

# DENSITY-DEPENDENT COOPERATION AS A MECHANISM FOR PERSISTENCE AND COEXISTENCE

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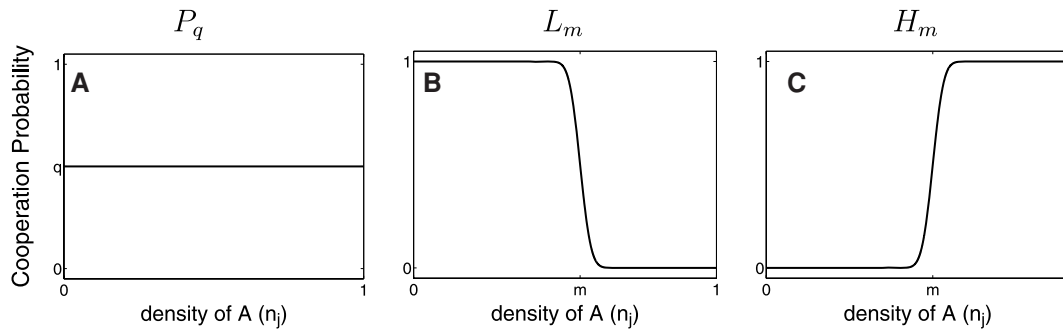
To overcome stress, such as resource limitation, an organism often needs to successfully mediate competition with other members of its own species. This may favor the evolution of defective traits that are harmful to the species population as a whole, and that may lead to its dilution or even to its extinction (the tragedy of the commons). Here, we show that this phenomenon can be circumvented by cooperation plasticity, in which an individual decides, based on environmental conditions, whether to cooperate or to defect. Specifically, we analyze the evolution of density-dependent cooperation. In our model, the population is spatially subdivided, periodically remixed, and comprises several species. We find that evolution pushes individuals to be more cooperative when their own species is at lower densities, and we show that not only could this cooperation prevent the tragedy of the commons, but it could also facilitate coexistence between many species that compete for the same resource.

**KEY WORDS:** Adaptive dynamics, coexistence, cooperation plasticity, tragedy of the commons.

A great challenge in ecology is to explain the enormous levels of heterogeneity and biodiversity sometimes exhibited in real systems, which stands in stark contrast to the naive view suggested by many models that predict relatively homogeneous ecosystems dominated by only a few species (Levin, 1999; Begon et al., 2006). One scenario that suppresses diversity and promotes extinction is competitive exclusion, in which the competition of several species over a single resource often results in the exclusion of the weaker species (Tilman, 1982). Another scenario is the “tragedy of the commons” (TOC), in which intraspecific competition induces the evolution of defective traits that eventually result in the extinction of the entire species (Hardin, 1968; Levin, 1999; Rankin et al., 2007). For instance, some micro-organisms cooperatively produce and secrete molecules that benefit the neighboring population (common good) but at a metabolic cost to the individual (Greig and Travisano, 2004; West et al., 2007; Kümmerli et al., 2009; Ross-Gillespie et al., 2009). Defectors that do not engage in the same activity for the common still enjoy its benefits without paying any cost, thereby conferring upon them a selective

advantage that allows them to take over the population. Eventually, the common good is no longer available, and the species is prone to extinction.

Mechanisms that may prevent competitive exclusion include: a temporally or spatially changing environment (niche differentiation) (Hutchinson, 1961; Harper, 1977); competition for multiple resources (Tilman, 1982, 1986); trade-off between competition and colonization abilities (Tilman, 1994); and others (Tilman, 1982; Begon et al., 2006). To prevent the TOC, a mechanism that allows cooperation to persist is needed. A basic feature of such mechanisms is positive relatedness: cooperators interact more frequently with other cooperators than with defectors, which results in an average higher benefit for cooperators (Hamilton, 1964; Wilson, 1975; Frank, 1998; Nowak, 2006; West et al., 2006). These mechanisms can be mediated by, for instance: kin discrimination (Griffin and West, 2003; West et al., 2006); social reciprocity (Trivers, 1971; Axelrod, 1984; Wilkinson, 1984; Milinski, 1987; Nowak, 2006); and limited dispersal (Wilson et al., 1992; Taylor, 1992; Nowak and Sigmund, 1992). Alternatively,



**Figure 1.** The possible strategies.  $P_q$  individuals cooperate with probability  $q$ , irrespective of the density;  $L_m$  ( $H_m$ ) individuals tend to cooperate if the density of  $A$  in the patch ( $n_j$ ) is below (above) the switching density  $m$ , and to defect otherwise.

cooperation may persist even if the common good serves the entire patch/group population equally, provided that the population is spatially subdivided into several patches, each of which is periodically seeded by several individuals (Wilson, 1975; Hauert et al., 2002; Nowak, 2006; Ackermann et al., 2008; Chuang et al., 2009). As such, each individual interacts more with its own relatives, which yields positive relatedness.

Still, the proposed effect does not guarantee the persistence of cooperation, and the conditions for avoiding the TOC are restrictive. Nevertheless, some experiments suggest that cooperative behavior may be tuned in response to the environment (cooperation plasticity). Specifically, switching to cooperation at lower densities has been recently observed in various systems and mechanisms: secretion of common good (Kümmerli et al., 2009); allelopathy restraint in bacteria (Buchman et al., 1988; de Ruyter et al., 1996; Kleerebezem et al., 1997; Riley and Wertz, 2002; Kleerebezem, 2004); competitive restraint in small mammals (Van Zegeren, 1979; Kalinin and Shchipanov, 2003; Shilova and Orlenev, 2004); and restraint of intraspecific brood parasitism in birds (Lyon and Eadie, 2008).

