The geographic scaling of biotic interactions

Miguel B. Araújo[1,2,3,4*] & Alejandro Rozenfeld[3*]

[1]Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot SL5 7PY, Berks, United Kingdom (miguel.araujo@imperial.ac.k)

[2]Department of Biogeography and Global Change, National Museum of Natural Sciences, CSIC, Calle José Gutiérrez Abascal, 2, 28006, Madrid, Spain

[3]'Rui Nabeiro' Biodiversity Chair, CIBIO, University of Évora, Largo dos Colegiais, 7000 Évora, Portugal

[4]Center for Macroecology, Evolution and Climate, University of Copenhagen, 2100 Copenhagen, Universitetsparken 15, 2100, Denmark

* Authors contributed equally

Abstract: A central tenet of ecology and biogeography is that the broad outlines of species ranges are determined by climate, whereas the effects of biotic interactions are manifested at local scales. While the first proposition is supported by ample evidence, the second is still a matter of controversy. To address this question, we develop a mathematical model that predicts the spatial overlap, i.e., co-occurrence, between pairs of species subject to all possible types of interactions. We then identify the scale in which predicted range overlaps are lost. We found that co-occurrence arising from positive interactions, such as mutualism (+/+) and commensalism (+/0), are manifested across scales of resolution. Negative interactions, such as competition (-/-) and amensalism (-/0), generate checkerboard-type co-occurrence patterns that are discernible at finer resolutions. Scale dependence in consumer-resource interactions (+/-) depends on the strength of positive dependencies between species. Our results challenge the widely held view that climate alone is sufficient to characterize species distributions at broad scales, but also demonstrate that the spatial signature of competition is unlikely to be discernible beyond local and regional scales.

Introduction

The question of whether the geographical ranges of species are determined by their ecological requirements and the physical characteristics of individual sites, or by assembly rules reflecting interactions between species, has long been a central issue in ecology (e.g., Andrewartha and Birch 1954, Diamond 1975, Gotelli and Graves 1996, Chase and Leibold 2003, Peterson et al. 2011). Evidence is compelling that the limits of species ranges often match combinations of climate variables, especially at high latitudes and altitudes (e.g., Grinnell 1917, Andrewartha and Birch 1954, Hutchinson 1957, Woodward 1987, Root 1988), and that these limits shift through time in synchrony with changes in climate (e.g., Walther et al. 2005, Hickling et al. 2006, Lenoir et al. 2008). However, recent evidence suggests that the thermal component of species climatic niches is more similar among terrestrial organisms than typically expected (Araújo et al. 2013), leading to the conclusion that spatial turnover among distributions of species might often result from non-climatic factors (see also for discussion Baselga et al. 2012a). The degree to which non-climatic factors shape the distributions of species has been focus of discussion in community ecology and biogeography for over a century, with several authors proposing that climate exerts limited influence at lower latitudes and altitudes (e.g., Wallace 1878, Dobzhansky 1950, Loehle 1998, Svenning and Skov 2004, Colwell et al. 2008, Baselga et al. 2012b). Specifically, much interest exists regarding the extent to which occurrences of species are constrained by the distributions of other species at broad scales of resolution and extent (e.g., Gravel et al. 2011). It has been argued that biotic interactions determine whether species thrives or withers in a given environment, but that the spatial effects associated with these interactions are lost at broad scales (e.g., Whittaker et al. 2001, Pearson and Dawson 2003, McGill 2010). In contrast, modelling studies have hinted that biotic interactions could leave broad-scale imprints on coexistence and, therefore, on species distributions (e.g., Araújo and Luoto 2007, Heikkinen et al. 2007, Meier et al. 2010, Bateman et al. 2012). But empirical evidence for the broad scale effects of biotic interactions is limited. A study has shown that with scales of few hundred kilometres the effects of competition on geographical ranges can still be discernible (Gotelli et al. 2010), but at scales of biomes such effects are often diluted (Russell et al. 2006, Veech 2006). How general are these patterns?

Empirical studies of the effects of biotic interactions on species distributions have historically focused on competition (e.g., Gause 1934, Hardin 1960, MacArthur 1972, Schoener 1982, Amarasekare 2003). However, several authors have pointed out that a greater variety of interactions can control for spatial patterns of overlap between species (e.g., Hairston et al. 1960, Connell 1975, Ricklefs 1987, Callaway et al. 2002, Bruno et al. 2003, Travis et al. 2005, Ricklefs 2010). Competition is a specific case involving two species that are worse off interacting with one another (which we annotate as: -/-). In its extreme form, competition leads to co-exclusion of the interacting species (MacArthur 1972). The reverse of competition is mutualism, whereby two species display mutual dependency (+/+). Different combinations of positive, negative, and neutral relationships exist and they generate consumer-resource interactions such as predation, herbivory, parasitism and disease (+/-), or amensalism (-/0) and commensalism (+/0).

