

- 35 Kjellén, N. *et al.* (2001) Timing and speed of migration in male, female and juvenile ospreys *Pandion haliaetus* between Sweden and Africa as revealed by field observations, radar and satellite tracking. *J. Avian Biol.* 32, 57–67
- 36 Fuller, M.R. *et al.* (1998) Routes and travel rates of migrating peregrine falcons *Falco peregrinus* and Swainson's hawks *Buteo swainsoni* in the western hemisphere. *J. Avian Biol.* 29, 433–440
- 37 Ristow, D. *et al.* (2000) Satellite tracking of Cory's shearwater migration. *Condor* 102, 696–699
- 38 Goldstein, M.L. *et al.* (1999) Monocrotophos-induced mass mortality of Swainson's hawks in Argentina. *Ecotoxicology* 8, 201–214
- 39 Waser, P.M. and Strobeck, C. (1998) Genetic signatures of interpopulation dispersal. *Trends Ecol. Evol.* 13, 43–44
- 40 Milá, B. *et al.* (2000) Genetic evidence for the effect of a postglacial population expansion on the phylogeography of a North American songbird. *Proc. R. Soc. London B Biol. Sci.* 267, 1033–1040
- 41 Merilä, J. *et al.* (1997) Historical demography and present day population structure of the greenfinch, *Carduelis chloris*—an analysis of mtDNA control region sequences. *Evolution* 51, 946–956
- 42 Haavie, J. *et al.* (2000) Discrepancies in population differentiation at microsatellites, mitochondrial DNA and plumage colour in the pied flycatcher—inferring evolutionary processes. *Mol. Ecol.* 9, 1137–1148
- 43 Hansson, M. *et al.* (2000) Range expansion and the possibility of an emerging contact zone between two subspecies of chiffchaff *Phylloscopus collybita* ssp. *J. Avian Biol.* 31, 548–558
- 44 Helbig, A.J. *et al.* (2001) Male-biased gene flow across an avian hybrid zone: evidence from mitochondrial and microsatellite DNA. *J. Evol. Biol.* 14, 277–287
- 45 Irwin, D.E. *et al.* (2001) Speciation in a ring. *Nature* 409, 333–337
- 46 Nesje, M. *et al.* (2000) Microsatellite analysis of population structure and genetic variability in peregrine falcons (*Falco peregrinus*). *Anim. Conserv.* 3, 267–275
- 47 Rintamäki, P.T. *et al.* (1998) Blood parasites of migrating willow warblers (*Phylloscopus trochilus*) at a stopover site. *Can. J. Zool.* 76, 984–988
- 48 Bensch, S. *et al.* (2001) Host specificity in avian blood parasites: a study of *Plasmodium* and *Haemoproteus* mitochondrial DNA amplified from birds. *Proc. R. Soc. London B Biol. Sci.* 267, 1583–1589
- 49 Sehgal, R.N.M. *et al.* (2001) Host specificity and incidence of *Trypanosoma* in some African rainforest birds: a molecular approach. *Mol. Ecol.* 10, 2319–2327
- 50 Tieszen, L.L. and Boutton, T.W. (1989) Stable carbon isotopes in terrestrial ecosystem research. In *Stable Isotopes in Ecological Research* (Rundel, P.W. *et al.*, eds), pp. 167–195, Springer-Verlag
- 51 Hobson, K.A. and Wassenaar, L.I. (1997) Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. *Oecologia* 109, 142–148
- 52 Chamberlain, C.P. *et al.* (1997) The use of isotope tracers for identifying populations of migratory birds. *Oecologia* 109, 132–141
- 53 DeNiro, M.J. and Epstein, S. (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim. Cosmochim. Acta* 42, 495–506
- 54 Blum, J.D. *et al.* (2000) Changes in Sr/Ca, Ba/Ca, and 87Sr/86Sr ratios between trophic levels in two forest ecosystems in the northeastern USA. *Biogeochemistry* 49, 87–101
- 55 Wassenaar, L.I. and Hobson, K.A. (2001) A stable-isotope approach to delineate catchment areas of avian migration monitoring stations in North America. *Environ. Sci. Technol.* 35, 1845–1850
- 56 Hobson, K.A. *et al.* (2001) Linking breeding and wintering grounds of Bicknell's thrush using stable isotope analysis of feathers. *Auk* 118, 16–23
- 57 Meehan, T.D. *et al.* (2001) Using hydrogen isotope geochemistry to estimate the natal latitudes of immature Cooper's hawks migrating through the Florida keys. *Condor* 103, 11–20
- 58 Hobson, K.A. and Wassenaar, L.I. (2001) Isotopic delineation of migratory wildlife populations in North America: loggerhead shrikes. *Ecol. Appl.* 11, 1545–1553
- 59 Chamberlain, C.P. *et al.* (2001) Stable isotopes examined across a migratory divide in Scandinavian willow warblers (*Phylloscopus trochilus trochilus* and *Phylloscopus trochilus acredula*) reflect their African winter quarters. *Proc. R. Soc. London B Biol. Sci.* 267, 43–48
- 60 Milot, E. *et al.* (2000) Phylogeography and genetic structure of northern populations of the yellow warbler (*Dendroica petechia*). *Mol. Ecol.* 9, 667–681

