from neotropical forests (Palmer, 2005) to urban environments (La Sorte et al., 2008); and at different spatial scales (Steinbauer et al., 2012). At local or regional scales, distance-decay curves are primarily shaped by the organisms' biological characteristics (e.g. niche requirements or dispersal ability) and their interaction with the environment (Morlon et al., 2008; Steinbauer et al., 2012). The biogeographic characteristics of the study area (such as spatial scale or latitude) also impact the patterns of distance-decay (Nekola & McGill, 2014; Nekola & White, 1999; Soininen et al., 2007). However, the links between distance-decay and key macroecological attributes, such as species range size, have received less attention, even though range size determines to which extent a given species can be found in two different sites. Moreover, species range size also depends on dispersal and niche processes (Brown et al., 1996; Willis, 1922). Thus, organisms with high vagility and wide niches would tend to have larger distributions. In turn, larger distributions increase the probability of different sites having the same species, thus leading to higher similarity in community composition. On the contrary, the distributions of organisms with low vagility and narrow niches are generally smaller and, thus, higher turnover in community composition is expected for these taxa. Therefore, we predict that species range size is a crucial link between the processes controlling species distributions and the shape of the relationship between community similarity and spatial (or environmental) distance.

The assessment of spatial turnover in community composition and, more precisely, its dependence on spatial/environmental distance relies on adequately modelling the shape of the relationship between community similarity and spatial/environmental distance. Non-linear regressions of community similarity (e.g. negative exponential or power-law models) are usually employed, and their parameters are interpreted in biological terms. For example, the intercept estimates the expected community similarity at short distances and the slope quantifies the rate at which communities change with distance (Nekola & White, 1999; Soininen et al., 2007). Therefore, when the same function is used to model distance-decay patterns of different biological groups, these statistical parameters provide a powerful tool to assess how the biological characteristics of different organisms (i.e. dispersal ability or ecological niche) impact the spatial turnover of biological communities (e.g. Gómez-Rodríguez & Baselga, 2018; Soininen et al., 2007). The most frequently used functions are the negative exponential (Nekola & McGill, 2014; Nekola & White, 1999; Preston, 1962; Whittaker, 1960) and the power-law (Nekola & McGill, 2014). It is not possible to opt for one of these mathematical models on first principles as we lack a theoretical foundation for the form of the relationship (Nekola & McGill, 2014) or how it may be affected by species' attributes, such as range size. For instance, when species have small spatial ranges (relative to the study extent), nearby sites are expected to have very different species composition, causing the similarity to rapidly decay from the shortest distances. In this case, power-law or negative exponential functions would suffice to model distance-decay curves. However, when species have large spatial ranges relative to the study extent, close-by biological communities may be very similar, resulting in a small or null rate of change in community composition at the shortest distances while the actual decrease in community similarity would start at intermediate distances. In consequence, the similarity among these communities would present a sigmoidal relationship with distance, being more or less constant (and close to 1) at short distances, rather than steeply decaying from the shortest distance. This shape in the relationship between biological similarity and spatial distance cannot be, a priori, captured by negative exponential or power-law models (Figure 1). In other words, when only these two functional forms are assessed, one of them will be identified as the best supported model, but it may still be an inadequate representation of the distance-decay pattern.

To accommodate scenarios in which the distance-decay relationship shows an initial plateau of high similarity, we introduce the use of the Gompertz function (Gompertz, 1825), which is a sigmoidal function (Godeau et al., 2020) that generalizes the negative exponential model,

$$f(x) = ae^{-be^{-cx}}$$

where a is the superior asymptote, b a position parameter, c the rate of change and x a distance metric between sampling sites. This function was designed for growth patterns and is widely used in many fields of biology, like microbiology, cytology or vegetal physiology (Baker et al., 1975; Booth, 1984; Çelekli et al., 2008; Johnsen et al., 2013; Rossi et al., 2003). Brownstein et al. (2012) also used it to fit the increase in biological dissimilarity with spatial distance (i.e. the inverse of a distance-decay relationship), in order to use its intercept as a proxy for randomness in community configuration. One of the main advantages of the Gompertz function is its theoretical versatility because, as a generalization of the negative exponential, it is expected to adequately fit curves with and without an initial plateau. If this is confirmed, distance-decay patterns parameterized with a Gompertz function can be compared across multiple taxa with varied distance-decay shapes. Such cross-taxon comparison is the basis for the identification of species traits related to distance-decay patterns and, hence, the inference of the main processes driving the spatial variation of those biological communities.