The spatial effects of the different biotic interactions have rarely, if ever, been investigated. Differences in patterns of co-occurrence arising from alternative biotic interactions are seldom stated and focus has been on identifying non-random patterns of co-occurrence between pairs of species (e.g., Gotelli and McCabe 2002, Horner-Devine et al. 2007, Gotelli et al. 2010). Substantial controversy exists regarding the appropriate null models in such analyses (for review and discussion see Gotelli and Graves 1996), but the more fundamental question of whether departures from randomness in co-occurrence patterns provide interpretable information regarding the underlying biotic interactions remains unanswered.

In practice, several biotic and abiotic factors can simultaneously affect the distributions of species (e.g., Soberón 2010, Peterson et al. 2011) and, therefore, co-occurrence (e.g., Cohen 1971, Leibold 1997, Amarasekare et al. 2004, Ovaskainen et al. 2010, Araújo et al. 2011). One approach to disentangle the relative importance of factors causing changes in species co-occurrence is through simulations (Urban 2005). Here, we develop a novel 'point-process' model that infers co-occurrence of species across the full space of potential biotic interactions between pairs of species: i.e., given all biotic interaction types (+/+, +/-, -/-, +/0, -/0) and all possible combinations of biotic interaction strength ($0 \leq I_x \leq 1$) (for more details see material and methods). Dynamic Lotka-Volterra-type models could also be used as they explicitly simulate the effects of different biotic interactions on population dynamics (e.g., predation, competition,

mutualism, see for review Kot 2001). However, Lotka-Volterra models require detailed parameterization of mortality and colonization rates that are highly contingent and are usually impossible to obtain. Furthermore, models predicting the spatial effects of repulsive and attractive interactions at steady state would be particularly useful if the goal is to examine these spatial effects rather than the underlying population dynamics that generate them (see also Dieckmann et al. 2000, Law and Dieckmann 2000). The critical issue is whether a simple point-process model, such as ours, simulates spatial patterns of co-occurrence comparable with dynamic Lotka-Volterra models at equilibrium. Preliminary analysis comparing our model with Markov-chain formulation of Lotka-Volterra models by Cohen (1970) supports this view and is being prepared for publication elsewhere (Rozenfeld & Araújo, unpublished).

In the current implantation of the proposed point-process model, and to control for the effects of species range sizes and environmental clustering on species distributions, simulations were replicated for species ranges with varying prevalence and spatial autocorrelation. Once co-occurrence between two species was estimated, we sampled ranges at increasingly coarser scales of resolution (i.e., by increasing grid-cell size) and identified the scale at which the original patterns of co-occurrences lost the signature of the biotic interactions effects. When the effects of biotic interactions on patterns of co-occurrence of species were maintained across scales of resolution we interpreted the pattern as providing evidence for scale independence. In contrast, biotic interactions generating patterns of co-occurrence that were lost at increasing scales of resolutions were interpreted as being strongly dependent on the scale.

Material and methods

The model

The primary assumption of our point-process model is that the signal of biotic interactions drives spatial attraction (for +) or repulsion (for -). It follows that if no interactions are present (0/0), co-occurrence between species ranges is dependent on their prevalence (ρ=fraction of the sites where the species is present). Formally, if species probabilities of occurrence are equal to their respective prevalence, i.e., $P(A) = \rho_A$ and $P(B) = \rho_B$, then the probability of co-occurrence between ranges of two non-interacting species is given by

$$P_{Null}(A \cap B) = \rho_A \rho_B \quad (1)$$

The probability of co-occurrence is the expected fraction of sites where species co-occur. If species A and B interact, then their overlap is a function of both their prevalence and the strength of their interactions I_A and I_B

$$P(A \cap B) = f(\rho_A, \rho_B, I_A, I_B) \quad (2)$$

Interactions can be either attractive I_x^+ or repulsive I_x^-, with $0 \leq I_{A\ or\ B}^{+\ or\ -} \leq 1$. It follows that I_A^+ stands for the intensity with which species A is attracted by B, and I_B^+ is the intensity with which species B is attracted by A. Likewise, I_A^- stands for the intensity with which species A repulses B, and I_B^- is the intensity with which species B repulses A.

In the particular case of mutualism (+/+), positive interactions will cause species to co-occur more often than expected under the null model

$$P_{(+/+)}(A \cap B) = \rho_A\rho_B + \max(I_A^+, I_B^+) \times [\min(\rho_A, \rho_B) - \rho_A\rho_B] \quad (3)$$

Where the second term in equation 3 estimates the excess of co-occurrence due to positive (+/+) interactions. The maximum fraction of sites where species co-occur is limited by the prevalence of the species with the most restricted range, i.e., $\min(\rho_A, \rho_B)$. So that $[\min(\rho_A, \rho_B) - \rho_A\rho_B]$ refers to the maximum excess of co-occurrence over the null model. With interactions (+/+), the species with the greatest positive dependence is the one that constrains co-occurrence between the two interacting species. That is, the maximum excess of co-occurrence is modulated by the maximum attracting index ($\max(I_A^+, I_B^+)$).

