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BRIEF COMMUNICATION

Variation in the degree of specialization can maintain local diversity in model communities

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Abstract We hypothesize that the continuum between generalist and specialist adaptations is an important general trade-off axis in the maintenance of local diversity, and we explore this idea with a simple model in which there are patch types to which species arrive as propagules and compete. Each patch type is defined by a competitive ranking of all species. A highly specialist species is the top competitor in one patch type but has a relatively low average ranking across different patch types, while a generalist species has a high average rank across patch types but is not the top competitor in any patch type. We use random dispersal and vary the fecundity of all species together to vary total propagule density and therefore recruitment limitation and density-dependent mortality. When fecundity is very high, each patch becomes occupied by its specialist species and generalists go extinct, so the number of species at equilibrium is equal to the number of patch types. If fecundity is very low, generalists dominate and specialists go extinct. There is a range of fecundity levels in which specialists, generalists, and intermediates coexist, and the number of species is substantially greater than the number of patch types. While coexistence of specialists and generalists has been considered a problem in evolutionary ecology, our results suggest to the contrary that this trade-off contributes to the maintenance of local diversity.

Keywords Coexistence · Dispersal · Generalist · Multidimensional niches · Recruitment limitation · Specialist

Introduction

There is a widespread agreement among researchers that trade-offs among different strategies are central to the maintenance of local species diversity (Rees 1993). While ecological theory has focused on one or two life history trade-off axes (e.g., MacArthur and Wilson 1967; Muller-Landau 2010; Yu and Wilson 2001), it has been argued that trade-offs occur in many dimensions, physiological and morphological as well as demographic (Clark et al. 2007), making the task of understanding their role in diversity daunting. There may be general patterns, however, which can be useful in summarizing the effects of numerous trade-off dimensions. We refer here to one such general trade-off axis, which is classical in ecological thinking but whose importance for maintaining diversity has not been appreciated: the continuum between generalists and specialists.

Variation in the degree of specialization is a compelling pattern in nature (Futuyma and Moreno 1988). Many organisms have very specific adaptations to certain conditions or threats, allowing them to be very successful relative to other species when such conditions or threats are present, but these adaptations have large costs, reducing competitive ability when these specific conditions are not present. Other species have evolved to be successful in many situations, but they are at a disadvantage when competing with a species that is specialized for the specific conditions in which they find themselves (Kneitel and Chase 2004; Chevin et al. 2010). For example, predators that specialize on a specific prey species will have an advantage over generalist predators when their preferred species is abundant, but they will be at a

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disadvantage in competition with generalist predators when their preferred food is rare or absent. Plants that have optimized their growth for a specific set of environmental conditions and resource levels will grow better than other species under these conditions, but they will be at a disadvantage in competition with more generalist plant species under other conditions (Marvier et al. 2004). While coexistence of specialists and generalists has been considered a problem for evolutionary ecology (Abrams 2006; Wilson and Yoshimura 1994), we hypothesize that this general trade-off axis plays an important role in maintaining local diversity, and we explore this hypothesis with a model in which trade-offs in different dimensions are described as competitive rankings in different patch types.

Model

We formulate the specialist–generalist continuum in terms of relative competitive ability (competitive rank) in different environments (patch types). We define a highly specialized species as one that is the top competitor in one patch type but has a low average competitive rank across patch types, while a generalist species is one with a high average competitive rank across all patch types but is not the top competitor in any patch type.

In our model, species allocate their total amount of resources, R_t, to different trade-off dimensions, which we define as competitive abilities in different patch types within a multidimensional trade-off space. Subscript i denotes a trade-off (patch type) dimension, and R_i is the amount of resources allocated to being competitive in patch type i, so $R_t = \sum R_i$ for each species. We assume that R_t is the same for all species, but that species vary in how they allocate their total resources to being competitive in the different patch types.