The aim of this paper is to evaluate how species range size affects the distance-decay functional form and which function (i.e. negative exponential, power-law or Gompertz) can better capture the distance-decay relationship under different range size scenarios.

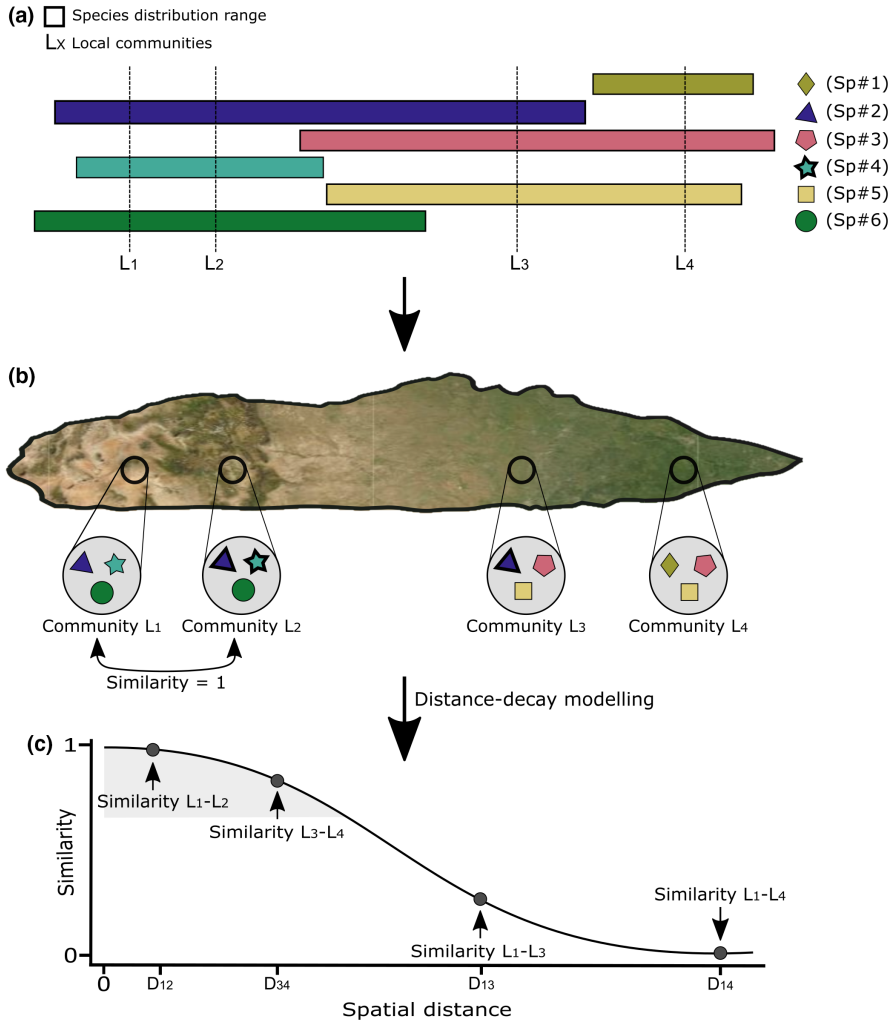

FIGURE 1 Hypothetical example showing how species ranges in a landscape (a) may lead to a spatial configuration of biological communities (b) with a sigmoidal distance-decay relationship (c)

We expect the Gompertz model to provide a better fit when all or most species ranges are large in relation to the distance between local communities. To do this, we used simulations to assess the relationship between the functional form of distance-decay patterns and (i) the frequency distribution of species range size (i.e. proportion of spatially restricted vs. widespread species), and (ii) the size of the smallest ranges. We also used data on the distribution of South American mammals as a case study of how range size influences the form of distance-decay patterns in empirical datasets.

