

REVIEW

Competitive coexistence in spatially structured environments: a synthesis

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Abstract

Theoretical developments in spatial competitive coexistence are far in advance of empirical investigations. A framework that makes comparative predictions for alternative hypotheses is a crucial element in narrowing this gap. This review attempts to synthesize spatial competition theory into such a framework, with the goal of motivating empirical investigations that adopt the comparative approach. The synthesis presented is based on a major axis, coexistence in spatially homogeneous vs. heterogeneous competitive environments, along which the theory can be organized. The resulting framework integrates such key concepts as niche theory, spatial heterogeneity and spatial scale(s) of coexistence. It yields comparative predictions that can guide empirical investigations.

Keywords

Competition, life history trade-offs, source-sink dynamics, spatial coexistence, spatial heterogeneity, storage effect.

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1 INTRODUCTION

Spatial competition theory has made great strides in advancing our understanding of competitive coexistence in patchy environments. Progress on the empirical front, however, has been comparatively slow. While theory is in advance of data in most areas in ecology, nowhere is it more apparent than in spatial ecology.

The most important element in narrowing the gap between theory and data is a theoretical framework that yields comparative predictions for multiple hypotheses. Most theory on spatial competition has focused on a single mechanism (e.g. Levins & Culver 1971; Levin 1974; Hastings 1980; Nee & May 1992; Tilman *et al.* 1994; Loreau & Mouquet 1999; Amarasekare & Nisbet 2001; Yu & Wilson 2001); very few studies have considered alternative mechanisms and comparative predictions to distinguish between them (e.g. Pacala & Rees 1998; Bolker & Pacala 1999). This single hypothesis approach has hampered the feedback between theory and data. For instance, empirical studies that fail to support a particular hypothesis for spatial coexistence are difficult to interpret, and hence uninformative for guiding future theory, because it is not clear whether they signify an absence of spatial effects altogether, or the presence of spatial mechanisms not tested for. Empirical studies that can simultaneously test several hypotheses are much more likely to shed light on spatial coexistence in

natural communities, and inform theory of areas that need development. While the paucity of comparative empirical studies may well be because of logistical difficulties in their implementation, the lack of a comparative theoretical framework is at least partly responsible.

This review attempts to synthesize spatial competition theory into a framework that can yield comparative predictions for alternative mechanisms. The goal is to stimulate empirical investigations that adopt the comparative approach. To this end, I begin with some well-known but under-appreciated ideas from classical competition theory. I then suggest major axes along which the large body of theory could be organized. I discuss the major mechanisms of spatial coexistence that fall under each axis, and predictions that distinguish among them. I end with suggestions for future directions, both theoretical and empirical.

2 A COMPARATIVE THEORETICAL FRAMEWORK FOR SPATIAL COMPETITION

2.1 Background

All species are to some extent limited by resources or natural enemies. In communities where species exploit common resources or experience common natural enemies, the species that can maintain a positive per capita growth rate at the lowest resource level (R^* rule in exploitative

competition; Tilman 1982) or highest natural enemy pressure (P^* rule in apparent competition; Holt *et al.* 1994) will drive all other species extinct. Coexistence requires species to be different in the way they affect, and are affected by, resources and natural enemies such that intra-specific competition is stronger than inter-specific competition. Following Chesson (2000a), the differences between species that allow coexistence are most usefully thought of as species' niches. Coexistence, therefore, requires some form of niche difference or partitioning between species that increases the strength of intra-specific competition relative to that of inter-specific competition.

Ecological differences between species that lead to niche partitioning can occur in three basic ways. First, different species may specialize on distinct resources (classical resource partitioning; MacArthur & Levins 1967; Tilman 1982) or be subject to density- or frequency-dependent predation (Murdoch & Oaten 1975). Second, different species may be limited by the same resources or natural enemies, but differ in terms of *when* they exploit the resource or respond to natural enemies (temporal niche partitioning; Armstrong & McGehee 1976, 1980; Chesson 1985, 2000a,b). Third, species could differ in terms of *where* they experience, and respond to, limiting factors (spatial niche partitioning; May & Hassell 1981; Chesson 2000a,b). Thus, a useful definition of a species' niche space is that it consists of four major axes: resources, natural enemies, space and time. The niche can then be thought of as species responses to, and their effects on, each point at this niche space (Chesson 2000a).

When species inhabiting a spatially structured environment lack the first two types of ecological differences (e.g. partitioning of two or more resources, frequency-dependent predation, temporal partitioning of a single resource), coexistence must involve some form of niche difference in space that arises from the interplay between competitive dynamics (i.e. the operation of R^* or P^* rules) within local communities, and spatial processes (e.g. emigration, immigration, colonization) that link local communities into a metacommunity (Wilson 1992). Such spatial niche differences can arise in two basic ways.

2.2 Coexistence in a spatially homogeneous competitive environment

Consider a community of species competing for a single limiting resource. The resource can be space itself, as in plants, sessile animals, or species that require nest sites or breeding territories for reproduction. Alternatively, species could be competing for a limiting resource whose abundance varies in space (e.g. patchily distributed food resources or essential nutrients). The competitive environment of a given species consists of abiotic (e.g. temperature,

humidity, nutrient availability) or biotic (e.g. natural enemies) factors that influence its ability to exploit space or the spatially variable resource.

A spatially homogeneous competitive environment is one in which species' competitive rankings (e.g. R^* values) do not change within the spatial extent of the landscape being considered (e.g. the metacommunity). Such a situation arises when differences in the way species exploit resources are intrinsic to the species themselves, and do not depend on the species' abiotic or biotic environment. In other words, species do not exhibit differential responses to the environment and there is no covariance between the environment and competition (*sensu* Chesson 2000a,b). Note that a spatially homogeneous *competitive* environment does not necessarily imply that the environment is completely uniform in space. The key distinction is that while species' vital rates may vary spatially, such variation does not alter species' competitive rankings.