In this work, we theoretically examine the evolution of density-dependent cooperation in a subdivided population model in which the population is spatially segregated and periodically remixed. We find that individuals that switch to cooperation at low densities and to defection at high densities are selectively favored. Particularly, a population of such individuals is evolutionarily stable and is not invaded by obligatory defectors. Motivated by these results, we ask what is the evolutionarily favored switching density (or densities), and whether this density-dependent behavior enhances the sustainability of species in general, thereby enabling them to avoid, in particular, the TOC and/or competitive exclusion.

## The Subdivided Population Model

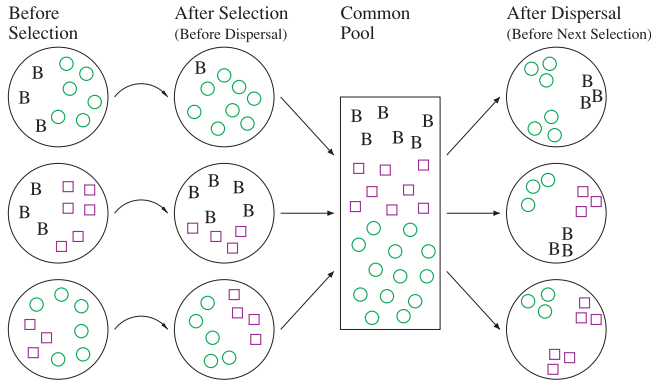
We consider a species  $A$  that is spatially subdivided into several identical patches, each of which can potentially support up to

$K$  individuals, but the actual number of  $A$  individuals may be smaller. The “density” of  $A$  in patch  $j$ ,  $n_j$ , is the number of  $A$  individuals in the patch divided by  $K$  ( $0 \leq n_j \leq 1$ ; Table 1). Each  $A$  individual may cooperate to benefit all  $A$  patch members, but that cooperation comes at an individual cost. Alternatively, that individual can defect and enjoy the benefits yielded by the cooperative  $A$  individuals but without paying the cost.

Cooperators and defectors may be obligatory and always behave the same. In addition, we allow for: (1) “probabilistic cooperators,”  $P_q$  ( $0 \leq q \leq 1$ ), which cooperate with a probability  $q$ , irrespective of the density<sup>1</sup> (Fig. 1A) (Doebeli et al., 2004; Rankin, 2007; Ackermann et al., 2008]; (2) “low-density (LD) cooperators,”  $L_m$  ( $0 \leq m \leq 1$ ), which tend to cooperate in patch  $j$  if  $n_j < m$  and to defect otherwise (Fig. 1B); and (3) “high-density cooperators,”  $H_m$ , which tend to cooperate if  $n_j > m$  and to defect otherwise (Fig. 1C). Specifically, we assume that the probability that  $L_m$  or  $H_m$  cooperate is given by a sigmoidal curve (error function) of  $n_j$  with a threshold (switching density) at  $n_j = m$ , and a small variance,  $\sigma \ll 1$ .

The evolutionary dynamics comprises sequential cycles, each of which includes a selection stage followed by a dispersal stage (Fig. 2). In the selection stage, deterministic selection takes place in each patch separately. Whenever both cooperators and defectors are present in a patch, defectors increase their ratio compared to cooperators. However, cooperation may be maintained if  $A$  populations in cooperator-rich patches grow faster than  $A$  populations in cooperator-poor patches (Simpson’s paradox (Chuang et al., 2009)). To incorporate this effect into our model, we assume a competitor species  $B$  such that each patch is occupied by  $K$  individuals, either  $A$  or  $B$ , and the growth rate of each subpopulation in patch  $j$  is determined by its relative fitness in the patch

<sup>1</sup>Alternatively,  $P_q$  can be regarded as deterministically investing  $q$  in cooperation and  $1 - q$  in defection.



**Figure 2.** The dynamics of a single cycle is illustrated for three patches and three subpopulations (B; □; ○). Each large circle represents a patch. The aggregation of the population within a patch is meaningless. In the selection stage, deterministic selection takes place in each patch separately. (○ have a higher tendency to cooperate than □). In the dispersal stage, all individuals from all patches assemble in a common pool, and then  $M = 3$  individuals are chosen randomly to seed each patch. Each seeder then establishes its own clade. Note that  $K = 9$  and three patches and subpopulations were chosen for clarity, but in the simulations we consider much larger numbers.

(replicator dynamics) (Maynard-Smith, 1982; Hofbauer and Sigmund, 1998):

$$\frac{dX_j}{dt} = X_j s (F_{x,j} - \Phi_j), \quad (1)$$

where  $X_j$  is the subpopulation's density in the patch (the subpopulation may be  $P_q/L_m/H_m/B$ ; we treat the densities as continuous variables),  $s$  is the selection strength,  $F_{x,j}$  is the fitness of an individual belonging to the subpopulation, and  $\Phi_j$  is the average fitness of all individuals in the patch.

$B$  individuals are not affected by the cooperation of  $A$ , and therefore their fitness is given by a constant,  $F_B > 0$ . The fitness of  $A$  individuals that cooperate and defect in patch  $j$  are given by

$$\begin{aligned} F_{c,j} &= b\tilde{C}_j - c, \\ F_{d,j} &= b\tilde{C}_j, \end{aligned}$$

respectively, where the constants  $b$  and  $c$  are the induced benefit and the paid cost, respectively, as mediated by the cooperators (this is a manifestation of the infinite-players prisoner's dilemma).  $\tilde{C}_j$  is the fraction of  $A$  individuals that cooperate among all  $A$  individuals in patch  $j$ , which is determined by the composition of the population in the patch, and therefore, may vary over time. It follows that if all  $A$  patch members cooperate, then their fitness is  $b - c$ , and if they all defect, then their fitness is 0. The fitness of a  $P_q$  individual is  $b\tilde{C}_j - qc$ , and the fitness of an LD or high-density cooperator is either  $F_{c,j}$  or  $F_{d,j}$ , in accordance with its actual behavior, which may change along the selection stage. The dura-

tion of the selection stage is normalized to one in dimensionless units.<sup>2</sup>

