Ecology, 95(8), 2014, pp. 2289–2302

Coexistence of competitors in marine metacommunities: environmental variability, edge effects, and the dispersal niche

Christopher M. Aiken[1] and Sergio A. Navarrete

Estación Costera de Investigaciones Marinas, Center for Marine Conservation, Laboratorio Internacional de Cambio Global (LINCGlobal, CSIC-PUC), Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

Abstract. Theoretical studies have shown that coexistence between competitors can be favored in a spatially heterogeneous environment by a number of mechanisms, which ultimately allow the expression of persistent or transitory variation in species competitive abilities, colonization, or reproduction. Four distinctive paradigms to model metacommunities have been identified according to assumptions about the biology of the species and essential aspects of the environment. Missing from these are mechanisms of coexistence that can arise from the dispersal process itself without explicit spatial heterogeneity or biological trade-offs. These mechanisms have only recently received attention, but they may be common in marine communities and other systems in which dispersal is obligatory and modulated by the physical environment. We investigate coexistence in spatially homogeneous metacommunities where there is no partitioning of resources, no competition–colonization trade-off, and no possibility of source–sink dynamics. Coexistence is shown to be possible through three distinct mechanisms related to the dispersal process itself. Firstly, in a neutral scenario, inclusion of temporal variability in the connectivity matrix, emulating an intrinsic attribute of ocean character and other turbulent environments, can promote the invasion of an equally matched competitor and, in a hierarchical competition scenario, the persistence of an otherwise unviable, inferior competitor (the dispersal variability mechanism). Secondly, a sufficiently large difference in the shape of the time-independent dispersal kernels of the two species, which may result from differences in larval-release timing, buoyancy, or behavior, can produce stable coexistence in the center of their shared range (the dispersal-shape mechanism). Thirdly, asymmetry in the dispersal process due to biased advection renders the metapopulation model reactive, such that small variations in the upstream abundances can be sufficient for the subordinate species to stably persist (the dispersal-bias mechanism). These results demonstrate that a subordinate species may persist by occupying a dispersal niche that differs sufficiently from that of the dominant species. Further theoretical research is necessary to develop simple empirical tests for these and other dispersal-based coexistence mechanisms.

Key words: coexistence; dispersal; environmental variability; metapopulation; niche; reactivity.

Introduction

The identification of mechanisms that can allow coexistence of multiple species that compete for a common resource has been a central issue in ecology for over 100 years (see Chesson [2000] for a review). The coexistence paradox is nontrivial because for any given set of environmental conditions one species will be best suited on average and hence could be expected to eventually drive all others to local extinction. Coexistence then would be limited to species that are either exactly the same in every aspect related to resource utilization (the neutral paradigm; Hubbell 1997) or that partition the available resources, thereby reducing the detrimental effects of competition (Adler et al. 2007). It has been recognized that the ubiquitous variability in the environment plays a fundamental role in many examples of persistent coexistence (Chesson 2000, Amarasekare 2003). Coexistence requires that differences in fitness be offset by ecological or niche differences (Chesson 1991, Adler et al. 2007), i.e., the difference in niche occupied by the inferior species must be such that competition with the dominant species (interspecific) is reduced relative to that with itself (intraspecific). When a species possesses a buffering stage that resists extinction under unfavorable conditions (such as a seed bank) it may coexist with a superior competitor that has a distinct response to environmental fluctuations. This general mechanism of coexistence has been termed the storage effect (Chesson and Warner 1981, Warner and Chesson 1985). Alternatively, a subordinate may offset its competitive disadvantages under average conditions by being less sensitive to resource variability, as reflected in distinct, nonlinear, functional resource dependence and hence referred to as relative nonlinearity of competition (Armstrong and McGehee 1980). In both cases,

Manuscript received 14 March 2013; revised 10 December 2013; accepted 18 December 2013; final version received 29 January 2014. Corresponding Editor: S. G. Morgan.

[1] E-mail: cm.aiken@yahoo.com

temporal variability in the environment is crucial to provide occasional opportunities for subordinate species to prosper. Thus, the ubiquitous temporal variability in environmental parameters, when occurring at timescales affecting biological vital rates, creates niche opportunities that may be exploited by species to permit their stable coexistence in the face of competitors better suited to average conditions.

Besides temporal variability leading to niche partitioning, the consideration of space and the idea of local populations of interactive species connected through dispersal of individuals (metacommunity) represented a milestone in our understanding of population persistence, coexistence mechanisms, and the maintenance of biodiversity (Chesson 2000, Shurin 2001, Amarasekare 2003, Kritzer and Sale 2004, Logue et al. 2011). In these spatially structured systems, the level of connectivity among local populations is of critical importance for species coexistence (Iwasa and Roughgarden 1986, Pulliam 1988, Leibold et al. 2004, Mouquet et al. 2005, Salomon et al. 2010, Bode et al. 2011, Figueiredo and Connolly 2012). Indeed, a large number of theoretical studies have shown that spatial heterogeneity in the environment, which ultimately generates spatial variation in the arrival of individuals to local populations, i.e., per capita recruitment rates, can foster coexistence either through source–sink subsidization dynamics (Iwasa and Roughgarden 1986, Mouquet et al. 2005), competition–colonization trade-offs (Tilman 1994, Amarasekare 2003), or through a spatial storage effect (Snyder and Chesson 2004). In a recent review, Leibold et al. (2004) provided a lucid and didactic conceptualization of the main theoretical approaches to model species coexistence in metacommunities. They identified four paradigms that make distinctive assumptions about the biology of the species, the relative timescales of local and regional processes, and about essential aspects of the environment within each patch. In all these models (except the neutral paradigm), the environment provides permanent or ephemeral spatial variability that affect ecological and/or reproductive performance of the species, which in turn affects coexistence through dispersal of individuals across space (Leibold et al. 2004). Their influential review has undoubtedly spurred the much needed field work to test these ideas in terrestrial, aquatic, and marine ecosystems (Logue et al. 2011). But because theoretical developments have been made only very recently, mechanisms of coexistence that can arise from the dispersal process itself, without spatial heterogeneity or biological trade-offs, were not considered in Leibold et al.'s (2004) paradigms or in previous reviews (Chesson 2000, Amarasekare 2003). We expand upon recent developments and provide new theory on dispersal-driven coexistence and maintenance of diversity in metacommunities. Together with previous developments (Berkley et al. 2010, Salomon et al. 2010, Figueiredo and Connolly 2012), our results show that these mechanisms may be quite common in marine communities and other systems in which dispersal is obligatory and modulated by the inherently variable physical environment. They therefore should be brought to attention of theorists and empirical marine ecologists alike.

In the case of marine species, the ability of larvae to arrive to a suitable habitat within their competency period is strongly conditioned by the character of the local ocean currents, even for those with sophisticated swimming behaviors (Largier 2003, Aiken et al. 2007, 2011, Mitarai et al. 2008, Siegel et al. 2008). While many studies of marine metapopulations have treated oceanic dispersal as spatially homogeneous and steady in time, in reality the ocean circulation and hence pelagic dispersal is highly variable with the result that, even for species without temporally variable spawning or larval swimming behavior, connectivity of populations along the coastline will commonly vary over a range of space- and time-scales (Kaplan 2006, Aiken et al. 2007, Mitarai et al. 2008, Siegel et al. 2008, Aiken and Navarrete 2011). Yet despite the importance of dispersal for all aspects of the ecology and evolution of species (Gaines et al. 2007), we are just beginning to explore the population and community consequences of its inherently variable nature (Kritzer and Sale 2004, Aiken et al. 2007, Siegel et al. 2008). The effects of stochastic dispersal on population persistence and on the metapopulation structure and dynamics were recently explored by Aiken and Navarrete (2011) and Watson et al. (2012). Aiken and Navarrete (2011) showed that under some quite general conditions even temporally uncorrelated (noise) forcing may profoundly alter metapopulation dynamics, sustaining an otherwise unviable metapopulation. As a result, it may be expected that stochastic forcing of metacommunities may also condition the ability of inferior competitors to survive. But the consequences of stochastic dispersal variability on species coexistence have only been considered in a landmark paper by Berkley et al. (2010), where the authors lucidly demonstrated that temporal variability in the recruitment of pelagic larvae can by itself permit a competitive subordinate to be sustained, provided only that the spawning seasons of the competitors are sufficiently offset. Unlike much of the previous work on the role of environmental fluctuations (e.g., McPeek and Holt 1992), Berkley et al.'s (2010) model is spatially homogeneous, contains no fitness–environment correlation and no interspecific differences in dispersal abilities, nor gregarious settlement. These features allow the authors to rule out the competition–colonization trade-off (Tilman 1994) or any other form of temporal or spatial niche partitioning (e.g., Klopfer and Ives 1997) as mechanisms of coexistence. Instead, they show that the coexistence process results from the inherently stochastic dispersal of species that release larvae into the water column at offset times, which generates a novel form of spatial storage effect due to highly ephemeral spatial heterogeneity. Thus, the authors

conclude that coexistence of species with stochastic dispersal does not necessarily depend on any form of fitness inequalities, but rather on the degree of overlap in their spawning seasons.