When the competitive environment is spatially homogeneous, coexistence is most likely to occur via inter-specific trade-offs between life history attributes that influence competition (e.g. fecundity, longevity) and those that allow species to escape or minimize competition (e.g. dispersal). The crucial point to note is that life history trade-offs allow coexistence only as long as they allow spatial niche differences between species. As discussed below, whether or not such trade-offs allow spatial niche partitioning depends crucially on the type of competitive interactions between species.

2.3 Coexistence in a spatially heterogeneous competitive environment

When life history or other intrinsic differences between species do not exist or are insufficient to generate spatial niche differences between species, coexistence can occur if the competitive environment is spatially heterogeneous. This means that species' R^* or P^* values vary in space because of spatial variation in the biotic or abiotic environment (Chesson & Huntley 1997). For example, a community of species may compete for a limiting resource, but the degree to which a given species' per capita growth rate is affected by resource limitation may depend on temperature or humidity, or the presence of a specialist natural enemy. Now, the species do exhibit differential responses to the environment, and covariance between the environment and competition is possible (Chesson 2000a,b).

When the competitive environment is spatially heterogeneous, coexistence can occur via three mechanisms (Chesson 2000a,b). Spatial relative nonlinearity occurs when competing species exhibit different *nonlinear* responses to a common competitive environment, which are enhanced by spatial variation in that environment. Spatial storage

effect occurs when species' responses to the competitive environment (which can be linear) vary spatially so as to lead to a covariance between the environment and competition. Growth-density covariance occurs when limited dispersal allows rare species to build up densities in favourable areas, thus increasing their overall per capita growth rate (see Section 4 for details).

2.4 Spatial scale of coexistence

The two spatial scales at which coexistence can occur are the local scale, i.e. within a local community, and the regional scale, i.e. within a metacommunity. A local community is defined as a set of species that occupy a spatial extent of the landscape within which routine feeding and breeding activities and species interactions such as competition and predation occur (Hanski & Gilpin 1997). A metacommunity is a set of local communities linked by dispersal of multiple interacting species (Wilson 1992).

Coexistence in a spatially homogeneous competitive environment occurs via mechanisms independent of spatial variation (e.g. life history trade-offs). Such mechanisms can operate at the scale of a local community and thereby ensure both local and regional coexistence, or they could operate at the scale of a metacommunity and allow only regional coexistence. The former is a more likely outcome than the latter because spatial homogeneity in the biotic or abiotic environment most likely manifests at the smaller spatial scale of a local community than at the larger, regional scale of a metacommunity. Strictly regional coexistence, while possible, requires somewhat restrictive conditions: (i) within-community (competitive) dynamics occur on a faster time scale than metacommunity dynamics (dispersal among communities; Levins & Culver 1971; Hastings 1980), and (ii) the competitive environment is homogeneous at both local and regional scales. Regional coexistence is most easily envisioned in species whose life history differences are not phenotypically plastic such that competitive rankings (e.g. R^* values) are invariant at the regional scale. In a spatially homogeneous competitive environment therefore, the most plausible outcome is local and regional coexistence via the same mechanism.

Coexistence in a spatially heterogeneous competitive environment occurs via mechanisms dependent on spatial variation (e.g. spatial storage effect, growth-density covariance). While these mechanisms can operate at the local scale and allow local and regional coexistence, local exclusion and regional coexistence is the more likely outcome. This is because spatial variation in the biotic or abiotic environment that affects species' competitive rankings is most likely to manifest at spatial scales larger than a local community. A key point to note is that if regional coexistence occurs via one or more variation-dependent mechanisms, dispersal

among communities can allow local coexistence of species (Levin 1974; Shmida & Ellner 1984; Holt 1993). Thus, in contrast to a spatially homogeneous competitive environment where the same mechanism can allow both local and regional coexistence, dual-scale coexistence in a spatially heterogeneous competitive environment occurs most plausibly with the simultaneous operation of two or more mechanisms.

The distinction between spatially homogeneous and spatially heterogeneous competitive environments provides a major axis for identifying basic categories of spatial coexistence mechanisms. It also integrates such key concepts such as niche theory, spatial heterogeneity, and the spatial scales at which coexistence occurs. As I show below, it lays the foundation for a comparative theoretical framework that can guide empirical investigations.

3 COEXISTENCE IN A SPATIALLY HOMOGENEOUS COMPETITIVE ENVIRONMENT

Mechanisms that lead to coexistence in a spatially homogeneous competitive environment are those that concentrate intra-specific competition relative to inter-specific competition in the absence of spatial variation in species' competitive rankings. Broadly speaking, all of these mechanisms involve some form of intra-specific clustering (because of reproduction and localized dispersal), and inter-specific segregation (because of competition that thins out overcrowded areas and creates negative spatial covariances between species; Bolker & Pacala 1999; Chesson 2000b). This can occur in two basic ways: (i) life history trade-offs, and (ii) differences in the spatial scales over which intra-specific vs. inter-specific competition occur. The fundamental distinction between these two classes of mechanisms is that in the former, intra-specific aggregation and inter-specific segregation results from life history differences between species (Bolker & Pacala 1999) while in the latter, it arises from differences in the interaction neighbourhoods within and between species in the absence of large life history differences (Murrell & Law 2003). I discuss each mechanism in turn.

3.1 Life history trade-offs

The general mechanism underlying coexistence via life history trade-offs is as follows: superior competitors are fecundity, recruitment or dispersal-limited, or lack the ability to exploit resource-rich conditions characteristic of recently disturbed (early successional) habitats. Inferior competitors on the other hand, have high fecundity, recruitment ability, or long dispersal ranges, and are thus able to exploit resource-rich or early successional habitats and disperse offspring before superior competitors arrive (the fugitive

strategy; Bolker & Pacala 1999). Because of fecundity, recruitment or dispersal limitations, superior competitors cannot exploit all the available space, or a spatially distributed limiting resource, and leave gaps in the landscape that inferior competitors can exploit. The resulting intra-specific clustering increases the strength of intra-specific competition relative to inter-specific competition, and promotes coexistence. The key point to appreciate is that life history differences allow coexistence by creating spatial niche differences between species that in turn arise from intra-specific clustering and inter-specific segregation. The stochastic spatial model of Bolker & Pacala (1999) illustrates how coexistence results from inter-specific trade-offs between competitive and colonization abilities (classical competition-colonization trade-off; Levins & Culver 1971; Hastings 1980), and between competitive and rapid resource exploitation abilities (successional niche; Pacala & Rees 1998). I next discuss these two modes of trade-off mediated coexistence and how to distinguish between them.

