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Disturbance-generated niche-segregation in a structured metapopulation model

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ABSTRACT

Question: Does limiting similarity apply for co-existence maintained by disturbance in a metapopulation?

Methods: In contrast to patch occupancy modelling, we follow both local- and metapopulation-scale dynamics explicitly. The theory of structured metapopulations is used for this purpose. Adaptive dynamics is employed to study evolution.

Key assumptions: Local catastrophes at a given rate. Fixed dispersal rate, trade-off between fecundity and local competitiveness.

Results: Co-existence of a few (up to 5) but not more species is observed. They are distinctly different along the trade-off variable and partition the patch-age axis. A series of evolutionary branchings leads to an evolutionarily stable coalition.

Conclusions: The usual niche theoretical picture of decreased competition with increased differentiation applies. The patch age is the proper niche axis. Niche differentiation along this axis is the requirement of co-existence. Constraints of co-existence are overlooked in patch occupancy models.

Keywords: disturbance, diversity, metapopulation, niche.

INTRODUCTION

Maintenance of species diversity via disturbance (Connell, 1978; Huston, 1979, 1994; Hastings, 1980) is a central issue of ecology. In the most commonly considered case, it is assumed that the ability to colonize and/or exploit an empty habitat can be increased at the cost of decreasing local competitiveness. In a constant environment, the better competitors (the '*K*-strategists') outcompete the good colonizers/exploiters (the '*r*-strategists') in each habitat, so that the latter disappear. If, however, the local sub-populations are destroyed regularly, the *r*-strategists may always have the chance to exploit a newly emptied habitat before they are expelled from the previous one. In this way, the long-term co-existence of the *r*- and

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K-strategist [or 'early successional' and 'late successional' species, respectively (Rees *et al*., 2001)] is maintained.

Such a mechanism requires a metapopulation (Levins, 1968) structure, i.e. a collection of local populations connected via dispersal. The usual way of modelling is based on a major simplification: a patch is either empty or fully occupied by a single species (e.g. Nee and May, 1992; Amarasekare *et al*., 2004). Occupied patches become empty due to catastrophes. Empty patches become occupied when colonized by dispersers from the occupied patches. In this context, better competitive ability is modelled via the possibility of over-colonization of the less competitive species.

These 'patch occupancy' models can also be interpreted outside the patch disturbance framework, as one can define a 'patch' as a single 'safe site', possibly occupied by a single individual (Tilman *et al*., 1994; Geritz, 1995; Geritz *et al*., 1999; Kisdi and Geritz, 2003; Calcagno *et al*., 2006). Gap dynamics models, where the successional process after the fall of a single tree is investigated, constitute a mixed case (Shugart, 1998, p. 217).

As we are interested in disturbance-mediated co-existence, we stick to the original 'population of populations' interpretation of metapopulation modelling. In this context, over-colonization is a process in which the more competitive species gradually ousts the less competitive one from the patch. This succession may take many generations. As traditional metapopulation models do not follow the local population dynamics, the details of the real process of colonization and competition remain hidden. Here we attempt a deeper understanding by following the population growth and the process of competitive exclusion within the patches explicitly, i.e. by considering both the local- and metapopulation-scale dynamics. To this end, we study the phenomenon in a structured metapopulation model (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001; Parvinen and Egas, 2004; Parvinen, 2006, 2007; Nurmi and Parvinen, 2008; Nurmi *et al*., 2008).

There are two basic ways of being an *r*-strategist (Pacala and Rees, 1998). First, a species can be a good colonizer by arriving first in the empty patch. Or, it can exploit the resource-rich environment of the new habitat faster than the *K*-strategist [successional niche-segregation (Pacala and Rees, 1998; Szabó and Meszéna, 2007)]. While the former has been widely investigated (Hastings, 1980; Nee and May, 1992; Tilman *et al*., 1994; Kinzig *et al*., 1999; Calcagno *et al*., 2006), the latter type of trade-off is our choice for the current study.

The relationship between the *r*- and the *K*-strategy is one of the oldest topics in evolutionary ecology (MacArthur and Wilson, 1967, p. 146), inherently linking ecological and adaptational issues. In this vein, we are equally interested in the purely ecological question of species co-existence and in the evolutionary regime this ecology generates. Here, we use adaptive dynamics (Metz *et al*., 1996; Geritz *et al*., 1997, 1998; for background, see Brown and Vincent, 1987; Vincent *et al*., 1993; Cohen *et al*., 1999) to study this connection.

MODEL DEFINITION

We adapt our model from the structured metapopulation model of Parvinen (2006) by introducing the following trade-off: decreased fecundity is the cost of increased within-patch, or local, competitiveness. The dispersal properties are the same for all variants. An infinite number of habitat patches is assumed. For numerical simplicity, discrete, non-overlapping generations are used. Individuals reproduce once and die afterwards; simulation steps follow the generations. In each step, after reproduction, a fraction d of the newborns enters the dispersal pool; the rest remain in their original

patch. Dispersers survive to the next step with probability k and immigrate into a randomly chosen patch with probability a.

The probability to survive dispersal under these assumptions is

$$F = \frac{\alpha k}{1 - (1 - \alpha)k}.$$

Parvinen (2006) showed that equilibria of the metapopulation dynamics and invasion fitness depend on k and α only through the probability to survive dispersal F. Our results would thus be unaltered, if we assume that dispersers survive dispersal and immigrate immediately with probability F or die otherwise.

In any patch, the immigrants and the non-dispersed individuals together form the parent population for the next reproduction. Catastrophes may occur randomly in any patch after the dispersal process. The probability μ of a catastrophe is independent of the local population size. A catastrophe kills all individuals in the patch. Nevertheless, the patch remains habitable, and can be re-colonized by dispersers from the disperser pool.

The fecundity $f(s, \Sigma N)$ of an individual depends on its inherited 'strategy' s that characterizes the species, and on the total density ΣN of the individuals in the patch. The latter dependence is of the Ricker-type (Ricker, 1954)

$$f\left(s, \sum N\right) = f_0(s) \exp\left(-\frac{\sum N}{K(s)} \ln f_0(s)\right),$$

where $f_0(s) = f(s, 0)$ is the fecundity at zero density. The carrying capacity $K(s)$ is the equilibrium density, when the strategy is alone in an isolated patch (i.e. $f(s, K(s)) = 1$ for all s). It can be considered a measure of the local competitiveness. In the absence of catastrophes, the species with the largest K outcompetes all others from all patches.