# Selection at the level of the community: the importance of spatial structure

Craig R. Johnson and Maarten C. Boerlijst

**To ask whether natural selection occurs at the level of the community is to consider whether communities represent a major transition in evolution – can particular community configurations evolve and maintain their integrity in the face of disruption arising from the self-interest of component individuals? This requires heritable variation among subcommunities in a landscape, and that alternative subcommunities maintain a degree of individuality in both time and space. Recently developed models show that spatial self-structuring in multispecies systems can meet both criteria and provide a rich substrate for community-level selection and a major transition in evolution.**

The long-running controversies about whether selection at several different levels of biological organization is possible, and whether it can be important, are in large part resolved. The theory of multilevel selection is well established [1–4]. Although genes or, using the lexicon of Dawkins [5], replicators are the units of selection, replicators reside within circumscribed vehicles on which selection acts directly [2]. Vehicles are entities that represent different levels of biological organization, such as genomes, cells, individual organisms and

populations. What remains controversial is the identity of levels of organization above the level of individual organisms on which selection can act, and the circumstances in which selection at levels above the individual are necessary to explain the evolution of particular traits at lower levels [2–4].

## The question and context

One of the grand unifying themes [6] in biology is how selection among selfish entities within one level of biological organization is prevented from overriding a common interest in the INTEGRITY (see Glossary) of a higher level of organization. There is a sound theoretical case that resolution of this problem has realized the major transitions in evolution that give rise to new, higher levels of biological organization: for example, evolution of cells from symbiotic protocells, of individual organisms from cells, and of societies from collectives of individuals [2,3]. Selection can act at higher levels when the variance in a trait among

### Box 1. What is community-level selection?

Selection occurs at the community level if it acts on properties that are manifest only at the level of the community and results in differential survival and reproduction among different subcommunities within a landscape. Note that evolution of traits of individuals might influence community-level properties with concomitant feedback (positive or negative) on the selection environment of individuals. However, this phenomenon is not explained simply by individual-level selection responding to a changing environment. Interpretation at the level of the individual fails, because it provides no insight into the mechanism by which traits of individuals are affected. The mechanism involves effects of community-level phenomena on fitness.

#### Craig R. Johnson\*

School of Zoology,  
University of Tasmania,  
GPO Box 252-05, Hobart,  
TAS 7001, Australia.  
\*e-mail: craig.johnson@  
utas.edu.au

#### Maarten C. Boerlijst

Institute for Biodiversity  
and Ecosystem  
Dynamics, University of  
Amsterdam, Kruislaan  
320, 1098 SM Amsterdam,  
The Netherlands.

different groups that define a higher level of biological organization exceeds the variance within the groups. Under these circumstances, selection at higher levels can favour traits of lower-level entities that confer an advantage to higher-level groups containing those entities, even if the trait is at a selective disadvantage at lower levels.

