

# 1 **Species-level selection reduces selfishness through competitive exclusion**

2 Daniel J. Rankin<sup>1</sup>, Andrés López-Sepulcre<sup>1,2</sup>, Kevin R. Foster<sup>1,3</sup> & Hanna Kokko<sup>1</sup>

3 <sup>1</sup> Laboratory of Ecological and Evolutionary Dynamics, Department of Biological and  
4 Environmental Sciences, University of Helsinki, Finland

5 <sup>2</sup> Evolutionary Ecology Research Unit, Department of Biological and Environmental Science,  
6 University of Jyväskylä, Finland

7 <sup>3</sup> Center for Systems Biology, Harvard University, Bauer Laboratories, 7 Divinity Avenue,  
8 Cambridge, MA 02138, USA

9 **Author E-mail addresses: DJR:** [daniel.rankin@helsinki.fi](mailto:daniel.rankin@helsinki.fi), **AL-S:**

10 [andres.lopezsepulcre@helsinki.fi](mailto:andres.lopezsepulcre@helsinki.fi) **KRF:** [kfoster@cgr.harvard.edu](mailto:kfoster@cgr.harvard.edu), **HK:**

11 [hanna.kokko@helsinki.fi](mailto:hanna.kokko@helsinki.fi)

12 **Corresponding author:** Daniel J. Rankin, Laboratory of Evolutionary and Ecological

13 Dynamics, Department of Biological and Environmental Science, University of Helsinki, P.O.

14 Box 65 (Viikinkaari 1), FIN-00014 Helsinki, Finland

15 **Telephone:** + 358-9-1915 7866. **Fax:** +358-9-1915 7694.

## 1 **Summary**

2 Adaptation does not necessarily lead to traits which are optimal for the population. This is  
3 because selection is often strongest at the individual or gene level. The evolution of  
4 selfishness can lead to a ‘tragedy of the commons’, where traits such as aggression or social  
5 cheating reduce population size and may lead to extinction. This suggests that species-level  
6 selection will result whenever species differ in the incentive to be selfish. We explore this  
7 idea in a simple model that combines individual-level selection with ecology in two  
8 interacting species. Our model is not influenced by kin or trait-group selection. We find that  
9 individual selection in combination with competitive exclusion greatly increases the  
10 likelihood that selfish species go extinct. A simple example of this would be a vertebrate  
11 species that invests heavily into squabbles over breeding sites, which is then excluded by a  
12 species that invests more into direct reproduction. A multi-species simulation shows that these  
13 extinctions result in communities containing species that are much less selfish. Our results  
14 suggest that species-level selection and community dynamics play an important role in  
15 regulating the intensity of conflicts in natural populations.

16 **Key-words:** Levels of selection, interspecific competition, selfishness, conflict

1 “Animals and plants are not quite such ruthlessly efficient strugglers as they would be if Darwinism were the  
2 whole truth... it does not pay a species to be too well adapted. A variation making for too great efficiency may  
3 cause a species to destroy its food and starve itself to death. This very important principle may explain a good  
4 deal of the diversity in nature, and the fact that most species have some characters which cannot be accounted  
5 for on orthodox Darwinian lines”. J.B.S. Haldane (Haldane, 1939)

## 6 **Introduction**

7 Ever since the group selection debate in the 1960s, it has been clear that selection acting at the  
8 level of the gene or the individual does not necessarily produce adaptations that are optimal  
9 for the population (Dawkins, 1976, Williams, 1966). Indeed, individual-interested behaviour  
10 can often be expected to cause resource depletion resulting in a the ‘tragedy of the commons’  
11 (Hardin, 1968), which in its most extreme form may cause population demise, or  
12 ‘evolutionary suicide’ (Dieckmann & Ferrière, 2004, Parvinen, 2005).

13 The concept of the tragedy of the commons has most often been evoked when studying the  
14 overexploitation of resources by humans (Hardin, 1998, Ostrom, 1999, Penn, 2003), where it  
15 is argued that short-sighted selfish behaviour will invariably lead to disaster for the  
16 individuals using that resource. However, it also applies to non-humans where selection for  
17 selfish competition is expected to be widespread (Frank, 1995, Leigh, 1977, Falster &  
18 Westoby, 2003, Foster, 2004, Rankin & Kokko, 2006, Wenseleers & Ratnieks, 2004). Moral  
19 restraint is often invoked as an argument for resolving the tragedy in humans (Hardin, 1968),  
20 and policing (Frank, 1995, Wenseleers & Ratnieks, 2006b) or sufficient relatedness (Frank,  
21 1995, Foster, 2004, Wenseleers & Ratnieks, 2004) can limit the tragedy in other species.  
22 However, the evolution of policing is only possible in some contexts (such as insect societies  
23 – e.g. Wenseleers & Ratnieks, 2006b), and not all species exist in kin-structured communities.  
24 This begs the question of whether evolutionary suicide commonly occurs in nature (Rankin &

1 López-Sepulcre, 2005), and whether such extinctions can act as an important higher level of  
2 selection (Foster, 2006).

3 An increasing number of empirical and theoretical studies show how individual selection has  
4 the potential to harm the population (e.g. Muir & Howard, 1999, Fiegna & Velicer, 2003). For  
5 example, territorial animals risk injury, as well as waste time and energy that could be better  
6 invested in reproduction and survival, in contests over space. Succeeding in this competition  
7 is essential for individual reproduction but the predicted patterns of space division reduce the  
8 number of individuals that can exist on any given area (López-Sepulcre & Kokko, 2005).

9 Conflicts can therefore result in a lowering of population density (López-Sepulcre & Kokko,  
10 2005). Figure 1 shows examples where wasteful within-species conflict may affect species  
11 persistence.

12 While a reduction in population density is not equivalent to extinction, it is likely to increase  
13 the extinction risk (Soulé, 1987, Leigh, 1981, Lande, 1993). Species extinctions, for example,  
14 have long been considered to be important in the evolution of sex, due to the higher extinction  
15 risk of asexuals (Fisher, 1930, Nunney, 1989, van Valen, 1975), and extinctions are also  
16 thought to be important in the evolution of cancer (Nunney, 1999). Despite a rich history on  
17 the relative importance of species-level selection as an adaptive force (Gould & Lloyd, 1999,  
18 Lloyd & Gould, 1993, Vrba, 1984), the population consequences of adaptive behaviour have  
19 been argued to act as a relatively weak selective pressure at the level of the species (e.g.  
20 Maynard Smith, 1964). However, in a community context, traits are expected to affect species  
21 persistence when they alter the likelihood of competitive exclusion by other members of the  
22 community (Hardin, 1960, Ciroso-Pérez et al., 2002), even if they do not cause evolutionary  
23 suicide by themselves.

1 Here we explore the effects of extinctions at the species-level on the evolution of conflict in  
2 multi-species communities. We specifically look at the joint effect of individual-level  
3 selection, where selection acts on individuals, and species-level selection, where species go  
4 extinct due to behavioural adaptation at the individual level. There is no spatial deme structure  
5 or trait-group selection (sensu Wilson, 1975) in the model. First, we incorporate selfish  
6 evolution into a simple two-species Lotka-Volterra competition model to illustrate the extent  
7 to which competitive exclusion may influence the population density of selfish species.  
8 Second, we use a simulation to investigate macroevolutionary effects, both in an isolated  
9 species and in a community setting. In particular, we ask the question that, given selfish  
10 competition within a species may harm populations, what part do community interactions  
11 play in the macroevolutionary consequences of such harm?

