



Espaço e diversificação:
uma perspectiva teórica

Space and diversification:
a theoretical perspective

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Dedicatória

À minha avó Irene,
por me ensinar a ver

Epígrafe

"Thoughts without content are empty, intuitions without concepts are blind. The understanding can intuit nothing, the senses can think nothing. Only through their unison can knowledge arise."

Immanuel Kant

"Every day should be a fight against the mundane."

RuPaul Charles

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Introdução Geral

Um prólogo poético

O Homem olha para a Natureza e vê padrões. O céu se separa das nuvens, frutas são doces mas folhas são amargas. Identificar um padrão é determinar uma escala onde a homogeneidade se rompe. Se sabemos que as noites são mais escuras que os dias é porque nossa atenção é detida por tempo suficiente para que percebamos a diminuição da luminosidade. No entanto, se nos perdêssemos olhando para o céu por centenas de anos, é possível que os dias e as noites se confundissem como as pulsações de uma lâmpada fluorescente e dessem lugar à clareza no discernimento dos ciclos de atividade solar.

Teorias científicas são abstrações de mecanismos através das quais tentamos compreender os padrões que colecionamos. Quando construímos teorias que nos permitem transportar informação entre escalas, ganhamos o poder de agrupar padrões aparentemente díspares em um corpo teórico abrangente. A Mecânica Estatística é um exemplo dessa arquitetura teórica: corpos com diferentes propriedades macroscópicas podem ser descritos a partir de uma teoria microscópica comum.

A abrangência do corpo teórico de muitas Ciências é contingente à hierarquização de padrões e teorias, e a Biologia não é uma exceção. Por exemplo, a generalidade de padrões ecológicos como fases de crescimento populacional exponencial, exclusão competitiva ou sucessão ecológica pode ser explicada a partir de processos de nascimento e morte comuns a todos os seres vivos. A Biologia é, entretanto, estruturada por um componente teórico pervasivo singular: a evolução.

Diferentemente do que ocorre com a Física ou a Química, as unidades mais fundamentais das teorias biológicas, os organismos vivos, são definidas por propriedades que estão em constante transformação. As escalas temporais e espaciais características dos padrões de evolução podem ser muito grandes quando comparadas ao tempo e área de vida de um organismo ou mesmo de uma população. Caracteres morfológicos podem transformar-se continuamente por milhões de anos e eventos de especiação podem ocorrer em escala planetária. A evolução é, portanto, guiada por padrões biológicos de

diversas escalas, mas seus resultados alteram as próprias dinâmicas que geraram esses padrões.

A Biologia é, assim, uma Ciência em que existem mecanismos de retorno entre escalas. Consequentemente a contextualização de um padrão biológico é contingente às dinâmicas de padrões passados. Em outras palavras, existe um caráter histórico inerente à Biologia. De fato, é difícil imaginar que a explicação para a presença de algum organismo em um determinado lugar possa ser independente dos processos que geraram a espécie à qual ele pertence ou que geraram as condições de que ele depende. Conversamente, o futuro de uma espécie será moldado pelos padrões para os quais essa espécie contribuir.

Nós, seres humanos, somos um instante em uma linha dentre os emaranhados da evolução biológica. Se vemos padrões, é porque nossos corpos foram moldados, por esses mesmos padrões, tornando-se máquinas de amplificação de contrastes. Se nossa visão é legado de nosso passado, por outro lado é ela que desenhará nosso futuro.

E o retorno ao pragmático

Desde o surgimento da vida, a Terra tem sido modificada de inúmeras formas por seus habitantes (Van Valen 1971). Atualmente, a espécie motriz dessas transformações tem sido o próprio ser humano. Por volta de 20% da superfície terrestre foi convertida em áreas urbanas, pastos ou extensões agrícolas (Olson, Watts, and Allison 1983) e aproximadamente 40% da produção primária líquida terrestre é apropriada por atividades humanas (Vitousek et al. 1986). As áreas relativamente intocadas remanescentes foram fragmentadas (Saunders, Hobbs, and Margules 1991), estão sujeitas a transformações na composição atmosférica e a mudanças climáticas (Forster et al. 2007). É seguro dizer que a interferência humana é uma força pervasiva em todos os ambientes do planeta (Vitousek et al. 1997).

O uso desproporcional dos recursos terrestres por parte dos seres humanos impactou profundamente a biodiversidade. Taxas de extinção se elevaram consideravelmente por toda a árvore da vida, e são comparáveis às das grandes extinções em massa do passado (Pimm et al. 1995). Além disso, a escala sem precedentes com que as invasões biológicas têm ocorrido desde a expansão da civilização ocidental assim

como a reorganização da biota causada por essas invasões são características únicas da fase atual de extinções (McKinney and Lockwood 1999). A habilidade de proteger o que restou da biodiversidade e restaurar ecossistemas degradados pode ser instrumental para a manutenção da prosperidade humana, e para isso é fundamental que compreendamos os padrões de biodiversidade e os processos pelos quais ela emerge e é mantida.

Tradicionalmente comunidades biológicas foram vistas como conjuntos estáveis de organismos que interagem direta ou indiretamente. As investigações a respeito de biodiversidade foram, portanto, por muito tempo pautadas pelo princípio da exclusão competitiva (Hardin 1960). De acordo com esse paradigma, a riqueza de uma comunidade pode ser interpretada como uma partição de um espaço de recursos, e o bloco da partição associado a cada espécie corresponde a seu nicho (R. MacArthur 1970). Para muitas comunidades, entretanto, a riqueza de espécies é consideravelmente maior que as partições do espaço de recursos baseada na eficiência de uso dos recursos (Hutchinson 1961). Muitos trabalhos foram dedicados a expandir a capacidade de suporte de diversidade teórica de ambientes com tipos finitos de recursos, usualmente recorrendo à heterogeneidade temporal (Tilman and Pacala 1993) ou espacial (Amarasekare and Nisbet 2001). Os modelos resultantes são extremamente ricos em parâmetros e não iluminam muito questões a respeito da consistência dos padrões de biodiversidade por diversos ecossistemas e clados (Hubbell 2001).

Em oposição à perspectiva clássica de que comunidades são montadas a partir de regras de partição de nichos, MacArthur e Wilson propuseram que a riqueza de espécies de ilhas poderia ser explicada como sendo resultante de um equilíbrio entre colonização e extinção. A teoria da biogeografia de ilha que propuseram incorporou à interpretação de padrões de biodiversidade três novos elementos. Em primeiro lugar, foi introduzida a idéia de que a estabilidade da biodiversidade de uma comunidade não necessariamente é consequência da persistência de suas espécies. Muito pelo contrário, é esperado que cada espécie seja em algum momento extinta e que novas espécies imigrantes ocupem seu lugar. Em segundo lugar, a ausência de uma espécie pode ser entendida pela falta de uma oportunidade de colonização, e não como a incapacidade de ela se estabelecer, talvez pela escassez de algum recurso. A teoria da biogeografia de ilha é, portanto, uma teoria de montagem por dispersão. Finalmente, a teoria da biogeografia de ilha se propõe a

explicar a biodiversidade sem ter de recorrer às particularidades fisiológicas de cada espécie (MacArthur and Wilson 1967).

Inspirado pela teoria da biogeografia de ilha, Hubbell desenvolveu sua teoria neutra unificada da biodiversidade e biogeografia, na qual incorporou limitação de dispersão, estocasticidade demográfica e especiação. A neutralidade da teoria reside na hipótese de que indivíduos pertencentes a qualquer espécie são demograficamente equivalentes. O grande sucesso dessa teoria neutra foi a capacidade de com poucos parâmetros produzir distribuições de biodiversidade extremamente similares às aquelas observadas na natureza (Hubbell 2001).

A especiação é um aspecto fundamental da teoria neutra, pois é ela que equilibra as extinções que inexoravelmente acompanham a estocasticidade demográfica. Originalmente Hubbell conjecturou que diferentes modos de especiação produziriam pouco impacto nas previsões da teoria neutra (Hubbell 2001). Trabalhos posteriores revelaram, no entanto, que as particularidades de cada modo de especiação afetavam drasticamente as distribuições de diversidade preditas (Rosindell, Hubbell, and Etienne 2011). Foram desenvolvidas versões da teoria neutra que incorporavam uma miríade de modos de especiação como fissão aleatória da espécie progenitora (Etienne and Haegeman 2011), emergência de espécies com tamanhos iniciais fixos e emergência de espécies com tamanhos iniciais sorteados de distribuições (Hubbell 2003). No entanto todas essas implementações são modelos fenomenológicos de especiação. Os critérios para a fissão de uma espécie, que poderiam ser inspirados em qualquer uma das muitas definições de o que é uma espécie (Coyne and Orr 2004), e os mecanismos pelos quais esses critérios são atingidos nunca são explicitados.

É possível que ausência de especificação de uma definição de espécie e de um correspondente mecanismo de especiação venha da percepção de que a maior parte desses mecanismos viola a neutralidade (Coyne and Orr 2004). Uma implementação consistente da teoria neutra com mecanismos explícitos de especiação depende do desenvolvimento de um modelo neutro e mecanístico de especiação. As paisagens adaptativas esburacadas propostas por Gavrilets forneceram um cenário quasi-neutro sobre o qual um mecanismo de especiação neutro pode ser definido (Gavrilets 2003). Simulações espaciais adotando modos de especiação realistas baseados em paisagens

adaptativas esburacadas geraram distribuições de diversidade compatíveis com as previsões originais da teoria neutra e também com padrões observados (de Aguiar et al. 2009). Posteriormente foi mostrado que esse tipo de mecanismo de especiação é contingente às propriedades geográficas das simulações (Martins, de Aguiar, and Bar-Yam 2013).

