LETTER

Species are not most abundant in the centre of their geographic range or climatic niche

Tad Dallas,[1,2]* (iD)
Robin R. Decker[1,2] and
Alan Hastings[1,2]

[1]*Center for Population Biology University of California Davis CA 95616, USA,* [2]*Department of Environmental Science and Policy University of California Davis, CA 95616, USA,*

Correspondence: E-mail: tdallas@ucdavis.edu

Abstract
The pervasive idea that species should be most abundant in the centre of their geographic range or centre of their climatic niche is a key assumption in many existing ecological hypotheses and has been declared a general macroecological rule. However, empirical support for decreasing population abundance with increasing distance from geographic range or climatic niche centre (*distance–abundance* relationships) remains fairly weak. We examine over 1400 bird, mammal, fish and tree species to provide a thorough test of *distance–abundance* relationships, and their associations with species traits and phylogenetic relationships. We failed to detect consistent *distance–abundance* relationships, and found no association between *distance–abundance* slope and species traits or phylogenetic relatedness. Together, our analyses suggest that *distance–abundance* relationships may be rare, difficult to detect, or are an oversimplification of the complex biogeographical forces that determine species spatial abundance patterns.

Keywords
Abundant-centre hypothesis, climatic niche, eBird, Forest Inventory and Analysis, geographic range, macroecology.

INTRODUCTION

A shared common goal of macroecology, biogeography and population ecology is to understand the distribution of species abundances across geographic space (Gaston & Blackburn 2003; Vandermeer & Goldberg 2013). One such species abundance pattern is the tendency for species to be most abundant in the centre of their geographic ranges (Hengeveld & Haeck 1982; Brown 1984; Holt *et al.* 1997; McGill & Collins 2003). This phenomenon, sometimes referred to as the *abundant centre hypothesis* (Sagarin *et al.* 2006), is one of many *distribution–abundance* relationships in macroecology, which attempt to relate species abundance patterns to geographic extent (e.g. occupancy, geographic range area, etc.). Under the umbrella of *distribution–abundance* relationships, the way both *distribution* and *abundance* are quantified can have a large influence on the resulting relationship. For instance, quantifying *distribution* as the number of occupied spatial grid cells typically yields positive relationships with abundance (abundance–occupancy relationships; Gaston & Blackburn 2003), but variation in this relationship exists when measured at different spatial scales, or if *distribution* is defined as geographic extent (Blackburn *et al.* 2006). *Distance–abundance* relationships are a subset of *distribution–abundance* relationships that relate the distance from the centre of a species geographic range to local population sizes, which tests the hypothesis that species are most abundant at their range centres. Further, the *distance–abundance* relationship is a common assumption of theoretical modelling efforts (Gaston & Blackburn 2003; Sagarin *et al.* 2006), has been used to inform conservation and management decisions (Borregaard & Rahbek 2010), and has served as the basis for many biogeographic and macroecological hypotheses (Sagarin *et al.* 2006).

However, empirical support for *distance–abundance* relationships is mixed (Sagarin & Gaines 2002; Pironon *et al.* 2016),

with no clear causal basis (Borregaard & Rahbek 2010). Studies on trees (Murphy *et al.* 2006; Ren *et al.* 2013) and coastal plants (Samis & Eckert 2007) failed to detect *distance–abundance* relationships, while evidence has been found for a small number of animal species (Martínez-Meyer *et al.* 2013). The variable support for *distance–abundance* relationships may relate to how distance is quantified, the spatial scale of studies, or ecological and biogeographic differences in species groups through conserved traits related to population growth and dispersal (Flügge *et al.* 2012). Logistical constraints have typically restricted researchers to examine *distance–abundance* relationships at smaller spatial scales and for a limited number of populations (Sagarin & Gaines 2002), which may not fully capture abundance patterns across species' geographic ranges. Understanding associations between species-level covariates may provide much needed insight into *when* a *distance–abundance* relationship is likely to be observed. For instance, species body size may be associated with the slope of the *distance–abundance* relationship, as macroecological patterns have suggested that body size is closely related to metabolic rate (Nagy 2005), range size (Diniz-Filho *et al.* 2005), and is central to many macroecological studies (see Smith & Lyons 2013).

Another confounding influence on the generality of *distance–abundance* relationships is the considerable variation in how distance is quantified, suggesting the need for an integrative and unified approach to examinations of *distance–abundance* relationships (McGill & Collins 2003). Distance may be measured from geographic range edge or centre (see table 2 of Sagarin & Gaines 2002), where range centre may be quantified in a number of ways (Borregaard & Rahbek 2010). Recently, Martínez-Meyer *et al.* (2013) demonstrated that the lack of a relationship between local population abundance and geographic distance from range centres of eleven animal species

belied a clear relationship between species abundance and environmental distance from species niche centres. The use of environmental distance provides a link between species niche requirements and corresponding geographic distribution (Pulliam 2000), and potentially explains the limited support for *distance–abundance* relationships to date. Further, this tests a slightly different assumption that is central to niche theory; species should be most abundant under optimal niche conditions (Weber *et al.* 2016). Together, these issues may underlie the limited support for *distance–abundance* relationships, and highlight a clear knowledge gap in a fundamental area of ecological research (Sagarin *et al.* 2006).