# 1 **The models**

## 2 **1. TWO-SPECIES DYNAMICS AND THE EVOLUTION OF SELFISHNESS**

3 Our goal is to evaluate the impact of a selfish and competitive trait  $z_i$  on population  
4 persistence and the resulting species-level selection. In this section, we describe a simple  
5 analytical model of two species, where species 1 suffers from wasteful and selfish within-  
6 species competition. The logic of the model is to calculate the evolved level of selfishness in  
7 species 1 (e.g. fighting), and then see how this affects its population density. By putting the  
8 effects of wasteful competition into the ecological context, we are able to evaluate how  
9 wastefulness within a species affects between-species competition, and ultimately, species  
10 persistence. We begin, however, by defining the two key terms in the models.

11 *Selfishness:* Competitive ‘selfishness’  $z_i$  is the degree to which individuals of species  $i$   
12 compete in a way that lowers the reproductive performance of the population, where  $0 \leq z \leq$   
13 1. Our use of ‘selfishness’ throughout the paper, therefore, refers to the strength of  
14 intraspecific conflict. A simple example is fighting over a breeding site where an individual  
15 allocating all of its energy into such fights would have a  $z$  of 1, while a non-fighting  
16 individual would have a value of  $z=0$ . Investing energy in fighting decreases the resources  
17 available for reproduction, and is expected to therefore decrease population density (López-  
18 Sepulcre & Kokko, 2005). Other potential examples include investment in slime production  
19 by bacteria that suffocates members of the same species but lowers overall growth rate  
20 (Xavier & Foster, 2007), or social insect larvae that become new queens rather than workers  
21 in colonies that already have a queen (Ratnieks et al., 2006, Wenseleers & Ratnieks, 2004).  
22 Figure 1 shows some example systems where wasteful selfishness may affect species  
23 persistence.

1 *Competitive Incentive:* The evolution of traits like fighting will depend not only on the  
2 demography and the environment, but also on the constraints and life history characteristics of  
3 the species in question. Because species differ in their constraints, the incentive to invest in  
4 selfish competition with other members of their species will also differ between species. For  
5 example, predator avoidance might constrain a bird's ability to fight, and in insect colonies  
6 with a discrete reproductive phase and no queen succession, there is no benefit to selfishly  
7 becoming a new queen apart from during a short period each year (e.g. vespine wasps, Foster  
8 & Ratnieks, 2001). We investigate how this incentive  $\alpha_i$  affects the level of conflict, and  
9 higher levels of selection. The value of  $\alpha_i$  can change, according to the extent to which this  
10 incentive covaries with population density (e.g. territorial aggression may be  
11 counterproductive if vacant breeding habitat is readily available, Kokko *et al.*, 2006), such  
12 that  $\alpha_i$  is the maximum incentive of individuals in species  $i$  to invest in selfishness in the  
13 absence of any influence of density on the behaviour.

14

15 *Individual-level selection*

16 We start by considering selection for selfish behaviour within species 1 by calculating the  
17 invasion fitness of a mutant  $z_i'$  invading a population of residents. The fitness of a mutant,  
18  $z_j'$  is then

19 
$$w(z_i', \bar{z}_1) = f(z_i', \bar{z}_1) R_1(\bar{z}_1) \tag{1}$$

20 Where  $R_1(\bar{z}_1)$  defines the group performance of species 1 (per capita growth rate), which is a  
21 function of selfishness in species 1 but is also affected by resource competition from species 2  
22 (see equation 2, below). The benefit gained from a mutant individual investing  $z_i'$  in  
23 competition in a population comprising individuals which invest  $\bar{z}_1$  in selfishness is described

1 by the function  $f(z_1', \bar{z}_1)$ . Following the logic of Frank (1995) and Foster (2004), we use  
2  $f(z_1', \bar{z}_1) = (z_1' / \bar{z}_1)^\alpha (1 - cz_1')$ , where  $\alpha$  scales the incentive to invest in selfish competition.  
3 For  $\alpha = 1$  and  $c = 0$ , the model becomes identical to Frank (1995), where selfishness leads to  
4 population collapse (a tragedy of the commons). However, for  $c > 0$ , the expression includes  
5 an individual cost of expressing the selfish traits, which puts an upper bound on the individual  
6 investment into competition (e.g. intense fighting is personally costly, Foster, 2004,  
7 Hammerstein & Reichert, 1988). A mutant with a phenotype of  $z'$  will be able to invade a  
8 population containing  $\bar{z}$  individuals if  $w(z_1', \bar{z}_1) - w(\bar{z}_1, \bar{z}_1) > 0$ , allowing us to calculate the  
9 direction of evolution (lower or higher  $z$  favoured) in  $z_1$ .

10

### 11 *Two-species interactions*

12 We now consider the impact of selfishness  $z$  in species 1 on the population dynamics and  
13 competition with species 2. In our example, we assume that species 2 does not exhibit selfish  
14 behaviour (e.g. does not fight with conspecifics), and therefore has a value of  $z$  fixed at zero.  
15 This allows us to look at the population consequences of the evolution of selfishness of  
16 species 1 (eq. 1), when undergoing interspecific competition. The two species compete over a  
17 common resource  $E$ , where  $E_i(x)$  is the maximum availability of resource  $x$  that an individual  
18 of species  $i$  could use. Critically, the *ability* of species 1 to translate the shared resource into  
19 reproduction decreases with increased selfishness  $z$  (equation 2 below).  $x$  denotes a resource  
20 gradient that may be interpreted in different ways, for example habitat with a specific  
21 microclimate ( $E_i(x)$  then gives the area of such habitat available to individuals of species  $i$ ), or  
22 food items of a specific size ( $E_i(x)$  is then the available density of such items). To provide an  
23 illustrative example, the amount of resources available to each species is defined by two



1 simple functions:  $E_1(x) = bExp(1-x)$  and  $E_2(x) = bExp(x)$ , such that the two species have a  
 2 significant degree of niche overlap but they are not ecologically identical (species 2 is better  
 3 at using large values of  $x$ ). The overlap makes interspecific competition an important factor  
 4 determining the densities of both species. The population density of species  $i$  is given as  $n_i$   
 5 and its dynamics can be described by the equation  $n_i(t+1) = R(\bar{z}_i)n_i(t)$ , where  $R$  indicates  
 6 average *per capita* population growth:

$$7 \quad R_i(\bar{z}_i) = \int \frac{E_i(x)q(\bar{z}_i)}{n_1E_1(x) + n_2E_2(x)} dx \quad (2)$$

8 The effect of density-dependence from within- and between-species competition is captured  
 9 by the denominator in equation 2: in the absence of species 2, the reproductive rate of species  
 10 1 is simply determined by the number of individuals in the population (i.e. it is density  
 11 dependent). In the presence of conflict with other individuals, the effect of wasteful  
 12 selfishness by members of species  $i$  on resource availability is captured by  $q_i(z_i)$ , where  $q_i$  is  
 13 the fraction of the resource that remains useful to individuals of a given species, and  
 14 selfishness ( $z$ ) has a negative effect on this fraction, such that  $\partial q_i(z_i)/\partial z_i < 0$ , and  $q(z_i) = (1-z_i)^\beta$ .  
 15 A low value of  $\beta$  means that competition in a species is very wasteful, and therefore  
 16 population-wide reproduction suffers greatly from individual selfishness, making a species  
 17 more likely to go extinct with a small increase in  $z$ . A larger value confers the opposite effect.  
 18 Note that  $q$  does not appear in the denominator, indicating that resources inefficiently used by  
 19 species 1 are not available to the other species. This assumption makes our model  
 20 conservative because if resources wasted by species 1 could be used by species 2 then this  
 21 would further promote the advantage of the latter. A nice example of this possibility is  
 22 territoriality. If species 1 is highly territorial over space and leaves a lot of resources

1 unexploited in the environment, this will not only lower its growth rate (López-Sepulcre &  
2 Kokko, 2005) but also increase the resources available to competing species.