The strategy $s \in [0, 1)$ characterizes the species along the r–K continuum. We assume the dependencies $K(s) = (1 - s)^{1/\beta}$ and $f_0(s) = 1 + \gamma s^{1/\beta}$. The value $s = 0$ corresponds to the extreme K-strategy that maximizes the carrying capacity; $K(0)$ is scaled to 1. When s approaches 1, fecundity increases, while the carrying capacity goes to zero. This end of the scale represents the r-strategy. Parameter β determines the shape of the trade-off (Fig. 1). It is convex for $0 < \beta < 1$ and concave for $\beta > 1$. Parameter γ determines the maximum possible value of fecundity.

To investigate the model, we need a proper and efficient notion of fitness. In general, fitness is the long-term exponential growth rate of an invader in an environment set by the resident coalition (Metz *et al.*, 1992). A newly arrived strategy invades if, and only if, its fitness is positive. The fitness is zero for an equilibrium population. In the metapopulation setting, we find it more convenient to study fitness as the logarithm of the basic reproduction ratio R_m of the dispersal generations. R_m is defined as the expected number of dispersers produced by the clan initiated by a mutant disperser in the environment set by the resident (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001). (Do not confuse dispersal generation with individual generation. The former constitutes a variable number of the latter.) Parvinen (2006) provided an efficient algorithm to calculate R_m and proved its (sign) equivalence with growth rate as a fitness measure in a fixed environment. Note that a realistic simulation of the evolutionary process cannot be based on R_m because evolution is accompanied by a continuously changing environment, where the equivalence does not hold.

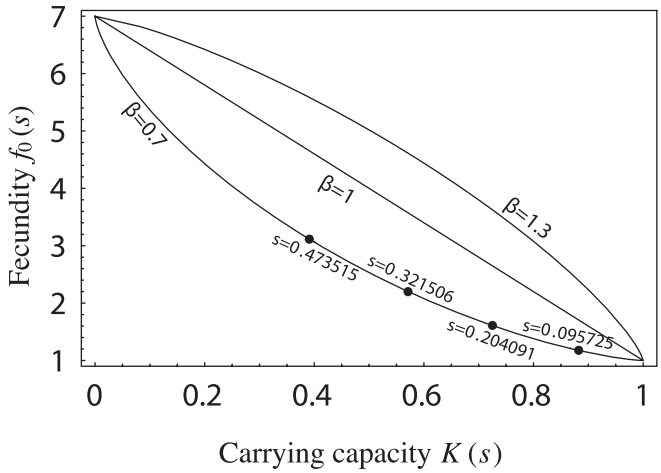

Fig. 1. Trade-off between fecundity $f_0(s)$ and local carrying capacity $K(s)$ for the parameter values $\beta = 0.7$ (convex trade-off), $\beta = 1$ (linear), and $\beta = 1.3$ (concave); $\gamma = 6$. The four dots on the concave curve represent the four strategies in Fig. 2.

RESULTS

Figure 2 illustrates the co-existence of four different species. Figure 2(a) plots their abundances $N_s(t)$ in a single patch as a function of the patch age $t = 0, 1, 2, \ldots$, since the last catastrophe. With the given parameters, the local population dynamical processes are much longer than the generation time, so although the dynamics is defined in discrete time, the curves shown in Fig. 2 are rather smooth. The probability that a patch survives until a given age is plotted as a thick curve. In Fig. 2(b) one can observe that, initially, the species with the largest colonization ability has the highest fecundity. It loses its advantage and is taken over by another species with lower colonization but higher competitive ability, when the total size of the local population increases and the local competition increases. This pattern of succession is repeated until the species with the largest competitive ability reaches its carrying capacity.

How many strategies can co-exist in the metapopulation? In particular, would it be possible to invade the established coalition by a new species? Figure 3e presents the fitness function when the coalition of Fig. 2 is established. The four established strategies have zero fitness, as expected. The non-trivial feature is that all other strategies have negative fitness. This means that the four strategies chosen for Fig. 2 form an uninvadable (i.e. an evolutionarily stable) coalition.

How does one reach such an uninvadable strategy coalition? Can it emerge evolutionarily starting from a single strategy? To address this question, we analyse the adaptive dynamics of a monomorphic one-dimensional strategy by drawing pairwise invasibility plots (PIP) (Matsuda, 1985; Van Tienderen and De Jong, 1986). In these plots, the sign of the invasion fitness proxy $\log R_m(y, E_x)$ (where y is the mutant strategy and E_x is the environment when the sole strategy x is established) is displayed in dependence on resident and mutant strategies. The pairwise invasibility plot for the parameter values used in Fig. 2 is illustrated in Fig. 3a. From the PIP in Fig. 3a, we observe that there exists an evolutionarily attracting singular

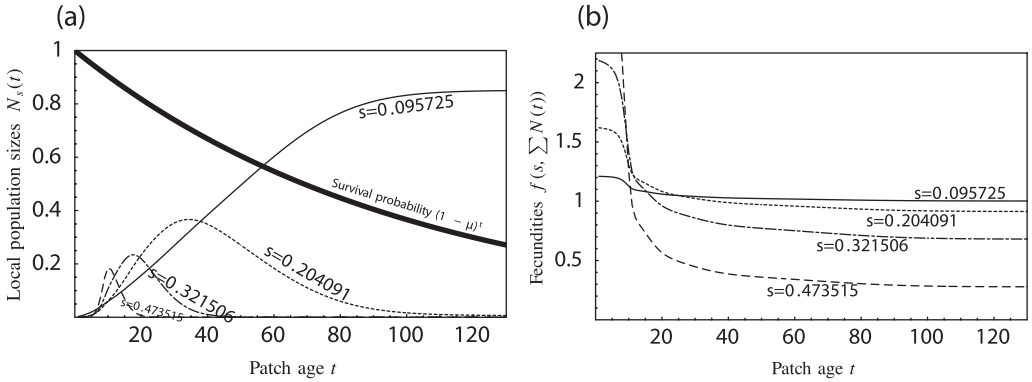

Fig. 2. Co-existence of four different strategies. Local population size (a) and fecundity (b) of the strategies as a function of patch age. The bold curve in (a) represents the survival probability of the patch until the specified age. Note that the strategy with the highest K dominates the old patches. However, only a fraction of the patches survive so long. Parameter values: $\beta = 0.7$, $\gamma = 6$, $d = 0.005$, $\mu = 0.01$, $k = 0.95$, $\alpha = 0.8$, $F \approx 0.938$. The same values are used in the other figures unless specified otherwise.

strategy $s^* \approx 0.110642$, which is not unbeatable, and is thus a branching point. An initially monomorphic population is thus expected first to adapt its strategy towards s^*, and then divergent selection pressure will cause it to split into two groups, and the strategies of the groups will, initially at least, evolve away from each other. What then happens during and as a result of such evolutionary branching? (Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998). This question can be addressed with the fitness function by drawing the set of protected dimorphisms P2 together with the direction of the dimorphic selection gradient. From Fig. 3b we observe that the dimorphic strategy pair is expected to reach the dimorphic singularity (s_1, s_2) or (s_2, s_1), where $s_1 \approx 0.0974$, $s_2 \approx 0.251$. Note that since the numbering of strategies is arbitrary, Fig. 3b is symmetric across the diagonal. From Fig. 3c we observe that this dimorphic singular strategy pair is not evolutionarily stable, and thus another branching event is expected, resulting in the evolving population becoming trimorphic. While difficult to illustrate, the direction of selection pressure on trimorphic strategies can again be calculated using the fitness function. The trimorphic strategy coalition is expected to approach the singular coalition (0.09607 0.2138 0.3940). As we observe from Fig. 3d, this trimorphic coalition is not evolutionarily stable, and yet another branching event is expected, resulting in the evolutionarily stable co-existence of four strategies, as illustrated in Fig. 3e.