Na natureza organismos frequentemente estão espaçados irregularmente pelo ambiente (Plotkin et al. 2000). Dentre as explicações mais comuns para a heterogeneidade na distribuição de organismos está a heterogeneidade subjacente de algum recurso ou condição ambiental. Entretanto um ambiente homogêneo também pode ser o palco de distribuições heterogêneas de organismos: apenas interações entre organismos e padrões de migração são suficientes para a emergência de padrões de distribuição não aleatórios dos organismos (Turing 1952). O mecanismo gerador de padrões espaciais mais geral, no entanto, pode ser a própria natureza auto-replicante dos organismos associada à correlação entre a posição dos progenitores e da prole (Bolker and Pacala 1997).

O presente trabalho aborda aquela que talvez seja a questão mais revisitada da Ecologia: de que forma o espaço limita a biodiversidade? Meu objetivo principal é explorar uma perspectiva heterodoxa para este problema: a idéia de que os padrões espaciais intrínsecos a comunidades possam influenciar os padrões de especiação e portanto a biodiversidade destas comunidades. Me propus a caracterizar os padrões de biodiversidade emergentes de sistemas com diferentes padrões espaciais e identificar os mecanismos através dos quais esses diferentes padrões de biodiversidade pudessem surgir. Espero assim lançar alguma luz sobre um dos elos das complexas possibilidades de interação entre escalas biológicas.

A phase transition in speciation modes can unify biodiversity patterns

Abstract. Some of the most consistent ecological patterns encountered in nature, such as species-area relationships and rank-abundance distributions, can be predicted from a class of neutral models. In this context, neutrality means demographic equivalence between individuals of all species. Within this class of neutral models, species extinction by demographic fluctuations is counterbalanced by some speciation mechanism. Each particular speciation mode leaves an imprint in the resulting patterns. A model with a mechanistic speciation implementation was shown to generate patterns dependent on geographic constraints. I used individual based simulations with a mechanistic speciation implementation to investigate whether the intrinsic spatial patterning of organisms could transform biodiversity patterns. I found out that there is a phase transition on speciation modes that is dependent on the spatial structure of the community. An extended range of the biodiversity patterns found in nature can be unified into a single model because of this phase transition. Clade richness and age relationships may be understood by the predicted critical slowdowns in diversification. A new interpretation is given to the post mass extinction "Dead Clade Walking" effect. An objective and biologically reasonable redefinition of allopatric speciation is explored by exploiting the phase transition. I propose the "speciation credit" effect, and its potential implications for long term biodiversity conservation.

Introduction

Since the advent of life, Earth has been modified in many ways by its inhabitants (Van Valen 1971). Most recently it is the human species that has been driving this change. Around 20% of the terrestrial surface was converted into urban areas, pastures or agricultural expanses (Olson, Watts, and Allison 1983) and an estimated 40% of the

terrestrial net primary production is appropriated by human activities (Vitousek et al. 1986). The remaining relatively untouched areas have been affected by fragmentation (Saunders, Hobbs, and Margules 1991), shifting atmospheric composition and climate change (Forster et al. 2007). It is safe to say that human interference is a pervasive force in all of Earth's environments (Vitousek et al. 1997).

Such a disproportionate use of Earth's resources by humans has taken its toll on biodiversity. Extinction rates have risen sharply throughout the tree of life and are comparable to those of the great mass extinctions of the past (Pimm et al. 1995). Furthermore, the unprecedented scale of biological invasions that accompanied the spread of western civilization and the resulting biota reorganization are unique features of the ongoing extinction process (McKinney and Lockwood 1999). The ability to protect remaining biodiversity and restore degraded ecosystems might be instrumental to the continuation of human prosperity, and for that we must understand biodiversity patterns and the processes by which they arise and are maintained.

Biological communities have traditionally been viewed as stable ensembles of interacting organisms and the study of biodiversity has therefore been lined by the principle of competitive exclusion (Hardin 1960). Within this framework the richness of a community is interpreted as a partition of a resource space, and the partition block associated to each species is its niche (MacArthur 1970). Yet, the species richness of many communities is far superior to any reasonable niche partitioning based on resource use efficiency (Hutchinson 1961). Much effort has gone into expanding the theoretical diversity capacity of environments with finite resource types, often resorting to spatial (Amarasekare and Nisbet 2001) or temporal heterogeneity (Tilman and Pacala 1993). The resulting models are extremely parameter rich and do not shed much light on the remarkable consistency of biodiversity patterns throughout ecosystems and clades (Hubbell 2001).

Contrasting to the classical niche assembly perspective, MacArthur and Wilson proposed that species richness of islands could be explained as an equilibrium between colonization and extinction. Their theory of island biogeography incorporated three new elements to the interpretation of biodiversity patterns. First, that persistence of species is not imperative for stable biodiversity, on the contrary, that species are expected to go

locally extinct and be replaced by new immigrants. Second, that the absence of a species might be due, not to some resource limitation, but to it not yet having reached that location: the theory of island biogeography is therefore a dispersal assembly theory. Finally, the theory of island biogeography sets to explain biodiversity without resorting to the physiological differences between species (MacArthur and Wilson 1967).

Inspired by the theory of island biogeography, Hubbell developed what he dubbed the unified neutral theory of biodiversity and biogeography, which incorporated dispersal limitation, speciation and demographic stochasticity. The neutrality of the theory refers to the assumption that individuals from different species are demographically equivalent. This neutral theory achieved great success in that with very few parameters it mechanistically produced biodiversity distributions that fit remarkably well many of the distributions encountered in nature (Hubbell 2001).

Speciation is a fundamental aspect of the neutral theory, as it offsets the inevitable extinctions that come with demographic stochasticity. Originally Hubbell conjectured that speciation modes would have little impact on the neutral theory's predictions (Hubbell 2001), but it was later shown that the particularities of each speciation mode had drastic outcomes on the predicted biodiversity distributions (Rosindell, Hubbell, and Etienne 2011). Versions of the neutral theory were developed incorporating many speciation modes such as random fission of the parent species (Etienne and Haegeman 2011), emerging species with fixed size and emerging species with size drawn from a variety of distributions (Hubbell 2003). All of these implementations, however, are phenomenological models of speciation in that the criteria that establish fission, which could be drawn from the vast pool of species definitions (Coyne and Orr 2004), and the mechanisms by which these criteria could be achieved are never explicated.

The avoidance of specifying a species definition and a speciation mechanism might come from the perception that most of these mechanisms violate neutrality (Coyne and Orr 2004). A consistent implementation of the neutral theory with explicit speciation mechanisms depends on the development of a neutral model of mechanistic speciation. The holey adaptive landscapes proposed by Gavrillets provided a quasi-neutral setting over which such a neutral speciation mechanism could be defined (Gavrillets 2003). Spatial simulations conducted adopting realistic speciation modes based on holey

adaptive landscapes showed good agreement with Hubbell's original predictions and with observations (de Aguiar et al. 2009). Latter work revealed, however, that realistic implementations of speciation were contingent on the geographical properties of the simulations (Martins, de Aguiar, and Bar-Yam 2013).

It is known that organisms are frequently irregularly spaced on their environments (Plotkin et al. 2000). Explanations for this heterogeneity in spatial distribution range from an actual spatial heterogeneity in resource distribution to patterning that emerges through interaction between organisms and dispersal (Turing 1952). Most generally, however, the self-replicative nature of individuals, and the expected correlation between the location of parents and their offspring is enough to induce spatial distribution heterogeneity (Bolker and Pacala 1997). This work explores how can these realistic spatial patterns in organism distribution affect speciation mechanisms and consequently determine biodiversity patterns.

Methods

The model

Simulations were performed using an agent based model. At the beginning of each run, individuals, which in some simulations could be predators or preys, were randomly placed at a grid. During a generation, individuals had the opportunity to take each of three actions: reproduction, death and migration.

Whenever a individual would migrate it would be repositioned on the grid on a random position drawn from a square area centered around its original position. Typically, the migration squares would be comprised by nine lattice units, but in some simulations predators were assigned larger motility. If an individual would be placed beyond the limits of the lattice, the steps that it would take outwards were instead reflected so that individuals could never leave the grid.

Following (de Aguiar et al. 2009) each prey was endowed with a haploid binary genome of 100 loci, initially all set to zero. In order to reproduce, a prey would select a potential mate within a geographic and genetic distance. The genetic distance between

two individuals was defined as the number of mismatched alleles in their genomes. Initially, the geographic search radius was six and the maximum genetic distance allowed was twenty. If a prey failed to find a potential mate, both the geographic and genetic search distances were progressively expanded until a mate could be found. The progeny was placed at the same site as its parent, with a genome built from a recombination of the parent and mate's genomes, with added point mutations occurring at some rate. As in (Martins, de Aguiar, and Bar-Yam 2013), at each generation, each individual would be replaced by an offspring, but also had the opportunity to leave an additional descendant with some reproduction probability. Different genomic recombination schemes were used, such as independent allele segregation and single point crossover with a random breaking point.

