



# Joint evolution of altruistic cooperation and dispersal in a metapopulation of small local populations

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## ABSTRACT

We investigate the joint evolution of public goods cooperation and dispersal in a metapopulation model with small local populations. Altruistic cooperation can evolve due to assortment and kin selection, and dispersal can evolve because of demographic stochasticity, catastrophes and kin selection. Metapopulation structures resulting in assortment have been shown to make selection for cooperation possible. But how does dispersal affect cooperation and vice versa, when both are allowed to evolve as continuous traits? We found four qualitatively different evolutionary outcomes. (1) Monomorphic evolution to full defection with positive dispersal. (2) Monomorphic evolution to an evolutionarily stable state with positive cooperation and dispersal. In this case, parameter changes selecting for increased cooperation typically also select for increased dispersal. (3) Evolutionary branching can result in the evolutionarily stable coexistence of defectors and cooperators. Although defectors could be expected to disperse more than cooperators, here we show that the opposite case is also possible: Defectors tend to disperse less than cooperators when the total amount of cooperation in the dimorphic population is low enough. (4) Selection for too low cooperation can cause the extinction of the evolving population. For moderate catastrophe rates dispersal needs to be initially very frequent for evolutionary suicide to occur. Although selection for less dispersal in principle could prevent such evolutionary suicide, in most cases this rescuing effect is not sufficient, because selection in the cooperation trait is typically much stronger. If the catastrophe rate is large enough, a part of the boundary of viability can be evolutionarily attracting with respect to both strategy components, in which case evolutionary suicide is expected from all initial conditions.

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## 1. Introduction

Cooperation – how can it emerge and be maintained when threatened by free-riders, individuals who do not cooperate themselves, but enjoy all the benefits from the cooperation of others? Various mechanisms promoting cooperation have been proposed. Potential cooperation events may be repeated many times between the same individuals. If an individual decides not to cooperate, the partner is likely to remember such defecting act, and not to give help in the future either. Therefore, direct reciprocity may promote cooperation (Trivers, 1971). In case pairwise interactions are repeated, but not between the same individuals, by defecting one may get a bad reputation, and that way risk the possibility of receiving help in the future. Therefore, indirect reciprocity (Alexander, 1979; Sugden, 1986; Alexander, 1987; Nowak and Sigmund, 1998a,b, 2005) may

promote cooperation, depending on the social norm (Ohtsuki and Iwasa, 2006).

Assortment has also been proposed to be a mechanism promoting cooperation (Fletcher and Doebeli, 2009). Whatever the mechanism causing assortment is, if a cooperating individual is more likely to interact with cooperating individuals than a defecting individual is, the direct benefit received from them may promote cooperation. Assortment can occur for example in populations that are not well-mixed, and in which cooperation is typically possible only among nearby individuals. In such a population individuals are likely to have some relatives around. Giving help to relatives is often beneficial from an evolutionary point of view, and thus kin selection (Hamilton, 1964a,b) may promote cooperation. Metapopulations, collections of local populations connected by dispersal (Levins, 1969, 1970), provide a natural setup for assortment. This has given motivation to study the evolution of cooperation in metapopulation models or in other spatially heterogeneous populations (Le Galliard et al., 2003; Parvinen, 2011).

Dispersal is a key feature in metapopulations, and its evolution has been widely studied in various types of models (for references

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see this and the following paragraphs). Already [Hamilton and May \(1977\)](#) observed that kin selection can promote dispersal even in stable habitats, see also ([Motro, 1982a,b, 1983](#); [Frank, 1986](#)): If the relatedness between a focal individual and other individuals in the present patch is high, by dispersing the focal individual reduces kin competition. In large local populations this mechanism is not effective, because the relatedness between individuals in a large local population is essentially zero. When large local populations show equilibrium dynamics, dispersal is typically selected against ([Hastings, 1983](#); [Parvinen, 1999](#)), because there is no benefit to disperse between patches with similar conditions. Temporal heterogeneity has been shown to be a mechanism promoting dispersal, because it results in sparsely populated patches, into which immigration typically is beneficial. Such temporal heterogeneity can result, e.g., from non-equilibrium local population dynamics ([Doebeli, 1995](#); [Doebeli and Ruxton, 1997](#); [Holt and McPeck, 1996](#); [Parvinen, 1999](#)) or catastrophes ([Gyllenberg and Metz, 2001](#); [Gyllenberg et al., 2002](#); [Parvinen, 2002, 2006](#); [Ronce et al., 2000](#)). In case of small local populations, local population dynamics is necessarily stochastic resulting in temporal heterogeneity, which together with kin selection promotes dispersal ([Metz and Gyllenberg, 2001](#); [Parvinen et al., 2003](#); [Parvinen and Metz, 2008](#); [Parvinen et al., 2012](#)).

Direct costs of dispersal are in general expected to select against dispersal, but also opposite effects have been observed ([Comins et al., 1980](#); [Gandon and Michalakis, 1999](#); [Heino and Hanski, 2001](#)). [Gandon and Michalakis \(1999\)](#) suggested that increases in the direct costs of dispersal may cause more and more competition between highly related philopatric individuals, which may eventually select for dispersal. Local adaptation ([Kisdi, 2002](#); [Nurmi and Parvinen, 2011](#)) is also expected to select against dispersal, because a dispersing individual who is well adapted to the conditions in the present location, takes the risk of arriving into a patch with conditions for which it is maladapted.

It is obvious that dispersal affects the evolution of cooperation: for low dispersal rates the relatedness between individuals in a small local population can be high, and cooperation can evolve. Increasing the dispersal rate is expected to have a direct decreasing effect on relatedness, and thus to make cooperation less favourable. This is, however, not always the case ([Parvinen, 2011](#)). Although such an effect may first seem counterintuitive, note that increasing the dispersal rate has also an indirect increasing effect on relatedness through decreasing the average local population size. Furthermore, for high dispersal rates, [Parvinen \(2011\)](#) observed evolution to too low cooperation resulting in evolutionary suicide ([Ferrière, 2000](#); [Parvinen, 2005](#); [Matsuda and Abrams, 1994](#)).

Cooperation is also likely to affect the evolution of dispersal. According to first intuition, a cooperating individual could be expected to be willing to remain close to its kin and thus to disperse only moderately. On the other hand, cooperation will also affect the evolution of dispersal by increasing the local population size, which is expected to select for dispersal. These effects give motivation for the study of the interplay of dispersal and cooperation, about which only few studies exist ([Hochberg et al., 2008](#); [Pfeiffer and Bonhoeffer, 2003](#)).

