Species-level selection reduces selfishness through competitive exclusion

D. J. RANKIN,* A. LÓPEZ-SEPULCRE*†, K. R. FOSTER*‡ & H. KOKKO*

*Laboratory of Ecological and Evolutionary Dynamics, Department of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland
†Evolutionary Ecology Research Unit, Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland
‡Bauer Laboratories, Center for Systems Biology, Harvard University, Cambridge, MA, USA

Abstract

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

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

Introduction

Ever since the group selection debate in the 1960s, it has been clear that selection acting at the level of the gene or the individual does not necessarily produce adaptations that are optimal for the population (Williams, 1966;

Correspondence: Daniel J. Rankin, Laboratory of Ecological and Ecological Dynamics, Department of Biological and Environmental Science, University of Helsinki, PO Box 65 (Viikinkaari 1), FIN-00014 Helsinki, Finland.
Tel.: +358 9 1915 7866; fax: +358 9 1915 7694;
e-mail: daniel.rankin@helsinki.fi

Dawkins, 1976). Indeed, individual-interested behaviour can often be expected to cause resource depletion resulting in the 'tragedy of the commons' (Hardin, 1968), which in its most extreme form may cause population demise, or 'evolutionary suicide' (Dieckmann & Ferrière, 2004; Parvinen, 2005).

The concept of the tragedy of the commons has most often been evoked when studying the overexploitation of resources by humans (Hardin, 1998; Ostrom, 1999; Penn, 2003), where it is argued that short-sighted selfish behaviour will invariably lead to disaster for the individuals using that resource. However, it also applies to nonhumans where selection for selfish competition is expected to be widespread (Leigh, 1977; Frank, 1995; Falster & Westoby, 2003; Foster, 2004; Wenseleers & Ratnieks, 2004; Rankin & Kokko, 2006). Moral restraint is often invoked as an argument for resolving the tragedy in humans (Hardin, 1968), and policing (Frank, 1995; Wenseleers & Ratnieks, 2006b) or sufficient relatedness (Frank, 1995; Foster, 2004; Wenseleers & Ratnieks, 2004) can limit the tragedy in

other species. However, the evolution of policing is only possible in some contexts (such as insect societies – e.g. Wenseleers & Ratnieks, 2006b), and not all species exist in kin-structured communities. This begs the question of whether evolutionary suicide commonly occurs in nature (Rankin & López-Sepulcre, 2005), and whether such extinctions can act as an important higher level of selection (Foster, 2006).

An increasing number of empirical and theoretical studies show how individual selection has the potential to harm the population (e.g. Muir & Howard, 1999; Fiegna & Velicer, 2003). For example, territorial animals risk injury, as well as waste time and energy that could be better invested in reproduction and survival, in contests over space. Succeeding in this competition is essential for individual reproduction but the predicted patterns of space division reduce the number of individuals that can exist in any given area (López-Sepulcre & Kokko, 2005). Conflicts can therefore result in a lowering of population density (López-Sepulcre & Kokko, 2005). Fig. 1 shows examples where wasteful within-species conflict may affect species persistence.

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

Here we explore the effects of extinctions at the species level on the evolution of conflict in multispecies communities. We specifically look at the joint effect of individual-level selection, where selection acts on individuals, and species-level selection, where species go extinct because of behavioural adaptation at the individual level. There is no spatial deme structure or trait-group selection (*sensu* Wilson, 1975) in the model. First, we incorporate selfish evolution into a simple two-species Lotka–Volterra competition model to illustrate the extent to which competitive exclusion may influence the population density of selfish species. Second, we use a simulation to investigate macroevolutionary effects, both in an isolated species and in a community setting. In particular, we ask the question,
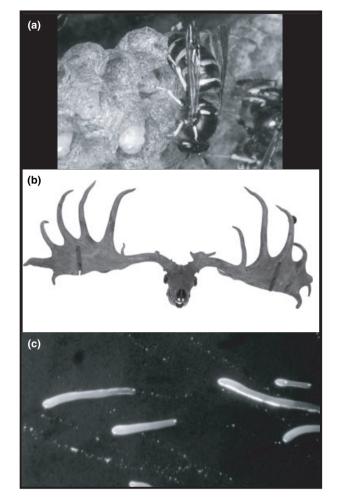

Fig. 1 Examples where wasteful within-species conflict may affect the probability of species persistence. (a) Worker laying in a small-colony yellow jacket species *Dolichovespula saxonica*. Laying by workers directs resources away from work into male production that conflicts with the queen (Ratnieks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

given that selfish competition within a species may harm populations, what part do community interactions play in the macroevolutionary consequences of such harm?