So,

$$P_{(+/+)}(A \cap B) = \begin{cases} \rho_A\rho_B & I_A^+ = 0 \quad and \quad I_B^+ = 0 \\ \min(\rho_A, \rho_B) & I_A^+ = 1 \quad or \quad I_B^+ = 1 \end{cases}$$

When both interaction strengths are 0 we recover the null expectation, and when one of the species is fully dependent on the other the co-occurrence range is maximal.

In the case of competition (-/-), negative interactions will cause the species to co-occur less often than expected under the null model

$$P_{(-/-)}(A \cap B) = \rho_A\rho_B \times [1 - \max(I_A^-, I_B^-)] \quad (4)$$

Co-occurrence will tend to zero as the interaction strength of at least one of the interacting species approaches 1. With interactions (-/-), the species with the greatest

negative (repulsive) interaction is the one that constrains co-occurrence between the two interacting species. That is, co-occurrence decreases below the null expectation proportionally to the maximum repulsion strength ($\max(I_A^-, I_B^-)$).

So,

$$P_{(-/-)}(A \cap B) = \begin{cases} \rho_A\rho_B & I_A^- = 0 \quad and \quad I_B^- = 0 \\ 0 & I_A^- = 1 \quad or \quad I_B^- = 1 \end{cases}$$

When both interaction strengths are 0 we recover the null expectation and, when one of the species is fully excluded by the other, co-occurrence is zero.

In the case of consumer-resource interactions (+/-) with A being the consumer and B the resource, both positive and negative interactions will cause co-occurrence to deviates from the null expectation

$$P_{(+/-)}(A \cap B) = [\rho_A\rho_B + I_A^+ \times (\min(\rho_{A,}\rho_B) - \rho_A\rho_B)] \times (1 - I_B^-) \qquad (5)$$

The equation 5 is a combination of equations 3 and 4. The first factor $[\rho_A\rho_B + (\min(\rho_{A,}\rho_B) - \rho_A\rho_B)I_A^+]$ corresponds to equation 3 with $I_B^+ = 0$, and it shows how co-occurrence is increased due to the positive dependence of species A on B. The second factor $(1 - I_B^-)$ reduces co-occurrence proportionally to the repulsive strength (I_B^-).

So,

$$P_{(+/-)}(A \cap B) = \begin{cases} \rho_A\rho_B & I_A^+ = 0 \quad and \quad I_B^- = 0 \\ \min(\rho_{A,}\rho_B) & I_A^+ = 1 \quad and \quad I_B^- = 0 \\ 0 & I_B^- = 1 \end{cases}$$

When both interaction strengths are 0 we recover the null expectation. When species A is fully dependent on B and species B does not repulse A then the co-occurrence reaches its maximum. Finally, when species B repulses A with maximum intensity co-occurrence is forbidden.

Notice that commensalism is a special case of mutualism (with $I_B^+ = 0$) or predation, parasitism and disease (with $I_B^- = 0$), while amensalism is a special case of competition (with $I_B^- = 0$). By varying the sign (+, -) and the strength I_x ($0 \leq x \leq 1$), our model predicts range overlaps across the full biotic interaction space.

Simulations

The general formulation of our point-process model defines rules of attraction and repulsion among species subject to different biotic interaction types and strengths, but

these interactions take place in non-heterogeneous landscapes where multiple drivers, in addition to interactions, can affect species ranges and, therefore, co-occurrence. Constraints to the general model can be added to take these drivers into account, such as varying the ecological niches of species (both in the sense of species affecting and being affected by the environment, e.g., Chase and Leibold 2003, Peterson et al. 2011), or dispersal (both in the sense of species having the ability to disperse and being prevented from it due to external barriers, e.g., Levin 1974, Pulliam 1988, Hanski 1998, Humphries and Parenti 1999). Here, we explore two features of species ranges that we deem relevant for studying the geographical scaling of biotic interactions. The first is prevalence (ρ). In one implementation of the model, the prevalence of species is relatively low: each species occupies 10% of the studied region (ρ=0.1). In the other implementation of the model species occupy 30% (ρ=0.3) of the studied region.

The second feature explored is the placement of ranges. In one implementation of the model, species B is randomly located and species A is constrained by species B. Under this model, environmental conditions are assumed to be homogenous across the studied area as it would be expected if range overlaps were measured within a given habitat type. In such a scenario, species B can be found anywhere in geographical space and range overlaps between species A and B are solely determined by prevalence and the attractive and repulsive effects of interactions. In the modified model, the distribution of species B is spatially structured while species A is a function of species B. This implementation of the model simulates range overlaps when the distribution of one of the species is highly autocorrelated (e.g., Legendre 1993, Dormann et al. 2007). Such autocorrelation can arise because strong environmental gradients exist and act to constrain species ranges (as might often occur at biogeographical extents) and/or when dispersal, demographic or behavioural factors cause individuals to aggregate in specific portions of geographical space (as might often occur at local and landscape extents). All simulations were performed in lattices of 100x100 pixels. In order to account for stochastic differences in the placement of the ranges, simulations were repeated 1000 times. Details on the generation of random and spatially autocorrelated distributions are provided in the supporting online material, together with the Mat Lab computer code written by AR and used to generate the species ranges (see supporting online material).