[Pfeiffer and Bonhoeffer \(2003\)](#) used a game-theoretical approach to study cooperation and dispersal in a spatial setting, in which cooperating cells produce ATP only with the efficient but slow method of respiration, and defectors use also the faster method of fermentation, which in total is less efficient. Population dynamics with two cell types, in case all cells are mobile, showed that cooperators dominate when cell motion is low, and defectors dominate when cell motion is high. This result is analogous to results in the model studied in this article, when only cooperation is evolving ([Parvinen, 2011](#)). Furthermore, [Pfeiffer and Bonhoeffer \(2003\)](#) assumed that non-dispersing (clustering) cells remain

attached to the mother cell in contrast with dispersing (mobile) cells. Population dynamics of the resulting four different cell types showed that for high resource influx, non-dispersing cooperators (clustering respirator) dominate. Although their result is interesting, it leaves open the question how will dispersal and cooperation evolve, when they are continuously varying traits under the natural selection. [Hochberg et al. \(2008\)](#) partly investigated this question by studying a model, in which the dispersal rate of cooperators and the dispersal rate of defectors were evolving. Cooperation itself was not allowed to evolve as a continuously varying trait, but in their model 2, the relative abundance of cooperators and defectors was allowed to change. However, they did “not explicitly consider dynamics, such as group founding, group numbers, individual emigration and immigration, and competition for limiting resources within or between groups”. The novelty of this article is in that we study the joint evolution of dispersal and cooperation, when both are continuously varying traits under natural selection, in a metapopulation model with realistic (local) population dynamics.

Our choice of a model is a metapopulation model with infinitely many patches with small (finite) local populations, in which the evolution of dispersal ([Cadet et al., 2003](#); [Metz and Gyllenberg, 2001](#); [Parvinen et al., 2003](#); [Parvinen and Metz, 2008](#); [Parvinen et al., 2012](#)) and the evolution of cooperation ([Parvinen, 2011](#)) and other traits ([Jesse et al., 2011](#)) have already been studied separately. The benefit of this model type is that it is rather realistic concerning local population dynamics, in which stochastic events of birth, death, emigration and immigration are accounted for. Also, a well-defined proxy for invasion fitness is available ([Metz and Gyllenberg, 2001](#)), which allows us to perform efficient evolutionary analysis with methods of adaptive dynamics, instead of relying only on time-consuming simulations.

## 2. Model and methods

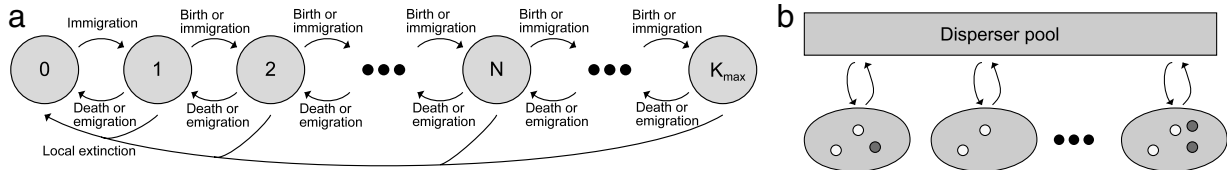
Our model is a structured metapopulation model with infinitely many habitat patches with small local populations ([Metz and Gyllenberg, 2001](#)). In short, our model is ecologically almost the same as the model by [Parvinen \(2011\)](#), but here in addition to studying the evolution of cooperation we allow also the dispersal rate to evolve. For the sake of completeness, we give the ecological details here. For the calculation of invasion fitness, see the references above.

### 2.1. Ecological dynamics

The strategy of an individual is a 2-dimensional vector  $s = \{c, m\}$ . The first strategy component describes the rate  $c$  at which individuals contribute resources locally. The value of the cooperative contributions to a public pool of local resources are multiplied with the factor  $\rho$ , and then shared among all individuals in the patch. Therefore, the average rate of received contributions in a local population of size  $N$  is  $\rho A = \frac{\rho}{N} \sum c_i N_i$ , where  $N_i$  is the size of the sub-population with cooperative strategy  $c_i$ , and  $N = \sum N_i$ . We assume that the received contributions have an increasing effect on the birth rate, which is the same among all individuals in the patch. More precisely, the per capita birth rate in a patch of  $N \geq 1$  individuals is

$$\beta_N = b(N) + h(\rho A) = b(N) + h\left(\frac{\rho}{N} \sum c_i N_i\right), \quad (1)$$

where  $b(N)$  is the birth rate in the absence of cooperation, and  $h$  describes the functional response in the effect of received contributions. The function  $h$  is assumed to be a smooth non-negative increasing function with  $h(0) = 0$ . In numerical examples we assume Holling type II functional response,  $h(\rho A) = \frac{\rho A}{1 + \gamma \rho A}$ .



**Fig. 1.** (a) Transition diagram for a single patch. Arrows describe the possible transitions in the state of the patch. Local population size is increased by one by birth and immigration events and decreases by one when a death or emigration event occurs. Local extinction events can kill all individuals in a patch, thus resetting its population size to zero. (b) Illustration of the metapopulation structure: local populations consist of a small number of individuals with different strategies. Dispersal occurs via a disperser pool.

The personal cost of contribution to the public good is an increase in the death rate of the contributor only. We assume that the death rate of an individual with contribution strategy  $c$  is

$$\delta_N(c) = d(N) + c \quad (2)$$

where  $d(N)$  is the death rate in the absence of cooperation.

In some cases, such as for bacteria producing exoproducts, allowing contributions to public resources when alone is realistic. As pointed out by Parvinen (2011), the condition  $1 < \rho \leq 2$  ensures that cooperation is altruistic in the sense that the direct benefit of cooperation as an increased birth rate never exceeds the cost of cooperation as increased death rate in patches of size 2 and larger. However, in patches of size 1, the increasing effect of cooperation on the birth rate does exceed the increasing effect of cooperation on the death rate, at least for small  $c$ . Such cooperative behaviour of a lonely individual cannot really be called altruistic. Therefore, like Hauert et al. (2006), we also study the case in which the public goods interactions occur only in local populations of size 2 and greater, in which case we set  $\beta_1 = b(1)$  and  $\delta_1(c) = d(1)$ . For simplicity of notation, we denote this case with  $\tilde{N} = 2$ , where  $\tilde{N}$  denotes the smallest local population size in which cooperation occurs.

No real-life patch can host an infinite number of individuals. Therefore (and also for technical reasons), we assume that there is an upper limit  $K_{\max}$  for the local population size, thus  $\beta_{K_{\max}} = 0$ . Following Parvinen (2011), in numerical examples we have assumed that per capita birth rates are unaffected by density,  $b(N) = b_0$  for  $N < K_{\max}$ , while per capita death rates increase linearly with local population size,  $d(N) = b_0 N / K$ . Therefore, in local populations of size  $K$  the birth rate equals the death rate in the absence of cooperation. In numerical examples we have used the value  $K_{\max} = 2K$  for the upper limit of local population size.

The second strategy component is the rate  $m$  at which individuals emigrate and enter a global disperser pool. While in the disperser pool, individuals experience mortality at rate  $\tilde{d}$ . They leave the disperser pool by settling into a new patch at rate  $\alpha$ . Dispersers choose the patch they immigrate into at random, independently of the local population size. Immigration into a full patch with local population size  $K_{\max}$  is not possible. Individuals encountering full patches simply remain in the dispersal pool. Occasionally a local catastrophe kills the local population. The patch remains habitable and can be recolonized by dispersers from the disperser pool. These extinctions of a local population due to external disturbances occur at rate  $\mu$ . The possible transitions in the state of a patch are illustrated in Fig. 1 together with the metapopulation structure.