The models

Two-species dynamics and the evolution of selfishness

Our goal is to evaluate the impact of a selfish and competitive trait z_i on population persistence and the

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

Selfishness

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

Competitive incentive

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

Individual-level selection

We start by considering selection for selfish behaviour within species 1 by calculating the invasion fitness of a mutant z_i' invading a population of residents. The fitness of a mutant, z_1' is then

$$w(z_1', \bar{z}_1) = f(z_1', \bar{z}_1) R_1(\bar{z}_1) \qquad (1)$$

where $R_1(\bar{z}_1)$ defines the group performance of species 1 (per capita growth rate), which is a function of selfishness in species 1, but is also affected by resource competition from species 2 (see eqn 2, below). The benefit gained from a mutant individual investing z_1' in competition in a population comprising individuals which invest $\bar{z}_1$ in selfishness is described by the function $f(z_1', \bar{z}_1)$. Following the logic of Frank (1995) and Foster (2004), we use $f(z_1', \bar{z}_1) = (z_1'/\bar{z}_1)^{\alpha}(1 - c z_1')$, where α scales the incentive to invest in selfish competition. For $\alpha = 1$ and $c = 0$, the model becomes identical to Frank (1995), where selfishness leads to population collapse (a tragedy of the commons). However, for $c > 0$, the expression includes an individual cost of expressing the selfish traits, which puts an upper bound on the individual investment into competition (e.g. intense fighting is personally costly, Hammerstein & Reichert, 1988; Foster, 2004). A mutant with a phenotype of z' will be able to invade a 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 direction of evolution (lower or higher z favoured) in z_1.

Two-species interactions

We now consider the impact of selfishness z in species 1 on the population dynamics and competition with species 2. In our example, we assume that species 2 does not exhibit selfish behaviour (e.g. does not fight with conspecifics), and therefore has a value of z fixed at zero. This allows us to look at the population consequences of the evolution of selfishness of species 1 (eqn 1), when undergoing interspecific competition. The two species compete over a common resource E, where $E_i(x)$ is the maximum availability of resource x that an individual of species i could use. Critically, the *ability* of species 1 to translate the shared resource into reproduction decreases with increased selfishness z (eqn 2). x denotes a resource gradient that may be interpreted in different ways, for example, habitat with a specific microclimate [$E_i(x)$ then gives the area of such habitat available to individuals of species i], or food items of a specific size [$E_i(x)$ is then the available density of such items]. To provide an illustrative example, the amount of resources available to each species is defined by two simple functions: $E_1(x) = b \exp(1-x)$ and $E_2(x) = b \exp(x)$, such that the two species have a significant degree of niche overlap but they are not ecologically identical (species 2 is better at using large values of x). The overlap makes interspecific competition an important factor determining the densities of both species. The population density of species i is given as n_i and its dynamics can be described by the equation

$n_i(t + 1) = R(\bar{z}_i)n_i(t)$, where R indicates average *per capita* population growth:

$$R_i(\bar{z}_i) = \int \frac{E_i(x)q(\bar{z}_i)}{n_1 E_1(x) + n_2 E_2(x)} \mathrm{d}x \qquad (2)$$

The effect of density dependence from within- and between-species competition is captured by the denominator in eqn 2: in the absence of species 2, the reproductive rate of species 1 is simply determined by the number of individuals in the population (i.e. it is density dependent). In the presence of conflict with other individuals, the effect of wasteful selfishness by the members of species i on resource availability is captured by $q_i(z_i)$, where q_i is the fraction of the resource that remains useful to individuals of a given species, and selfishness (z) has a negative effect on this fraction, such that $[\partial q_i(z_i)/\partial z_i] < 0$, and $q(z_i) = (1-z_i)^{\beta}$. A low value of β means that competition in a species is very wasteful, and therefore population-wide reproduction suffers greatly from individual selfishness, making a species more likely to go extinct with a small increase in z. A larger value confers the opposite effect. Note that q does not appear in the denominator, indicating that resources inefficiently used by species 1 are not available to the other species. This assumption makes our model conservative because if resources wasted by species 1 could be used by species 2 then this would further promote the advantage of the latter. A nice example of this possibility is territoriality. If species 1 is highly territorial over space and leaves a lot of resources unexploited in the environment, this will not only lower its growth rate (López-Sepulcre & Kokko, 2005) but also increase the resources available to competing species.