2 | METHODS

2.1 | Data simulation

To assess whether species range size affects the functional form of the distance-decay relationship, we compared the fit of the negative exponential, power-law and Gompertz functions in different scenarios of varying (i) proportion of spatially restricted vs. widespread species, and (ii) range size of spatially restricted species. We simulated the distribution of 300 species with different range sizes (depending on each scenario) in a virtual landscape and computed the compositional similarities between randomly allocated sampling sites, which correspond to our "virtual communities." To do so, we first created 300 circular spatial polygons, each representing the range of a species, using the R package "sp" (Bivand et al., 2013; Pebesma & Bivand, 2005). Each polygon had a different diameter, which was drawn from the frequency distribution of species range size in each simulation scenario. The polygon centre was located at a random point in a virtual landscape of 3000 x 3000 cells. Finally, n sampling sites were randomly allocated in the virtual landscape using the *grf* function of the package "geoR" (Ribeiro & Diggle, 2018). The species composition in each site was computed by identifying the species' polygons that overlap on that site, using the function *gIntersects* of the package "rgeos" (Bivand & Rundel, 2019). This procedure was repeated for different number of sites (n = 10, 50, 500, 5000) to assess the effect of sample size on the functional form of distance-decay patterns. Therefore, we obtained four presence/absence matrices of 300 simulated species in n = 10, 50, 500 and 5000 sites, respectively. We also assessed the effect of absences within a species' potential range (e.g. due to imperfect species detection or unsuitable conditions) on the functional form of distance-decay patterns. To do so, the presence/absence of species within its potential range was assigned using a Bernoulli trial with

four different probabilities of success ($p = 0.25$, $p = 0.50$ or $p = 0.75$, representing different degrees of incomplete species detection, and $p = 1.00$, representing perfect detection).

The differences in species range sizes among simulation scenarios were set following two axes of variation: (i) the ratio between spatially restricted and widespread species (ratio-classes 1–3) and (ii) the range size of spatially restricted species (size-classes A–C) (Figure 2). The combination of these two axes of variation leads to nine simulation scenarios. For the first axis of variation, we simulated three ratio-classes with an increasing proportion of widespread species (diameter of widespread species drawn from a uniform distribution U [3000, 5000]): ratio-class 1 (10 species with widespread distributions and 290 with spatially restricted distributions); ratio-class 2 (20 widespread species and 280 spatially restricted species); and ratio-class 3 (200 widespread species and 100 spatially restricted species). For the second axis of variation, we simulated spatially restricted species with increasingly larger ranges. Hence, in each size-class the polygon diameters were drawn from different distributions: size-class A with U [500, 1000]; size-class B with U [1000, 1500] and size-class C with U [2000, 2500].

2.2 | Distance-decay models of simulated data

We performed non-linear regressions of pairwise assemblage similarity against spatial distance to fit distance-decay models using three different functions: negative exponential, power-law and Gompertz. We computed the similarity in species composition between pairs of sites with the Simpson pairwise similarity index, 1-β_{sim} (Baselga, 2010; Koleff et al., 2003), using the *beta.pair* function of the package "betapart" (Baselga & Orme, 2012). Spatial distances were calculated as the Euclidean distance between pairs of sampling sites. The negative exponential, power-law and Gompertz functions were fitted using the *nlsLM* function of the package "minpack.lm" (Elzhov et al., 2016), which performs a non-linear least squares regression using the Levenberg–Marquardt algorithm (Levenberg, 1944; Marquardt, 1963). We empirically compared the fit of each model based on two independent criteria: AIC and pseudo-r^2 value. For algebraic details on the Gompertz function, please see Appendix S1 in Supplementary Material. The code for the simulation of virtual communities and the assessment of distance-decay models is provided in Appendix S2.

2.3 | Real data

To study the relationship between species' range size and the functional form of distance-decay models in empirical data, we used distribution data of South American terrestrial mammals from the IUCN red list (*IUCN Red List of Threatened Species*). We created four subsets of data based on quartiles of species range size (Q1, Q2, Q3 and Q4). Thus, the species with the smallest distribution ranges were included in Q1 while the ones with the largest distribution ranges were included in Q4. For each species, we computed range size as