At the metapopulation level we study the local population size distribution  $p_n$ , where  $p_n$  is the probability that a randomly selected patch has a local population of size  $n$ . The differential equations for  $p_n$ , which are also called as forward Kolmogorov equations, are obtained by straightforward book-keeping of the events described above (see, e.g., Parvinen, 2011).

## 2.2. Adaptive dynamics

In the framework of adaptive dynamics (Metz et al., 1996; Geritz et al., 1997, 1998), invasion fitness (Metz et al., 1992) is defined as the long-term exponential growth rate  $r(s_{\text{mut}}, E_{\text{res}})$  of a mutant phenotype  $s_{\text{mut}}$  in an environment  $E_{\text{res}}$  set by the resident. If the invasion fitness is positive,  $r(s_{\text{mut}}, E_{\text{res}}) > 0$ , the mutant phenotype may grow in (meta)population size, invade and possibly replace the former resident. Adaptive dynamics investigates the long-term outcomes of such invasion events.

In structured metapopulation models, the direct computation of fitness is complicated. For this reason, Gyllenberg and Metz (2001) and Metz and Gyllenberg (2001) presented the metapopulation reproduction ratio

$$R_m(s_{\text{mut}}, E_{\text{res}}). \quad (3)$$

Consider a single mutant disperser arriving in a patch. This mutant may reproduce and thus gain descendants in this patch, but this will not necessarily happen because of demographic stochasticity. As long as this mutant or at least one of its descendants is present in the local population, we call it a mutant colony. Again, because of demographic stochasticity and catastrophes, the mutant colony will eventually go extinct. During its lifetime, some mutants will emigrate from this mutant colony to the disperser pool. Their average number is the metapopulation reproduction ratio  $R_m$  of the mutant. In other words, it is the expected number of successful dispersers produced by a typical mutant colony initiated by a single mutant disperser. For details, see also Parvinen et al. (2003) and Parvinen and Metz (2008). The invasion condition  $r(s_{\text{mut}}, E_{\text{res}}) > 0$  is equivalent to  $R_m(s_{\text{mut}}, E_{\text{res}}) > 1$ , and thus  $R_m$  is a proxy for invasion fitness, and can be used to study evolution in metapopulation models.

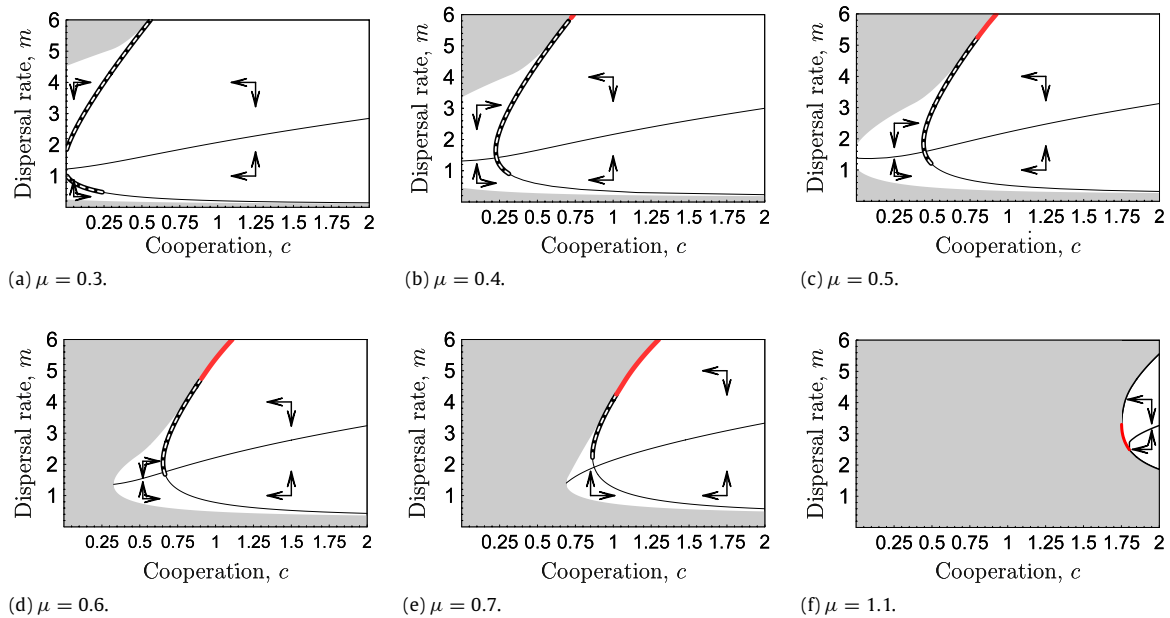
The fitness gradient, which for vector-valued strategies consists of derivatives  $\frac{\partial}{\partial s_{i,\text{mut}}} r(s_{\text{mut}}, E_{\text{res}})|_{s_{\text{mut}}=s_{\text{res}}}$  with respect to each strategy component, gives the direction into which strategies are expected to change with mutations of small size. The components of the fitness gradient are sign-equivalent with the corresponding derivatives of the fitness proxy

$$D_i(s_{\text{res}}) = \frac{\partial}{\partial s_{i,\text{mut}}} R_m(s_{\text{mut}}, E_{\text{res}}) \Big|_{s_{\text{mut}}=s_{\text{res}}}. \quad (4)$$

Strategies for which the fitness gradient is zero, or equivalently  $D(s_{\text{res}}) = 0$ , are called singular strategies (Geritz et al., 1997, 1998). For determining the expected direction of selection and finding singular strategies we have used the direct calculation method for the fitness-proxy gradient (4), provided by Parvinen (2011) for this class of structured metapopulation models. For determining other properties of the singular strategies, calculating (3) is necessary, which can be done using the algorithm provided by Metz and Gyllenberg (2001).

