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The influence of stochasticity, landscape structure and species traits on abundant–centre relationships

Tad A. Dallas and Luca Santini

T. A. Dallas (https://orcid.org/0000-0003-3328-9958) ✉ (tad.a.dallas@gmail.com), Dept of Biological Sciences, Louisiana State University, Baton Rouge, LA, 70802, USA. – L. Santini (https://orcid.org/0000-0002-5418-3688), Dept of Environmental Science, Institute for Wetland and Water Research, Faculty of Science, Radboud University, GL Nijmegen, the Netherlands, and: National Research Council, Inst. of Research on Terrestrial Ecosystems (CNR-IRET), Monterotondo (Rome), Italy.

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Species have been commonly hypothesized to have high population densities in geographic areas which correspond to either the centre of the species geographic range or climatic niche (abundant–centre hypothesis). However, there is mixed empirical support for this relationship, and little theoretical underpinning. We simulate a species spreading across a set of replicated artificial landscapes to examine the expected level of support for abundant–centre relationships in geographic and niche space. Species niche constraints were modeled as a single axis which was related directly to population growth rates. We found strong evidence for abundant–centre relationships when populations follow deterministic growth, dispersal is high, environmental noise is absent and intraspecific competition is low. However, the incorporation of ecological realism reduced the detectability of abundant–centre relationships considerably. Our results suggest that even in carefully constructed artificial landscapes designed to demonstrate abundant–centre dynamics, the incorporation of small amounts of demographic stochasticity, environmental heterogeneity or landscape structure can strongly influence the relationship between species population density and distance to species geographic range or niche centre. While some simulated relationships were of comparable strength to common empirical support for abundant–centre relationships, our results suggest that these relationships are expected to be fairly variable and weak.

Keywords: abundance, distance–abundance, distribution–abundance, geographic distribution, macroecology, niche

Introduction

According to the abundant–centre hypothesis, species should have higher population density in the centre of their geographic distribution (Brown 1984, Sagarin and Gaines 2002). However, empirical support for this remains fairly low (Pironon et al. 2016, Dallas et al. 2017) (but see Waldock et al. 2019), as this hypothesis makes numerous assumptions concerning the geographic distribution of a species. For instance, populations are assumed to be well connected throughout the geographic range, be at their carrying capacity and in equilibrium with the environment. These assumptions

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are largely untenable (Sagarin et al. 2006, Dallas et al. 2017, Santini et al. 2019). However, it has been proposed that while species may not be most abundant in their geographic range centre, they may be most abundant in their niche centre (Martínez-Meyer et al. 2013). Interpreting the abundant–centre hypothesis across the niche space ('abundant–niche centre hypothesis') provides a closer link to existing theory of the ecological niche (Maguire Jr 1973). However, framing the abundant–centre hypothesis in niche space does not address many of the abundant–centre assumptions. This version of the hypothesis focuses on the fundamental niche (Hutchinson 1957), however, niche is typically estimated from occurrence data (implicitly linking the species niche and geographic distribution; Pulliam 2000) and thus producing something closer to the realized niche (Soberón 2007). Yet, realized niches are expected to be a partial representation of the fundamental niche (Peterson et al. 2011) and can have holes (Blonder 2016). Further, population density is assumed to be equilibrial and unaffected by dispersal or competition (Pironon et al. 2016).

The core idea of the abundant–niche centre hypothesis is that the density of a species and the distance from the niche centre should be negatively related, such that species density should be lowest closest to the edge of the niche (Martínez-Meyer et al. 2013). This makes intuitive sense, as those conditions near the edge of the niche boundary represent the niche extremes for that species. Translating species performance curves into niche axes, it would be expected that population growth rates, fecundity or survival would be highest in the niche centre and lowest at the niche edge (Maguire Jr 1973, Sagarin and Gaines 2002, Pironon et al. 2018). Ultimately, this treats the niche not as a persistence boundary (Holt 2009), but as a surface where more interior environments correspond to 'better' conditions for population growth. Further, the empirical support for this relationship is also quite low (Tuya et al. 2008, Dallas et al. 2017, Santini et al. 2019), potentially because of the failure to estimate appropriate niche axes, the non-equilibrial nature of population dynamics or the multitude of other factors influencing population density (e.g. competition, dispersal, predation).

It is potentially due to these factors that the abundant–centre and abundant–niche centre hypotheses have received mixed support so far in natural systems. Understanding when and why we observe abundant–centre and abundant–niche centre relationships (Martínez-Meyer et al. 2013, Waldock et al. 2019, Osorio-Olvera et al. 2020), and when we do not (Sagarin and Gaines 2002, Pironon et al. 2016, Dallas et al. 2017, Santini et al. 2019) is a pressing need. Presently, abundant–centre relationships are largely a collection of observational studies at different scales and encompassing a wide range of taxa, but without any clear consensus or synthetic understanding of the underlying cause (Sagarin and Gaines 2002, Pironon et al. 2016). Perhaps this focus on documenting abundant–centre relationships in natural systems has undercut the development and testing of the underlying theoretical framework. One possible way to explore the hypothetical mechanisms of the abundant–centre hypothesis is through spatially-explicit simulations of population dynamics. One recent attempt to address this theoretical shortcoming used a deterministic model based on a shrew species in Mesoamerica to explore the relationship between density of a species and distance from a niche centre (Osorio-Olvera et al. 2019). The authors enforced a covariance structure between niche axes by modeling population growth rate as a function of Mahalanobis distance in a ellipsoidal niche structure, directly linking distance in niche space and population growth rates. Previously, Osorio-Olvera et al. (2019) found that incorporating Allee effects and dispersal into a deterministic model of a single species spreading across a constructed landscape could result in a failure to detect abundant–centre relationships.