During the dispersal stage, the populations of different patches mix as follows (Wilson, 1975; Griffin et al., 2004; Ackermann et al., 2008). First, the patches are deserted, and the dispersed individuals assemble in a common pool. In the common pool,  $A$  individuals are subject to random rare mutations that slightly tune their strategy. In addition, we do not allow for extinction of species  $B$ , so we enforce a small lower bound  $\epsilon_B \ll 1$  on the  $B$  population abundance in the pool.<sup>3</sup> Next, each patch is recolonized by being seeded with  $M$  randomly chosen individuals from the common pool ( $M \ll K$ ). Each seeder then establishes a clade of  $K/M$  clones. Consequently, a patch may contain up to  $M$  subpopulations that differ from one another based on their respective cooperative strategies.

## Low-Density Cooperation Prevents Extinction

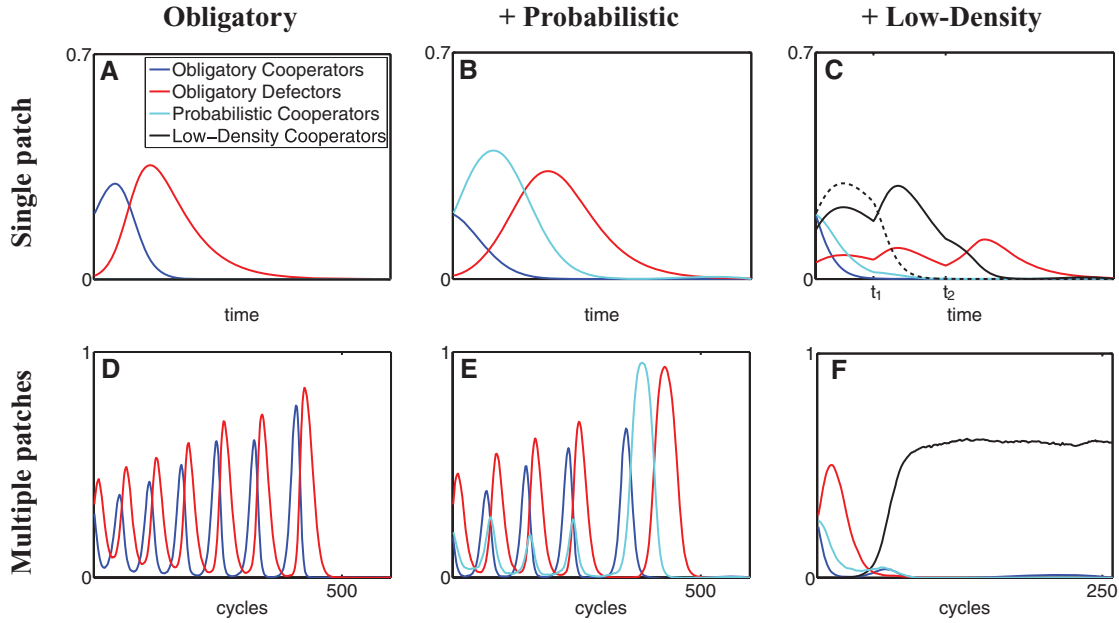
In a single patch without dispersal, the dynamics simply follows the replicator equation (1). Because defectors enjoy the benefit without paying any cost, their fitness is never smaller than the fitness of any other  $A$  individual, and as a result, they take over the  $A$  population. Then their fitness becomes zero, which is lower than  $F_B$ , and they lose to  $B$  individuals and become extinct (TOC; Fig. 3A–C).

In a subdivided population of obligatory cooperators and defectors, numerical simulations show that defectors may still proliferate on the account of cooperators, which in turn results in the decreased “relative abundance” of  $A$  (relative proportion of  $A$ , sampled in the common pool). This time, however, cooperators may recover due to Simpson's effect, which results in population cycles whose dominant types are first cooperators, then defectors, then  $B$  individuals, then again cooperators, etc. (Fig. 3D). However, the cycles are amplified, until eventually one species does not seed any patch. Because  $B$  cannot become extinct, and because cooperators can mutate and become defectors, the process eventually ends with the extinction of cooperators, which in turn leads to the extinction of species  $A$  (still TOC; Figs. 3D and S1).

This dynamics is not altered much in the presence of probabilistic cooperators (Fig. 3E) or of high-density cooperators (not shown). In contrast, the existence of LD cooperators may indeed prevent the TOC in a subdivided population. Certain LD cooperators are able to outcompete both obligatory cooperators and

<sup>2</sup>A duration of  $T$  is normalized to one by the transformation  $s \rightarrow s \times T$ . Therefore, the selection strength  $s$  indicates the magnitude of the coupling between patches, where a small  $s$  corresponds to strong coupling and vice versa.

<sup>3</sup>The lower bound is justified as  $B$  may represent any competitor species, and such always exists.