If the invasion fitness is negative for all mutant strategies different from the resident strategy,

$$r(s_{\text{mut}}, E_{\text{res}}) < 0 \quad \text{for all } s_{\text{mut}} \neq s_{\text{res}}, \quad (5)$$



**Fig. 2.** Zero-isoclines of the components of the two-dimensional fitness gradient (4) for different values of the catastrophe rate  $\mu$ , which illustrate the direction of expected evolutionary change without mutational covariance. Areas of unviable strategies are shown in grey. The zero-isocline curves are either drawn thin or black bold curves with white dashes. Thin curves correspond to strategies that are uninvadable (local fitness maxima) with respect to the strategy component for which the selection gradient vanishes. Black bold curves with white dashes correspond to local fitness minima, which means that they are branching points with respect to the corresponding strategy component. The thick red (grey in the printed version) curve in panels b–e corresponds to a boundary of viability, which is evolutionarily attracting with respect to the cooperation component, and may allow for evolutionary suicide. All visible boundaries of viability in panel f are evolutionarily attracting with respect to the cooperation component, and the boundary drawn with the thick red curve is evolutionarily attracting also with respect to the dispersal component. Therefore, evolutionary suicide is inevitable. Parameters:  $b_0 = 1$ ,  $K = 5$ ,  $K_{\max} = 10$ ,  $\bar{d} = 0.0555$ ,  $\alpha = 0.5$ ,  $\gamma = 0.01$ ,  $\rho = 2$ , and  $\bar{N} = 2$ .

this singular strategy is uninvadable, and thus an evolutionarily stable strategy, ESS (Maynard Smith, 1976). A singular strategy  $s^*$  is an evolutionary attractor (Eshel, 1983) if the repeated invasion of nearby mutant strategies into resident strategies will lead to the convergence of resident strategies towards  $s^*$ . For scalar strategies, the condition for such convergence is  $D'(s^*) < 0$ , whereas the situation with vector-valued strategies is more complicated (Christiansen, 1991; Geritz et al., 1998; Leimar, 2001; Marrow et al., 1996; Matessi and Di Pasquale, 1996; Meszéna et al., 2001).

Because cooperation and dispersal are physiologically rather different traits, we find it realistic to assume that these traits evolve independently. Each mutation thus affects only one trait, and therefore mutational covariance is equal to zero. Furthermore, the variance–covariance matrix  $\sigma^2$  of the mutation distribution is a diagonal matrix. Under this assumption, the direction of expected evolutionary change can be illustrated by showing the signs of the fitness gradient vector (such as in Fig. 2). We have assumed the diagonal elements of the variance–covariance matrix to be equal to 1, thus  $\sigma^2 = \text{diag}\{1, 1\}$ .

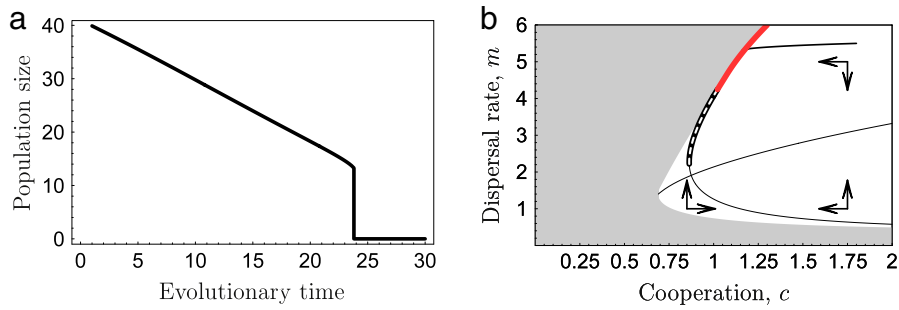
For one-dimensional strategy spaces, singular strategies, which are convergence stable, but not uninvadable, are of special interest. In a neighbourhood of such a singular strategy there is an area of protected coexistence, which means that two strategies are mutually invadable, and cannot oust each other out (Geritz et al., 1997, 1998). Furthermore, the two strategies will evolve away from each other because of disruptive selection. This process is called evolutionary branching, and therefore such singular strategies are called branching points. The general conditions for evolutionary branching in higher-dimensional trait spaces is an open question in adaptive dynamics. Nevertheless, in this article we found singular strategies near which evolutionary branching with respect to the cooperation strategy is expected to happen, after which the dispersal strategy components may also evolve away from each other.

### 3. Results

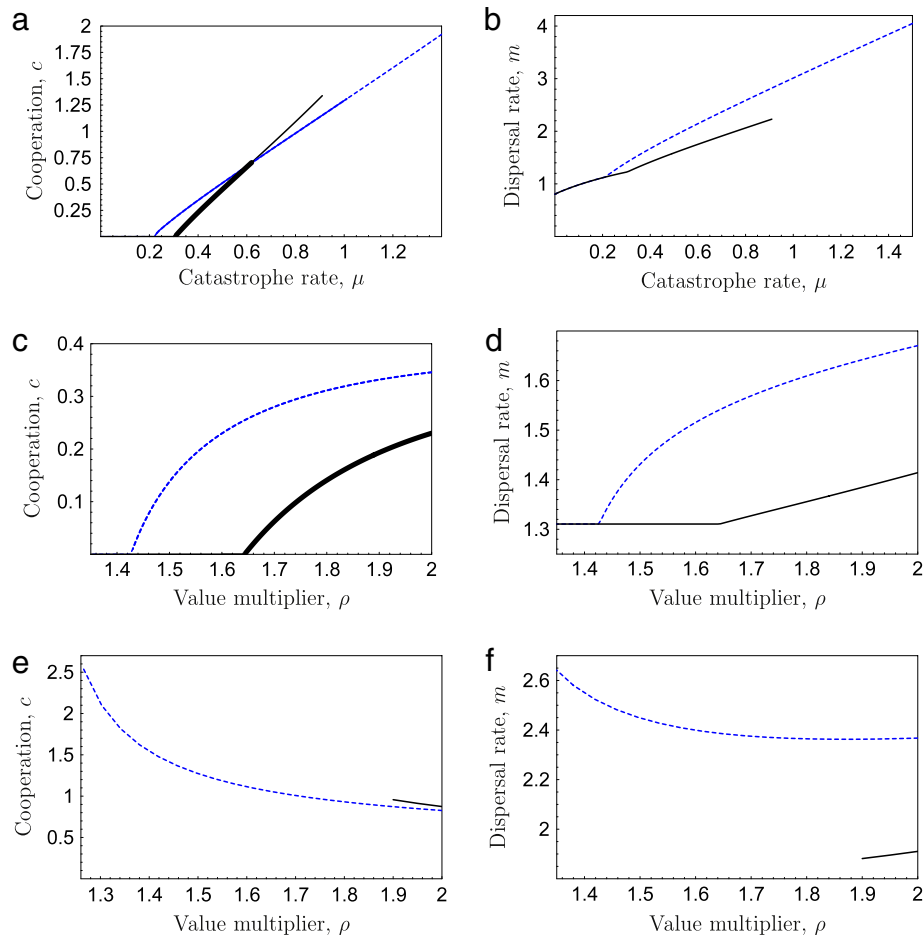
First we investigate the joint evolution of cooperation and dispersal in the absence of cooperation in local populations of size one ( $\bar{N} = 2$ ). Fig. 2 shows zero-isoclines of the components of the fitness gradient, and thus illustrates the potential direction of monomorphic adaptive dynamics of cooperation and dispersal, as well as possible outcomes, in the absence of mutational covariance.