Building on this, Holt (2019) demonstrate that niche asymmetry, spatial variation in density dependence and nonlinear environmental feedbacks can also strongly influence resulting abundant–centre relationships. Together, this suggests that even when conditions are constructed to be quite favorable, abundant–centre relationships may be quite difficult to detect in natural systems. One of the larger potential reasons for this could be that demographic processes (e.g, survival, fecundity) can be completely unrelated to geographic range position or species niche limitations, or have opposite relationships to what would be expected from an abundant–centre relationship through population processes such as demographic compensation (Doak and Morris 2010, Villellas et al. 2015). Understanding the conditions where an abundant–centre relationship might manifest is a clear research need, and could help to explain the low levels of empirical support. In addition to the concerns raised by Holt (2019), we posit that at least two large classes of effects could further influence the detectability and strength of abundant–centre relationships.

First, the assumption that all populations across a species range are at equilibrium is difficult to reconcile with our knowledge of population dynamics in both natural (Lundberg et al. 2000, Benincà et al. 2015) and experimental (Shorrocks 1970, Laakso et al. 2003) systems. Dynamic demographic processes may strongly influence abundant–centre relationships. For example, spatial synchrony in species population dynamics – caused by the underlying response of population growth rates to distance from the range centre – may lead to jointly fluctuating populations and resulting temporal change in the strength of abundant–centre relationships. Additionally, the data used to explore the abundant–centre relationships are often based on surveys from different time periods instead of simultaneous sampling (Pérez-Tris et al. 2000, Martínez-Meyer et al. 2013, Dallas et al. 2017, Santini et al. 2019). While out of necessity, this practice makes the assumption that population densities are comparable across a set of geographic sites sampled under different local environmental conditions (commonly aggregate measures like annual mean temperature are used to define niche axes) and at different times (creating a clear issue for seasonally fluctuating species).

Relatedly, deterministic models simulated for many timesteps will approach an equilibrial density across a landscape, which may inflate abundant–centre correlations from what would actually be seen over any realistic timescale.

Second, there are likely both landscape and species-level processes which influence the detectability and strength of abundant–centre relationships. For instance, the spatial distribution and autocorrelation of environmental conditions likely strongly constrains whether a geographic abundant–centre relationship is observed for a given species. Further, species vary in terms of intraspecific competition and dispersal ability, which may strongly influence population demography and abundant–centre support by placing constraints on maximum population density and the rate and variation within the spatial spread of a species, respectively.

To explore the influence of these factors, we created artificial landscapes for a single species to grow and spread within. To start, we assumed that the geographic centre of the landscape also corresponded to the niche centre (this is modified by the η parameter), that a single niche axis was directly proportional to population growth rate, and enforced the landscape to follow an abundant–centre gradient in terms of the distribution of population growth rates. We ran simulations by varying a set of species-specific (intraspecific competition, dispersal probability and distance) and landscape (spatial variation in environment and shape of the linear gradient in population growth rates) conditions. We explore the extent to which abundant–centre relationships are sensitive to non-equilibrial population dynamics by incorporating demographic stochasticity into simulations of species spatial population dynamics, using both a deterministic and stochastic Ricker model to examine spatial population dynamics. We evaluate the strength of the abundant–centre relationship by estimating the rank correlation between abundance per cell, and geographic and niche-centre distance, respectively. The strength of abundant–centre relationships for the stochastic model approximate many of the correlation strengths from empirical studies (Tuya et al. 2008, Rivadeneira et al. 2010, Baldanzi et al. 2013, Scrosati and Freeman 2019). However, the degree to which these relationships can be used to make predictions of species abundance given geographic or niche information remains unclear (Dallas et al. 2018). The incorporation of spatial population dynamic models which incorporate realistic ecological processes (e.g. competition, dispersal variation, stochasticity) are essential for understanding the conditions required to observe abundant–centre relationships in terms of either geographic or climatic niche space.

Methods

Constructing artificial landscapes

Artificial landscapes consisted of a 200 × 200 lattice, where each cell contained a population. The goal of constructing these landscapes was to explore the most simple case, where we could easily expect abundant–centre relationships to manifest. To this end, geographic and niche gradients corresponded directly to population growth rates, and the landscapes were formed so that niche and geographic gradients were identical, creating a 1:1 correspondence between geographic and niche space. Assuming this, combined with reasonable access to all sites (removing the influence of dispersal limitation), we create a situation where the fundamental and realized niche are equivalent, and where population growth rates are directly proportional to geographic and niche position.

To construct the landscape, we assumed an initial abundance of 20 individuals located in a 21 × 21 square centred on the landscape. From the central point, we modeled population growth rate as a decreasing linear function in x and y dimensions, creating nested squares of population growth rates with the largest values in the centre of the landscape. Population growth rates (R) varied between 0 and 2, where values less than 1 correspond to decreasing population sizes and greater than 1 correspond to increasing populations. This value of R encompasses a realistic range of population growth rates, and does not come close to producing oscillatory dynamics or dynamic phenomena observed in the logistic map.

