# Stabilization of species coexistence in spatial models through the aggregation–segregation effect generated by local dispersal and nonspecific local interactions

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## ABSTRACT

Spatial interactions are widely acknowledged to play a significant role in sustaining diversity in ecological communities. However, theoretical work on this topic has focused on how spatial processes affect coexistence of species that differ in their strategies, with less attention to how spatial processes matter when competitors are equivalent. Furthermore, though it is recognized that models with local dispersal and local competition may sustain higher diversities of equivalent competitors than models in which these are not both localized, there is debate as to whether this reflects merely equalizing effects or whether there is also a stabilizing component. In this study, we explore how dispersal limitation and nonspecific local competition influence the outcome of species coexistence in communities driven by stochastic drift. We demonstrate that space alone acts as a stabilizing factor in a continuous space model with local dispersal and competition, as individuals of rare species on average experience lower total neighborhood densities, causing per capita reproductive rates to decrease systematically with increasing abundance. These effects prolong time to extinction in a closed system and enhance species diversity in an open system with constant immigration. Fundamentally, these stabilizing effects are obtained when dispersal limitation interacts with local competition to generate fluctuations in population growth rates. Thus this effect can be considered a fluctuating mechanism similar to spatial or temporal storage effects, but generated purely endogenously without requiring any exogenous environmental variability or species dissimilarities.

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## 1. Introduction

In ecological communities where individuals have limited ability to move (e.g. plants and soil microbes), local spatial dynamics often play a central role in determining population and community structure and dynamics (Chesson, 2000a,b; Pacala, 1997; Stoll and Prati, 2001; Turnbull et al., 2007; Webb et al., 2007). The ecological importance of space has motivated the development of spatially explicit theoretical approaches (Dunning et al., 1995; Durrett and Levin, 1994; Perc et al., 2013). This includes individual-based simulation models (on a lattice or continuous space) and approximate analytical models such as moment equations (Bolker and Pacala, 1997) and reaction–diffusion equations (Britton, 1986). Spatially explicit theory has demonstrated the limitations of spatially implicit competition models and classical neutral theory;

for example, spatial dynamics can alter the parameter space in which stable coexistence is possible (Bolker et al., 2003) and lead to biased estimations and interpretations of model parameters (Etienne and Rosindell, 2011; Pacala and Levin, 1997).

To date, spatial ecological theory has generated many interesting results on how spatial processes alter niche mechanisms of coexistence, though little attention has been paid to exactly how spatial interaction terms matter when competitors are equivalent. Spatial dynamics have been investigated extensively in models of resource or apparent competition (Bonsall and Hassell, 2000; Molofsky et al., 2002; O'Brien et al., 2007; Pacala, 1987), habitat partitioning (Chesson, 2000a,b), competition–colonization and other life history tradeoffs (e.g. Bolker and Pacala, 1999; Chave et al., 2002, King and Hastings, 2003), and specialized natural enemies (e.g. Adler and Muller-Landau, 2005; Sedio and Ostling, 2013). It has been recognized that even in the absence of species differences, spatial localization matters (Hanski, 1981; Slatkin, 1974); however, there is a dearth of research on how the spatial interaction terms affect population and community dynamics in these

cases. Models with ecologically identical species are typically addressed only in the context of null model comparison, where the focus is on understanding spatial niche mechanisms (e.g. Sedio and Ostling, 2013).

Surprisingly, there remains a fundamental disagreement as to whether spatial effects on their own can contribute to *stabilizing* species coexistence, or if they are merely *equalizing*. A mechanism is said to be stabilizing if it increases intraspecific negative density-dependence relative to interspecific negative density dependence, thus leading a species per capita population growth rate to increase if it becomes rare (Chesson, 2000a,b). In contrast, equalizing mechanisms reduce fitness differences among species, thereby slowing eventual extinction, but provide no advantage to a species when rare nor disadvantage when abundant.

Classical niche mechanisms such as resource partitioning, life history tradeoffs, and habitat specialization are all well understood to be stabilizing. Proper understanding of the role of spatial processes alone is an important starting point for any quantification of stabilizing effects of these or other niche mechanisms in spatial models and observations. If local interactions themselves have stabilizing effects that are not considered, these may confound the stabilization provided by spatial niche mechanisms.

Local dispersal and competition lead to conspecific aggregation and species segregation, and thereby increases the frequency of neighborhood interactions with conspecifics relative to interactions with heterospecifics (Holyoak and Loreau, 2006; Murrell et al., 2001). By reducing heterospecific competition, these spatial structures could slow ecological dynamics (Hurtt and Pacala, 1995), a finding that has motivated the formulation of a *segregation hypothesis*. This hypothesis states that "finite dispersal and spatially local interactions lead to spatial structure that enhances ecological stability (resilience) and biodiversity (Pacala, 1997)".