3.1.1 *Competition-colonization trade-off*

Most theory on competition-colonization trade-offs is based on patch occupancy models where the fraction of the available habitat occupied by a species, rather than its abundance, is the state variable of interest (e.g. Levins & Culver 1971; Hastings 1980; Nee & May 1992; Tilman *et al.* 1994; Yu & Wilson 2001). The spatial scale at which coexistence occurs depends on the two scales considered in these models. A strict interpretation of the underlying mathematics, derived from the Levins patch occupancy framework (Levins 1969, 1970), translates to the smaller spatial scale (patch or microsite) being equivalent to a single individual of a given species, and the larger scale (collection of a large number of patches or microsites) being equivalent to a local community within which different species can coexist (e.g. Tilman *et al.* 1994; Yu & Wilson 2001). If one assumes that local competitive dynamics occur on a faster time scale than spatial dynamics, then a patch can be interpreted as a local community within which coexistence is impossible and the collection of patches, a metacommunity within which regional coexistence is possible (e.g. Levins & Culver 1971; Hastings 1980). Empirical evidence for trade-off mediated coexistence is stronger for coexistence at the local community scale rather than the regional, metacommunity scale (see below).

Patch occupancy models consider two types of competitive interactions between species: dominance competition, where superior competitors can displace inferior competitors from occupied patches, and preemptive (lottery) competition, where all species compete for empty patches (or a patchily distributed limiting resource) and superior competitors are species with greater capability of replacing an individual once it dies and leaves an empty patch

(Comins & Noble 1985). One simplifying feature of patch occupancy competition models is that fecundity, recruitment, dispersal tendency and dispersal rate are subsumed into a single parameter termed the colonization rate (e.g. Levins & Culver 1971; Hastings 1980; Nee & May 1992; Tilman *et al.* 1994). Perhaps because of this assumption, dominance and preemptive competition have quite different consequences for trade-off mediated coexistence in patch occupancy models. I discuss several representative models in the two sections that follow.

3.1.1.1 *Dominance (displacement) competition* Because competitive superiority is defined in terms of a species' ability to displace another species from an occupied patch, the appropriate trade-off is between displacement ability and colonization ability. As mentioned above, colonization ability is a composite of fecundity, recruitment from the natal patch to other patches, and dispersal ability (rate and distance). Coexistence requires that competing species exhibit a strict dominance hierarchy, i.e. superior competitors can displace inferior competitors from occupied patches, but inferior competitors cannot displace superior competitors (Hastings 1980; Nee & May 1992; Tilman *et al.* 1994). It is this feature that allows spatial niche differences between species. As competition involves displacement, inferior competitors do not have access to patches that superior competitors occupy. Because of their superior colonization ability however, inferior competitors can establish in patches that superior competitors do not colonize. Thus, a trade-off between displacement ability and colonization ability allows competing species to partition space or another limiting factor (e.g. food, natural enemies) that varies in space.

Studies in which fecundity and dispersal ability are considered as separate parameters (e.g. Holmes & Wilson 1998) have shown that when the superior competitor is not very common, an inferior competitor can invade and establish itself provided it has a longer dispersal range rather than greater fecundity. This suggests that as long as a strict dominance hierarchy is present, the requisite trade-off for coexistence can be that between displacement ability and fecundity (in which case coexistence is not strictly spatial), or between displacement ability and long-distance dispersal ability.

Several recent studies have shown that when the assumption of a strict dominance hierarchy is relaxed, the number of species that can coexist via a competition-colonization trade-off is greatly reduced (Geritz *et al.* 1999; Adler & Mosquera 2000; Levine & Rees 2002). Two sets of circumstances make coexistence restrictive: (i) if the functional form of the trade-off changes from a step function to a continuous one such that a small difference in fecundity or mortality no longer translates into a large

difference in competitive ability (Geritz *et al.* 1999; Adler & Mosquera 2000), and (ii) if there is imperfect competitive asymmetry such that inferior competitors can negatively affect superior competitors (Levine & Rees 2002). These findings strongly suggest that it is stepwise asymmetric competition rather than spatial processes that allows coexistence (Murrell & Law 2003). This makes intuitive sense, because it is the displacement ability of superior competitors that allows for spatial niche differences between species. A trade-off in itself cannot lead to coexistence if it does not generate such differences.

3.1.1.2 Preemptive (replacement) competition Coexistence via a competition-colonization trade-off is not possible under preemptive competition. This is because of the lack of spatial niche differences between species. As no displacement is possible and all species compete for the same amount of empty habitat (or another limiting resource), they experience complete niche overlap. Moreover, competitive ability is determined by a given species' ability to replace individuals of another species once the latter die. As replacement ability itself is determined by life history traits such as fecundity, recruitment, or dispersal ability, a trade-off between competition and colonization cannot arise. The species with the highest local growth rate (ratio of colonization to extinction rate) will exclude all others (Comins & Noble 1985; Loreau & Mouquet 1999; Yu & Wilson 2001). Thus, coexistence under preemptive competition requires additional process(es) that allow for spatial niche partitioning.