Under abundant–centre assumptions, populations towards the geographic or niche centre would have larger values of R. In our constructed landscapes, we placed the largest R values in the middle of the landscape, with population growth rates decreasing towards landscape margins with step size β at a decay rate of 0.2, which means each step of size β away from the centre of the landscape results in a population growth rate reduction of 0.2, until a minimum value was reached (minimum R was set to 0). The artificial landscapes were large enough such that inhospitable habitat was always included, so no odd boundary behavior was observed, as dispersal off the grid was impossible. This creates a flexible approach to construct landscapes with different potential species range sizes, but that strictly adhere to the assumptions of the abundant–centre hypothesis.

To add some realistic spatially autocorrelated environmental variation, we superimposed a Gaussian random field on the artificial growth matrix (Fig. 1) using the R package gstat (Pebesma 2004). The random field was generated with range parameter (ω) set to 10, which controls the degree of spatial autocorrelation, generating ecologically realistic spatial landscapes. We varied the relative role of this autocorrelated variation and the artificial growth rate matrix using the parameter η (Supplementary material Appendix 1 Fig. A2), which represents spatial heterogeneity in population growth rates due to variation in habitat structure, composition, resource distribution and biotic interactions. Even more simply, this spatial variation in population growth rates would just correspond to spatial variation in the dominant niche axis (i.e. the environment is not perfectly spatially autocorrelated). If η is set to 0, there is no spatially-autocorrelated environmental variation added. When η is equal to 1, the role

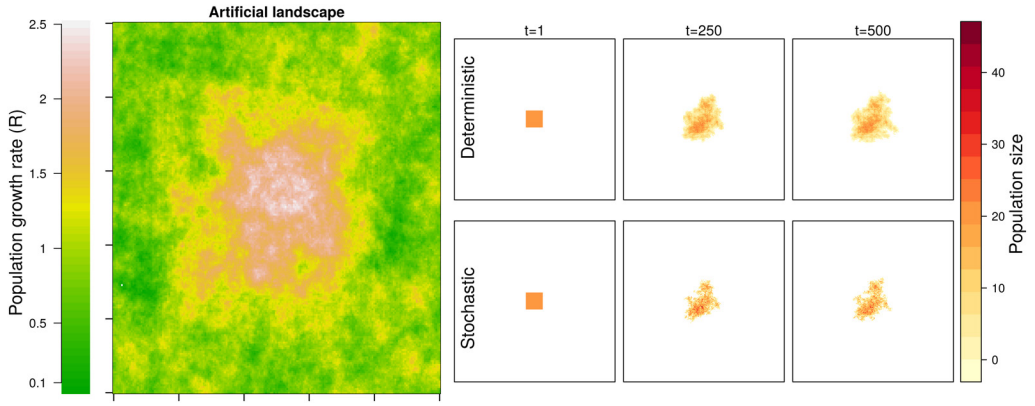

Figure 1. An example of a constructed landscape, where colors correspond to population growth rates, clearly linking the species niche requirements along a single simple axis and the species geographic distribution. Populations of 20 individuals were distributed centrally in the landscape (in 441 cells) and allowed to spread for 500 generations. The deterministic dynamics (upper panel) match the simple landscape structure well, and demonstrate that an abundant–centre relationship should be observed under these conditions. However, the stochastic simulations (lower panel) show that even a small amount of demographic stochasticity can influence the spatial distribution of abundance quite strongly.

of the spatially-autocorrelated environmental variation is the same as the artificial growth rate matrix.

Species dispersal may influence spatial synchrony and the spatial distribution of individuals (Paradis et al. 1999) partially independent of population growth rates (i.e. through source–sink dynamics). Dispersal was implemented by varying both dispersal probability and dispersal distance (Table 1). Dispersal probability P_d was modeled as a binomial variable determining the total number of individuals from any population that would disperse at least one cell in each timestep. Dispersal kernel shape was modeled using a negative exponential dispersal kernel, whose shape was determined by a negative exponential parameter, controlling the steepness of the exponential decline in probability with increasing dispersal rate (γ; Table 1). Each individual dispersed in x and y directions of the landscape independently following the negative exponential dispersal kernel ($\delta_i = e^{-\gamma}$), where i in the number of cells in either x or y dimensions and $i > 0$. In order to constrain the maximum possible dispersal distance an individual could go, we impose a limit d, corresponding to the maximum dispersal distance. This essentially truncates the negative exponential dispersal kernel at its low probability tail. This value was set at 20 cells for all simulations, which corresponds to 10% of the total size of artificial landscape in either direction (see Supplementary material Appendix 1 Fig. A3 for more information on dispersal kernel shape). However, the probability of any individual moving 20 cells is incredibly small, given the negative exponential dispersal kernel. This creates dispersal dynamics where P_d determines the number of dispersing individuals (all of which will travel at least 1 cell away), d constrains the overall distance any dispersing individual might travel, and γ determines the shape of the dispersal kernel.

Table 1. Parameter definitions and ranges used in the spatial Ricker model describing species dispersal characteristics and landscape structure. These values are meant to encompass a wide range of species and conditions, spanning from low to high intraspecific competition, low to high dispersal probability, short to long tail dispersal kernels, from steep gradients (where only the centre shows positive growth rates) to less steep gradients (where almost the entire landscape can show positive growth rates) and from no to high environmental noise that shifts the niche centre substantially with respect to the geographic centre (Supplementary material Appendix 1 Fig. A1–A5). Parameters were not changed through time in the simulations.

