



# Cooperation can promote rescue or lead to evolutionary suicide during environmental change

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The adaptation of populations to changing conditions may be affected by interactions between individuals. For example, when cooperative interactions increase fecundity, they may allow populations to maintain high densities and thus keep track of moving environmental optima. Simultaneously, changes in population density alter the marginal benefits of cooperative investments, creating a feedback loop between population dynamics and the evolution of cooperation. Here we model how the evolution of cooperation interacts with adaptation to changing environments. We hypothesize that environmental change lowers population size and thus promotes the evolution of cooperation, and that this, in turn, helps the population keep up with the moving optimum. However, we find that the evolution of cooperation can have qualitatively different effects, depending on which fitness component is reduced by the costs of cooperation. If the costs decrease fecundity, cooperation indeed speeds adaptation by increasing population density; if, in contrast, the costs decrease viability, cooperation may instead slow adaptation by lowering the effective population size, leading to evolutionary suicide. Thus, cooperation can either promote or—counterintuitively—hinder adaptation to a changing environment. Finally, we show that our model can also be generalized to other social interactions by discussing the evolution of competition during environmental change.

**KEY WORDS:** Cooperation, environmental change, evolutionary rescue, evolutionary suicide, moving optimum, public goods.

Throughout evolutionary history, populations have experienced constantly changing environmental conditions. Examples of large-scale environmental changes with profound evolutionary legacies include the rise of atmospheric oxygen during the Proterozoic (Lyons and Reinhard 2014), continental movements like the emergence of the Isthmus of Panama during the Pliocene (Stehli and Webb 1985), and climatic alterations such as the Pleistocene glaciations (Hewitt 2004). In recent times, natural populations are increasingly facing anthropogenic directional environmental shifts, ranging from habitat degradation and climate change (reviewed in Gienapp et al. 2008; Sih et al. 2011; Hoffmann and Sgrò 2011) to exposure to increasing concentrations of antibiotics (Klein et al. 2018).

Because populations are often locally adapted (Hereford 2009), environmental changes may lead to decreased fitness and

to a decline in population size. Ultimately, this may lead to extinction, as the population's phenotype is unable to track the shifting environmental optimum. This fate may be prevented when genetic adaptation counters population decline and prevents extinction, a process called evolutionary rescue (Gomulkiewicz and Holt 1995; Bell 2017). The effects of environmental change (and ultimately the possibility of evolutionary rescue) will, in general, depend on within- and between-species biotic interactions (Tylanakis et al. 2008; Harmon et al. 2009; Lavergne et al. 2010; Collins 2011; Lawrence et al. 2012). Although most theoretical models of adaptation to changing environments ignore ecological interactions—reviews of theory by Alexander et al. (2014) and Bell (2017) barely discuss the subject, only very briefly mentioning competition—there is a growing body of modeling work on the effects on evolutionary rescue of ecological interactions,

both within and between species, such as competition (e.g., Johansson 2007; Osmond and De Mazancourt 2012) and predation (e.g., Jones 2008; Mellard et al. 2015; Osmond et al. 2017).

Here we focus on how adaptation to a changing environment is affected by a different type of interaction, cooperation. Because high levels of cooperation can increase population mean fitness, and therefore, population abundance (Hauert et al. 2006a; Chuang et al. 2009; Tekwa et al. 2017)—and larger populations are both less prone to extinction from demographic stochasticity and can adapt faster due to a larger mutational input and less genetic drift—we predict that cooperation can reduce the chance that a population will go extinct due to environmental change.

Following a well-established game-theoretical tradition (reviewed in Archetti and Scheuring 2012), we will model cooperative interactions as public goods games: events in which individuals pay a cost to contribute toward a public good. The benefit generated by this public good is then equally enjoyed by all interacting partners. Public goods interactions can describe many instances of cooperative behavior in nature (Levin 2014). For example, many microbes secrete extracellular molecules which can be used by nonproducers (West et al. 2006; Tarnita 2017); these include, for example, adhesive polymers in *Pseudomonas* (Rainey and Rainey 2003), invertase in yeast (Gore et al. 2009), and indole (a signaling molecule providing antibiotic resistance) in *Escherichia coli* (Lee et al. 2010). Similarly, in many costly or risky behaviors such as cooperative breeding (Rabenold 1984), cooperative hunting (Bednarz 1972; Packer et al. 1990; Yip et al. 2008), alarm calls against predators (Clutton-Brock et al. 1999), or the formation of fruiting bodies in social amoebae (Strassmann et al. 2000), benefits are equally distributed to all participants. Even cancer cells share costly diffusible products, such as growth factors (Axelrod et al. 2006; Archetti et al. 2015). Thus, public goods interactions are a useful general framework to model cooperation, applicable to a wide range of natural scenarios.

The public goods framework also permits a seamless articulation between evolutionary game dynamics and ecological or demographic dynamics (such as changes in population size, as might be caused by environmental shifts). Models that make this connection explicit (called “ecological public goods games,” Hauert et al. 2006a, 2008; Wakano et al. 2009; Parvinen 2010; Gokhale and Hauert 2016) are based on the feedback between population size and the fitness of cooperators. In these models, the marginal benefits of cooperation decrease with higher group sizes, meaning that cooperation is favored only when groups are small (Hauert et al. 2006a, this is sometimes called “weak altruism,” e.g., in Fletcher and Doebeli 2009). This is also true (or true under some conditions) in other models of cooperation (Cornforth et al. 2012; Shen et al. 2013; Powers and Lehmann 2017; Peña and Nöldeke 2018), and it matches at least some empirical observations: for example, the amount of time that meerkats

spend on guard decreases with group size (Clutton-Brock et al. 1999), and *Pseudomonas* “cheaters” that do not produce siderophores perform better at high cell densities (Ross-Gillespie et al. 2009). Therefore, if low population densities correspond to small interaction group sizes (e.g., Johnson 1983; Pépin and Gerard 2008; Blank et al. 2012; Vander Wal et al. 2013), they allow cooperation to gain a foothold. As cooperation increases, so does the population mean fitness, and, consequently, the population density. This feedback between ecology and evolution can lead to the maintenance of stable, intermediate frequencies of cooperators (Hauert et al. 2006a, 2008). Laboratory experiments in sucrose-growing yeast (Sanchez and Gore 2013; Chen et al. 2014; Harrington and Sanchez 2014) confirm the empirical relevance of these feedbacks between population density and the evolution of cooperation. Populations whose growth is mediated by cooperative production of invertase approach intermediate densities and frequencies of cooperators, consistent with ecological public goods dynamics (Sanchez and Gore 2013).

Binary-action public goods games describe bimorphic populations where individuals are either cooperators (who produce a fixed amount of public good) or defectors (nonproducers). For example, wild-type yeast cells produce invertase, whereas mutant “cheaters” do not (Gore et al. 2009). This is the approach used in most models of ecological public goods games (Hauert et al. 2006a, 2008; Wakano et al. 2009). However, in some systems it may be more appropriate to model cooperation as a quantitative trait. For instance, meerkat females can provide more or less assistance with babysitting and pup feeding (Clutton-Brock et al. 2001). In continuous public goods games (Killingback and Doebeli 2002; Doebeli et al. 2004; Molina and Earn 2017; Gylling and Brännström 2018) individuals are described by a continuous trait value that quantifies how much they invest into the public good. Parvinen (2010) showed that, if cooperation is modeled as a continuous trait, ecological public goods games can exhibit evolutionary branching—that is, the population can evolve into a highly cooperating and a noncooperating strain. In other words, the continuous public goods framework can also (depending on the parameters of the model) give rise to distinct cooperators and defectors, a process called “tragedy of the commune” by Doebeli et al. (2004) who first described it in the context of the continuous snowdrift game. In our model, we will use the continuous public goods game. As we will see, depending on the shape of the function that describes the costs of cooperation, we may observe a tragedy of the commune. If this happens, the model will resemble a binary-action public goods game, where cooperation evolves through changes in the relative frequencies of the two fixed strategies rather than a shift in the value of a quantitative trait (cf. Section S3.1, particularly equation S29). Thus, the same framework will allow us to investigate the interaction between cooperation and environmental change, both in those cases where

all individuals cooperate to a similar degree and in those cases where cooperators and defectors coexist.

Under directional environmental change, species keep track of the moving environmental optimum at a certain phenotypic distance or “lag” (Lynch and Lande 1993; Bürger and Lynch 1995). The size of the lag will depend on the speed of environmental change, as well as the population’s ability to adapt (Bürger and Lynch 1995; Lynch and Lande 1993). The lag reaches an equilibrium when the rate of environmental change equals the rate of adaptation, which, for mutation-limited evolution, is proportional to population size and mutation rate (Dieckmann and Law 1996). The larger the lag, the lower the size of the population. If the lag becomes too large, the population will get trapped in a vicious cycle: it will grow so small that it cannot adapt fast enough to keep up with the environmental optimum. The result is an extinction vortex (Gilpin and Soulé 1986; Fagan and Holmes 2006; Brook et al. 2008): an amplifying feedback that will ultimately lead the population to extinction (Johansson 2007); in the quantitative genetics literature, a similar cycle exists with genetic variance taking the place of population size (Bürger and Lynch 1995; Osmond and Klausmeier 2017). However, a population engaged in ecological public goods games could potentially break free from this vicious cycle, because the decline in population density would favor cooperation. This matches experimental evidence that, as environments deteriorate, public goods producers increase in frequency (Chen et al. 2014). Thus, our hypothesis is that environmental change favors the evolution of cooperation, and that this process may rescue a population that would otherwise have been unable to keep track with the optimum.

## Methods

### MODEL DESCRIPTION

#### Inheritance and life cycle

We model a population of individuals, each of which are characterized by a cooperation trait  $x > 0$  and a functional quantitative trait  $y$ . The multidimensional phenotype  $\vec{z} = (x, y)$  is assumed to be completely genetically determined. We assume clonal reproduction such that offspring inherit their parent’s phenotype exactly with probability  $(1 - \mu_x)(1 - \mu_y)$ ; with probability  $\mu_x$  a random normal deviate with standard deviation  $\sigma_x$  is added to the cooperative trait and with probability  $\mu_y$  a random normal deviate with standard deviation  $\sigma_y$  is added to the functional trait. If such a mutation would result in a negative value of  $x$ , the offspring’s cooperative trait is set to zero. We ignore genetic correlations between  $x$  and  $y$ .