Figure 4 presents an evolutionary simulation starting from a single strategy. Here we iterated the real local population dynamics (reproduction and dispersal) and random catastrophes in 1000 patches. Every 1000th generation was considered a single evolutionary step. In each of these steps, a single random mutation occurs. (A strategy slightly different from a randomly chosen present strategy is introduced with a small population size. Mutation step size follows a Gaussian distribution with standard deviation 0.01.) Repeated mutations and invasions result in the change of the strategies constituting the coalition. As expected from the fitness-based results in Fig. 3, one can observe several consecutive events of evolutionary branching (Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998). The evolutionary process ends up in an uninvadable coalition of four strategies with a cloud of mutants.

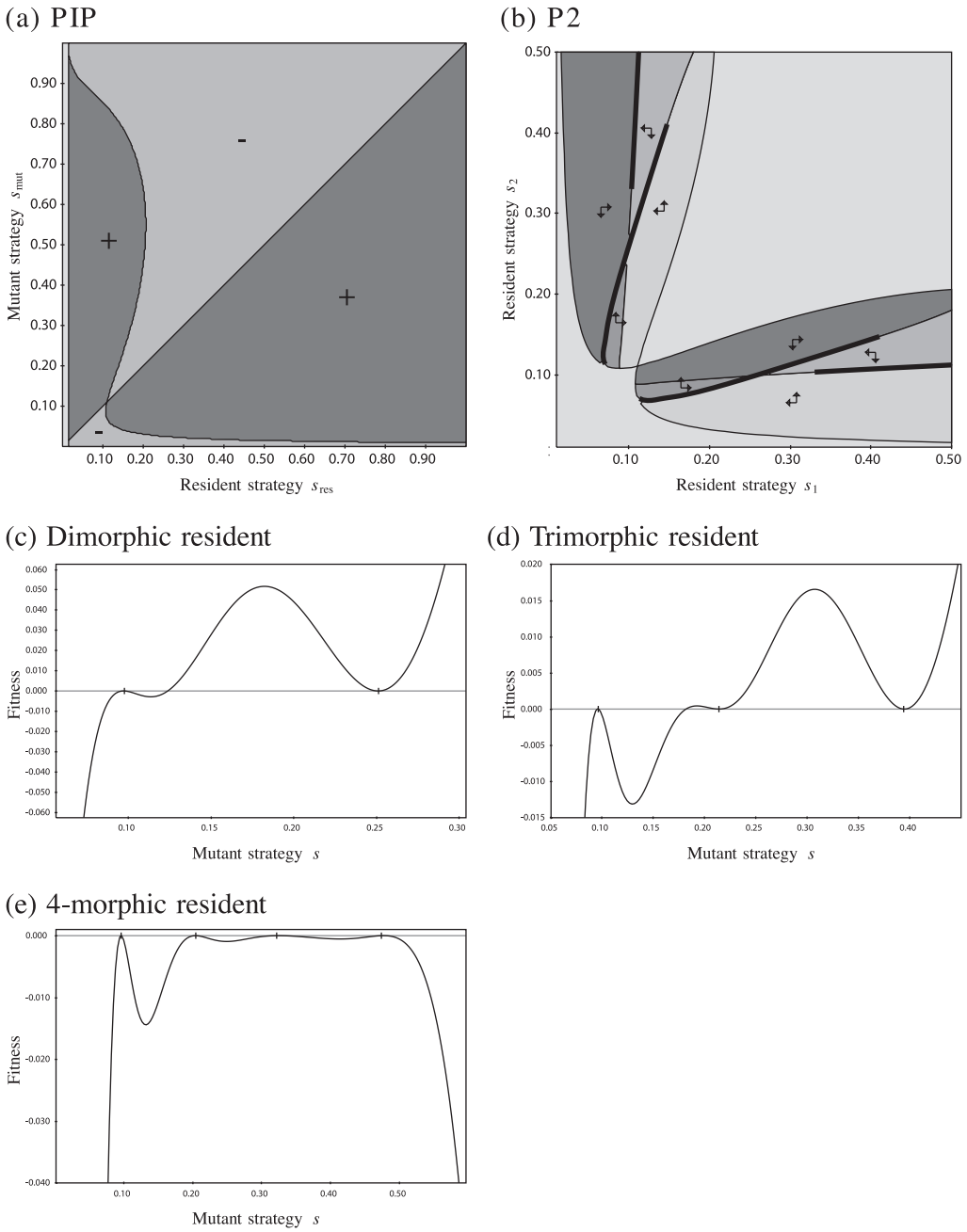

Fig. 3. Fitness-based evolutionary analysis. (a) Pairwise invasibility plot with a branching point at $s \approx 0.110642$. (b) Set of protected dimorphisms P2 with the direction of the selection gradient. Bold curves illustrate isoclines for which the corresponding strategy is a local fitness maximum. The dimorphic singularity $s_1 \approx 0.0974$, $s_2 \approx 0.251$ is evolutionarily attracting, but not evolutionarily stable, as can be seen from panel (c), thus another branching event is expected. (c–e) Fitness of the mutant for different evolutionarily singular resident coalitions. (d) The trimorphic coalition is not evolutionarily stable, and another branching event can occur. (e) The coalition of four different strategies illustrated in Fig. 2 is evolutionarily stable, and thus an evolutionary endpoint. Parameters are the same as in Fig. 2.

