

The population consequences of territorial behavior

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Theoretical work on competition for space, like mathematical ecology more generally, has followed a trajectory beginning with a basic model that predicts a population-level pattern in terms of some average characteristics of the population, leads on to empirical work showing the model is too simple, and then produces further theory that seeks to show how the phenomenon arises from local interactions.

An example of this trajectory is work on 'self-thinning' in populations of trees that compete for light and nutrients, both of which are resources linked to space. In early work on density dependence in plants¹, the goal was to see how, in a population of sessile organisms, neighbor effects on survivorship and mortality might influence both spatial distributions and population dynamics. The self-thinning rule relates the number of trees in a population to its size distribution. The size distribution of the population is characterized by the mean biomass, and the 3/2 power law of self-thinning is that a log-log plot of biomass against number has a slope of -3/2. Empirical work has shown that the self-thinning rule is often too simple. For example, competitive effects change as a tree ages², and the suppression of new trees by neighbors may have different dynamics from those of neighbor effects on the mortality of large trees³. When competition between two neighbors is asymmetric⁴, the self-thinning rule does not hold. Recent theoretical work shows that when local conditions are considered, both the 3/2 law and deviations from it can be derived⁵. Adler's model⁵ includes a term for how the effect of competition depends on each focal individual's body size, and a term for how the effect of competition scales with neighbor size and distance.

In general, theory on competition for space is usually intended to contribute to the broader theory of population dynamics. Most models are based on plant populations. Unlike animals, plants do not move around. There is, however, a growing body of theoretical work (e.g. Ref. 6) on spatial distributions of populations of sessile animals, which, as Harper said of plants⁷, stand still and wait to be counted.

Competition for space is clearly related to population dynamics. The events that determine population dynamics, such as growth, recruitment, and spatial and temporal heterogeneity in resources, are all crucial to spatial distributions. Models of competition for space often examine the effects of growth or recruitment on population size; for example, they specify the conditions for the coexistence of two or more species, or for the persistence of populations in a metapopulation⁸, or predict the course of succession⁹. Mathematical ecology in general has moved toward greater

Many organisms compete for space, or for resources that are linked to space.

Territorial behavior in animals is one expression of competition for space.

Models of competition for space seek to predict how the arrangement of individuals in a population changes as new individuals appear, others die, and neighbors interact with each other; studies of territorial behavior examine how neighbor interactions lead animals to establish and maintain their use of space. In recent work on competition for space and on territorial behavior, there has been a shift from simple, general models to ones that incorporate heterogeneity in the spatial and temporal distribution of resources, and in the ways individuals use resources.

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recognition of the effects of heterogeneity on population dynamics; theory on competition for space has joined in this trend.

Territorial behavior, like population dynamics, influences the distribution of individuals that compete for space. Territoriality was originally defined as the behavior used to defend or capture space, but it is now recognized that a great diversity of behavior, including but not restricted to defense, influences animals' use of space. Stamps¹⁰ has written an excellent recent review of the literature on territoriality. The main generalization to emerge from recent work is that territories are not fixed parcels of real estate. Instead, territories are the fluid outcome of behavioral interactions that determine where individuals settle and how long they stay, and produce the continual adjustment

of shared boundaries. The interactions of neighbors depend on many characteristics of the individuals involved, such as age, size and sex, and on the fluctuating distribution of neighbors and resources in space. Thus in territorial behavior, as in spatial ecology more generally, both local conditions and individual differences are important.

Linking individual behavior and population-level patterns

Interactions among neighbors produce patterns in space, but how this happens is difficult to trace. It is much easier to model the average behavior of a population than to piece together the combined local effects that influence the population. This is because every individual has a unique configuration of neighbors, and if each individual affects its neighbors' growth and survival, then the conditions at each site are perpetually changing the conditions nearby. An example is the behavior of people in an elevator. Where you stand in an elevator depends on where the other passengers are standing. Whenever a person gets on or off, everyone adjusts their position relative to the people nearby. As Slatkin and Anderson¹¹ put it: 'Models of competition for space are intrinsically difficult because the intensity of interactions among individuals depends on their locations, and the interactions themselves modify the distributions of those locations'.