Generations are nonoverlapping, that is, individuals are semelparous (they reproduce only once) and reproduce synchronously. Every generation, each individual survives to repro-

ductive age with a probability  $V$  (viability) that depends on the individual’s phenotype as well as the state of the environment (including both abiotic and biotic components). Should they survive, each gives birth to a Poisson number of offspring with an expectation  $F$  (fecundity) that is also dependent on the individual’s phenotype and the environment. Due to stochasticity in both survival and reproduction, the number of individuals in the population,  $n \in \mathbb{Z}_0^+$ , varies stochastically over time.

#### Fitness components

Viability and fecundity are assumed to depend on four factors: environmental mismatch, density regulation, and the costs and benefits of cooperation. We discuss each factor in turn.

**Environmental mismatch:** The state of the environment,  $\theta$ , is measured in the same scale as the functional trait,  $y$ . Defining  $\mathcal{L}(y) = |\theta - y|$  as a phenotypic lag, we assume the fitness effect of environmental mismatch is a Gaussian function of lag:

$$M(y) = \exp\left(-\frac{1}{2}s\mathcal{L}(y)^2\right), \quad (1)$$

which is 1 when  $\mathcal{L}(y) = 0$  and declines to 0 as lag increases, with larger values of  $s$  increasing the rate of this decline.

**Density regulation:** We implement density regulation similarly to Beverton and Holt (1957). The fitness effect of density is assumed to be a decreasing function of population size,  $n$ ,

$$D(n) = \frac{1}{1 + dn}, \quad (2)$$

which is 1 when  $n = 0$  and declines to 0 as  $n \rightarrow \infty$ , with larger values of  $d$  increasing the rate of decline.

**Cost of cooperation:** Any investment into cooperation is assumed to come at a cost, with fitness effect

$$C(x) = \exp(-cx^k), \quad (3)$$

which is 1 when  $x = 0$  and declines to 0 as cooperation increases, with larger values of  $c$  and  $k$  increasing the rate and concavity of this decline, respectively. Note that because this is a decreasing function, the cost of cooperation is higher when  $C(x)$  is smaller, and vice versa.

**Benefits of cooperation:** Each cooperative interaction begins with a focal individual assembling an interaction group. Every individual in the population has the same probability  $p$  of joining the interaction group (i.e., there is no spatial structure or heritable variation in interaction tendency). Sampling without replacement, the probability  $\Pr(g|n)$  that an interaction group size will

equal  $g$  is then given by a hypergeometric distribution. Here we approximate this with the simpler binomial distribution,

$$\Pr(g|n) = \binom{n-1}{g-1} p^{g-1} (1-p)^{n-g}, \quad (4)$$

which is accurate as long as group sizes are small relative to the total population size,  $g \ll n$ . This includes the possibility that the focal individual is the sole member of an interaction group ( $g = 1$ ).

Equation (4) mechanistically connects population dynamics to public goods dynamics. Variations in population size,  $n$ , will affect the group size, which in turn (see next) changes the incentives for cooperation. This feedback loop promotes the maintenance of cooperation at intermediate levels, and it makes our model an example of an ecological public goods game (Hauert et al. 2006a, 2008; Wakano et al. 2009; Parvinen 2010; Gokhale and Hauert 2016). Although previous models implemented eco-evolutionary feedbacks by limiting reproductive opportunities, thus implicitly incorporating space (Hauert et al. 2006a, 2008; Wakano et al. 2009; Parvinen 2010; Gokhale and Hauert 2016), equation (4) accomplishes the same qualitative effect via a different mechanism (by assigning each individual a probability of joining interaction groups).

In each interaction, every individual contributes to a common pool of public good. The total quantity is multiplied by a factor  $r$ , generating a benefit that is equally distributed among the members of the group. Therefore, for each interaction, the benefit to a focal individual with trait value  $x$  in a group with  $g - 1$  other individuals is  $(x + \sum_{i=1}^{g-1} x_i)r/g$ , where the  $x_i$  are the cooperative trait values of the nonfocal individuals. Here we assume there is little variation in trait values among the population, so that this can be approximated by

$$B(x|\bar{x}, g) = \frac{r}{g} (x + (g-1)\bar{x}), \quad (5)$$

where  $\bar{x}$  is the mean cooperative trait value in the population.

Over the course of a lifetime, we assume all individuals will have participated in many interaction groups. Therefore, we can normalize the benefit (i.e., interpret  $r$  to be the interest rate per interaction times the number of interactions) such that the fitness effect depends only on the average benefit received across a lifetime,

$$\begin{aligned} \bar{B}(x|\bar{x}, n) &= \sum_{g=1}^n \Pr(g|n) B(x|\bar{x}, g) \\ &= r \left[ \bar{x} + \frac{1 - (1-p)^n}{np} (x - \bar{x}) \right], \end{aligned} \quad (6)$$

which can vary from 0 to infinity. This assumption of many interactions is a simple caricature of a species that interacts at a much higher rate than individuals die. Relaxing this assumption, so that

the group sizes experienced and therefore the benefits received each generation are stochastic, would be an interesting extension.

Our main results are robust to alternative functional forms for the cost and benefit (see Discussion).

### Partitioning fitness components

We partition these factors into viability and fecundity. We assume the benefits of cooperation,  $\bar{B}(x|\bar{x}, n)$ , which in this framework are not bounded between 0 and 1, always affect fecundity while the other three components multiplicatively decrease either this baseline fecundity or a baseline viability of 1. For instance, costs may affect fecundity while density and mismatch affect viability, giving  $F = \bar{B}(x|\bar{x}, n)C(x)$  and  $V = D(n)M(y)$  (recall that higher values of  $C(x)$  correspond to smaller costs, equation 3). We refer to the  $2^3 = 8$  different alternatives as “fitness partitions.”

### SIMULATIONS

We have implemented the stochastic process described above as an individual-based (or agent-based) simulation in R, deposited in Dryad (Henriques and Osmond 2020). Note that we do not explicitly simulate group size formation but instead directly use equation (6). To avoid numerical issues, cooperation trait values below  $10^{-6}$  are set to  $10^{-6}$ . We begin all simulations with monomorphic populations.

### ADAPTIVE DYNAMICS

To gain deeper intuition we also analyzed an approximation of this individual-based process. As a modeling framework, we used adaptive dynamics (Dieckmann and Law 1996; Metz et al. 1996; Geritz et al. 1998) to follow the change, over time, of a population's traits and density. This approach makes a number of assumptions.

First, adaptive dynamics assumes that evolution is much slower than ecological population dynamics (demography). This will be the case, for example, if evolution is limited by the arrival of rare small-effect mutations, rather than occurring from standing genetic variation. This timescale separation allows the population to always reach ecological equilibrium (i.e., a monomorphic population at carrying capacity) before the introduction of new advantageous phenotypes. Note that this implies that we are primarily concerned only with environmental changes that occur on the evolutionary timescale, that is, during the time it takes for a population to reach ecological equilibrium the environmental state changes only by a negligible amount. If the environment were to change much faster than the evolutionary timescale evolutionary rescue would be impossible and extinction certain; if the environment were to change much slower persistence would be trivial. As a consequence of the separation of timescales, the population is nearly monomorphic, with nearly all individuals having a resident phenotype  $\vec{z} = (x, y)$ . Mutations are so rare

that, at any given time, no more than one mutant segregates in the population; such mutants are denoted  $\vec{z}' = (x', y')$ . The distribution of group sizes formed by this mutant is therefore binomial (equation 4).

Second, adaptive dynamics assumes that the population size is large and that there is no demographic stochasticity in the resident population. This is, of course, problematic in a model that purports to describe the dynamics of populations that are approaching extinction. Quantitatively, this assumption means that our approximation will get worse at small population sizes; however, as we will see, it still captures the qualitative differences observed (on average) across the individual-based simulations.

A final approximation that we make to translate the stochastic process to a deterministic dynamical system is that we redefine  $n$  as the expected population size, which is not in general an integer and therefore violates the binomial sampling assumption in the model (equation 4). Despite this, we use this expected population size in the final line of equation (6) (and elsewhere) as an approximation of the underlying individual-based sampling process (Section S1.2), which qualitatively recapitulates stochastic realizations of the individual-based process, as we will see next.

## Results

### RESIDENT DYNAMICS

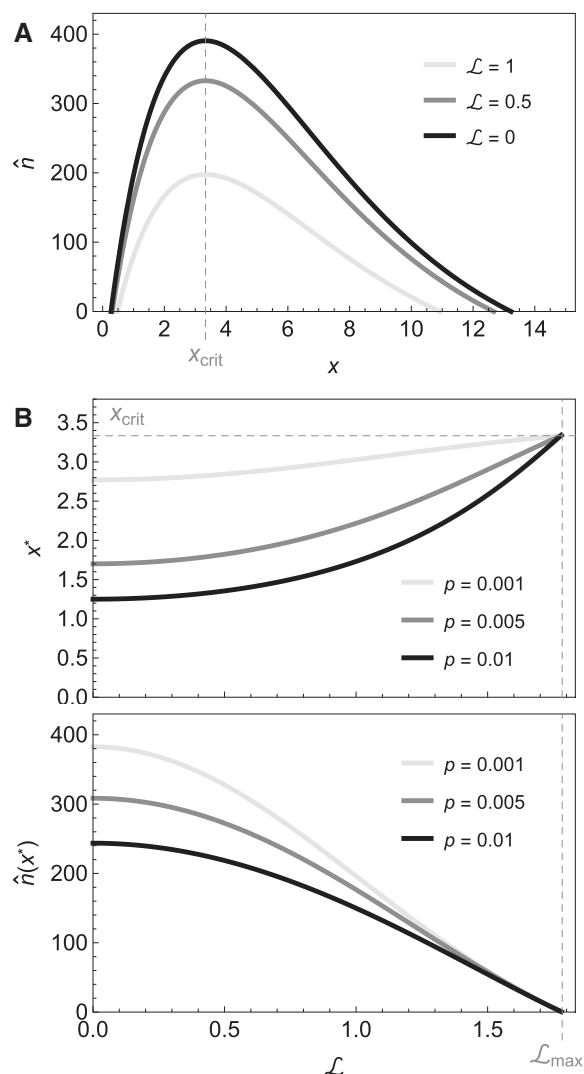
Under these adaptive dynamic assumptions, the average benefit of cooperation (equation 6) for a rare mutant with cooperative trait value  $x'$  is  $\bar{B}(x'|x, n)$ , where the mean trait value,  $\bar{x}$ , has been replaced by the resident trait value,  $x$ . Fitness, the expected number of offspring a focal individual leaves in the next generation, is then  $W(\vec{z}|\vec{z}) = VF = \bar{B}(x'|x, n)C(x)D(n)M(y)$ , which depends on both focal and resident phenotypes,  $\vec{z}'$  and  $\vec{z}$ , as well as population size,  $n$ . (Again, recall that costs are highest, and hence fitness is lower, at small values of  $C(x)$ .)