However, it is possible for local aggregation of a species to accelerate exclusion and reduce the parameter space where coexistence occurs (Chesson and Neuhauser, 2002; Neuhauser and Pacala, 1999). Similarly, in models of invasion, spatial structures and life-history tradeoff play a central role in determining the outcome of an invasion, but intraspecific competition intensifies so much that competitive dynamics are actually faster than in the nonspatial case (Bolker and Pacala, 1999).

It is unclear if these mechanisms are expected to have larger effects among similar competitors, and therefore to be particularly important for spatially explicit neutral community models. Analytical approximations derived by spatial stochastic processes, which describe the average population dynamics, have shown that asymmetry in conspecific and heterospecific interaction scales is necessary to achieve stable coexistence of otherwise equal competitors (Murrell and Law, 2003).

It is important to note that the presence of conspecific aggregation and heterospecific segregation alone, which emerge in many simulations, is not a sufficient condition for stabilization. In neutral lattice models in which all cells are occupied, for example, total neighborhood densities of conspecifics plus heterospecifics remain invariant even though conspecifics are highly clustered, and in this case there can be no stabilization as all individuals experience equal local competition. In such models spatial structures could enhance coexistence by reducing potential rate of change in abundance of species, i.e. reducing the stochastic drift. This mechanism acts in a similar manner of an equalizing mechanism (Chave et al., 2002; Neuhauser and Pacala, 1999), even though the definition of equalization does not apply well here because all species are identical, so fitness differences cannot be reduced.

In continuous systems with local dispersal and competition, spatial structures continuously form and dissipate (Detto and Muller-Landau, 2016). These spatiotemporal dynamics may generate covariance between local population densities and population growth rates, for example, isolating individuals of species that are at low abundance and in danger of drifting to extinction. Such temporary spatial *refugia* alleviate competitive pressure and increase the probability that these species recover from rarity. Although spatial segregation is unlikely to be permanent, it could last long enough to significantly affect population dynamics, but the extent of its potential contribution to species persistence has not yet been investigated (Holyoak and Loreau, 2006). If these mechanisms create an advantage for the less abundant species, they should be classified as stabilizing, like temporal or spatial storage effects, but without invoking any differences among competitors or extrinsic environmental variation (Bertuzzo et al., 2011).

Here, we test the segregation hypothesis by thoroughly investigating how local dispersal and local non-specific negative density dependence impact coexistence of equivalent competitors in model communities. The model under examination is a point process in continuous space where individuals disperse offspring according to a dispersal kernel and have a rate of mortality dependent on neighborhood density. Although extremely simplified, these models are able to generate a wide variety of spatial patterns consistent with mapped species distribution of large tropical forest plots (Detto and Muller-Landau, 2013). We show how the spatial structure in these models develops such that there are systematic differences with focal species abundance in neighborhood densities of conspecifics and heterospecifics, and how this in turn translates to stabilization as evidenced by negative density-dependence (i.e., a rare species advantage). We explore the full parameter space which differentiates our model from the classic analytically tractable neutral model – i.e., varying dispersal distance, interaction strength and interaction range – and show how these parameters affect time to extinction in the 2-species closed system (Gandhi et al., 1998) and species diversity in the multi-species open system, two classic cases investigated in neutral theory (Beres, 2005). We also examine the effects of local community size and metacommunity species diversity, and evaluate the robustness of our results to the zero-sum assumption. This study complements the rich existing literature on spatially explicit ecological models, constituting an intermediate and necessary step towards fully understanding how niche mechanisms function in communities where individuals have limited mobility.

## 2. Methods and theory

### 2.1. Model description and simulation methods

We first consider a closed system of $N$ individuals and two ecologically equivalent species. Parents disperse offspring according to a dispersal kernel and individual survival is a linear negative function of local density weighted by an interaction kernel, as defined below. The total number of individuals is constant, meaning that for each death there is a birth (zero-sum game). There is no immigration. The system reaches an absorbing state when one of the two species goes extinct.

In the second case study, we consider a variant of the previous model in which immigration is allowed with rate $\nu$ from a metacommunity with $S$ species. For simplicity, the $S$ species are equally abundant in the metacommunity (hence an immigrant has equal probability of being any one of the $S$ species). As before, the system has $N$ individuals, all species are ecologically equivalent, dispersal follows a dispersal kernel, and survival is a negative function of local density of all individuals.

We simulate these cases as point processes with $N$ individuals on a square arena of area $A$, with periodic boundary conditions to minimize edge effects. Every birth event or immigration is paired with a death event such that the total number of individuals is maintained constant. For every death event, an individual is chosen