In addition to Berkley et al.'s (2010) contribution on coexistence under stochastic dispersal, a series of theoretical studies published over the past three years have demonstrated that fixed but spatially variable connectivity among populations in which some patches of habitat export more larvae per capita to the metapopulation than they receive can foster coexistence of space-limited competitors (Salomon et al. 2010, Figueiredo and Connolly 2012) and that this mechanism can be an important mechanism supporting the high diversity of tropical reef fish (Bode et al. 2011). These authors concentrate on the positive effect that an unequal geographical distribution of recruits can have upon coexistence by elegantly manipulating patterns of connectivity in small metacommunities. Considering the enormous consequences of these recent theoretical developments for our views about maintenance of biodiversity in the ocean and other turbulent dispersive environments, we further explore the role of the dispersal phase in the coexistence of species.

An important aspect addressed here is the finiteness of the environment in which adult populations can exist, in particular in the presence of a mean drift in realized dispersal. Metapopulation models often assume an infinite range, and even when range boundaries are included they are often modeled as periodic or reflective (e.g., Berkley et al. 2010). While mathematically convenient, such boundary conditions are clearly not realistic in the majority of dispersal scenarios. In the marine environment in particular, the phenomenon of larval waste, i.e., larvae produced on the shore but dying before reaching adult habitat, has always been identified as a major factor of larval ecology (Thorson 1950). The finiteness of a species' ranges can, in fact, have a profound influence on metapopulation dynamics that extends beyond the abundances of edge populations. This is particularly apparent when dispersal has a nonzero drift, as the metapopulation can become highly sensitive to the upstream populations (Lutscher et al. 2007, Aiken and Navarrete 2011, Pringle et al. 2011). The finite geographical extent of the metacommunity also renders connectivity heterogeneous, even when the advective environment is spatially homogeneous, raising the possibility for coexistence of the type detailed in Salomon et al. (2010) and Figueiredo and Connolly (2012) in a two-patch system.

Our intent is to present the various routes by which coexistence can occur between two species that occupy a finite geographical region under three different competitive–dispersal scenarios: (1) the neutral case in which dispersal character (probability density kernel), mortality rates, and fecundities are identical (equal competitors), (2) hierarchical competition due to differences in mortality rates, but identical dispersal abilities, and (3) both dispersal kernel and mortality rate differ. In all cases, resource use of species overlaps completely, preventing typical resource partitioning, and spatial homogeneity in species fitness and their response to competition prevents spatial source–sink dynamics (Iwasa and Roughgarden 1986, Muko and Iwasa 2000, Mouquet et al. 2005). Competition intensity is spatially homogeneous; there is no differing covariance with environmental factors and no differences in death rates and lifespans, preventing relative nonlinearity of competition or storage effects. The statistics of dispersal are assumed to be stationary and spatially homogeneous, ruling out source–sink coexistence of the type described by Iwasa and Roughgarden (1986). Nonetheless, we demonstrate that this simple model can sustain various modes of coexistence, wherein environmental variability in dispersal, in combination with asymmetrical advection and a finite geographical range, enhances the probability for survival of species that could not exist under constant conditions.

Methods

Dispersal-based metapopulation model for two species that compete for space

We extend the single species metapopulation model of Aiken and Navarrete (2011) to include a second species that competes for the available space. Each metapopulation is composed of a finite number of discrete populations that occupy geographically distinct sites. For convenience the sites may be envisaged to fall upon a straight section of coastline, although the geographical relationship between sites is, in fact, irrelevant. The model is based on that of Roughgarden et al. (1985) modified to explicitly include spatial patterns of larval exchange via a connectivity matrix. Competition for space is effectively of the lottery type (sensu Chesson and Warner 1981), in that all recruits of both species have the same probability of settling to the available substrate. The model can be written as

$$\mathrm{d}\mathbf{n}_1/\mathrm{d}t = \Big(f_1\mathbf{S}(\mathbf{n}_1+\mathbf{n}_2)\mathbf{C}_1(t) - \mathbf{M}_1\Big)\mathbf{n}_1 \qquad (1)$$

$$\mathrm{d}\mathbf{n}_2/\mathrm{d}t = \Big(f_2\mathbf{S}(\mathbf{n}_1+\mathbf{n}_2)\mathbf{C}_2(t) - \mathbf{M}_2\Big)\mathbf{n}_2 \qquad (2)$$

where $\mathbf{n}_i$ is the time-dependent state vector containing the number of individuals of species i in each patch, $\mathbf{C}_i(t)$ is the time-dependent connectivity matrix, which defines the probability of competent larval delivery to each of the J local populations at time t, such that the diagonal of $\mathbf{C}$ determines the level of self-recruitment, and f_i is the rate of production of competent settlers of species i per adult per unit time at each local population. This factor includes the effects of larval production and mortality. $\mathbf{S}(\mathbf{n}_1+\mathbf{n}_2)$ is the density dependent settlement rate, which in this case decreases linearly with the availability of substrate and may be cast in matrix form as

$$\mathbf{S}(\mathbf{n}_1 + \mathbf{n}_2) = \mathbf{I} - \sum(\mathbf{n}_1) - \Sigma(\mathbf{n}_2) \quad (3)$$

where $\mathbf{I}$ is the identity matrix, $\mathbf{\Sigma}(\mathbf{n}) = \mathrm{diag}(\mathbf{n})/N$, diag() denotes the matrix with the elements indicated along the diagonal and zeros elsewhere, and N is the maximum possible abundance at each site, determined by a fixed availability of free space for both species in that location and the per capita use of this resource. $\mathbf{M}_i = m_i\mathbf{I}$ is the mortality rate matrix, where the m_i is the mortality rate of species i per unit time.

We have, for simplicity but without loss of generality, assumed that the per capita use of space (e.g., individual size) is identical for both species and across the metapopulation. Introducing differences in the adult per capita usage of space results in proportional linear changes in the population abundances, but no qualitative change in the results that follow. The density dependent term couples the two equations and renders the model nonlinear in abundance. It may be noted that the density dependent term is identical in both Eqs. 1 and 1, and hence there is no difference between intraspecific and interspecific competition. Each individual competes for space on equal terms with members of its own and other species at all local populations (equal competitors). This symmetry rules out the possibility for stable coexistence in the model through relative nonlinearity of competition (there is no low density advantage) or a temporal storage effect.

While our model is similar to that of Berkley et al. (2010), there are a number of differences that should be noted. The Beverton-Holt recruitment function in Berkley et al. (2010) enforces hyperbolic density-dependent competition on recruits. While this functional form for competition has been shown to be appropriate for intracohort competition in fisheries (White 2009), this is not the case for populations of coastal invertebrates (e.g., Roughgarden et al. 1988, Hughes et al. 2000, Navarrete and Manzur 2008) and for many fish species (Iles 1994). The interspecific competition for available space used here provides a simpler and arguably more realistic representation of competition among marine invertebrates (see also Salomon et al. 2010). Secondly, and importantly, we explicitly incorporate open boundaries at the edges of the metapopulations. While in Berkley et al. (2010) the mean settlement success rate is identical across the metacommunity, the result of using periodic or reflective boundaries, we will show that the inclusion of open boundaries, as is generally the case in nature, can provide additional mechanisms for coexistence under otherwise homogeneous conditions. Our goal is not to revisit the Berkley et al. (2010) study, but to evaluate the turbulence-based mechanism under our model assumptions and, if corroborated, assess the sensitivity to the time structure of stochastic process. Recognizing that dispersal is typically a red-noise process and by varying the decorrelation timescale of the stochastic forcing, we also evaluate the sensitivity of Berkley et al.'s and our own results to representations of dispersal variability that may be generalized beyond the ocean context. Our general model is also similar to that recently developed by Salomon et al. (2010; see also Figueiredo and Connolly [2012]), but we follow a different approach. These authors investigated the effects of temporally fixed spatial variation in patterns of dispersal of competing species by recreating different scenarios of connectivity matrices in an essentially closed metacommunity. We instead let a fixed or stochastically variable dispersal kernel determine the elements of connectivity matrices in a metacommunity with explicitly open boundaries, as would occur in a spatially homogeneous ocean (or any other advective environment) that extends beyond the range of species. We will show that Salomon et al.'s (2010) results are quite general and can be expanded to situations that do not impose specific patterns of dispersal sources/sinks across the metapopulation.