The resources that a species allocates to each trade-off dimension (patch type) determine its competitive ability relative to other species in that patch type. When propagules of different species arrive in a patch, one propagule of the species that has the highest allocation of resources to that patch type survives to adulthood and reproduces. A "perfect specialist" would be a species that allocates all its R_t to one patch type, so it has the maximum competitive ability in that patch type, whereas its competitive ability in other patch types is zero. When present, it always wins in its patch type, and it always loses when competing with a propagule of another species in another patch type. The "perfect generalist" is a species that allocates its resources equally to all patch types, so it has a high mean competitive ability on average across patch types, but it is not the top (or the bottom) competitor in any patch type. The degree of specialization across all trade-off dimensions is reflected in the coefficient of variation (CV) of a species' R_i values. A higher CV means more specialization because a high CV occurs when a species allocates all or almost all its resources to one patch type and little or none to other patch types.

We use an individual-based patch model (e.g., Hurtt and Pacala 1995). Species inhabit 10,000 cells or patches. Each cell is randomly assigned one of T patch types, so each patch type has, on average, the same number of patches out of the 10,000. Propagules of all species can survive and reproduce in any patch type if there are no other propagules present, but if more than one propagule arrives in a patch, one individual of the species that has the highest R_i survives and becomes an adult. If more than one individual has the same highest R_i, one is selected randomly to survive.

A patch is occupied until its occupant dies. Death is random, and the probability of an adult dying (d) is the same for all species. Individuals that do not die reproduce, producing a number of offspring (m), which are dispersed randomly among the patches. Propagules can compete and become adults only in patches not occupied by an adult, i.e., when the adult occupant has died. For simplicity, we assume the probability of adult mortality (d) and fecundity (m) are the same for all species, and the dispersal pattern of the propagules is global, i.e., a propagule can disperse to any patch with the same probability.

The sequence is (1) adult plants die with a probability d, (2) surviving adults produce m propagules, which are dispersed randomly among all patches, (3) if only one propagule arrives in an available patch, it survives; if more than one propagule arrives in an unoccupied patch, one individual of the species with the highest rank of those arriving in the patch survives.

To investigate our hypothesis in a very simple way, we started with contrived communities that consist of five patch types, one perfect generalist, and five perfect specialist species. We also investigated the randomly generated initial communities of 100 species for the five patch types. To do this, we used a sequential version (Tokeshi 1990) of the traditional "broken stick" model (MacArthur 1957) to define how the R_t of a species are allocated to different trade-off axes (competitive abilities in different patch types). For a given number of patch types (here is five), we start by randomly selecting one trade-off dimension i and allocate a random number between zero and R_t to this dimension. Then, we randomly select another trade-off dimension j and set R_j equal to a random number between zero and the residual total unallocated resource (R_t–R_i). This procedure is repeated until resources are allocated to every patch type except one. This last patch type receives the remaining uninvested resources. We chose a sequential broken stick model because it generates large variation in allocation to the different dimensions, i.e., large variation in the degree of specialization. Each species starts with the same number of individuals, and all individuals are randomly distributed among the 10,000 patches. Therefore, at the initial step of the simulations, there are a total of 10,000 individuals with each species having 10,000/S individuals.

All simulations are started with all patches occupied randomly by one individual and run for 20,000 time steps to allow the community to reach equilibrium. The values presented are the mean values of 100 independent replicate runs at the 20,000th step. The parameters used in the simulations are $R_t=1$, $d=0.2$, and $T=5$. Thus, we focus here on the question: how many species of varying degrees of specialization can coexist if there are only five patch types? We explored the robustness of our model with different parameter combinations, and the results were qualitatively similar to those reported below. Simulations were performed in NetLogo (Wilensky 1999), a freely available multiagent programmable modeling environment.

Results

In our simple contrived community consisting of five patch types, one perfect generalist, and five perfect specialists, the generalist species excluded all the specialists when fecundity was low, whereas the specialists outcompeted the generalist when fecundity was high, but there was a range of fecundity levels in which all the six species survived (Fig. 1).

In the broken stick model with 100 initial species but only five patch types, most species go extinct, but the number of species surviving varies with the propagule density, which is determined by the fecundity. At very high levels of fecundity, only five species, the most specialized for each patch type (i.e., high CV in allocation to different patch types), survive, whereas at very low levels of fecundity, only the single most generalist species (lowest CV in performance across patch types) survives.