For a given population size  $n$ , we can calculate the intergeneration change in the expected population size:  $\Delta n = n W(\vec{z}|\vec{z}) - n$ , where  $W(\vec{z}|\vec{z}) = \bar{B}(x|x, n)C(x)D(n)M(y)$  is the fitness of a resident individual. When the population size is constant,  $\Delta n = 0$ , the population is at ecological equilibrium and will have size  $\hat{n}(\vec{z})$  (Fig. 1A):

$$\hat{n}(\vec{z}) = \begin{cases} \frac{M(y)rx \exp(-cx^k) - 1}{d} & \text{if } x_{\min} \leq x \leq x_{\max} \\ 0 & \text{otherwise,} \end{cases} \quad (7)$$

where  $x_{\min}$  and  $x_{\max}$  are, respectively, the minimum and maximum amounts of cooperation beyond which the population goes extinct.

As expected, the population size is higher when public goods are cheaper to produce (low  $c$ ) or provide higher benefits (high  $r$ ), as well as when density regulation is less intense (low  $d$ ). Fur-



**Figure 1.** The population size depends on distance to the optimum and on the amount of cooperative investment. (A) The population size at ecological equilibrium ( $\hat{n}$ ) increases with cooperation ( $x$ ) up to a maximum ( $x_{\text{crit}}$ , equation 9), and decreases for higher values. At very low (equation 8) or very high values of cooperative investment, the population goes extinct. Population size also decreases with distance  $\mathcal{L}(y)$  to the environmental optimum (equation 7), such that at very large lags (equation 10), the population goes extinct. (B) *Top*: the equilibrium value of cooperation with a constant lag ( $x^*$ , calculated from equation 11) increases for higher lags ( $\mathcal{L}$ ) and smaller interaction group sizes (smaller  $p$ ). *Bottom*: corresponding population size at equilibrium ( $\hat{n}(x^*)$ ). Parameters:  $d = 0.01$ ,  $s = 1$ ,  $c = 0.3$ ,  $r = 4$ ,  $k = 1$ ,  $p = 0.01$  (except when otherwise stated in the figure).

thermore, even in a constant environment, a minimum amount of cooperation is necessary to sustain the population and avoid extinction (Fig. 1A):

$$x_{\min} = \sqrt[k]{-\frac{\mathcal{W}(-ck(M(y)r)^{-k})}{ck}}, \quad (8)$$



where  $\mathcal{W}(\cdot)$  denotes the Lambert  $W$ -function, also known as the product logarithm (Corless et al. 1996; Lehtonen 2016). As individuals invest more in cooperation, the population size increases (Fig. 1A), up to a critical value,  $x_{\text{crit}}$ :

$$x_{\text{crit}} = \sqrt[k]{\frac{1}{ck}}. \quad (9)$$

Beyond this point, the costs of cooperation are so high that further investment leads to smaller populations. Therefore, there is a maximum amount of cooperation,  $x_{\text{max}}$  beyond which the population cannot persist (Fig. 1A).

The equilibrium population size declines with the lag between the population's trait and the environmental optimum (Fig. 1A). Substituting equation (1) into equation (7) and solving  $\hat{n}(\bar{z}) = 0$  for  $\mathcal{L}(y)$ , we can calculate the maximum value of lag above which the population goes extinct:

$$\mathcal{L}_{\text{max}} = \sqrt{\frac{2}{s}(\ln(rx) - cx^k)}. \quad (10)$$

## EVOLUTION OF COOPERATION FOR A CONSTANT LAG

We now focus on the fate of a rare mutant with trait value  $x'$  and consider the case of a constant lag ( $\mathcal{L}(y) = \mathcal{L}$ ) in a constant environment (i.e.,  $\theta$  is constant). Because we are concerned with adaptation in  $x$  and the lag is fixed, we will drop the dependence of various functions on  $y$  for the remainder of this section. The mutant's fitness is then given by  $W(x'|x) = \bar{B}(x'|x, \hat{n}(x))C(x')D(\hat{n}(x))M$ .

The direction and strength of selection on cooperation can be measured by the selection gradient of cooperative investment (the slope of the fitness landscape experienced by the mutant), which is given by

$$\mathcal{S}(x) = \left( \frac{\partial W(x'|x)}{\partial x'} \right) \Big|_{x'=x} \quad (11)$$

$$= \frac{1 - (1-p)^{\hat{n}(x)} - cpx^k \hat{n}(x)}{px \hat{n}(x)}. \quad (11)$$

The evolutionary dynamics will be at equilibrium when there is no directional selection. At this point the selection gradient vanishes,  $\mathcal{S}(x^*) = 0$ , and  $x^*$  is said to be an evolutionarily singular point (Geritz et al. 1998). Although an explicit analytical solution is impossible to calculate, we can solve for  $x^*$  numerically (Fig. 1B). Furthermore, we can analytically show that  $\mathcal{S}(x)$  is positive when  $x$  is small enough, declines with  $x$  when  $x < x_{\text{crit}}$  (at least for  $k \geq 1$ , i.e., a sufficiently concave cost) and is negative when  $x = x_{\text{crit}}$  (Section S2.1). Therefore, in a monomorphic population, if  $x$  starts below  $x_{\text{crit}}$  it will converge to the only singular point  $x^*$  that exists below  $x_{\text{crit}}$ . Intuitively, selection does not drive cooperation above the value which causes decreases in

population size. This convergence to the singular point can be visualized from a pairwise invasibility plot, which indicates the mutant strategies  $x'$  that can invade any given resident strategy  $x$  (van Tienderen and de Jong 1986; Geritz et al. 1998). Figure 2Ai and 2Bi shows, for two sets of parameters, that the singular point is convergent stable. We are also able to show with implicit differentiation, again for  $k \geq 1$ , that the equilibrium level of cooperative investment,  $x^*$ , increases with lag and decreases with group size, as driven by increases in  $p$  (see Fig. 1B for a numerical example and Section S2.2 for derivations).

## Evolutionary stability

Once the population reaches equilibrium there are two possible outcomes. If the singular strategy is a fitness maximum then evolution will come to a halt and cooperation will remain constant at  $x^*$  (evolutionarily stable strategy). Otherwise (if the singular strategy is a fitness minimum) the monomorphic population can simultaneously be invaded by mutants on either side of  $x^*$ . This leads the population to split into two distinct and diverging phenotypes—a process called evolutionary branching (Geritz et al. 1998). Depending on the model parameters,  $x^*$  can either be evolutionarily stable (Fig. 2A) or unstable (Fig. 2B). For individual-based simulations illustrating both possibilities, see Figures S1A (evolutionarily stable) and S1B (evolutionary branching).

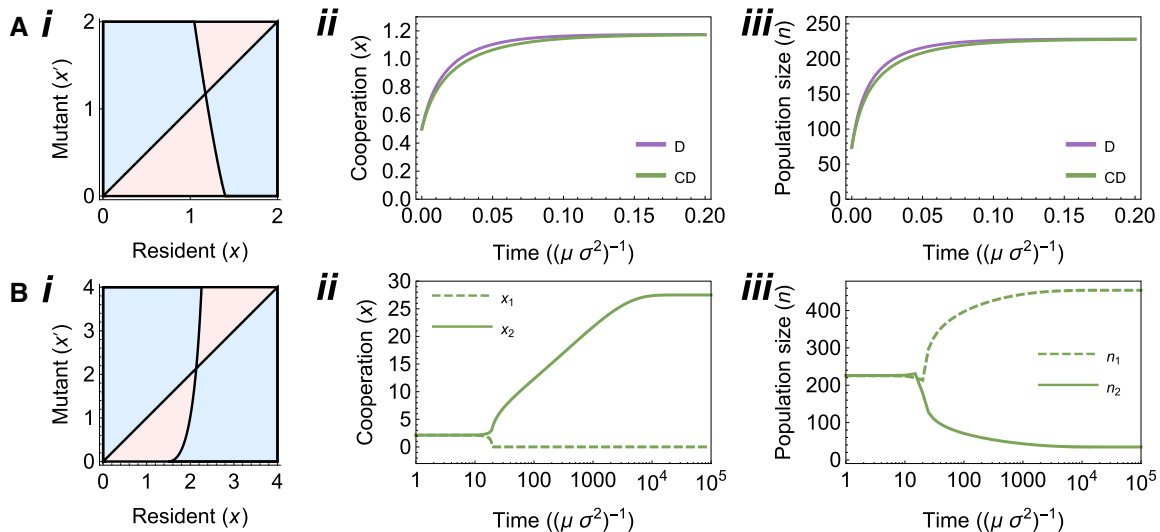
The singular strategy will be a fitness minimum if

$$\frac{\partial^2 W(x'|x)}{\partial (x')^2} \Big|_{x'=x=x^*} > 0 \iff k(1 + cx^{*k}) < 1, \quad (12)$$

(see equations S23–S24 for more details). This means that the singular strategy will be a branching point only when the cost is sufficiently weak (small  $c$ ) and convex (small  $k$ ), and the equilibrium level of cooperation is low.

If the singularity is a branching point the population branches into a defector strain and a cooperator strain (a process called tragedy of the commune, see Doebeli et al. 2004) with trait values  $x_1$  and  $x_2$ , respectively (Fig. 2B). At evolutionary equilibrium  $x_1^*$  and  $x_2^*$  are values that do not depend on the lag (as shown in Section S3.1). In contrast to the case where branching does not occur (in which the equilibrium trait value changes with the lag in a quantitative fashion), after branching the trait values evolve to a stable equilibrium, so that cooperation evolves in response to environmental change only through changes in their relative frequencies (cf. Section S3.1, particularly equation S29). This situation resembles a binary-action public goods game.