Simulations of metacommunity dynamics

The role of temporal variability upon metacommunity dynamics and coexistence was examined using Eqs. 1 and 2 under a number of forcing and dispersal scenarios. Each modeled metapopulation was composed of $J = 50$ equally spaced local populations inhabiting a finite section of coast. The results that follow are qualitatively insensitive to the choice of J. The limiting abundance at each site was nominally set to $N = 100$, such that the abundance values may equivalently be interpreted as percentages of the total population size summed over both species. Mortality rates and dispersal characteristics varied between simulations, but in all cases were uniform across all patches. The settler production rate (fecundity) was nominally set to be $f_i = 1$ settler per adult per unit time for both species (and hence no competition–colonization trade-off sensu Tilman 1994), which in all cases is above the critical level required for persistence in the absence of the competitor. Eqs. 1 and 2 were solved numerically in MATLAB using the code included in the Supplement. Positive definiteness (all elements of $\mathbf{n} \geq 0$) of the abundances was enforced at each time step. It may be noted that Eqs. 1 and 2 do not explicitly include a spatial dimension, as it is the connectivity patterns rather than the geographical spacing between sites that is relevant. Nonetheless, in the generation of the connectivity matrices outlined below we arbitrarily assume that all sites are evenly spaced by 1 unit. The results are independent of the units of distance.

Environmental variability was incorporated in two ways. Firstly, direct effects of the environment upon the adult abundances were simulated through the random addition and removal of individuals from each local population, represented in the model through the addition of a stochastic forcing term $\boldsymbol{\xi}(t)$ to the state vector $\mathbf{n}$, where each element $\xi_i(t)$ of $\boldsymbol{\xi}(t)$ was an independent, normally distributed random variable with

mean $\langle \xi_i(t) \rangle = 0$ and variance $\langle \xi_i(t)^2 \rangle = 0.001$. This term effectively parameterizes spatiotemporal variability in mortality, predation, or maternal fitness. It makes no net contribution of individuals to either metapopulation and is sufficiently small to avoid the production of negative abundances. These small fluctuations in adult abundance may also be interpreted as a buffering term in the storage effect sense (Chesson 2000), given that they ensure a low background level of both species that effectively prevents complete extinction under unfavorable conditions.

Secondly, the effect of dispersal variability upon the fluxes of competent larvae between populations was represented through a time-dependent connectivity matrix. The ocean circulation is dominated by coherent flow structures that result in settlement events that are sporadic and patchy (Largier 2003, Mitarai et al. 2008, Siegel et al. 2008, Berkley et al. 2010). This is likely true for dispersal in other fluids in which the dominant eddy timescales are comparable to dispersal durations. Although such patchy individual instances of recruitment differ from the conceptual advection–diffusion model of dispersal, nonetheless Gaussian statistics, or some related distribution, are commonly recovered in the long term (Aiken et al. 2007, Mitarai et al. 2008). We therefore approximate dispersal as patchy in space and randomly fluctuating in time, but with a Gaussian-average kernel in the long-term mean. Given that the ocean circulation, and geophysical fluids in general, commonly have red spectra (Frankignoul and Hasselmann 1977), it is appropriate to model the fluctuations in connectivity as a red-noise process. The redness of the spectrum is determined by a decorrelation timescale τ. Either periodic or open boundaries were imposed by appropriate normalization of the connectivity matrices. The method used to simulate time-dependent connectivity is explained in Appendix A.

In *Results*, biased or asymmetrical dispersal refers to cases where the mean dispersal kernel is noncentered, as used in previous publications examining dispersal in advective environments with a nonzero mean drift (Speirs and Gurney 2001, Byers and Pringle 2006, Aiken and Navarrete 2011, Pringle et al. 2011). We note that our use of the term asymmetrical differs from the spatial asymmetry of Salomon et al. (2010) and Figueiredo and Connolly (2012), which refers to the existence of net sources and sinks of dispersal propagules in the connectivity matrix of the metapopulation, which could be generated by unspecified dispersal kernels.

Results

The neutral scenario: coexistence of equally fit species

As the two species with identical mortality and dispersal kernels occupy an identical niche in the model, they may also be seen as two allotypes of the same species. The fact that the model includes no distinct intraspecific competition and no low-density demographic benefit means that species who share larval production and mortality rates have identical growth rates, i.e., equal competitors or neutral species (sensu Hubbell 2005), with the consequence that the equilibrium abundances remain in direct proportion to those found initially. That is, in the absence of any form of external stochastic forcing, and independently of the choice of model parameters, the identical properties of the two species assure their ability to coexist.

In the unforced model (no stochastic variation of abundances or of dispersal), a new species or allotype introduced in small numbers to a habitat already at maximum capacity by the other species remains scarce, at the level at which it was introduced (Fig. 1). Given the equal competitive abilities of the two species and the spatial homogeneity of the environment, no mechanism exists by which the new species, when rare, can gain space at the expense of the resident at equilibrium abundance (Chesson 2000, Siepielski and McPeek 2010). Nonetheless, when temporal variability is included in the connectivity matrix of each species, the abundance of the newly introduced species may grow and eventually coexist with the resident at the same mean abundance (Fig. 1). That is, the dispersal fluctuations, which are uncorrelated to ecological performance, can by themselves facilitate invasion and promote coexistence in the neutral system. The rate at which the invasion occurs, however, depends upon the decorrelation timescale of the variability (Fig. 1a–d). Invasion of the new species does not occur for white-noise dispersal variability ($\tau = 0$), but is increasingly rapid as the average time between settlement events increases.

Invasion is also possible in the neutral model in the absence of temporally variable dispersal whenever the mean dispersal distance μ is sufficiently large, even when the dispersal statistics of both species are exactly the same (Fig. 1e–h). When dispersal is symmetrical about the release location (i.e., $\mu = 0$) the newly introduced species cannot invade. Once the mean dispersal distance is large enough that self recruitment is low (e.g., when $\mu > 2\sigma$), invasion and therefore coexistence becomes possible and occurs increasingly rapidly with further dispersal asymmetry, i.e., increases in μ. The finiteness of the domain is fundamental for this mechanism. When periodic boundaries are used, no invasion is possible without dispersal variability, irrespective of the value of μ (cf. Fig. 1g, h). In the finite domain with open boundaries, increasing μ reduces the mean abundance summed over both species, due to the increase in larval waste at the habitat edge.

Coexistence between hierarchical competitors with the same time-mean dispersal kernel

While stable coexistence is trivial for equal competitors, this is no longer the case once a competitive ranking is enforced. A competitive hierarchy can be produced in the model by either increasing the fecundity of one species (as in Berkley et al. 2010), or, as we do here, by increasing the mortality rate of the second