It is difficult to specify how a spatial distribution arises, and this difficulty is related to, and compounded by, another one: how to describe or to characterize a spatial distribution¹². We speak of 'spatial patterns' but there are few aspects of real spatial distributions that we can describe quantitatively. One is whether a set of points are distributed in space at random or not, on the scale of distances between nearest neighbors. Two types of non-random distributions

can be distinguished: one in which the points tend to be farther away from each other, or more regularly spaced, than those distributed randomly; and one in which the points tend to be grouped into a few clumps. Regular spacing can arise from competition of neighboring individuals, and such spacing is sometimes taken to be evidence of competition for space. This notion has been tested empirically in a great variety of organisms (e.g. Ref. 13). However, Pielou¹⁴ and others¹⁵ have shown that competition does not necessarily lead to regular spacing.

Recent work shows that realistic predictions of spatial distributions will require new, more sophisticated models (see reviews in Refs 8, 16–18). The work of the past 10 years shows that local conditions matter: spatial heterogeneity of resources¹⁹, effects of size or age structure²⁰, and temporal patterns arising from small random fluctuations^{21,22}, all strongly influence population dynamics. In response, models are being developed that explicitly consider more of the population dynamic processes that could affect spatial distributions, and devote more attention to the effects of stochasticity.

As models have become more realistic, modeling methods have grown more diverse. Comparing models has an important lesson: the way that a model treats space will determine its conclusions. Early population dynamics models of competition for space were often set in a grid of cells (e.g. Ref. 23), and tracked the number of occupied cells as a function of negative interactions between neighbors. Real organisms do not occupy cells in a grid, though for some organisms this assumption is realistic enough to guide empirical work – for instance, predicting the size distribution of age-structured plant populations²⁴. Lattice models have been used to develop analytical methods such as pair-approximation to predict effects of neighbor interactions on nearest-neighbor distances²⁵. In the variety of approaches developed since Skellam's pioneering work, Durrett and Levin²⁶ trace four ways of modelling spatial behavior: (1) as if all individuals mix fully with each other; (2) as if relatively tiny individuals diffuse in a large, continuous space; (3) as if space were divided into a collection of discrete patches; (4) as if individuals move around a lattice of point locations. Each of these types of model gives a different equilibrium solution to the same problem, because each treats space differently. The implication is that the ways that real organisms occupy and partition space on the local scale will strongly affect the dynamics and distributions of populations on a larger scale. This suggests that spatially explicit models are needed²⁷.

Territorial behavior and spatial distributions of populations

In theoretical work that links territorial behavior and spatial distributions of animal populations, three approaches have emerged: (1) economic models that use optimization methods to predict individual behavior, then try to scale up to population-level patterns; (2) projections from individual-level behavior (for instance, effects of neighbors on growth or recruitment) to characterize the population-level distribution that might result; and (3) hypothetical descriptions of individual-level behavior that can be shown to produce the observed population-level pattern.

Economic models

Economic models of territorial behavior outline the costs and benefits of some aspect of territorial behavior, such as territory size^{28,29}. The models seek to determine what territorial behavior would be optimal for individuals, given the

resources available from a territory and the costs of defending it. Early models treated individuals as independent of each other. Subsequent models often use a game-theoretic approach: there is a set of alternative ways each individual might behave, and the costs and benefits of each alternative, for any individual, depend on the frequency of that behavior in the population.

Most economic models of territorial behavior are not concerned with predicting the spatial distribution of a population; they focus on individual behavior. But there are important exceptions. The ideal free distribution is the spatial distribution that would ensue if all individuals were completely informed about the resources available throughout the habitat (i.e. if information were 'ideal'), and if all individuals were able to move anywhere (i.e. 'free'), such that every individual ends up with the same amount of resources. The 'ideal despotic distribution' takes into account territorial behavior, in which some individuals prevent others from occupying some regions (e.g. the regions with the best resources). This leads to a different spatial distribution from the ideal free³⁰.

Empirical tests of economic models of territorial behavior have demonstrated the importance of local conditions. The costs and benefits of an individual's territorial behavior are related to the resources it obtains from its territory, and resources vary in time and space. Moreover, needs for resources vary during an individual's lifetime. This means it is not simple to extend models of what the optimal individual should do, to determine the various different ways individuals should behave if they respond optimally to the fluctuating mosaic of conditions they encounter. Then there is the further question of whether real individuals are actually behaving optimally.