Most attempts to uncover processes that allow coexistence under pre-emptive competition involve a spatially heterogeneous competitive environment (see Section 4 below). Two studies deserve mention here, both of which allow for niche partitioning in a spatially homogeneous competitive environment. Skellam (1951) and Kisdi & Geritz (2003) have investigated coexistence under replacement competition for annual and perennial plants respectively. In their models competition, although involving replacement, is asymmetric such that species with competitively superior seedlings can establish in all patches that are free of adults, while species with competitively inferior seedlings can only establish in adult-free patches that do not contain a seedling of the superior species. (In pure replacement competition all species compete equally for adult-free patches, and in a weighted lottery, in proportion to their relative abundances; Comins & Noble 1985.) There is also small-scale spatial variation because of random dispersal of a limited number of seeds. Thus, seed numbers within a given patch are subject to demographic stochasticity. The combination of demographic stochasticity and asymmetry in replacement competition provide opportunities for spatial niche partitioning: inferior competitors can only establish in patches that because of demographic stochasticity, superior com-

petitors have failed to colonize. In this framework, it is small-scale spatial variation because of demographic stochasticity, rather than colonization limitation of superior competitors, that allows inferior competitors to persist (Kisdi & Geritz 2003).

It is important to emphasize that asymmetry in replacement competition is the key to spatial niche partitioning in these models. In essence, coexistence under replacement competition becomes possible because asymmetry in replacement ability creates a dominance hierarchy just as asymmetry in displacement ability does under dominance competition.

3.1.2 Successional niche

A second spatial coexistence mechanism mediated by life history trade-offs involves the successional niche (Pacala & Rees 1998; Bolker & Pacala 1999). The major differences between this mechanism and the competition-colonization trade-off are that (i) the successional niche allows for imperfect competitive asymmetry (i.e. inferior competitors can invade patches occupied by superior competitors), and (ii) superior competitors are not recruitment or dispersal limited. Inferior competitors have greater resource-exploitation ability by virtue of higher fecundity and faster growth. Thus the appropriate trade-off is between competitive (displacement) ability and rapid resource exploitation. Inferior competitors specialize on resource-rich conditions typical of recently disturbed patches (early successional stages of the habitat), and hence cannot be excluded by late successional dominants even when the latter have unlimited recruitment or colonization ability. On the other hand, patches not subject to recent disturbances (late successional stages of the habitat) contain only the superior competitors and are resistant to invasion by inferior competitors. The mosaic of successional stages driven by the interplay between succession and disturbance ensures that species do not have complete overlap in space: inferior competitors experience intra-specific aggregation in patches subject to recent disturbances, as do superior competitors in patches not subject to disturbance. This concentrates intra-specific competition relative to inter-specific competition, thus promoting coexistence.

Under the successional niche hypothesis, spatial niche differences arise not just from the superior competitors displacing inferior competitors from occupied patches (which happens slowly because of succession), but because succession makes some patches completely resistant to invasion by inferior competitors. Under the competition-colonization trade-off hypothesis, inferior competitors can only persist in patches that the superior competitors fail to reach because of recruitment or colonization limitation. Under the successional niche, inferior competitors persist because high fecundity and faster growth rates allow them

Table 1 Comparative predictions to distinguish between spatial coexistence mechanisms involving life history trade-offs

	Competition-colonization trade-off	Successional niche
1. Trade-off	Displacement ability vs. fecundity, recruitment or dispersal ability	Displacement ability vs. resource exploitation ability
2. Competition	Strictly asymmetric, instantaneous exclusion	Imperfect asymmetry, slow exclusion
3. Disturbance	Large scale (many patches or microsites)	Small scale (single patch or microsite)
4. Invasion by inferior competitor	Patches not reached by superior competitors after disturbance	All recently disturbed patches regardless of superior competitors' presence

to capitalize on resource rich conditions of recently disturbed patches regardless of the presence of superior competitors.

The successional niche can operate in conjunction with a competition-colonization trade-off, which can complicate its detection in practice. However, there are important differences that can be detected by appropriately designed experiments (Table 1). The key difference is that superior competitors are recruitment or dispersal limited under the competition-colonization trade-off hypothesis, but not under the successional niche hypothesis. This is a difference that could be detected by seed sowing experiments (Pacala & Rees 1998). Second, under a competition-colonization trade-off inferior competitors can only invade patches not reached by superior competitors, whereas under the successional niche inferior competitors can invade all recently disturbed patches regardless of the presence of superior competitors. This difference can be detected by species introduction experiments. Third, coexistence via a competition-colonization trade-off is most likely when disturbances occur on a large scale (encompassing many patches) and are sufficiently severe to destroy colonizing propagules already present at a patch. In contrast, successional niche is most likely when disturbances occur on a small spatial scale (individual patches), particularly in productive habitats (Pacala & Rees 1998).

3.2 Heteromyopia

A second mechanism of spatial coexistence that results from intra-specific clustering and inter-specific segregation is called heteromyopia (Murrell & Law 2003). Factors such as allelopathy and natural enemies can cause differences in the spatial scales of intra- and inter-specific competition in species that are otherwise ecologically similar. Thus, coexistence can occur in the absence of large differences in life history traits among competing species. For instance, if competitive interactions among heterospecific individuals occur over shorter distances than those among conspecific individuals, strong intra-specific competition lowers the density of the more common species and creates small gaps in the landscape

that can be invaded by the rarer species. The concentration of intra-specific competition relative to inter-specific competition requires differences between the size of interaction neighbourhoods within and between species, and that dispersal be localized. Global dispersal reduces intra-specific aggregation, and eliminates effects of heteromyopia on coexistence (Murrell & Law 2003).

The characteristic feature of heteromyopia that distinguishes it from trade-off mediated coexistence is that species need differ only in the distances over which they interact with conspecifics vs. heterospecifics. Unlike competition-colonization trade-offs where coexistence requires strong competitive asymmetries, coexistence via heteromyopia results from spatial structure generated by the interplay between competition and dispersal (i.e. intra-specific clustering because of reproduction and dispersal, and inter-specific segregation because of competition). Coexistence cannot occur via mere variation in dispersal parameters, in which case the species with the longer dispersal distance always wins. While coexistence via heteromyopia does not require dispersal differences between species (as long as the competitive neighbourhoods are different), coexistence can be augmented by the inclusion of a competition-dispersal trade-off such that the inferior competitor can disperse over longer distances (Murrell & Law 2003).

Biologically, heteromyopia can arise if host-specific natural enemies increase the distance over which conspecific interactions occur relative to heterospecific interactions. Allelopathy against heterospecifics, which is likely to operate over short distances, can also reduce the distance over which heterospecific interactions occur (Murrell & Law 2003).