Parameter	Definition	Range
α	Intraspecific competition	0.005–0.1
P_d	Dispersal probability	0.0001–0.1
γ	Dispersal kernel shape	0.25–2.5
β	Shape of linear growth rate gradient (step size)	1–10
η	Environmental noise weight added to landscape	0–6

Species population dynamics

Each cell of the artificial landscape contained a population, which is connected by immigration and emigration to neighboring habitat patches. We considered population dynamics within each cell to be determined by a discrete single species Ricker model (Eq. 1), where population size in the next timestep (N_{t+1}) is determined by the population size at time t (N_t) and the per capita population growth rate R, discounted by the effects of intraspecific competition (αN_t). The Ricker model enforces non-overlapping generations, meaning that competition constrains population abundance on generational time.

$$N_{t+1} = N_t R e^{-\alpha N_t} \quad (1)$$

To this deterministic framework, we included demographic stochasticity by treating both the number of offspring

produced by each adult (R) and offspring survival as random variables. Specifically, the number of offspring per adult was modeled as a Poisson random variable with mean $N_t \times R$. However, only a portion of these offspring survive, and the survival of offspring to generation $t+1$ was modeled as a binomial random variable with probability proportional to the density-dependent adult effects on offspring; Bin(N_{t+1}, $\exp(-N_t \times \alpha)$). This corresponds to the Poisson Ricker model as described and analyzed in Melbourne and Hastings (2008, 2009), Dallas et al. (2019). We provide more conceptual detail on the influence of intraspecific competition α and population growth rates R_n on population dynamics in the deterministic (Supplementary material Appendix 1 Fig. A4) and stochastic model formulations (Supplementary material Appendix 1 Fig. A5) in the Supplementary materials Appendix 1.

The underlying Ricker model is the same for deterministic and stochastic approaches, with stochasticity introduced by allowing the production and survival of offspring to be random variables. This realistic process results in an integer-valued population size at any time N_t. This stochastic model has been used to explore variability in spatial spread (Melbourne and Hastings 2009) and the effects of competition and dispersal on maintaining interspecies range boundaries (Dallas et al. 2019). Previously, an expanded set of Ricker models was fit to experimental populations of flour beetles, finding that even in controlled situations, multiple forms of stochasticity influenced population dynamics (Melbourne and Hastings 2008). For simplicity, we only incorporate demographic stochasticity here, but note that environmental stochasticity, stochastic sex ratios and the existence of age or stage structured birth–death processes could further influence population dynamics (Melbourne and Hastings 2008).

Model simulations

We simulated spatial abundance dynamics using the deterministic and stochastic Ricker models on artificial landscapes for 500 generations. This period was chosen to avoid transient dynamics and allow sufficient time for the stabilization of species spatial abundance distributions, which typically occurred around 250 generations (Supplementary material Appendix 1 Fig. A19–A24). In the main text, we report the relationships after 50 generations, but also examine how the relationships change at 250 and 500 generations in the Supplementary material Appendix 1. The relationships stabilized after 300 timesteps (Supplementary material Appendix 1 Fig. A7–A14), and there was no appreciable change across all timepoints examined (50, 250 and 500 generations). Using both deterministic and stochastic implementations of the Ricker model across simulated landscapes, we thoroughly test how abundant–centre relationships are influenced by step size (β), dispersal probability (P_d), dispersal rate (γ), degree of environmental noise (η) and species intraspecific competitive ability (α). See Table 1 for parameter definitions, default values and ranges examined. These parameter ranges represent a broad spectrum, putatively capturing or exceeding what would be seen in natural systems.

We sampled the parameter space of these five parameters 10 000 times using latin hypercube sampling using the lhs R package (Carnell 2019), allowing us to more fully explore the parameter space. In the Supplementary material Appendix 1, we also report results for simulations where all other parameter values were fixed except a focal parameter, where we explored a gradient of values to see the effect of a single parameter independent of other parameters. The results of both approaches are qualitatively similar (Supplementary material Appendix 1 Fig. A15–A17).

We calculated Spearman's rank correlations of population abundance in each cell to 1) the Euclidean distance between the geographic range centre (which corresponds to the area of highest population growth rate), and 2) the difference of population growth rates from the maximum. This first relationship addresses the abundant centre relationship in terms of distance from the geographic range centre of the species. The second relationship is a simplified way to address distance from niche centre, making the implicit assumption that the highest value population growth rate corresponds to the centre of the niche. We further assume that this niche axis is directly proportional to population growth rate. We explore if the method used to quantify distance from geographic range or climatic niche centre influences the overall results, measuring distance as Mahalanobis distance in the Supplementary material Appendix 1, finding no appreciable differences between distance measures, as the two are strongly correlated (see Supplementary material Appendix 1 or Dallas et al. 2018).

All simulation and analytical code was written in R (<www.r-project.org>) and is available on figshare (Dallas and Santini 2020).

Results

Abundant–centre relationships in geographic space

The abundant–centre hypothesis was originally conceptualized in geographic space. We found relatively weak evidence for a geographic abundant–centre relationship after 50 generations for both deterministic (abundant–centre correlation; mean $\pm$ SD = -0.50 ± 0.27) and stochastic (abundant–centre correlation; mean $\pm$ SD = -0.31 ± 0.23) models given the amount of simplifying assumptions made (Fig. 2–4). While the overall strength of abundant–centre relationships decreased when demographic stochasticity was included, model parameters influenced both deterministic and stochastic model formulations proportionally.