In this manuscript we will focus on the case where the singular strategy is evolutionarily stable (Fig. 2A). Individual-based simulations suggest that, although branching is possible



**Figure 2.** Monomorphic evolutionary dynamics for a constant lag when the singular point  $x^*$  is a stable point (A) and when it is a branching point (B). The leftmost panels are pairwise invasibility plots, where blue (red) areas correspond to mutants with higher (lower) fitness than the resident. The point at which the black lines cross is the singular point ( $x^*$ ); this point cannot be invaded by any mutants in (A), but it is invulnerable on both sides in (B). For visual reference,  $x_{\text{crit}} \approx 2.74$  in (A) and  $x_{\text{crit}} \approx 44.44$  in (B). The other panels show the monomorphic evolutionary dynamics of cooperation ( $x$ , middle panels) and corresponding population size ( $n$ , rightmost panels). In (A), a population starting away from the singular point evolves toward  $x^*$  and remains at equilibrium. Purple and green curves correspond, respectively, to the fitness partitions  $d$  and  $cd$  (see “The evolution of cooperation rescues populations from extinction” section). In (B), only one fitness partition ( $cd$ ) is shown; a population starting at singular point branches into a defector ( $x_1$ ) and a cooperator ( $x_2$ ) strain. Parameters:  $d = 0.01$ ,  $r = 4$ ,  $c = 0.3$ ,  $M = 1$ ,  $p = 0.01$ . For (A)  $k = 1.1$ ; for (B)  $k = 0.5$ .

(Fig. S1B), the parameter range under which this process actually occurs, resulting in a stable dimorphic equilibrium, is relatively narrow when compared to the analytical predictions above. In particular, the population size of the cooperator is often so small that stochastic extinction of that branch quickly occurs. Nonetheless, we present some remarks regarding the postbranching dynamics in Section S3.1.

#### Monomorphic evolutionary dynamics for a constant lag

The selection gradient can also be used to determine the rate of evolution. Using a traditional adaptive dynamics approach (Dieckmann and Law 1996; Geritz et al. 1998; Metz et al. 1996), adapted for a life cycle with nonoverlapping generations (Section S1), we obtain a differential equation for the time dynamics of cooperative investment ( $\dot{x}$ ):

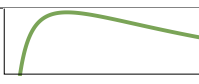






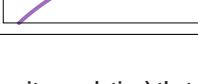
$$\dot{x} = \frac{1}{\sigma_W^2(x)} \hat{n}(x) \mu_x \sigma_x^2 S(x), \quad (13)$$

where  $\sigma_W^2(x)$  refers to the variance in the resident’s reproductive success. Equation (13) is analogous to the canonical equation of adaptive dynamics (Dieckmann and Law 1996). In contrast to the canonical equation, the rate of adaptation in equation (13) is inversely proportional to the variance in reproductive success,  $\sigma_W^2(x)$ . Given the same expected number of offspring, variance in number of offspring increases the chance that an ad-

vantageous mutant is lost through genetic drift; therefore, variance in reproductive success slows adaptation down (Supporting Information, see also Durinx et al. 2008). Given that survival is Bernoulli-distributed with expectation  $V$  and fecundity is Poisson-distributed with expectation  $F$ , the variance in reproductive success is  $\sigma_W^2 = W(1 + F - W)$ . At ecological equilibrium (when  $W = VF = 1$ ), this becomes  $\sigma_W^2 = F = 1/V$ , which depends on how the fitness components are partitioned into viability and fecundity (Section 2.1.3). The intuition for this result is that, if population size is at equilibrium, any increase in fecundity must be balanced out by a decrease in viability, and vice versa. Additionally, the number of offspring is more variable when fecundity is high. Therefore, viability and fecundity have opposite effects on reproductive variance.

Substituting equations (7) and (11) into equation (13) we are able to determine the time dynamics of cooperation. At this point, however, we need to be explicit about the fitness partition for the species we are studying. Because the rate of adaptation depends on the variance in reproductive success,  $\sigma_W^2(x)$ , the evolutionary trajectory will depend on how the different model elements—environmental mismatch (equation 1), cost of public good production (equation 3), and density regulation (equation 2)—are partitioned among the two fitness components (viability and fecundity, see the “Partitioning fitness components” section). Each of the three components in our model can affect either viability

**Table 1.** Possible fitness partitions in the model.

Fitness partition	Viability includes...			$\hat{n}(x)/\sigma_W^2(x)$	
	Cost	Mismatch	Density regulation		
CMD	✓	✓	✓	$\frac{e^{-cx^k} M(y) - \frac{1}{rx}}{d}$	
CM	✓	✓		$\frac{e^{-2cx^k} M(y) (-e^{cx^k} + M(y)rx)}{d}$	
CD	✓		✓	$\frac{e^{-cx^k} - \frac{1}{M(y)rx}}{d}$	
C	✓			$\frac{e^{-2cx^k} (-e^{cx^k} + M(y)rx)}{d}$	
MD		✓	✓	$\frac{-e^{cx^k} + M(y)rx}{d rx}$	
M		✓		$\frac{M(y) (e^{-cx^k} M(y)rx - 1)}{d}$	
D			✓	$\frac{1 - \frac{e^{cx^k}}{M(y)rx}}{d}$	
∅				$\frac{e^{-cx^k} M(y)rx - 1}{d}$	

**Note:** Partitions are named after the initial letter of the model elements (cost of cooperation, environmental mismatch, or density regulation) that decrease viability. Elements that do not decrease viability decrease fecundity instead. Abscissae indicate cooperation level ( $0 < x < x_{crit}$ , equation 9), and ordinates indicate  $\hat{n}(x)/\sigma_W^2(x)$ . Parameters:  $d = 0.01$ ,  $r = 4$ ,  $c = 0.3$ ,  $p = 0.01$ ,  $M(y) = 1$ ,  $k = 1$ .

or fecundity, for a total of eight possible partitions (Table 1). For example, the mismatch between the environmental state and the functional trait may conceivably decrease either viability or fecundity, depending on the species. The choice of fitness partition will turn out to qualitatively affect the outcome of adaptation to changing environments, via its effect on variance in reproductive success ( $\sigma_W^2$ ).

Two qualitatively different behaviors will be observed, depending on whether the costs of public good production (which are high when  $C(x)$  is small, see equation 3) decrease viability (green curves in Table 1) or fecundity (purple curves). Throughout the text, we will illustrate the effect of fitness partition choice by contrasting two example fitness partitions (which we call CD and D, see Table 1). In partition CD, the costs of public good production decrease viability, whereas in partition D, they decrease fecundity. As we will see, which fitness component is affected by density regulation and environmental mismatch has no qualitative effect. In both example fitness partitions, density regulation decreases viability, whereas environmental mismatch decreases fecundity (Table 1).

The viability of a resident individual with fitness partition D is  $V_D = D(\hat{n}(x)) = \exp(cx^k)/(M(y)rx)$ , and that of a resident individual with fitness partition CD is  $V_{CD} = C(x) \cdot D(\hat{n}(x)) = 1/(M(y)rx)$ . As evolution drives the population toward higher lev-

els of cooperative investment, the costs of cooperation increase (i.e., lower values of  $C(x)$ ), which reduces  $1/\sigma_W^2$ , so that CD-species adapt slower and slower when contrasted with D-species (Table 1). As we will see later on, this will lead to qualitative differences in the capacity for evolutionary rescue, but in the case of adaptation toward a stable singular point with a constant lag the long-term outcome of evolution is the same (Fig. 2A).

## EVOLUTION OF COOPERATION DURING ENVIRONMENTAL CHANGE

In the “Evolution of cooperation for a constant lag” section, we considered the dynamics of cooperation when the functional trait is at some constant distance to the environmental optimum. In the long term, populations that track moving environments will indeed always evolve to exhibit a constant lag (or, alternatively, they will fail to track the optimum and go extinct). However, the dynamics from the “Evolution of cooperation for a constant lag” section do not take into account the feedback between cooperation and lag distance. We will now track how populations evolve while the environmental optimum,  $\theta$ , increases at some constant velocity  $v$ , that is,  $\theta = vt$ .

We imagine that populations are initially well matched to the environment (and at evolutionary equilibrium, see the



“Evolution of cooperation for a constant lag” section). Recall that, if the evolutionary singular point  $x^*$  is an evolutionary branching point (equation 12), then the initially well-adapted population will be participating in a binary-action ecological public goods game (i.e., it will consist of two distinct strains: cooperators and defectors, whose frequencies may fluctuate as the environment changes; for more details see Section S3.1). Otherwise, it will be engaged in a continuous ecological public goods game (i.e., it will be a monomorphic population characterized by a quantitative trait, describing the amount of cooperative investment). Here, we will consider the latter scenario; for some remarks on the prior case see Section S3.1.

### The rate of evolution

We again focus on the fate of a rare mutant, with phenotype  $\vec{z} = (x', y')$  and fitness  $W(\vec{z}|\vec{z}) = \bar{B}(x'|\vec{z})C(x')D(\vec{z})M(y')$ . The formula for the selection gradient of cooperation is given by equation (11) (with the added dependence of  $M$  on  $y'$ ). As for the functional trait, its selection gradient is given by

$$S(y) = \left( \frac{\partial W(\vec{z}|\vec{z})}{\partial y'} \right) \Big|_{\vec{z}=\vec{z}} = s(tv - y). \quad (14)$$

In contrast to the “Monomorphic evolutionary dynamics for a constant lag” section, there is now no endpoint to evolution because, if the population manages to change fast enough to avoid extinction, it will approach a state in which  $y$  is constantly evolving at the same velocity as the environment ( $\dot{y} = v$ ). Nonetheless, this implies there can be a “dynamical” equilibrium where the lag stabilizes at some constant value. To find the dynamical equilibrium, we are ultimately interested in finding the values of  $x$  and  $\mathcal{L}$  for which  $\dot{x} = 0$  and  $\dot{\mathcal{L}} \equiv v - \dot{y} = 0$ . As there is no explicit analytic solution for equation (11), we will solve for  $x$  and  $\mathcal{L}$  numerically. Then, we will further clarify our results by analytically determining the maximum velocity of environmental change that the population is able to track without going extinct (i.e., the critical rate of environmental change).