How might one distinguish between heteromyopia and trade-off mediated coexistence in practice? In the case of heteromyopia, the interaction neighbourhoods between conspecifics and heterospecifics (quantified in terms of competition kernels) are different, competition does not involve strict dominance hierarchies, and superior competitors are not recruitment or colonization limited (Table 2). The empirical challenge lies in estimating competition kernels for interacting species. As suggested by Murrell & Law (2003), this can be done if spatially referenced time series data are available for multi-species communities.

Table 2 Comparative predictions for coexistence mechanisms in a spatially homogeneous competitive environment

	Life-history trade-offs	Heteromyopia
1. Life history differences	Large	Small*
2. Spatial scales of intra- vs. inter-specific competition	Similar	Larger for intra-specific competition
3. Spatial scales of dispersal	Different, greater for inferior competitor	Similar and localized for both species
4. Coexistence	For similar spatial scales of competition but not dispersal†	For similar spatial scales of dispersal but not competition

*Heteromyopia can occur in the presence of large life history differences between species provided spatial structure is sufficiently strong, but is most likely when such differences are small (Murrell & Law 2003).

†Given appropriate trade-offs.

3.3 Empirical evidence for coexistence in a spatially homogeneous competitive environment

3.3.1 Trade-off mediated coexistence

Most empirical evidence for trade-off mediated coexistence comes from species engaging in strong asymmetric competition that exhibit trade-offs between displacement ability and recruitment or colonization ability. Examples involve annual plants (Tilman *et al.* 1994; Tilman 1994) and insect parasitoids (Lei & Hanski 1998). Most of the evidence suggests coexistence via spatial niche differences at the local (community) scale rather than the regional (meta-community) scale.

Several studies have failed to find evidence of coexistence via a competition-colonization trade-off. These include studies of annual plants (Levine & Rees 2002), insect herbivores (Harrison *et al.* 1995), and parasitoids (Amarasekare 2000a,b). In the plant studies the failure of coexistence was attributed to imperfect asymmetry in competition, while in the insect studies it was the absence of a trade-off between competitive and dispersal abilities. The insect studies (Harrison *et al.* 1995; Amarasekare 2000a,b), which tested for regional coexistence, also found that competition and dispersal operated on the same time scale. This similarity in time scales allows for immigration between extant communities to counteract local competitive exclusion (Amarasekare & Nisbet 2001), an aspect not considered by the theory on regional coexistence via trade-offs. Thus, at least some of the negative results are because of a mismatch between theory and data regarding the spatial scales at which trade-offs operate (local communities vs. metacommunities), and the time scales of competition and dispersal.

The fact that most theory and data supporting trade-off mediated coexistence involve plants raises the issue of the applicability of this mechanism to other taxa. Insect parasitoid guilds that engage in both exploitation and interference competition for a common host provide perhaps the best example (Force 1970; Zwolfer 1971). Such parasitoid species engage in within-host larval competition

where one species wins via direct aggression or physiological suppression. The biology is thus consistent with a strict dominance hierarchy determined by displacement ability. The parasitoids also engage in exploitative competition for unparasitized hosts. Coexistence is possible, both in theory and practice, if species inferior at within-host larval competition are superior at exploiting unparasitized hosts via superior search efficiency and dispersal ability (Briggs 1993; Holt & Polis 1997; Amarasekare 2000a,b, 2003). This could be thought of as a trade-off between competitive (displacement) and dispersal abilities, with the parasitoid species superior at larval competition being able to displace (kill) other species from a single host individual that is multiply parasitized by several species. There are however, important differences from a competition-dispersal trade-off as envisioned in the theory discussed above. This is because there is local resource partitioning involved, i.e. the species superior at larval competition effectively has two resources, unparasitized hosts and the other parasitoid species it kills during larval competition. Coexistence cannot occur if the superior competitor displaces the inferior competitor, but does not gain a reproductive benefit from it (Briggs 1993; Amarasekare 2002).

3.3.2 Heteromyopia

Coexistence via differences in the spatial scales of intra- vs. inter-specific competition is a relatively new idea (Murrell *et al.* 2002; Murrell & Law 2003), and empirical evidence of its operation in nature is yet to be obtained. Some work has been carried out on estimating competition kernels in plants (e.g. Benjamin 1999; Purves & Law 2002), but comparative information on competition and dispersal kernels is not yet available.

3.4 Future directions

3.4.1 Theoretical

Coexistence mechanisms in a spatially homogeneous competitive environment have been quite exhaustively studied in

models of dominance competition. This is not the case for preemptive competition. Most theory on preemptive competition has focused on competition-colonization trade-offs, and used the patch occupancy approach to investigate them. This brings up the issue of whether the failure to find trade-off mediated coexistence under pre-emptive competition is an artefact of the patch occupancy approach of lumping fecundity, recruitment and dispersal into a single parameter so that trade-offs between these traits are not possible. Alternatively, it is possible that pre-emptive competition, because of its dependence on initial conditions, has fundamentally different consequences for spatial coexistence than dominance competition. Resolution of this issue is an important future direction, and can be achieved by extending the theory on successional niche and heteromyopia to incorporate preemptive competition.

3.4.2 Empirical

There are several crucial steps in empirical testing of coexistence mechanisms in a spatially homogeneous competitive environment. First, one needs to establish (i) the type of limiting factor involved (e.g. space or spatially distributed resource), (ii) the type of competitive interaction (e.g. dominance vs. preemptive competition), (iii) the spatial scales at which competition occurs (e.g. local community vs. metacommunity), and (iv) whether species' competitive rankings are invariant in space. Determining these attributes requires studying several local communities, the minimum number of which has to be sufficiently high for detecting a statistically distinguishable effect. *A priori* power analyses (Zar 1996) can determine the minimum number of communities needed.