Considering an all-or-nothing system for reproductive compatibility may seem arbitrary and unrealistic at first glance. It has been shown, however, that such a threshold compatibility function arises from a certain generalization of Bateson-Dobzhansky-Muller (BDM) incompatibilities (Gavrilets 2003). BDM incompatibilities, which are essentially pairs of genes that, if co-occurring, would render a genome unviable, were proposed to explain how the genome of diverging populations could eventually reach a degree of isolation through mutual incompatibility without ever reducing each population's fitness (Bateson 1909; Dobzhansky 1937; Muller 1942). It suffices that there exists a sequence of allelic substitutions such that at any given moment no pair of alleles in a population is responsible for a BDM incompatibility. This idea was later expanded to allow for incompatibilities being defined by larger sets of alleles. Alleles which might be involved in higher order BDM incompatibilities have lower chances of being purged by natural selection than those involved in lower order BDM incompatibilities, which is argued to be a reason for higher order BDM incompatibilities to be more common in nature (Orr 1995). Increasing the order of the BDM incompatibilities quickly leads to a viability threshold function of the genetic distance like the one adopted (Gavrilets 2004).

In accordance to the biological species concept, a species was defined to be a maximal set of organisms such that a path can be built between any pair of elements by connecting those which are genetically compatible (Mayr 1942; Templeton 1989). In other words, a species is a set of organisms which are each genetically incompatible with

all other organisms, and such that any two organisms may, through some breeding series, generate common descendents.

Three types of systems were simulated:

- One dimensional system with no local density dependent rates (1D)

A one dimensional system was approximated by means of a rectangular grid measuring 8192 x 8. The population was kept at a constant size. Deaths occurred with constant probability per individual per generation. Whenever an individual died, a neighbor within the reproductive range was randomly selected to produce an offspring that would take the place of the deceased. As births and deaths are associated and cancel each other out, there are effectively no population dynamics, and organisms are always homogeneously distributed.

- Two dimensional system with no local density dependent rates (2D-H)

The space for these simulations consisted of a 256 x 256 grid. The populations were also kept at a constant size. Reproductive dynamics took place as in the 1D systems. Consequently, at any given time organisms are also homogeneously distributed.

- Two dimensional system with local density dependent rates

The space for these simulations also consisted of a 256 x 256 grid. For these simulations, reproduction and death probabilities were functions of population densities around each individual. Two different kinds of dynamics were explored.

1- *Single guild systems with density dependant rates (2D-SG)*. Reproduction probabilities were constant for all individuals. Death probabilities, however, were a linear function of the local organism density of which the inclination can be interpreted as a competition parameter. Local organism density was calculated on a surrounding square area, and three different sizes were simulated (9, 49 and 121 lattice units).

2- *Predator prey systems (2D-PP)*. Reproduction probabilities were constant for all prey individuals. Death probabilities were constant for all predator individuals. Predator reproduction probabilities were assumed to be a saturating increasing function of the prey density given by $r_p(v)$ where α represents the maximum predator attack probability and v is the local prey density.

$$r_p(v) = \alpha \frac{v}{v + 1}$$

Prey death probabilities were the same as in the 2D-SG systems, with an additional mortality by consumption probability given by $\mu_v(v, p)$, where p is the local predator density.

$$\mu_v(v, p) = \alpha \frac{\frac{p}{v}}{\frac{p}{v} + 1}$$

For these simulations, local organism density was always calculated on a surrounding square area measuring 9 lattice units. Supplementary simulations where predator death rates were linear functions of predator density were also explored for robustness.

Parameter sweeping

Predator-prey dynamics can follow a multitude of dynamical behaviors. The solution of a Lotka-Volterra like differential equation with density dependent rates can converge to a fixed point representing either stable coexistence of both guilds, the extinction of the predator guild or total extinction. Alternatively, the solution can converge to a stable cycle with alternating peaks of predator and prey populations (Rosenzweig and MacArthur 1963). When spatial effects and the random fluctuations intrinsic to individual based simulations are factored in, even chaotic behavior might emerge (Baurmann, Gross, and Feudel 2007; Wilson, Deroos, and McCauley 1993).

Population fluctuations are known to have important effects on the genetic structure of a population (Wright 1931), and are central in some proposed scenarios of speciation (Gavrilets and Hastings 1996). Extinction rates are also thought to be affected by population sizes, increasing with small populations (Caswell 1976). However, the focus of this work is on the influence of spatial patterns on diversification processes, and

in order to minimize the confounding diversification patterns generated by global population bottlenecks, demographic parameters were restricted to the portion of the parameter space that results in stable population points.

For a generic system with demographic stochasticity, there is no guarantee that, given initial conditions, the trajectory described by the population sizes will ever be bounded. Also, demographic stochasticity might induce resonant oscillations and the distinction between a stable point and a limit cycle is, therefore, clouded (McKane and Newman 2005). For the purpose of this work, however, it suffices that population fluctuations be somewhat contained. I considered that a simulation has reached a stable population size if its coefficient of variation is below five percent.

The effective population size is also critical for diversification processes and acts in composite fashion. Having more individuals means more genetic variants arise, which is fundamental for speciation (Kondrashov 2003). A larger population can, however, sustain a longer bridge of genetic intermediaries between two diverging populations, which could possibly hinder speciation (de Aguiar and Bar-Yam 2011). To control for these effects, the simulated maximum predator attack probability and prey competition parameters were selected from a hypersurface of the parameter space that yielded the same mean population sizes (ten thousand individuals).

The variance in reproductive success enjoyed by the individuals is also an important factor influencing effective population sizes (Wright 1938). In a system that has reached a population size equilibrium, for one time step, the probability that an individual reproduces is equal to the mean probability that an individual dies. If individuals live enough so that we can approximate each of their average death probabilities per time step by the population's average death probability per time step, then it is reasonable to assume that the variance in reproductive success is a function of only the per time step reproduction probability. To minimize the influence of the variance in reproductive success, all simulations were performed using the same reproduction probability per time step (fifteen percent).

The migration distance of the prey is also expected to affect the rate of speciation, as it promotes the spread of emerging genetic diversity, and consequently decelerates regional differentiation (de Aguiar et al. 2009). Because of this, comparisons where only

drawn between simulations where prey migrated taking the same step sizes (one lattice unit). On the other hand, three different maximum migration distances were simulated for predators (one, ten and thirty lattice units).

For each set of demographic parameters selected, simulations were ran once for each mutation rate between fifty and three hundred per ten thousand. Each run lasted fifteen thousand generations, throughout which species numbers were registered as well as the position of each individual of each species.

Spatial analysis

Ripley's K function is a common way to describe spatial clustering. It represents how much more crowded it is in a region around an individual than what would be expected if individuals were evenly spaced (Fortin and Dale 2005). I wish to extract from the K function some statistics that encapsulate the geographical features that might influence speciation. The number of clusters together with the typical cluster radius of a geographical pattern can be used to estimate the mean distance between clusters, which can be taken as a measurement of the geographical isolation imposed by the patterning. The K function, however, does not provide a direct estimate of the typical size of a cluster or the number of clusters in a observed pattern.

The Matérn cluster process is a model for spatial patterning. It is defined by poisson distributed cluster seeds, around which points are distributed according to uniform distributions with a certain radius. Three parameters are needed to completely specify a Matérn cluster process: the parameter of the poisson distribution of the seeds, the cluster radius and the mean point density. The expected K function of a Matérn cluster process realization is well known, and this can be explored to find parameters that specify a Matérn cluster process with an expected K function that has a minimal distance from the K function of an observed pattern (Stoyan 1992). The parameters of the optimized Matérn cluster can then be used to characterize observed patterns in terms of cluster sizes and distances (Plotkin et al. 2000).

For each set of demographic parameters selected during the parameter sweep, simulations were ran for fifteen thousand generations. Every generation, the position of each individual was registered, and a the resulting spatial pattern was fitted with a Matérn

cluster process. This was performed using the `kppm` function of the `spatstat` R package. Mean parameter values of the fitted Matérn cluster processes were used as the descriptive spatial statistics for each simulation.

Paralyzed spatial patterns

Simulations were also performed in environments with non dynamic spatial patterns. For each set of demographic parameters selected for 2D-PP and 2D-SG simulations, a corresponding paralyzed spatial pattern was created by choosing a random generation of each of these simulations and registering the position of each individual. Parallel simulations were then performed having each of these paralyzed patterns as starting positions for individuals.

Migration was disabled for these simulations. Two different death mechanisms were tested: equal death probabilities for all individuals, as they were in the 1D and 2D-H simulations or preserve the death probabilities defined by the spatial patterns. Regardless of the mode of assignment of death probabilities, whenever an individual died, it was replaced by the offspring of some neighbor on its reproductive vicinity. The initial spatial patterns were thus preserved throughout the full course of these simulations.

The main difference between both death-birth mechanisms is that assuming a constant death rate throughout all of the population ensures a constant birth rate for the whole population, as in the dynamic pattern systems. However, this mechanism also implies that the variability in offspring production is constant throughout the range of the simulation, whereas in the dynamic pattern systems regions with higher mortality rates would have larger fecundity variability. For each initial paralyzed pattern, mutation rates were swept as was done for 2D-SG and 2D-PP simulations.

Results and Discussion

General patterns of diversification

Through the course of the simulations, diversification occurred in up to two stages. In accordance to earlier work (de Aguiar et al. 2009), an initial period of

diversification rapidly ceased as raising extinction rates counteracted speciation. After this initial diversification phase, two distinct behaviors were observed in the simulations. Single-stage simulations quickly reached a biodiversity steady state, extinction rates balancing out speciation. Two-stage simulations, however, exhibited a second diversification period, typically occurring over a different timescale than the first, leading finally to the steady state (figure 1).