A final note on the ambiguity of *distance–abundance* relationships relates to the quantification of abundance itself. The inherent difficulty in measuring population abundance has resulted in the use of standardised counts of individuals in place of overall abundance. That is, although *abundance* is the commonly applied term, *density* is a perhaps more sensible term, and, in most cases, the only possible measure. In keeping with previous terminology, we use the term *abundance*, but it is important to note that perhaps *density* would be more accurate.

To address the degree of empirical support for *distance–abundance* relationships, we proposed a simple test: if species are most abundant at their range or niche centres, then a negative correlation should exist between species abundance and distance from either geographic or niche centre. To this end, we used a number of extensive datasets on natural populations to examine *distance–abundance* relationships, and how they can be influenced by species-level traits and evolutionary relationships. First, we investigated the relationship between distance – measured as either geographic distance or climatic niche distance – and species abundance for a diverse set of mammals, birds, fishes, and trees distributed across a broad latitudinal gradient through the Americas. When data were available, species *distance–abundance* correlations were related to species body size and range size in order to determine the presence of a species-level trait basis for *distance–abundance* relationships. Lastly, we related *distance–abundance* correlation coefficients to measures of phylogenetic distance to determine associations between the strength of *distance–abundance* relationships and species evolutionary history. We found very little support for *distance–abundance* relationships when distance was defined as either geographic distance from range centre or environmental distance from niche centre. Further, we failed to detect associations between the *distance–abundance* relationship slope and species body size, geographic range area, climatic niche area, or phylogenetic relatedness. Together, our findings suggest that *distance–abundance* relationships may be rare, difficult to detect, or are an oversimplification of the complex biogeographical forces that determine species spatial abundance patterns.

METHODS

Data sources

To examine the relationship between species abundance and the distance from species geographic range centre or climatic niche centre, we used estimates from databases based on published work (Thibault *et al.* 2011), aggregated data from large-scale citizen science efforts (Sullivan *et al.* 2009), and government-sponsored repeated sampling efforts (Woudenberg *et al.* 2010). As we noted above, these estimates are, strickly speaking, estimates of density, not abundance. Data spanned a broad latitudinal gradient (see Fig. S8) and a diverse set of taxa, including mammals (MCDB; Thibault *et al.* 2011), birds (eBird database; Sullivan *et al.* 2009), tree seedlings (USDA Forest Inventory and Analysis database; FIA; Woudenberg *et al.* 2010), and fish species (EPA Environmental Monitoring and Assessment Program – EPA-EMAP; https://www.epa.gov/emap/ and a subset of the USGS National Water Quality Assessment – NAWQA; Knouft & Anthony 2016a; https://water.usgs.gov/nawqa).

The total number of species examined represents the largest investigation of *distance–abundance* relationships to date, including a total of bird ($n = 1109$), fish ($n = 63$), mammal ($n = 81$), and tree ($n = 166$) species for which enough data were available to calculate *distance–abundance* correlations. Further, the number of observations tended to be large, including over a million total observations among the data sources (birds = 593 288; trees = 389 850; fishes = 9375 and mammals = 20 412).

We limited the scope of our analyses to species occurring in the Americas with more than 10 sampled populations, resulting in a data set consisting of over 118 000 sampled and geo-referenced localities (see Fig. S8 for sampling locations). We discuss the sensitivity of our results to this threshold in Supporting Information. Also, the spatial extent of the eBird data was constrained to the Americas, while the other data sources occupied either the Americas (Mammal Community Database) or were restricted to the United States (tree and fish data). For datasets restricted to the United States (USDA-FIA tree seedlings and fish data from the EPA-EMAP and NAWQA data), we discarded species whose northernmost or southernmost abundance was greater than the mean abundance observed over all sampled populations for that species. This was an effort to remove species whose geographic range exceeds the sampled range. Sampled populations on distant islands were removed, as these potentially dispersal-limited populations may strongly influence *distance–abundance* relationships. Lastly, migratory status might influence species range estimation in the eBird data. We examine this further in Supporting Information, demonstrating our results are robust to the inclusion/exclusion of migratory species.

Species abundance estimation

Species abundance was estimated from sampling data; either repeated samples of variable (MCDB) or standardised (USDA-FIA) plot sizes, rarefied estimates of abundance based on repeated sampling (NAWQA), or acoustic and visual surveys (eBird). For these analyses, species abundance was estimated as the number of individuals within a sampling area, standardised by either sampling area or sampling intensity. This approach results in standardised species counts most akin to a measure of species density, as abundance may not be sensibly measured at the scale we examine here. There is

also little assurance that sampling was equal across study sites or across species, as this is an impossibly high bar given the spatial scale examined. However, we accounted for sampling biases in a number of ways. First, some data sources were based on rigorous national efforts, which used standardised plot sizes (USDA FIA data), which means that abundance estimates are comparable across space. That is, even if estimates do not capture true abundance, abundance estimates will be proportional to true abundance as a function of sampling design. Other data sources contained sufficient detail to allow for rarefaction (NAWQA; Knouft & Anthony 2016a), a form of statistical standardisation of sampling effort. For data based on published literature (MCDB data), raw species abundance was standardised by the number of trap nights, a commonly used measure of sampling effort (Richards & Schnute 1986). Lastly, abundance estimates from citizen science efforts (eBird) were standardised by the duration of time spent sampling, while data for which duration was not available was discarded. While other factors (e.g. time of day, length of transect, etc.) may also influence observations, these variables were less often recorded by users.