Model results

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

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

Figure 3 shows the isoclines of a case where the competitive incentive is lower, and both species can coexist even after species 1 has undergone selection for increased selfishness. Even here, the combination of

(a) Without individual-level selection
(b) With individual-level selection
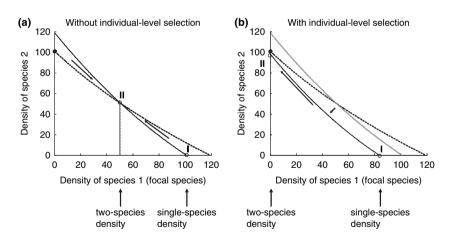
two-species density — single-species density

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

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

Evolution of selfishness in a multispecies simulation

Our isocline model is a proof of principle that selfishness selected at the individual level can have important consequences for the probability that a species will persist. We now use a simulation to evaluate its macroevolutionary consequences in communities containing many evolving species (our previous example only allowed one species to evolve). Our focus is on the competitive incentive (α_i), which is the central parameter defining the level of selfishness in a focal species. This is a species property or life-history character which drives the benefit gained from investing in conflict. Low values of α mean that there is relatively little to be gained from investing more in selfishness z, whereas higher values of
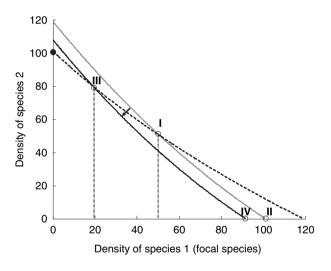

Fig. 3 Individual-level selection for selfishness and ecological competition without extinction. Zero-growth isoclines of two competing species when the incentive to invest in competition is low ($\alpha = 0.05$, $c = 1$, $\beta = 1$). The grey line represents the zero-growth isocline of species 1 when there is no selfishness ($z_1 = 0$), the solid line represents the zero growth isocline of species 1 when the population is allowed to evolve towards an ESS and the dashed line represents the zero-growth isocline of species 2. Closed circles indicate the equilibrium density of species 2 in the absence of species 1. Open circles represent different equilibria of species 1, indicated by roman numerals. I corresponds to the equilibrium density under interspecific competition, when there is no selfishness ($z_1 = 0$). II corresponds to the equilibrium density when species 1 is in isolation, with no selfishness. III represents the equilibrium density once z has evolved to an ESS. IV corresponds to the ESS of z when species 1 does not face interspecific competition.

α mean the opposite. We examine its distribution before and after the simulation to ascertain whether species-level selection affects the overall selfishness of species. In addition, we compare community simulations to the case of a single species (isolated-species simulations) to examine whether community interactions amplify any effects of species-level selection.

The community simulation allows speciation to take place, with daughter species being ecologically similar to the immediate ancestor, and species going extinct if they fail to satisfy current conditions for ecological coexistence. We continually update the equilibrium population density for each evolved level of selfishness, and hence take every species to be at its ecological equilibrium density. As such, we assume a separation of ecological and evolutionary time scales such that individual-level selection takes place at a much slower rate than the population dynamics (see Appendix). The ecological and evolutionary dynamics generate extinction events intermittently across the simulation whenever selfishness evolves to levels which result in population densities below a certain extinction threshold, ε. Full details of the simulation are provided in the Appendix.