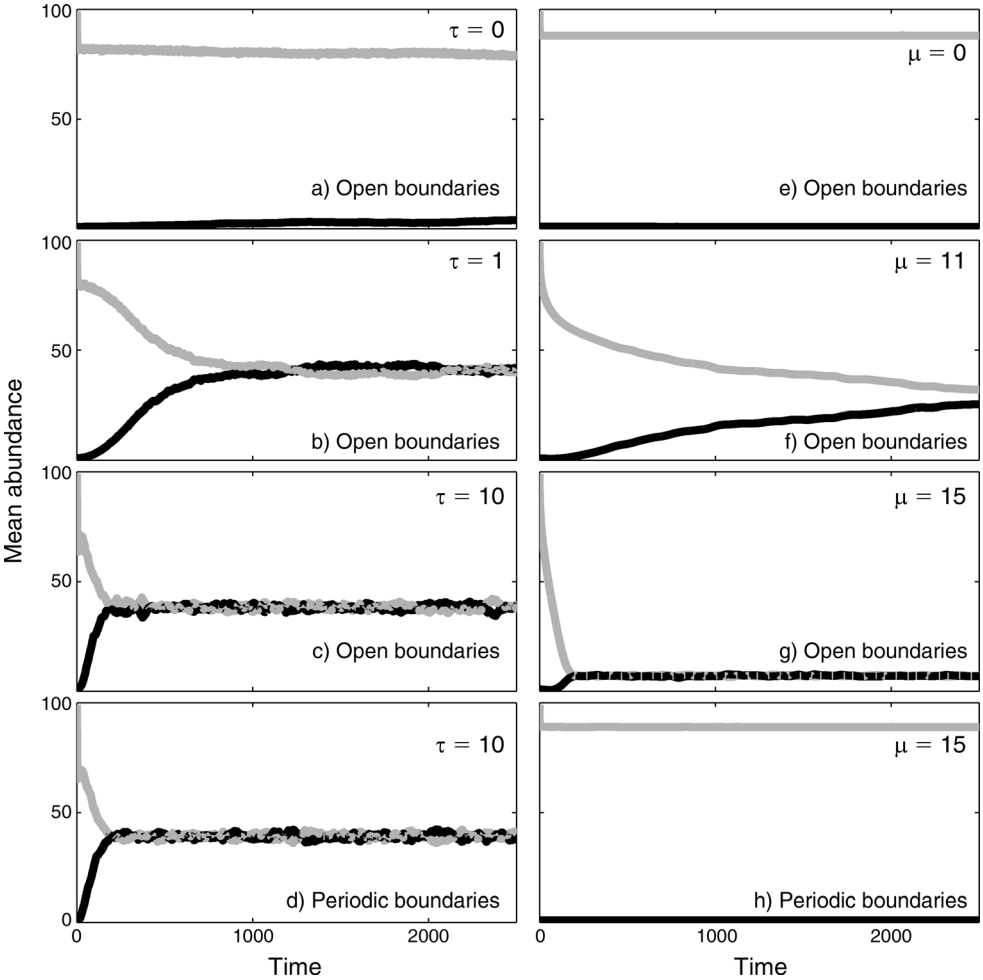

FIG. 1. Time taken for an equivalent species (black line) to invade an established population (gray line) as a function of the decorrelation timescale τ of the dispersal variability (left panels) and of the mean dispersal distance μ in the absence of dispersal variability (right panels). Each of the curves represents an ensemble average from 50 independent simulations using the metacommunity Eq. 1. Panels d and h were generated using the same parameters as panels c and g, respectively, but with periodic boundaries. In all experiments $\sigma = 5$, while the values of μ and τ are indicated in the upper right corner of each panel. The initial abundance was 99 for the resident species and 1 for the invader. The units of time are arbitrary.

species (m_2), rendering it subordinate at all local populations. As expected from the competitive exclusion principle, in the absence of resource partitioning and of all externally imposed variability, the species with lower mortality rate (the dominant species) saturates the metapopulation and drives the subordinate to global extinction, regardless of initial abundances (Fig. 2).

The inclusion of temporal dispersal variability, however, can have a quite dramatic positive effect upon the long-term mean abundance of the subordinate species as a fraction of the total interspecies abundance, and this positive effect on coexistence increases with increasing decorrelation timescales (Fig. 2a). A nominal fixed value of $\sigma = 5$ was used for the illustration, but the result is qualitatively insensitive to the value used. Coexistence is possible even for the case of a 100% difference in mortality rates, which would lead to the rapid and global exclusion of the subordinate in the steady, purely diffusive system. For each subordinate mortality rate m_2, there is a minimum dispersal decorrelation timescale τ below which coexistence is not possible, and a second timescale beyond which there is little additional benefit for the subordinate. Thus, under the dispersal variability mechanism, the subordinate will persist only if the temporal variability is of sufficiently long timescale in the dispersal phase to offset the fitness difference.

Coexistence of unequal competitors is also possible in the absence of temporal dispersal variability whenever the mean dispersal distance is sufficiently large relative to its variance, i.e., dispersal is asymmetrical, and the habitat is finite (Fig. 2b). The subordinate may then be sustained solely through an extremely low level of stochastic modulation of the metapopulation abundanc-

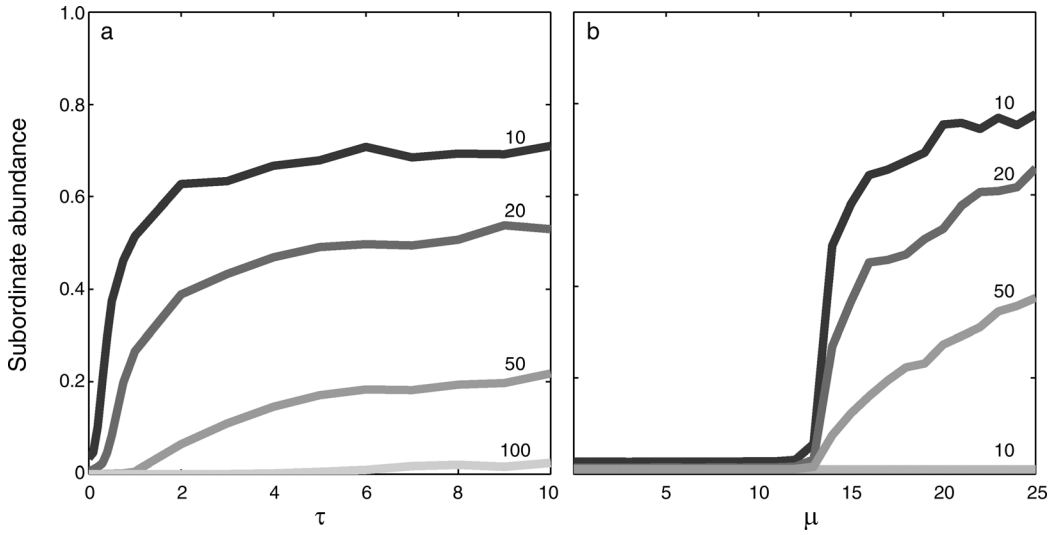

FIG. 2. Long-term average abundance of the subordinate relative to that of the dominant as a function of (a) decorrelation timescale τ, and (b) mean dispersal distance μ, for a range of subordinate mortality rates. The percent difference between the mortality rates of subordinate and dominant are denoted on each curve. In panel (b), the lightest gray line corresponds to the case of periodic boundary conditions. Each of the curves represents an ensemble average from 50 distinct stochastically forced simulations.

es. When both species experience low levels of self-recruitment at the upstream edge of their domain, stable coexistence can be sustained even when the subordinate mortality rate is twice that of the dominant (Fig. 2b). The dispersal bias mechanism of coexistence is not possible when the habitat is essentially infinite (periodic boundaries; Fig. 2b, lightest gray line).

In both the dispersal variability and dispersal bias scenarios, large-amplitude temporal fluctuations occur in the relative abundances of dominant and subordinate (Fig. 3). There are no long-term trends in the metapopulations nor in the amplitude of the oscillations, indicating that the coexistence in each case is stable. Although both coexistence processes rely on temporal variability, the mechanisms differ significantly. In the case of dispersal variability, each species satisfies, albeit sporadically, the invasibility criteria. The variable dispersal conditions intermittently favor the subordinate, causing ephemeral reversals in the competitive rankings, as evidenced by the fact that the exponential growth rate of small changes in the subordinate abundance occasionally exceeds that of the dominant (Fig. 3b). In the dispersal bias scenario, however, dispersal does not vary over time, the competitive rankings do not change, and the subordinate does not satisfy the standard invasibility criteria, even fleetingly. This is because the stochastically forced increases in the subordinate abundances are transient by nature. As we discuss in *Results: Coexistence of species with distinct mean larval-disperal kernals* and show in Appendix B, a more suitable measure of the possibility for coexistence in such cases is based on the maximum instantaneous growth rate (Fig. 3f).

Coexistence of species with distinct mean larval-dispersal kernels

Even when the competitor's propagules are advected in the same velocity field, identical interspecific mean dispersal kernels are likely to be the exception rather than the rule. In the pelagic context, such mean dispersal differences may arise from distinct larval development times, different larval buoyancy, larval behavior, or spawning synchronized to different phases of a periodic component of the advective environment (e.g., crab larval release; Morgan and Anastasia 2008). It is therefore pertinent to consider the case in which the two hierarchically competing species differ in their time mean dispersal kernels. We explore the case in which the mean (μ_1) and standard deviation (σ_1) of the dispersal distance of the dominant species differ to those of the subordinate species (μ_2 and σ_2, respectively). This is essentially a generalization of some of the scenarios explored by Salomon et al. (2010), but in a system with open boundaries. We arbitrarily define stable coexistence as occurring when neither species accounts for more than 99% of the combined abundance. We find that persistence of the subordinate is possible without any externally imposed variability, provided only that its dispersal kernel differs sufficiently from that of the dominant and that the geographical range is finite.