First consider small values of the catastrophe rate  $\mu$ , Fig. 2a. Although a part of the boundary of the strategy space without cooperation ( $c = 0$ ) is evolutionarily repelling, the part near the zero-isocline of the dispersal component is evolutionarily attracting. Because the isoclines do not intersect, there is no internal singular strategy of the joint evolution of cooperation and dispersal. In this case joint evolution will lead to the boundary of strategy space without cooperation, and the value of dispersal rate will become approximately 1.1. For  $\mu \approx 0.305$  this boundary at the singular dispersal rate becomes evolutionarily repelling, and an internal singular strategy appears (see also Fig. 4). From the shape of the zero-isoclines and directions of the arrows near the singular strategy it is clear that strategies will converge to this singular strategy (see Matessi and Di Pasquale, 1996). This singular strategy is first a fitness minimum with respect to the cooperation component (Fig. 2b, c, d), but becomes evolutionarily stable for larger values of  $\mu$ , around  $\mu \approx 0.62$  (Fig. 2e). As illustrated also by Parvinen (2011, his Figs. 3a and 4b), for large values of the dispersal rate  $m$  and the catastrophe rate  $\mu$ , the boundary of viability may become evolutionarily attracting with respect to the cooperation strategy, and thus evolutionary suicide (Ferrière, 2000; Gyllenberg and Parvinen, 2001; Gyllenberg et al., 2002; Parvinen, 2005; Rankin and López-Sepulcre, 2005; Webb, 2003) may take place. However, as we observe from Fig. 2c, d, e, near this boundary there can be selection for decreased dispersal, which means that this boundary is evolutionarily repelling with respect to the dispersal component. Therefore it depends on the initial strategy values, mutational variance and chance, whether the joint





**Fig. 3.** A trait substitution sequence resulting in evolutionary suicide when  $\tilde{N} = 2$ . In each step, a mutation in the direction of the fitness gradient is assumed to occur. Although the extinction boundary is evolutionarily repelling with respect to the dispersal component, selection in the cooperation component causes the evolution towards the extinction boundary, at which the population size (a) suddenly drops to zero. Panel (b) shows the trajectory of strategies together with the isocline plot (Fig. 2f). Parameters:  $\mu = 0.7$ . Other parameters as in Fig. 2.



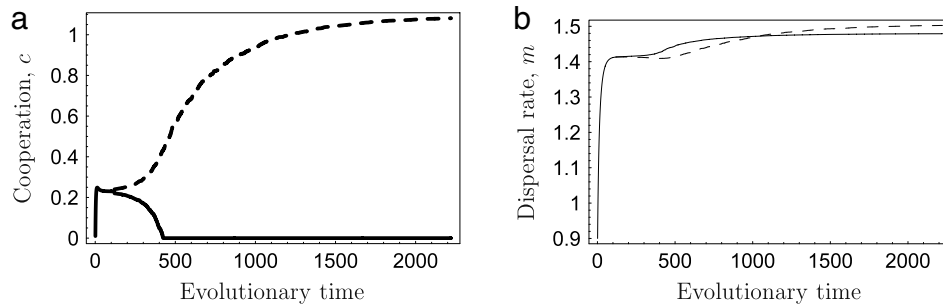
**Fig. 4.** Cooperation (a, c, e) and dispersal (b, d, f) components of vector-valued singular strategies for different values of the (a, b) catastrophe rate  $\mu$  and (c–f) multiplier parameter  $\rho$  when cooperation in patches of size one is allowed ( $\tilde{N} = 1$ , dashed blue curves) or is not allowed ( $\tilde{N} = 2$ , continuous curves). Bold curves correspond to fitness minima with respect to the cooperation component. Parameters: (a, b)  $\rho = 2$ , (c, d)  $\mu = 0.4$ , (e, f)  $\mu = 0.7$ . Other parameters as in Fig. 2.

evolution of cooperation and dispersal will result in evolutionary suicide (see Fig. 3). We can nevertheless conclude, that allowing the dispersal rate to evolve can potentially have a rescuing effect on the metapopulation. For even larger values of the catastrophe rate  $\mu$ , a part of the boundary of viability is evolutionarily attracting with respect to both strategy components, in which case evolutionary suicide is expected from all initial conditions (Fig. 2f).

The zero-isoclines of the components of the fitness gradient in case cooperation occurs also in local populations of size one ( $\tilde{N} = 1$ ) are otherwise qualitatively similar to those illustrated in Fig. 2, except that we did not observe evolutionarily attracting

boundaries of viability, which means that evolutionary suicide is not expected to happen (isocline-plots not shown).

At least for the parameter values used in Fig. 2, at most one evolutionarily attracting (monomorphic) singular strategy vector exists. Fig. 4 illustrates the dependence of this singular strategy on various parameter values, and also the effect of the presence ( $\tilde{N} = 1$ ) or absence ( $\tilde{N} = 2$ ) of cooperation in local populations of size one. Increasing the catastrophe rate increases the amount of empty or sparsely populated patches, into which immigration is beneficial. Indeed we observe from Fig. 4, that increasing the catastrophe rate has an increasing effect on



**Fig. 5.** A trait substitution sequence resulting in evolutionary branching when  $\tilde{N} = 2$ . In each step, a mutation in the direction of the fitness gradient is assumed to occur. At first, each mutant is able to take over the resident, and becomes the new resident itself. Once the strategies are close enough to a monomorphic singular strategy, the mutant population will coexist with the resident, and thus the population becomes dimorphic. The strategies of the dimorphic population will diverge until an evolutionarily stable strategy coalition is reached. After the evolving population has become dimorphic, the strategy components corresponding to the more cooperating strategy are illustrated with dashed curves. Parameters:  $\mu = 0.4$ . Other parameters as in Fig. 2.

dispersal. Note, however, that also non-monotonic dependence of evolutionarily stable dispersal rates on catastrophes have been observed (Gyllenberg et al., 2002; Parvinen et al., 2003; Parvinen, 2006; Ronce et al., 2000). Once catastrophes are very frequent, most individuals reside in thinly populated patches anyway, and thus benefits of dispersal can decline. Concerning the cooperation component, increasing the catastrophe rate decreases average local population sizes, and therefore increases within-patch relatedness. For low values of the catastrophe rate, relatedness is too low for cooperation to evolve. Once the catastrophe rate is large enough ( $\mu \approx 0.3$  for  $\tilde{N} = 2$  or  $\mu \approx 0.22$  for  $\tilde{N} = 1$ ), positive cooperation strategies  $c$  do evolve, and  $c$  increases with  $\mu$ . In case of  $\tilde{N} = 2$ , for  $\mu \gtrsim 0.92$ , no evolutionary singular strategy exists, and evolutionary suicide occurs from all initial conditions.

Increasing the multiplication factor  $\rho$  is expected to make cooperation more beneficial. Fig. 4c, d indeed illustrates that once cooperation evolves ( $\rho > 1.65$  for  $\tilde{N} = 2$ ,  $\rho > 1.43$  for  $\tilde{N} = 1$ ), the value of the cooperation component at the singular strategy will increase with  $\rho$ . In the absence of cooperation, the factor  $\rho$  has no effect on the benefits of dispersal. Therefore the dispersal component changes only when  $\rho$  is above the threshold. Fig. 4e, f, however, shows that increasing the multiplication factor  $\rho$  may also decrease the cooperation component of the singular strategy. In this case the catastrophe rate is relatively high ( $\mu = 0.7$ ), and so is cooperation. Although increasing  $\rho$  increases the birth rate, the marginal benefit of cooperation may even decrease because of the functional response.