227 *Measuring spatial dependencies in biotic interactions*

228 To address the question of how co-occurrences emerging from different biotic
229 interactions affect species distributions at different spatial resolutions we used a
230 hierarchical framework (Allen and Starr 1982). We compared co-occurrence scores
231 (measured as the ratio of the number of geographical cells where species A and B co-
232 occur to the total number of occupied cells) at the original resolution used to fit all of
233 our models (the cell in our lattice landscape) with co-occurrences measured at
234 progressively larger scales of resolution. This hierarchical framework for scaling was
235 achieved by increasing the size of the blocks where individuals occur, and then
236 quantifying the resulting co-occurrence. The quantification of co-occurrence was done
237 using two approaches. The first seeks to preserve information about the 'true' co-
238 occurrence of species that exists within geographical blocks and counts species as co-
239 occurring if, and only if, they co-occur within one or more cell within the larger block.
240 The second emulates the traditional approach of 'sampling' species occurrences' data in
241 macroecology (e.g., Rahbek and Graves 2001, McPherson et al. 2006, Nogués-Bravo
242 and Araújo 2006), and counts species as co-occurring if both species are present
243 somewhere in the block regardless of whether they co-exist in the cells.
244
245 The 'true' and 'sampled' co-occurrence scores measured at the cell level are then
246 plotted against progressively larger block sizes. The area between the curves
247 representing the 'true' and 'sampled' co-occurrence percentages between species A and
248 B, across the range of block sizes, provides a measure of scale dependence of co-
249 occurrence patterns (see Figure 1). The greater the area between the two curves the
250 more the effects of given biotic interaction on species' distributions depend on spatial
251 resolution, and vice versa (see Figure 1). The area between the 'true' and the 'sampled'
252 co-occurrences is calculated for the full set of possible biotic interactions that can arise
253 from combining interactions of varying signs (+, -) and strengths I_x ($0 \leq x \leq 1$).

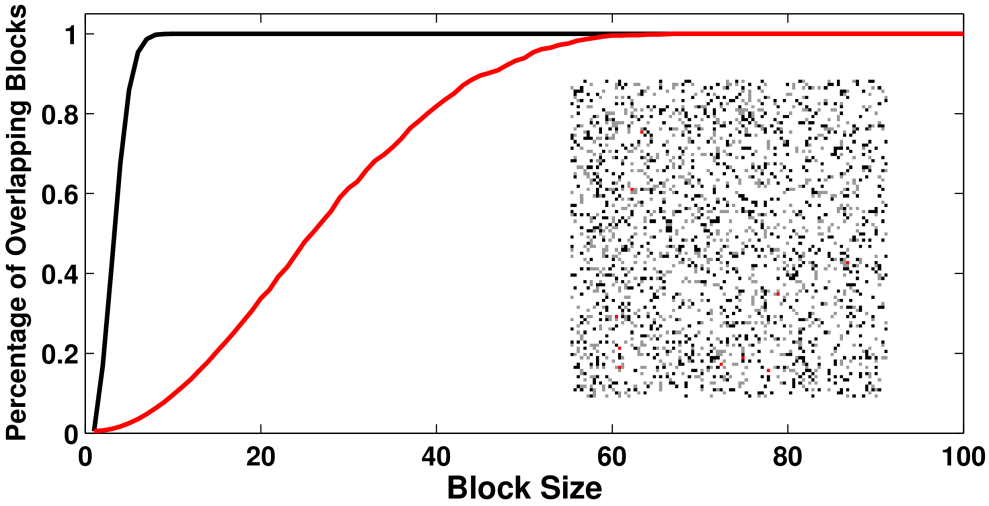

Figure 1 – **Scale dependence of biotic interactions**. Right (squared landscape): after the range of species A and B have been simulated, co-occurrence between the two species is calculated. Black squares indicate occurrence of species A but not species B, gray squares indicate occurrence of B but not A, and red squares indicate co-occurrence of A and B. Left (diagram): by progressively increasing the size of the squares, 'sampling' would lead to classifying species has co-occurring if both occurred somewhere in the square (black line indicates 'resampled' co-occurrence), while species would only co-occur if species overlapped within the square (red line indicates 'true' co-occurrence). The greater the area between the red and black lines the greater the scale dependence of biotic interactions.