Increasing the spatial variation in environmental conditions (η; Fig. 3) reduced support for abundant–centre relationships in geographic space in both deterministic ($\rho = 0.71$) and stochastic ($\rho = 0.50$) models. Similarly, decreasing the 'steepness' of the growth rate gradient (β; Fig. 4) reduced abundant–centre support for deterministic ($\rho = 0.20$) and

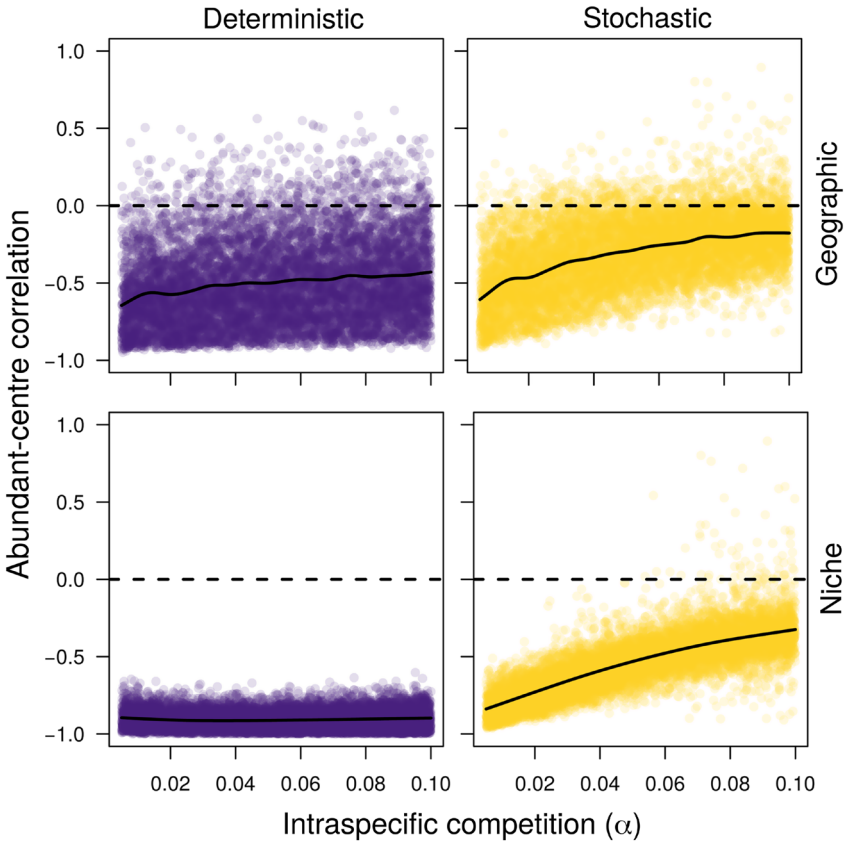

Figure 2. Abundant–centre relationships – quantified using Spearman's rank correlations – in geographic space (top row) and niche space (bottom row) and in a deterministic model (left column) and a stochastic model (right column). Abundant centre relationships in geographic space were especially susceptible to intraspecific competition (α), though incorporating a small degree of stochasticity caused intraspecific competition to strongly affect evidence for abundant centre relationships in geographic and niche space. Smoothed splines are plotted to show the general trends.

stochastic ($\rho = 0.23$) models. Dispersal kernel shape ('dispersal rate', γ) and dispersal probability did not appear to strongly influence abundant–centre patterns (Fig. 5), especially when compared to the effect of incorporating demographic stochasticity.

Abundant–centre relationships in niche space

Niche distance was quantified as the difference in population growth rates from the maximum. This value was related to species density for all occupied cells, as cells with the highest population growth rates should attain the highest densities. We found this was especially true in the deterministic model (abundant–centre correlation mean $\pm$ SD $= -0.96 \pm 0.03$), owing to the assumption of a perfectly measured one-dimensional niche gradient that captures population growth rates (Fig. 2–4). The relationships estimated in niche space for the deterministic model were consistently greater than what has been observed in natural populations, due to the simplifying assumptions of the simulations. Abundant–centre relationships for the determinstic model in niche space were completely insensitive to environmental noise (Fig. 3), rate of change in population growth rates (i.e. step size; Fig. 4), and dispersal dynamics (Fig. 5).

Introducing demographic stochasticity – modeling the number of offspring for each individual as a Poisson distribution random variable – consistently produced weaker abundant–centre relationships (abundant–centre correlation mean $\pm$ SD $= -0.54 \pm 0.19$) relative to the deterministic model. In the stochastic model, the abundant–centre relationship was strongly influenced by intraspecific competition (α; Fig. 2; $\rho = 0.81$), but only weakly influenced by spatial variation in environmental conditions (η; Fig. 3; $\rho = 0.16$) and the 'steepness' of the growth rate gradient (β; Fig. 4; $\rho = 0.15$).