Here, we address the possibility of selection at the level of the COMMUNITY (Box 1), conflicts between selection at the community level and that at lower levels of biological organization, and how selection at the community level influences the traits of individuals. The controversial idea of community-level selection is an extension of modern thinking on

group selection at the population level (Box 2) and addresses whether the evolutionary principles that underpin the major transitions in evolution at lower levels of biological organization extend to communities. Do communities represent another major transition in evolution, in which community integrity is maintained in spite of the self-interest of component individuals? In some measure, the question addresses whether communities are 'real'. Do they constitute a natural level of biological organization, or are they artificial and arbitrary assemblages that have been devised for the convenience of tidy-minded biologists?

In addressing community-level selection, a key issue is the identification of properties unique to communities on which selection can act. The most general EMERGENT PROPERTY on which selection can act is PERSISTENCE STABILITY. A less obvious emergent property is spatial pattern in the distribution of species in communities.

#### Models: the importance of spatial structure

Selection at the community level requires variability among multiple SUBCOMMUNITIES that can each maintain some minimum level of integrity for a period long enough for selection to act. Integrity can be the maintenance of a nonrandom pattern in the spatial arrangement of individuals – an amount of spatial order in the system.

### Box 2. The group selection controversy

Because community-level selection is closely linked with modern views of group selection, it is necessary to clarify aspects of the group selection debate about which there has been considerable confusion [a–c]. Ideas about group selection on populations (and more general multilevel selection) and of kin selection are alternative views of gene selection, and they do not invoke fundamentally different evolutionary processes [a,c,d]. For example, consider trait-group models of the evolution of altruistic behaviour in a system with altruists and nonaltruists. If altruists benefit the fitness of recipients in their group by an amount  $b$  at personal cost to individual fitness  $c$ , then altruism can evolve, providing that altruists tend to associate with altruists (and nonaltruists with nonaltruists), except during mating [c]. This can be interpreted as arising from a conflict between individual-level selection (favouring nonaltruists) and group selection (favouring altruists) [c]. Alternatively, Maynard Smith [e] argues that this result can be explained entirely at the individual level by the mechanism of kin selection; that the level of association of individuals and values of  $b$  and  $c$  necessary for altruism follows from Hamilton's [f] inequality  $rb > c$ , where  $r$  is the degree of relatedness among individuals. Thus, Maynard Smith suggests that the argument is semantic.

Two points arise from this debate. In the sense that one can define, *de novo*, any mechanism that increases INCLUSIVE FITNESS (see Box Glossary) as selection at the individual level, the debate is about semantics. However, it is not semantic in the sense that changes in inclusive fitness may be conditional upon dynamics at levels of organization above the individual. Under these circumstances,

multilevel selection provides an added understanding of the underlying mechanism that kin selection does not.

Note that, in principle, altruism can arise by kin selection or by any other mechanism that tends to group together altruists (whether or not they are related by recent descent [g]) – it is just that kin selection is often a plausible mechanism in nature. Notably, Hamilton [h] emphasized that the inclusive fitness concept is 'more general than "kin selection"'.

#### References

- a Bourke, A.F.G. and Franks, N.R. (1995) *Social Evolution in Ants*, Princeton University Press
- b Keller, L., ed. (1999) *Levels of Selection in Evolution*, Princeton University Press
- c Sober, E. and Wilson, D.S. (1998) *Unto Others: The Evolution and Psychology of Unselfish Behaviour*, Harvard University Press
- d Leigh, E.G. (1999) Levels of selection, potential conflicts, and their resolution: The role of the 'common good'. In *Levels of Selection in Evolution* (Keller, L., ed.), pp. 15–30, Princeton University Press
- e Maynard Smith, J. (1998) The origin of altruism. *Nature* 393, 639–640
- f Hamilton, W.D. (1964) The genetical evolution of social behaviour. I & II. *J. Theor. Biol.* 7, 1–52
- g Pepper, J.W. (2000) Relatedness in trait group models of social evolution. *J. Theor. Biol.* 206, 355–368
- h Hamilton, W.D. (1975) Innate social aptitudes of man: an approach from evolutionary genetics. In *Biosocial Anthropology* (Rox, R., ed.), pp. 133–155, Malaby Press