Davies's³¹ study of dunnock (*Prunella modularis*) mating systems provides an example. A long series of observational and experimental studies has enabled Davies to relate the mating and territorial behavior of individual birds to the spatial distribution of a population. Mating behavior depends on territory size and overlap, which is linked to spatial variation of food resources. Because males and females vary in reproductive investment, and because food availability varies greatly in space, an economic model yields no single optimal strategy for territorial behavior. In fact, optimal strategies for different individuals are often in conflict. The habitat is a mosaic of male and female territories that vary in size and may overlap, and the extent to which male and female territories overlap determines the numbers of mates an individual of each sex obtains. Davies explains the shifting spatial distributions of the population as a consequence of the different costs and benefits experienced by different types of individuals, all operating in a fluctuating, spatially heterogeneous environment.

Projection from observed individual behavior to population-level pattern

A second approach uses data on the observed movements and use of space of individuals, to predict the resulting spatial distribution of the population. Here the procedure is first to determine how individuals use space without reference to any model. This means finding out how interactions of neighbors affect each individual's spatial behavior. The effects of neighbor interactions may depend on individual differences in age, sex, size, duration of residence and so on, and may also vary with spatial and temporal heterogeneity in the resources that space provides. From these data on the interactions of neighboring individuals, it may be possible to project the dynamics of spatial distributions in the population.

An example of this approach is my study of seed-eating ants (*Pogonomyrmex barbatus*) in the Arizona desert, USA. Space use depends on colony age and size. A colony lives for 15–20 years, and age and size are related: the colony grows larger, in numbers of ants, for the first five years, when it reaches a stable size and begins to reproduce^{32–34}. Neighbors interact when foragers of the two colonies meet, so spatial interactions between colonies are related to the configuration, which shifts from day to day, of each colony's foraging trails. Larger colonies tend to prevent the recruitment of new ones³⁵. After the founding stage, neighbors have little effect on survival but more on reproductive success³⁶. Like a forest, the spatial distribution of the population results from the way each colony's neighbors affect its survival, and this depends on the sizes of a colony and its neighbors.

Projection from individual behavior to observed population-level pattern

A model that links individual-level spatial behavior to a population-level spatial pattern offers a way to investigate empirically the processes that determine spatial patterns. Such models show quantitatively how small changes in individual space use will influence the resulting population-level pattern. Diffusion models have been used very successfully in this way^{37–39}. For example, White *et al.*⁴⁰ used a reaction–diffusion model to describe the individual behavior that might produce the population-level distribution, observed in the field by Mech⁴¹, of wolves (*Canis lupus*) in Minnesota, USA. The model uses four aspects of an individual wolf's behavior: dispersal for foraging, avoidance of scent marks left by another pack, attraction to familiar scent marks, and movement back to the den. The results show how the details of individual movement, such as whether wolves travel directly back to the den after foraging, can determine the distribution of a population of wolf packs. Further empirical work is needed to test whether real wolves actually behave as individuals do in the model. If so, then the model shows how the territorial and foraging behavior of individual wolves at a local scale determine distances between packs in a population.

Future directions for behavioral ecology

Behavioral ecologists who study territoriality are ready to move beyond models in which space is homogeneous, all individuals are the same, and space use has only one form (such as Huxley's⁴² model of bird territories as a set of crowded elastic disks). Mathematical ecologists are exploring ways to consider how age, size and sex lead to differences among individuals in space use, and to incorporate the effects of particular ways of moving around, claiming, defending and maintaining territory. To learn how an animal's territorial behavior contributes to its ecology, we must link individual behavior to the spatial patterns of populations. The legacy of 20 years of work on competition for space, mostly by plant ecologists, is a theoretical perspective we could learn from in developing studies of territorial animals.

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Biodiversity, biospecifics, and ecological services

Recent commentaries in *TREE* by Williams *et al.*¹ and Perrings² present a this-versus-that perspective on biodiversity that obscures not only useful common ground but also possible limitations of ecological services as incentives for biodiversity protection.