The strength of abundant–centre relationships may change with time, as population dynamics reach equilibrium or become synchronous through shared response to environment or dispersal processes. We find that the deterministic model demonstrates a smooth transition to the long-term stable abundant–centre relationship slope across a range of parameter values, while the inclusion of demographic stochasticity causes the abundant–centre relationship slope to fluctuate much more strongly in geographic (Supplementary

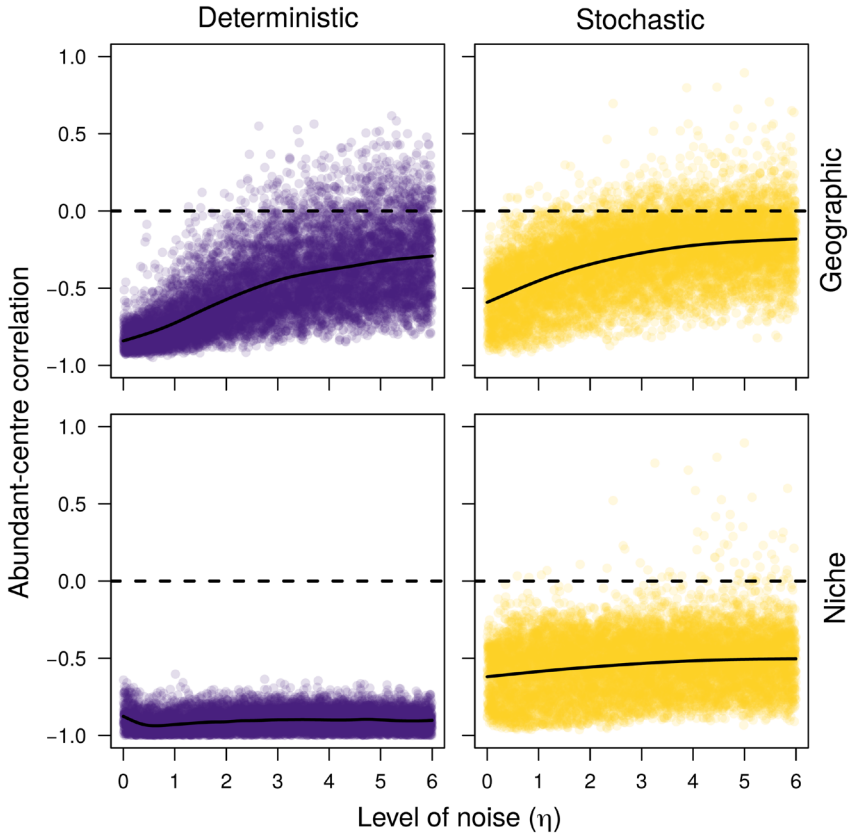

Figure 3. A realistic amount of environmental variation (η) – overlaid on the artificial relationship imposed between species geographic location, niche limits and rate of population growth – reduced evidence for abundant centre relationships strongly in geographic space. Abundant centre relationships – quantified as Spearman's rank correlations – in terms of niche position were relatively unaffected by this variation, but were sensitive to very small amounts of demographic stochasticity (lower right panel). Smoothed splines are plotted to show the general trends.

material Appendix 1 Fig. A19–A22) and climatic niche (Supplementary material Appendix 1 Fig. A23–A26) space.

Discussion

Using a combination of deterministic and stochastic model simulations with population dynamics based on the Ricker model, we demonstrated the sensitivity of abundant–centre and abundant-niche centre relationships to demographic stochasticity, landscape structure and species-specific parameters. We artificially constructed landscapes with a linearly decaying population growth rate with the highest value in the centre of the species geographic range, and calculated the difference from the maximum population growth rate as a measure of niche distance. In the absence of any deviation from this gradient – and when species dynamics were modeled as deterministic – abundant–centre and abundant-niche centre relationships were commonly observed and were quite strong (Fig. 2–4). However, this treats the niche as directly proportional to population growth rate; a strong assumption. This is perhaps why abundant–centre relationships detected in the deterministic model tend to be much stronger than typically observed in natural systems (Martínez-Meyer et al. 2013, Pironon et al. 2016, Dallas et al. 2017, Santini et al. 2019). But species population dynamics do not take place on a perfectly structured linear environmental gradient, in the absence of environmental variation, with homogeneously distributed biotic interactions, and deterministic population dynamics. The incorporation of demographic stochasticity strongly reduced support for abundant–centre and abundant–niche centre relationships, suggesting that incorporating a certain degree of ecological realism can negate an otherwise perfectly designed abundant–centre landscape.

Apart from demographic stochasticity, aspects of species ecology strongly influenced the degree of support for abundant–centre and abundant–niche centre relationships. Species with strong density-dependence in their demographic rates – imposed through intraspecific competition here – had reduced abundant–centre and abundant–niche centre relationships in the stochastic model. Dispersal probability and dispersal kernel shape weakly influence abundant–centre relationships, with steeper exponential dispersal kernels and larger dispersal probabilities reduced abundant–centre support. Finally, the spatial distribution of species demographic rates is critical to abundant–centre support, as the strongest