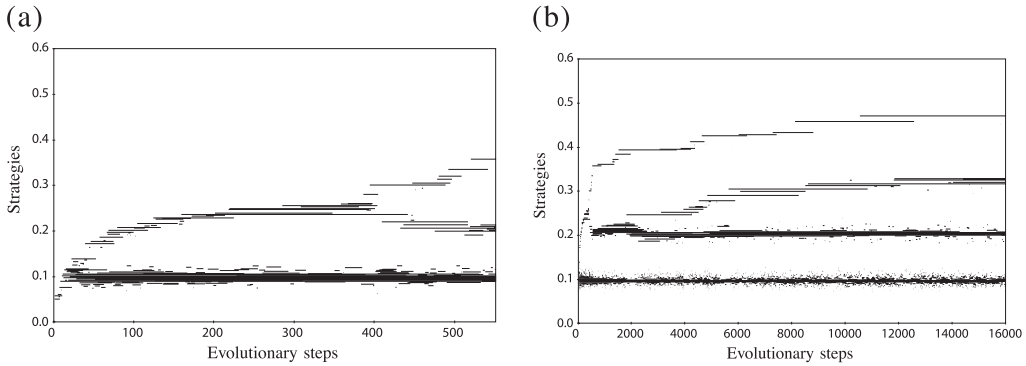

Fig. 4. Evolutionary simulation with mutation starting from a single strategy plotted on two different time-scales. The events expected to occur based on Fig. 3 are observed. Parameters are the same as in Figs. 2 and 3.

It is interesting to investigate the effect of various parameters on co-existing evolutionarily stable strategy coalitions as in Fig. 3e. Our results are depicted in Fig. 5. For some parameter values there is bistability, thus two (or more) different locally unbeatable coalitions exist. In the case of observed bistability, Fig. 5 illustrates the coalition with the largest number of strategies present. We observe that co-existence of four or even five strategies is common. The β dependence in Fig. 5b shows that, given the other parameters, the investigated trade-off curve with $\beta = 0.7$ is about optimal to maintain diversity, both in the sense of the number of co-existing strategies and the variance of strategies. Figure 5a illustrates the effect of the catastrophe probability, μ. If the disturbance rate is high, i.e. the average patch lifetime $1/\mu$ is short, only the extreme *r*-strategist survives. Longer patch ages allow co-existence such that the average strategy of all individuals moves to the direction of the *K*-strategy. At low disturbance rates, the most competitive species becomes dominant, as one can observe from the change in the average strategy. Figure 5c illustrates the effect of the dispersal probability, d. We observe that polymorphisms are possible only with relatively low values of d. High values of d and thus high immigration cause local populations to grow quickly after a catastrophe has occurred. Therefore, only one strategy with a high carrying capacity is evolutionarily stable. In the limit to no dispersal, the strategy with the highest r should be favoured, but this limit is difficult to study numerically, because the average local population sizes go to zero.

In our explorations we did not observe evolutionarily stable coalitions of more than five strategies. Although we cannot exclude the possibility of model versions supporting a slightly larger coalition, limited maintenance of high diversity in this way is a clear conclusion.

INTERPRETATION

Our model is a clear demonstration of the non-existence of a principal difference between equilibrium and non-equilibrium ecology. We considered the very ecological situation that is the archetype of fluctuation-maintained diversity. Nevertheless, the same pattern can also be seen as an equilibrium one. At the metapopulation level, the dynamical variables of the model are the functions, $N_s(t)$, which specify the abundances of the different strategies s in

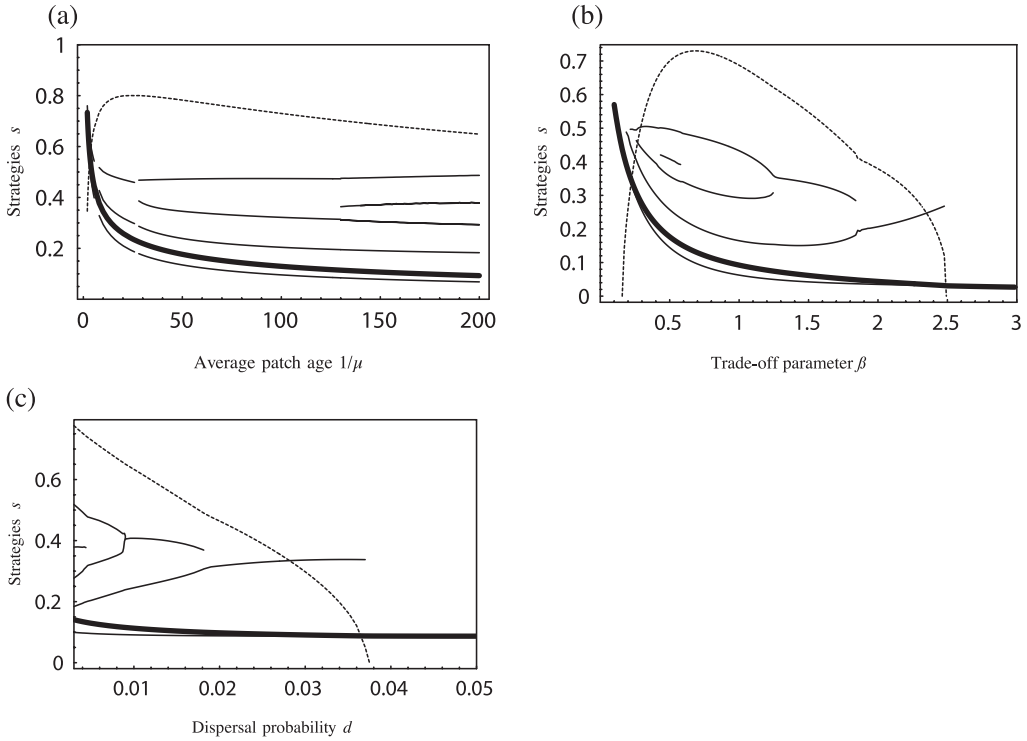

Fig. 5. Locally evolutionarily unbeatable strategy coalitions. (a) Dependence on average patch age $1/\mu$. (b) Dependence on the trade-off parameter β. (c) Dependence on dispersal probability d. The average overall strategy is plotted with a bold solid curve, and the standard deviation (multiplied by a factor 10 for better visibility) of the strategy distribution with a dotted curve. Except for μ in panel (a), β in panel (b), and d in panel (c), the parameters are the same as in Figs. 2 and 3.

the patches of age t. In terms of these variables, the dynamics is deterministic and converges to the equilibrium distribution displayed in Fig. 2.

The model-independent theory of niche-segregation, proposed by Meszéna *et al.* (2006) and formulated for equilibrium, is applicable for our model without caveats. The theory is based on the notion of the regulating variables (the environmental variables involved in the feedback loop of population regulation) and on the concept of robustness (with respect to the change of the external parameters) of co-existence. The relevance of robustness stems from the fact that co-existence of an arbitrary set of strategies can be arranged by fine-tuning within any model with sufficient numbers of parameters to adjust. Therefore, no absolute lower bound of similarity for the co-existing populations can be established. The meaningful question is not the possibility but the robustness of co-existence (cf. Abrams, 1983). The theory states that robust co-existence requires the species to be sufficiently different with respect to the regulating variables. More specifically, they should differ both on their (differential) impact on, and sensitivity towards, the regulating variables. Similarity in these respects restricts co-existence to a narrow range of the parameters, i.e. makes it unlikely (for case studies, see Szilágyi and Meszéna, 2009a, 2009b). Moreover, Gyllenberg and Meszéna (2005) showed that any model that allows a continuum of strategies (or an infinite number of strategies) to

co-exist is structurally unstable, i.e. such co-existence can always be destroyed by an arbitrarily small perturbation.