Fig. 4 illustrates also the effect of the presence ( $\tilde{N} = 1$ ) or absence ( $\tilde{N} = 2$ ) of cooperation in local populations of size one on the singular strategy. From Fig. 4a we observe that it depends on parameters which case results in a higher value of the cooperation component  $c$ . The corresponding quantitative effect on the dispersal component seems to be clearer (Fig. 4b, d). Although for  $\tilde{N} = 1$  the cooperation component  $c$  can be smaller than with  $\tilde{N} = 2$ , in case  $\tilde{N} = 1$  the total level of cooperation can be higher, which can result in higher average local population size, and therefore in higher dispersal rates (Fig. 4b, d).

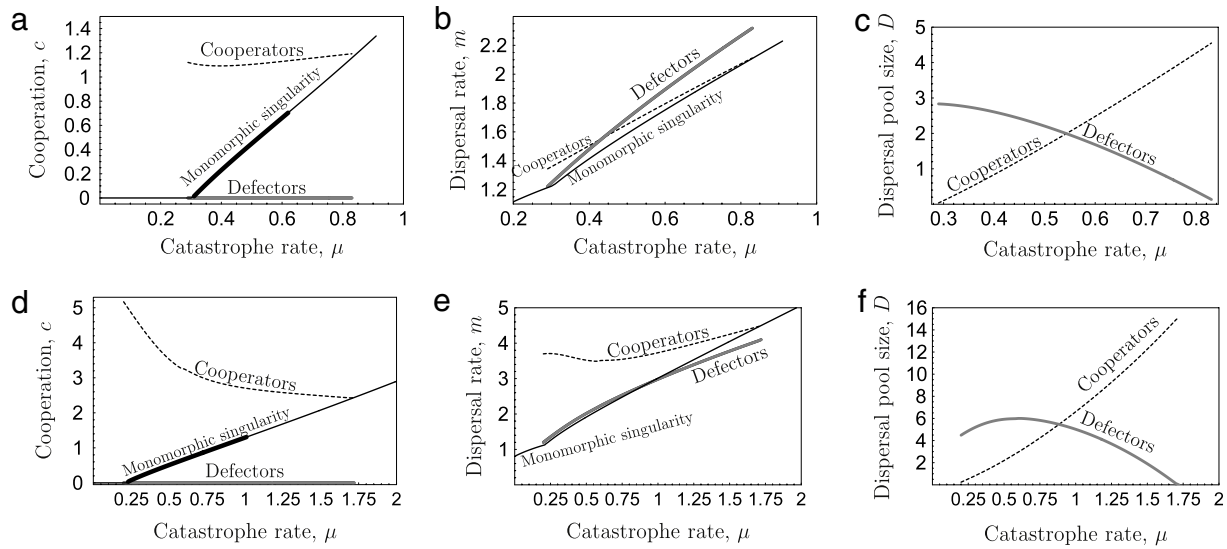
From Fig. 4 one can make the conclusion that in the studied metapopulation model, cooperation and dispersal appear mainly to be positively correlated: changes in parameters making cooperation more beneficial seem to cause crowding, and thus make dispersal more beneficial. Note, however, that from this result we cannot make the conclusion that cooperators should disperse more than defectors. Each observation in Fig. 4 namely corresponds to a different set of parameters, and thus to a different environment experienced by individuals. In order to make this kind of conclusions, we should investigate situations, which result in the coexistence of cooperators and defectors, and then study to which extent does their dispersal behaviour differ.

Fig. 5 illustrates evolutionary dynamics, when there is an internal singular strategy ( $c \approx 0.23$ ,  $m \approx 1.41$ ), which is a fitness minimum with respect to the cooperation component. Starting from a monomorphic population with  $c = 0$ ,  $m = 0.9$ , evolution first takes the evolving strategy near the internal singular strategy. Eventually two strategies are able to coexist, and their cooperation strategies evolve away from each other. The difference in their cooperation strategies causes also different selective pressures on their dispersal strategies. Finally, the dimorphic population reaches an evolutionarily stable strategy coalition of two strategies, a defector with  $\{c, m\} \approx \{0, 1.480\}$  and a cooperator with  $\{c, m\} \approx \{1.091, 1.505\}$ . Such a coexistence is possible, because each of the two strategies have their own niche: cooperators are good colonizers and perform well in sparsely populated patches where defectors have not yet arrived, and defectors perform well in the presence of cooperators. In this case, surprisingly the cooperator disperses more frequently than the defector. One could namely expect that the cooperator would benefit more from a sessile strategy due to kin cooperation.

In order to better understand the results of dimorphic evolution, Fig. 6 illustrates how the evolutionarily stable strategy coalition of two strategies varies with respect to the catastrophe rate  $\mu$ . The less cooperative population always evolves to full defection,  $c = 0$ . Fig. 6a–c show results in the absence of cooperation in local populations of size one ( $\tilde{N} = 2$ ). In this case the cooperation strategy of the cooperative population evolves to  $c \approx 1.1$ . Although the cooperation strategy value of the cooperator only slightly varies with  $\mu$  (Fig. 6a), Fig. 6c shows that increasing  $\mu$  increases the relative frequency of cooperators. The dispersal components of these two strategies are more affected by the catastrophe rate. For moderate catastrophe rates,  $0.3 \lesssim \mu \lesssim 0.45$ , the defectors have a majority. Therefore, cooperators disperse more frequently than the defectors to be able to take advantage of empty or sparsely populated patches. This effect diminishes, when increasing  $\mu$  increases the amount of cooperators, to the extent that for  $\mu \gtrsim 0.45$  cooperators disperse less frequently than the defectors. Fig. 6d–f show results in the presence of cooperation in local populations of size one ( $\tilde{N} = 1$ ). The results are mostly qualitatively similar to the previous case ( $\tilde{N} = 2$ ), but now cooperators always disperse more than the defectors.

#### 4. Conclusion

In addition to direct (Trivers, 1971) and indirect reciprocity (Alexander, 1979, 1987; Nowak and Sigmund, 1998a,b, 2005; Ohtsuki and Iwasa, 2006; Sugden, 1986), assortment (Fletcher and Doebeli, 2009) has been proposed as a general mechanism for promoting cooperation. Such assortment naturally occurs in



**Fig. 6.** Cooperation (a, d) and dispersal (b, e) components of vector-valued singular strategies in the monomorphic singularity and in the dimorphic singular strategy coalition with respect to the catastrophe rate  $\mu$ . Panels (c, f) show the dispersal pool sizes of cooperators and defectors in the dimorphic singular strategy coalition, and thus illustrate their relative frequencies. The bold curves in panels (a, d) correspond to fitness minima with respect to the cooperation component. Upper row (a–c): no cooperation in local populations of size one, lower row (d–f) cooperation also in local populations of size one. Other parameters as in Fig. 2.

metapopulation models, which consist of small local populations connected with dispersal. As observed previously (Parvinen, 2011), dispersal affects the population distribution and the average relatedness in local populations, and therefore also the evolution of cooperation. On the other hand, cooperation naturally affects the local population dynamics, and therefore also the evolution of dispersal. There are numerous studies, in which the evolution of one of these traits has been studied (see the introduction for references). In this article we have studied the joint evolution of dispersal and cooperation, when both are continuously varying traits under natural selection, in a metapopulation model with realistic (local) population dynamics.