Model results

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

We checked the robustness of our results against several alternative assumptions. The results of our model were qualitatively the same (i.e. shifts of distributions show similar patterns) if density dependence of the incentive (see Appendix) was removed. Similarly, the results remained qualitatively similar when: (1) the daughter species had a low population size (set at a value slightly larger than the extinction threshold), as opposed to parent and daughter species both taking half of the
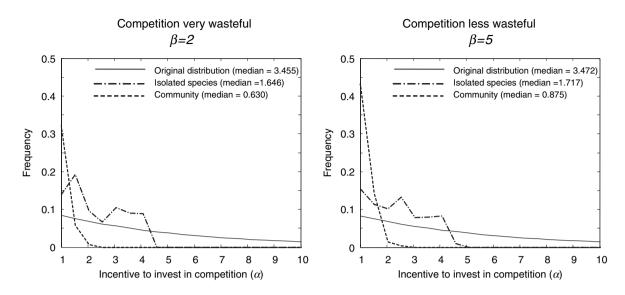
Fig. 4 The effects of species-level selection on the degree of wasteful competition within a species in the simulation. Solid lines represent the original (exponential) distribution, dotted-dashed lines represent the distribution of properties of surviving species in the isolated-species model, and dashed lines represent the distribution of properties of surviving species in the community model. Medians are given for the distributions of the respective species properties for the original distribution from which the properties are drawn, the results of the isolated-species model and the results of the community model. Note that the tails of the distributions have not been included in the graphs. Other parameters: $\gamma = 0.02$, $\delta_i = 0.001$, $p_S = 0.05$, $\varepsilon = 0.05$.

original population density; (2) longer simulation times (10 000 vs. 3000 generations) were used; and (3) there was variation in the initial distribution of α.

Discussion

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

A central finding from our model is that it is not required that species commit true evolutionary suicide for

species-level selection to work. Selfishness need only weaken a species, such that it more easily falls victim to competitive exclusion (Fig. 2). This shows that Hardin's (1960) competitive exclusion principle can function to make the effects of his tragedy (Hardin, 1968) more severe. Competitive exclusion is a common finding in ecological communities, which suggests that these processes have important consequences for real communities. This is consistent with the work on sexual and asexual populations of rotifers (Ciros-Pérez *et al.*, 2002). In single-species populations, costs associated with sex had no effect on population density (Ciros-Pérez *et al.*, 2002). However, in multispecies communities the increased levels of sexual reproduction resulted in increased risk of competitive exclusion and extinction, generating species-level selection against sexuality. Although the study by Ciros-Pérez *et al.* (2002) did not consider selfishness *per se*, it clearly highlights the potential effects of community interactions upon extinctions.

The evolutionary effects in our model are driven by the fact that species differ in traits associated with selfishness (which is reflected in α). There are many ways that this can come about, including basic differences in ecology: a species foraging on concentrated patchy resources that can be defended might have a higher propensity for competition and selfishness than one living on dispersed resources. Although not required for our model to function, variation in the incentive for selfishness can also be driven by factors that promote sociality, such as the degree to which individuals interact with relatives (Fig. 1a,c; Hamilton,

1964; Griffin & West, 2003; Ratnieks *et al.*, 2006) and enforcement mechanisms (Wenseleers & Ratnieks, 2006a, b). That is, species-level selection may function to favour social species that interact with relatives and have enforcement systems.

Another mechanism, which can be associated with enforcement (Foster *et al.*, 2007), is the degree of pleiotropy where one gene affects multiple traits. This phenomenon is both extremely common in all genomes and highly variable in its effects (Foster *et al.*, 2004, 2007). When a pleiotropic relationship happens to be present in the genome that ties a potential selfish trait to a personal cost, this will reduce the incentive for selfishness (α). Our model predicts that this reduced incentive will increase species persistence, and, therefore, that such pleiotropic relationships should commonly occur in nature. An example can be found in a social amoeba, *Dictyostelium discoideum*, which forms social aggregations where some cells die in an apparent act of altruism to form a stalk that allows other cells to disperse as spores. Pleiotropy of the gene *dimA* links this altruistic act of stalk production to the ability to make spores, thereby reducing the incentive to be selfish and limiting the evolution of cheaters that produce fewer stalk cells (Foster *et al.*, 2004).

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

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

Conclusion

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

Acknowledgments

References

Burt, A. & Trivers, R. 2006. *Genes in Conflict: The Biology of Selfish Genetic Elements*. Belknap Press, Harvard.

Ciros-Pérez, J., Carmona, M. & Serra, M. 2002. Resource competition and patterns of sexual reproduction in sympatric sibling rotifer species. *Oecologia* **131**: 35–42.

Clavero, M. & García-Berthou, E. 2005. Invasive species are a leading cause of animal extinctions. *Trends Ecol. Evol.* **20**: 110.