The set of regulating variables constitutes the niche 'space' to be partitioned between the species. Segregation in this space (i.e. differentiation in the way of population regulation) is the prerequisite of robust co-existence. In the case of a resource continuum (e.g. a continuum of food size), this set/space is a continuous one: the resource concentrations for all food-sizes have to be considered as separate regulating variables. This way the theory reduces to the well-known picture of resource partitioning. In the corresponding competitive Lotka-Volterra model, it is easy to arrange co-existence of the full continuum of the species along the resource quality axis, for example by choosing both the carrying capacity curve and the competition kernel to be Gaussians. However, as it should be, this co-existence is structurally unstable. A relatively small modification of the exceptional carrying capacity curve leads to a situation where the usual idea of niche-segregation prevails (Szabó and Meszéna, 2006; Barabás and Meszéna, 2009).

In our model, the total density $\Sigma N(t)$ for the patch-age t plays the role of a regulating variable. It describes the resource exploitation, i.e. the strength of competition in patches of age t. If this quantity is known for all patch-ages, then the fecundities of the different strategies in any patch are calculable. This way, we have a continuum of the regulating variables along the patch-age axis. This is in complete analogy with the continuum of resource densities (more exactly, the exploitations thereof) in the food-size case. As in the Lotka-Volterra case, the continuum of the regulating variables will not generically support unlimited co-existence; sufficient segregation along the niche axis is required.

If fine-tuning of the shape of the trade-off curve were allowed, one would be able to provide an advantage/disadvantage to any strategy arbitrarily and, therefore, to arrange arbitrary co-existence artificially. In a complicated model, such as the current one, there is no analytic way to determine the shape of the trade-off that allows continuous co-existence. Instead of searching for this exceptional case numerically, we opted to restrict our attention to a reasonable one-parameter family of the trade-off curve. This family turned out to be 'normal' in the sense that it did not allow the exceptional behaviour of unlimited co-existence. In light of the general and Lotka-Volterra studies reviewed above, we expect that our experience represents the typical case.

Note that our model was defined in discrete time, even if the parameters were chosen so that the behaviour was essentially continuous. If discreteness of time t is taken into account, then the regulating variables $\Sigma N(t)$ form an infinite series, instead of a continuum, of variables. This series is truncated to a finite set by the convergence of the local dynamics. Then, finiteness of the number of regulating variables implies an upper bound for the number of co-existing species. However, the actual co-existence is more restricted because of the need for sufficient segregation.

DISCUSSION

Understanding the factors that shape species diversity is a fundamental problem and of great practical relevance for nature conservation. The role of environmental fluctuations is an important focus of investigation. Here we analysed the possibility of co-existence maintained and generated by a trade-off between fecundity and local competitiveness via a structured metapopulation model. The novelty of our approach was that we followed the local- as well as the metapopulation-scale dynamics. This way we acquired a clearer picture

of the possibility of disturbance-related co-existence than provided by patch-occupancy models. We found that co-existence is based on, and constrained by, the possibility of successional segregation along the patch-age axis. Evolutionary stability of the co-existing coalition was analysed.

The applicability of limiting similarity (MacArthur and Levins, 1967; Abrams, 1983) for patch occupancy models has already been noted (Tilman *et al*., 1994). However, one is free to choose the parameters describing over-colonization in that framework. Therefore, co-existence of an arbitrary number of species can be arranged. Augmentation of the picture with the possibility of back-colonization results in further constraining of the co-existence of similar species (Kinzig *et al*., 1999). Still, one can arrange arbitrarily large coalitions without fine-tuning just by increasing the asymmetry of the competition (Adler and Mosquera, 2000). This behaviour is in line with the fact that the patch-occupancy models are isomorphic to the asymmetric version of the Lotka-Volterra competition model (Kisdi, 1999). The existence, or non-existence, of back-colonization corresponds to the non-extreme, or extreme, asymmetry of competition, respectively. The very same relationship between limiting similarity and the non-extremely asymmetric nature of competition was recognized by Geritz and his colleagues (Geritz, 1995; Geritz *et al*., 1999) in a model that cannot be reduced to a Lotka-Volterra one.

When the mechanistic details of the local replacement process are factored in, as in the current investigation, the possibilities are more constrained. The expected patch lifetime should be long enough to allow several successional steps that cannot be speeded up arbitrarily. However, longevity of the patches is detrimental for the *r*-strategists: the lower rate of disturbances decreases the ratio of the fresh patches needed for them. Although the number of co-existing strategies is still relatively high for large patch ages in Fig. 5, the relative population size of the *r*-strategists is fairly low. The highest diversity measured as highest variance in strategies is observed for average patch ages around 30. Therefore, in line with the intermediate disturbance hypothesis (Connell, 1978), neither the low nor the high level of disturbance supports significant diversity. In between, for intermediate levels of the catastrophe, the co-existence of several, but not very many, successional states was observed.

For an analogy, consider the Lotka-Volterra model of symmetric competition (MacArthur and Levins, 1967). One can arrange an arbitrarily high number of co-existing species by narrowing the niches. This freedom would be lost, however, if the physiological constraints determining niche-widths were part of the model.

It is also possible to model the successional replacement process within a single patch (e.g. Figure 6.1 in Tilman, 1988, p. 187; Figure 10.5 in Shugart, 1998, p. 307). However, if a single habitat of finite lifetime is considered on its own, the long-term survival of the species at the metapopulation scale is outside the scope of the study by definition. In this case, one has to postulate the set of species that has the possibility to enter the habitat.

To see the complete picture, parallel consideration of the local and the global scales was essential. Global-scale competitive exclusion determines the species composition of the metapopulation. In turn, study of the local operation of successional replacement provides the constraints for the global-level processes. Note that a similar two-level approach was previously applied for a different type of spatial co-existence that was based on the dispersal–competitiveness trade-off and which does not rely on patch disturbance (Amarasekare and Nisbet, 2001; Abrams and Wilson, 2004) [see also Szabó and Meszéna (2007) on the importance of the local or global nature of competition].

The results presented here are consistent with the general impression of real-word processes. In particular, our Fig. 2a is reminiscent of empirically observed succession (e.g. Figure 8.22 of Tilman, 1988, p. 284).