**Figure 3.** Low-density cooperation prevents extinction. Single-patch (top row): Time evolution of the subpopulations’ densities are plotted for different sets of strategies (solution of eq. (1), no dispersal is considered). (A) We assume only obligatory cooperators and defectors. The defectors outcompete the cooperators and then become extinct (the tragedy of the commons). (B) We introduce probabilistic cooperators that cooperate half of the time ( $P_{1/2}$ ). The obligatory defectors still outcompete the others and become extinct. (C) We simultaneously introduce two types of low-density cooperators that cooperate if and only if the species density in the patch is below  $1/2$  ( $L_{1/2}$ ; dashed black line) or  $1/6$  ( $L_{1/6}$ ; solid black line). They initially defect, but resort to cooperation at  $t_1$  ( $L_{1/2}$ ) or at  $t_2$  ( $L_{1/6}$ ). The species is still extinction prone. Parameters:  $x$ -axis  $\in [0, 25/s]$ ,  $b = 2$ ,  $c = 1$ ,  $F_B = 0.4$ ; (c)  $\sigma = 0$ . Multiple patches (bottom row): Time evolution of the relative abundances of the subpopulations at the common pool is demonstrated. (D) Only obligatory cooperators and defectors are present. Cyclic dynamics of the subpopulations eventually ends with the extinction of the species. (E) Probabilistic cooperators ( $P_{1/2}$ ) are introduced, but the species is still extinction prone. (F) Low-density cooperators ( $L_{1/2}$ ) are introduced. They invade and persist at a constant density. Obligatory defectors are quickly eliminated in the presence of  $L_{1/2}$ , and therefore, the species is no longer extinction prone (the tragedy of the commons is prevented). Parameters:  $b = 2$ ,  $c = 1$ ,  $F_B = 0.4$ ,  $M = 3 \cdot 10^4$  patches,  $s = 0.5$ , mutations between  $A$  subpopulations occur with probability  $10^{-6}$ ,  $\epsilon_B = 10^{-4}$ ; (f)  $\sigma = 0$ .

defectors and stably coexist with  $B$  individuals. A steady state with approximately constant relative abundance of LD cooperators is obtained. This steady-state population is immunized against invasion by obligatory defectors (Figs. 3F and S2).

This phenomenon can be explained by two major mechanisms that favor LD cooperators in our model. First, cooperation is needed to compete with species  $B$ . At high densities of species  $A$ , species  $B$  is almost absent, and therefore, cooperation is associated with almost no gain. Specifically, it follows from (1) that the average per-capita growth rate of  $A$  at patch  $j$  is given by<sup>4</sup>

$$\frac{1}{n_j} \frac{dn_j}{dt} = s(1 - n_j) [(b - c)\tilde{c}_j - F_B].$$

At high densities, this growth rate is less sensitive to cooperation. For example, if initially  $n_j = 1$ , then it is kept unchanged along

<sup>4</sup>  $\frac{1}{n_j} \frac{dn_j}{dt} = s\tilde{c}_j [b\tilde{c}_j - c - \Phi_j] + s(1 - \tilde{c}_j) [b\tilde{c}_j - \Phi_j] = s[(b - c)\tilde{c}_j - \Phi_j]$ , where  $\Phi_j = n_j [\tilde{c}_j (b\tilde{c}_j - c) + (1 - \tilde{c}_j)b\tilde{c}_j] + (1 - n_j)F_B = n_j [(b - c)\tilde{c}_j] + (1 - n_j)F_B$ .

the selection stage, irrespective of the cooperators’ proportion. In this case, the number of cooperators can only decrease due to the presence of defectors. Therefore, it is always worthwhile to defect at  $n_j = 1$ . However, if  $n_j$  is small, then the growth of  $A$  can potentially compensate for the reduced proportion of cooperators within the  $A$  population. In other words, Simpson’s paradox is stronger at lower densities.

Second, lower density is correlated with higher relatedness, that is, lower density may indicate that a larger fraction of the  $A$  population in the patch has originated from the same seeder. For example, at the beginning of each selection stage, each clade fills  $1/M$  of the patch, and therefore, the number of  $A$  seeders in patch  $j$  is given by  $Mn_j$ . Thus,  $n_j = 1/M$  at the beginning of a selection stage implies that only one  $A$  seeder seeded patch  $j$ , and it is worthwhile to cooperate because only its clade members stand to benefit. Nevertheless,  $n_j = 1$  implies that  $M$  different  $A$  seeders seeded the patch, and therefore, the benefit induced by a cooperator on its own clade is lower (see section “Dominance of the Monomorphic LD Cooperators”

**Table 1. Summary of notations.**

Symbol	Definition
TOC	Tragedy of the commons.
LD	Low-density.
$A$	A species of facultatively cooperative individuals.
$n_j$	The density of $A$ individuals in patch $j$ .
$P_q$	The strategy that determines cooperation with probability $q$ (Fig. 1A).
$L_m (H_m)$	The strategy that determines tendency to cooperate if the density of $A$ in the patch is below (above) a threshold $m$ and to defect otherwise (Fig. 1B,C).
$\sigma$	The variance in the behavior of $L_m$ and $H_m$ .
$B$	A competitor species.
$s$	Selection strength.
$F_B$	The fitness of $B$ .
$b, c$	Induced benefit and paid cost by cooperative individuals, respectively.
$\tilde{C}_j$	The fraction of $A$ individuals that cooperate among all $A$ individuals in patch $j$ .
$\epsilon_B$	Lower bound on the fraction of $B$ population in the common pool.
$M$	The number of patch seeders.
relative abundance	The relative proportion of the subpopulations in the common pool.
$m_c$	The convergence stable switching density.
$ \rho^* $	The steady-state relative abundance of the entire $A$ species.
$A_k$	The $k$ th species in the multiple species model.
$\delta$	The difference in base fitness of consecutive species in the multiple species model.
$N_s$	The number of coexisting species.
$ \rho_k^* $	The steady-state relative abundance of the entire $A_k$ species.

Population at Extremely Weak Selection” for a more detailed analysis).