Cronin, H. 1993. *The Ant and the Peacock: Altruism and Sexual Selection from Darwin to Today*. Cambridge University Press, Cambridge.

Dawkins, R. 1976. *The Selfish Gene*. Oxford University Press, Oxford.

Dercole, F., Ferrière, R. & Rinaldi, S. 2002. Ecological bistability and evolutionary reversals under asymmetrical competition. *Evolution* **56**: 1081–1090.

Dieckmann, U. & Ferrière, R. 2004 Adaptive dynamics and evolving biodiversity. In: *Evolutionary Conservation Biology* (R. Ferriere, U. Dieckmann & D. Couvet, eds), pp. 188–224. Cambridge University Press, Cambridge.

Dieckmann, U., Marrow, P. & Law, R. 1995. Evolutionary cycling in predator-prey interactions: population dynamics and the red queen. *J. Theor. Biol.* **176**: 91–102.

Falster, D.S. & Westoby, M. 2003. Plant height and evolutionary games. *Trends Ecol. Evol.* **18**: 337–343.

Fiegna, F. & Velicer, G.J. 2003. Competitive fates of bacterial social parasites: persistence and self-induced extinction of *Myxococcus xanthus* cheaters. *Proc. R. Soc. Lond. B* **270**: 1527–1534.

Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.

Foster, K.R. 2004. Diminishing returns in social evolution: the not-so-tragic commons. *J. Evol. Biol.* **17**: 1058–1072.

Foster, K. 2006. Balancing synthesis with pluralism in sociobiology. *J. Evol. Biol.* **19**: 1394–1396.

Foster, K.R. & Ratnieks, F.L. 2001. Paternity, reproduction and conflict in vespine wasps: a model system for testing kin selection predictions. *Behav. Ecol. Sociobiol.* **50**: 1–8.

Foster, K.R., Fortunato, A., Strassmann, J.E. & Queller, D.C. 2002. The costs and benefits of being a chimera. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **269**: 2357–2362.

Foster, K.R., Shaulsky, G., Strassmann, J.E., Queller, D.C. & Thompson, C.R.L. 2004. Pleiotropy as a mechanism to stabilise cooperation. *Nature* **431**: 693–696.

Foster, K.R., Parkinson, K. & Thompson, C.R.L. 2007. What can microbial genetics teach sociobiology? *Trends Genet.* **23**: 73–80.

Frank, S.A. 1995. Mutual policing and repression of competition in the evolution of cooperative groups. *Nature* **377**: 520–522.

Gould, S.J. & Lloyd, E.A. 1999. Individuality and adaptation across levels of selection: how shall we name and generalize the unit of Darwinism? *Proc. Natl Acad. Sci.* **96**: 11904–11909.

Griffin, A.S. & West, S.A. 2003. Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. *Science* **302**: 634–636.

Gyllenberg, M. & Parvinen, K. 2001. Necessary and sufficient conditions for evolutionary suicide. *Bull. Math. Biol.* **63**: 981–993.

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

Haldane, J.B.S. 1985. *On Being the Right Size and Other Essays by J.B.S. Haldane* (J. Maynard Smith, ed.), Oxford University Press, Oxford.

Hamilton, W.D. 1964. The genetical evolution of social behaviour. I & II. *J. Theor. Biol.* **7**: 1–52.

Hammerstein, P. & Reichert, S.E. 1988. Payoffs and strategies in territorial contests: ESS analyses of two ecotypes of the spider *Agelenopsis aperta*. *Evol. Ecol.* **2**: 115–138.

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

Hardin, G. 1968. The tragedy of the commons. *Science* **162**: 1243–1248.

Hardin, G. 1998. Extensions of 'the tragedy of the commons'. *Science* **280**: 682–683.

Howard, R.D., DeWoody, J.A. & Muir, W.M. 2004. Transgenic male mating advantage provides opportunity for Trojan gene effect in a fish. *Proc. Natl Acad. Sci.* **101**: 2934–2938.

Hubbell, S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.

Keller, L. (Ed.) 1999. *Levels of Selection in Evolution*. Princeton University Press, Princeton, NJ.

Knowlton, N. & Parker, G.A. 1979. Evolutionarily stable strategy approach to indiscriminate spite. *Nature* **279**: 419–421.