Our investigation is inherently related to a major debate on community ecology. Niche theory (Hutchinson, 1978; Leibold, 1995; Chase and Leibold, 2003), a centrepiece of classical ecology, asserts that competitive exclusion operates between species attempting to occupy the same niche, so the availability of different niches constrains diversity. In contrast, the theory of disturbances (Connell, 1978; Hastings, 1980; Huston, 1979, 1994) argues that repeated disturbances in a non-equilibrium ecosystem are able to increase diversity beyond the prediction of the equilibrium theory via weakening competition.

The controversy about, and the axiomatic status of, the competitive exclusion principle ('complete competitors cannot co-exist') was reviewed in a seminal paper by Hardin (1960). While the principle played a key role in Hutchinson's concept of niche (Hutchinson, 1978), he also introduced the doubt that the non-equilibrium situations may be entirely different ['paradox of the plankton' (Hutchinson, 1961)]. These distinctions between equilibrium and non-equilibrium, niche and disturbance used to be regarded as fundamental (Huston, 1979, 1994).

However, Hardin's argument about the unavoidability of niche-segregation was reformulated for fluctuating situations by Chesson (1991). A general theory of fluctuation-mediated co-existence was developed on this basis (Chesson, 1994, 2000a, 2000b). The fallacy of the idea that 'disturbance' decreases 'competition' in some general way was discussed in detail by Chesson and Huntly (1997). Fluctuation may contribute to species diversity not because it alleviates the need for ecological diversification; instead, it provides additional ways of being different. In particular, the storage effect of Chesson (1994), which is an important mechanism for fluctuation-mediated co-existence, can be seen as temporal niche-segregation (Amarasekare, 2003). In line with the emergence of this new synthesis, disturbance-maintained co-existence is now also considered a niche-segregation along life-history trade-offs (Rees *et al*., 2001; Amarasekare, 2003).

In our model, from the local point of view, the less competitive *r*-strategist species are able to survive temporarily because catastrophes transitionally reduce local competition. However, the global situation cannot be described as if 'competition', in general, would be weaker than in equilibrium. Nor is it justified to regard the *r*-strategist as a weak competitor on the metapopulation scale. As the branching pattern of the evolutionary simulations (Fig. 4) demonstrates, metapopulation-level competition is reduced only between sufficiently different strategies that present in different periods during the succession process. After reaching the evolutionarily stable coalition, the fitness curves have minima between the established strategies (Fig. 3e). In this sense, competition remains strong against the intermediate strategies. This is exactly the picture of niche-segregation: co-existence is made possible by the reduced between-species competition. In turn, weakening of competition is caused by adaptations to different ecological roles. In our case, these roles are the presence of the species at the different successional stages. That is, the essential issue is the partitioning of patch age, as a niche dimension. An *r*-strategist species, if it survives, is the best competitor in its own niche.

The controversy about competitive exclusion is strongly related to the one about population regulation. For a single population, regulation is necessary to ensure balanced birth and death. For a coalition, further regulation is needed to balance the populations against each other. This additional regulation is provided by differentiation with respect

to the form of population regulation (Meszéna *et al.*, 2006). [See Turchin (1999) for the unavoidability of regulation by density-dependent factors; Berryman *et al.* (2002) for the same, but especially for fluctuating populations; Hixon *et al.* (2002) about the importance of considering a closed population; and Hanski *et al.* (1996) for the metapopulation context.]

In this study, we opted to keep the dispersal parameters constant. In reality, one can expect the dispersal rate to be selected towards a higher value for an *r*-strategist than for a *K*-strategist. Moreover, the higher migration rate itself [even without higher fecundity, as in the pure case of competition–colonization trade-off (cf. Pacala and Rees, 1998)] can contribute to the *r*-strategist nature of a species. In general, one should consider a trade-off between three variables: fecundity, dispersal, and competitiveness. However, the mathematical structure would remain similar to ours. If the populations within a single patch are regulated by a single factor, then the metapopulation as a whole is regulated by the patch-age continuum of this factor. Co-existence in such a system is an issue of niche-segregation along the patch-age axis.

The issue of the evolutionarily stable value of dispersal parameters (Parvinen, 1999, 2006, 2007; Ronce *et al.*, 2000; Mathias *et al.*, 2001; Gyllenberg *et al.*, 2002; Parvinen *et al.*, 2003) is related to the evolutionary origin of the *r*-strategy. Tilman (1988) considers fast vegetative growth, which may or may not be coupled to fast reproduction, as an adaptation to a high rate of biomass loss (e.g. by herbivory). Such *r*-strategists need not have a high dispersal rate, and will not have one because of the trade-off between migration ability and the other life-history parameters. However, they will dominate the early stages of succession if they happen to find their way to the patch. In contrast, if the early stages of the succession in a metapopulation with repeated patch catastrophes constitute the typical niche of an *r*-strategist, then it is necessarily selected for a higher migration rate. Note, however, that non-monotonous relationships between the evolutionarily stable dispersal parameters and local extinction rates have been observed in several models (Ronce *et al.*, 2000; Gyllenberg *et al.*, 2002; Parvinen *et al.*, 2003; Parvinen, 2006).

Note that the term 'disturbance' is not always defined with a clear distinction between a constantly high loss rate and repeated patch catastrophes (Pásztor *et al.*, submitted a). While both situations select for high growth rate, only the latter is able to maintain diversity by providing a new opportunity for niche-segregation. A constant high rate of biomass loss does not introduce any new regulating variable. This, again, is in line with the conclusion of Chesson and Huntly (1997) that 'harshness' of the environment alone neither decreases competition nor increases diversity.

In our model, the local abiotic environment remains constant between catastrophes. It is like secondary succession, when fertile soil is available from the very beginning. In the case of primary succession, one should take into account the facilitating effects of the populations. Then, additional variables, such as soil nitrogen level (cf. Tilman, 1988, p. 214), should be followed as a function of patch age. Still, age remains a full characterization of the state of a patch. Therefore, the picture of niche-segregation along the patch-age axis survives. If the 'resource ratio hypothesis' of the primary succession (Tilman, 1988, p. 217) is to be modelled explicitly, then one should consider two local regulating variables (e.g. soil nitrogen level and light intensity on the soil surface) instead of a single one, such as the total density used here. Then, at the metapopulation level, the set of regulating variables consists of the two patch-age continuums of the two local regulating variables.

Nevertheless, the *complete* extinction at patch catastrophe was an essential ingredient of our model. Only this assumption ensures that patch-age (i.e. the time spent since the last

catastrophe in the patch) is a full descriptor of the state of the patch. The possibility of partial catastrophes would require consideration of the complete history of disturbances at a locality. Niche analysis of such a situation is beyond the scope of this paper.