When the dispersal kernels are similar (i.e., μ_1 and σ_1 close to μ_2 and σ_2, respectively) and in the absence of dispersal variability and external abundance fluctuations, stable coexistence does not occur anywhere in the model. However, a sufficient increase in μ_1 with respect to μ_2 will eventually drive the dominant species to

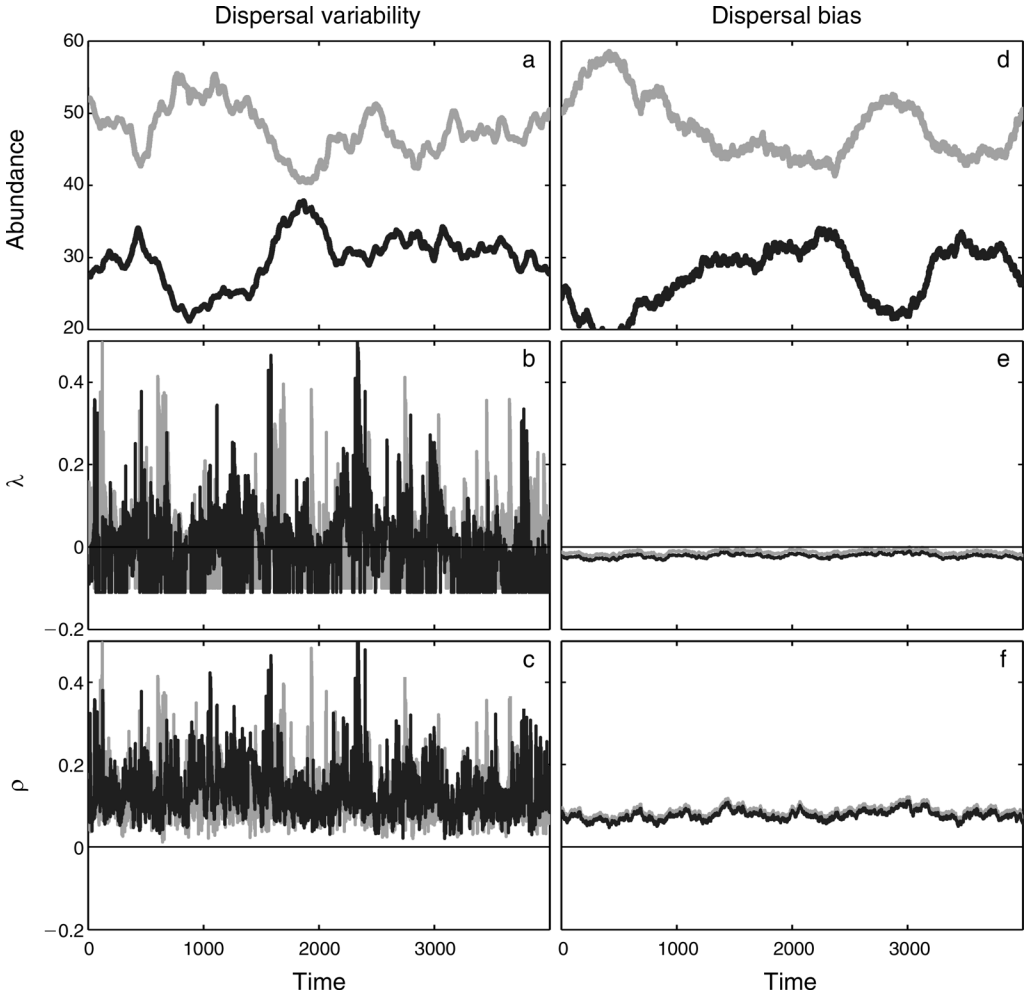

FIG. 3. Example of the evolution of the dominant (gray, $m_1 = 0.1$) and subordinate (black, $m_2 = 0.11$) species in the stochastically forced metacommunity model with (a) time-varying dispersal ($\mu = 0$, $\sigma = 5$, $\tau = 10$) and (d) constant spatially asymmetrical dispersal ($\mu = 10$, $\sigma = 5$). For each of these simulations the corresponding exponential growth rate λ and maximum instantaneous growth rate ρ of each species at each point in time are shown in panels (b) and (c), and (e) and (f), respectively. As described in Appendix B, growth rates above zero indicate the possibility for the species abundance to increase. The units of time are arbitrary and of abundance are the percentage of the maximum population.

extinction, allowing the subordinate to persist; for a fixed subordinate dispersal kernel defined by $\mu_2 = 0$ and $\sigma_2 = 5$, extinction of the dominant occurs for $\mu_1 > 4$ (Fig. 4a). This amounts to a reversal of competitive hierarchies driven solely by biased dispersal and the finiteness of the habitat. When μ_1 falls between these two limiting values (i.e., in the range 0–4), coexistence of dominant and subordinate is possible under a range of values of σ_1 (Fig. 4a). The removal of the dominant's competitive advantage is due to the greater larval loss through the edges of the domain that it experiences when either μ_1 or σ_1 are increased. As such, coexistence occurs when the fitness reduction of the dominant due to increased larval waste is sufficient to allow the subordinate to persist at one or both edges of the domain. Unlike the previous two cases, the resulting coexistence through variation in dispersal shape is spatially structured (coexistence does not occur throughout the metapopulation) and time independent. In the case of nonzero μ, the dominant is found predominantly in the center and downstream extent of the habitat, and the species coexist locally in a transition zone leading from the upstream edge to the center of the habitat (Fig. 4b). That is, stable coexistence at the metapopulation level ensues once the subordinate is able to stably occupy the site located furthest upstream. The critical importance of the open boundaries is confirmed by the fact that coexistence ceases if periodic boundaries are used and further demonstrates that this coexistence mechanism is essentially different from the classic competition–colonization trade-off or settlement aggregation effects

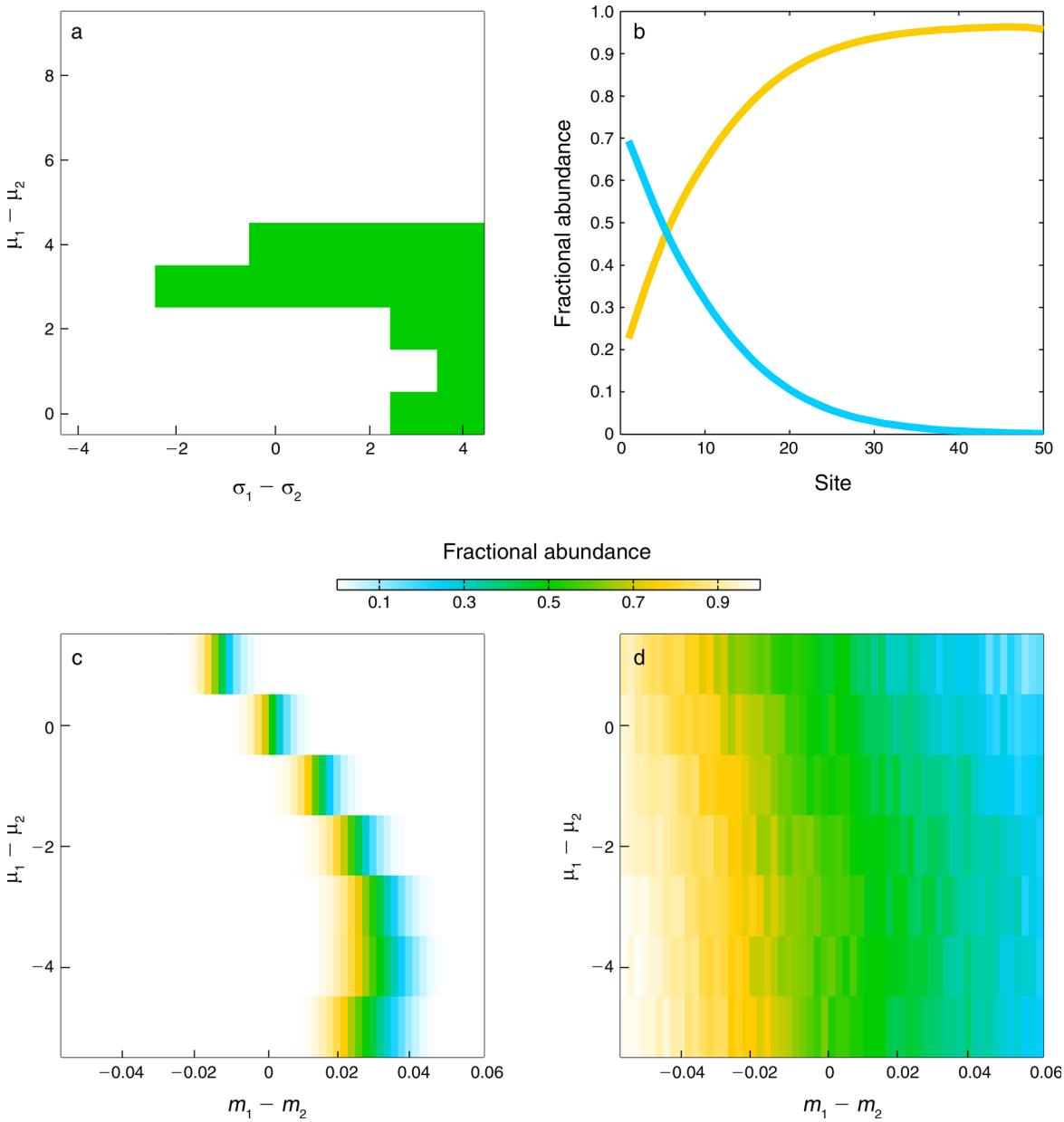

FIG. 4. (a) Green indicates the region of μ–σ space in which stable coexistence is possible in the unforced metacommunity model with constant dispersal, when $m_1 = 0.1$, $m_2 = 0.11$, $\mu_2 = 0$, and $\sigma_2 = 5$; (b) fractional abundance of the dominant (yellow) and subordinate (blue) at each site when $m_1 = 0.1$, $m_2 = 0.11$, $\mu_1 = 3$, $\sigma_1 = 4$, $\mu_2 = 0$, and $\sigma_2 = 5$; (c) fractional abundance of species 2 as a function of m_2 and μ_2 ($m_1 = 0.1$, $\mu_1 = 5$, $\sigma_1 = 5$, $\sigma_2 = 5$); (d) as in panel (c) but with the inclusion of dispersal variability with decorrelation timescale $\tau = 1$.