Distance calculation

We examined the *distance–abundance* relationship by measuring the distance of all sampled populations from a central point (Fig. 1a), which was represented either as the geographic centre of the species range or the species climatic niche centre. The geographic range centre was determined by finding the centre point of a convex hull around observed populations. Meanwhile, the climatic niche centre was determined by first translating the multivariate climate space into a two-dimensional space

comparable to geographic space. To do this, we calculated the first two principal components (PCA) of the set of 56 BioClim/ WorldClim variables (Hijmans *et al.* 2005), translating geographic points into climatic niche space, and finding the centre of the convex hull of points in niche space (Kriticos *et al.* 2014; T. Dallas and J.M. Drake, unpublished). WorldClim variables ($n = 36$) contain monthly information on minimum and maximum temperature and precipitation, while the BioClim variables ($n = 19$) are derived quantities (e.g. temperature seasonality, mean annual precipitation). Together, these climate data (plus altitude) represent the best available data for defining species niches and modelling species geographic distributions (Barbet-Massin & Jetz 2014). While species likely vary in their sensitivities to these variables, previous work has demonstrated high predictive accuracy from models trained on these climatic covariates (Barbet-Massin & Jetz 2014).

The first two PCA axes explained 77% of the variation in the global climate (T. Dallas and J.M. Drake, unpublished). We make the assumption that favourable climatic conditions will result in larger population sizes, as we don't have detailed information on species growth responses to various environmental variables. This is a common assumption of niche modeling efforts, and evidence suggests that climatic suitability does capture aspects of local abundance (VanDerWal *et al.* 2009). Geographic distance from species range centres was calculated as Haversine distance, while distance in species niche space was calculated, using Euclidean distance between points in niche space created by the two PCA niche axes. We used Pearson's correlations to quantify the relationship between distance and abundance (Fig. 1a,b), and explore the possibility of non-linear relationships, using Spearman's rank correlation coefficients in Supporting Information.
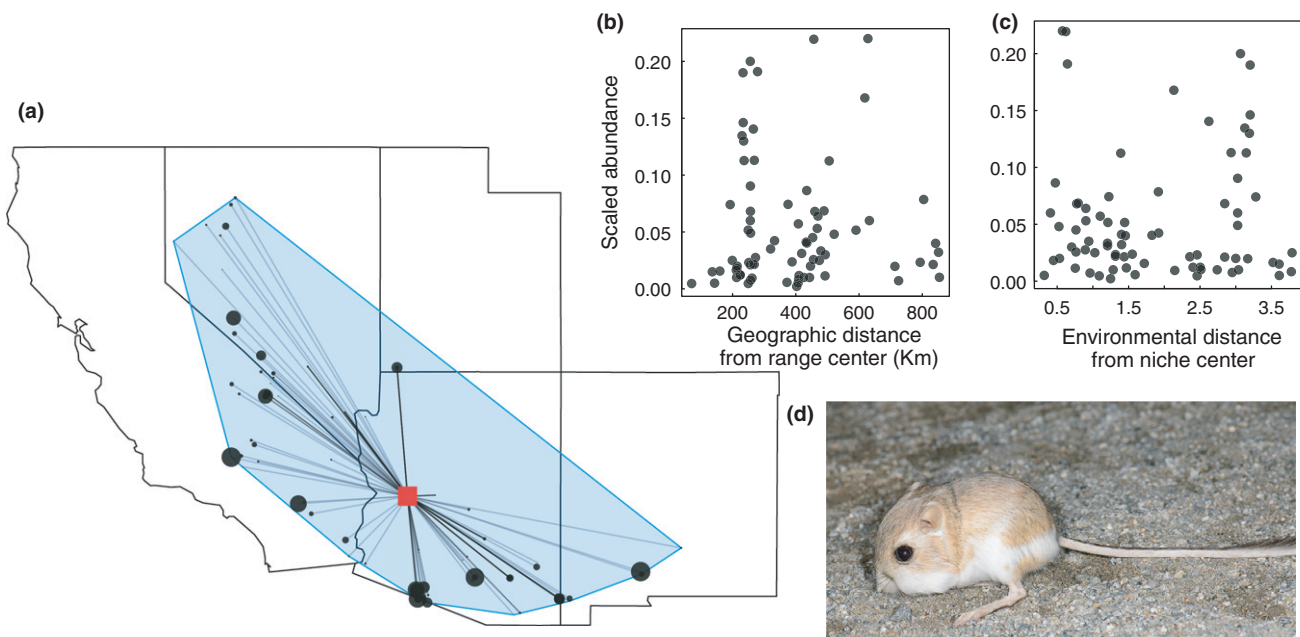

Figure 1 An example of the spatial distribution of abundance for *Dipodomys merriami*, whose range is outlined by a blue convex polygon, and whose centre is denoted by a red square (panel a). Lines connecting this centroid to each population – black points with population size proportional to point size – provide a means to measure geographic distance. The relationship between scaled abundance of *D. merriami* and geographic (b) and environmental (c) distance provide an instance of the lack of a clear *distance–abundance* relationship. Photograph of *D. merriami* (d) is by Marshal Hedin.