#### Box Glossary

**Inclusive fitness:** fitness that takes into account the reproductive success of all individuals sharing a particular gene.

### Box 3. Spatial effects influence the evolution of parasite virulence and transmissibility in model systems

In spatial models of host–parasite systems with constant (high) virulence and single infections per host, transmission rates evolve to an intermediate level [a–c]. Individual-level selection favours higher transmission rates locally, but as transmission rates approach a critical threshold, local extinction of hosts leads to local extinction of parasites. By this mechanism, the landscape self-organizes into patches (subcommunities of hosts and parasites). If transmission rates within a patch become too high, that subcommunity is likely to collapse, often before transmission of the parasite to another patch. Thus, the global process of community-level selection (between patches) limits the local effects of individual-level selection (within patches). When transmission and virulence are both allowed to evolve independently, evolution to an intermediate balance between transmission and virulence occurs by the same mechanism [c].

Keeling, Rand and colleagues have shown that this behaviour also occurs if within-patch dynamics are modelled nonspatially and the spatial component is included only at the between-patch dynamics level [b,c]. This emphasizes the importance of processes at the patch (subcommunity) level. Importantly, these

results do not arise in completely mixed populations [a–c], and in partially mixed systems mean virulence increases as the dispersal of parasites becomes less local [d]. Similarly, if dead hosts are replaced instantaneously with susceptible hosts, local extinction of hosts is not possible and so the spatial mechanism is removed and transmission increases unbounded [e].

#### References

- a Haraguchi, Y. and Sasaki, A. (2000) The evolution of virulence and transmission rate in a spatially structured population. *J. Theor. Biol.* 203, 85–96
- b Keeling, M.J. (2000) Evolutionary dynamics in spatial host–parasite systems. In *The Geometry of Ecological Interactions: Simplifying Spatial Complexity* (Dieckmann, U. *et al.*, eds), pp. 271–291. Cambridge University Press
- c Rand, D.A. *et al.* (1995) Invasion, stability and evolution to criticality in spatially extended, artificial host–pathogen ecologies. *Proc. R. Soc. London B Biol. Sci.* 259, 55–63
- d Boots, M. and Sasaki, A. (1999) 'Small worlds' and the evolution of virulence: infection occurs locally and at a distance. *Proc. R. Soc. London B Biol. Sci.* 266, 1933–1938
- e Claessen, D. and de Roos, A. (1995) Evolution of virulence in a host–pathogen system with local pathogen transmission. *Oikos* 74, 401–413

Spatial order is emergent in a range of spatial models of multispecies interactions. Unsurprisingly, spatial models of multispecies systems often manifest very different behaviours from their MEAN-FIELD counterparts. Two important general features of spatial models of multispecies systems are that they allow the possibility of global persistence in spite of local extinctions and so are usually more stable than their mean-field equivalents, and have a tendency to self-organize spatially [7–9]. SPATIAL SELF-STRUCTURING produces nonrandom spatial patterns at scales much larger than the scale of interaction among individuals, even in a continuous and abiotically homogeneous environment. This structure is not explicitly coded but is emergent from local interactions among individuals and (usually) local dispersal. It is 'order for free' [10].

#### Evolution to critical stability of subcommunities

The most basic form of community-level selection in a spatial system occurs when selection at the individual level changes a trait to the point where the community dynamic of discrete patches (subcommunities) on a landscape becomes unstable. This instability leads to loss of individuals with those traits, and the subsequent collapse of the subcommunities that contain them. Local subcommunities with individuals that exceed this threshold go extinct at higher rates, so community-level selection maintains the trait below that threshold.