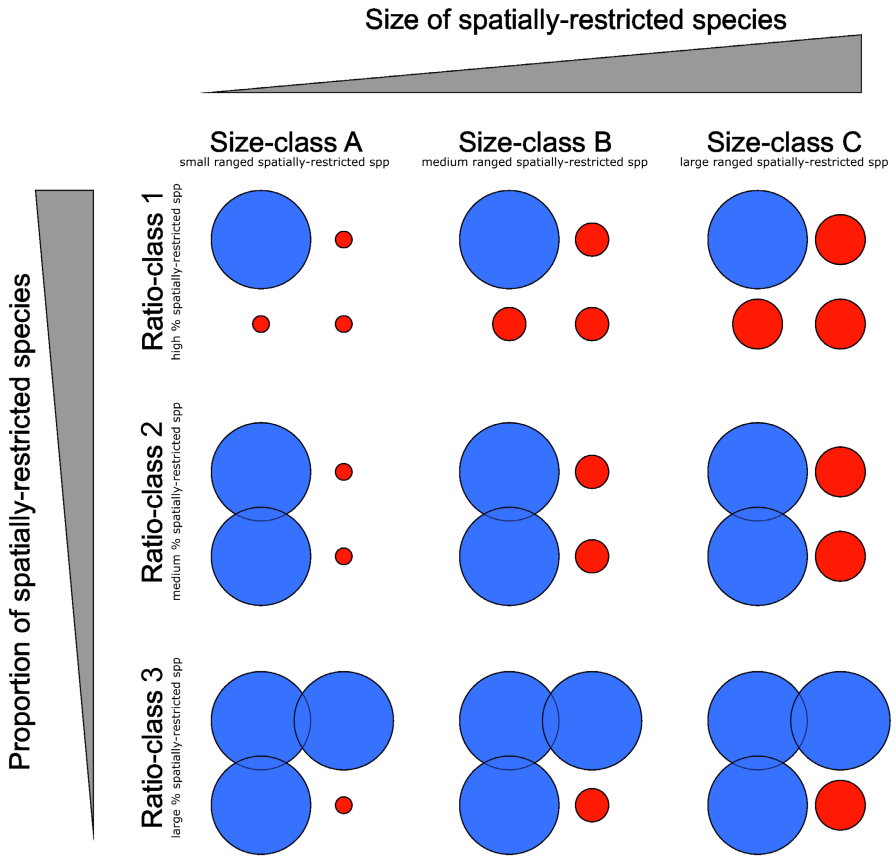

FIGURE 2 Schematic representation of the two axes of variation in simulation scenarios: the proportion of spatially restricted species (ratio-classes 1–3) and the range size of spatially restricted species (size-classes A-C)

the total area it occupies with the *area* function of the package "raster" (Hijmans, 2021).

To obtain a presence/absence matrix for each subset, we constructed a 1°x1° cell grid over South America using the *spsample* function of the package "sp" to define the cells centroids and the function *SpatialPixelsDataFrame* of the same package to obtain the final grid. Then, we computed the species present in each cell with the *gIntersects* function. This function does not work with spatial pixels, so we converted the grid into spatial polygons with the function *Grid2Polygons* of the package "inlmisc" (Fisher, 2020). The 1°×1° cells with less than five species were excluded from further analyses. Presence/absence tables were used to compute independent distance-decay curves for each quartile of range sizes (Q1, Q2, Q3 and Q4). We used the same procedure as in the simulated data, except for the calculation of spatial distances, which were here computed as the geodesic distance between cell centroids using the *geodist* function of the package "geodist" (Padgham & Sumner, 2020). We finally assessed the best fitting model (power-law, negative exponential or Gompertz) based on the AIC and pseudo-r^2 value, as in the simulation study. To evaluate whether the results are robust to sample size variation, for each quartile dataset (Q1, Q2, Q3 and Q4), we repeated the distance-decay analyses for 100 resamples of 50 sites each.

3 | RESULTS

We used simulated community data to study how the functional form of the distance-decay curve varies with species range sizes. For the smallest range size and the lowest proportion of widespread species (ratio-class 1 and size-class A, hereinafter scenario 1A), the power-law function presented a better fit (Table 1), in a pattern characterized by the rapid decay of initial similarities (results for $n = 50$ and $p = 1$ are shown in Figure 3). An increase in range size and/or the proportion of widespread species (scenarios 1B, 2A and 2B) resulted in biological similarity still decaying from the shortest distances, but with a less steep shape. In these scenarios, the negative exponential function better fitted the data. For the largest range sizes and the highest proportion of widespread species (all scenarios involving either ratio-class 3 or size-class C), the similarity remained constant at short or intermediate distances, approaching a sigmoidal shape. In these scenarios, the Gompertz function was the one that presented a better fit (Figure 3, Table 1). Remarkably, when negative exponential or power-law functions fitted the data best, the performance of the Gompertz function was still relatively good (i.e. with pseudo-r^2 values close to the best fitting model). Sample size and species detection probability had small effects on the relationship between species range size and the best fitting model of the distance-decay curve. Only with a very low sample size ($n = 10$) and/or very low detection probability ($p = 0.25$), the best fitting model may be different to the one found with larger sample sizes and detection probabilities (see Tables S1–S4). Importantly, inconsistencies in the identification of the best functional form only occurred when the fit of distance-decay models was very low (i.e. pseudo-$r^2 < 0.1$, Table S4).