In this investigation, we have taken the advantage of a well-defined (proxy for) invasion fitness, the metapopulation reproduction ratio (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001). An efficient numerical calculation method exists for the invasion fitness (see also Parvinen et al., 2003; Parvinen and Metz, 2008), as well as for the fitness gradient directly (Parvinen, 2011). This allows us to use the framework of adaptive dynamics (Geritz et al., 1997, 1998; Metz et al., 1992, 1996) for evolutionary studies.

We observed four qualitatively different evolutionary outcomes in the joint evolution of cooperation and dispersal.

1. The population can evolve to full defection ( $c = 0, m > 0$ ).
2. The population evolves to a monomorphic singular strategy with positive cooperation ( $c > 0, m > 0$ ). In this case, parameter changes selecting for increased cooperation typically also select for increased dispersal.
3. The population first evolves to the monomorphic singular strategy, but then evolutionary branching results in the evolutionarily stable coexistence of a defector ( $c_1 = 0, m_1 > 0$ ) and a cooperator ( $c_2 > 0, m_2 > 0$ ). Depending on parameters, either one of them can be the more frequently dispersing strategy ( $m_1 > m_2$  or  $m_1 < m_2$ ).
4. For moderate catastrophe rates, if the initial dispersal rate is large enough, selection for less cooperation can result in evolutionary suicide, although the extinction boundary is evolutionarily repelling with respect to the dispersal component. If the catastrophe rate is large enough, a part of the boundary of viability can be evolutionarily attracting with respect to both strategy components, in which case evolutionary suicide is expected from all initial conditions.

Outcome (4) was observed only in the absence of cooperation in local populations of size one ( $\bar{N} = 2$ ).

The case (3) is especially interesting. For better understanding of the observed results (Fig. 6) it is essential to identify the “niches” of different strategies, which enable the coexistence of cooperators and defectors. A cooperator performs well (better than a defector) when arriving into empty or sparsely populated patches, whereas defectors exploit the high abundance of cooperators. For low catastrophe rates, the average local population size is high, and there are not enough sparsely populated patches so that cooperation could evolve. When the catastrophe rate is increased, also the amount of empty patches increases, so that cooperation can evolve. Initially, the relative benefit of catastrophes to cooperators is small, and thus the coexistence of cooperators and defectors is possible. When the catastrophe rate is further increased, the proportion of cooperators in the evolutionarily stable dimorphic population increases, until cooperators overtake the defectors. Although it has been observed previously that evolutionary branching (Geritz et al., 1997, 1998) provides a mechanism for the evolutionary emergence of cooperators and defectors (Brännström and Dieckmann, 2005; Doebeli et al., 2004; Parvinen, 2010, 2011), here we have been able to investigate the question how should defectors and cooperators disperse? In a dimorphic population, cooperators and defectors observe different benefits of dispersal. When the proportion of cooperators is small, cooperators disperse more frequently than the defectors to be able to take advantage of empty or sparsely populated patches. When the proportion of cooperators is large and their cooperation strategy is large enough, it is advantageous for defectors to disperse frequently to avoid kin competition, so that not too many defectors exploit the cooperators in a patch. Similar effect of the proportion of cooperators on the relative dispersal behaviour of cooperators and defectors was observed also by Hochberg et al. (2008), but note that their starting point was the presence of cooperators and defectors, whereas in our approach the coexistence of cooperators and defectors is a result of a long-term evolutionary process including evolutionary branching. To conclude, defectors tend to disperse less than cooperators when the overall cooperation in the dimorphic population is low enough.