Range area, niche area, body size and phylogeny

The slope of the *distance–abundance* relationship could be associated with species traits or with overall geographic range or climatic niche area. This could, in part, explain the variable support for *distance–abundance* relationships. To explore variation in *distance–abundance* relationships as a function of species ecology or distribution, we examined relationships between the slope of the *distance–abundance* relationship and species geographic range, climatic niche area, body size and phylogenetic relatedness.

Species geographic range size and climatic niche area were determined by calculating the area of the minimum convex polygon that encompassed all sampling locations for a given species either in space (i.e. geographic range size) or in the phase space of the first two climatic niche axes (i.e. niche area). Species body size estimates were obtained in terms of mass for bird (Myhrvold *et al.* 2015) and mammal (Jones *et al.* 2009) species, length for fish species (Froese & Pauly 2000), and height for tree species (Kattge *et al.* 2011). Species body size and range size, either geographic range area or niche area, were related to the slope of the *distance–abundance* relationship obtained from a best fit linear model relating species abundance to either geographic or niche distance. Some species were not sampled in enough unique geographic locations ($n < 4$) or environments to estimate geographic or niche area accurately, resulting in slightly reduced numbers of species that could be used to examine relationships between slope of the *distance–abundance* relationship and species traits. This number was also reduced for some species where estimates of body size were unavailable (see Table 1). We explore the sensitivity of *distance–abundance* relationships to the number of occurrence points in Supporting Information. For the set of species for which data were available (*n* column of Table 1), we fit linear models to each taxa (mammal, bird, fish and tree species) including species body mass, estimated geographic range size and climatic niche area as covariates.

Phylogenetic data were obtained from the mammal (Bininda-Emonds *et al.* 2007) and bird (Myhrvold *et al.* 2015)

phylogenetic supertrees. Branch lengths were not included in the avian supertree, but were calculated using the well-established *Grafen* method (Grafen 1989). Taxonomic dissimilarity was used instead of phylogenetic distance for trees and fishes. We used Moran's *I* to determine if the slope of the *distance–abundance* relationship contained a phylogenetic (or taxonomic) signal. Taxonomic data was accessed using *taxise* (Chamberlain & Szöcs 2013; Chamberlain *et al.* 2016), and *ape* was used for the calculation of Moran's *I* statistic (Paradis *et al.* 2004). Some species in the data were not found in the supertree or through *taxise*, constraining our analyses to 713 bird, 48 fish, 39 mammal and 152 tree species.

RESULTS

Distance–abundance relationships

Distance–abundance relationships were rarely observed when measuring distance as geographic distance from a species range centre (Fig. 2a) and environmental distance from a species niche centre (Fig. 2b). The mean correlation coefficients between geographic distance and species abundance were near zero for birds ($\bar{\rho}_{bird} = -0.015$), fishes ($\bar{\rho}_{fish} = -0.041$), mammals ($\bar{\rho}_{mammal} = 0.002$), and trees ($\bar{\rho}_{tree} = 0.015$). Significant correlations, both positive and negative, were detected for some bird ($n_+ = 151$; $n_- = 123$), fish ($n_+ = 1$; $n_- = 3$), mammal ($n_+ = 2$; $n_- = 2$), and tree ($n_+ = 35$; $n_- = 8$) species. However, these significant correlations tended to occur for species with limited sampling (Fig. S6). Further, relative to the number of species examined the percent of significant *distance–abundance* relationships in bird ($p_+ = 0.12$; $p_- = 0.10$), fish ($p_+ = 0.02$; $p_- = 0.06$), mammal ($p_+ = 0.04$; $p_- = 0.04$), and tree ($p_+ = 0.12$; $p_- = 0.03$) species was quite low, and positive relationships – indicating higher abundance at range edges – were just as common as negative relationships. These findings were robust to using Spearman's correlation coefficients to capture potentially nonlinear relationships between distance and abundance (Fig. S4) and when defining species range and climatic niche centroids (and subsequent distance

Table 1 Species body size, geographic range area (log km^2 + 1), and climatic niche area (log area + 1) explained very little of the variation in *distance–abundance* slope, treating distance either as geographic distance from species range centre (models identified by subscript *G*) or environmental distance from species climatic niche centre (identified by subscript *E*). Due to limited data availability, species body size was estimated as mass (g) for mammals and birds, length (cm) for fish and height (m) for trees. The number of species for which data were available is given by *n*. β are model coefficients (with standard errors *SE*), and *t* and *P* are the *t*-statistic and *P*-value associated with model coefficients