A simple example of this behaviour arises in spatial models of the evolution of virulence in parasites. In spatial models in which singly infected hosts infect their neighbours and hosts reproduce locally, patch formation in the distribution of hosts

and parasites is emergent. If transmission (or virulence) becomes too high, hosts die too quickly, creating isolated patches that are doomed to extinction (Box 3). Thus, selection at the level of the individual increases transmission rates to the border of host-patch persistence stability, which limits further increases. This results in evolution to intermediate transmission rates (Box 3). Evolution to critical stability in host dynamics can arise through a similar spatial mechanism [11].

Evolution to intermediate levels of transmission (and/or virulence) also arises in nonspatial models, provided there is an explicit tradeoff between parasite virulence and transmissibility [12,13]. This is often interpreted as a tradeoff between individual-level selection (acting to increase the reproductive rate of parasites within hosts) and community-level selection (limiting virulence). This idea underpins predictions that virulence should increase with: multiple infection of single hosts by unrelated parasites [14–16]; increased frequency of HORIZONTAL TRANSMISSION OVER VERTICAL TRANSMISSION [17–19]; increased likelihood of horizontal transmission [17]; the capacity of the parasite to survive outside the host [17,20]; the parasite-independent mortality rate of the host; and the mortality rate of the parasite [21]. In these models, the tradeoff is usually not interpreted in a spatial context.

The important point here is that in nonspatial models, these behaviours depend on an explicit tradeoff between virulence and transmissibility. If transmission and virulence are decoupled in mean-field models, with single infections per host, evolution tends to highest transmission rates and zero virulence as a result of community-level selection. With multiple unrelated genotypes co-infecting each

host, virulence increases unbounded as a result of individual-level selection within hosts.

Note that mean-field models in which virulence and transmissibility are explicitly coupled simply assume that the tradeoff exists, but they do not offer an explanatory mechanism for it. In spatial models, the mechanism that limits virulence is an emergent spatial phenomenon; transmissibility (or virulence) is limited, because it affects the probability of extinction of host patches. Thus, the system can be understood in terms of the direction of selection within and between host patches on a landscape. This is a truly community-level phenomenon. It contrasts with mean-field models, in which the dynamics are determined by selection within and between hosts.

The conceptual framework that underpins evolution of virulence also applies to the dynamics of exploitation of prey by other types of consumers. For example, van Baalen and Sabelis [22] identify comparable tradeoffs between selection at the level of the individual and that at the level of the community. Although research in this area is in its infancy, these ideas are being increasingly addressed [23,24].

Competitive interactions can also show evolution to critical stability in spatial systems where competition is for space [25]. If species self-organize into modular colonies, one colony can protect another from its competitor, depending on the spatial arrangement of the colonies. If the COMPETITION NETWORK is a simple INTRANSITIVE LOOP (i.e. *A* overgrows *B*, *B* overgrows *C*, *C* overgrows *A*), selection at the individual level will always act to increase competitive ability (i.e. growth rate). However, when the difference in growth rate among species becomes too large, subcommunities with very fast growers become locally unstable and collapse, with loss of the fast growers. This occurs because fast growers locally eliminate their competitor's competitor (e.g. if a fast-growing *A* eliminates *B*, *C* will overgrow *A* unimpeded by *B*). The mechanism depends on self-organized spatial structure and the indirect interactions among species.

In all these spatial models, individuals evolve to be as fit as they can be locally, while allowing their subcommunity to persist. The dynamic reflects a simple tradeoff between individual-level selection (which increases the fitness of individuals locally) and community-level selection (which acts to limit it). The key point here is that limiting fitness provides no benefit to the individual in its local environment, and there is no net benefit at the population group level. The benefit arises only at the community level. Spatial structure in populations is an essential ingredient for the mechanism, as has been similarly shown to enable population-level selection for altruism in other systems [26]. Most of the models described above show that community-level selection becomes less important as spatial pattern becomes increasingly homogeneous.