All simulations that took place in one-dimensional environments followed the single-stage diversification behavior. On the other hand, simulations set in two-dimensional environments exhibited both possible behaviors. For a given set of demographic parameters, which determines a spatiotemporal organism distribution pattern (figure 2), and a given genetic architecture, there is a critical mutation rate above which the system will display the second diversification stage. For simulations that generate patchier organism distributions in space, the critical mutation rates are lower (figure 3). In fact, the largest critical mutation rate was found for the simulations lacking predators and with no local density dependence on death rates.

The existence of a critical mutation rate was consistent throughout all genetic architectures simulated, as well as for all the spatial pattern generating mechanisms. This indicates that this effect is probably not an artifact of a particular implementation of the model. Accordingly to ecological data and previous theoretical investigations, simulations set in one-dimensional environments reached a more biodiverse steady state than those set in two-dimensional environments (de Aguiar et al. 2009; Moyle and Cech 2004), as long as the mutation rates were below the critical value. However, for mutation rates above the critical values, the species richness steady states for simulations ran in both one and two-dimensional environments were equivalent regardless of the mechanism behind the spatial patterning (figure 3) as well as the species distributions (figure 4).

The two-stage diversification behavior hints that there might be more than one process responsible for the fragmentation of a species. The second stage is in many ways distinct from the first: it might take its course over a much longer time scale than the first, richness levels often lingering at what seems to be intermediate semistable states. The second stage diversity transients seem to be influenced by particular spatial histories the

system might have gone through, which is not the case for the first stage transients (figure 1B). I propose that these diversification behaviors are associated with two distinct spatial features in the distribution of a species: the clumping within the range of a species and the borders of the range.

For mutation rates below the phase transitions shown in figure 3, diversification is always a single stage process which leads to biodiversity patterns that closely match those of less clumped systems. The corresponding paralyzed pattern simulations are slightly more diverse than the dynamic ones, which is to be expected, as the lack of migration reinforces spatial isolation (Gavrilets, Li, and Vose 2000). The diversification patterns and equilibrium biodiversity are not qualitatively affected by the paralysis of the spatial pattern. The insensitivity of the diversification process to diminishing clumping for pre-critical simulations leads to the conclusion that the most important spatial feature in these systems should be the border of a species range. If this were indeed the case, new species would arise close to the periphery of the mother species range, budding of a poorly connected lobe. The breaking point between the species would be extremely asymmetric. In fact systems displaying this pattern of diversification have rank-abundance distributions that are very well fit by a zero-sum multinomial (figure 4B), which is derived from neutral dynamics assuming a maximum asymmetry speciation mode (Hubbell 2003).

For mutation rates above the phase transitions shown in figure 3, simulations display the second diversification stage. Notwithstanding the corresponding paralyzed pattern simulations never undergo the second diversification stage, which is therefore dependent on the temporal dynamics of organism clumping. It follows that the spatial patterning within species range must be an important driver for the second stage of diversification. As the clumps arise independently of the species range, they are expected to break the species in random chunks, and speciation events induced by these breaks are expected to have random breaking points. Accordingly the rank-abundance distributions of systems that undergo the second diversification stage are very well fit by a broken-stick distribution (figure 4D), which is derived when the point speciation process in Hubbell's neutral biodiversity theory is replaced by random fission speciation (Etienne and Haegeman 2011).

The one-dimensional space simulations display no spatial patterning, and therefore the only spatial feature of a species distribution is the species range border. However, the one dimensionality implies that all individuals of a species are in some sense close to the border of the species range. This increased symmetry on the geometrical properties of the individuals of a species favor random breaking points for speciation, and, accordingly, the rank-abundance distributions of these systems are very well fit by a broken-stick distributions (figure 4C). It is worth pointing out that MacArthur first proposed his broken-stick distribution thinking about a one dimensional resource being randomly partitioned (MacArthur 1957). I obtain the same species distribution in a neutral setting with a one dimensional space taking the place of the original one dimensional niche.

Spatial organization of biodiversity

Both 1D simulations and post critical 2D simulations converge to very similar species abundance distributions, because both display spatial mechanisms that promote random species fission. The diverse nature of these mechanisms is reflected not only on the different time-scales at which they act (figure 1B), but also on the distinct species-area relationships that they generate (figure 5). 1D simulations resulted in biphasic species-area relationships that were consistent with earlier theoretical results, both analytic and simulation based, that considered point mutation speciation and two-dimensional space (Durrett and Levin 1996; Hubbell 2001). The transition between phases occurs close to area sizes where exactly one species can be found, and the inclination of the species-area curve approaches unity for the second phase. Such high slopes for the second phase denote that species accumulation becomes proportional to the sampled area, and consequently that there is a lack of species with ranges comparable to the system size (Durrett and Levin 1996) and are common in nature when the sampled areas are very large (Rosenzweig 1995). The slope of the first phase is very shallow, which can be interpreted as very little superposition of the ranges of different species.

The inflection point of such a curve can be interpreted as the typical range of a species, and is the dominating spatial scale for the diversification process. In a system with point mutation speciation, this inflection point corresponds to an area with radius

known as correlation length which is expected to be proportional to the inverse of the square root of the speciation rate (Durrett and Levin 1996). This is because, when speciation is a point mutation process, there is a strong correlation between the age of a species and its range. Namely, a species can be found as far as it has random walked since it came into being. Conversely, in a system with random fission speciation and little range superposition, there is no relation between the range of a species and its age. The random fission rate is a factor determining the equilibrium number of species, and the mean species range is the total system area divided by the number of species, which is very close to the inflection point obtained for the species-area curves for 1D.

The species-area curves for 2D simulations are markedly different from those of 1D simulations. Instead of the shallow species-area curves that 1D simulations generate for small areas, a much steeper initial slope is obtained for 2D simulations. As sampled areas increase, an inflection point leads the species-area curve to a less inclined section. This kind of inflection is very common in nature, and is usually explained as a sampling effect on a homogeneous patch, an interpretation that is corroborated by analytic results (Hubbell 2001). It is interesting to note that for the 2D simulations with spatial patterning, the position of this inflection is close to the typical area sizes of clusters of those patterns.

If the second stage of diversification that is displayed by post critical 2D simulations is indeed driven by the spatial patterning, then one would expect that the species-area relationships of a system with a mutation rate just below the critical value and of a system with a mutation rate just above the critical value should only diverge for areas larger than those of spatial clusters. Accordingly, post critical 2D systems have a triphasic species-area relationship, with a second inflection point located just above maximum cluster area sizes, beyond which the slope increases as in the 1D systems. The correlation range for post critical 2D systems is therefore more related to the parameters that determine the spatial patterns than to the species fission rate itself. There is evidence for correlation ranges being determined by biogeographic patterning in nature. Families of Panamanian trees and shrubs have distinct biodiversity patterns, and are thus expected to have characteristic speciation and dispersal rates. They do, however, have the same correlation range (D'Arcy 1987; Hubbell 2001), just as the presented findings predict for

families with different genetic structures but immersed in a common biogeographic pattern.

It is curious that pre critical 2D systems have biphasic species-area curves, with no clear correlation range, in discordance with most similar works, analytic or simulation based. One fundamental theoretical difference might be responsible for this divergence. Even though pre critical speciation is a very asymmetric fission process, which approximates a point mutation process, it is spatially structured in a different way. What limits the range of a species in a model with point mutation speciation is the occurrence of a speciation event on the expansion front of a species. The new species then proceeds to expand in place of its progenitor. In the pre critical 2D simulations, however, fission tends to occur towards the borders of the range of a massive species, which means that small nascent species are protected from fission until they have expanded enough. This leads to species ranges comparable to the size of the system, and therefore no correlation range.

Biodiversity transients

In nature, it is not just the individual abundances that are unevenly distributed over the species richness. Species diversity is also remarkably uneven throughout the tree of life (Hodkinson and Parnell 2010). Two kinds of explanations are usually given to why some clades are richer than others. Any diversification process must eventually hit some bound. It is impossible, for instance, to have more species than there are individuals in a guild. If clades have reached a diversity equilibrium, then the difference between the diversities of each clade should be explained by the particular diversity dependencies that regulate the diversification processes (Head and Rodgers 1997; Hubbell 2003). On the other hand, if clades are still away from the diversities for which diversification rates become regulated, a major factor for the differences in clade diversity should be clade age (Ricklefs 2007).

It is believed that for the vast majority of extant clades there is no correlation between clade diversity and age (Rabosky, Slater, and Alfaro 2012). This is consonant with earlier theoretical work as well as with the results here presented. Simulations reach a diversity equilibrium very fast, so the relation between clade age and diversity fades for

all but the youngest clades (Rabosky 2009). Accordingly, the pattern of very brief diversification transients seems to be widespread in nature (Jaramillo, Rueda, and Mora 2006). There are, however, groups for which the age-diversity relation is robust, and previous theoretical work has not addressed why this should be possible albeit rare. The two stage diversification process here proposed might be the solution for this conundrum.

Distinct clades have different typical birth and death rates, different migration patterns and inhabit different geographies. They also have different mating mechanisms, genetic architectures and even different per generation mutation rates. This can be interpreted as each clade being defined by a unique sample of the genetic and demographic parameter space. Over the subset of the parameter space for which simulations had a one stage diversification processes, richness equilibrium was swiftly achieved. For two stage simulations, however, the time-frame of the second diversification stage was dependent on how far from the critical point was the mutation rate. Much longer diversification transients were observed for simulations with a mutation rate just above the critical point. This is a case of critical slowdown, and is a hallmark of systems undergoing phase transitions (Scheffer et al. 2009). For the rare clades that are represented by this narrow slice of the parameter space, the positive age-diversity relationship would be expected. More so, if this is the true explanation for the existence and rarity of the age-diversity relationship, all clades that display such relationship would be expected to be undergoing the second stage of diversification, and would, therefore, be expected to be more biodiverse than the average clade. This appears to be the case, with only relatively biodiverse clades displaying the age-diversity relation (Rabosky, Slater, and Alfaro 2012).