| Taxa	Variable	*n*	β_G	SE_G	*t*	*P*	R^2	β_E	SE_E	*t*	*P*	R^2
Birds	Body mass	1047	−0.001	0.003	−0.397	0.69	0.03	−0.004	0.003	−1.058	0.29	0.002
	Range size	1137	0.024	0.005	4.680	< 0.001		−0.002	0.010	−0.205	0.84	
	Niche area	1137	−0.007	0.010	−0.672	0.50		0.006	0.005	1.174	0.24	
Trees	Height	48	−0.006	0.014	−0.410	0.68	0.03	−0.004	0.014	−0.299	0.77	0.13
	Range size	48	0.011	0.006	1.810	0.07		0.003	0.018	0.174	0.86	
	Niche area	48	−0.006	0.018	−0.338	0.74		−0.008	0.006	−1.332	0.18	
Mammals	Body mass	39	0.019	0.054	0.345	0.73	0.04	−0.041	0.045	−0.915	0.37	0.06
	Range size	42	−0.070	0.062	−1.136	0.26		−0.098	0.082	−1.207	0.24	
	Niche area	42	0.078	0.098	0.795	0.43		0.051	0.051	0.991	0.33	
Fishes	Length	209	−0.016	0.031	−0.529	0.60	0.02	0.040	0.034	1.174	0.25	0.01
	Range size	294	0.037	0.071	0.522	0.60		0.112	0.140	0.796	0.43	
	Niche area	294	−0.025	0.127	−0.195	0.85		−0.111	0.078	−1.419	0.16	
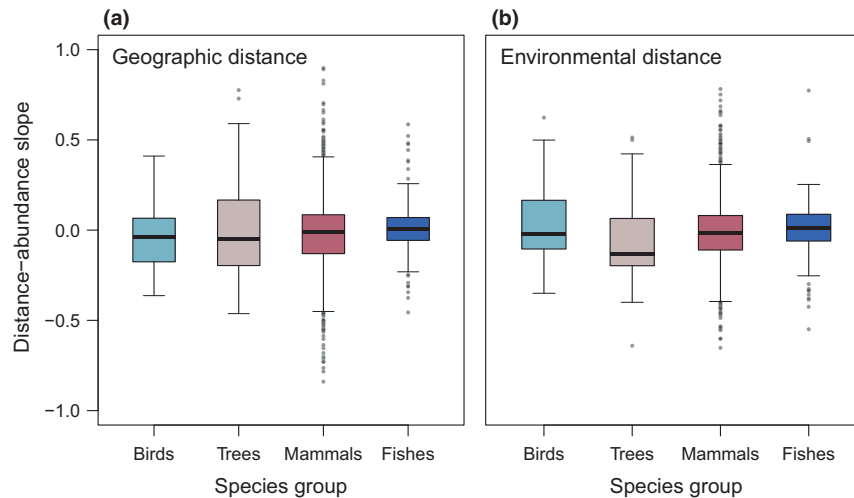
Figure 2 *Distance–abundance* correlations for over 1600 species reveal a lack of support for the hypothesis that populations should have the highest abundance in the (a) centre of their geographic distribution or (b) in the interior of their niche. Distance from the geographic or niche centre was calculated either as spatial distance (a) or Euclidean distance in climatic niche space from species niche centroid (b).

to centroid) based on occurrence data instead of abundance data (Fig. S3). Lastly, we failed to detect consistently strong relationships between geographic distance to species range centroids and environmental distance to species niche centroids (Fig. 3), though these relationships did tend to be positive.

Examining the *distance–abundance* relationship in terms of environmental distance from the niche centroid did not increase the detectability of *distance–abundance* relationships; environmental distance from centroid and species abundance had near zero correlation coefficients for birds ($\bar{\rho}_{bird} = -0.010$), fishes ($\bar{\rho}_{fish} = 0.018$), mammals ($\bar{\rho}_{mammal} = -0.068$), and trees ($\bar{\rho}_{tree} = 0.009$). Similarly when distance was measured as the geographic distance from species range centres, significant correlations, both positive and negative, were detected only rarely for bird ($n_+ = 109$; $n_- = 101$), fish ($n_+ = 2$; $n_- = 1$), mammal ($n_+ = 1$; $n_- = 1$), and tree ($n_+ = 34$; $n_- = 15$) species. As with geographic *distance–abundance* relationships, these numbers represented small portions of the number of species tested, and the percent of significant *distance–abundance* relationships in bird ($p_+ = 0.09$; $p_- = 0.08$), fish ($p_+ = 0.04$; $p_- = 0.02$), mammal ($p_+ = 0.02$; $p_- = 0.02$), and tree ($p_+ = 0.11$; $p_- = 0.05$) species was quite low, and positive relationships – indicating higher abundance at climatic niche edges – were just as common as negative relationships.

Ecological and phylogenetic covariates to distance–abundance slope

Species body size, geographic range area and climatic niche area were unrelated to the slope of the relationship between species population abundance and geographic distance to range centre or environmental distance from niche centre (Table 1). Further, we failed to detect evidence for a phylogenetic signal in the *distance–abundance* slope for any species group, regardless of whether distance was defined in terms of geographic distance from species range centroid or niche distance from species niche centre (Table 2).
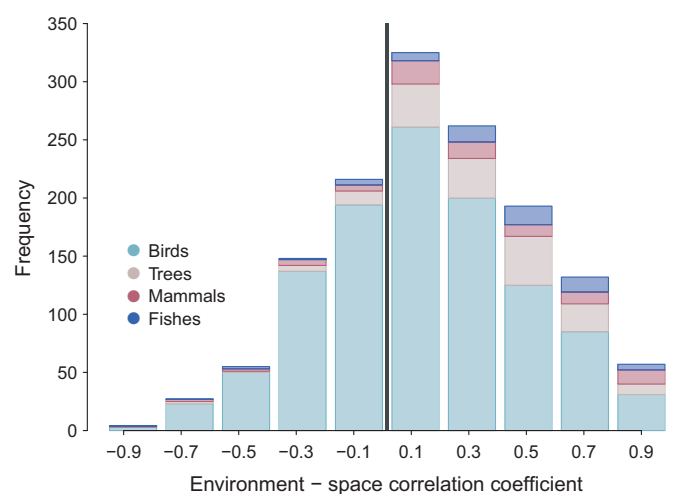

Figure 3 Pearson's correlation coefficients between spatial and environmental distance from geographic or niche centres reveals that geographic distance and niche distance are often only weakly related, and can even be negatively related, corresponding to a situation where nearby environmental conditions are less similar than those in geographically distant areas.