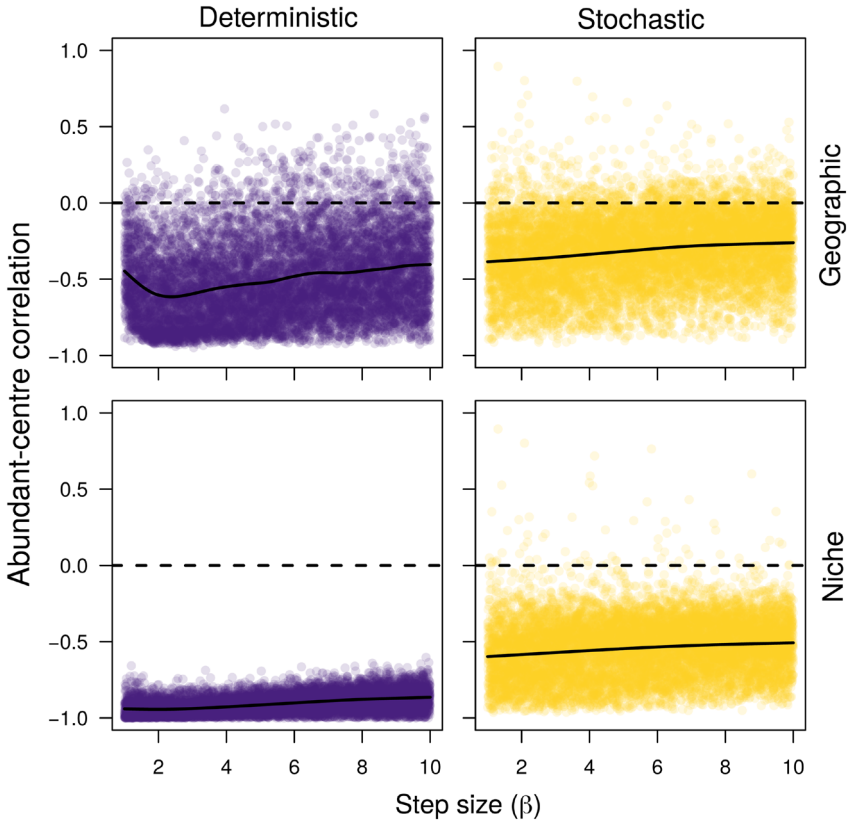

Figure 4. The rate of change in population growth rates across the artificial landscapes (β) reduced evidence for abundant centre relationships – quantified as Spearman's rank correlations – in geographic space for both deterministic and stochastic model formulations. In the deterministic model, an abundant–centre in niche space is inveitable as a function of the simulation design. Smoothed splines are plotted to show the general trends.

abundant–centre evidence occurs when the structuring niche axis – which relates directly to species demographic rates – is spatially autocorrelated. This conflates the species niche with the corresponding geographic distribution (Pulliam 2000), which is why recently abundant–centre relationships have been re-defined in climatic niche space (Martínez-Meyer et al. 2013). Even in climatic niche space, the spatial distribution and density of environmental conditions can strongly influence abundant–niche centre relationships, and the implied relationship between climatic suitability and species density may be a gross oversimplification (Van Couwenberghe et al. 2013, Dallas and Hastings 2018). A better integration with existing ideas from metapopulation biology, niche theory and macroecology may clarify the relative roles of environmental heterogeneity and species ecology on potential abundant–centre and abundant–niche centre relationships.

Here we have shown that the theoretical support for the theory is expected to be fairly low in semi-realistic settings, dependent on the level of demographic stochasticity, the structure of the landscape and the relationship between niche axes and species demographic rates. However, the empirical support is expected to be even lower. First, several approaches exist to estimate the niche of a species and distance from centroid or edges (Dallas et al. 2017, Soberon et al. 2018, Santini et al. 2019, Osorio-Olvera et al. 2020). Second, all these approaches rely on the proper estimation of species' niche axes (Synes and Osborne 2011, Fourcade et al. 2018), and the direct relationship between species niche axes and species demographic rates. A failure in any of these two can already undermine the estimated relationship. Third, species abundance estimates are rare in the literature, can be obtained from heterogeneous methods, and those used in macroecological modeling are normally collected opportunistically and thus suffer of known biases (Santini et al. 2018, Soberon et al. 2018). If the abundant–centre relationship is weak and close to zero, an incomplete, heterogeneus, and biased sample can easily flatten or reverse the estimated relationship. As such, assuming the relationship exists, its empirical support is expected to be absent or extremely weak on average, and show strong negative or positive correlations by chance, which may result in publication biases.

Our results support previous findings incorporating ecological realism into a deterministic model of abundant–centre dynamics (Holt 2019, Osorio-Olvera et al. 2019), but perhaps with a different overall conclusion. (Osorio-Olvera et al. 2019) developed a simulation model, finding similar difficulty in detecting abundant–centre relationships at realistic timescales or when incorporating ecologically realistic population