What does allopatry mean?

The most prevalent system of mode of speciation classification is based on the spatial context in which divergence occurred (Coyne and Orr 2004). Geographical structure is commonly summarized as a one-dimensional quantity: the gene flow between diverging populations. Most theoretical work has been conducted on the extremes of this spectrum: sympatry, in which geography does not hinder gene-flow at all and allopatry, in which geography prevents all gene flow between the diverging populations (Gavrilets

2003). Much criticism has been drawn towards this framework (Butlin, Galindo, and Grahame 2008). It has been pointed out that total isolation is probably very rare in nature, as is attested by the colonizing capacities of many species (Endler 1977). Also, the total lack of spatial structure assumed in strict sympatry models can only be observed for very specific reproductive strategies, as broadcast spawners with planktonic larval stages (Gavrilets 2003). Additionally, there is no reason to suppose beforehand that the whole process of speciation elapses within a single spatial context (Bolnick and Fitzpatrick 2007). Therefore, most, if not all, speciation events must have occurred in parapatry, that is, with an intermediate intensity of gene flow.

The further one drifts from the extreme points of the gene flow spectrum, the more problematic it becomes to project the entirety of the spatial structure over a one dimensional parameter. This caricature might be useful to describe situations of well mixed populations or total isolation, because these conditions imply that any two paths connecting populations are roughly equivalent. However, there is no good mathematical reason to disregard spatial complexity when one can no longer assume connectivity symmetry between populations. The importance of a higher order of spatial organization for speciation has been acknowledged, at least verbally, for a long time (Mayr 1982).

Much has been said about which parts of the range of a species are more prone to see a speciation event. Proponents of peripatric speciation argue that lower population densities on the periphery of a species range could be responsible for lower patch connectivity and more genetic drift, which would culminate in a boost of speciation rates (Mayr 1982). On the other hand, most of the genetic diversity of a species, which is understood to be an essential ingredient for speciation, arises at the center of a species range, which makes a case for speciation being more common at the core of a species range (Brown 1957). To tackle this controversy one must adopt a theoretical framework capable of describing multiple spatial scales and, therefore, a single parameter description of space is unsuitable (Gavrilets, Li, and Vose 2000).

Even though the concept of allopatry is widely invoked in evolutionary biology, it seems to have evaded a definition that is both biologically reasonable and mathematically accurate (Turelli, Barton, and Coyne 2001). Either one adopts a strict view of isolation, which is mathematically sound, but incompatible with observation or one accepts partial

population connectivity, which requires spatial structure to be summarized over a single parameter and subjected to an arbitrary cutoff (Butlin, Galindo, and Grahame 2008). I believe that the failure to solve this issue is due to an unnecessary focus on describing isolation.

When recounting a case of assumed allopatric speciation, a Biologist will tell a two part story. An ancestral population is first geographically subdivided and differences accumulate between the newly formed subpopulations. Speciation is established on the second arc, when the geographical separation subsides and the organisms from each subpopulation no longer are reproductively compatible (Mayr 1982; Hoskin et al. 2005). Theoreticians have focused their attention on the first half of this story (Orr 1995). If a more holistic approach is taken, the necessity of a precise definition of isolation might be curtailed. The core of the allopatric speciation process is the successive separation of populations and their reencounter. One can, therefore, define allopatric diversification as a process which is contingent on a shifting spatial structure. Conversely, sympatric (or parapatric) diversification is a process which has the average spatial structure as its only spatial contingency.

This work supports that, for at least a range of realistic spatiotemporal population structures, there are two distinct diversification patterns, only one of which is contingent on dynamical spatial structures and is therefore consistent with being called allopatric. Moreover, even though parameters describing spatial structure (such as the clumpiness of a spatial distribution), the rate at which spatial structure evolves (such as the autocorrelation function of spatial parameters) or the rate at which organisms differentiate (such as the mutation rate) may vary continuously, there is a sharp transition between the diversification patterns (figure 3). Such a sharp transition exempts using these diversification patterns as a definition for allopatry from the arbitrariness of applying a gene flow cutoff.

Speciation credit

It has been widely documented that the effect of human interference in ecosystems might not be immediate. The decline in species richness of a fragmented region may extend itself for many years beyond the initial disturbance (Hanski and

Ovaskainen 2002). Estimates of ecological impact might severely underestimate the ultimate burden of human interference. The delayed decrease in richness is usually credited to the often long transients that lead to extinctions, and this effect is thus known as extinction debt (Tilman et al. 1994). However, the species composition of an ecosystem is forged by the antagonistic forces of speciation and extinction, and by focusing only on the destructive force, we might be missing an important aspect of the full picture (Myers and Knoll 2001).

This work supports the idea that even a small disruption in the resource availability of a certain guild, even though insufficient to significantly reduce total population sizes and thus increase extinction rates, alters spatio-temporal organism distribution patterns, which in turn might drastically reduce speciation rates. The lingering shadow of biodiversity loss might be even taller than expected. In addition to extinction debts, we might be depleting a speciation credit that our ecosystems can no longer maintain. If this is indeed the case, a new richness equilibrium might be down along a much longer and deeper transient than that predicted solely by delayed extinctions.

The evolutionary persistence of a clade is frequently linked to how prolific it is, that is, the rate at which new species arise within it (Jablonski 1986). The genetic isolation of species is thought to protect genetic and functional diversity as well as promote vaster ranges (Garcia-Ramos and Kirkpatrick 1997), which may in turn serve as a buffer against extinctions caused by shifts in environmental conditions (Jablonski and Raup 1995). The mechanisms by which the prolificacy of many clades plummeted throughout Earth's history, leading to their demise, is still poorly understood (Jablonski 2001). This work suggests that an important factor for these steep transitions in speciation rates might have been the transformation in the spatiotemporal organism distribution patterns.

If human activities have indeed induced a transition in speciation rates, the clades in which this has occurred will be progressively more vulnerable to extinction, as their internal richness is reduced. This can be understood as a higher order extinction debt. Just as a species that has a fertility below replacement rates is set to be eventually extinct, a clade which loses diversity faster than it replenishes it is bound to disappear.