3

#### 4 *Model results*

5 Figures 2 and 3 show the zero-growth isoclines of this two species system, along with the  
6 respective population densities when species 1 has reached evolutionary stability. This  
7 assumes that populations are always at their ecological equilibria i.e. that ecological processes  
8 are much faster than evolutionary ones. First we consider the dynamics of species 1 if species  
9 2 is absent (points along the  $x$  axis, Figure 2). Individual-level selection then has a fairly  
10 minor effect on the population density of species 1 (compare the location of point I in Figure  
11 2a with Figure 2b). Now consider coexistence if neither species has yet evolved selfishness  
12 (point II in the left-hand figure); the different but symmetrical use of the resource gradient  
13 results in coexistence where both species have equal population density.

14 When individual-level selection and between-species competition are considered in  
15 combination, the outcome is dramatically different. Individual level selection for wasteful  
16 resource use in species 1 reduces its ability to compete with species 2. As a result competitive  
17 exclusion occurs and species 1 goes extinct (point II in the right-hand figure). For example,  
18 this could mean that within-species fighting in species 1 reduces the population growth rate so  
19 much that species 2 can drive it extinct. Or comparably, that within-group competition in a  
20 slime mould slug limits its migration (Foster et al., 2002) so much that a second conflict-free  
21 species is able to out-compete it by reaching resources more efficiently.

22 Figure 3 shows the isoclines of a case where the competitive incentive is lower, and both  
23 species can coexist even after species 1 has undergone selection for increased selfishness.  
24 Even here, the combination of individual-level selection and competition from species 2

1 combines to result in a greatly reduced population density of species 1, which in a stochastic  
2 world could imply increased vulnerability to extinction (Leigh, 1981, Lande, 1993). This may  
3 reflect the situation in the yellowjacket wasps where species with high levels of intracolony  
4 conflict over male production tend to have smaller colonies (Foster & Ratnieks, 2001).

## 5 **2. EVOLUTION OF SELFISHNESS IN A MULTI-SPECIES SIMULATION**

6 Our isocline model is a proof-of-principle that selfishness selected at the individual level can  
7 have important consequences for the probability that a species will persist. We now use a  
8 simulation to evaluate its macroevolutionary consequences in communities containing many  
9 evolving species (our previous example only allowed one species to evolve). Our focus is on  
10 the competitive incentive ( $\alpha_i$ ), which is the central parameter defining the level of selfishness  
11 in a focal species. This is a species property or life-history character which drives the benefit  
12 gained from investing in conflict. Low values of  $\alpha$  mean that there is relatively little to be  
13 gained from investing more in selfishness  $z$ , while higher values of  $\alpha$  mean the opposite. We  
14 examine its distribution before and after the simulation in order to ascertain whether species-  
15 level selection affects the overall selfishness of species. In addition, we compare community  
16 simulations to the case of a single species (isolated-species simulations) to examine whether  
17 community interactions amplify any effects of species-level selection.

18 The community simulation allows speciation to take place, with daughter species being  
19 ecologically similar to the immediate ancestor, and species going extinct if they fail to satisfy  
20 current conditions for ecological coexistence. We continually update the equilibrium  
21 population density for each evolved level of selfishness, and hence take every species to be at  
22 its ecological equilibrium density. As such, we assume a separation of ecological and  
23 evolutionary time-scales such that individual-level selection takes place at a much slower rate  
24 than the population dynamics (see appendix). The ecological and evolutionary dynamics

1 generate extinction events intermittently across the simulation whenever selfishness evolves  
2 to levels which result in population densities below a certain extinction threshold,  $\epsilon$ . Full  
3 details of the simulation are provided in the appendix.

#### 4 *Model results*

5 Figure 4 shows the initial distribution of the incentive for selfishness, and the distributions of  
6 the trait in the surviving species at the end of the simulation for both the isolated simulation  
7 and the community simulation. Analysing the results of all simulations reveals that species-  
8 level selection has a strong effect on the distribution of species properties: the starting  
9 distribution differed significantly with the distribution after individual-level selection in an  
10 isolated species (Kolmogorov-Smirnov  $p < 0.0001$  both when  $\beta = 2$  and  $\beta = 5$ ). Taking  
11 interactions with other species into account in the community simulation revealed that  
12 community ecology greatly intensified species-level selection: the distribution of surviving  
13 species in the community simulation differed significantly from both the original distribution  
14 (Kolmogorov-Smirnov  $p < 0.0001$  both when  $\beta = 2$  and  $\beta = 5$ ) and from the surviving species  
15 in the single-species simulation (Kolmogorov-Smirnov  $p < 0.0001$  both when  $\beta = 2$  and  $\beta = 5$ ).  
16 This is well illustrated by the medians of the incentive  $\alpha$ , which were roughly halved from  
17 their initial values in the single species simulation, and halved again in the community  
18 simulation (figure 4). Means of distributions undergo changes of similar magnitude (not  
19 shown).

20 We checked the robustness of our results against several alternative assumptions. The results  
21 of our model were qualitatively the same (i.e. shifts of distributions show similar patterns) if  
22 density-dependence of the incentive (see appendix) was removed. Likewise, the results  
23 remained qualitatively similar when (1) the daughter species had a low population size (set at  
24 a value slightly larger than the extinction threshold), as opposed to parent and daughter

1 species both taking half of the original population density, (2) for longer simulation times  
2 (10,000 versus 3000 generations) were used and (3) for variation in the initial distribution of  
3  $\alpha$ .

4

## 5 **5. Discussion**

6 There is a strong feeling in the evolutionary literature that adaptations should be primarily  
7 viewed as a result of selection acting at the level of the individual (or further below, at the  
8 gene, e.g. Keller, 1999, Burt & Trivers, 2006). It is a telling example that Haldane was  
9 ridiculed for our opening quotation by Cronin (1993), who suggested that he was playing to  
10 socialist ideology “rather than attempting to propagate a genuine Darwinian unorthodoxy”.  
11 Our model supports Haldane’s (1939) argument. We know that the individual-level selection  
12 point of view can explain why species can be so short-sighted that they become extinct  
13 (Matsuda & Abrams, 1994a, Gyllenberg & Parvinen, 2001, Rankin & López-Sepulcre, 2005).  
14 Our model shows that this very shortsightedness necessarily creates conditions in which  
15 higher levels of selection become important, and this applies particularly strongly in a  
16 community context. We did not allow for kin or group selection to occur that might promote  
17 cooperation, yet species with more cooperative habits (lower  $z$ ) prevailed. If ‘selfishness’  
18 ultimately leads to population extinction, species in which individuals have a high incentive to  
19 behave selfishly will eventually be removed. This will consequently affect the properties of  
20 species that we see in nature.

21 A central finding from our model is that it is not required that species commit true  
22 evolutionary suicide for species-level selection to work. Selfishness need only weaken a  
23 species, such that it more easily falls victim to competitive exclusion (figure 2). This shows  
24 that Hardin’s competitive exclusion principle (Hardin, 1960) can function to make the effects

1 of his tragedy (Hardin, 1968) more severe. Competitive exclusion is a common finding in  
2 ecological communities, which suggests that these processes have important consequences for  
3 real communities. This is consistent with work on sexual and asexual populations of rotifers  
4 (Ciros-Pérez *et al.*, 2002). In single-species populations, costs associated with sex had no  
5 effect on population density (Ciros-Pérez *et al.*, 2002). However, in multispecies communities  
6 the increased levels of sexual reproduction resulted in increased risk of competitive exclusion  
7 and extinction, generating species-level selection against sexuality. Although the study by  
8 Ciros-Pérez *et al.* (2002) did not consider selfishness *per se*, it clearly highlights the potential  
9 effects of community interactions upon extinctions.