The second step involves deciding which classes or subclasses of coexistence mechanisms to test. This requires careful matching of models with the system being studied, making sure that the biology of the species being studied is consistent with model assumptions. The two major classes of coexistence mechanisms are life history trade-offs and heteromyopia, the crucial distinction between which is the size of the interaction neighbourhoods within and between species (see Table 2 for comparative predictions). If interaction neighbourhoods are similar, heteromyopia is unlikely to be driving coexistence. One then needs to establish whether species exhibit the appropriate life history trade-offs (competition-colonization or successional niche; Table 1) required for coexistence.

Given that most existing studies have focused on spatial coexistence mechanisms in plant communities, it is important to expand empirical investigations to cover other taxa. Parasitoid guilds and social insects (e.g. Acacia ants; Yu & Wilson 2001) provide good model systems for testing spatial coexistence mechanisms in insect communities. Investigations of parasitoid guilds also have practical applications in

biological control because whether or not parasitoid natural enemies coexist via spatial processes is likely to have important consequences for pest population abundance and variability (Hassell 2000; Bogran *et al.* 2002).

In situations where it is difficult to distinguish between alternative mechanisms via experimentation alone, mechanistic models that are appropriately parameterized can aid in identifying the most likely mechanism(s). Recent work by Yu & Wilson (2001) and Levine & Rees (2002) constitute important steps in this direction.

4 COEXISTENCE IN A SPATIALLY HETEROGENEOUS COMPETITIVE ENVIRONMENT

The coexistence mechanisms discussed above involve ecological differences between species in a spatially homogeneous competitive environment. Because species are limited by a single factor (e.g. resources or natural enemies) and their competitive rankings are invariant in space, opportunities for coexistence are likely to be the most restrictive under this scenario. Spatial heterogeneity in the competitive environment provides additional axes over which species can differ, thus broadening opportunities for coexistence.

As noted in Section 2.3, three mechanisms can allow coexistence in a spatially heterogeneous competitive environment (Chesson 2000a,b). I focus mainly on the spatial storage effect, because it arises under a wide variety of circumstances and thus appears to be the most biologically feasible. Where appropriate I also discuss how the growth-density covariance broadens opportunities for coexistence.

4.1 Regional coexistence via a spatial storage effect

A spatial storage effect enables coexistence by concentrating intra-specific competition relative to inter-specific competition. This requires three important ingredients: (i) differential responses to the environment, (ii) covariance between the environment and competition, and (iii) buffered population growth (Chesson 2000a,b). I explain each of these elements in turn.

Competing species may differ in their responses to a spatially varying competitive environment. This can occur if species' R^* and P^* values vary in space because of spatial variation in abiotic or biotic factors that affect species differently (Chesson & Huntley 1997).

If spatial heterogeneity in the biotic or abiotic environment leads to spatial variation in the strength of competition, then a covariance between the environment and competition can arise. For example, if a natural enemy that affects competing species differently, say via frequency-dependent predation (the environmental response), is present in some areas of the landscape and not others, the

competitor that is more susceptible to the natural enemy will build up densities in areas free of the natural enemy and hence experience strong intra-specific competition relative to inter-specific competition. Its densities will however be low in areas where the natural enemy is present, subjecting it to stronger inter-specific competition from other species that are less susceptible to the natural enemy. Thus a covariance between competition and natural enemy presence arises such that intra-specific competition is strongest in spatial locations where the environment is favourable for the focal species (e.g. natural enemy is absent), and inter-specific competition is strongest in locations where the environment is unfavourable (e.g. natural enemy is present). Note that a trade-off between resource limitation and susceptibility to natural enemies is a coexistence mechanism that is independent of spatial variation. Here I refer not to such a trade-off, but to spatial variation in natural enemy abundance that affects competing species differently in different locations of the landscape.

When differential responses to the environment generate a covariance between the environment and competition, buffered population growth ensures that the reduction in a species' per capita growth rate because of negative effects of competition in unfavourable spatial locations is compensated for by an increase in growth rate because of release from competition in favourable spatial locations (Chesson 2000a). A positive average per capita growth rate will allow an initially rare species to invade a community of resident species that have reached their stationary abundances in the absence of the invader (Chesson 2000b).

Coexistence via a spatial storage effect can be thought of as resulting from competing species exhibiting differences along multiple niche axes. As pointed out in Section 2.1 (see also Chesson 2000a), a species' niche consists of four major axes: resources, natural enemies, space and time. Thus, if species compete for a limiting resource, differential responses to the competitive environment would necessarily constitute how resource exploitation varies over space, time or in response to natural enemies. For instance, if the presence or absence of a natural enemy alters the relative strengths of intra- vs. inter-specific competition for a limiting resource in different locations of the landscape, then spatial variation in natural enemy abundance constitutes a second limiting factor (niche axis) along which species exhibit differences. Similarly, if spatial variation in abiotic factors such as temperature, humidity, salinity or presence of an essential nutrient (or toxin) alters the strength of competition, then space itself constitutes a second niche axis.

Given that a spatial storage effect results from species differences on multiple niche axes, the question arises as to what spatial scale at which coexistence is most likely to occur. This depends crucially on the scale at which spatial

heterogeneity in the competitive environment occurs. More often than not, spatial variation in biotic or abiotic factors that alters species' R^* s is likely to occur on spatial scales larger than a single, local community. Thus, a spatial storage effect is most likely to lead to regional coexistence of competing species.

The next two sections discuss several biological mechanisms for regional coexistence via a spatial storage effect.

4.1.1 *Spatial variation in habitat area*

Yu & Wilson (2001) have shown, by explicitly incorporating inter-specific competition to a patch occupancy model, that species engaging in preemptive competition cannot coexist locally via a competition-colonization trade-off, but can coexist regionally provided there is spatial variation in habitat area. For instance, in areas where the habitat available for colonization is large, the superior competitor excludes the inferior competitor, but in areas where habitat available for colonization is small, the inferior competitor's greater colonization (or recruitment) ability sufficiently outweighs its competitive inferiority to exclude the superior competitor.