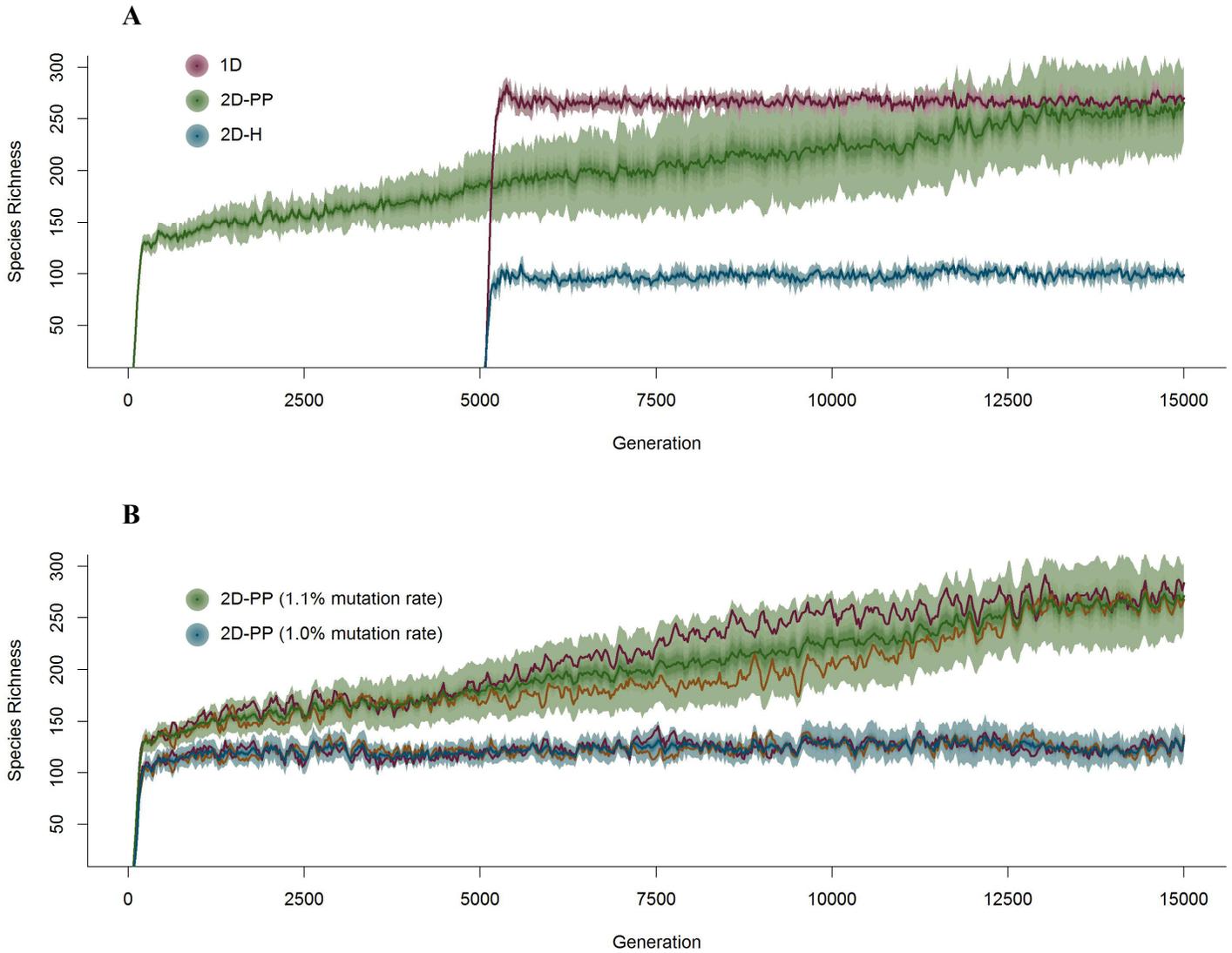


Fig. 1. Each curve represents the mean species richness through time measured in generations. Means were taken from 80 simulations for each curve. In **(A)**, the red curve describes simulations ran in a one dimensional space and no local density dependence on demographic rates (1D), the blue curve describes simulations ran in a two dimensional space and no local density dependence on demographic rates (2D-H) and the green curve describes simulations ran in a two dimensional space and with mortality rates depending on the local densities of other organisms as well as on the local densities of a predator species (2D-PP). All simulations had the same mean number of organisms as well as the same mutation rate (1,1%). Note how the simulations with local density rate dependences (2D-PP) display two diversification stages. Simulations with no local density dependant rates (1D & 2D-H) are delayed and only begin in generation 5000 because these simulations reach a steady state much faster. In **(B)**, both green and blue curves describe simulations ran in a two dimensional space and with predator dependant mortality rates (2D-PP), however simulations for the green curve had a higher mutation rate (1,1%) than simulations for the blue curve (1,0%). Yellow and red curves represent simulations ran repeating the same spatial history. Note that the two stage diversification only happens for simulations ran with a high enough mutation rate. Also, each particular spatial history is only correlated with species richness during the second diversification stage, if it exists.

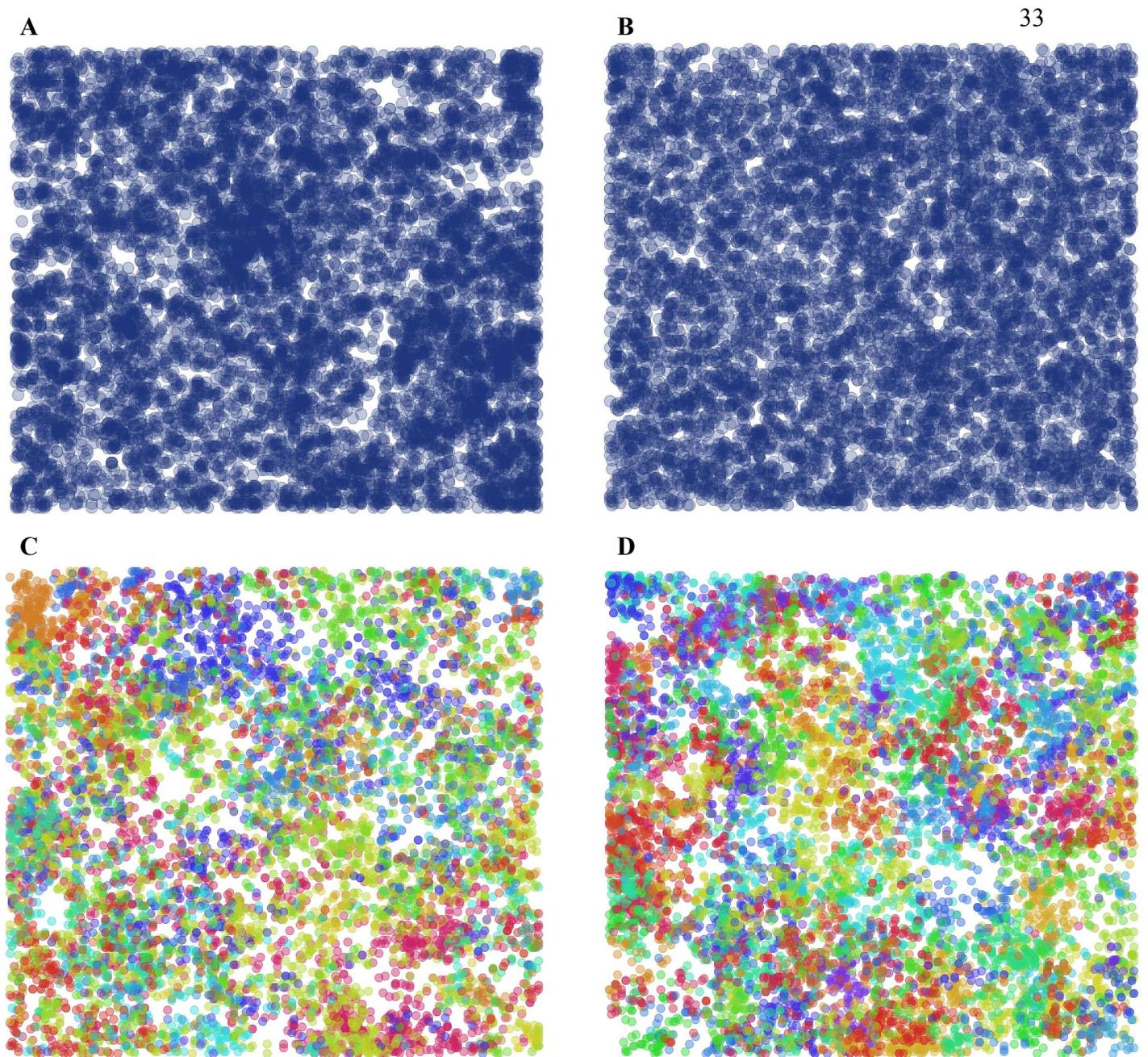


Fig. 2. Snapshots of the simulations (2D-PP) after 15.000 generations. (A) shows the spatial distribution of a highly clumped simulation (eight times more clumped than expected at random), obtained with high local support capacities and predator induced mortality. (B) shows the spatial distribution of a much less clumped simulation, obtained by lowering local support capacities. Both (C) and (D) are snapshots of spatially equivalent and highly clumped simulations. Each species is shown a different color. In (C), mutation rates were such that there was only one stage of diversification (1,0%), and in (D) mutation rates were just enough to observe the second diversification stage (1,1%).

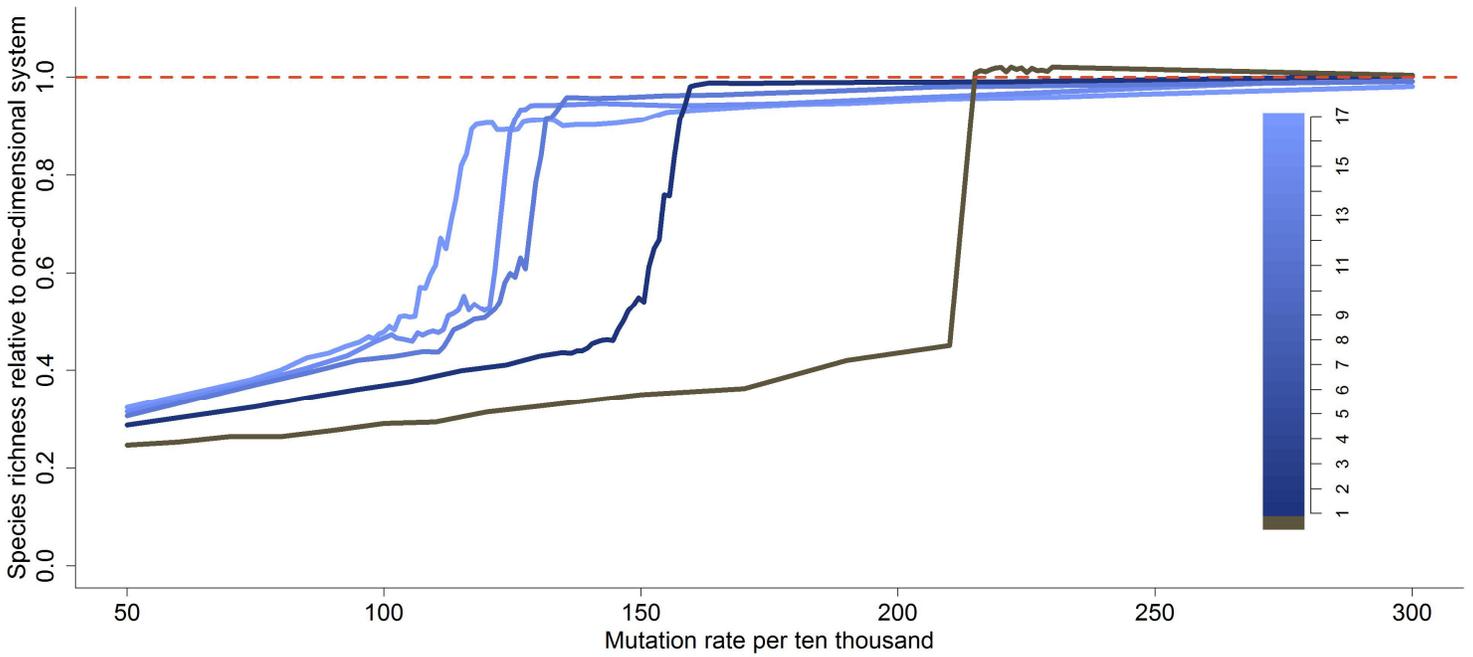


Fig. 3. Each curve represents the results of simulations performed in two dimensional spaces with a set of demographic parameters, but sweeping the mutation rate. The color of each curve represents the mean spatial clustering observed for that set of demographic parameters. Clustering was measured as the relation between the parameter of a Poisson distribution that fits the mean organism density and the parameter of the Poisson distribution of the seeds of the best fitting Matern cluster process. Lighter blue means more clustered and darker blue means more dispersed. The grey curve is that obtained for simulations with no local density dependant rates, and, therefore, random spatial clustering (2D-H). Blue curves were obtained from simulations with predator-prey interactions (2D-PP). For each simulation, the mean species richness after 15.000 generations is divided by the mean species richness of a one dimensional space simulation with the same number of individuals and same mutation rate. The dashed orange line marks when the richness of a two dimensional space system is equivalent to that of the correspondent one dimensional space system. For this set of 2D-PP simulations, the adopted value of maximum predator attack efficiency was 10%.