DISCUSSION

The assumption that species abundance – or perhaps more properly termed *density* – is highest at the geographic range or climatic niche centre is a central assumption of many hypotheses in macroecology (Brown 1984; Gaston & Blackburn 2003) and population ecology (Pulliam 2000), with qualitative evidence for the pattern dating back to the formation of ecology as a discipline (Gause 1930; Whittaker 1952). However, empirical support remains limited, for a number of factors including variation in environmental conditions, incomplete sampling of species ranges, or interactions with competitors and parasites (Sagarin *et al.* 2006; Borregaard &

Table 2 We failed to detect a phylogenetic signal in the relationship between spatial distance from either the geographic (*G*) or niche (*E*) centroid for any species group examined. The analysis uses a permutation approach of Moran's *I* values to test for the presence of a phylogenetic signal in *distance–abundance* relationships

Taxa	Obs_G	Exp_G	SD_G	P_G	Obs_E	Exp_E	SD_E	P_E
Birds	0.001	−0.001	0.02	0.80	−0.01	−0.001	0.02	0.72
Trees	−0.003	−0.004	0.002	0.70	−0.004	−0.004	0.002	0.65
Mammals	−0.03	−0.004	0.03	0.48	0.02	−0.004	0.03	0.46
Fishes	−0.02	−0.016	0.01	0.52	−0.02	−0.016	0.01	0.82

Rahbek 2010). We suggested a simple test of the *distance–abundance* relationship; if species are most abundant in the centre of their spatial range, then a negative correlation should exist between species abundance and distance from either geographic or niche centroid. We failed to detect a signal of *distance–abundance* relationships using a dataset consisting of over 118 000 sampled populations across over 1400 species across a wide range of species, including birds, mammals, trees, and fishes. Further, we have provided the first attempt to relate the strength of the *distance–abundance* correlation to species traits, range size and evolutionary history. We failed detect any influence of body size, range size, or evolutionary history on the correlation between species abundance and spatial or environmental distance. Together, our findings suggest that *distance–abundance* relationships may not be as general as previously believed, and that hypotheses and models based upon the assumption that species abundance is highest in the interior of a species geographic range or niche may need to be reconsidered.

Some previous studies have found support for *distance–abundance* relationships (references within Pironon *et al.* 2016; Sagarin & Gaines 2002), and the closely related relationship between mean abundance and species range size (Gaston *et al.* 2000), leading to classification of *distance–abundance* relationships as a general rule in macroecology (Hengeveld & Haeck 1982). However, several recent studies have failed to detect any effect of spatial distance from species range centre or to species niche edges on species local abundance (see meta-analysis by Sagarin & Gaines 2002). More recently, researchers have begun to explore the conditions under which *distance–abundance* relationships should be observed. For instance, several recent studies have recognised that geographic distance may simply be a surrogate for environmental distance, in which niche constraints are responsible for the relationship between distance from a species range centre and abundance (Martínez-Meyer *et al.* 2013; Knouft & Anthony 2016a). However, we failed to detect strong associations between distance and species abundance regardless whether distance was measured as geographic distance or environmental distance. Further, we arrived at different conclusions than Knouft & Anthony (2016a), though we used the same data on freshwater fish abundance (Knouft & Anthony 2016b). This disparity stems from a key difference between our conceptual approaches; Knouft & Anthony (2016a) uses a model selection procedure to examine if principal component axes representing climatic variation can explain local abundance, while we examine the shape of decay relationship between local abundance and geographic or environmental distance. While relating climatic conditions to species abundance is important

to understand patterns of species abundance, the application of regression analyses from niche modelling may not be appropriate to address macroecological *rules* like the *distance–abundance* relationship, as the ability to predict species abundance as a function of climatic covariates does not directly test if species abundance declines from a species range or niche centre.

There are at least two classes of mechanisms that reduce the probability of observing a *distance–abundance* relationship. First, species abundances may not be strongly constrained by the environmental variables measured here. This suggests that unmeasured environmental variation may underlie *distance–abundance* relationships, or that species interactions and community structure may be more important in regulating population abundance than the environment. Second, the spatial distribution of abundance, and subsequent *distance–abundance* relationships, may be limited by dispersal boundaries or unmeasured ecological interactions. For instance, coasts and mountain ranges represent obvious barriers to species spread. Species abundance may be highest at the barrier (Brown *et al.* 1996), with the putative explanation being directional dispersal against a barrier, and an environment capable of sustaining relatively high species abundance. To address this in our analyses, we discarded species with greater than average abundance at sampling limits present in the USDA FIA seedling data and the eBird data (sampling locations in Fig. S8). Though we used the most extensive data available, temporal variation in abundance, changing environmental conditions, and the role of interspecific interactions with competitors and natural enemies (Hastings *et al.* 1997; Frick *et al.* 2010; Robinson *et al.* 2010) may further confound detection of *distance–abundance* relationships. Understanding how interspecific interactions, natural enemies, environmental forces and dispersal barriers influence the existence of *distance–abundance* relationship remains an open question; one, when answered, may provide an underlying basis for the emergence of the macroecological pattern.