Williams *et al.* respond to Perrings' claimed consensus that 'the main value of biodiversity... is... derived from the role of a combination of species in supporting specific ecological services', by substituting their own characterization of the 'most widely held value of biodiversity' as that residing in 'the variety of expressed genes or characters among organisms'. But that counter-claim and their assertion that 'ecological services should not be conflated with biodiversity' neglects Perrings' argument² (also presented in the *Global Biodiversity Assessment*³) that biodiversity's value is 'derived from' ecological services because biodiversity provides insurance value related to ecosystem resilience.

Broadly, more species will imply greater insurance value. Beyond that, the expected contribution of a given species to insurance value depends on its particular properties⁴. In practice, the corresponding degree to which a species is not redundant⁵ but rather complementary³ to others may be inferred from functional patterns (e.g. whether the species is the sole representative of a functional group, or increases some other measure of functional diversity³).

If insurance value is recognized as a form of option value⁴, and phylogenetic pattern is substituted for functional pattern in the above description, there is a striking similarity to the feature diversity/option value framework^{6,7} endorsed by Williams and colleagues^{1,8,9}. Both endeavour to keep options open in the face of incomplete knowledge by 'maximizing' biodiversity at the level of phylogenetic/functional diversity. Both are also accompanied by corresponding 'biospecifics' efforts – determining that a specific species deserves high priority because it has a specific property, supporting a specific service.

Ecological services are therefore 'conflated' with biodiversity (*contra* Williams *et al.*), through the link with resilience-based option value. But this link does cast doubt on how effectively ecological services can provide the incentives,

optimistically anticipated by Perrings², for biodiversity protection within individual regions. Even if insurance value is accepted as a strong incentive, it may prioritize species differently from other forms of option value, and so not guarantee overall biodiversity protection. Also troubling is the reference by Perrings² to 'specific ecological services', as this may imply an incentive to protect only those specific species that are judged adequate to maintain those specific services. Management of individual regions for resilience then may be more about biospecifics than biodiversity.

Williams *et al.*'s unease about linking biodiversity value primarily to ecological services may be justified, not because ecological services have no place in principle on the bandwagon of biodiversity, but because in practice maintaining specific key services is largely the concern of that important but relatively bland-wagon of biospecifics. If maintenance of ecological services consequently is not much of an incentive for protecting all forms of option value in a region, the challenge is to recognize and take advantage of common ground in the use of 'pattern diversity'^{7,10} in order to combine different assessments of option value.

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Reply from P. Williams *et al.*

We are pleased that Dan Faith agrees with our central point¹ that, *whatever their relative popularity*, it is important to recognize the distinction between, on the one hand, the value of biodiversity that comes from an expected insurance value of variety², and on the other, the value of ecosystem services³ that are provided by presently identifiable 'biospecifics'. Contrary to his assertions, however, we were careful not simply to substitute one value for another (a social question), but merely to distinguish between the two (a biological question).

We are pleased also to see agreement on the use of pattern for predicting the distribution of characters of value, whether they be genetic, morphological or functional². One of the problems with choosing to value functional characters (e.g. those providing ecosystem services) is in recognizing them: there are so many of them, they have both spatial and temporal dynamics, and they can often be subtle. We have considered possible uses of functional patterns, for example, based on dietary similarity⁴. However, genealogical pattern was considered likely to be more robustly predictive of valued characters (including functional characters) than our simple function-based classification, if valued characters were inherited, because the pattern model (genealogy) could then be linked with a general process model (descent with modification).

Perrings⁵ and Faith argue that common ground between incentives for diversity and ecological service protection might be found by shifting the emphasis within ecological service value towards insurance for future ecosystem resilience (in the sense of capacity to absorb disturbance). However, because the insurance value lies in variety whereas the value of present services lies in fewer 'biospecifics' as agreed above, it is unlikely that protection for both can be maximized simultaneously. Thus, while emphasizing resilience may strengthen the insurance-based arguments for conserving biodiversity for some people, for others, the consequent de-emphasis of present ecological service value will not promote consensus.

This discussion serves to highlight an important question: is there a conflict between maintaining ecological services in the present and in the future? It is not clear that the 'biospecifics' with