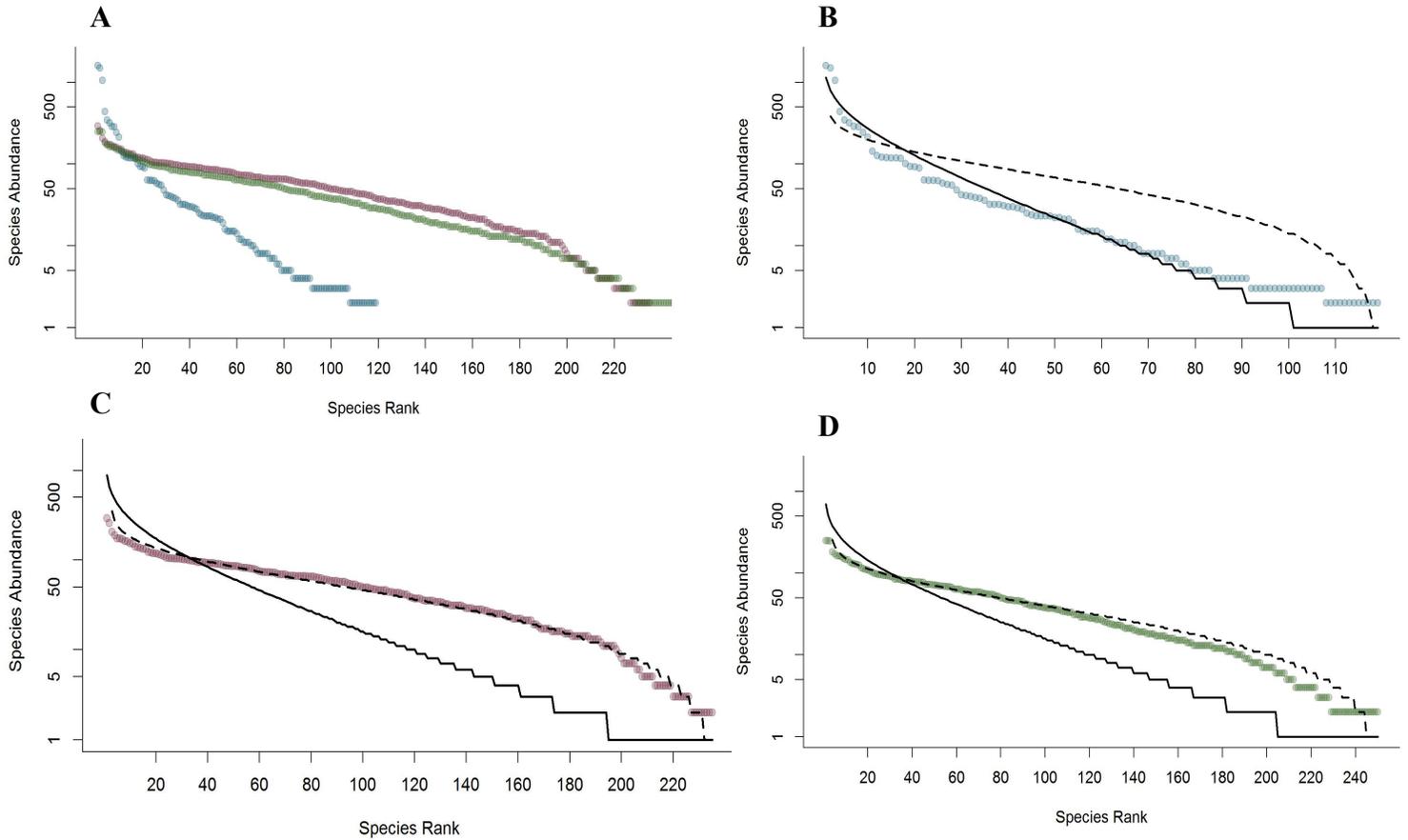


Fig. 4. Rank abundance curves for single simulations. In blue and green are the results for simulations ran in two dimensional spaces with density dependant mortality and predator induced mortality (2D-PP). The results shown in blue are for a simulation with mutation rate such that it displayed only one diversification stage (1,0%). The results shown in green are for a simulation with mutation rate such that it displayed two diversification stages (1,1%). The results shown in red are for a simulation ran in a one dimensional space (1D) and with mutation rate of 1,0%. Solid black lines are the best fitting zero-sum multinomial distributions for each of the simulations and dashed black lines are the best fitting broken stick distributions for each of the simulations. The zero-sum multinomial is the most likely distribution for the single stage diversification simulation on a two dimensional space and the broken stick is the most likely distribution for both the simulation ran on a one dimensional space and the simulation with a two stage diversification.

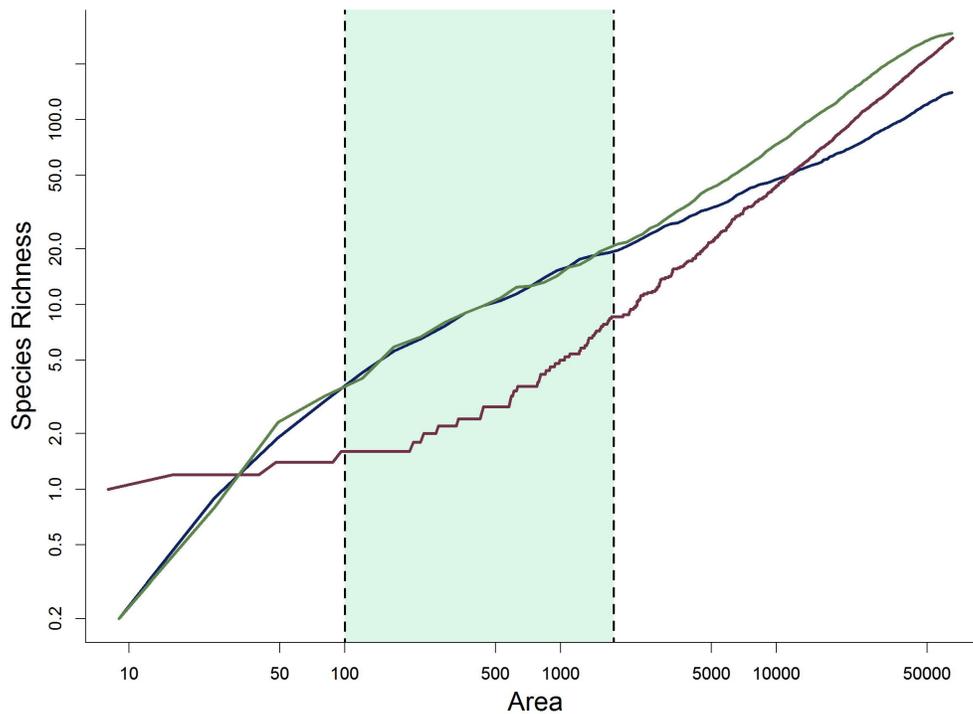


Fig. 5. Species area curves for single simulations on a log-log scale. In blue and green are the results for simulations ran in two dimensional spaces with density dependant mortality and predator induced mortality (2D-PP). The results shown in blue are for a simulation with mutation rate such that it displayed only one diversification stage (1,0%). The results shown in green are for a simulation with mutation rate such that it displayed two diversification stages (1,1%). The results shown in red are for a simulation ran in a one dimensional space (1D) and with mutation rate of 1,0%. The shaded region is the range of areas within which reside the areas of 95% of the clumps determined by the set of demographic parameters for which the simulations were ran. The species area curve for the one dimensional simulation is left skewed, denoting a lack of species with wide ranges. The species area curve for both two dimensional simulations is coincident at small scales. Note that they only diverge for scales larger than those defined by the clumping of the system.

Conclusions

In the quest to understand how biological diversity is distributed on Earth, space is not only part of the question ("Why is this particular organism here?"), but also a fundamental ingredient of the possible answers. The presence of a species in a given environment is ultimately dependant on it having somehow originated or arrived there, and both speciation and migration are processes that are contingent on spatial structure. The main result of this work is that for a range of realistically structured spatial patterns, and for a realistic speciation mechanism, there are two modes of speciation that result in two distinct species abundance and distribution patterns. Moreover, the two speciation modes are separated by a phase transition, in other words, a smooth variation of the parameters regulating spatial patterning or speciation can cause an abrupt shift on the speciation mode.

I have shown that rank-abundance distributions that are well fit by a zero-sum multinomial and rank-abundances distributions that are well fit by a broken-stick distribution can be both obtained from a single model. Both of these distributions are amongst the most common in nature and have shown up in numerous theoretical investigations (MacArthur 1957; Hubbell 2001). Even though the relationship between the zero-sum multinomial and the broken-stick distribution has been explored (Etienne and Haegeman 2011), this is the first time, to the best of my knowledge, that they have emerged as alternate distributions for a single model.