Macroecological relationships, such as those examining spatial abundance patterns, are interesting due to their perceived generality (Brown 1984; McGill & Collins 2003; Lennon & Locey 2017). However, the development of macroecological *laws* is confounded when researchers use different measures of abundance or distribution. This confusion may promote the construction of hypotheses which assume these general relationships. Clear definitions of terms used to refer to macroecological variables (e.g. distribution, abundance), the application of mechanistic approaches to the study of macroecological relationships (Eckert *et al.* 2008; Alexander *et al.* 2016), and closer examination of hypotheses assuming the

existence of *distance–abundance* relationships are necessary to determine support for *distance–abundance* relationships, and macroecological relationships in general

AUTHOR CONTRIBUTIONS

TAD, RD and AH developed the protocol. TAD performed the analyses and drafted the manuscript. All authors contributed to manuscript editing.

DATA ACCESSIBLITY

R code is available on figshare at https://doi.org/10.6084/m9.figshare.5023232. Data are available for eBird data (Sullivan *et al.* 2009), EPA-EMAP data (https://www.epa.gov/emap/), NAWQA data (Knouft & Anthony 2016a; https://water.usgs.gov/nawqa), Forest Inventory and Analysis data (Woudenberg *et al.* 2010; https://www.fia.fs.fed.us/), and the mammal community database (Thibault *et al.* 2011). While authors should cite the original data sources, we also provide data used in the analyses and analytic code.

REFERENCES

Alexander, J.M., Diez, J.M., Hart, S.P. & Levine, J.M. (2016). When climate reshuffles competitors: a call for experimental macroecology. *Trends Ecol. Evol.*, 31, 831–841.

Barbet-Massin, M. & Jetz, W. (2014). A 40-year, continent-wide, multispecies assessment of relevant climate predictors for species distribution modelling. *Divers. Distrib.*, 20, 1285–1295.

Bininda-Emonds, O.R., Cardillo, M., Jones, K.E., MacPhee, R.D., Beck, R.M., Grenyer, R. *et al.* (2007). The delayed rise of present-day mammals. *Nature*, 446, 507–512.

Blackburn, T.M., Cassey, P. & Gaston, K.J. (2006). Variations on a theme: sources of heterogeneity in the form of the interspecific relationship between abundance and distribution. *J. Anim. Ecol.*, 75, 1426–1439.

Borregaard, M.K. & Rahbek, C. (2010). Causality of the relationship between geographic distribution and species abundance. *Q. Rev. Biol.*, 85, 3–25.

Brown, J.H. (1984). On the relationship between abundance and distribution of species. *Am. Nat.*, 124, 255–279.

Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996). The geographic range: size, shape, boundaries, and internal structure. *Annu. Rev. Ecol. Syst.*, 27, 597–623.

Chamberlain, S.A. & Szöcs, E. (2013). taxize: taxonomic search and retrieval in R. *F1000Res.*, 2, doi: 10.12688/f1000research.2-191.v2.

Chamberlain, S., Szocs, E., Boettiger, C., Ram, K., Bartomeus, I., Baumgartner, J. *et al.* (2016). taxize: taxonomic information from around the web. R package version 0.7.8.

Diniz-Filho, J.A.F., Carvalho, P., Bini, L.M. & Tôrres, N.M. (2005). Macroecology, geographic range size–body size relationship and minimum viable population analysis for new world carnivora. *Acta Oecologica*, 27, 25–30.

Eckert, C., Samis, K. & Lougheed, S. (2008). Genetic variation across species geographical ranges: the central–marginal hypothesis and beyond. *Mol. Ecol.*, 17, 1170–1188.

Flügge, A.J., Olhede, S.C. & Murrell, D.J. (2012). The memory of spatial patterns: changes in local abundance and aggregation in a tropical forest. *Ecology*, 93, 1540–1549.

Frick, W.F., Pollock, J.F., Hicks, A.C., Langwig, K.E., Reynolds, D.S., Turner, G.G. *et al.* (2010). An emerging disease causes regional population collapse of a common north american bat species. *Science*, 329, 679–682.

Froese, R. & Pauly, D. (2000). *FishBase 2000: Concepts Designs and Data Sources*, vol. 1594. WorldFish, ICLARM, Los Baños, Laguna, Philippines.

Gaston, K.J. & Blackburn, T.M. (2003). Dispersal and the interspecific abundance-occupancy relationship in british birds. *Glob. Ecol. Biogeogr.*, 12, 373–379.

Gaston, K.J., Blackburn, T.M., Greenwood, J.J., Gregory, R.D., Quinn, R.M. & Lawton, J.H. (2000). Abundance–occupancy relationships. *J. Appl. Ecol.*, 37, 39–59.

Gause, G. (1930). Studies on the ecology of the Orthoptera. *Ecology*, 11, 307–325.

Grafen, A. (1989). The phylogenetic regression. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 326, 119–157.

Hastings, A., Harrison, S. & McCann, K. (1997). Unexpected spatial patterns in an insect outbreak match a predator diffusion model. *Proc. R. Soc. Lond. B Biol. Sci.*, 264, 1837–1840.