Distance-decay patterns in South American terrestrial mammals showed similar shifts in the shape of the distance-decay relationship across the range size classes (Q1-Q4). The negative exponential was the best fitting model for the datasets including the species with smaller range sizes (Q1 and Q2), while the Gompertz function was the best fitting model for the datasets including the species with larger range sizes (Q3 and Q4) (Figure 4, Table 2). Similar results were found when the sample size was smaller, as in the analyses of 100 random samples of 50 sites in each dataset. The negative exponential was the best fitting model in 89 and 93 of the 100 samples taken for Q1 and Q2, respectively, while the Gompertz function was the

TABLE 1 Model comparison, based on AIC values, of the power-law, negative exponential and Gompertz functions in distance-decay simulations of different frequency distribution of species range size, from a higher proportion of spatially restricted species (ratio-class 1) to a smaller proportion (ratio-class 3); and different range size of spatially restricted species, from smaller ranges of spatially restricted species (size-class A) to larger ranges of spatially restricted species (size-class C). Best fitting models are shown in bold

		Size-class A small ranged spatially restricted spp		Size-class B medium ranged spatially restricted spp		Size-class C large ranged spatially restricted spp	
		Pseudo-r^2	AIC	Pseudo-r^2	AIC	Pseudo-r^2	AIC
Ratio-class 1 high % spatially restricted spp	Power-law	**0.67**	**-2077**	0.65	−1339	0.54	−161
	Negative exponential	0.66	−2040	**0.88**	**−2667**	0.87	−1697
	Gompertz	0.62	−1912	0.86	−2466	**0.94**	**−2747**
Ratio-class 2 medium % spatially restricted spp	Power-law	0.67	−2185	0.72	−1862	0.56	−401
	Negative exponential	**0.76**	**−2547**	**0.89**	**−2959**	0.88	−2020
	Gompertz	0.74	−2473	0.85	−2598	**0.95**	**−3029**
Ratio-class 3 low % spatially restricted spp	Power-law	0.52	−2218	0.57	−2328	0.59	−2016
	Negative exponential	0.78	−3160	0.82	−3384	0.86	−3318
	Gompertz	**0.86**	**−3703**	**0.87**	**−3788**	**0.90**	**−3774**

Note: Results are here shown for simulations of 50 sampling sites ($n = 50$) and perfect detection probability of species ($p = 1$). See Appendix S3 for results with different sampling sizes and detection probabilities.