I have also reproduced the range of features of species-areas relationships observed in nature (Rosenzweig 1995). The speciation mode phase transition is responsible for the shift from biphasic to triphasic species-area relationships. I therefore predict an association between features of species-area relationships and types of rank-abundance distributions. I also show that the correlation range of a pre critical process is determined mainly by the genetic structure and parameters, whereas the correlation range of a post critical process is a function of the spatial structure.

The theory of speciation has since its inception been observant of the importance of spatial context (Coyne and Orr 2004). Problems have arisen when classification schemes for speciation processes were proposed based on spatial isolation (Turelli, Barton, and Coyne 2001). It has been argued that a compromise between biological realism and the arbitrariness of classification bounds would be unavoidable. I propose that the existence of a phase transition for speciation modes provides theoretical grounds to reconcile the biological narrative of allopatry with mathematical precision.

This developing theory of phase transitions for speciation modes expands the conceptual toolbox through which observations might be interpreted. I suggest two examples of well known observations over which light might be shed. The relative rarity of the association of clade age and diversity (Rabosky, Slater, and Alfaro 2012) can be explained resorting to the idea of critical slowing down. The long transients observed for systems close to criticality might sustain the age-diversity association for a relatively long period. Sudden crashes in diversification rates that are observed in the periods following mass extinctions, which some posit are responsible for the "dead clade walking" effect (Jablonski 2002), might be caused by transformations in the spatial structure of the organisms, which might be enough to transverse the critical point.

I raise new environmental concerns. I show that we might be changing the capacity of species replenishment by ecosystems under human interference, which could lead to catastrophic biodiversity losses over long periods. I simulated human action as a homogeneous decrease in the local carrying capacity of each system. The robustness of these conclusions to realistic patterns of anthropogenic habitat loss and motility restriction is yet to be tested.

Null models often serve the double role of providing the backdrop against which alternative hypothesis are tested, but also of revealing the fundamental properties of a system. This work establishes phase transitions for speciation modes when there is a lack of selective pressure. However, it is well known in the theory of speciation that natural selection plays a central role in the fragmentation of a species (Coyne and Orr 2004). Therefore, the effect of natural selection on the mutation rate thresholds becomes of foremost importance to the comprehension of the biodiversity patterns one might come across.

Conclusões

Na busca para que se compreenda como a diversidade biológica está distribuída pela Terra, o espaço não é apenas parte da pergunta ("Por que é que este organismo está aqui?"), como também um ingrediente fundamental de muitas das possíveis respostas. A presença de uma espécie em um dado ambiente é dependente, em última instância, de ela ter se originado nesse local ou então alcançado esse local, e ambas especiação e migração são processos contingentes à estrutura espacial. O principal resultado deste trabalho é que para uma gama de padrões espaciais realistas e para um mecanismo de especiação realista há dois modos de especiação que geram dois padrões de abundância e distribuição distintos. Além disso, os dois modos de especiação estão separados por uma transição de fase, isto é, uma variação contínua dos parâmetros que regulam a formação de padrões espaciais ou dos parâmetros que controlam a especiação pode causar um deslocamento abrupto no modo de especiação.

Eu mostrei que distribuições de rank-abundância que se ajustam bem a uma multinomial de soma zero e distribuições de rank-abundância que se ajustam bem a uma distribuição do tipo broken-stick podem ser ambas obtidas a partir de um único modelo. Ambas essas distribuições estão entre as mais comuns na natureza, e apareceram em múltiplas investigações teóricas (MacArthur 1957; Hubbell 2001). Muito embora a relação entre a multinomial de soma zero e a broken-stick já tenha sido explorada (Etienne and Haegeman 2011), ao que me consta essa é a primeira investigação em que elas emergem como distribuições alternativas para um único modelo.

Eu também reproduzi a gama de características das relações entre número de espécies e área amostrada encontrada na natureza (Rosenzweig 1995). A transição de fase no modo de especiação também marca a mudança de relações bifásicas para relações trifásicas. Portanto, eu prevejo uma associação entre características das relações entre número de espécies e área amostrada e características das distribuições de rank-abundância. Eu também mostro que a distância de correlação de um sistema pré-crítico é determinada mormente pela estrutura e pelos parâmetros genéticos, ao passo que a

distância de correlação de um sistema pós crítico é mormente uma função da estrutura espacial.

Desde seu início, a teoria de especiação levou em consideração a importância do contexto espacial (Coyne and Orr 2004). Problemas surgiram, no entanto, quando esquemas de classificação para processos de especiação baseados em isolamento foram propostos (Turelli, Barton, and Coyne 2001). Um compromisso entre realismo e arbitrariedade dos limites aceitáveis de conectividade parecia inevitável. Eu proponho que a existência de uma transição de fase nos modos de especiação provê um sustentáculo teórico para a reconciliação entre a narrativa biológica da alopatria e a precisão matemática.

Essa incipiente teoria de transições de fase para modos de especiação expande a caixa de ferramentas conceitual através da qual observações podem ser interpretadas. Eu sugiro dois casos de observações bem estabelecidas as quais acredito que possam ser melhor compreendidas à luz dessa teoria. Como primeiro exemplo, a relativa raridade de grupos nos quais a idade de um clado está associada a seu número de espécies (Rabosky, Slater, and Alfaro 2012) pode ser explicada usando-se a idéia de desaceleração crítica. Os longos transientes observados para sistemas perto dos parâmetros nos quais há a transição de fase pode sustentar a relação entre idade e diversidade por tempos prolongados. Como segundo exemplo, as quedas nas taxas de diversificação que podem ser observadas em alguns grupos depois das extinções em massa, que alguns acreditam ser o que causa o efeito conhecido como "clado morto andando" (Jablonski 2002), podem ser causadas por transformações nos padrões espaciais de distribuição dos organismos.

Eu levanto novas inquietações conservacionistas. Eu mostro que existe a possibilidade de que estejamos erodindo a capacidade dos ecossistemas impactados pelo ser humano de repor a diversidade perdida, o que pode a longo prazo acarretar em perdas líquidas de biodiversidade muito maiores que o previsto por modelos que não levam mecanismos de especiação em consideração. A robustez desse padrão de perda a padrões realistas de destruição antropogênica de hábitat não foi testada ainda.

Modelos nulos frequentemente desempenham o papel duplo de prover o pano de fundo contra o qual hipóteses alternativas são testadas, mas também de revelar propriedades fundamentais do sistema. Este trabalho estabelece que há transições de fase

para modos de especiação quando não há forças seletivas atuando. A seleção natural tem, entretanto, um papel central na fragmentação de uma espécie (Coyne and Orr 2004). Torna-se de suma importância para a compreensão dos padrões de biodiversidade entender o efeito que a seleção natural pode provocar sobre as transições de fase aqui descritas.

Resumo

Alguns dos padrões ecológicos mais consistentemente encontrados na natureza, como as relações espécie-área e as distribuições de rank-abundância, podem ser previstas por uma classe de modelos neutros. Nesse contexto, neutralidade quer dizer que há equivalência demográfica entre os indivíduos de todas as espécies. Para os modelos dessa classe, extinções causadas por flutuações demográficas são contrabalanceadas por algum mecanismo de especiação. Cada modo de especiação deixa uma marca nos padrões ecológicos emergentes. Foi mostrado que um modelo com uma implementação mecanística de especiação gera padrões de diversidade que dependem de limites geográficos. Eu usei simulações baseadas em indivíduos com uma implementação mecanística de especiação para investigar se padrões espaciais intrínsecos das comunidades poderiam transformar os padrões de biodiversidade. Eu descobri que existe uma transição de fase no modo de especiação que depende da estrutura espacial da comunidade. Uma gama extensa de padrões encontrados na natureza puderam ser unificados em um único modelo dada essa transição de fase. Relações entre riqueza e idade de um clado podem ser melhor compreendidas considerando-se o efeito previsto de desaceleração crítica da diversificação. Uma nova interpretação foi dado ao efeito "Clado Morto Andando", característico dos períodos seguintes a extinções em massa. Uma redefinição objetiva e biologicamente razoável para especiação alopátrica é explorada, graças às propriedades da transição de fase descrita. Eu proponho a existência de um "crédito de especiação", e exploro suas possíveis implicações para a conservação a longo prazo da biodiversidade.

Abstract

Some of the most consistent ecological patterns encountered in nature, such as species-area relationships and rank-abundance distributions, can be predicted from a class of neutral models. In this context, neutrality means demographic equivalence between individuals of all species. Within this class of neutral models, species extinction by demographic fluctuations is counterbalanced by some speciation mechanism. Each particular speciation mode leaves an imprint in the resulting patterns. A model with a mechanistic speciation implementation was shown to generate patterns dependent on geographic constraints. I used individual based simulations with a mechanistic speciation implementation to investigate whether the intrinsic spatial patterning of organisms could transform biodiversity patterns. I found out that there is a phase transition on speciation modes that is dependent on the spatial structure of the community. An extended range of the biodiversity patterns found in nature can be unified into a single model because of this phase transition. Clade richness and age relationships may be understood by the predicted critical slowdowns in diversification. A new interpretation is given to the post mass extinction "Dead Clade Walking" effect. An objective and biologically reasonable redefinition of allopatric speciation is explored by exploiting the phase transition. I propose the "speciation credit" effect, and its potential implications for long term biodiversity conservation.

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