### *Selection for spatial pattern in communities*

When self-organized subcommunities are inherently stable, such that stability within subcommunities is not influenced by selection at the individual level, a qualitatively different mechanism can arise in which selection operates on emergent spatial patterns. This phenomenon can be observed in models in which spiral structures arise in the arrangement of individuals (Box 4). In these examples, individual-level selection is largely irrelevant to the overall dynamic, because it is overridden by selection for properties of the spiral (i.e. of the entire subcommunity). Where a variety of different global spatial patterns arise (spirals, spiral chaos and turbulence), EVOLUTIONARY ATTRACTORS in the system are ultimately determined by the global pattern (Box 5).

The models discussed in Boxes 4 and 5 show that selection at the level of emergent mesoscale patterns can work in the opposite direction to that of selection at the level of individuals. The evolutionary attractors do not convey a fitness benefit to either individuals or groups of individuals of the same species. The benefit is evident only at the community level, and the phenomenon is entirely dependent on spatial structure.

### **Empirical evidence**

#### *Experimental tests*

As with all areas of evolutionary biology, theoretical development advances more quickly than does empirical evidence. The most powerful empirical approach is to conduct experiments in which evolution can be measured directly, but this area has been slow to develop. This is due, in part, to difficulties in the design and interpretation of this kind of experiment because of potential confounding effects [21,27]. Notably, explicit tests of the importance of emergent spatial structure in influencing selection have not been attempted.

Notwithstanding these difficulties, SERIAL PASSAGE EXPERIMENTS show that virulence increases rapidly relative to unmanipulated controls when there are frequent serial transfers of parasites to environments with uninfected hosts [28]. This result is in keeping with tradeoffs between selection at the level of the individual and that at the level of the community. Similar increases in virulence are observed in other systems with increased rates of horizontal transmission [28–31]. At least some of these experiments have been interpreted in a spatial context [32]. Experiments allowing multiple infections arguably provide the richest ground for appropriate tests, but the likelihood of complex dynamics [15] and SOFT SELECTION (e.g. where competition between different parasites within a host reduces their virulence [33,34]) makes for difficult interpretation.

Artificial selection experiments using multispecies communities, such as those of Swenson *et al.* [35], are

#### Box 4. Evolution that is dependent on emergent spiral patterns in multispecies systems

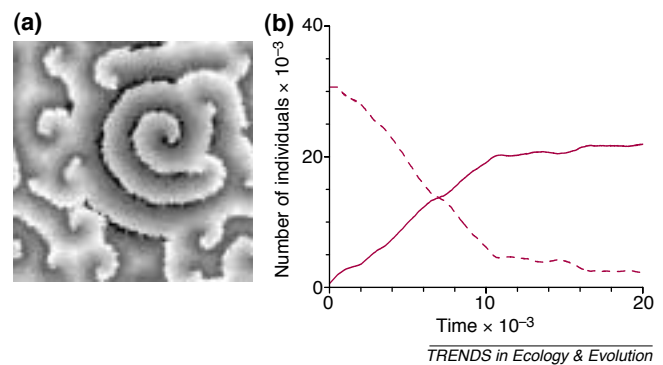
Even when different subcommunities are inherently stable, they can demonstrate differential survival depending on how their spatial properties affect the nature of their interactions. An example of this is provided by the multispecies models of Boerlijst and Hogeweg [a], in which molecules interact in catalytic hypercycles. These systems self-structure spatially to form rotating 'spirals' in which molecular species propagate from the core of the spiral and track each other on a two-dimensional surface (Fig. 1). Individual-level selection invariably favours molecules with a low decay rate (i.e. longer lifespan). However, spirals (subcommunities) composed of molecules with high decay rates rotate more quickly than do those composed of longer-lived molecules and, at the spiral level, quickly rotating spirals annihilate the more slowly rotating spirals.