### Emergence of Polymorphic Populations of LD Cooperators

To find which switching density ( $m$ ) is evolutionarily favored, we consider long-term evolution and allow different LD cooperators for all values of  $0 \leq m \leq 1$ , as well as high-density and probabilistic cooperators for all values of  $0 \leq m \leq 1$  or  $0 \leq q \leq 1$ , respectively. We consider infinitely many patches, which results in deterministic dynamics (Tilman, 1994; Nowak and May, 1994; Geritz et al., 1999; Ackermann et al., 2008). This is implemented by considering a discrete set of possible  $m$  and  $q$  values (e.g.,  $m = \Delta m, 2\Delta m, 3\Delta m, \dots$ ), and simulating the replicator dynamics many times, where every possible initial patch-realization is

substituted, in turn, as the initial condition<sup>5</sup>. To obtain the relative abundance of each subpopulation in the common pool at the  $(T + 1)$ th cycle, each realization is weighted by its occurrence probability/frequency, based on the relative abundance at the  $(T)$ th cycle.

These simulations show that, in time, the relative abundances of all subpopulations reach a steady state in which only LD cooperators coexist with  $B$  individuals, whereas high-density and probabilistic cooperators become extinct. For small selection strengths, one LD subpopulation dominates, namely that with a switching density  $m = m_c$ , together with some others with  $m \approx m_c$  that appear due to mutational load (monomorphic population; Fig. 4A,B). However, as the selection strength surpasses a certain threshold, the steady-state population becomes polymorphic and comprises several subpopulations with strictly different switching densities (Fig. 4C,D). The steady-state relative abundance of the entire  $A$  species monotonically decreases from almost one ( $A$  solely dominates) at  $F_B = 0$  to zero ( $A$  vanishes) at  $F_B = b - c$  (Fig. 5).

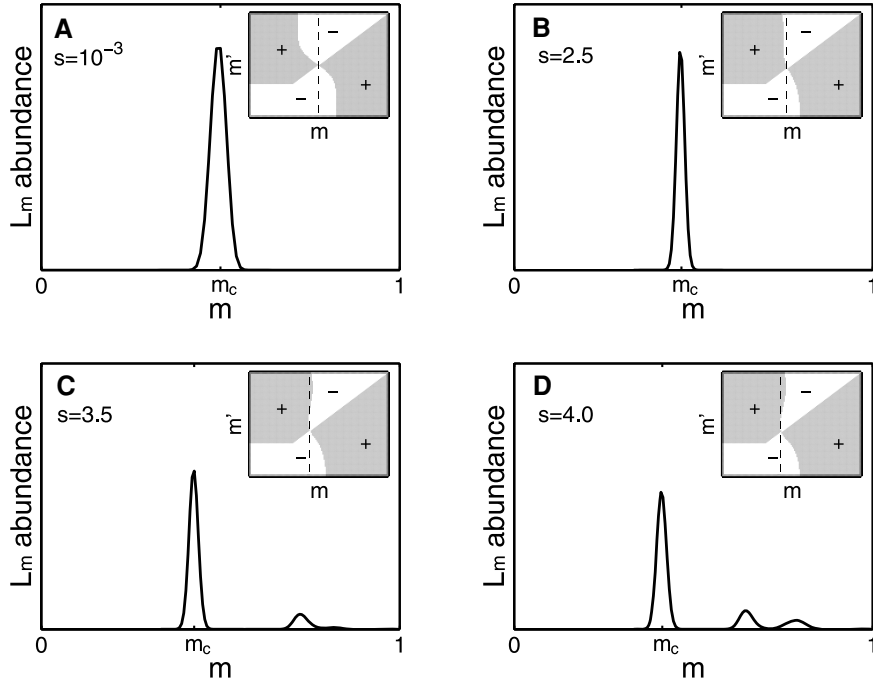
### Adaptive Dynamics Analysis

#### DOMINANCE OF A MONOMORPHIC LD COOPERATORS' POPULATION AT EXTREMELY WEAK SELECTION

To gain quantitative insight, we first consider the limit where the distribution within each patch hardly changes during a single selection stage ( $s \rightarrow 0$  or  $s \ll 1/b$ ). Generally, to sustain, cooperators have to interact among themselves more than with defectors, that is, they need a positive average relatedness (Frank, 1998). Because patches are randomly seeded by the dispersed individuals, there is no positive average relatedness among the  $M$  different seeders of each patch. The only source of positive average relatedness at  $s \rightarrow 0$  is therefore ascribed to the fact that each clade fills  $1/M$  of the patch (Ackermann et al., 2008). (The dynamics is therefore analogous to an  $M$ -players hawk–dove game in a well-mixed population.) Therefore, it is selectively advantageous to cooperate if and only if such cooperation directly increases the relative fitness of the clade. Cooperation of the clade members of subpopulation  $x$  in patch  $j$  increases  $\tilde{C}_j$  by

$$\Delta \tilde{C}_j = \frac{1}{n_j M},$$

<sup>5</sup>Each possible choice of  $M$  strategies generates a possible patch configuration in which each strategy initially occupies  $1/M$  of the patch. The number of possible strategies,  $L_s$ , is determined by the resolution mediated by the discretization. We are interested in the case  $\Delta m \ll 1$ , for which  $L_s \gg 1$  and the number of required replicator dynamics simulations can be approximated by  $L_s^M$ .