The differential equation for the dynamics of the two traits  $\vec{z} = (x, y)$ , with selection gradients  $\vec{S}(\vec{z}) = (S(x), S(y))$ , can be calculated similarly to equation (13) (cf. also Section S1 and equation 6.1 in Dieckmann and Law 1996):

$$\dot{\vec{z}} = \frac{1}{\sigma_w^2(\vec{z})} \hat{n}(\vec{z}) \vec{\mu} \vec{\Sigma} \vec{S}(\vec{z}), \quad (15)$$

where  $\vec{\mu} = (\mu_x, \mu_y)^T$  is a vector of the mutation rates and  $\vec{\Sigma} = \begin{pmatrix} \sigma_x^2 & 0 \\ 0 & \sigma_y^2 \end{pmatrix}$  is the variance–covariance matrix for the mutational distribution (assuming no genetic correlation in the two traits).

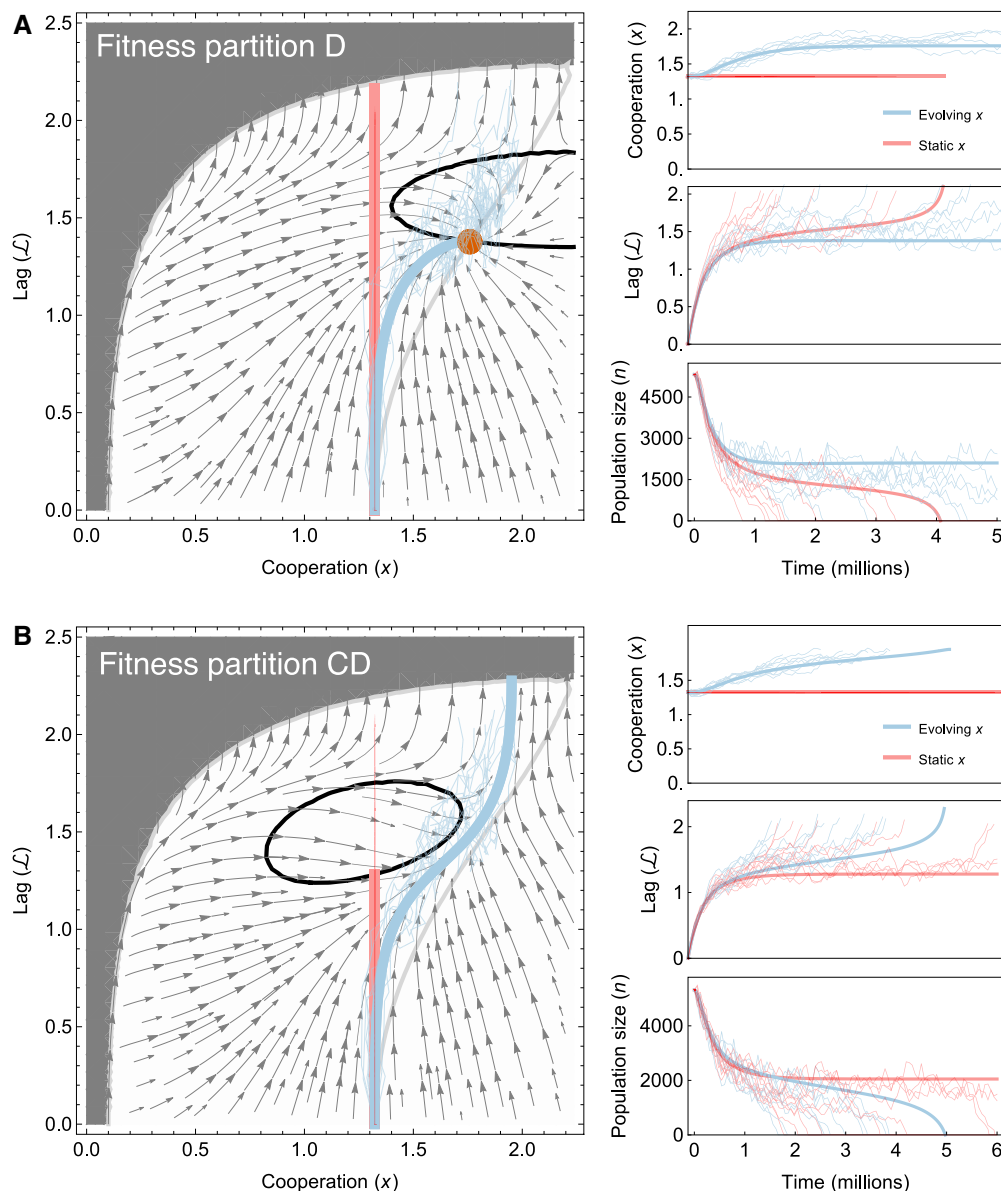
### The evolution of cooperation rescues populations from extinction

Intuitively, one may expect that because increased phenotypic lag favors the evolution of cooperation and cooperation increases population size, the evolution of cooperation may counteract decreases in population size caused by changing environments. If this is so, there may be rates of environmental change for which populations with a fixed level of cooperation tend to go extinct while those with an evolving level of cooperation do not, meaning that the evolution of cooperation facilitates evolutionary rescue. This process can indeed be observed for some fitness partitions.

For example, Figure 3A shows the evolutionary dynamics of a population belonging to a species with fitness partition D (Table 1). The pink curves depict the dynamics of a population where cooperation is fixed at a constant value ( $\mu_x \sigma_x^2 = 0$ ). At the beginning of the numerical simulation, the population is perfectly adapted to the environment, and the level of cooperation is at equilibrium. As the optimum starts moving at a constant velocity, the population size decreases. For some time, adaptation in  $y$  keeps the population afloat, by lowering the rate of increase in the lag and the rate of decrease in population size. But as the population becomes ever smaller, adaptation decelerates, limited by the supply of beneficial mutations. The positive feedback between decreased population size and slower adaptation leads the population to extinction. Compare this with the blue curves, which differ from the red curves only in allowing cooperation to evolve on a timescale more similar to that of the moving optimum (i.e., larger  $\mu_x \sigma_x^2$ , parameters in figure caption). The initial dynamics are very similar to the previous case: an increase in the lag and a corresponding decrease in population size. But this very decrease in population size rewards higher cooperative investments. As cooperation increases, it slows the rate of population decline and thus allows the population to adapt faster to the environmental change. Confirming our intuition, the evolution of cooperation rescues the population and leads to a dynamical equilibrium (orange dot in Fig. 3A).

If the environment changes too fast, no dynamical equilibrium will exist. Higher environmental velocities result in a narrower lag nullcline (black line in Fig. 3A’s stream plot); if the velocity is too high, the nullcline vanishes, meaning that the population will fail to track the optimum and will go extinct regardless of the initial conditions (Fig. 4A). That said, species where cooperation can evolve will survive faster environmental changes compared to species where cooperation cannot evolve (Fig. 4A). Even when the velocities are low enough that both types of species can avoid extinction, species where cooperation can evolve will equilibrate at higher population sizes and lower lags (Fig. 4A).

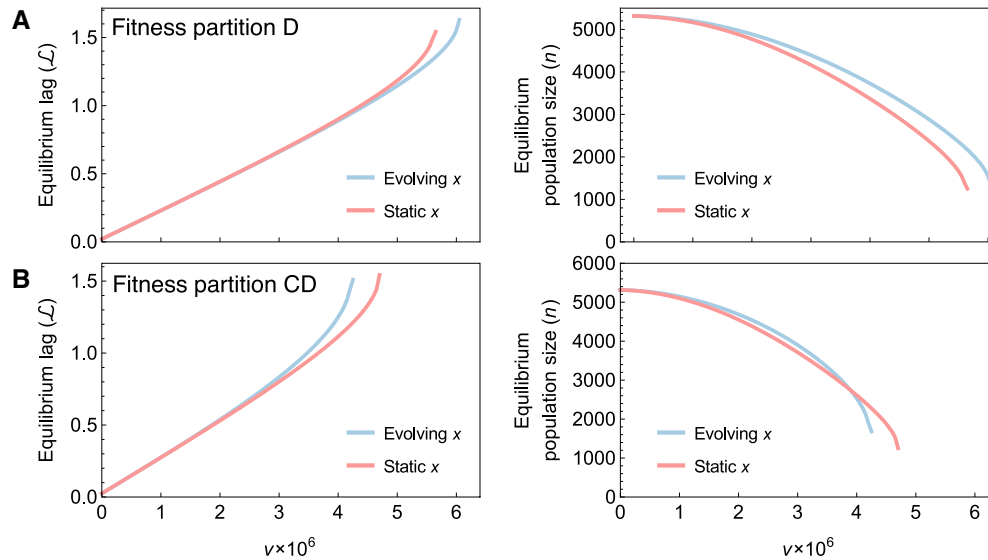
A dynamical equilibrium may also not exist if the game parameters do not favor the evolution of high cooperation. For



**Figure 3.** Evolution of cooperation with a moving optimum, for a species with fitness partition  $d$  (panel A) or fitness partition  $cd$  (panel B). The stream plot to the left indicates the change in a population's lag ( $L$ ) and cooperation ( $x$ ) over time, for a population where cooperation evolves fast relative to the environmental change. The nullclines for lag ( $\dot{L} = 0$ ) and cooperation ( $\dot{x} = 0$ ) are in black and light gray, respectively. Within the dark gray region, the population goes extinct. The thick blue curves are the result of numerical simulations, starting with zero lag and with  $x = x^*$ . For comparison, the thick pink curves are the result of numerical (deterministic) simulations, with identical starting conditions, where cooperation does not evolve ( $\mu_x = 0$ ). The panels on the right show the time dynamics of cooperation, lag, and population size for the same simulations. Thin lines show the mean cooperation value, mean lag, and population size of individual-based simulations (10 replicates for each treatment). Parameters:  $r = 10$ ,  $c = 0.1$ ,  $s = 1$ ,  $k = 2$ ,  $\mu_x = \mu_y = 10^{-4}$ ,  $\sigma_x = \sigma_y = 0.01$ ,  $d = 0.0019$ ,  $p = 5 \times 10^{-4}$ ; for (A)  $v = 5.8 \times 10^{-6}$ ; for (B)  $v = 4.5 \times 10^{-6}$ . In contrast to (A), the velocity in (B) was chosen such that the nullclines do not intersect. Using the higher velocity in panel (B) would lead to extinction of both populations, whereas using the lower velocity in panel (A) would lead to persistence of both populations (see also Fig. 4).