10 The evolutionary effects in our model are driven by the fact that species differ in traits  
11 associated with selfishness (which is reflected in  $\alpha$ ). There are many ways that this can come  
12 about, including basic differences in ecology: a species foraging on concentrated patchy  
13 resources that can be defended might have a higher propensity for competition and selfishness  
14 than one living on dispersed resources. Although not required, variation in the incentive for  
15 selfishness will be also affected by factors that promote cooperation, such as the degree to  
16 which individuals interact with relatives (Figure 1a,c; Hamilton, 1964, Griffin & West, 2003,  
17 Ratnieks *et al.*, 2006) and enforcement mechanisms (Wenseleers & Ratnieks, 2006a,  
18 Wenseleers & Ratnieks, 2006b). Another mechanism, which can be associated with  
19 enforcement (Foster *et al.*, 2007), is the degree of pleiotropy where one gene affects multiple  
20 traits. This phenomenon is both extremely common in all genomes and highly variable in its  
21 effects (Foster *et al.*, 2004, Foster *et al.*, 2007). When a pleiotropic relationship happens to be  
22 present in the genome that ties a potential selfish trait to a personal cost, this will reduce the  
23 incentive for selfishness ( $\alpha$ ). Our model predicts that this reduced incentive will increase  
24 species persistence, and, therefore, that such pleiotropic relationships should commonly occur  
25 in nature. An example can be found in a social amoeba, *Dictyostelium discoideum*, which

1 forms social aggregations where some cells die in an apparent act of altruism to form a stalk  
2 that allows other cells to disperse as spores. Pleiotropy of the gene *dimA* links this altruistic  
3 act of stalk production to the ability to make spores, thereby reducing the incentive to be  
4 selfish and limiting the evolution of cheaters that produce fewer stalk cells (Foster *et al.*,  
5 2004).

6 An associated assumption of our model is that, given that species differ in the traits associated  
7 with selfishness, the variation is great enough to be important in species persistence. An  
8 alternative explanation for the absence of traits that lead to ‘too tragic’ outcomes is that the  
9 incentives to invest in intraspecific competition are simply never great enough to be an  
10 important cause of extinctions. In our model this would correspond to values of the incentive  
11  $\alpha$  that are always constrained to low values that have little effect on species persistence  
12 compared to other traits or chance events. Evidence against this alternative come from a  
13 number of studies that suggest that individual selection can drive population demise (Rankin  
14 & López-Sepulcre, 2005). Analogously to *D. discoideum*, cells of the social bacterium  
15 *Myxococcus xanthus* form complex fruiting structures, where individuals in the fruiting body  
16 are then released as spores (Fiegna & Velicer, 2003). Artificially selected cheater strains,  
17 which produce a higher number of spores than wild-types, can invade wild-type strains under  
18 laboratory conditions. However, although such cheaters do well in competition with the  
19 wildtype, they can cause population extinction because their strategy compromises fruiting  
20 body development and they are unable to produce spores alone (Fiegna & Velicer, 2003).  
21 Further support that conflict can increase the risk of extinction comes from comparative  
22 studies. For example, the intensity of sperm competition in birds (Morrow & Pitcher, 2003),  
23 and larger genome size, associated with a higher prevalence of selfish DNA (Vinogradov,  
24 2003), have been found to be associated with extinction risk.

1 Several studies, therefore, suggest that species-level selection can be important. Nevertheless,  
2 it remains a challenge for future research to distinguish between our hypothesis that species-  
3 level selection drives down selfishness and the alternative that variation in species properties  
4 (as shown by the effects on  $\alpha$  in our model) is rarely important enough to cause extinctions.  
5 Naturally, both predict that extant species should not exhibit values that do not allow  
6 persistence. The observation that species introductions to new geographical areas are often  
7 detrimental and can cause extinctions (Clavero & García-Berthou, 2005) provides a basis to  
8 test the idea that strong intraspecific conflict predicts failure in novel situations of  
9 interspecific competition. For example, previous work has predicted that, as species richness  
10 increases, so does the extinction rate (Weatherby *et al.*, 1998). We predict these extinctions to  
11 depend not only on the degree of niche overlap, but also on how intense intraspecific conflicts  
12 are in the species concerned. All else being equal, we predict that extreme forms of  
13 intraspecific conflict are less likely to be observed in species-rich communities than in those  
14 with low species richness.



## 1 *Conclusion*

2 Despite the plethora of recent work demonstrating that individual-level selection can lead to  
3 extinction (Matsuda & Abrams, 1994a, Matsuda & Abrams, 1994b, Muir & Howard, 1999,  
4 Gyllenberg & Parvinen, 2001, Gyllenberg et al., 2002, Dercole et al., 2002, Dieckmann &  
5 Ferrière, 2004, Howard et al., 2004), the macroevolutionary consequences of such extinctions  
6 have remained unexplored. Our model demonstrates that such ‘evolutionary suicide’ can have  
7 strong effects on the distribution of traits in nature. Importantly, we show that species-level  
8 selection can operate through competitive exclusion whenever selfishness weakens the  
9 competitive ability of a species, even in the absence of true evolutionary suicide. This  
10 principle may indeed explain why species “*are not quite such ruthlessly efficient strugglers*”  
11 (Haldane, 1939) as they might be.

## 12 **Acknowledgements**

13 Funding was provided by the Academy of Finland. We are grateful to Katja Bargum, Katja  
14 Heubel and two anonymous referees, whose comments helped us to improve the manuscript.  
15 We also thank Astrid van Teffelen, Mike Fowler and John Reynolds for valuable discussions.

## 1 **References**

- 2 Burt, A. & Trivers, R. 2006. *Genes in Conflict: The Biology of Selfish Genetic Elements*.  
3 Belknap Press, Harvard.
- 4 Ciroso-Pérez, J., Carmona, M. & Serra, M. 2002. Resource competition and patterns of sexual  
5 reproduction in sympatric sibling rotifer species. *Oecologia* **131**: 35-42.
- 6 Clavero, M. & García-Berthou, E. 2005. Invasive species are a leading cause of animal  
7 extinctions. *Trends in Ecology and Evolution* **20**: 110.
- 8 Cronin, H. 1993. *The Ant and the Peacock : Altruism and Sexual Selection from Darwin to*  
9 *Today*. Cambridge University Press, Cambridge.
- 10 Dawkins, R. 1976. *The Selfish Gene*. Oxford University Press, Oxford.
- 11 Dercole, F., Ferrière, R. & Rinaldi, S. 2002. Ecological bistability and evolutionary reversals  
12 under asymmetrical competition. *Evolution* **56**: 1081-1090.
- 13 Dieckmann, U. & Ferrière, R. (2004) Adaptive dynamics and evolving biodiversity. In:  
14 *Evolutionary Conservation Biology*, (Ferriere, R., Dieckmann, U. & Couvet, D., eds.).  
15 pp. 188-224. Cambridge University Press, Cambridge.
- 16 Dieckmann, U., Marrow, P. & Law, R. 1995. Evolutionary cycling in predator-prey  
17 interactions: population dynamics and the red queen. *Journal of Theoretical Biology*  
18 **176**: 91-102.
- 19 Falster, D. S. & Westoby, M. 2003. Plant height and evolutionary games. *Trends in Ecology*  
20 *and Evolution* **18**: 337-343.

- 1 Fiegna, F. & Velicer, G. J. 2003. Competitive fates of bacterial social parasites: persistence  
2 and self-induced extinction of *Myxococcus xanthus* cheaters. *Proceedings of the Royal*  
3 *Society of London B* **270**: 1527-1534.
- 4 Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.
- 5 Foster, K. 2006. Balancing synthesis with pluralism in sociobiology. *Journal of Evolutionary*  
6 *Biology* **19**: 1394-1396.
- 7 Foster, K. R. 2004. Diminishing returns in social evolution: the not-so-tragic commons.  
8 *Journal of Evolutionary Biology* **17**: 1058-1072.
- 9 Foster, K. R., Fortunato, A., Strassmann, J. E. & Queller, D. C. 2002. The costs and benefits  
10 of being a chimera. *Proceedings of the Royal Society of London Series B-Biological*  
11 *Sciences* **269**: 2357-2362.
- 12 Foster, K. R., Parkinson, K. & Thompson, C. R. L. 2007. What can microbial genetics teach  
13 sociobiology? *Trends in Genetics*: In Press.
- 14 Foster, K. R. & Ratnieks, F. L. 2001. Paternity, reproduction and conflict in vespine wasps: a  
15 model system for testing kin selection predictions. *Behavioral Ecology and*  
16 *Sociobiology* **50**: 1-8.
- 17 Foster, K. R., Shaulsky, G., Strassmann, J. E., Queller, D. C. & Thompson, C. R. L. 2004.  
18 Pleiotropy as a mechanism to stabilise cooperation. *Nature* **431**: 693-696.
- 19 Frank, S. A. 1995. Mutual policing and repression of competition in the evolution of  
20 cooperative groups. *Nature* **377**: 520-522.