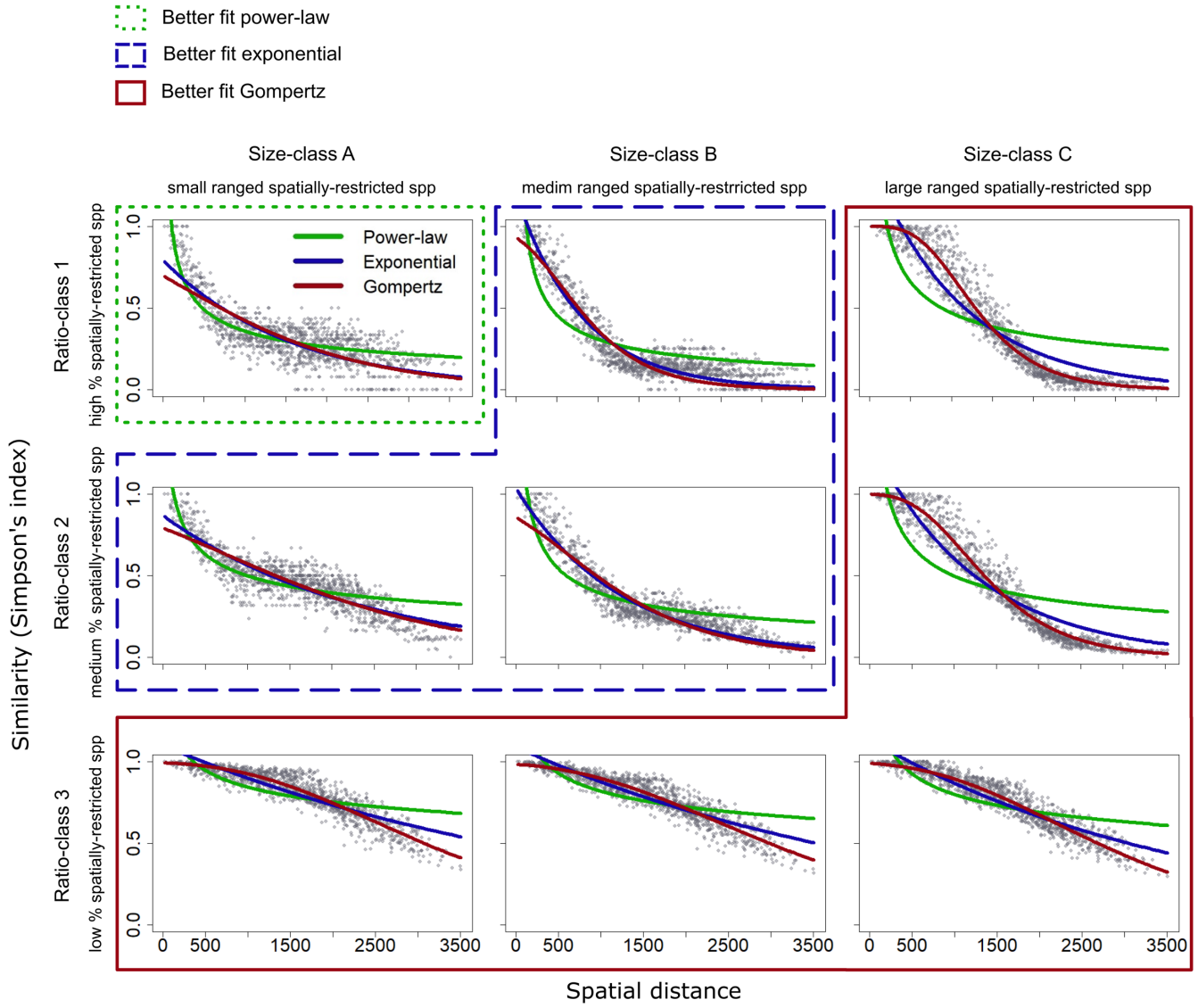

FIGURE 3 Distance-decay models of simulated data under different range size scenarios. Simulated scenarios differ in the proportion of spatially restricted species (ratio-classes 1 to 3) and in the average range size of the smallest size class (size-classes A to C). The adjustment of three different functions is shown: negative exponential, power-law and Gompertz. The model with the best fit for each scenario is also indicated

best fitting model in 76 and 68 of the 100 samples taken for Q3 and Q4, respectively.

4 | DISCUSSION

Our results show that a key biogeographical attribute, species range size, drives the functional form of distance-decay patterns. More importantly, when range sizes are large compared with the study extent, distance-decay can take a sigmoidal form that cannot be accurately captured by the most frequently used models: the negative exponential and the power-law. This relationship between the functional form of distance-decay models and the species range size is observed both in simulated and empirical data. The simulated data show that when species ranges are comparatively small, even biological communities at close distance have different species, leading to a rapid decay of biological similarity from the shortest distances in the form of a power-law relationship. When species ranges are comparatively larger, the initial decay is still present but the decay in similarity is not so steep, being constant and proportional across distances, with the negative exponential being the model that better fits the data. With even larger species ranges, no decay occurs at the shortest distances, with community similarity remaining high and almost constant at short and intermediate distances (i.e. forming an initial plateau of high similarity). This sigmoidal relationship is observed when the distribution range of most species is larger than the spatial distances separating the closest sampling sites. In this scenario, the Gompertz function outperforms the negative exponential and power-law models due to its ability to adapt to this plateau of constant similarity. More