**Figure 4.** The transition from monomorphic to polymorphic populations of low-density cooperators. The steady-state relative abundance distribution of low-density cooperators bifurcates from one peak into several peaks as  $s$  increases. (A,B) For small values of  $s$ , the evolutionarily stable strategy is  $L_{m_c}$ : cooperate if and only if the density of the species in the patch is below  $m_c$ . (C,D) For larger values of  $s$ , the steady-state population becomes polymorphic and comprises several subpopulations with strictly different switching densities. Note that in all cases, both obligatory cooperators ( $L_1$ ) and obligatory defectors ( $L_0$ ) are eliminated. The insets depict the pairwise invasibility plots: gray (white) regions denote that an  $L_{m'}$  mutant has a selective advantage (disadvantage) over the  $L_m$  wild-type in a resident population of  $L_m$  individuals. The convergence-stable switching density,  $m_c$ , appears at the intersection of the two gray and two white regions: an initially monomorphic population that adopts any  $L_m$  strategy is expected to gradually evolve toward the  $L_{m_c}$  strategy. In (A,B), the vertical line across  $m_c$  (dashed line in the inset) is in the white region, which implies that  $L_{m_c}$  is an evolutionarily stable strategy, whereas in (C,D) the line crosses a gray segment, which implies that  $L_{m_c}$  loses stability, and the population splits and becomes polymorphic. Parameters:  $M = 3, b = 2, c = 1, F_B = 0.4, \sigma = 0.05, \epsilon_B \rightarrow 0$ .

and therefore, the change in the fitness of the clade members due to their own cooperation is given by

$$\Delta F_{x,j} = b\Delta\tilde{C}_j - c = \frac{b}{n_j M} - c,$$

whereas  $\Phi_j$  increases by

$$\Delta\Phi_j = b\Delta\tilde{C}_j n_j - \frac{c}{M} = \frac{b-c}{M}.$$

Cooperation is beneficial to the clade as long as  $\Delta F_{x,j} > \Delta\Phi_j$ , which implies

$$n_j < \frac{b/c}{b/c + M - 1}.$$

When  $s \rightarrow 0$ ,  $Mn_j$  indicates the number of  $A$  seeders in patch  $j$ , which is an integer, and therefore two strategies  $L_{m_1}$  and  $L_{m_2}$  for which  $Mm_1$  has the same integer part as  $Mm_2$  ( $\lfloor Mm_1 \rfloor = \lfloor Mm_2 \rfloor$ ) can be distinguished only due to positive values of  $s, \sigma$ , and mutation rate. Therefore, the selectively favored strategy,  $m_c$ ,

satisfies

$$\frac{\lfloor Mm_0 \rfloor}{M} \leq m_c \leq \frac{\lfloor Mm_0 \rfloor}{M} + \frac{1}{M},$$

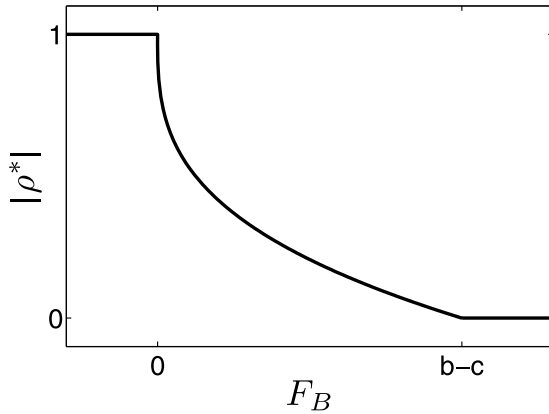
where

$$m_0 = \frac{b/c}{b/c + M - 1},$$

and the actual value of  $m_c$  is determined by the values of  $s$  and  $\sigma$ . In our simulations, we consider  $\sigma = 0.05$ , which removes the degeneracy (Fig. 4A). The result of this Section is demonstrated in Appendix S2 for  $M = 3$ . Note that  $m_0$  is independent of  $F_B$ , but that the steady-state relative abundance of the entire  $A$  species decreases as  $F_B$  increases (Fig. 5; see Appendix S3 for the derivation).

#### FROM MONOMORPHIC TO POLYMORPHIC POPULATION AT STRONGER SELECTION

To analyze the evolution of LD cooperators for larger values of  $s$ , we numerically follow the guidelines of adaptive dynamics



**Figure 5.** The steady-state relative abundance of the entire  $A$  species,  $|\rho^*|$ , decreases as the fitness of the competitor species,  $F_B$ , increases. Parameters:  $s \rightarrow 0$ ,  $M = 5$ ,  $b = 2$ ,  $c = 1$ .

analysis (insets of Fig. 4) (Geritz et al., 1998). Assume that, initially, all  $A$  individuals are LD cooperators with the same switching density  $m$ , and that the fixation rate of mutations is much higher than the mutation rate itself, so that the monomorphic  $L_m$  population reaches a fixed relative abundance,  $\Gamma(m)$ , which is determined by its competition with  $B$ . A mutant  $L_{m'}$  is said to invade the resident  $L_m$  population if and only if a rare  $L_{m'}$  subpopulation in the common pool increases in size in the consecutive cycle. Equivalently,  $L_{m'}$  invades if and only if the average contribution of an  $L_{m'}$  seeder to the common pool is larger than the average contribution of an  $L_m$  seeder, provided that no more than one  $L_{m'}$  individual seeds the same patch (Geritz et al., 1999; Ackermann et al., 2008). If an  $L_{m'}$  mutant with  $m' \approx m$  invades, then the population becomes a monomorphic  $L_{m'}$  population (Dieckmann and Law, 1996; Geritz et al., 1998).

In our model, if  $m$  is large ( $m \lesssim 1$ ), then the resident  $L_m$  population is abundant and  $B$  individuals are scarce ( $\Gamma(m) \lesssim 1$ ), and hence, defection is selectively advantageous and only mutants with switching density  $m' < m$  may invade. However, if  $m$  is small ( $m \gtrsim 1/M$ )<sup>6</sup>, then the resident  $L_m$  population abundance is close to zero ( $\Gamma(m) \gtrsim 0$ ), and hence, a mutant seeder has a high probability to be the only  $A$  seeder in the patch and cooperation is advantageous because it is most likely to take place among kins originating from the same seeder. Therefore, if  $m$  is small then only mutants with a switching density  $m' > m$  may invade. Consequently, there is a unique value of  $m$ , denoted by  $m_c$ , toward which a monomorphic population approaches (see insets of Fig. 4;  $L_{m_c}$  is the convergence stable strategy (Eshel, 1996; Geritz et al., 1998)).