(Amarasekare 2003). Coexistence of species in our model is of the type documented by Salomon et al. (2010) in the scenarios where net propagule contribution of the dominant varies over space with respect to the subordinate.

The range of mortality rates over which the two species coexist increases slightly with increasing disparity in μ (Fig. 4c). That is, it can be possible for a subordinate to offset increased competitive disadvantages in the adult phase by increasing the disparity in the larval dispersal kernels. While stable coexistence is possible in the absence of dispersal variability, it is confined to particular choices of kernel shapes and relative mortality rates. Addition of dispersal variability, however, broadens substantially the parameter range over which stable coexistence is possible (Fig. 4d). Indeed, as shown above, a sufficient level of dispersal variability can promote coexistence independently of the differences in the dispersal kernels, only dependent upon the relative mortality rates and amplitude of the external

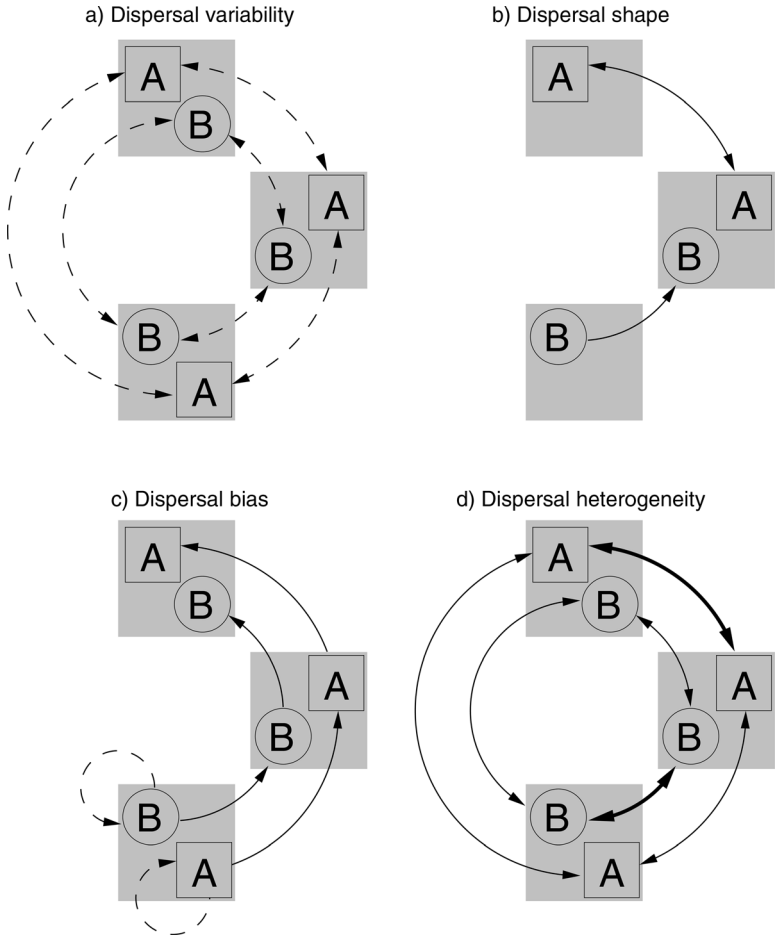

FIG. 5. Schematic representation of the four dispersal-mediated coexistence mechanisms, following Leibold et al. (2004). In each case, the three gray squares represent three sites, and A and B represent the presence of the two species. The fact that A appears in a box indicates that it is the dominant competitor to B (in circles) in all locations. The arrows indicate the direction of larval flows between populations. Dashed lines indicate time-varying dispersal.

forcing. As a result, dispersal shape processes may only be of primary importance in the absence of dispersal variability.

DISCUSSION AND CONCLUSIONS

The complexity of the ecological interactions in the real world, where space is finite, the range is limited, and environmental conditions are variable, as occurs in all marine benthic ecosystems, provides a variety of mechanisms by which coexistence between competitors may occur. Here we have shown that even a very simple, homogeneous, spatially limited metapopulation model can support coexistence of unequally matched species in the absence of life-history trade-offs, which commonly drive coexistence in homogeneous competitive environments (Amarasekare 2003), without resource partitioning and limiting similarity (MacArthur and Levins 1967, Adler et al. 2007) and with no distinction between each species' response to the environment or between inter- and intraspecific competition (Chesson 1985, Snyder and Chesson 2004). Our results therefore confirm recent theoretical developments on dispersal-based coexistence (Berkley et al. 2010, Salomon et al. 2010, Bode et al. 2011), expand (though sometimes restrict) their generality to situations that should be commonly encountered in the ocean or other advective systems, and identify new mechanisms of competitive coexistence. We synthesize these findings into three distinct mechanisms of dispersal-based coexistence in spatially homogeneous environments, which are illustrated in schematic form in Fig. 5a–c. If spatial variation in the advective environment is allowed, then a fourth coexistence mechanism can emerge, as shown by Salomon et al. (2010).

The first coexistence mechanism, dispersal variability, was driven solely by fluctuations in connectivity, representative of that associated with the ubiquitous fluctuations in the ocean circulation. The stochastic variability in the advective medium ensures that the realized dispersal of each species differs at each instant, even when both species have larval dispersal kernels that are identical when averaged in time. This mechanism

was previously explored in the groundbreaking work of Berkley et al. (2010) and was shown there to be equivalent to a spatial storage effect (Warner and Chesson 1985), with the distinction that the ephemeral spatial niche partitioning requires no underlying spatial heterogeneity. Here we show that environmental fluctuations in the dispersal phase provide occasional opportunities in which the subordinate can locally out-recruit the dominant, as evidenced by the intermittent superior exponential growth rate of the subordinate (Fig. 3b). The color of the stochastic dispersal is also important. By increasing the decorrelation timescale of the dispersal variability, which is equivalent to increasing the eddy scales of the advective medium, favorable events become longer and provide more time for the subordinate abundance to increase in the transiently less competitive environment, although a longer-lasting buffering stage is required to prevent extinction during the correspondingly longer unfavorable events.

Although this mechanism has been referred to as turbulent coexistence by Berkley et al. (2010), as noted by those authors deterministic, even periodic, dispersal variability can foster coexistence in the same way, provided only that the dispersal phase gives opportunities for a subordinate to sufficiently differentiate the timing of settlement. In a stochastically varying ocean, offset recruitment timing can occur even when reproduction timing is synchronous, and relatively subtle differences in larval behavior can also be sufficient to guarantee asynchronous settlement. Therefore, the need for offset reproduction times between competitors, highlighted by Berkley et al. (2010) as the main mechanism for coexistence in these environments, can in fact be relaxed. This is an important point since empirical tests designed to evaluate this mechanism cannot be based on reproductive patterns of competing species.

The second coexistence mechanism, dispersal bias, did not require dispersal variability, but rather a finite geographical range combined with a dispersal phase in which advection dominates diffusion. Under these circumstances, self-recruitment is low, and downstream populations are strongly subsidized by those located further upstream. As a result, the stochastic fluctuations of the adult abundances at the upstream edge of the range control the downstream population dynamics. Small changes to the abundances upstream are magnified as they propagate downstream. In a strongly advective environment, the addition of a very few subordinates, or the removal of a very few dominants, at the upstream edge of the range can create a bloom of the subordinate downstream that, although transient, can reach large amplitude (e.g., Fig. 3b). Sufficiently frequent excitation of the transient blooms by the high levels of variability ubiquitous in the environment can allow the subordinate to persist. Weak self-recruitment is increasingly likely for propagules with long dispersal times. In the marine context, mean along-shore flow is a feature common to virtually all coastlines (Largier 2003) such that, save for larvae with extremely sophisticated swimming behaviors and comparatively large body size, there is very low possibility for self-recruitment over small to moderate spatial scales with long larval durations.