example, larger interaction groups deter cooperation (because they decrease the fraction of investment benefits that return to the cooperator). Increasing  $p$  makes groups larger, and therefore it moves the cooperation nullcline (gray line in Fig. 3A's

stream plot) to the left, thus causing the dynamical equilibrium to vanish. Finally, even if a dynamical equilibrium exists, the population will be unable to reach it if it evolves too slowly in  $x$ . The pink curve in Figure 3 represents the most extreme such



**Figure 4.** Lag (left) and population size (right) at the dynamical equilibrium, in populations with fitness partition d (panel A) or fitness partition cd (panel B), for different velocities of environmental change ( $v$ ). The curves are interrupted at high velocities because the populations become extinct: at high  $v$ , the nullclines for lag ( $\dot{\mathcal{L}} = 0$ ) and cooperation ( $\dot{x} = 0$ ) no longer intersect, so that there is no equilibrium lag. Note that in A, for high values of  $v$ , the evolution of cooperation rescues populations that would otherwise undergo extinction; in contrast, in B, the opposite happens. The parameters are the same as in Figure 3.

scenario ( $\mu_x = 0$  or  $\sigma_x = 0$ ). Note that the position of the equilibrium itself does not depend on  $\mu_x$  or  $\sigma_x$ , provided that  $\mu_x > 0$  and  $\sigma_x > 0$ .

#### The evolution of cooperation causes extinction

Surprisingly, small differences in fitness partition can result in a diametrically opposite outcome. Consider now a species with fitness partition CD (Table 1). Recall that the only difference between the two fitness partitions is that in CD, the costs of cooperation decrease viability instead of fertility (as in D). In the one-dimensional dynamics, the differences between the two fitness partitions are relatively minor (Fig. 2A): although adaptation is slightly slower for CD, the evolutionary equilibrium is the same in both fitness partitions. However, the differences between the fitness partitions turn out to have important qualitative consequences for a population's capacity to track a moving optimum.

Because cooperation can slow the rate of adaptation in fitness partition CD (by increasing reproductive variance), it is possible that the evolution of cooperation could hinder persistence in a changing environment. To examine this possibility, Figure 3B considers a scenario where the rate of environmental change is small enough that a population with a fixed cooperative investment would persist (all other parameters are the same as in panel A). Such a population is represented by the pink curve in Figure 3B. In contrast, a population with an evolving level of cooperation now goes extinct (blue curve in Fig. 3B). In effect, the changing environment causes the population to decline, which favors more cooperation to evolve. Although increases in coop-

eration may temporarily make the population larger relative to a population where cooperation does not evolve (Fig. 4B), speeding adaptation by increasing the supply of mutations, increases in cooperation also increase the variance in reproductive success (and thus the strength of genetic drift). Eventually the increase in the variance in reproductive success overwhelms the positive effect of increased population size, making adaptation slower and thereby causing extinction. More generally, in stark contrast to fitness partition D, the evolution of cooperation in fitness partition CD results in higher equilibrium lags (compare Fig. 4B for CD to Fig. 4A for D).

#### The critical rate of environmental change

To more formally understand the difference between D and CD, consider the rate of change in lag,  $\dot{\mathcal{L}} = v - \dot{y}$ . If a dynamical equilibrium exists, then at such an equilibrium,  $\dot{y} = v$ . From equation (15) we can write:

$$\dot{y} = \frac{s\mathcal{L}\mu_y\sigma_y^2}{\sigma_W^2(\bar{z})d} \left( rxe^{-\frac{1}{2}s\mathcal{L}^2 - cx^k} - 1 \right), \quad (16)$$

which, for fitness partitions D and CD, equals

$$\dot{y} = \begin{cases} s\mathcal{L}\mu_y\sigma_y^2 \frac{rx - e^{-cx^k + \frac{1}{2}s\mathcal{L}^2}}{drx} & \text{if d} \\ s\mathcal{L}\mu_y\sigma_y^2 \frac{rx - e^{cx^k + \frac{1}{2}s\mathcal{L}^2}}{drx} e^{-cx^k} & \text{if cd.} \end{cases} \quad (17)$$

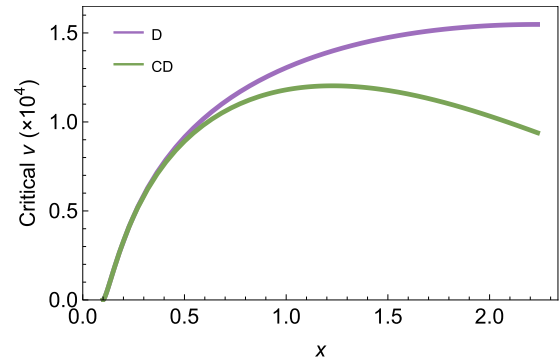
With fitness partition D,  $\dot{y}$  increases with  $x$  up to  $x = x_{\text{crit}}$ . Thus, the evolution of higher levels of cooperation will always increase the population's capacity to track the moving optimum—decreasing lag—because  $x$  will never evolve to values higher than  $x_{\text{crit}}$  (Section S2.1). In contrast, in fitness partition CD  $\dot{y}$  is maximized at a value of  $x$  below  $x_{\text{crit}}$ . Therefore, once a sufficiently high level of cooperation has evolved, further increases will impair the ability of the population to track the moving environment—increasing lag.

To understand how this leads to extinction we next turn to calculating the critical rate of environmental change. First, note that equation (16) has a maximum in  $\mathcal{L}$ , implying a saddle-node bifurcation in the dynamical equilibrium lag. This bifurcation corresponds to the fact that an equilibrium lag ceases to exist at high velocities (Fig. 4); it is an “evolutionary tipping point” (Osmond and Klausmeier 2017). This bifurcation also explains why simulated populations rapidly go extinct (Fig. 3) as they can transition quickly from large positive growth rates to large negative ones as they pass through the bifurcation. We can find the critical lag that maximizes the rate of evolution ( $\mathcal{L}_{\text{crit}}$ ) by calculating the root of  $d\dot{y}/d\mathcal{L}$ :

$$\mathcal{L}_{\text{crit}} = \sqrt{\frac{2\mathcal{W}\left(\frac{rx}{2}e^{1/2-cx^k}\right) - 1}{s}}, \quad (18)$$

where  $\mathcal{W}$  again denotes the Lambert  $W$ -function.

Having calculated the critical lag, we can plug it into equation (17) to obtain the maximum velocity of environmental change that can be tolerated by the population before it goes extinct (for a given value of  $x$ ). Although the resulting expressions are not particularly insightful, a plot of this critical velocity confirms that increases in  $x < x_{\text{crit}}$  have qualitatively different effects for the fitness partitions D and CD (Fig. 5). In particular, we see that the evolution of increased cooperation cannot drive extinction in fitness partition D because it never decreases the maximum rate of evolution in  $y$  (as seen from equation 17 and argued above). In contrast, Figure 5 shows that it is possible for increased cooperation to drive extinction in fitness partition CD, if cooperation evolves to such an extent that it lowers the critical rate of environmental change (e.g., beyond  $x \approx 1.25$  in Fig. 5). And this indeed can happen; increases in lag lower the population size, driving increases in cooperation that stimulate yet further increases in lag and declines in population size, and thus more cooperation. Through this feedback cooperation can eventually reach levels that preclude a stable lag, as seen in Figure 3. In other words, the evolution of cooperation promotes a vicious cycle that drives the population to an extinction that would not have occurred if cooperation were fixed, an example of evolutionary suicide (Ferrière 2000; Gyllenberg and Parvinen 2001). For this reason, in contrast to D, the lag nullcline in CD (black line of



**Figure 5.** Critical velocity (maximal velocity of environmental change for which the population is able to track the moving optimum without undergoing extinction) as a function of the level of cooperative investment ( $x < x_{\text{crit}}$ ), for fitness partitions d (purple) and cd (green). The evolution of increasing levels of cooperation makes populations able to endure faster rates of environmental change in d, but it has the opposite effect in cd. The critical velocity is calculated by subbing  $\mathcal{L}_{\text{crit}}$  (equation 18) into  $\dot{y}$  (equation 17). Parameters:  $r = 10$ ,  $c = 0.1$ ,  $s = 1$ ,  $k = 2$ ,  $\mu_x = \mu_y = 10^{-4}$ ,  $\sigma_x = \sigma_y = 0.05$ ,  $d = 0.0015$ ,  $p = 5 \times 10^{-4}$ .

Fig. 3B) vanishes for high values of cooperation. Of course, equilibria may still exist if the velocity is small, which widens the area enclosed by the lag nullcline, or if the game parameters are such that equilibrium cooperation is low. For example, in Figure 3,  $p$  is relatively small, so that the average group size is  $np \approx 3.5$ . In populations where a larger proportion of the population composes any one group (i.e., larger  $p$ ) a lower level of cooperation is favored, so that the  $x$  nullcline in Figure 3B moves to the left and may intersect the  $\mathcal{L}$  nullcline. In such a case, faster environmental change would be needed to see evolutionary suicide.

In general, for any fitness partition where the costs of cooperation decrease viability,  $\hat{n}(\bar{z})/\sigma_W^2(\bar{z})$  will decline as  $x$  approaches  $x_{\text{crit}}$ , whereas for any fitness partition where the costs instead decrease fecundity, it will be maximized exactly at  $x = x_{\text{crit}}$ . This is because the slope at  $x_{\text{crit}}$ ,  $\frac{\partial}{\partial x} \frac{\hat{n}(\bar{z})}{\sigma_W^2(\bar{z})} \Big|_{x=x_{\text{crit}}}$  only depends on the derivative of  $V(\bar{z}) = 1/\sigma_W^2(\bar{z})$  (because  $\hat{n}(\bar{z})$  is maximized at  $x_{\text{crit}}$ ). The viability, in turn, can depend on  $x$  only through  $C(x)$  and/or  $D(\hat{n}(\bar{z}))$ . If the viability is affected by neither (fitness partition  $\emptyset$ ), then its derivative will be zero. The same is true when the viability depends on  $x$  only through  $D(\hat{n}(\bar{z}))$ , again because  $\hat{n}(\bar{z})$  is maximized at  $x_{\text{crit}}$ . Thus, all fitness partitions in which the costs of cooperation do not affect viability have a maximum rate of evolution in  $y$  at  $x = x_{\text{crit}}$ . In contrast, when the viability is affected by the costs of cooperation, its derivative also depends on the derivative of  $C(x)$ , which is always negative. Therefore, if the costs of cooperation decrease viability, then  $\hat{n}(\bar{z})/\sigma_W^2(\bar{z})$  is declining with  $x$  at  $x_{\text{crit}}$ , and increasing cooperation can slow evolution.