4.1.2 *Spatial variation in habitat suitability*

Levine & Rees (2002) have shown that for annual plant species engaging in dominance competition with partial asymmetry (i.e. inferior competitors can exert negative effects on superior competitors), spatial variation in habitat suitability can allow regional coexistence. Note that it is not habitat area that varies in space, as in Yu & Wilson's (2001) model, but its suitability in terms of allowing rare species to maintain positive per capita growth rates. For instance, plant species that are competitively superior by virtue of having larger seeds that disperse little are restricted to the most favourable habitats, whereas competitively inferior species with smaller seeds (and higher seed output) that disperse farther can invade even the suboptimal habitats. Long-term regional coexistence however, depends on the ability of inferior competitors to persist in suboptimal habitats (see Section 4.2).

Two specific examples of spatial variation in habitat suitability involve natural enemy effects and resource supply ratios. As discussed in Section 4.1, spatial variation in the abundance of a specialist natural enemy can allow regional coexistence if it causes spatial variation in the relative strengths of intra-specific vs. inter-specific competition. The best-known examples come from the rocky intertidal, where competitive dominance between algal species shifts with the presence of a keystone predator (Paine 1966; Connell 1971).

In species that compete for two or more limiting resources (e.g. essential nutrients), the ratio of supply rates determines which combination of species can coexist at a particular location of the landscape (resource ratio

hypothesis; Tilman 1982). A given resource supply ratio can also cause competitive exclusion, with one species being the best competitor at a particular location (Pacala & Tilman 1994). In this latter case, spatial variation in the resource supply ratio can favour different species at different locations, leading to regional coexistence of species that would exclude each other locally. Even when resource supply ratios do allow local coexistence, a spatial storage effect will lead to greater regional diversity because spatial variation in resource supply ratios will favour different species combinations at different locations.

4.2 Local coexistence via a spatial storage effect and dispersal

That competing species could coexist regionally via a spatial storage effect is not too surprising given that inter-specific differences over multiple niche axes ensures that species have favourable locations in the landscape where they suffer relatively little inter-specific competition. The more challenging issue is whether a spatial storage effect can allow local coexistence.

A large body of theory exists to show that a spatial storage effect combined with dispersal can lead to local coexistence via source-sink dynamics (e.g. Skellam 1951; Levin 1974; Pacala & Roughgarden 1982; Shmida & Ellner 1984; Chesson 1985; Loreau & Mouquet 1999; Amarasekare & Nisbet 2001; Codeco & Grover 2001; Levine & Rees 2002; Mouquet & Loreau 2002). I first discuss general models of spatial storage effect and dispersal. I then turn to specific biological mechanisms that allow local coexistence via source-sink dynamics.

4.2.1 General models of spatial storage effect and dispersal

A spatial storage effect automatically implies the existence of sources and sinks, localities where an initially rare species has a positive per capita growth rate because inter-specific competition is weaker than intra-specific competition, as opposed to localities where it has a negative growth rate because of stronger inter-specific competition. Dispersal from sources can prevent the exclusion of inferior competitors from sinks. Exclusion is prevented because dispersal creates a negative density-dependent effect that increases the strength of intra-specific competition relative to inter-specific competition (Holt 1993; P. Amarasekare *et al.*, unpublished manuscript).

A key point to note is that local coexistence via source-sink dynamics is unprotected because no inter-specific niche differences exist at the local scale (Amarasekare 2000c). Continued immigration from source communities is, therefore, necessary to maintain inferior competitors in sink communities. Another crucial requirement is permanent spatial heterogeneity in the competitive environment (Muko

& Iwasa 2000). If variation is spatiotemporal rather than purely spatial, the spatial storage effect is ephemeral (Chesson 2000a), as is local coexistence. Even in the presence of permanent spatial heterogeneity, long-term coexistence depends on the mode of dispersal (P. Amarasekare *et al.*, unpublished manuscript). If dispersal involves surplus individuals who do not contribute to local reproduction of sources, sinks are rescued from extinction with no cost to sources. In this case, a spatial storage effect coupled with dispersal ensures local coexistence of competing species regardless of the dispersal rate. In contrast, if dispersal involves individuals that contribute to local reproduction of sources, per capita growth rate of the source itself will be depressed. If losses due to emigration are sufficiently large, source communities themselves can experience negative growth rates, resulting in region-wide exclusion of the species (Amarasekare & Nisbet 2001; Mouquet & Loreau 2002). In such a situation, growth-density covariance can broaden opportunities for coexistence (Chesson 2000b; Snyder & Chesson 2003). In the presence of permanent spatial heterogeneity, localized dispersal (or equivalently, low rates of global dispersal) allows an initially rare species to build up densities in favourable areas of the landscape and hence achieve a higher per capita growth rate than in an unfavourable area. This will increase the average per capita growth rate of an invading species across the landscape, and promote coexistence (Snyder & Chesson 2003). The combination of a spatial storage effect and growth-density covariance, therefore, can substantially increase opportunities for local coexistence.

Local coexistence via source-sink dynamics has been demonstrated for both dominance and preemptive competition, via a wide variety of modelling approaches. Thus it appears to be a general mechanism that applies across a broad range of taxa and systems. Most source-sink competition models however, consider a spatial storage effect phenomenologically without incorporating a specific biological mechanism. I next discuss studies that provide a mechanistic basis for the spatial storage effect.

4.2.2 Mechanistic models of spatial storage effect and dispersal

As discussed in Section 4.2.1, spatial variation in habitat area and suitability provide a mechanistic basis for the spatial storage effect under both preemptive (Yu & Wilson 2001) and dominance competition (Levine & Rees 2002). Dispersal from areas favourable to each species can prevent its exclusion in unfavourable areas, thus enabling local coexistence.

Codeco & Grover (2001) have shown that spatial variation in the supply ratios of Carbon and Phosphorous combined with dispersal can allow local coexistence of algal and bacterial species that cannot otherwise coexist (because bacteria exclude algae at high C : P ratios and vice versa).

Spatial variation in C : P ratios can favour different algal or bacterial species at different spatial locations. Dispersal from such source localities prevents competitive exclusion in localities that are unfavourable for a particular species (sinks). The model, however, failed to accurately predict species' abundance patterns, suggesting that other processes besides source-sink dynamics may influence such patterns.