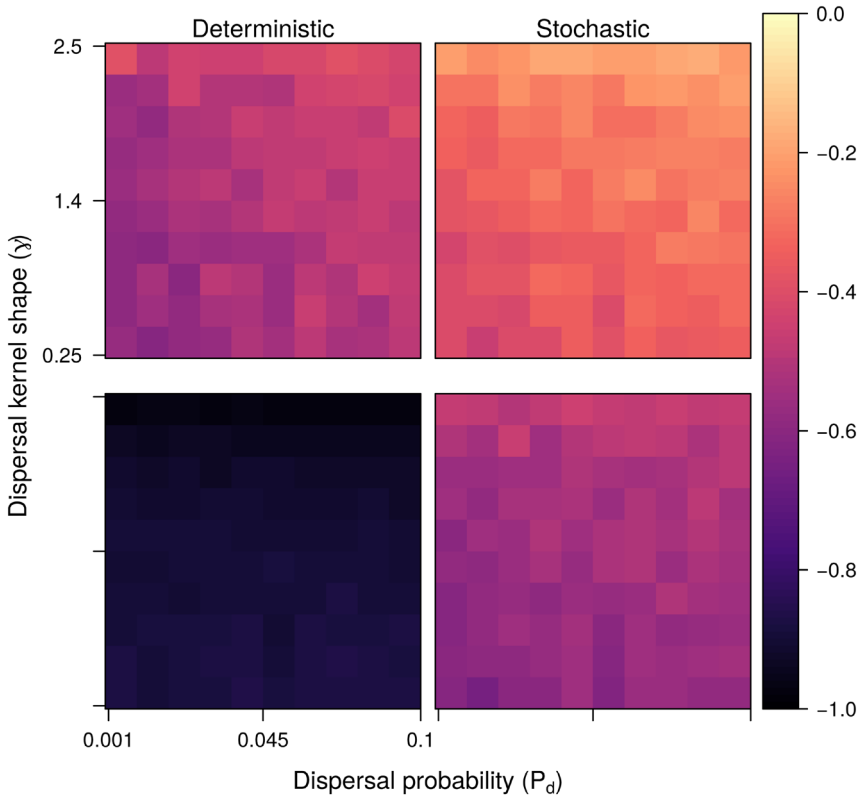

Figure 5. The joint effects of dispersal probability (P_d; x-axis) and dispersal kernel shape parameter (γ) on abundant–centre relationship strength (color scale) in geographic space (top row) and niche space (bottom row) for both the deterministic (left column) and stochastic (right column) model formulations. All relationships were negative on average, and dispersal probability and distance did not appear to strongly influence resulting abundant–centre patterns in our simulations.

processes (e.g. Allee effects), but claimed to have found general support for abundant–centre relationships. Despite the strong relationships we document here when conditions are perfect for abundant–centre relationships to be maintained, we find small perturbations in parameter estimates, and the incorporation of demographic stochasticity strongly reduce the artificially-imposed abundant–centre. Based on these results, we conclude that abundant–centre relationships tend to be weak even in simulations designed to demonstrate the phenomenon (e.g. a single, simplified, perfectly estimated niche axis directly proportional to population growth rates), and therefore empirical support for the hypothesis is expected to be rare at best.

However, there are aspects of our simulation framework which may fail to capture the reality of natural systems. For instance, the spatial distribution of population growth rates follows the niche gradient linearly in the absence of environmental noise, creating an artificial link between the species niche and corresponding geographic distribution (Pulliam 2000). The use of more realistic niche structures and the incorporation of more than one niche axis are likely to further reduce support for strong abundant–centre and abundant–niche centre relationships. Further, this model can be extended to examine the sensitivity of species spatial population dynamics to other forms of stochasticity, different dispersal kernels, competing species or natural enemies. One clear example is the incorporation of environmental stochasticity, as most natural systems have temporally varying climatic conditions. Incorporating this temporal scale into macroecological studies is an interesting next step, as support for macroecological relationships may depend on temporal scale, and environmental variability may alter niche centroid and distance estimates.

The clear difficulty in detecting abundant–centre relationships highlights the role of species life history and landscape structure on the spatial distribution of species abundance. The predictions made by our model simulations may be generally testable in observational data by carefully considering the structure of the niche in n-dimensional space and species-specific attributes related to dispersal and intraspecific competition. Abundant–centre relationships observed in our simulations with a single niche axis, a single species and many simplifying assumptions resulted in estimated correlation coefficients comparable to many empirical studies (Martínez-Meyer et al. 2013, Pironon et al. 2016, Dallas et al. 2017, Osorio-Olvera et al. 2020). This is striking, as natural systems are likely far more complex than our simulated landscapes, as it is likely that species demographic rates are not simply controlled by a single niche axis. Given the simplifying assumptions of our simulations, the correlation coefficients

estimated here can be seen as an upper bound of what can be realistically estimated in empirical case studies. While data quality and availability are constant concerns (Conde et al. 2019), exploring species variation in abundant–centre support may provide an idea of the range of correlation coefficients attainable in empirical systems relative to simplified simulation exercises such as this. Large databases of species densities (Santini et al. 2018), occurrences (Sullivan et al. 2009, Telenius 2011) and traits (Maitner et al. 2018) can be used to explore the sensitivity of abundant–centre and abundant–niche centre relationships to species traits and geographic structure (Dallas et al. 2020, Osorio-Olvera et al. 2020).

Despite this, the low levels of support for abundant–centre relationships from both observational (Pironon et al. 2016, Dallas et al. 2017, Santini et al. 2018) and theoretical (Osorio-Olvera et al. 2019) studies suggests that the abundant–centre hypothesis cannot be used for the prediction of species densities. Further, the failure to detect abundant–centre relationships may not be because of small methodological or measurement differences between studies (Soberon et al. 2018), but simply because species spatial population dynamics at large scales do not follow from such simple predictions. Further conceptual refinement of abundant–centre ideas, and a better integration of population and community level theory, can help clarify the role of abundant–centre relationships in natural systems.

Data accessibility

R code is available on Figshare at <https://doi.org/10.6084/m9.figshare.11553534.v1> (Dallas and Santini 2020).

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Supplementary material (available online as Appendix ecog-05164 at <www.ecography.org/appendix/ecog-05164>). Appendix 1.

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