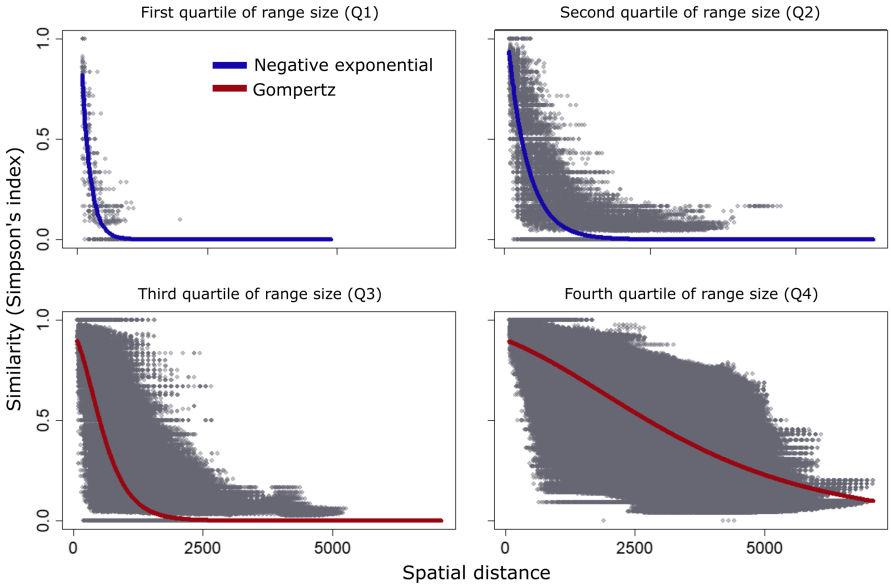

FIGURE 4 Distance-decay models for the four range size groups (quartiles 1 to 4, Q1–Q4) of South American mammals. Note the shift in the shape of the distance-decay relationship from the smallest range size subsets, best fitted by the negative exponential function (Q1–Q2), to the largest size subsets, best fitted by the Gompertz function (Q3-Q4)

TABLE 2 Pseudo-r^2 and AIC of the power-law, negative exponential and Gompertz models of the distance-decay pattern of South American terrestrial mammals. Best fitting models are shown in bold

	Power-law		Negative exponential		Gompertz	
	Pseudo-r^2	AIC	Pseudo-r^2	AIC	Pseudo-r^2	AIC
First quartile of range size (Q1)	0.77	−3775	**0.80**	**−3995**	0.79	−3971
Second quartile of range size (Q2)	0.65	−84451	**0.71**	**−94365**	0.70	−93148
Third quartile of range size (Q3)	0.56	−1389354	0.71	−1792540	**0.71**	**−1801573**
Fourth quartile of range size (Q4)	0.41	−560855	0.52	−807862	**0.53**	**−822159**

Note: Species have been classified into quartiles (Q1, Q2, Q3 and Q4) according to their range size and distance-decay models have been fit for each subset.

importantly, even when species ranges are small and no initial plateau exists, the Gompertz function performs relatively well in all scenarios, showing a performance (in terms of pseudo-r^2) close to the model with the best fit. The results obtained from simulated data were in agreement with those based on an empirical dataset, the distribution data of South American mammals. The negative exponential models showed a better fit of distance-decay patterns in species with smaller ranges (Q1 and Q2), while the Gompertz function was the best fitting model for more widespread species (Q3 and Q4).

Our results reveal that the size of the species ranges (relative to the distances between sampling sites) plays an important role in shaping distance-decay patterns. This inference seems robust to variations in sample size and detection probability. While the most widely used functions in distance-decay analyses (i.e. negative exponential and power-law) work well when species have relatively small ranges, their performance is worse when the distance-decay relationship takes a sigmoidal form associated with the existence of species with widespread distributions. On the contrary, the Gompertz function can accommodate such sigmoidal relationship. More importantly, as a generalization of the negative exponential function, the Gompertz is a versatile function that performs relatively well in all simulation scenarios, independently of the species range size. This is particularly relevant when the goal is to analyse the variation in distance-decay parameters across multiple taxa or biological systems (as in Baselga & Gómez-Rodríguez, 2021; Gómez-Rodríguez & Baselga, 2018; Soininen et al., 2007). In this type of studies, the shape of distance-decay might differ across taxa or systems, so having a general function that performs well under multiple scenarios, as the Gompertz function does, is of crucial importance.