While both the dispersal variability and dispersal bias scenarios depend on the continued presence of environmental variability, only the former occasionally satisfies the invasibility criteria (Fig. 3b, e). In the dispersal variability case, the dynamics of the metacommunity change in time such that the competitive rankings occasionally reverse, making possible intermittent invasion of a subordinate. For dispersal bias, however, the dynamics do not change, and hence neither do the competitive rankings, and the exponential growth rate of the subordinate is never positive (Fig. 3e). Nonetheless, when the dynamical operator is reactive (Neubert and Caswell 1997), as occurs when dispersal is sufficiently biased (asymmetrical), episodes of transient growth of the subordinate (and of transient decay of the dominant) may occur frequently enough to mediate coexistence. As shown in Appendix B, the maximum instantaneous (rather than asymptotic) growth rate is a more appropriate metric for quantifying the possibility for coexistence in reactive systems (Fig. 3f). The transients can in fact occur over sufficiently long times as to be relevant, or indeed dominant. In contrast, the exponential solution may emerge on such long timescales as to be irrelevant in practice (see examples for single populations in Hastings and Higgins 1994). This is especially true when metacommunities are not hermetic, as sporadic arrivals of potential colonizers from outside the metacommunity may be sufficient to sustain the transients.

Finally, we demonstrated that, whenever the section of coastline occupied by the species is finite, differences in dispersal kernel shape alone may permit coexistence, even when the dispersal environment is homogeneous and time invariant. This time-independent stable coexistence is a direct consequence of the finite extent of the available geographic range, which has the effect of altering the larval source–sink relationship (sensu Iwasa and Roughgarden 1986), only at the edges of the habitat, and introducing spatial heterogeneity into the otherwise homogeneous connectivity matrix. Even though the dispersal kernels of each species are uniform across the metapopulation, consistent with a homogeneous dispersal environment, larval fluxes towards the edges of the domain differ from those in the center. Because the two species' mean dispersal kernels are distinct, the amount by which the recruitment rate reduces towards the domain edges also differs. When the recruitment rate reduction of the dominant exceeds that of the subordinate at the edges and is sufficient to overcome the homogeneous difference in mortality rates, then the local competitive rankings (considering mortality and arrival of individuals) reverse, allowing

the (global) subordinate to be locally dominant, i.e., regional-scale processes that drive changes in the number of individuals overcome the local process of competitive exclusion produced by per capita differences (see Leibold et al. [2004] for a review of metacommunity models and terminology). At the habitat edge, a subordinate with strong self-recruitment can out compete a species that is dominant away from the edge, but whose dispersal is more diffuse and/or asymmetrical.

This coexistence effect is similar to the spatial source–sink competitive dynamics identified in similar models (Iwasa and Roughgarden 1986, Pulliam 2000) and to the advection-mediated coexistence discussed in Cantrell et al. (2007) and Salomon et al. (2010), except that here heterogeneity is not imposed explicitly, but rather is a consequence of the spatially limited geographical range of the species and species-specific dispersal kernels. A number of recent studies have addressed the possibility for differences in the time-mean dispersal kernel to mediate coexistence. Bode et al. (2011) demonstrate how heterogeneous patch spacing can open a niche for a subordinate whose mean dispersal distance is better matched to at least one pair of patches. In a series of studies, Salomon, Connolly, Bode, and coworkers develop a powerful theory for predicting the coexistence outcome for unequal competitors with differing fixed dispersal patterns (Salomon et al. 2010, Bode et al. 2011, Figueiredo and Connolly 2012). They characterize dispersal in terms of the spatial asymmetry of the connectivity matrices, which refers to an uneven distribution of viable settlers among the patches within a closed metacommunity. This interpretation differs from the asymmetrical connectivity matrices that results in our study due to biased (asymmetrical) but spatially homogeneous dispersal. While there is substantial support for the existence of spatially variable dispersal kernels under realistic ocean flows (Aiken et al. 2007), Salomon et al.'s (2010) approach makes it difficult to isolate the effects of noncentered dispersal from spatially variable dispersal kernels. Yet, a number of their results anticipate the dispersal shape coexistence shown here. As in Salomon et al. (2010), increasing asymmetry of propagule contribution among patches of the dominant and/or increasing self-recruitment of the subordinate tend to favor coexistence. However, in contrast to Salomon et al.'s proposition 4, we find that increasing self-recruitment of either species can inhibit persistence of the other when its dispersal is biased. This difference owes to the fact that the increased larval waste of edge patches is explicitly incorporated into our connectivity matrices. The result of the process is similar to that which would occur for species with overlapping ranges and spatial niche partitioning. However, the model contains no explicit heterogeneity, and the spatial partitioning is solely a consequence of the interaction of the geographically finite species range with the distinct dispersal kernels.

An important characteristic of each of the mechanisms for coexistence produced in our simple model is that the subordinate differentiates itself from the dominant through dispersal strategies alone. A subordinate can avoid the direct competition that would guarantee its extinction by possessing a dispersal phase that differs in space and/or time from that of the dominant, even in an otherwise homogeneous environment. If the dispersal environment is heterogeneous over space, as might be the case in most real systems, then more venues for dispersal-based coexistence can arise (Salomon et al. 2010). In this way, the dispersal phase can represent a niche axis through which species may differentiate themselves to promote their chances of survival. Until recently, these types of coexistence mechanisms had not been considered in existing metacommunity models, summarized by Leibold et al. (2004), or in the empirical assessment of these models (reviewed by Logue et al. [2011]). In the case of pelagic larvae in the highly variable ocean circulation, a species may establish a unique dispersal niche via differences in the larval development time, behavior in the water column, or simply in the timing of larval release or larval settlement at the end of dispersal, for instance, through variable competence times (Hadfield et al. 2001). As the amplitude of the dispersal variability or its decorrelation timescale increases, the degree of differentiation of the dispersal phase required for coexistence diminishes. On the other hand, when the geographical extent of the metacommunity is finite, very low levels of external variability in adult abundances or differences in mean dispersal kernel can promote coexistence in the absence of dispersal variability.

Interestingly, our results also show that low levels of environmental variability and net advection in the dispersal environment can facilitate stable coexistence between competitively and demographically identical (neutral) species by allowing the invasion of a previously saturated system. It is unclear to what extent these types of mechanisms are implicit in the colonization dynamics of neutral biodiversity models (Alonso et al. 2006) or even whether the dispersal representation in such models is commensurate with the model presented here. This seems a fertile field to further theoretical research.

We explicitly address the issue of finite geographical ranges with open boundaries and find that they can play an important role in facilitating coexistence, either in their own right or in concert with environmental variability. Increased larval waste from edge populations introduces heterogeneity into an otherwise homogeneous metacommunity, providing coexistence opportunities such as those described in Bode et al. (2011) and Salomon et al. (2010). In addition, a bias in the direction of propagule transport renders the entire metacommunity sensitive to fluctuations at its upstream end. For example, Great Barrier Reef populations located at the bifurcation of the New Caledonia jet may exert control on the downstream dynamics. A greater examination of

the importance of border populations is especially relevant in a climate change context wherein species ranges are in flux and where fishing pressures can change dramatically at political boundaries.

Given that connectivity asymmetry is extremely common in the ocean due to the presence of a mean alongshore larval transport (e.g., Largier 2003, Aiken et al. 2007, Mitarai et al. 2008), the dynamics of populations with a dispersive life stage may commonly be reactive and hence display a high degree of sensitivity to environmental fluctuations. Such systems may be especially benevolent towards subordinate competitors, as even very small levels of stochastic environmental variability can be sufficient to support coexistence. Our results demonstrate that this mechanism may result in large amplitude fluctuations in the abundances of dominant and subordinate (e.g., Fig. 3). This implies that observed fluctuations in metapopulation abundances may not have an immediately identifiable deterministic source, but rather may reflect natural variability of the stochastically forced system. That is, it is possible that observed changes in spatial and temporal patterns and trends in species range and abundance may not necessarily indicate alterations in the underlying mean conditions. On the other hand, given the fact that climate change is likely to affect species ranges and the strength and variability of coastal currents (e.g., Bakun 1990), coming decades may see some degree of reorganization in coastal metacommunities due solely to altered larval dispersal patterns.

In summary, multiple opportunities exist in the simple model presented by us and by others for species to coexist by occupying distinct dispersal niches. A species may compensate its lower fitness simply by using a larval dispersal strategy that ensures that its own recruitment is uncorrelated in space or time with that of its competitors. Marine ecologists interested in understanding patterns of biodiversity must therefore pay closer attention to the dispersal stages of these species, for the key to high biodiversity may not be in features of the adult habitat, but in characteristics of the ocean circulation. Unfortunately, the state of the art of dispersal theory does not yet allow for powerful empirical tests. However, qualitative comparisons of model predictions and empirical patterns, as those shown by Bode et al. (2011) for the highly diverse Great Barrier Reef fish are highly promissory. Further theoretical research should combine the great advances made in recent years in modeling ocean flows with the theory of dispersal niche to provide more powerful empirical tests to evaluate the importance of these mechanisms on the maintenance of biodiversity.