- 1 Gould, S. J. & Lloyd, E. A. 1999. Individuality and adaptation across levels of selection: How  
2 shall we name and generalize the unit of Darwinism? *Proceedings of the National*  
3 *Academy of Sciences* **96**: 11904-11909.
- 4 Griffin, A. S. & West, S. A. 2003. Kin discrimination and the benefit of helping in  
5 cooperatively breeding vertebrates. *Science* **302**: 634-636.
- 6 Gyllenberg, M. & Parvinen, K. 2001. Necessary and sufficient conditions for evolutionary  
7 suicide. *Bulletin of Mathematical Biology* **63**: 981-993.
- 8 Gyllenberg, M., Parvinen, K. & Dieckmann, U. 2002. Evolutionary suicide and evolution of  
9 dispersal in structured metapopulations. *Journal of Mathematical Biology* **45**: 79-105.
- 10 Haldane, J. B. S. (1939) Science and Everyday Life. In: *On being the right size and other*  
11 *essays by J.B.S. Haldane*, (Maynard Smith, J., ed.). pp. Oxford University Press.
- 12 Hamilton, W. D. 1964. The genetical evolution of social behaviour. I & II. *Journal of*  
13 *Theoretical Biology* **7**: 1-52.
- 14 Hammerstein & Reichert, S. E. 1988. Payoffs and strategies in territorial contests: ESS  
15 analyses of two ecotypes of the spider *Agelenopsis aperta*. *Evolutionary Ecology* **2**:  
16 115-138.
- 17 Hardin, G. 1960. The competitive exclusion principle. *Science* **131**: 1292-1297.
- 18 Hardin, G. 1968. The tragedy of the commons. *Science* **162**: 1243-1248.
- 19 Hardin, G. 1998. Extensions of "the tragedy of the commons". *Science* **280**: 682-283.

- 1 Howard, R. D., DeWoody, J. A. & Muir, W. M. 2004. Transgenic male mating advantage  
2 provides opportunity for Trojan gene effect in a fish. *Proceedings of the National*  
3 *Academy of Sciences* **101**: 2934-2938.
- 4 Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton  
5 University Press, Princeton.
- 6 Keller, L. (Ed.) (1999) *Levels of Selection in Evolution*, Princeton, Princeton University Press.
- 7 Knowlton, N. & Parker, G. A. 1979. Evolutionarily stable strategy approach to indiscriminate  
8 spite. *Nature* **279**: 419-421.
- 9 Kokko, H., Lopéz-Sepulcre, A. & Morrell, L. J. 2006. From Hawks and Doves to Self-  
10 Consistent Games of Territorial Behavior. *American Naturalist* **167**: 901-912.
- 11 Lande, R. 1993. Risks of population extinction from demographic and environmental  
12 stochasticity and random catastrophes. *American Naturalist* **142**: 911-972.
- 13 Leigh, E. G. 1977. How does selection reconcile individual advantage with the good of the  
14 group? *Proceedings of the National Academy of Sciences* **74**: 4542-4546.
- 15 Leigh, E. G. 1981. The average lifetime of a population in a varying environment. *Journal of*  
16 *Theoretical Biology* **90**: 213-239.
- 17 Lloyd, E. A. & Gould, S. J. 1993. Species selection on variability. *Proceedings of the*  
18 *National Academy of Sciences* **90**: 595-599.
- 19 López-Sepulcre, A. & Kokko, H. 2005. Territorial defense, territory size and population  
20 regulation. *American Naturalist* **166**: 317-329.

- 1 Matsuda, H. & Abrams, P. A. 1994a. Runaway evolution to self-extinction under  
2 asymmetrical competition. *Evolution* **48**: 1764-1772.
- 3 Matsuda, H. & Abrams, P. A. 1994b. Timid consumers: self-extinction due to adaptive  
4 change in foraging and anti-predator effort. *Theoretical Population Biology* **45**: 76-91.
- 5 Maynard Smith, J. 1964. Group selection and kin selection. *Nature* **201**: 1145-1147.
- 6 Morrow, E. H. & Pitcher, T. E. 2003. Sexual selection and the risk of extinction in birds.  
7 *Proceedings of the Royal Society of London B* **270**: 1793-1799.
- 8 Muir, W. M. & Howard, R. D. 1999. Possible ecological risks of transgenic organism release  
9 when transgenes affect mating success: sexual selection and the trojan gene  
10 hypothesis. *Proceedings of the National Academy of Sciences* **96**: 13853-13856.
- 11 Nunney, L. 1989. The maintenance of sex by group selection. *Evolution* **43**: 245-257.
- 12 Nunney, L. (1999) Lineage selection: natural selection for long-term benefit. In: *Levels of*  
13 *Selection in Evolution*, (Keller, L., ed.). pp. Princeton University Press, Princeton.
- 14 Ostrom, E. 1999. *Governing the commons*. Cambridge University Press, Cambridge.
- 15 Parvinen, K. 2005. Evolutionary suicide. *Acta Biotheoretica* **53**: 241-264.
- 16 Penn, D. J. 2003. The evolutionary roots of our environmental problems: toward a Darwinian  
17 ecology. *The Quarterly Review of Biology* **78**: 275-301.
- 18 Rankin, D. J. 2007. Resolving the tragedy of the commons: the feedback between population  
19 density and intraspecific conflict. *Journal of Evolutionary Biology* **20**: 173-180.
- 20 Rankin, D. J. & Kokko, H. 2006. Sex, death and tragedy. *Trends in Ecology and Evolution*  
21 **21**: 225-226.

- 1 Rankin, D. J. & López-Sepulcre, A. 2005. Can adaptation lead to extinction? *Oikos* **111**: 616-  
2 619.
- 3 Ratnieks, F. L. W., Foster, K. R. & Wenseleers, T. 2006. Conflict resolution in insect  
4 societies. *Annual Review of Entomology* **51**: 581-608.
- 5 Soulé, M. E. (Ed.) (1987) *Viable populations for conservation*, Cambridge, Cambridge  
6 University Press.
- 7 Stuart, A. J., Kosintsev, P. A., Higham, T. F. & Lister, A. M. 2004. Pleistocene to Holocene  
8 extinction dynamics in giant deer and woolly mammoth. *Nature* **431**: 684-9.
- 9 van Valen, L. 1975. Group selection, sex and fossils. *Evolution* **29**: 87-94.
- 10 Vinogradov, A. E. 2003. Selfish DNA is maladaptive: evidence from the plant Red List.  
11 *Trends in Genetics* **19**: 609-614.
- 12 Vrba, E. S. 1984. What Is Species Selection. *Systematic Zoology* **33**: 318-328.
- 13 Weatherby, A. J., Warren, P. H. & Law, R. 1998. Coexistence and collapse: an experimental  
14 investigation of the persistent communities of a protist species pool. *Journal of Animal*  
15 *Ecology* **67**: 554-566.
- 16 Wenseleers, T. & Ratnieks, F. L. W. 2004. Tragedy of the commons in *Melipona* bees.  
17 *Proceedings of the Royal Society of London B* **271**: S310-S312.
- 18 Wenseleers, T. & Ratnieks, F. L. 2006a. Comparative analysis of worker reproduction and  
19 policing in eusocial hymenoptera supports relatedness theory. *Am Nat* **168**: E163-79.
- 20 Wenseleers, T. & Ratnieks, F. L. 2006b. Enforced altruism in insect societies. *Nature* **444**: 50.