4.3 Empirical evidence for coexistence in a spatially heterogeneous environment

Empirical evidence for coexistence via a spatial storage effect and source-sink dynamics is scant, largely because of the difficulty of testing these ideas in natural communities. Some evidence does exist for their operation in plant and insect communities (Shmida & Ellner 1984; Kadmon & Shmida 1990; Harrison *et al.* 1995). The best evidence to date comes from gradostat studies of microbes. Codeco & Grover (2001) investigated the role of dispersal and spatial variation in resource supply ratios in local coexistence of one algal species and two bacterial species. They found that while the algae and bacteria dominated at different resource supply ratios, dispersal from areas favourable to each species allowed local coexistence in unfavourable areas.

4.4 Future directions

4.4.1 Theoretical

Although a large body of theory exists on spatial coexistence mechanisms, most of the theory has focused on either trade-off mediated coexistence or source-sink dynamics. Very few studies have attempted a comparative analysis of coexistence mechanisms in spatially homogeneous vs. heterogeneous competitive environments. The recent work of Yu & Wilson (2001) and Levine & Rees (2002) constitute an important step in this direction. Both have combined trade-offs and source-sink dynamics in a single model, and obtained the important result that while life history trade-offs in themselves cannot lead to coexistence, a trade-off combined with source-sink dynamics can do so. Levine & Rees (2002) further show that a competition-colonization trade-off operating in combination with spatial heterogeneity and source-sink dynamics can accurately predict the abundance patterns of annual plants in natural communities. These results and those of Codeco & Grover's (2001) suggest that elements of different mechanisms may operate in concert, an issue that requires further theoretical exploration. Yu and Wilson's and Levine and Rees' studies, while pushing the theory in important new directions, are restricted to one type of competition (preemptive or dominance) and geared mostly towards plants. What is missing is a comparative theoretical framework that can accommodate different modes of competition, dispersal, and regimes of spatial

heterogeneity. Such a framework can investigate the relative importance of difference classes of spatial coexistence mechanisms, and identify situations where several mechanisms are likely to operate simultaneously. It can also predict which classes or subclasses of mechanisms tend to be mutually exclusive. Most importantly, a framework that accommodates these different aspects can yield comparative predictions that apply across a wide range of life histories and regimes of environmental heterogeneity.

4.4.2 Empirical

Empirical tests of the spatial storage effect require quantifying differential responses of species to their common environment, and the resulting covariance between the environment and competition (Chesson 2000a,b). The first step in testing for source-sink dynamics involves quantifying per capita growth rates of species at multiple spatial locations to verify that sources and sinks in fact exist. Species abundances or reproductive rates are not surrogates for the per capita growth rate because sinks can support large populations under certain circumstances (Watkinson & Sutherland 1995), and reproductive rates do not take into account the effects of emigration and immigration. A measure of the per capita growth rate is essential for determining dispersal constraints on coexistence, for it is the excess of emigration over reproduction that causes per capita growth rates of source communities to become negative (Gundersen *et al.* 2001). In fact, quantifying the relationship between the per capita growth rate and the relative density of a rare species can reveal whether a growth-density covariance (Snyder & Chesson 2003) reduces emigration losses to sources.

Once the existence of source and sink communities has been verified, the role of dispersal in local coexistence can be tested by varying dispersal rates (or distances between experimentally created local communities) between sources and sinks. It is also possible to create sinks artificially, as has been carried out in single species source-sink studies (Gundersen *et al.* 2001). The expectations based on source-sink models are: regional coexistence in the absence of dispersal (i.e. each species is restricted to its favourable habitat), local coexistence under low dispersal rates, and regional exclusion of the species with the weaker storage effect under high dispersal rates (or in the absence of a growth-density covariance). Designing experiments to test these predictions can be logistically quite challenging. In such situations, mechanistic models, appropriately parameterized, can simplify experimental designs by predicting the range of dispersal rates likely to induce qualitative changes in dynamical behaviour (e.g. from regional to local coexistence, or from local coexistence to regional exclusion).

Experiments that simultaneously test for coexistence with and without spatial heterogeneity are likely to be the most

Table 3 Comparative predictions for coexistence mechanisms in spatially homogeneous vs. heterogeneous competitive environments

	Homogeneous competitive environment	Heterogeneous competitive environment
1. Differential responses to competitive environment	No	Yes
2. Covariance between environment and competition	No	Yes
3. Spatial variation in competitive rankings	No	Yes
4. Intra-specific clustering and inter-specific segregation	Yes	Yes if SSE and/or GDC*, No if SSE + dispersal but no GDC
5. Spatial scale of Intra-specific clustering and inter-specific segregation	Local (within a community)	Regional (metacommunity) if SSE only
6. Spatial scale of coexistence	Local and regional via same mechanism†	Local and regional via different mechanisms: local (SSE and/or GDC + dispersal), regional (SSE and/or GDC)

*SSE, spatial storage effect, GDC, growth-density covariance.

†Trade-offs, successional niche or heteromyopia.

informative (see Table 3 for comparative predictions), but pose an even bigger challenge in terms of implementation. Mechanistic models along the lines of Yu & Wilson (2001) and Levine & Rees (2002) can be used to eliminate mechanisms that are inconsistent with the species' biology and to predict the conditions under which plausible mechanisms are likely to operate. Statistical approaches such as metaanalyses (Gurevitch *et al.* 1992; Gurevitch & Hedges 1999) can be particularly useful in combining information from studies that have focused on one class of mechanism.

5 CONCLUDING REMARKS

This review attempts to synthesize spatial competition theory into a framework that can guide empirical investigations. It utilizes a major axis, coexistence in spatially homogeneous vs. heterogeneous competitive environments, along which theory and data can be organized. The resulting framework identifies important gaps in the theory, and yields predictions that can be empirically verified. Most importantly, it lays the foundation for a comparative approach to both theory and empiricism that emphasizes the simultaneous analysis and tests of multiple mechanisms.

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