Throughout we assume the benefits of cooperation affect fecundity. If the benefits were instead scaled in such a way to keep

them bounded between 0 and 1 (e.g.,  $\tilde{B} = 1 - \exp(B)$ ), we could also allow them to affect viability. This would complicate our conclusions but the outcome can be intuited from the above reasoning. On the one hand, if the benefits affected viability but the costs affected fecundity then increasing cooperation would speed up evolution (because the derivative of  $V$  would be positive), whereas on the other hand, if both affected viability the effect of cooperation on evolution would be determined by the slope of their product,  $\tilde{B}C$ , with respect to  $x$ .

## Extension to other types of social interactions

The results above are consequence of a series of ecoevolutionary feedbacks (interactions between population density and selection on trait values) that arise during the process of environmental change. Changes in one trait,  $x$  (in this case, cooperation), affect the evolutionary rate of a second trait,  $y$ , that is undergoing adaptation to a changing environment, through both its effect on population density and the strength of genetic drift. The rate of evolution in both traits was found to be proportional to  $\hat{n}(\bar{z})/\sigma_W^2(\bar{z})$  (equation 15). As explored above (Section 3.3.4), we can see the effect of  $x$  on the rate of evolution in  $y$  by taking the derivative of this quantity with respect to  $x$ , giving  $(\frac{\partial \log \hat{n}(\bar{z})}{\partial x} - \frac{\partial \log \sigma_W^2(\bar{z})}{\partial x})\hat{n}(\bar{z})/\sigma_W^2(\bar{z})$ . When this derivative is positive an increase in  $x$  will speed evolution in  $y$ , lowering the lag and favoring persistence (potentially leading to evolutionary rescue). When it is negative an increase in  $x$  will slow evolution in  $y$ , increasing the lag and favoring extinction (potentially leading to evolutionary suicide). In this article, we were concerned with the effects of evolving cooperation. In our model of cooperation, the first term of the derivative is positive (because cooperation increases population size,  $\partial \log \hat{n}(\bar{z})/\partial x > 0$ ) but the second term can be negative for some fitness partitions (because cooperation can also increase drift,  $\partial \log \sigma_W^2(\bar{z})/\partial x > 0$ ). The balance between these two terms underlies the diversity of results we have reported.

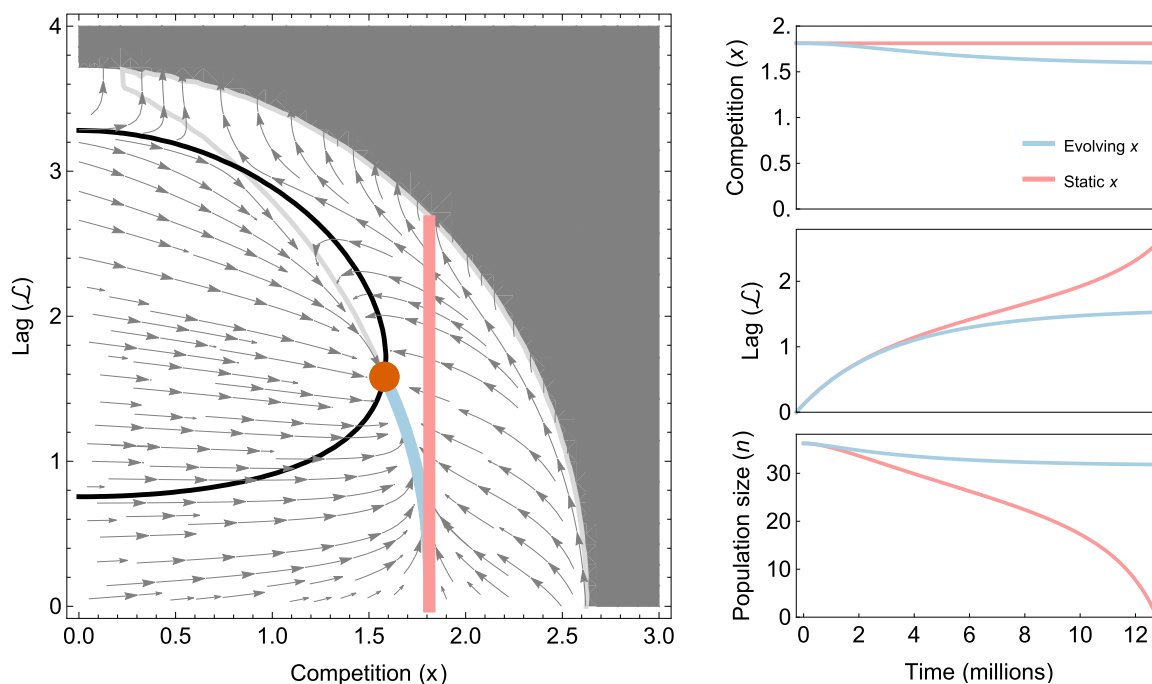
Although this work has been motivated by cooperation, the same framework can be used, more generally, to explore other types of social interactions. As an example, we have implemented in our framework a well-known model of competition (Matsuda and Abrams 1994). In this model, individuals are characterized by a costly trait  $x$  determining their resource preference and competitive ability. Individuals with more similar traits compete more strongly and individuals with larger traits out-compete those with smaller (for details, see Section S5 and the accompanying *Mathematica* notebook, deposited in Dryad; Henriques and Osmond 2020). Matsuda and Abrams (1994) showed how this competition kernel leads to the runaway evolution of extreme competitive abilities, despite the imposed cost, resulting in one of the earliest examples of evolutionary suicide.

Here we add a second trait  $y$  to this model, and explore how the evolution of competitive ability  $x$  affects the ability of a population to track a moving environmental optimum through evolution in  $y$ . As in the cooperation model, there are ecoevolutionary feedback loops between population density and trait values. In particular, population density decreases with higher levels of competition (Fig. S11A). This implies that the first term in our derivative of evolutionary rate above is now negative ( $\partial \hat{n}(\bar{z})/\partial x < 0$ ), meaning increased competition will tend to slow the evolution of  $y$  through this pathway. However, as the lag increases population size declines, lowering the equilibrium level of competition (Fig. S11C). As a result, evolution leads to reduced competition and larger population sizes than would occur if competition was fixed. In some cases, this means that the evolution of competition (which, in static environments, can result in population extinction through evolutionary suicide) can actually rescue populations from extinction during environmental change (Fig. 6). Interestingly, however, despite the fact that in some fitness partitions the evolution of reduced competition results in more genetic drift ( $\partial \log \sigma_W^2(\bar{z})/\partial x < 0$ ) and as a consequence increased lags, we did not find numerical examples where the evolution of competition lowered the critical rate of environmental change and thus caused extinction in a changing environment (in contrast to our model of cooperation). This is particularly interesting given this model was originally introduced as a model of evolutionary suicide in a constant environment. We expect that alternative functional forms of the fitness components would allow evolutionary suicide in changing environments as well, but leave this as a conjecture.

## Discussion

In this manuscript, we have studied the role that the evolution of cooperation may play during adaptation to environmental change. By modeling cooperation as an ecological public goods game (Hauert et al. 2006a, 2008; Wakano et al. 2009; Parvinen 2010; Gokhale and Hauert 2016), we were able to connect the dots between changes in environmental conditions and the evolution of social behavior. Our prediction was that changes in the environment would promote the evolution of cooperation, which would compensate for decreases in population size and permit populations to keep up with moving environments. When the population is polymorphic (cooperators and defectors), we indeed observed these dynamics (see Section S3.1). However, when the population is monomorphic for an intermediate level of cooperation, we found out that widely different outcomes are possible, depending on how the different factors that affect fitness (costs of cooperation, environmental mismatch, and density regulation) are partitioned between viability and fecundity.





**Figure 6.** Evolution of competition with a moving optimum, for a species with viability equal to 1 and a fecundity that depends on competition ( $x$ ) and lag ( $L$ ). The stream plot to the left indicates the change in a population's lag and competition over time, for a population where competition evolves fast relative to the environmental change. The nullclines for lag ( $\dot{L} = 0$ ) and competition ( $\dot{x} = 0$ ) are in black and light gray, respectively. Within the dark gray region, the population goes extinct. The thick blue curves are the result of numerical simulations, starting with zero lag and with  $x$  at equilibrium. For comparison, the thick pink curves are the result of numerical simulations, with identical starting conditions, where competition does not evolve ( $\mu_x = 0$ ). The panels on the right show the time dynamics of competition, lag, and population size for the same simulations. Parameters:  $\lambda = 1000$ ,  $a = 0.1$ ,  $c = 1$ ,  $s = 1$ ,  $k = 2$ ,  $\mu_x = \mu_y = 10^{-4}$ ,  $\sigma_x = \sigma_y = 0.01$ ,  $v = 0.5 \times 10^{-6}$ . For more details on the model, and for parameter interpretation, see Section S5.

We contrasted a fitness partition where the costs of cooperation affect fecundity (D: Figs. 3A and 4A), to one where they affect viability (CD: Figs. 3B and 4B). In the former case the evolution of cooperation promoted rescue, whereas in the latter it led to evolutionary suicide. This seemingly paradoxical result arose because, in the latter case, while cooperation increased census population sizes, it also increased variance in reproductive success, thus decreasing the effective population size (Kimura and Crow 1963; Hedrick 2005) and slowing down adaptation by increasing the effect of genetic drift. The evolution of a population toward extinction—evolutionary suicide (Ferrière 2000; Gyllenberg and Parvinen 2001)—has often been discussed in the context of evolution favoring selfish individuals (Gyllenberg and Parvinen 2001; Gyllenberg et al. 2002; Rankin et al. 2007), which leads to a tragedy of the commons (Hardin 1968). However, here we have shown the opposite effect, where the evolution of increased levels of cooperation underlies evolutionary suicide.