1 Williams, G. C. 1966. *Adaptation and Natural Selection: a critique of some current*  
2 *evolutionary thought*. Princeton University Press, Princeton.

3 Wilson, D. S. 1975. A Theory of Group Selection. *PNAS* **72**: 143-146.

4 Xavier, J. B. & Foster, K. R. 2007. Cooperation and conflict in microbial biofilms.  
5 *Proceedings of the National Academy of Sciences* **104**: 876-881.

6

7



## 1 **Appendix – Multi-species simulation**

2 For the simulation, we assume that evolutionary and ecological dynamics occur over separate  
3 timescales, such that the ecological equilibria (population densities) are approached much  
4 faster than evolutionary changes occur. The notation of the isocline model is here modified to  
5 yield an individual performance function  $f_i(z_{ij}, \alpha_i)$ , that is used to calculate the fitness  $w_{ij}$  for  
6 individual  $j$  of species  $i$ , according to its share of the resources available to the whole species:

$$7 \quad w_{i,j}(z_{ij}, \bar{z}_i) = \frac{f_i(z_{ij}, \alpha_i)}{f_i(\bar{z}_i, \alpha_i)} R_i(\bar{z}_i) \quad (\text{A1})$$

8 The function  $R(z)$  is based on equation (1), and describes the total *per capita* resource  
9 available to species  $i$ , extended to include the niche use by all members of the community  
10 (note that the sum includes species  $i$ ):

$$11 \quad R_i(\bar{z}_i) = \int_x \frac{E_i(x)q(\bar{z}_i)}{\sum_j n_j E_j(x)} dx, \quad (\text{A2})$$

12 The first part of the RHS of equation (A1) defines the share of available resources that focal  
13 individual gets as a function of its competitiveness, and the second part weights this by the  
14 overall amount of resources available (from equation 1), which is a function of both intra- and  
15 interspecific competition. We assume that there is relatively little variation in  $z$  at any point in  
16 time, such that  $f_i(\bar{z}_i, \alpha_i)$  can be used as a good approximation of the mean of  $f_i(z_{ij}, \alpha_i)$ , taken  
17 over different values of  $z_{ij}$  used in the population. We use the function

18  $f_i(z_i, \alpha_i) = z_i \exp(-z_i / \alpha_i m(n_i))$  in our examples. This function allows us to consider cases  
19 where ‘too selfish’ behaviour simply brings about costs (e.g., superfluous aggression) to the  
20 individual while no longer increasing the benefits gained (Knowlton & Parker, 1979, Foster,

1 2004). From this function, it follows that  $\frac{\partial f_i(z_{ij}, \alpha_i)}{\partial z_{ij}} = c \exp(-z_i / \alpha_i m(n_i))(1 - z_i / \alpha_i m(n_i))$ ,

2 and therefore selfish gains from competitive behaviour peak at  $z_i = \alpha_i m(n_i)$  and decline after  
3 that.

4 The incentive to be selfish is likely to be small at lower population densities than at higher  
5 population densities, which will tend to reduce the potential for selfishness to drive extinction  
6 (e.g. Rankin, 2007). To use our earlier example of fighting, there will be less incentive to  
7 compete aggressively for resources when the population density is so low that many resources  
8 remain undefended (Kokko *et al.*, 2006), which will make the incentive positively density-  
9 dependent. In order to be conservative, therefore, we include such density dependence in our  
10 model. The function  $m(n_i)$  describes the relationship between the overall incentive and  
11 population density. We assume that  $m(n_i)$  reaches its highest possible value  $\alpha_i$  when the  
12 population is very dense, and declines with lowering density; the speed of this decline is  
13 scaled by the parameter  $\gamma_i$ , the density-dependence of the incentive. In our examples we use  
14 the function  $m(n_i) = (1 - \exp(-n_i / \gamma_i))$ . Note that positive density-dependence of the incentive  
15 is a distinct process from the negative density-dependence that affects population growth  
16 (which is represented in the function  $R(z)$ ), which also has to be included in our model in  
17 order to regulate population sizes.

### 18 *The effect of selection on the evolution of selfishness ( $z$ )*

19 To investigate the effect of selection on selfishness  $z$  we assume constant heritabilities of  $z$   
20 across species, and calculate the selection gradient as

$$21 \Delta \bar{z}_i = \delta_i \frac{\partial w_{ij}(z_{ij}, \bar{z}_i)}{\partial z_{ij}}, \quad (\text{A3})$$

1 Here, the factor  $\delta_i$  is proportional to  $\sigma_{Aij}^2/w_{ij}$  where  $\sigma_{Aij}^2$  is additive genetic variance for  $z$ . Our  
 2 assumption that evolutionary change is slow compared to ecological change is reflected in  
 3 low values of  $\delta_i$ . We can write the change in  $z$  over time as  $\bar{z}_i(t+1) = \bar{z}_i(t) + \Delta\bar{z}_i$ , where

4 
$$\frac{\partial w_{ij}(z_{ij}, \bar{z})}{\partial z_{ij}} = \frac{R_i(\bar{z}_i)}{f_i(\bar{z}_i, \alpha_i)} \frac{\partial f_i(z_{ij}, \alpha_i)}{\partial z_{ij}}$$
 is obtained by evaluating the right-hand side of equation

5 A3.

6 To follow the evolutionary and ecological dynamics of a species, we define the maximum  
 7 amount of resource available to a given species,  $E(x) = v(x, \mu_i, \sigma_i^2)$ , where the niche  
 8 distribution  $v(x, \mu_i, \sigma_i)$  follows a normal distribution evaluated at  $x$ , with mean  $\mu_i$  and  
 9 variance  $\sigma_i^2$ . In other words, species  $i$  uses resources that match its niche midpoint,  $x = \mu_i$ ,  
 10 with the highest efficiency.

### 11 *Ecological and evolutionary dynamics*

12 To link evolution and population dynamics, we assume ‘fast-slow’ dynamics (Matsuda &  
 13 Abrams, 1994a, Dieckmann et al., 1995), such that ecological processes happen considerably  
 14 faster than evolutionary ones. Thus, to derive the ecological equilibria, we may assume fixed  
 15 behaviour  $\{\bar{z}_i, \dots, \bar{z}_k\}$  of all species. The population dynamics of the  $i$ th species  
 16 is  $n_i(t+1) = n_i(t)R_i(\bar{z}_i, \beta_i)$ . Here we are assuming that the per capita resources  $R_i$  determine  
 17 population growth. Due to the low value of  $\delta_i$ , the population dynamics are assumed to  
 18 change at a faster rate than the evolutionary dynamics. It is important to note that extinctions  
 19 are a result of both ecological and evolutionary processes, so the rate of extinctions is not  
 20 defined *a priori* but is an emergent property of the simulation.

### 21 *Starting values*

1 The functions described above are made species-specific by giving each species different  
2 properties of competitive incentive ( $\alpha_i$ ). Initial, positive, values of  $\alpha_i$  were chosen from  
3 exponential distributions to avoid artificial constrains, while making lower, more realistic,  
4 values more likely. However, our results remained qualitatively identical if a normal  
5 distribution was used in place of our exponential distribution (not shown) or if we used  
6 substantially higher or lower starting values of  $\alpha_i$ . Each simulation started with niche  
7 parameters  $\mu_i=0$ ,  $\sigma_i^2 = 0.01$ , and an initial low value of  $z_i=0.01$ . Every time step, the  
8 dynamics were updated to calculate the population density and current value of  $z$  for all  
9 species in the community. Then the properties of each species were shifted proportionally to  
10 the selection gradient given by equation A3, which is a discretised approximation of a  
11 separation in ecological and evolutionary time-scales.