Kokko, H., López-Sepulcre, A. & Morrell, L.J. 2006. From hawks and doves to self-consistent games of territorial behavior. *Am. Nat.* **167**: 901–912.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* **142**: 911–972.

Leigh, E.G. 1977. How does selection reconcile individual advantage with the good of the group? *Proc. Natl Acad. Sci.* **74**: 4542–4546.

Leigh, E.G. 1981. The average lifetime of a population in a varying environment. *J. Theor. Biol.* **90**: 213–239.

Lloyd, E.A. & Gould, S.J. 1993. Species selection on variability. *Proc. Natl Acad. Sci.* **90**: 595–599.

López-Sepulcre, A. & Kokko, H. 2005. Territorial defense, territory size and population regulation. *Am. Nat.* **166**: 317–329.

Matsuda, H. & Abrams, P.A. 1994a. Runaway evolution to self-extinction under asymmetrical competition. *Evolution* **48**: 1764–1772.

Matsuda, H. & Abrams, P.A. 1994b. Timid consumers: self-extinction due to adaptive change in foraging and anti-predator effort. *Theor. Popul. Biol.* **45**: 76–91.

Maynard Smith, J. 1964. Group selection and kin selection. *Nature* **201**: 1145–1147.

Morrow, E.H. & Pitcher, T.E. 2003. Sexual selection and the risk of extinction in birds. *Proc. R. Soc. Lond. B* **270**: 1793–1799.

Muir, W.M. & Howard, R.D. 1999. Possible ecological risks of transgenic organism release when transgenes affect mating success: sexual selection and the trojan gene hypothesis. *Proc. Natl Acad. Sci.* **96**: 13853–13856.

Nunney, L. 1989. The maintenance of sex by group selection. *Evolution* **43**: 245–257.

Nunney, L. 1999 Lineage selection: natural selection for long-term benefit. In: *Levels of Selection in Evolution* (L. Keller, ed.), pp. 238–252. Princeton University Press, Princeton, NJ.

Ostrom, E. 1999. *Governing the Commons*. Cambridge University Press, Cambridge.

Parvinen, K. 2005. Evolutionary suicide. *Acta Biotheor.* **53**: 241–264.

Penn, D.J. 2003. The evolutionary roots of our environmental problems: toward a Darwinian ecology. *Q. Rev. Biol.* **78**: 275–301.

Rankin, D.J. 2007. Resolving the tragedy of the commons: the feedback between population density and intraspecific conflict. *J. Evol. Biol.* **20**: 173–180.

Rankin, D.J. & Kokko, H. 2006. Sex, death and tragedy. *Trends Ecol. Evol.* **21**: 225–226.

Rankin, D.J. & López-Sepulcre, A. 2005. Can adaptation lead to extinction? *Oikos* **111**: 616–619.

Ratnieks, F.L.W., Foster, K.R. & Wenseleers, T. 2006. Conflict resolution in insect societies. *Annu. Rev. Entomol.* **51**: 581–608.

Soulé, M.E. (Ed.) 1987. *Viable Populations for Conservation*. Cambridge University Press, Cambridge.

Stuart, A.J., Kosintsev, P.A., Higham, T.F. & Lister, A.M. 2004. Pleistocene to Holocene extinction dynamics in giant deer and woolly mammoth. *Nature* **431**: 684–689.

van Valen, L. 1975. Group selection, sex and fossils. *Evolution* **29**: 87–94.

Vinogradov, A.E. 2003. Selfish DNA is maladaptive: evidence from the plant Red List. *Trends Genet.* **19**: 609–614.

Vrba, E.S. 1984. What is species selection. *Syst. Zool.* **33**: 318–328.

Weatherby, A.J., Warren, P.H. & Law, R. 1998. Coexistence and collapse: an experimental investigation of the persistent communities of a protist species pool. *J. Anim. Ecol.* **67**: 554–566.

Wenseleers, T. & Ratnieks, F.L.W. 2004. Tragedy of the commons in Melipona bees. *Proc. R. Soc. Lond. B* **271**: S310–S312.

Wenseleers, T. & Ratnieks, F.L. 2006a. Comparative analysis of worker reproduction and policing in eusocial hymenoptera supports relatedness theory. *Am. Nat.* **168**: E163–E179.