Results

Although positive interactions generate range overlaps and negative interactions generate non-overlaps, equivalent degrees of overlap were recorded for species exposed to different types of biotic interactions (Figure 2). For example, the spatial patterns of range overlap for commensalism (I_A^+, I_B^0) can be identical to range overlaps arising from mutualistic interactions (I_A^+, I_B^+) (Figure 1). Range overlaps from amensalism (I_A^-, I_B^0) can also mach range overlaps from competition (I_A^-, I_B^-). Patterns of range overlap from consumer-resource interactions (I_A^-, I_B^+) can be like that of any type of biotic interaction.

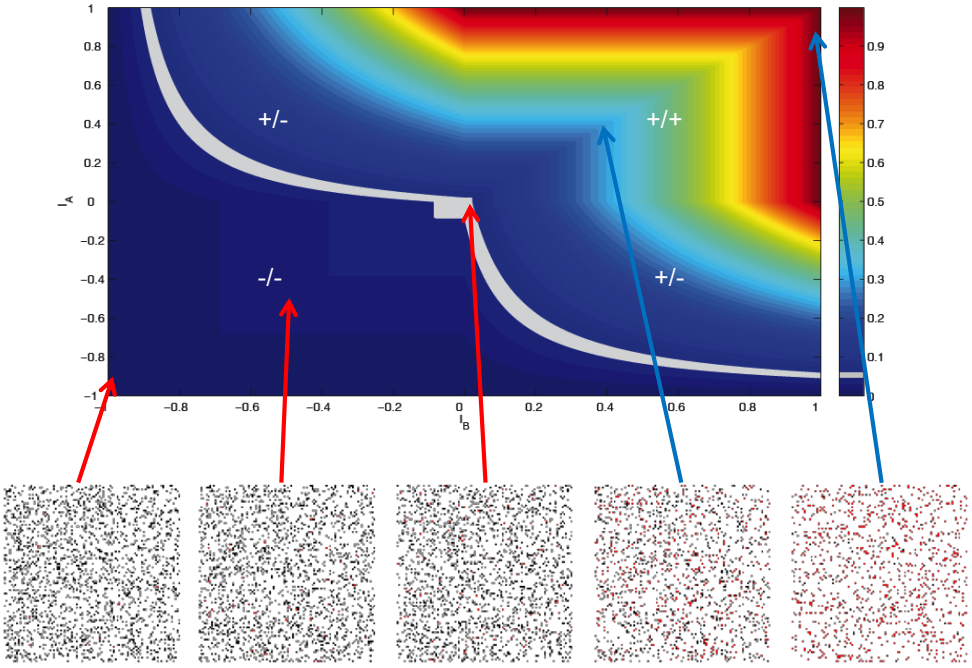

Figure 2 – **Expected range overlap in biotic-interaction space**. Colours on the top graph indicate the intensity of the predicted range overlaps between species A (y axis) and B (x axis), where increasing gradients of red indicate increased range overlap while increasing gradients of blue indicate increased non-overlap. The light gray line indicates the portion of biotic-interaction space where range overlaps between species are no different from the null model. The numbers on the y and x axes represent interactions (I) of varying signal (+, -, 0) and strength (≥0 ≤1). The lower scatter diagrams provide examples of simulated distributions of species A (black) and B (gray), with their respective overlap (red), for interactions of varying sign and strength. Both species have prevalence ρ=0.1.

When data are sampled from the cell to progressively larger blocks, estimated co-occurrence between species increases until an asymptote of complete overlap is reached (Figure 3). The difference between 'sampled' and 'true' co-occurrence (our metric of scale independence, see Figure 1) varies with the spatial resolution, but also with the signal and the strength of the biotic interactions (Figure 3). The stronger the negative interactions, the more scale dependent local patterns of co-occurrence are; in contrast, the stronger the positive interactions the greater the scale independence. In the extreme case of obligate positive dependencies between species pairs, i.e., strong mutualism, no difference exists between 'sampled' and 'true' co-occurrence across spatial scales.