There were intermediate fecundity levels in which some generalist and some specialists continued to coexist, with as many as 15 species coexisting after 20,000 time steps (Fig. 2a). As fecundity increases, the CV in allocation to different patch types of the surviving species increases (Fig. 2b). At low fecundity, the few surviving species are generalists, while at high fecundity levels, the surviving species are specialists (Fig. 3). Fecundity and therefore the degree of recruitment limitation are also reflected in the proportion of empty (nonoccupied) patches. When $m=5$, 5% of the patches are unoccupied. At $m=10$, which results in the highest diversity, 2.5% of the patches are empty, whereas when $m=30$, where only five highly specialized species survive, only 0.84% of the patches are unoccupied.

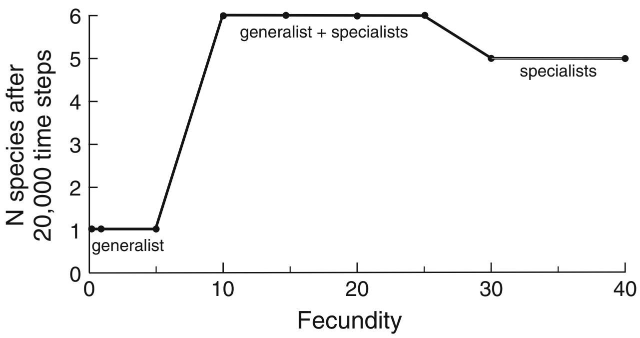

Fig. 1 Number out of six initial species surviving after 20,000 time steps versus fecundity (number of propagules produced per surviving individual per time step). There are five patch types, one perfect generalist species, and five perfect specialist species

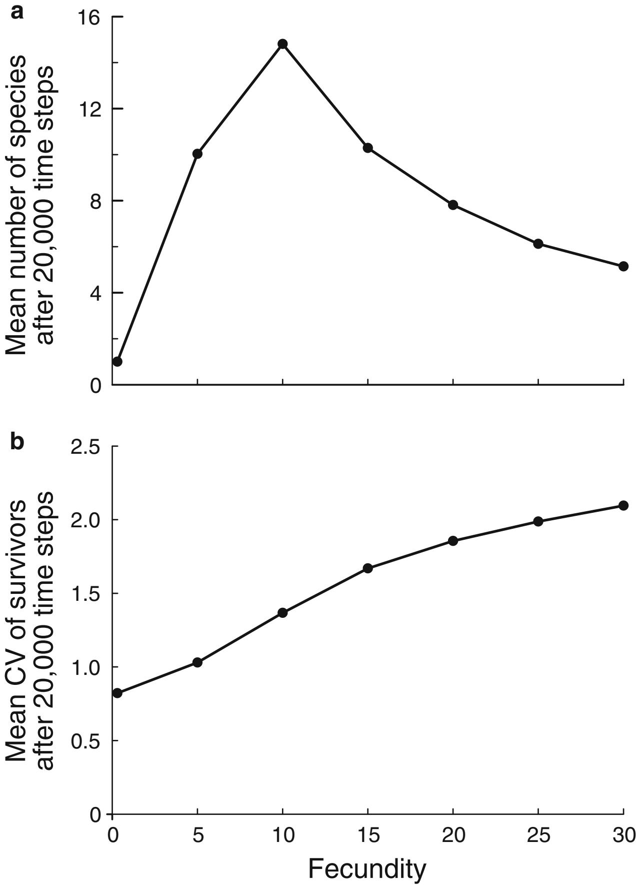

Fig. 2 a Mean number of species surviving out of 100 initial species and b mean CV of allocation to different patch types among survivors versus fecundity after 20,000 times steps when allocation to five different patch types is determined by the sequential broken stick model. All results are means of 100 replicate runs

There was a negative relationship between the mean performance of a species across all patch types and the CV in its allocation to different patch types (Fig. 4).