Acknowledgments

This study was financed through *Iniciativa Científica Milenio* grant P10-033F to the Center for Marine Conservation provided by the *Fondo de Innovación para la Competitividad* of the Chilean government *Ministerio de Economía, Fomento y Turismo*; the *Laboratorio Internacional de Cambio Global* (Linc-Global, CSIC-PUC); Fondap-Fondecyt 15001-001 grant to S. A. Navarrete; Fondecyt grant 1100646 to C. M. Aiken; and Fondecyt 1120158 to S. A. Navarrete. Comments by Sean Connolly and two anonymous reviewers have greatly improved this presentation.

Literature Cited

Adler, P. B., J. HilleRisLambers, and J. M. Levine. 2007. A niche for neutrality. Ecology Letters 10:95–104.

Aiken, C. M., and S. A. Navarrete. 2011. Environmental fluctuations and asymmetrical dispersal: generalized stability theory for studying metapopulation persistence and marine protected areas. Marine Ecology Progress Series 428:77–88.

Aiken, C. M., S. A. Navarrete, M. I. Castillo, and J.-C. Castilla. 2007. Along-shore larval dispersal kernels in a numerical ocean model of the central Chilean coast. Marine Ecology Progress Series 339:13–24.

Aiken, C. M., S. A. Navarrete, and J.-L. Pelegri. 2011. Potential changes in larval dispersal and along-shore connectivity on the central Chilean coast due to an altered wind climate. Journal of Geophysical Research 116:G04026.

Alonso, D., et al. 2006. The merits of neutral theory. Trends in Ecology and Evolution 21:451–457.

Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. Ecology Letters 6: 1109–1122.

Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. American Naturalist 115:151–170.

Bakun, A. 1990. Global climate change and intensification of coastal ocean upwelling. Science 247:198–201.

Berkley, H. A., et al. 2010. Turbulent dispersal promotes species coexistence. Ecology Letters 13:360–371.

Bode, M., L. Bode, and P. R. Armsworth. 2011. Different dispersal abilities allow reef fish to coexist. Proceedings of the National Academy of Sciences USA 108:16317–16321.

Byers, J. E., and J. M. Pringle. 2006. Going against the flow: retention, range limits and invasions in advective environments. Marine Ecology Progress Series 313:27–41.

Cantrell, R. S., C. Cosner, and Y. Lou. 2007. Advection-mediated coexistence of competing species. Proceedings of the Royal Society of Edinburgh: Section A Mathematics 137: 497–518.

Chesson, P. 1991. A need for niches. Trends in Ecology and Evolution 6:26–28.

Chesson, P. 2000. General theory of competitive coexistence in spatially varying environments. Theoretical Population Biology 58:211–237.

Chesson, P. L. 1985. Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. Theoretical Population Biology 28:263–287.

Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. American Naturalist 117:923–943.

Figueiredo, J., and S. R. Connolly. 2012. Dispersal-mediated coexistence under recruitment limitation and displacement competition. Ecological Modelling 243:133–142.

Frankignoul, C., and K. Hasselmann. 1977. Stochastic climate models, Part II Application to sea-surface temperature anomalies and thermocline variability. Tellus 29:289–305.

Gaines, S. D., B. Gaylord, L. R. Gerber, A. Hastings, and B. P. Kinlan. 2007. Connecting places: the ecological consequences of dispersal in the sea. Oceanography 20:90–99.

Hadfield, M., E. Carpizo-Ituriarte, K. Carmen, and B. Nedved. 2001. Metamorphic competence, a major adaptive convergence in marine invertebrate larvae. American Zoologist 41: 1123–1131.

Hastings, A. and K. Higgins. 1994. Persistence of transients in spatially structured ecological models. Science 263:1133–1136.

Hubbell, S. P. 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forest and coral reefs. Coral Reefs 16:s9–s21.

Hubbell, S. P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. Functional Ecology 19:166–172.

Hughes, T. P., A. H. Baird, E. A. Dinsdale, N. A. Moltschaniwskyj, M. S. Pratchett, J. E. Tanner, and B. L. Willis. 2000. Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. Ecology 81: 2241–2249.

Iles, T. C. 1994. A review of stock–recruitment relationships with reference to flatfish populations. Netherlands Journal of Sea Research 32:399–420.

Iwasa, Y., and J. Roughgarden. 1986. Interspecific competition among metapopulations with space-limited subpopulations. Theoretical Population Biology 30:194–214.

Kaplan, D. 2006. Alongshore advection and marine reserves: consequences for modeling and management. Marine Ecology Progress Series 309:11–24.

Klopfer, E., and A. R. Ives. 1997. Aggregation and the coexistence of competing parasitoid species. Theoretical Population Biology 52:167–178.

Kritzer, J. P., and P. F. Sale. 2004. Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. Fish and Fisheries 5:131–140.

Largier, J. L. 2003. Considerations in estimating larval dispersal distances from oceanographic data. Ecological Applications 13(Supplement):S71–S89.

Leibold, M. A., et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Logue, J. B., N. Mouquet, H. Peter, and H. Hillebrand. 2011. Empirical approaches to metacommunities: a review and comparison with theory. Trends in Ecology and Evolution 26:482–491.

Lutscher, F., R. M. Nisbet, and E. Pachepsky. 2010. Population persistence in the face of advection. Theoretical Ecology 3: 271–284.

MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. American Naturalist 101(921):377–385.

McPeek, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. American Naturalist 140:1010–1027.

Mitarai, S., et al. 2008. A numerical study of stochastic larval settlement in the California Current system. Journal of Marine Systems 69:295–309.

Morgan, S. G., and J. R. Anastasia. 2008. Behavioral tradeoff in estuarine larvae favors seaward migration over minimizing visibility to predators. Proceedings of the National Academy of Sciences USA 105:222–227.

Mouquet, N., et al. 2005. The world is patchy and heterogeneous! Trade-off and source sink dynamics in competitive metacommunities. Pages 237–262 in M. Holyoak, M. A. Leibold, and R. Holt, editors. Metacommunities: spatial dynamics and ecological communities. Chicago University Press, Chicago, Illinois, USA.

Muko, S., and Y. Iwasa. 2000. Species coexistence by permanent spatial heterogeneity in a lottery model. Theoretical Population Biology 57:273–284.

Navarrete, S. A., and T. Manzur. 2008. Individual- and population-level responses of a keystone predator to geographic variation in prey. Ecology 89:2005–2018.

Neubert, M. G., and H. Caswell. 1997. Alternatives to resilience for measuring the responses of ecological systems to perturbations. Ecology 78:653–665.

Pringle, J. M., A. M. H. Blakeslee, J. E. Byers, and J. Roman. 2011. Asymmetric dispersal allows an upstream region to control population structure throughout a species' range. Proceedings of the National Academy of Sciences USA 108: 15288–15293.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Pulliam, H. R. 2000. On the relationship between niche and distribution. Ecology Letters 3:349–361.

Roughgarden, J., et al. 1985. Demographic theory for an open marine population with space-limited recruitment. Ecology 66:54–67.

Roughgarden, J., et al. 1988. Recruitment dynamics in complex life cycles. Science 241(4872):1460–1466.

Salomon, Y., S. R. Connolly, and L. Bode. 2010. Effects of asymmetric dispersal on the coexistence of competing species. Ecology Letters 13:432–441.

Shurin, J. B. 2001. Interactive effects of predation and dispersal on zooplankton communities. Ecology 82:3404–3416.

Siegel, D. A., et al. 2008. The stochastic nature of larval connectivity among nearshore marine populations. Proceedings of the National Academy of Sciences USA 105:8974–8979.

Siepielski, A. M., and M. A. McPeek. 2010. On the evidence for species coexistence: a critique of the coexistence program. Ecology 91:3153–3164.

Snyder, R. E., and P. Chesson. 2004. How the spatial scales of dispersal, competition, and environmental heterogeneity interact to affect coexistence. American Naturalist 164:633–650.

Speirs, D. C., and W. S. C. Gurney. 2001. Population persistence in rivers and estuaries. Ecology 82:1219–1237.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews 25(1):1–45.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75:2–16.

Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. American Naturalist 125:769–787.

Watson, J. R., B. E. Kendall, D. A. Siegel, and S. Mitarai. 2012. Changing seascapes, stochastic connectivity, and marine metapopulation dynamics. American Naturalist 180:99–112.

White, C. 2009. Density dependence and the economic efficacy of marine reserves. Theoretical Ecology 2:127–138.

Supplemental Material

Appendix A

Generation of the time-dependent connectivity matrices (*Ecological Archives* E095-203-A1).

Appendix B

A generalized invasibility criteria (*Ecological Archives* E095-203-A2).

Supplement

MATLAB source code of the metacommunity model (*Ecological Archives* E095-203-S1).