We have seen that for  $s \rightarrow 0$ ,  $m_c \approx (bc)/(bc + M - 1)$ . In the other extreme, where  $s \rightarrow \infty$ , the population in each

<sup>6</sup>A monomorphic  $L_m$  population with  $m \leq 1/M$  is prone to extinction ( $\Gamma(m) = 0$  if  $m \leq 1/M$ ).

patch fixates during every selection stage. By the end of selection stage, a clade that is seeded by a rare  $L_{m'}$  mutant with  $m' < m$  fills a fraction  $m'$  of the entire patch population, irrespective of the composition of the other seeders. Therefore, a mutant seeder results, on average, in  $Mm'$  seeders in the next cycle. This means that  $L_{m'}$  invades  $L_m$  if and only if  $1/M < m' < m$ , which implies  $m_c \rightarrow 1/M$ .

What happens when  $m$  approaches  $m_c$  and all LD cooperators have a switching density at approximately  $m_c$ ? For sufficiently small  $s$ , the population does not lose stability to any mutant invader ( $L_{m_c}$  is an evolutionarily stable strategy). In this case,  $L_{m_c}$  individuals solely dominate (Fig. 4A,B). However, as  $s$  surpasses a certain threshold,  $L_{m'}$  individuals with some  $m'$  that is strictly larger than  $m_c$  are able to invade (insets of Fig. 4C,D; global instability). The reason is that  $m_c$  becomes small, and hence, so does the  $L_{m_c}$  population abundance. Therefore,  $L_{m'}$  mutants compete mostly against  $B$  individuals and are even likely to be the only  $A$  seeders in many patches. The invasion of  $m'$  results in the appearance of coexisting  $A$  subpopulations (Fig. 4C,D). This coexistence ensues because the  $L_{m_c}$  subpopulation is hardly affected by the invading subpopulations. For even higher values of  $s$ , additional splits may occur, thereby leading to the coexistence of more different subpopulations (Fig. 4D).

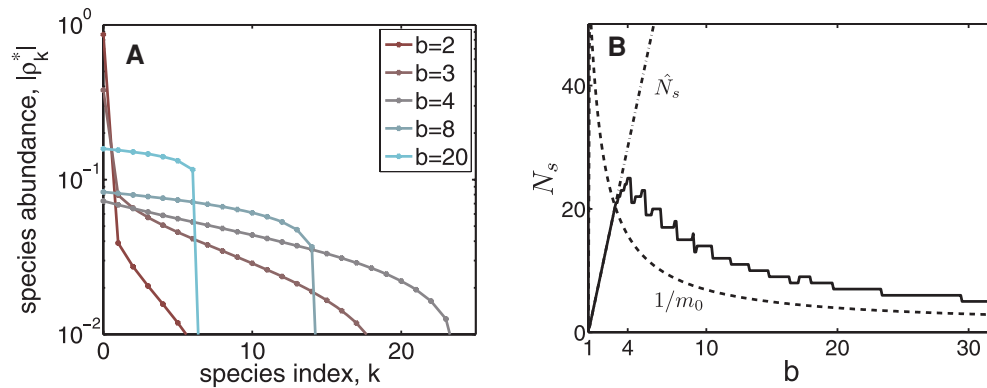
## Multiple Species and Coexistence

Up to now, we have seen that LD cooperators may stably coexist with a competitor species. Next, we examine the more general problem of several species, namely  $A_k$  ( $k = 0, 1, 2, \dots$ ), that compete for the same resource. We allow each species to evolve its own distribution of LD cooperative strategies. The dynamics follows exactly the same selection and dispersal stages as before, where the fitness is calculated based on the following considerations: (1) the fitness of each species is not affected by the cooperative behavior of the other species; (2) the values of the induced benefits,  $b$ , and of the paid costs,  $c$ , are the same for all species; and (3) for all  $k$ , the base fitness of species  $A_k$  surpasses that of species  $A_{k+1}$  by  $\delta$ . Consequently, the fitness of cooperative and defective  $A_k$  individuals in patch  $j$  are

$$\begin{aligned} F_{c,k,j} &= b\tilde{C}_{k,j} - c - k\delta, \\ F_{d,k,j} &= b\tilde{C}_{k,j} - k\delta, \end{aligned}$$

respectively, where  $\tilde{C}_{k,j}$  is the fraction of  $A_k$  individuals that cooperate among all  $A_k$  individuals in patch  $j$ , and the fitness of an LD cooperator is either  $F_{c,k,j}$  or  $F_{d,k,j}$ , in accordance with its actual behavior.

Consider the limit  $s \rightarrow 0$ , at which the evolutionarily stable strategy of all species is the same: each individual cooperates if



**Figure 6.** (A) The steady-state relative abundances of the species,  $|\rho_k^*|$ , and (B) the number of coexisting species,  $N_s$ , are demonstrated for various values of the induced benefit,  $b$ . For small values of  $b$ , the strongest species  $A_0$  constitutes most of the population. As  $b$  increases,  $|\rho_k^*|$  flattens and  $N_s$  increases until  $b = 4$ . As  $b$  further increases,  $N_s$  decreases while the species distribution remains nearly uniform. The dashed asymptotic lines in (B) correspond to  $\hat{N}_s$  and  $1/m_0$  (see text). Parameters:  $s \rightarrow 0, c = 1, M = 60, \sigma = 0.1$ .

and only if the density of its own species in the patch is below  $m_0 = (b/c)/(b/c + M - 1)$ , because this strategy maximizes the fitness of the clade, irrespective of the fitness of the competitors, as proven in the section “Dominance of the Monomorphic LD Cooperators’ Population at Extremely Weak Selection.” Therefore, at a steady state, the fitness of  $A_k$  individuals in patch  $j$  is

$$F_{A,k,j} = \begin{cases} b - c - k\delta & \text{if } n_{k,j} < m_0 \\ -k\delta & \text{otherwise,} \end{cases} \quad (2)$$

where  $n_{k,j}$  is the density of species  $A_k$  in patch  $j$ .