Discussion

In our model, generalists exclude specialists when fecundity and therefore overall propagule density and density-dependent mortality are very low, such that there are few, if

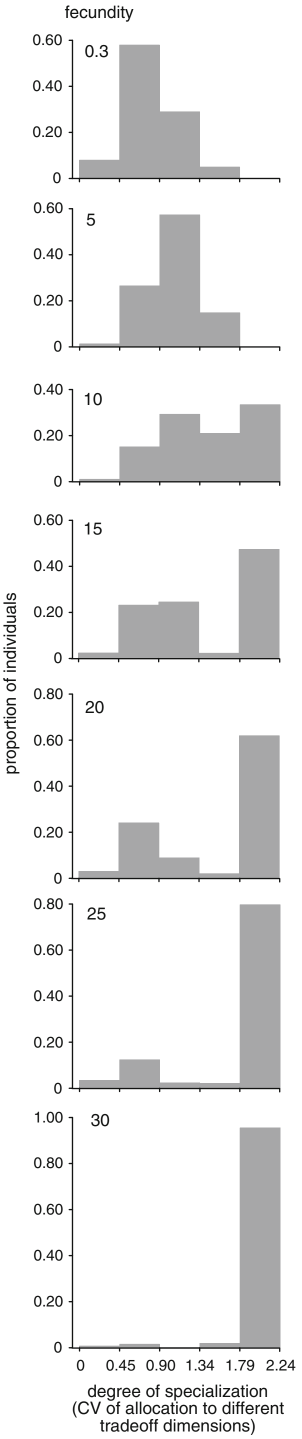

Fig. 3 Frequency distribution of the CV in allocation to five different trade-off dimensions (patch types) of survivors after 20,000 times steps for different levels of fecundity (propagules produced per individual). The simulations started with 100 species with allocation to different patch types according to the sequential broken stick model

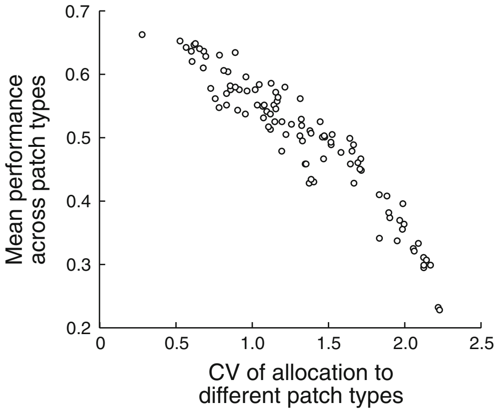

Fig. 4 Mean performance of a species across all patch types (proportion of times that propagules of a species win in competition with propagules of other species) versus CV in allocation to the different patch types. Specialization (high CV) carries a high cost in average performance

any, propagules arriving in most patches. Even though the average R_i is the same for all species ($=R_t/T$), generalists win more contests than specialists when there are relatively few contests. A perfect specialist will always win in "its" patch, but it will always lose in competition with another species in every other patch type. Thus, if all patch types are equally frequent, the perfect specialist will win, on average, in $1/T$ proportion of contests (20% in our simulations) in which its propagules are in competition with those of another species, while the perfect generalist will win in the remaining $(T{-}1)/T$ proportion of cases, even though the average allocation to different patch type dimensions of all species is equal. Specialists pay a high cost in rank in other patch types for their ability to always win in one patch type (Fig. 4). Specialists win often by a large margin in R_i within the patch types for which they are specialized, whereas generalists win by a smaller margin but more often. But since winning versus losing is binary, the margin doesn't matter: the generalists win more often when competing with one or few randomly selected opponents in randomly selected patch types. This, by itself, creates what Levins (1962, 1979) and others (Wilson and Yoshimura 1994) called a "concave fitness set," which allows coexistence of a specialist and a generalist species in their models. While coexistence of specialists and generalists has been considered a problem in evolutionary ecology when only two species are being compared (Abrams 2006; Wilson and Yoshimura 1994), our results suggest to the contrary that this trade-off, when combined with some degree of recruitment limitation, contributes to the maintenance of local diversity.

