studies [4,5,7] are in clear agreement with Stoll and Prati [2], the question 'can the initial spatial configuration promote a long-term species coexistence?' still remains. Realistic cellular automaton models for clonal perennials with initial intraspecific aggregation predict that survival of weaker competitors can last for up to 500 years [8]. Delays of this kind could contribute to the long-term maintenance of species diversity even if the asymptotic outcomes of such spatial models are monocultures of the strongest competitors [9].

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Intraspecific aggregation and species coexistence

Comment from Chesson and Neuhauser

It is hard not to be enthusiastic about possible major advances in the understanding of diversity maintenance mechanisms that stem from recent work in spatial ecology, a subject discussed by Murrell *et al.* [1] in a recent research news article. There are, however, very serious dangers from superficial understanding of spatial models. Unfortunately, Murrell *et al.* [1] miss some crucial advances in the theory and, although advising caution, nevertheless manage to encourage a dangerously simplistic view of aggregation as a mechanism of coexistence of plant species.

When spatial niches underlie aggregation, there is no problem theoretically demonstrating that coexistence can result quite broadly for a wide range of different sorts of spatial niche [2,3], but most people expect that there is more to it than this. For example, Murrell *et al.* [1] make much of the fact that, at equivalent densities, individual plants are likely to have more conspecific neighbors than heterospecific neighbors when they are aggregated intraspecifically, an outcome that might result simply from local dispersal. Pacala and Levin [4,5] try to quantify the potential effects of such aggregation on species interactions in spatial models of Lotka–Volterra competition using landscape-level interspecific competition coefficients, which are much lower than neighborhood-level interspecific competition coefficients when the latter are large. This suggests that the effect of aggregation is to reduce the likelihood of competitive exclusion. However, the opposite outcome is possible. In the absence of life-history tradeoffs, mathematically rigorous methods have demonstrated that the region of parameter space consistent with coexistence becomes smaller in the presence of aggregation in spatial Lotka–Volterra models [6].

The reason that aggregation can promote competitive exclusion in spatial Lotka–Volterra competition is easy to understand. Competitive exclusion takes place by the expansion of monospecific clusters of the superior competitor [6]. The important interactions are near cluster boundaries, and therefore local-scale competition coefficients are relevant. The species with the larger interspecific effect on the other species will have a higher probability of excluding the other species near cluster boundaries. In the interior of a cluster, interactions are exclusively intraspecific, but, because only conspecific replacement can occur there, competitive exclusion is not affected. Thus, a focus on the relative frequencies of heterospecific versus conspecific neighbors, encouraged by Murrell *et al.* [1], or on the resulting landscape-level competition coefficients of Pacala and Levin [4,5], can be misleading.

However, variation in species densities in space can lead to new opportunities for coexistence when combined with tradeoffs between life-history parameters, a feature examined in an approximate analytical study by Bolker and Pacala [7]. They identified two coexistence mechanisms, one of which is the now-familiar competition–colonization tradeoff, and the other of which is a variation on competition–colonization relying on rapid local population growth of the inferior competitor to a high carrying capacity before it is locally excluded. It is the existence of regions of low density (relative to the inferior competitor's carrying capacity) that are available for colonization and exploitation, rather than aggregation, that is at the heart of coexistence in their study.

Recent work in spatial models has the potential to yield a sophisticated understanding of spatial coexistence mechanisms, but the challenge is to identify those features that are truly behind coexistence rather than distracting characteristics that are associated with a mechanism but are not fundamental to it. This caution applies not only to plants, but also to animals, where aggregation of insects was originally suggested as a broad mechanism of species coexistence, but was later shown to reduce to spatial niches [8,9], or to depend on tradeoffs greatly at variance with the original idea [10].

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Intraspecific aggregation and species coexistence

Response from Murrell, Purves and Law

Our recent article in *TREE* [1] was motivated by the lack of empirical information on the effect of spatial structure on competition. We thank Rejmánek [2] for drawing attention to several further empirical studies.

Chesson and Neuhauser [3] create the impression that, in the absence of life-history tradeoffs, coexistence of competing species becomes less likely when spatial structure is considered. The basis for this is an analysis by Neuhauser and Pacala [4] that concluded that local interactions in a spatial version of the Lotka–Volterra competition model would reduce the parameter space of coexistence. We offer the following counterexample (model from [4] with small modifications) in which the spatial extension causes the coexistence of two species (Fig. 1).

In this example, the first species is a stronger competitor and leads to extinction of the second in the nonspatial Lotka–Volterra system. But the distance over which interactions between species occur is shorter than that within species. This, together with the spatial segregation of the species, reduces the strength of interspecific competition sufficiently to permit either species to invade the other. We have not invoked a life-history tradeoff (e.g. the familiar competition–colonization tradeoff) to achieve coexistence here. Moreover, there is nothing intrinsic to coexistence here that says that it has to be due to niche differentiation. But, this is not to say that, if competition extends to conspecific neighbors that are more distant than heterospecifics, niche differentation is not a potential mechanism; different distances could, for instance, be caused by host-specific enemies that aggregate around parents (the Janzen–Connell hypothesis).

That we get dynamics different from [4] is not surprising – the models have several different assumptions. Six extra functions are needed in the spatial version of the two-species Lotka–Volterra competition model to deal fully with local interactions and local dispersal, and each function has at least one parameter [5]. To make analysis tractable, theoreticians have had to use simplifying symmetries in the interactions; investigation of how the extended parameter space affects asymptotic and transient coexistence has barely begun.

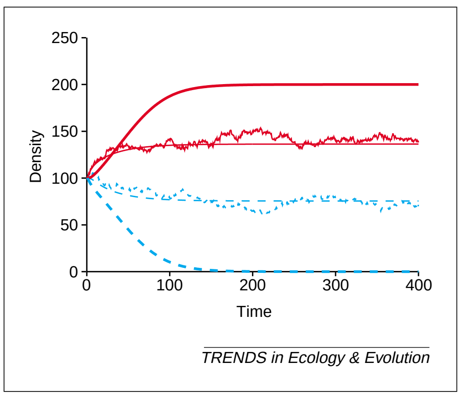

Fig. 1. In the non-spatial Lotka–Volterra model (heavy solid and dashed lines), the strong competitor (red) drives the weak one (blue) to extinction. In the spatial model, by allowing interspecific interactions to occur over a shorter range than do the intraspecific interactions, the weaker competitor is able to coexist with its rival. This is shown both in a stochastic model (uneven lines) averaged over 40 realizations and also in a deterministic approximation based on moment dynamics (light solid and dashed lines). Apart from the weak and strong competition, the two species have the same parameter values.

Coupling of spatial structure to population dynamics is intricate and it would be unwise to assume either that aggregation always leads to exclusion or the reverse. It is most likely that there are some conditions under which spatial structure promotes coexistence and others under which it does not: the former obviously deserve special attention.

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