Wenseleers, T. & Ratnieks, F.L. 2006b. Enforced altruism in insect societies. *Nature* **444**: 50.

Williams, G.C. 1966. *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton University Press, Princeton, NJ.

Wilson, D.S. 1975. A theory of group selection. *PNAS* **72**: 143–146.

Xavier, J.B. & Foster, K.R. 2007. Cooperation and conflict in microbial biofilms. *Proc. Natl Acad. Sci.* **104**: 876–881.

Appendix: Multispecies simulation

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

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

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

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

The first part of the RHS of eqn A1 defines the share of available resources that focal individual gets as a function

of its competitiveness, and the second part weighs this by the overall amount of resources available (from eqn 1), which is a function of both intra- and interspecific competition. We assume that there is relatively little variation in z at any point in 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 over different values of z_{ij} used in the population. We use the function $f_i(z_i, \alpha_i) = z_i \exp(-z_i/\alpha_i m(n_i))$ in our examples. This function allows us to consider cases where 'too selfish' behaviour simply brings about costs (e.g. superfluous aggression) to the individual while no longer increasing the benefits gained (Knowlton & Parker, 1979; Foster, 2004). From this function, it follows that

$$\frac{\partial f_i(z_{ij}, \alpha_i)}{\partial z_{ij}} = c \exp\left(-\frac{z_i}{\alpha_i m(n_i)}\right)\left(1 - \frac{z_i}{\alpha_i m(n_i)}\right),$$

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

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

The effect of selection on the evolution of selfishness

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

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

Here, the factor δ_i is proportional to σ^2_{Aij}/w_{ij}, where σ^2_{Aij} is additive genetic variance for z. Our assumption that evolutionary change is slow compared with ecological change is reflected in low values of δ_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

$$\frac{\partial w_{ij}(z_{ij}, \bar{z})}{\partial z_{ij}} = \frac{R_i(\bar{z}_i)}{f_i(\bar{z}_i, \alpha_i)} \frac{\partial f_i(z_{ij}, \alpha_i)}{\partial z_{ij}}$$

is obtained by evaluating the right-hand side of eqn A3. To follow the evolutionary and ecological dynamics of a species, we define the maximum amount of resource available to a given species, $E(x) = v(x, \mu_i, \sigma_i^2)$, where the niche distribution $v(x, \mu_i, \sigma_i)$ follows a normal distribution evaluated at x, with mean μ_i and variance σ_i^2. In other words, species i uses resources that match its niche midpoint, $x = \mu_i$, with the highest efficiency.

Ecological and evolutionary dynamics

To link evolution and population dynamics, we assume 'fast–slow' dynamics (Matsuda & Abrams, 1994a; Dieckmann *et al.*, 1995), such that ecological processes happen considerably faster than evolutionary ones. Thus, to derive the ecological equilibria, we may assume fixed behaviour $\{\bar{z}_i, \ldots, \bar{z}_k\}$ of all species. The population dynamics of the *i*th species 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 population growth. Due to the low value of δ_i, the population dynamics are assumed to change at a faster rate than the evolutionary dynamics. It is important to note that extinctions are a result of both ecological and evolutionary processes, so the rate of extinctions is not defined *a priori* but is an emergent property of the simulation.

Starting values

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

Speciation and extinctions

In the community simulations, new species were added by speciation. At each time step, a species could speciate with a small probability, p_S. We assume a simple 'point mutation' mode of speciation (Hubbell, 2001); the population was split into half, and the daughter species mutated to take different values of α, and also of the niche parameters μ and σ^2. The new value of a trait after mutation, u', was calculated with the formula $u' = \exp(\log(u) + \psi(M, V))$, where u is the original value of either the incentive to invest in competition or the niche overlap (i.e. α_i or σ_i^2) and ψ is a normally distributed random number with mean M and variance V (taken to be 0 and 0.1 respectively). A normal distribution is required in this case because in this case any individual species may experience competition from either side on the niche axis (this is in contrast to the two-species model, where an exponential was used to allow tractability). This scales properly in our setting, ensuring values remain positive. The mean of the niche can take negative values, and therefore the niche mean (μ_i) was mutated by adding a normally distributed small random number (with mean 0 and variance 0.01) to the original value of μ_i.

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

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