One of the challenges in the modeling of both ecological and genetic variation since the classical work by Levins (1962) is that, in most models of diversity, the genotype (or species) with the best overall performance usually dominates and excludes others at equilibrium. Many modeling efforts have focused on how diversity can be maintained in the face of this tendency for the most optimal genotype or species to dominate in the long run. In our model, whether specialists or one generalist exclude all other species, is a function of overall propagule density. Based on the results of Levins and others, we might therefore expect that there will be an optimal degree of specialization for each propagule density, and one or a few species with or near this optimal degree of specialization for that propagule density would exclude all others, but this does not appear to be the case. Recruitment limitation in the broad sense—the fact that propagules of all species do not arrive in all patches (Primack and Miao 1992; Ehrlén and Eriksson 2000)—allows generalists and specialists to coexist. In other models (e.g., Hurtt and Pacala 1995), recruitment limitation slows the rate of diversity loss, but in our model, it appears to have an effect at equilibrium (or at least after many thousands of generations). Recruitment limitation makes the generalist–specialist trade-off stabilizing (sensu Chesson 2000). One of the lessons of research in community ecology over the past two decades is that, contrary to the hypothesis of Baas-Becking (1934), “Everybody is not available everywhere.” Limits on the availability of species to reach all local habitats in which they could establish and persist (Ehrlén and Eriksson 2000) can be an important determinant of local diversity (Ricklefs 2004). In our model, over a range of propagule densities, specialists reach some, but not all, of the places/situations for which they are specialized, while generalists succeed in reaching some places/situations where the specialist competitor is not present. We hypothesize that this is important in nature, not just in our model. This could also help explain selection for generalism, which recent theory finds problematic (Ravigné et al. 2009).

We do not find our hypothesis or similar ones in the literature on the maintenance of local diversity. There are many studies in which there is a trade-off between competitive ability and other abilities (e.g., colonization; Tilman 1994), but in our model, all species have the same amount of resources, and only trade-off is in competitive abilities in different patch types. We assume no differences among species in dispersal and that individuals of all species can live everywhere their propagules arrive if they are not outcompeted by individuals of other species (fundamental niche). The realized niche of each species is defined by the competitive relationships among species in different patch types and is a function of the availability as well as the characteristics of other species.

We argue that the mechanism maintaining diversity in our model of trade-offs in many dimensions, resulting in a general trade-off in the degree of specialization, is fundamentally different from that in other models, which focus on a single trade-off axis, e.g., competition–colonization (Yu and Wilson 2001). The multidimensionality of niches and therefore trade-offs holds one of the keys in understanding the maintenance of diversity (Hutchinson 1957; Clark et al. 2007).

Our idea of trade-offs among competitive abilities in different patch types is similar to Tilman’s model of trade-offs among affinities for different potentially limiting resources (Tilman 1982). The hypothesis that the number of potentially limiting resources determines the maximum number of coexisting competitors corresponds to the situation at very high levels of fecundity in our model, where the maximum number of coexisting species is simply the number of patch types. Continuing the analogy, we suggest here that spatial heterogeneity in resource levels plus variation in uptake abilities across resources could allow species that are not the best at taking up any one resource to coexist at equilibrium with those that are. This could be an important mechanism by which spatial structure promotes species diversity.

Our model leads to the following predictions:

- High species density should be associated with a high variation in the degree of specialization. Low diversity communities should tend to be dominated by generalists.
- Highest local diversity should be found at intermediate levels of propagule availability. Species diversity should decrease at very high and very low levels of propagule density and diversity.

Our simple simulation model is only a first step in exploring the ideas presented here. There may be analytically tractable generalizations of our model, which would allow us to analyze the full parameter space and could provide more testable hypotheses. We hope mathematical ecologists will pursue this.

Concluding remarks

Natural selection produces a continuum from highly specialized to broadly generalist species, and this continuum can be seen as a “major axis” in multidimensional trade-off space. Variation in the degree of specialization, in combination with dispersal limitation, may be an important contributor to the maintenance of local species diversity.

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