## 12 *Speciation and extinctions*

13 In the community simulations, new species were added by speciation. At each time step, a  
14 species could speciate with a small probability,  $p_s$ . We assume a simple ‘point mutation’  
15 mode of speciation (Hubbell, 2001); the population was split in half, and the daughter species  
16 mutated to take different values of  $\alpha$ , and also of the niche parameters  $\mu$  and  $\sigma^2$ . The new  
17 value of a trait after mutation,  $u'$ , was calculated with the formula  
18  $u' = \exp(\log(u) + \psi(M, V))$ , where  $u$  is the original value of either the incentive to invest in  
19 competition or the niche overlap (i.e.  $\alpha_i$  or  $\sigma_i^2$ ) and  $\psi$  is a normally distributed random  
20 number with mean  $M$  and variance  $V$  (taken to be 0 and 0.1, respectively). A normal  
21 distribution is required in this case because in this case any individual species may experience  
22 competition from either side on the niche axis (this is in contrast to the two species model,  
23 where an exponential was used to allow tractability). This scales properly in our setting,  
24 ensuring values remain positive. The mean of the niche can take negative values, and

1 therefore the niche mean ( $\mu_i$ ) was mutated by adding a normally distributed small random  
2 number (with mean 0, and variance 0.01) to the original value of  $\mu_i$ .

3 We ran simulations with no speciation ( $p_S = 0$ , isolated-species simulation) as well as with a  
4 speciation rate of  $p_S = 0.05$  (community simulation) in order to investigate the influence of  
5 community structure on species-level selection. Additionally, we ran a considerable number  
6 of simulations providing sensitivity checks with some of the assumptions altered (i.e. length  
7 of simulation run, initial distributions of  $\alpha_i$ , and the details of the speciation process; details  
8 provided in the results).

9 Extinction occurred if the density of a species fell below a certain, small, threshold  $\varepsilon$ . At each  
10 time step all species with population densities below this threshold were removed from the  
11 community. Using such thresholds for extinction make use of the assumption that very low  
12 population sizes will be driven extinct due to stochastic processes (Matsuda & Abrams,  
13 1994a, Dieckmann & Ferrière, 2004). We recorded the values of  $\alpha$  for all species which  
14 survived at the end of the simulation. Unless all species went extinct, the simulation  
15 proceeded until a set time was reached (3000 time steps in this model). In both the isolated  
16 species model, and the community model, the complete simulation was repeated until we  
17 obtained 500 simulations in which at least one species remained at the end. The values of  $\alpha$   
18 were recorded for all surviving species. The results of each simulation were pooled for  
19 analysis. A Kolmogorov-Smirnov test was used to see if the distribution of  $\alpha$  differed  
20 between the isolated-species and the community simulation, as well as from the original  
21 exponential distribution.

22

## 1 **Figure and Table Legends**

2 Figure 1. Examples where wasteful within-species conflict may affect the probability of  
3 species persistence. a) Worker laying in a small-colony yellow jacket species *Dolichovespula*  
4 *saxonica*. Laying by workers directs resources away from work into male production that  
5 conflicts with the queen (Ratnieks *et al.*, 2006). b) Skull of the extinct Irish Elk *Megaloceros*  
6 *giganteus* showing the massive antlers. Although far from certain (Stuart *et al.*, 2004), these  
7 may have contributed to the species' demise. c) Migrating slug of the slime mould  
8 *Dictyostelium discoideum*, chimeric slugs containing multiple clones migrate poorly  
9 compared to pure clones, suggesting that conflict inhibits their dispersal (Foster *et al.*, 2002).  
10 All photos by KRF.

11 Figure 2. Extinction driven by the synergistic effects of individual-level selection for  
12 selfishness and competitive exclusion on population density. (a) There is no extinction  
13 without individual-level selection for selfishness ( $z_1 = 0$ ). Zero-growth isoclines are shown for  
14 the two competing species (solid line is species 1). Long arrows on the graph show the  
15 trajectory of population growth. Open circles represent equilibrium population densities for  
16 the focal species (species 1): I is population density without species 2, II is with species 2.  
17 Closed circles represent the equilibrium density of species 2 without species 1. (b), When  
18 species 1 is allowed to evolve towards its ESS level of selfishness, it is driven extinct before it  
19 can reach it. The grey line in (b) represents the isocline of species 1 in the absence of any  
20 selfishness ( $z_1=0$ ). This example assumes an incentive for selfishness ( $\alpha = 0.1, c = 1, \beta=1$ ),  
21 which in the single species case results in an an ESS for species 1 at  $z_1 = 0.0909$ .

22

23 Figure 3. Individual-level selection for selfishness and ecological competition without  
24 extinction. Zero-growth isoclines of two competing species when the incentive to invest in

1 competition is low ( $\alpha = 0.05$ ,  $c = 1$ ,  $\beta=1$ ). The grey line represents the zero-growth isocline of  
2 species 1 when there is no selfishness ( $z_1 = 0$ ), the solid line represents the zero growth  
3 isocline of species 1 when the population is allowed to evolve towards an ESS and the dashed  
4 line represents the zero-growth isocline of species 2. Closed circles indicate the equilibrium  
5 density of species 2 in the absence of species 1. Open circles represent different equilibria of  
6 species 1, indicated by roman numerals. I corresponds to the equilibrium density under  
7 interspecific competition, when there is no selfishness ( $z_1 = 0$ ). II corresponds to the  
8 equilibrium density when species 1 is in isolation, with no selfishness. III represents the  
9 equilibrium density once  $z$  has evolved to an ESS. IV corresponds to the ESS of  $z$  when  
10 species 1 does not face interspecific competition.

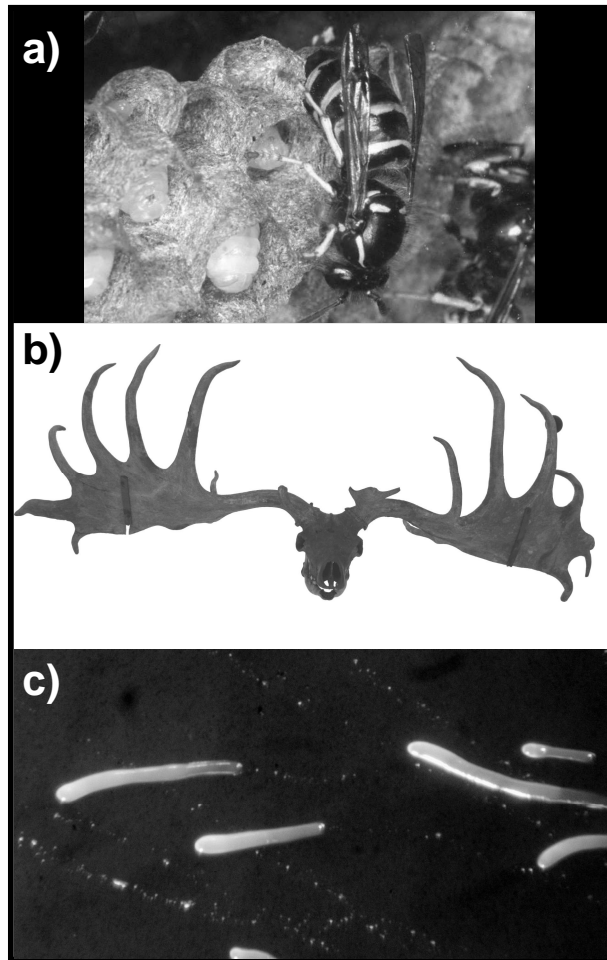
11 Figure 4. The effects of species-level selection on the degree of wasteful competition within a  
12 species in the simulation. Solid lines represent the original (exponential) distribution, dotted-  
13 dashed lines represent the distribution of properties of surviving species in the isolated-  
14 species model, and dashed lines represent the distribution of properties of surviving species in  
15 the community model. Medians are given for the distributions of the respective species  
16 properties for the original distribution from which the properties are drawn, the results of the  
17 isolated-species model and the results of the community model, respectively. Note that the  
18 tails of the distributions have not been included in the graphs. Other parameters:  $\gamma = 0.02$ ,  $\delta_i =$   
19  $0.001$ ,  $p_S = 0.05$ ,  $\varepsilon = 0.05$ .