The Gompertz function informs about two important aspects of diversity patterns: species turnover at the shortest distances (position parameter) and the rate of change in community composition (slope). Contrary to other distance-decay models, in which the intercept is a key parameter that informs about similarity at short distances (Morlon et al., 2008; Qian & Ricklefs, 2012; Soininen & Hillebrand, 2007), in the Gompertz model both the extent of the initial plateau and the intercept mathematically depend on the position parameter (b, see Appendix S1). The higher the value of the position parameter, the longer the distance at which the initial similarity remains constant before it starts decaying. Thus, the position parameter of this sigmoidal distance-decay pattern informs about the existence and magnitude of turnover at short distances. Moreover, the ability of the Gompertz function to fit the initial

plateau of constant similarity, if it exists, has also important implications in the estimation of the rate at which similarity decays with distance (i.e. the model's slope). It must be highlighted that the slope in a Gompertz model is estimated only over the spatial distances at which similarity actually decays with distance, because the data points in the initial plateau do not bias the estimation of the slope. On the contrary, in convex functions such as the exponential and power-law models, the complete range of spatial distance has an influence on the slope. In other words, the existence of an initial plateau would affect the estimation of the slope, biasing the estimation of the rate at which similarity decays with distance. Thus, the Gompertz model informs about similarity at short distances (i.e. the intercept); how far the initial similarity is maintained, and hence if species turnover occurs at short-intermediate distances (i.e. position parameter); and the rate of similarity decay with the increase in spatial separation among sites (i.e. slope). Additionally, the Gompertz function is bounded between 0 and 1 (see Appendix S1), and thus is in accordance with the bounds of biological similarities (also 0 and 1), contrary to the negative exponential and power-law functions, which can take values higher than one at short distances, a result lacking biological meaning.

Understanding the link between species range size and how community similarity decreases with spatial distance is relevant for conservation biogeography. Biotic homogenization, that is, "the replacement of local biotas with non-indigenous species, usually introduced by humans" (McKinney & Lockwood, 1999), is one of the major threats for biodiversity (Baiser et al., 2012; Olden et al., 2004; Yang et al., 2021). Biotic homogenization is usually linked to human activities that lead to range expansions of invasive species and range contraction of specialist and endemic species (Clavel et al., 2011; Olden & Poff, 2003). Our results on the relationship between the shape of distance-decay patterns and range size are relevant in the context of biotic homogenization in two ways. First, from a theoretical standpoint, understanding the links between species range size and distance-decay patterns is crucial, because biotic homogenization (i.e. the increase in spatial community similarity over time) is the result of range expansion of some generalist species. Second, from a practical standpoint, accurately measuring the shape of distance-decay patterns and assessing changes in their shapes (from convex to sigmoid functions) can help detecting processes of biotic homogenization and allow quantifying its strength.

In conclusion, species range size is here revealed as a key biogeographical attribute that shapes distance-decay patterns. Previous studies had evidenced the relationship between distance-decay patterns and species biological attributes (Gómez-Rodríguez & Baselga, 2018; Soininen et al., 2017) or the spatial scale of the study (Nekola & McGill, 2014). Our results show that species range size is also a crucial biogeographical driver of the functional form of the distance-decay relationship. From the smallest range sizes to the largest ones, the shape of the distance-decay curve varies from a power-law, negative exponential to a sigmoidal form, which can be accurately fitted with a Gompertz function. Importantly, the Gompertz function provides a general good fit in all situations and, therefore, can be considered a general model to study distance-decay patterns and the best option to model, study and compare distance-decay patterns across different taxa or biological systems.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The code for data simulation is available as supplementary material (Appendix S2), and a Gompertz function fitting method is to be implemented in the R package *betapart* (Baselga & Orme, 2012). All data analysed during the current study are already available in public repositories (https://www.iucnredlist.org). No new data are used in this paper. Presence/absence tables of the Q1-Q4 data subsets with the respective coordinates are available as supplementary material (Data S1–S4).

PEER REVIEW

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BIOSKETCH

The Biogeography Lab (RM-D, SM-S, CG-R and AB, at BiBiCI, University of Santiago de Compostela) focuses on assessing macroecological patterns to better understand the processes driving biodiversity.

Author contributions: All authors conceived the ideas. R.M.-D. designed the simulations and wrote the code. R.M.-D, R.M.C. and A.B. analysed the data. R.M.-D. led the writing of the manuscript. All authors revised and critically contributed to the drafts and gave final approval for publication.

SUPPORTING INFORMATION

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