Other models have previously shown that the fitness component being affected by cooperation (viability or fecundity) has important consequences for the evolution of altruism. In spatially structured populations, the “scaled relatedness coefficient” (i.e.,

a cost-to-benefit ratio of cooperation that incorporates both local competition effects and effects of population structure, as in Lehmann and Rousset 2010; Van Cleve and Lehmann 2013) depends on life-cycle properties, so that in certain models, the evolution of cooperation is contingent on whether the benefits and costs of sociality affect fecundity (“death–birth updating”) or survival (“birth–death” updating), cf. (Ohtsuki and Nowak 2006; Grafen 2007; Taylor et al. 2007; Débarre et al. 2014).

Although we focused on models with nonoverlapping generations, there are other possibilities. At the opposite end of the life-history spectrum, we may consider another extreme whereby generations overlap and in which individuals reproduce asynchronously by producing a single offspring at a time (as may be the case with microbes that reproduce by binary fission or by budding). Such a life history resembles a continuous-time birth–death process, and is commonly modeled using the standard canonical equation of adaptive dynamics (Dieckmann and Law 1996). A species with this life history has a rate of evolution that is proportional to  $n/2$  (Dieckmann and Law 1996), rather than  $n/\sigma_w^2$ , which is always increased by cooperation (up to  $x_{\text{crit}}$ , which is the maximum value of cooperation that will evolve). Thus, such a species will qualitatively behave like a species with

fitness partition D, meaning that the evolution of cooperation would favor persistence.

There is, of course, a wide range of possible life histories between synchronous semelparity and asynchronous budding. Species may be iteroparous, having multiple broods throughout their lives. Furthermore, in iteroparous species reproduction may be either synchronous (as with many perennial plants) or asynchronous (as with most mammals). The canonical equation of adaptive dynamics for iteroparous diploids and haplodiploids (Metz and de Kovel 2013) is similar to equation (13) in that it includes the term  $1/\sigma_W^2$ , meaning that qualitatively, CD-type effects may be at play in such species (i.e., the evolution of cooperation may lead to evolutionary suicide in changing environments). The same is true for physiologically (e.g., age or stage) structured populations (Durinx et al. 2008).

Many of the analytical results discussed so far (e.g., equations 7–11, 16–18) depend on the specific functional forms we chose in the “Partitioning fitness components” section, and in particular on the cost and benefit functions. However, our qualitative result—namely, that the evolution of cooperation as a response to environmental change can either promote or hurt persistence, depending on the specific fitness partition—can be observed for a variety of functional forms. The benefit function adopted in equation (5) assumes that the benefits of cooperation increase linearly with the level of cooperative investment,  $x' + (g - 1)x$ . This assumption of linearity is inherited from the continuous-strategy form of the traditional multiplayer prisoner’s dilemma. However, nonlinearity is mathematically more general, and empirically, nonlinear public goods are more common than linear public goods in biological systems (Archetti and Scheuring 2012). Two types of nonlinear benefits that are particularly relevant from a biological point of view are discounted and synergistic benefits (examples of which have been studied by Motro 1991; Hauert et al. 2006b; Cornforth et al. 2012, and, in the context of ecological public goods games, by Gokhale and Hauert 2016). Discounted benefits grow sublinearly with investment (i.e., they are a concave function of cooperation), whereas synergistic benefits grow super-linearly (convex function). In Section S4.1, we provide examples of numerical simulations showing that our main results are robust to at least small deviations from linear benefits.

The same concern exists for the cost function. In this manuscript, we chose a cost function that changes nonlinearly with cooperative investment  $x$  (equation 3), but linear costs ( $C(x) = 1 - cx$ ) are also possible. (We use the word “linear” in slight abuse of terminology; more precisely, we considered a piecewise linear function,  $C(x) = \max(1 - cx, 0)$ , to avoid nonsensical negative values.) Numerical simulations show that our main results can also be obtained for linear costs (see Section S4.2.1). Note, however, that this alternative functional form ren-

ders the evolutionary branching scenario impossible (at least when benefits are also linear).

Traditional models of public goods games assume that the cost of cooperation is additive (i.e., subtracted from fitness) rather than multiplicative. The choice of a multiplicative cost function in our model has a number of advantages: it constrains fitness to biologically meaningful (positive) values and it facilitates comparison with continuous-time models. Ignoring, for simplicity, the fitness components that do not relate to cooperation, Wrightian fitness equals  $W(x'|x) = \bar{B}(x'|x, n)C(x')$ . In continuous time, we can define  $m(\cdot) = \log(W(\cdot))$  as the Malthusian fitness (Crow and Kimura 1970; Wu et al. 2013); we then have  $m(x'|x) = \log(\bar{B}(x'|x, n)) + \log(C(x'))$ . In particular, for the functional form in equation (3), we have  $\log(C(x')) = -cx'^k$ , which is comparable to previous implementations of the ecological public goods game (Hauert et al. 2006a), where costs are subtracted from benefits. Regardless, our main results can still be obtained using additive costs (Section S4.2.2), provided that one is careful to avoid biologically impossible fitness partitions, at which fecundity or viability turn negative.

The evolution of cooperation is critically dependent on the size of the interaction groups. In our model, cooperation is more beneficial when groups are small. The average group size is given by the product of the population size and the interaction probability  $p$ . Note that in many of our numerical simulations (including some in Figs. 1–3), group sizes are often small, which allows for the maintenance of cooperation. In some of these cases, the most frequent “group” consists solely of the focal individual (which can hardly be described as cooperation). In this sense, our results do not depend on the presence of cooperation, only on the evolution of trait  $x$  (see the “Extension to other types of social interactions” section). However, even in those simulations, cooperation in the sense of public good sharing still takes place, because there is variation in group size. Further, the “The critical rate of environmental change” section explains how our results are expected to hold regardless of the specific parameter values chosen.

Previous models (Brännström et al. 2011; Peña 2012; Peña and Nöldeke 2016) have shown that variation in group size influences the evolution of cooperation. In our model the benefits of cooperation (equation 6) are calculated using the entire distribution of group sizes and are therefore influenced by its variance ( $np(1 - p)$ ). We follow the approach of previous models of ecological public goods games (Hauert et al. 2006a, 2008; Parvinen 2010; Gokhale and Hauert 2016) in assuming that individuals engage in enough interactions that fitness depends only on the mean benefit accrued across all group sizes. In the future it would be interesting to relax this assumption and study how the outcomes of ecological public goods games change when there are fewer interactions per generation. In such cases the benefits of

cooperation would be stochastic and perhaps then depend more strongly on the variance in group size.

Overall, our results highlight that species engaging in cooperative interactions may exhibit disparate and counterintuitive responses to environmental change. For example, mammals and birds engaging in public goods provisioning (although they are most often iteroparous) have a relatively low number of offspring, and low reproductive variance. In contrast, many social insects, which engage extensively in cooperative interactions, have nonoverlapping generations and very high numbers of offspring, implying the possibility of high reproductive variance. Whether reproductive variance indeed increases with fecundity depends on the distribution of offspring number. In this model, we assumed that it does (by modeling fecundity as a Poisson distribution), which had a major influence in our results, but other choices could lead to different outcomes. Overall, whether the evolutionary dynamics of social behavior will ultimately be beneficial or detrimental during adaptation to environmental change is contingent on the species' specific life history.

In the future, it would be interesting to extend the model to include other biologically realistic possibilities, such as environmental noise and plasticity, as well as alternative features such as diploidy and sexual reproduction. Furthermore, it would be interesting to consider whether these results apply also to other mechanisms of cooperation. For example, if cooperation is modeled through kin selection, declines in population size can increase or decrease the degree of relationship between individuals (depending on life cycle and spatial structure, cf. Table 1 in Van Cleve and Lehmann 2013). This provides the opportunity for dynamics very similar to the ones we have described. In contrast, other mechanisms of cooperation may affect adaptation in quite different ways. Particularly, in the case of between-species cooperation (mutualism), environmental change would set up coevolutionary feedback loops (Northfield and Ives 2013) that are not well described by our framework.

## AUTHOR CONTRIBUTIONS

GJBH conceived of the project, wrote the simulations, and wrote the article. MMO supervised the project and contributed substantially to the simulations and to writing. Both authors participated in developing the model.

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## DATA ARCHIVING

Data and code are available in a Dryad digital repository: <https://doi.org/10.5061/dryad.bg79cnp83>.

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## Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Figure S1.** Individual-based simulations showing cooperation values (left) and population size (right) for both monomorphic and polymorphic dynamics, with static environments.

**Figure S2.** Equilibrium strain sizes in a bimorphic population with a constant lag.

**Figure S3.** As the environment changes, the frequency of cooperators increases (A) which, after a period of oscillations, stabilizes the population size (B) and the distance to the optimum (C).

**Figure S4.** Frequency of cooperators (A), strain sizes (B), and distance to the optimum (C) at dynamical equilibrium, for different velocities of environmental change ( $v$ ).

**Figure S5.** Effects of small deviations from linearity with a constant lag, for low (top) and high (bottom) values of  $p$ .

**Figure S6.** Lag (left) and population size (right) at the dynamical equilibrium, in populations with fitness partition d (panel A) or fitness partition cd (panel B), for different velocities of environmental change ( $v$ ).

**Figure S7.** Ecological and evolutionary dynamics are qualitatively similar between the nonlinear multiplicative cost scenario (main text) and the linear multiplicative cost scenario.

**Figure S8.** Evolution of cooperation with a moving optimum in a model with linear multiplicative costs, for a species with fitness partition d (panel A) or fitness partition cd (panel B).

**Figure S9.** Ecological and evolutionary dynamics are qualitatively similar between the nonlinear multiplicative cost scenario (main text) and the linear additive cost scenario.

**Figure S10.** Evolution of cooperation with a moving optimum in a model with linear additive costs, for a species with fitness partition cmd (panel A) or fitness partition cd (panel B).

**Figure S11.** Competition  $x$  decreases the ecological equilibrium of population density  $\hat{n}(A)$ , creating an ecoevolutionary feedback loop.

Data S1

Data S2