Numerical simulations for  $M = 60$  ( $m_0 \approx 0.03$ ) demonstrate two characteristic distributions of coexisting species (Fig 6A): at low values of  $b$ ,  $A_0$  constitutes most of the population, whereas at large values of  $b$ , the distribution is more uniform. The number of coexisting species,  $N_s$ , is maximized at intermediate values of  $b$  that appear at the intersection between these two distributions (Fig. 6B).

To gain insight into the mechanisms underlying this behavior, note that  $N_s$  is bounded from above by  $\hat{N}_s \equiv (b - c)/\delta$  (because  $A_{[\hat{N}_s]}$  individuals always have a fitness lower than that of  $A_0$  individuals). This upper bound is reachable at small values of  $b$ . However, the steady-state abundance of  $A_k$  ( $1 \leq k \leq N_s - 1$ ) cannot be much smaller than  $m_0$ , because in such a case, the species members tend to cooperate in most patches and consequently obtain a relatively high fitness (and the cooperation of  $A_k$  individuals directly affects only other  $A_k$  individuals). Therefore, as  $b$  surpasses a certain threshold where  $\hat{N}_s \approx 1/m_0$ , the distribution of the steady-state relative abundance of coexisting species becomes comparatively uniform. The interplay between the bounds  $\hat{N}_s$  and  $1/m_0$  also leads to the maximal  $N_s$  at intermediate values of  $b$  (Fig. 6B).

## Discussion

In this article, we first demonstrated that low-density cooperation can prevent the TOC: a subdivided population of obligatory cooperators and defectors is extinction prone in our model, whereas a subdivided population of individuals that cooperate only below a certain density of their own species (LD cooperators) persists at an approximately constant abundance, and is immune to invasion by obligatory defectors.

In addition, we performed a quantitative analysis to show that the steady-state population bifurcates from a monomorphic population, where all individuals have essentially the same switching density, to a polymorphic population, where two or more switching densities are present.

We considered a scenario in which the environmental stress is mediated by a competitor species, but the main results hold for other cases in which cooperation is essential for survival. Moreover, the effect of LD cooperation may be even stronger if the resource is subject to fluctuations. Assume that a good (resource rich) year is followed by a bad (resource poor) year. Without LD cooperators, obligatory defectors may easily take over the population in the good year only to become extinct in the bad year. LD cooperators, however, are able, in the good year, to endure together with the defectors, whom they outcompete in the following bad year.

One reason why LD cooperators are evolutionarily favored is because individuals are pushed to be more cooperative as the external stress becomes stronger. In our model, lower densities indicate that interspecific competition is more important than intraspecific competition, whereas high densities indicate that intraspecific competition is more important. This is also the reason why a density-dependent mechanism is needed, and it is inadequate to consider a resource-dependent mechanism that cannot distinguish between interspecific- and intraspecific-induced stress.

It would be interesting to further test experimentally the direct role of density versus the role of resource-abundance in determining cooperation at low densities in nature. This can be done either by tuning the density without affecting the per-capita available resource (Van Zegeren, 1979; Kalinin and Shchipanov, 2003; Kümmerli et al., 2009), or by detecting the microscopic (molecular) mechanism that triggers cooperation (Buchman et al., 1988; de Ruyter et al., 1996).

Other mechanisms that enhance density-dependent cooperation have been previously suggested, but whatever the mechanism, we expect LD cooperation to enhance species persistence. Examples for such mechanisms include: (1) avoid overexploitation of resources (Brown, 1999; Brown et al., 2002); (2) cooperation that is more efficient at certain densities (Brown and Johnstone, 2001; Velicer, 2003; Kleerebezem, 2004; MacLean and Gudelj, 2006; Greig and Travisano, 2004; Ross-Gillespie et al., 2009); and (3) resource-dependent cooperation, where resource is correlated with density (Dugatkin, 1997; Rankin, 2007; Knell, 2009). Mechanism (1) enhances high-density cooperation, whereas mechanisms (2) and (3) may enhance either high-density or LD cooperation.

Although these mechanisms mostly concern single species conflicts, in this study we explored the effects of interspecific competition on the social behavior within each species, and then we explored the reverse problem, namely the effect of intraspecific conflict on interspecific competition. We found stable coexistence among many species that exhibit LD cooperation, even though they all compete for the same, single resource. This may occur even when all species exhibit the same cooperative strategy. A possible interpretation of this outcome is that intraspecific competition plays the dynamical role of an internal resource. The manifestation of this resource corresponds to the cooperative mechanism. That cooperative mechanism could be, for example, the common good or the restraint of intraspecific agonistic behavior. Therefore, intraspecific cooperation may play an important role in the formation and maintenance of biodiversity.

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## Supporting Information

The following supporting information is available for this article:

**Appendix S1.** Dynamics of obligatory strategies at extremely weak selection.

**Appendix S2.** Demonstration of the evolutionarily stable switching density for  $M = 3$  at extremely weak selection.

**Appendix S3.** The steady-state relative abundance of the entire species at extremely weak selection.

**Figure S1.** The tragedy of the commons in sub-divided populations.

**Figure S2.** Persistence of low-density cooperators.

Supporting Information may be found in the online version of this article.

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