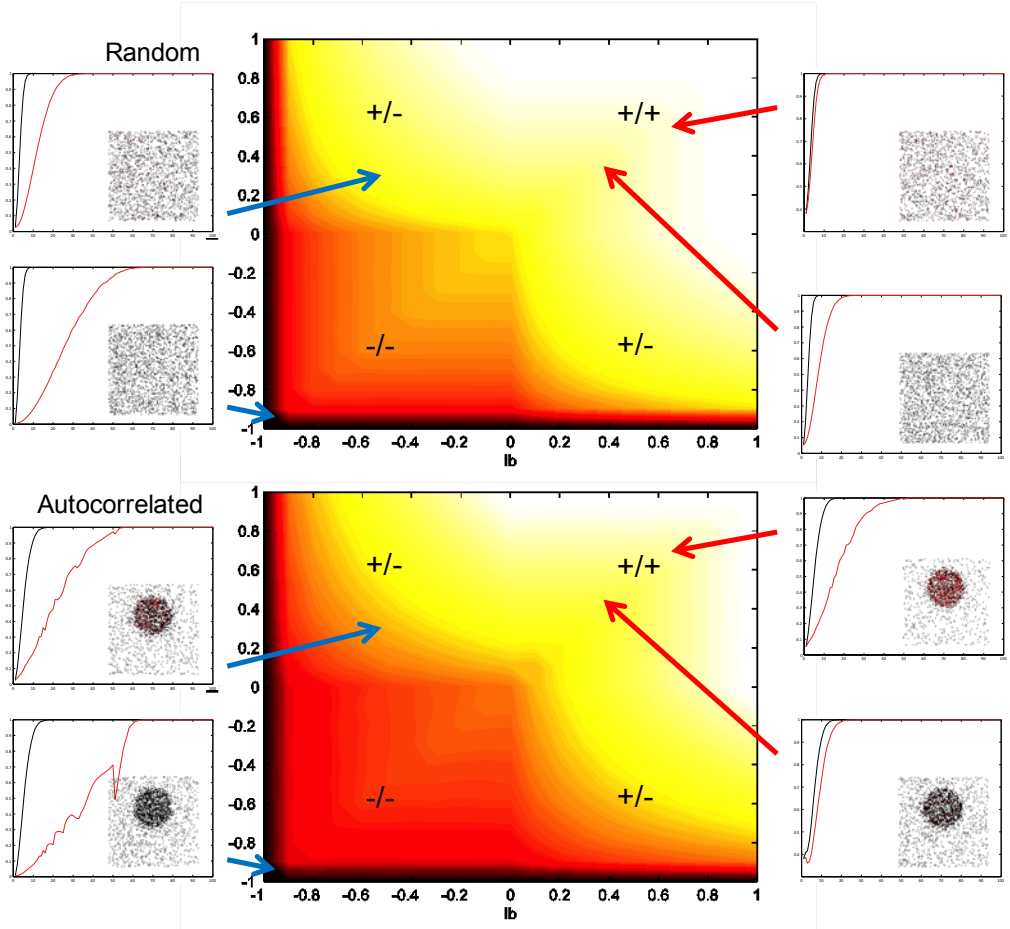

Figure 3 – **Scale dependence across biotic interaction space.** In the outer scatter plots, red lines indicates 'true' co-occurrence (y axis) between species A and B at increased scales of resolution (x axis), while black lines represent estimated co-occurrence after sampling occurrence data at increased scales of resolution. The greater the area between the two curves, the greater the scale dependence in the geographical signatures of biotic interactions. Lattice diagrams are examples of the geographical distribution of species A (black) and B (grey) and their respective overlaps (red) for interactions of varying signal and strength. In the central column of graphs, increasing gradients of red indicate increased scale dependence (i.e., increased area between red and black lines in outer scatter diagrams), while decreasing gradients of red indicate increased scale independence (i.e., decreased area between red and black lines in outer scatter diagrams): a) when A and B have prevalence ρ=0.1 and both are randomly distributed; b) when A and B have ρ=0.1 and B is geographically structured. Colour scales are log transformed. Estimates of range overlap underlying measurements of scale dependence were obtained with 1000 model runs and values provided are averages across all runs. Summary statistics are provided in table 1.

Co-occurrence patterns generated by consumer-resource interactions are also discernible across spatial scales, when at least one of the interacting species has strong positive dependency on the other. The same qualitative trend is maintained when species prevalence and autocorrelation increases (Table 1). However, scale independence tends to increase when interacting species have higher prevalence and ranges have weak spatial autocorrelation structure (Table 1). Spatially autocorrelated ranges also generate higher variance in patterns of scale dependence, chiefly across competitive interaction space (Table 1, Figure S1).

Table 1 – Mean and SD (after 1000 repetitions) of scale dependence values across sections of biotic interaction space for mutualism (+/+), competition (-/-), consumer-resource interactions (+/-), commensalism (+/0), amensalism (-/0). The greater the mean values, the greater the scale dependence of co-occurrence patterns generated by biotic interactions (large SDs indicate large uncertainties). Results are provided for two different prevalence (10% and 30%) and for two types of distributions (random and autocorrelated). See figure S1 for a visual representation of these results.

Prevalence		10%		30%	
Distribution		random	autocorrelated	random	autocorrelated
+/+	Mean	0.3414	1.0758	0.1000	0.1203
	SD	0.5188	1.3736	0.1390	0.1627
-/-	Mean	29.5011	35.4663	21.7188	21.9117
	SD	32.9402	29.0701	36.9765	36.9117
+/-	Mean	12.5640	15.6700	11.0573	11.1537
	SD	28.1500	26.6214	28.9997	28.7860
+/0	Mean	0.8284	2.2766	0.2235	0.2634
	SD	0.9412	2.2639	0.2295	0.2646
-/0	Mean	19.5134	26.1670	12.3791	12.5908
	SD	26.2082	23.5428	28.5864	28.3371