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## References

- Alexander, R.D., 1979. Darwinism and human affairs. University of Washington Press, Seattle.
- Alexander, R.D., 1987. The biology of moral systems. Aldine de Gruyter, New York.
- Brännström, Å., Dieckmann, U., 2005. Evolutionary dynamics of altruism and cheating among social amoebas. *Proc. R. Soc. Lond. B* 272, 1609–1616.
- Cadet, C., Ferrière, R., Metz, J.A.J., van Baalen, M., 2003. The evolution of dispersal under demographic stochasticity. *Am. Nat.* 162, 427–441.
- Christiansen, F.B., 1991. On conditions for evolutionary stability for a continuously varying character. *Am. Nat.* 138, 37–50.
- Comins, H.N., Hamilton, W.D., May, R.M., 1980. Evolutionarily stable dispersal strategies. *J. Theoret. Biol.* 82, 205–230.
- Doebeli, M., 1995. Dispersal and dynamics. *Theor. Popul. Biol.* 47, 82–106.
- Doebeli, M., Hauert, C., Killingback, T., 2004. The evolutionary origin of cooperators and defectors. *Science* 306, 859–862.
- Doebeli, M., Ruxton, G.D., 1997. Evolution of dispersal rates in metapopulation models: branching and cyclic dynamics in phenotype space. *Evolution* 51, 1730–1741.
- Eshel, I., 1983. Evolutionary and continuous stability. *J. Theoret. Biol.* 103, 99–111.
- Ferrière, R., 2000. Adaptive responses to environmental threats: evolutionary suicide, insurance, and rescue. In: *Options spring 2000*. IIASA, Laxenburg, Austria, pp. 12–16.
- Fletcher, J.A., Doebeli, M., 2009. A simple and general explanation for the evolution of altruism. *Proc. R. Soc. Lond. B* 276, 13–19.
- Frank, S.A., 1986. Dispersal polymorphisms in subdivided populations. *J. Theoret. Biol.* 122, 303–309.
- Gandon, S., Michalakis, Y., 1999. Evolutionarily stable dispersal rate in a metapopulation with extinctions and kin competition. *J. Theoret. Biol.* 199, 275–290.
- Geritz, S.A.H., Kisdi, É., Meszéna, G., 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., Metz, J.A.J., Kisdi, É., Meszéna, G., 1997. Dynamics of adaptation and evolutionary branching. *Phys. Rev. Lett.* 78, 2024–2027.
- Gyllenberg, M., Metz, J.A.J., 2001. *J. Math. Biol.* 43, 545–560.
- Gyllenberg, M., Parvinen, K., 2001. Necessary and sufficient conditions for evolutionary suicide. *Bull. Math. Biol.* 63, 981–993.
- Gyllenberg, M., Parvinen, K., Dieckmann, U., 2002. Evolutionary suicide and evolution of dispersal in structured metapopulations. *J. Math. Biol.* 45, 79–105.
- Hamilton, W.D., 1964a. The genetical evolution of social behaviour i. *J. Theoret. Biol.* 7, 1–16.
- Hamilton, W.D., 1964b. The genetical evolution of social behaviour ii. *J. Theoret. Biol.* 7, 17–52.
- Hamilton, W.D., May, R.M., 1977. Dispersal in stable habitats. *Nature* 269, 578–581.
- Hastings, A., 1983. Can spatial variation alone lead to selection for dispersal. *Theor. Popul. Biol.* 24, 244–251.
- Hauert, C., Holmes, M., Doebeli, M., 2006. Evolutionary games and population dynamics: maintenance of cooperation in public goods games. *Proc. R. Soc. Lond. B* 273, 2565–2570.
- Heino, M., Hanski, I., 2001. Evolution of migration rate in a spatially realistic metapopulation model. *Am. Nat.* 157, 495–511.
- Hochberg, M.E., Rankin, D.J., Taborsky, M., 2008. The coevolution of cooperation and dispersal in social groups and its implications for the emergence of multicellularity. *BMC Evol. Biol.* 8, 238.
- Holt, R.D., McPeck, M., 1996. Chaotic population dynamics favors the evolution of dispersal. *Am. Nat.* 148, 709–718.
- Jesse, M., Mazzucco, R., Dieckmann, U., Heesterbeek, H., Metz, J.A.J., 2011. Invasion and persistence of infectious agents in fragmented host populations. *PLoS one* 6, e24006 1–12.
- Kisdi, É., 2002. Dispersal: risk spreading versus local adaptation. *Am. Nat.* 159, 579–596.
- Le Galliard, J.-F., Ferrière, R., Dieckmann, U., 2003. The adaptive dynamics of altruism in spatially heterogeneous populations. *Evolution* 57, 1–17.
- Leimar, O., 2001. Evolutionary change and Darwinian demons. *Selection* 2 65–72.
- Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* 15, 237–240.
- Levins, R., 1970. Extinction. In: Gerstenhaber, M. (Ed.), *Some mathematical problems in biology*. American Mathematical Society, Providence, RI, pp. 77–107.
- Marrow, P., Dieckmann, U., Law, R., 1996. Evolutionary dynamics of predator–prey systems: An ecological perspective. *J. Math. Biol.* 34, 556–578.
- Matessi, C., Di Pasquale, C., 1996. Long-term evolution of multilocus traits. *J. Math. Biol.* 34, 613–653.
- Matsuda, H., Abrams, P.A., 1994. Timid consumers: self-extinction due to adaptive change in foraging and anti-predator effort. *Theor. Popul. Biol.* 45, 76–91.
- Maynard Smith, J., 1976. Evolution and the theory of games. *Amer. Sci.* 64, 41–45.
- Meszéna, G., Kisdi, É., Dieckmann, U., Geritz, S.A.H., Metz, J.A.J., 2001. Evolutionary optimisation models and matrix games in the unified perspective of adaptive dynamics. *Selection* 2 193–210.
- Metz, J.A.J., Geritz, S.A.H., Meszéna, G., Jacobs, F.J.A., van Heerwaarden, J.S., 1996. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In: van Strien, S.J., Verduyn Lunel, S.M. (Eds.), *Stochastic and spatial structures of dynamical systems*. North-Holland, Amsterdam, pp. 183–231.
- Metz, J.A.J., 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., Geritz, S.A.H., 1992. How should we define “fitness” for general ecological scenarios? *Trends Ecol. Evol.* 7, 198–202.
- Motro, U., 1982a. Optimal rates of dispersal. I. haploid populations. *Theor. Popul. Biol.* 21, 394–411.
- Motro, U., 1982b. Optimal rates of dispersal. II. diploid populations. *Theor. Popul. Biol.* 21, 412–429.
- Motro, U., 1983. Optimal rates of dispersal. III. parent offspring conflict. *Theor. Popul. Biol.* 23, 159–168.
- Nowak, M.A., Sigmund, K., 1998a. The dynamics of indirect reciprocity. *J. Theoret. Biol.* 194, 561–574.
- Nowak, M.A., Sigmund, K., 1998b. Evolution of indirect reciprocity by image scoring. *Nature* 393, 573–577.
- Nowak, M.A., Sigmund, K., 2005. Evolution of indirect reciprocity. *Nature* 437, 1291–1298.
- Nurmi, T., Parvinen, K., 2011. Joint evolution of specialization and dispersal in structured metapopulations. *J. Theoret. Biol.* 275, 78–92.
- Ohtsuki, H., Iwasa, Y., 2006. The leading eight: Social norms that can maintain cooperation by indirect reciprocity. *J. Theoret. Biol.* 239, 435–444.
- Parvinen, K., 1999. Evolution of migration in a metapopulation. *Bull. Math. Biol.* 61, 531–550.
- Parvinen, K., 2002. Evolutionary branching of dispersal strategies in structured metapopulations. *J. Math. Biol.* 45, 106–124.
- Parvinen, K., 2005. Evolutionary suicide. *Acta Biotheoretica* 53, 241–264.
- Parvinen, K., 2006. Evolution of dispersal in a structured metapopulation model in discrete time. *Bull. Math. Biol.* 68, 655–678.
- Parvinen, K., 2010. Adaptive dynamics of cooperation may prevent the coexistence of defectors and cooperators and even cause extinction. *Proc. R. Soc. Lond. B* 277, 2493–2501.
- Parvinen, K., 2011. Adaptive dynamics of altruistic cooperation in a metapopulation: Evolutionary emergence of cooperators and defectors or evolutionary suicide? *Bull. Math. Biol.* 73, 2605–2626.
- Parvinen, K., Dieckmann, U., Gyllenberg, M., Metz, J.A.J., 2003. Evolution of dispersal in metapopulations with local density dependence and demographic stochasticity. *J. Evol. Biol.* 16, 143–153.
- Parvinen, K., Metz, J.A.J., 2008. A novel fitness proxy in structured locally finite metapopulations with diploid genetics, with an application to dispersal evolution. *Theor. Popul. Biol.* 73, 517–528.
- Parvinen, K., Seppänen, A., Nagy, J.D., 2012. Evolution of complex density-dependent dispersal strategies. *Bull. Math. Biol.* 74, 2622–2649.
- Pfeiffer, T., Bonhoeffer, S., 2003. An evolutionary scenario for the transition to undifferentiated multicellularity. *Proc. Natl. Acad. Sci. USA* 100, 1095–1098.
- Rankin, D.J., López-Sepulcre, A., 2005. Can adaptation lead to extinction? *Oikos* 111, 616–619.
- Ronce, O., Perret, F., Olivieri, I., 2000. Evolutionarily stable dispersal rates do not always increase with local extinction rates. *Am. Nat.* 155, 485–496.
- Sugden, R., 1986. The evolution of rights, co-operation and welfare. Oxford, Blackwell.
- Trivers, R., 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.* 46, 35–57.
- Webb, C., 2003. A complete classification of Darwinian extinction in ecological interactions. *Am. Nat.* 161, 181–205.