1 **Figures**

2 **Figure 1**

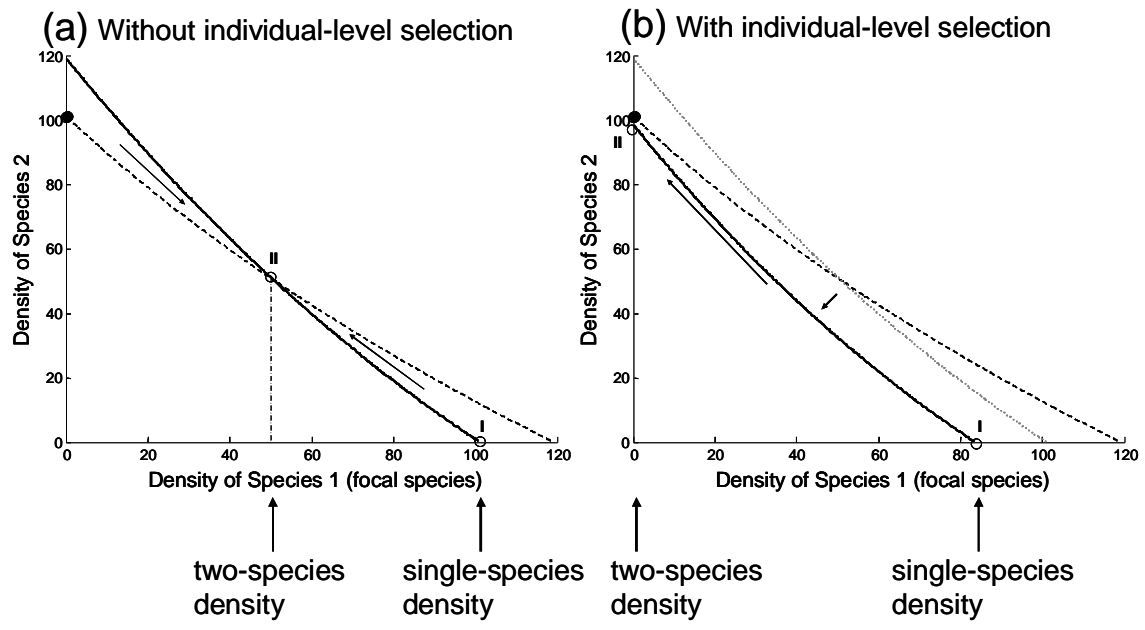
3

4





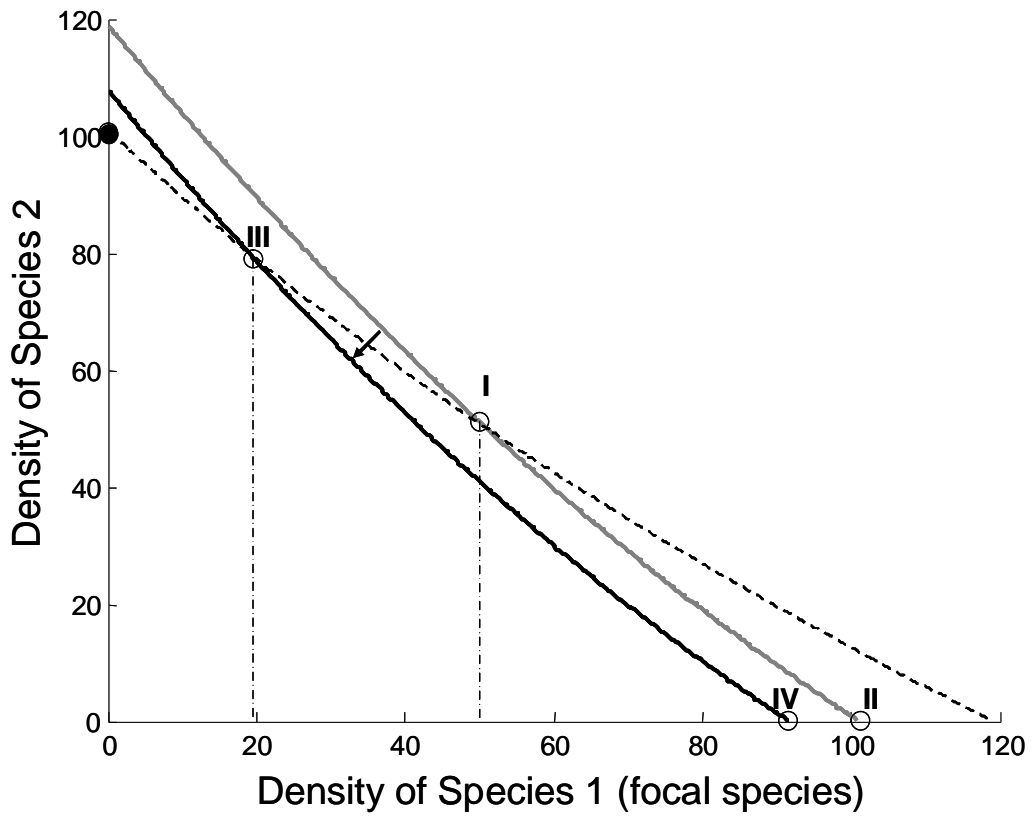
1 Figure 2.



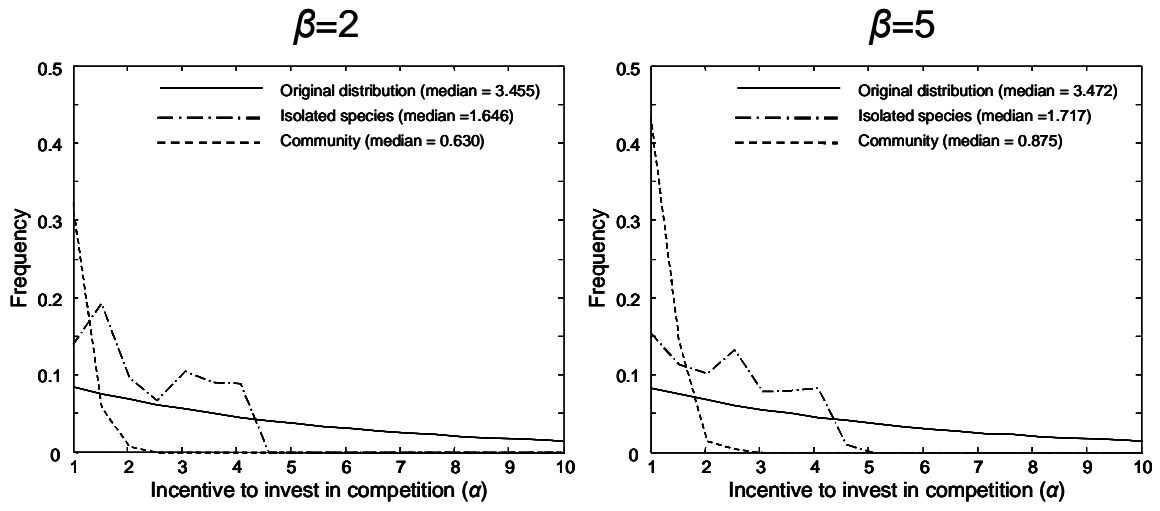
2

1 Figure 3

2



1 Figure 4



2