Discussion

Inferring process from pattern across scales is a critical challenge for ecology, biogeography, as well as for other branches of science (Levin 1992). Our point-process models offer a novel and general framework for studying the signature of any type of

biotic interactions across scales. The results illustrate how relatively simple mathematical models can make testable predictions about species co-occurrence across spatial scales, thus enhancing understanding of community patterns in ecology. Specifically, our findings shed light onto the long-standing controversy of whether the geographical signature of biotic interactions is maintained across spatial scales (Wiens 1989, Schneider 2001). It is typically assumed that the geographical signature of biotic interactions is scale dependent, with climate structuring the broad outlines of species ranges and biotic interactions affecting patterns of local abundances (e.g, Whittaker et al. 2001, Pearson and Dawson 2003). Competition is often given as an example of the localized effects of biotic interactions (Connor and Bowers 1987, Whittaker et al. 2001, Pearson and Dawson 2003). Our extensive model simulations support the view that the spatial signature of negative interactions is sensitive to scale, i.e., exclusion by competitors or predators at local scales tends not manifest at coarser scales. In contrast, we also demonstrate that interactions involving positive dependencies between species, such as mutualism (+/+) and commensalism (+/0), are more likely to be manifested across scales. Consumer-resource interactions, such as predation, herbivory, parasitism, or disease (+/-) can also generate scale-independent patterns of coexistence providing that the dependency of the consumer on the resource is higher than the repulsion of the resource on the consumer.

Previous studies have suggested that consumer-resource interactions could modify the regional composition of species pools (Ricklefs 1987) and control for species range limits (Hochberg and Ives 1999) and diversity (Jabot and Bascompte 2012). Recent findings also highlighted the disproportionate effects of consumers in shaping local responses of resources to climate change (Post 2012). Our results generalize and extend these inferences. Specifically, we identify circumstances in which biotic interactions are likely to generate scale-invariant patterns of co-occurrence among species thus enabling us to propose a new scaling law: the degree to which the signatures of biotic interactions on local co-occurrences scale up depends on the strength of the positive dependencies between species.

Even though our simulations suggest that competitive interactions generate patterns of co-occurrence that tend not to scale up (for recent empirical evidence of the same pattern see also Segurado et al. 2012), there are circumstances in which the

consequences of competition are expected to be manifested at wide geographical extents and resolutions. Such is the case when competitive exclusion leads to splitting of species ranges at biogeographical scales (Hardin 1960, Horn and MacArthur 1972, Connor and Bowers 1987). To explore this exceptional circumstance we repeated our simulations for the extreme case of repulsion $I_A^- = 1$ and $I_B^- = 1$ (i.e., competition being such that species never co-occur), with highly spatially autocorrelated ranges and subject to varying degrees of range exclusion ($0 \leq \mu_{excl} \leq 1.5$, see supporting online material). With the extremes: 0 representing no enforced range exclusion, potentially leading to checkerboard distributions when ranges are not spatially autocorrelated (the rule used in all previous simulations); and 1.5 representing fully enforced range exclusion leading to range splitting with not edge contact (see supporting online material for more details). We find, as expected, that the greater the degree of exclusion (μ_{excl}) between the ranges of two competing species the greater the degree of scale independence of the resulting geographical patterns (Figure 4). For example, the area between the curves of the 'sampled' and 'true' co-occurrences when no range exclusion is enforced (μ_{excl}=0) is 77, while when full range exclusion is enforced (μ_{excl}=1.5) the area between the curves is 82. These areas between curves are, however, well above mean values across biotic interaction space (Table 1) thus supporting our conclusions regarding strong scale-dependence of the co-occurrence patterns with competition. Whether strong forms of range exclusion have an impact in structuring of regional species pools partly depends on the degree to which they are a common feature at biogeographical scales; this question is beyond the scope of our discussion (but see Connor and Bowers 1987).