Hengeveld, R. & Haeck, J. (1982). The distribution of abundance. I. Measurements. *J. Biogeogr.*, 9, 303–316.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.*, 25, 1965–1978.

Holt, R., Lawton, J., Gaston, K. & Blackburn, T. (1997). On the relationship between range size and local abundance: back to basics. *Oikos*, 78, 183–190.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L. *et al.* (2009). Pantheria: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, 90, 2648–2648.

Kattge, J., Diaz, S., Lavorel, S., Prentice, I., Leadley, P., Bönisch, G. *et al.* (2011). TRY–a global database of plant traits. *Glob. Change Biol.*, 17, 2905–2935.

Knouft, J.H. & Anthony, M.M. (2016a). Climate and local abundance in freshwater fishes. *R. Soc. Open Sci.*, 3, 160093.

Knouft, J.H. & Anthony, M.M. (2016b). Data from: climate and local abundance in freshwater fishes. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.1d1t5.

Kriticos, D.J., Jaroˇsik, V. & Ota, N. (2014). Extending the suite of bioclim variables: a proposed registry system and case study using principal components analysis. *Methods Ecol. Evol.*, 5, 956–960.

Lennon, J.T. & Locey, K.J. (2017). Macroecology for microbiology. *Environ. Microbiol. Rep.*, 9, 38–40.

Martínez-Meyer, E., Díaz-Porras, D., Peterson, A.T. & Yáñez-Arenas, C. (2013). Ecological niche structure and rangewide abundance patterns of species. *Biol. Let.*, 9, 20120637.

McGill, B. & Collins, C. (2003). A unified theory for macroecology based on spatial patterns of abundance. *Evol. Ecol. Res.*, 5, 469–492.

Murphy, H.T., VanDerWal, J. & Lovett-Doust, J. (2006). Distribution of abundance across the range in eastern north american trees. *Glob. Ecol. Biogeogr.*, 15, 63–71.

Myhrvold, N.P., Baldridge, E., Chan, B., Sivam, D., Freeman, D.L. & Ernest, S. (2015). An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology*, 96, 3109–3109.

Nagy, K.A. (2005). Field metabolic rate and body size. *J. Exp. Biol.*, 208, 1621–1625.

Paradis, E., Claude, J. & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290.

Pironon, S., Papuga, G., Villellas, J., Angert, A.L., García, M.B. & Thompson, J.D. (2016). Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm. *Biol. Rev.*, doi:10.1111/brv.12313.

Pulliam, H.R. (2000). On the relationship between niche and distribution. *Ecol. Lett.*, 3, 349–361.

Ren, H., Condit, R., Chen, B., Mi, X., Cao, M., Ye, W. *et al.* (2013). Geographical range and local abundance of tree species in china. *PLoS ONE*, 8, e76374.

Richards, L.J. & Schnute, J.T. (1986). An experimental and statistical approach to the question: is cpue an index of abundance? *Can. J. Fish Aquat. Sci.*, 43, 1214–1227.

Robinson, R.A., Lawson, B., Toms, M.P., Peck, K.M., Kirkwood, J.K., Chantrey, J. *et al.* (2010). Emerging infectious disease leads to rapid population declines of common british birds. *PLoS ONE*, 5, e12215.

Sagarin, R.D. & Gaines, S.D. (2002). The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecol. Lett.*, 5, 137–147.

Sagarin, R.D., Gaines, S.D. & Gaylord, B. (2006). Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends Ecol. Evol.*, 21, 524–530.

Samis, K.E. & Eckert, C.G. (2007). Testing the abundant center model using range-wide demographic surveys of two coastal dune plants. *Ecology*, 88, 1747–1758.

Smith, F.A. & Lyons, S.K. (2013). *Animal Body Size: Linking Pattern and Process Across Space, Time, and Taxonomic Group*. University of Chicago Press, Chicago, Illinois, US.

Sullivan, B.L., Wood, C.L., Iliff, M.J., Bonney, R.E., Fink, D. & Kelling, S. (2009). ebird: a citizen-based bird observation network in the biological sciences. *Biol. Cons.*, 142, 2282–2292.

Thibault, K.M., Supp, S.R., Giffin, M., White, E.P. & Ernest, S. (2011). Species composition and abundance of mammalian communities. *Ecology*, 92, 2316–2316.

Vandermeer, J.H. & Goldberg, D.E. (2013). *Population Ecology: First Principles*. Princeton University Press, Princeton, New Jersey, US.

VanDerWal, J., Shoo, L.P., Johnson, C.N. & Williams, S.E. (2009). Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. *Am. Nat.*, 174, 282–291.

Weber, M.M., Stevens, R.D., Diniz-Filho, J.A.F. & Grelle, C.E.V. (2016). Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. *Ecography*, 40, 817–828.

Whittaker, R.H. (1952). A study of summer foliage insect communities in the great smoky mountains. *Ecol. Monogr.*, 22, 1–44.

Woudenberg, S.W., Conkling, B.L., OConnell, B.M., LaPoint, E.B., Turner, J.A. & Waddell, K.L. (2010). The forest inventory and analysis database: database description and users manual version 4.0 for phase 2. General Technical Reports RMRS-GTR-245. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.