Frequency dependence is the essential link between ecology and evolution (Brown and Vincent, 1987; Christiansen, 1988; Cohen *et al.*, 1999). The most striking consequence of frequency dependence is the possibility of evolution to a fitness minimum (see, for example, Vincent *et al.*, 1993). If it happens, the population undergoes evolutionary branching (Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998). There is an ongoing debate whether the evolutionary branching of adaptive dynamics that occurs in the clonal models can be interpreted as a minimal representation of (the ecological aspects of) speciation (for opposing views, see Dieckmann *et al.*, 2004; Gavrilets, 2005; for model studies, see Dieckmann and Doebeli, 1999; Pennings *et al.*, 2008). Note also that species that co-exist along the r–K continuum are often not closely related. Therefore, their evolution cannot be described solely in our context. However, the observed branching pattern of Fig. 4 demonstrates, in principle, that the relationship between ecology and evolution is the same for disturbance-maintained and for resource-competition-maintained diversity. In both cases, the niche-theoretic 'decreasing competition with increasing difference' translates to the possibility of disruptive selection and evolutionary branching.

The concept of decreased competition between dissimilars was a defining element of Darwin's theory (Darwin, 1859, Chapter 3; for analysis, see Pásztor *et al.*, submitted b; cf. Reznick and Ricklefs, 2009). He needed to understand natural selection and species diversity within the same mental framework. However, the neo-Darwinian synthesis, based on frequency-independent relative fitnesses, emphasized only the first of these two, complementary, aspects. In ecology, which has become disconnected from evolutionary theory, the Darwinian understanding was undermined by the controversy about the principle of competitive exclusion. If, for example, disturbance eliminates competition, then how does it affect natural selection? This article contributes to the complete picture again: competition between similars, co-existence of dissimilars.

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REFERENCES

Abrams, P.A. 1983. The theory of limiting similarity. *Annu. Rev. Ecol. Syst.*, **14**: 359–376.

Abrams, P.A. and Wilson, W.G. 2004. Coexistence of competitors in metacommunities due to spatial variation in resource growth rates: does R^* predict the outcome of competition? *Ecol. Lett.*, **7**: 929–940.

Adler, F.R. and Mosquera, J. 2000. Is space necessary? Interference competition and limits of biodiversity. *Ecology*, **81**: 3226–3232.

Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. *Ecol. Lett.*, **6**: 1109–1122.

Amarasekare, P. and Nisbet, R.M. 2001. Spatial heterogeneity, source–sink dynamics and the local coexistence of competing species. *Am. Nat.*, **158**: 572–584.

Amarasekare, P., Hoopes, M.F., Mouquet, N. and Holyoak, M. 2004. Mechanism of coexistence in competitive metacommunities. *Am. Nat.*, **164**: 310–326.

Barabás, G. and Meszéna, G. 2009. When the exception becomes the rule: the disappearance of limiting similarity in the Lotka-Volterra model. *J. Theor. Biol.*, **258**: 89–94.

Berryman, A.A., Arce, M.L. and Hawkins, B.A. 2002. Population regulation, emergent properties, and a requiem for density dependence. *Oikos*, **99**: 600–606.

Brown, J. and Vincent, T.L. 1987. A theory for the evolutionary game. *Theor. Pop. Biol.*, **31**: 140–166.

Calcagno, V., Mouquet, N., Jarne, P. and David, P. 2006. Coexistence in a metacommunity: the competition–colonization trade-off is not dead. *Ecol. Lett.*, **9**: 897–907.

Chase, J.M. and Leibold, M.A. 2003. *Ecological Niches: Linking Classical and Contemporary Approaches*. Chicago, IL: University of Chicago Press.

Chesson, P. 1991. A need for niches? *Trends Ecol. Evol.*, **6**: 26–28.

Chesson, P. 1994. Multispecies competition in variable environments. *Theor. Pop. Biol.*, **45**: 227–276.

Chesson, P. 2000a. General theory of competitive coexistence in spatially varying environments. *Theor. Pop. Biol.*, **58**: 211–237.

Chesson, P. 2000b. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, **31**: 343–366.

Chesson, P. and Huntly, N. 1997. The role of harsh and fluctuating conditions in the dynamics of ecological communities. *Am. Nat.*, **150**: 519–553.

Christiansen, F.B. 1988. Frequency dependence and competition [and discussion]. *Proc. R. Soc. Lond. B*, **319**: 587–600.

Cohen, Y., Vincent, T.L. and Brown, J.S. 1999. A *G*-function approach to fitness minima, fitness maxima, evolutionarily stable strategies and adaptive landscapes. *Evol. Ecol. Res.*, **1**: 923–942.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs – high diversity of trees and corals is maintained only in non-equilibrium state. *Science*, **199**: 1302–1310.

Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray.

Dieckmann, U. and Doebeli, M. 1999. On the origin of species by sympatric speciation. *Nature*, **400**: 354–357.

Dieckmann, U., Metz, J.A.J., Doebeli, M. and Tautz, D. eds. 2004. *Adaptive Speciation*. Cambridge: Cambridge University Press.

Gavrilets, S. 2005. 'Adaptive speciation' – it is not that easy: a reply to Doebeli *et al. Evolution*, **59**: 696–699.

Geritz, S.A.H. 1995. Evolutionary stable seed polymorphism and small scale spatial variation in seedling density. *Am. Nat.*, **146**: 685–707.

Geritz, S.A.H., Metz, J.A.J., Kisdi, É. and Meszéna, G. 1997. Dynamics of adaptation and evolutionary branching. *Phys. Rev. Lett.*, **78**: 2024–2027.

Geritz, S.A.H., Kisdi, É., Meszéna, G. and Metz, J.A.J. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*, **12**: 35–57.

Geritz, S.A.H., van der Meijden, E. and Metz, J.A.J. 1999. Evolutionary dynamics of seed size and seedling competitive ability. *Theor. Pop. Biol.*, **55**: 324–343.

Gyllenberg, M. and Meszéna, G. 2005. On the impossibility of coexistence of infinitely many strategies. *J. Math. Biol.*, **50**: 133–160.

Gyllenberg, M. and Metz, J.A.J. 2001. On fitness in structured metapopulations. *J. Math. Biol.*, **43**: 545–560.

Gyllenberg, M., Parvinen, K. and Dieckmann, U. 2002. Evolutionary suicide and evolution of dispersal in structured metapopulations. *J. Math. Biol.*, **45**: 79–105.

Hanski, I., Foley, P. and Hassell, M. 1996. Random walks in a metapopulation: how much density dependence is necessary for long-term persistence? *J. Anim. Ecol.*, **65**: 274–282.

Hardin, G. 1960. Competitive exclusion principle. *Science*, **131**: 1292–1297.

Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. *Theor. Pop. Biol.*, **18**: 363–373.

Hixon, M.A., Pacala, S.W. and Sandin, S.A. 2002. Population regulation: historical context and contemporary challenges of open vs. closed systems. *Evolution*, **83**: 1490–1508.

Huston, M.A. 1979. General hypothesis of species diversity. *Am. Nat.*, **113**: 81–101.

Huston, M.A. 1994. *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge: Cambridge University Press.

Hutchinson, G.E. 1961. The paradox of the plankton. *Am. Nat.*, **45**: 137–145.

Hutchinson, G.E. 1978. *An Introduction to Population Ecology*. New Haven, CT: Yale University Press.

Kinzig, A.P., Levin, S.A., Dushoff, J. and Pacala, S. 1999. Limiting similarity, species packing, and system stability for hierarchical competition–colonization models. *Am. Nat.*, **153**: 371–383.

Kisdi, É. 1999. Evolutionary branching under asymmetric competition. *J. Theor. Biol.*, **197**: 149–162.

Kisdi, É. and Geritz, S.A.H. 2003. On the coexistence of perennial plants by the competition–colonization trade-off. *Am. Nat.*, **161**: 350–354.

Leibold, M.A. 1995. The niche concept revisited: mechanistic models and community context. *Ecology*, **76**: 1371–1382.

Levins, R. 1968. *Evolution in Changing Environments*. Princeton, NJ: Princeton University Press.

MacArthur, R.H. and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.*, **101**: 377–385.

MacArthur, R.H. and Wilson, E.O. 1967. *The Theory of Island Biogeography*. Monographs in Population Biology. Princeton, NJ: Princeton University Press.

Mathias, A., Kisdi, É. and Olivieri, I. 2001. Divergent evolution of dispersal in a heterogeneous landscape. *Evolution*, **55**: 246–259.

Matsuda, H. 1985. Evolutionarily stable strategies for predator switching. *J. Theor. Biol.*, **115**: 351–366.

Meszéna, G., Gyllenberg, M., Pásztor, L. and Metz, J.A.J. (2006). Competitive exclusion and limiting similarity: a unified theory. *Theor. Pop. Biol.*, **69**: 68–87.

Metz, J.A.J. and Gyllenberg, M. 2001. How should we define fitness in structured metapopulation models? Including an application to the calculation of ES dispersal strategies. *Proc. R. Soc. Lond. B*, **268**: 499–508.

Metz, J.A.J., Nisbet, R.M. and Geritz, S.A.H. 1992. How should we define 'fitness' for general ecological scenarios? *Trends Ecol. Evol.*, **7**: 198–202.

Metz, J.A.J., Geritz, S.A.H., Meszéna, G., Jacobs, F.J.A. and van Heerwaarden, J.S. 1996. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In *Stochastic and Spatial Structures of Dynamical Systems* (S.J. van Strien and S.M. Verduyn Lunel, eds.), pp. 183–231. Amsterdam: North-Holland.

Nee, S. and May, R.M. 1992. Dynamics of metapopulations – habitat destruction and competitive coexistence. *J. Anim. Ecol.*, **61**: 37–40.

Nurmi, T. and Parvinen, K. 2008. On the evolution of specialization with a mechanistic underpinning in structured metapopulations. *Theor. Pop. Biol.*, **73**: 222–243.

Nurmi, T., Geritz, S.A.H., Parvinen, K. and Gyllenberg, M. 2008. Evolution of specialization on resource utilization in structured metapopulations. *J. Biol. Dynamics*, **2**: 297–322.

Pacala, S. and Rees, M. 1998. Models suggesting field experiments to test two hypotheses explaining successional diversity. *Am. Nat.*, **152**: 729–737.

Parvinen, K. 1999. Evolution of migration in a metapopulation. *Bull. Math. Biol.*, **61**: 531–550.

Parvinen, K. 2006. Evolution of dispersal in a structured metapopulation model in discrete time. *Bull. Math. Biol.*, **68**: 655–678.

Parvinen, K. 2007. Evolutionary suicide in a discrete-time metapopulation model. *Evol. Ecol. Res.*, **9**: 619–633.

Parvinen, K. and Egas, M. 2004. Dispersal and the evolution of specialization in a two-habitat type metapopulation. *Theor. Pop. Biol.*, **66**: 233–248.

Parvinen, K., Dieckmann, U., Gyllenberg, M. and Metz, J.A.J. 2003. Evolution of dispersal in metapopulations with local density dependence and demographic stochasticity. *J. Evol. Biol.*, **16**: 143–153.

Pennings, P.S., Kopp, M., Meszéna, G., Dieckmann, U. and Hermisson, J. 2008. An analytically tractable model for competitive speciation. *Am. Nat.*, **171**: E44–E71.

Rees, M., Condit, R., Crawley, M., Pacala, S. and Tilman, D. 2001. Long-term studies of vegetation dynamics. *Science*, **293**: 650–655.

Reznick, D.N. and Ricklefs, R.E. 2009. Darwin's bridge between microevolution and macroevolution. *Nature*, **457**: 837–842.

Ricker, W.E. 1954. Stock and recruitment. *J. Fish. Res. Board Can.*, **11**: 559–623.

Ronce, O., Perret, F. and Olivieri, I. 2000. Evolutionarily stable dispersal rates do not always increase with local extinction rates. *Am. Nat.*, **155**: 485–496.

Shugart, H.H. 1998. *Terrestrial Ecosystems in Changing Environments*. Cambridge: Cambridge University Press.

Szabó, P. and Meszéna, G. 2006. Limiting similarity revisited. *Oikos*, **112**: 612–619.

Szabó, P. and Meszéna, G. 2007. Multi-scale regulated plant community dynamics: mechanisms and implications. *Oikos*, **116**: 233–240.

Szilágyi, A. and Meszéna, G. 2009a. Limiting similarity and niche theory for structured populations. *J. Theor Biol.*, **258**: 27–37.

Szilágyi, A. and Meszéna, G. 2009b. Two-patch model of spatial niche-segregation. *Evol. Ecol.*, **23**: 187–205.

Tilman, D. 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton, NJ: Princeton University Press.

Tilman, D., May, R.M., Lehman, C.L. and Nowak, M.A. 1994. Habitat destruction and the extinction debt. *Nature*, **371**: 65–66.

Turchin, P. 1999. Population regulation: a synthetic view. *Oikos*, **84**: 153–159.

Van Tienderen, P.H. and De Jong, G. 1986. Sex ratio under the haystack model: polymorphism may occur. *J. Theor. Biol.*, **122**: 69–81.

Vincent, T.L., Cohen, Y. and Brown, J. 1993. Evolution via strategy dynamics. *Theor. Pop. Biol.*, **44**: 149–176.