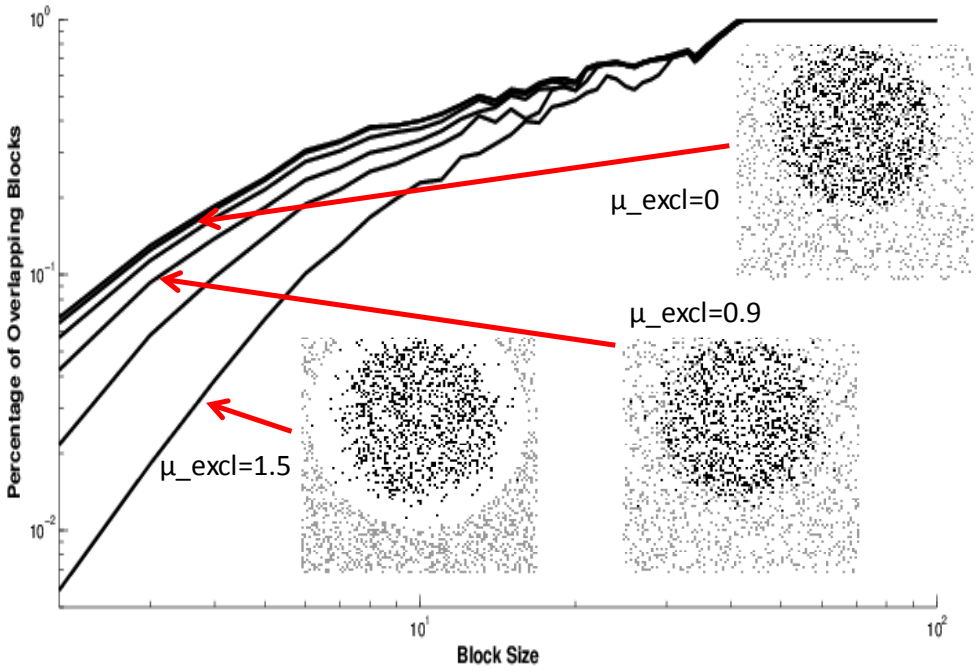

Figure 4 – **Variation in scale dependence of species distributional patterns arising from varying levels of competitive exclusion**. With extreme -/- interactions involving $I_A^- = 1$ and $I_B^- = 1$, populations of species A and B never co-occur. So, 'true' co-occurrence is zero (coincident with the x axis) independently of the size of blocks. By progressively increasing the size of the blocks, sampling leads to classifying species has co-occurring if both species occurred somewhere in the block (black lines). The greater the area between black lines and the horizontal x axis line the greater the scale dependence of distributional patterns arising from competition.

Our results have important implications for predictions of the effects of environmental changes on species distributions. For example, microcosms experiments have demonstrated that models of species responses to climate change that ignore competition and parasitoid-host interactions could lead to serious errors (Davis et al. 1998). However, our results suggest that errors arising from discounting the effects of competition would unlikely scale up to biogeographical scales (see also Hodkinson 1999). In contrast, models failing to account for strong positive dependencies between species would likely exclude mechanisms affecting species ranges across scales. Consistent with our prediction, studies have shown that mutualism (Callaway et al. 2002), commensalism (Heikkinen et al. 2007), predation (Wilmers and Getz 2005), herbivory (Post 2012) and parasitism (Araújo and Luoto 2007) could significantly affect species responses to climate change (see also Fordham et al. 2013). If predictions from

our models are correct, the bad news is that accurate predictions of climate change effects on species distributions would require the development of more complex models that include biotic interactions. The good news is that only a subset of all conceivable biotic interactions would likely matter. Since, most interactions between species are weak and non-obligate (Bascompte 2007, Araújo et al. 2011), and species with strong positive interactions are a subset of a relatively small number of species with strong interactions, the critical question would then be to identify the species with properties that are capable of affecting distributions and coexistence across scales. The task of identifying such species is of daunting magnitude, but is less so than documenting and modelling the full web of interactions among species.

Outlook

We are aware that our models can raise scepticism among empirical and theoretical community ecologists. The standard practice is to predict spatial-population processes from models that explicitly and dynamically account for consumer-resource interactions. Here, assumptions about these processes are implicit rather than explicit (arguably because they are impossible to parameterize in nature meaning that we need simplified models and assumptions to make progress). Instead, we characterize the spatial effects on coexistence of biotic interactions based on the expected attractive and repulsive consequences of these processes. The next step is to test our model predictions through extensive model-model (Rozenfeld & Araújo, unpublished) and model-data comparisons. By assuming distributions at steady-state the first comparison that becomes necessary is between expected co-occurrence of species achieved with dynamic Lotka-Volterra models and with static 'point-process' models like the ones proposed here. The problem with such comparisons is that consistency with predictions from alternative models lends to conditionally supporting them, but inconsistency leads to inconclusive results as we have no objective way to validate them unless we compare results with data (e.g., Araújo and Guisan 2006). Comparing model results with data is more powerful. However, such tests are difficult to undertake because fully-controlled and fully-replicated experiments at a variety of spatial scales are difficult to undertake and they are extremely costly (Marschall and Roche 1998). Furthermore, our predictions span a full spectrum of biotic interactions rather than focusing on specific types of interaction, thus adding an extra degree of difficulty to experimentation. A possible way forward is to compare predictions from models with smaller scale

experiments. They too have their limitations (Lawton 1998), but a pluralistic approach for testing models is likely the only possible way forward.

Acknowledgements

We thank François Guilhaumon and Michael Krabbe Borregaard for discussion, and Regan Early, Raquel Garcia, and François Guilhaumon for comments on the manuscript. MBA acknowledges the Integrated Program of IC&DT Call No 1/SAESCTN/ALENT-07-0224-FEDER-001755, and the Danish NSF for support of his research. AR is funded through a Portuguese FCT post-doctoral fellowship (SFRH/BPD/ 75133/2010).

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