In this system, there is no tradeoff between levels of selection, because community-level selection (i.e. among spirals) overrides individual-level selection. Selection at the community level selects for increased rotational velocity of spirals to an upper limit of spiral stability (spirals break down if the rotational velocity becomes too great). Thus, selection is for an asymptotic minimum fitness (i.e. maximum decay rate) of individuals. There is no benefit of a high decay rate at the level of individual molecules, or at the level of groups of molecules of the same type. Indeed, the asymptotic population size of an invasive mutant with a relatively high decay rate is inevitably smaller than that of the 'fitter' wild type it displaces [a]. The key point here is that the benefit arises only at the community level.

Spiral structures also arise in spatial models of host–parasitoid dynamics [b]. If inefficient mutant parasitoids with a relatively poor growth rate (i.e. low fitness) are introduced into the centre of a spiral, they eventually replace their locally fitter wild-type counterparts, in spite of the local growth rate of the wild type being always greater than that of the mutant [c]. The mechanism depends on the dynamics of the spirals. Because individuals are propagated to the entire domain of the spiral from the core, mutants introduced to the core eventually dominate the spiral.

important insofar that they show that community-level phenotypic traits are variable and have a heritable basis. However, this approach also has limitations. An obvious issue is that these experiments demonstrate a phenomenon, not a mechanism, and therefore do not control for the possibility of individual-level selection. Because it is possible that the same result could emanate from individual-level selection, interpretation is confounded. In this context, we note that many group behaviours in vertebrates (which, in principle, could be selected for artificially) can be explained by self-interest [36,37]. Another problem is that artificial selection can achieve what natural selection never will. It must be demonstrated that natural selection at the community level can overwhelm disruptive self-interest at the individual level, which can be arranged through artificial selection.

Note that although community-level selection can reinforce individual-level selection [38], in such



**Fig. 1.** Selection for a fast-decaying mutant in a hypercycle of catalytic molecular species [a]. The mutant (black) is introduced into the core of a spiral wave, where it completely replaces the wild type (white). The mutant decays 50% faster than the wild type, but all other parameters are the same. In (a), after 6500 time steps, the spiral with the mutant increases its domain, because of its faster rotation speed. This process continues, and the mutant gradually replaces the wild type until an equilibrium is reached (b), after ~10 000 time steps. In this equilibrium, the spiral with the mutant dominates most of the field (solid line), and a few reinforced wild-type spirals remain (dotted line), because the wild type locally outcompetes the mutant. The y-axis shows a running average over 1000 time steps.

Spirals with inefficient (mutant) parasitoids rotate more quickly than do 'uninfected' spirals with wild-type parasitoids, and faster-rotating spirals outcompete slowly rotating spirals. Again, selection occurs at the level of spirals. Spirals with inefficient parasitoids rotate more quickly, because host density increases more rapidly at the front of waves of inefficient parasitoids.

#### References

- Boerlijst, M.C. and Hogeweg, P. (1991) Self-structuring and selection: spiral waves as a substrate for evolution. In *Artificial Life II* (Langton, C.G., ed.), pp. 255–276. Addison–Wesley
- Hassell, M.P. *et al.* (1994) Species coexistence and self-organizing spatial dynamics. *Nature* 370, 290–292
- Boerlijst, M.C. *et al.* (1993) Evolutionary consequences of spiral waves in a host–parasitoid system. *Proc. R. Soc. London B Biol. Sci.* 253, 15–18

circumstances, it is difficult to separate the two effects empirically. Thus, a crucial test will show natural selection for a trait in one direction at the individual level, but in another direction at the community level. Results of serial passage experiments and other experiments in which the likelihood of horizontal transmission is manipulated [28–31] can be interpreted in this light.

The need for more experimental studies to determine the importance of natural selection at the community level remains. In particular, there is an urgent need to test whether selection at the level of emerging spatial structure influences the traits of individuals, and how these traits feed back to community dynamics.

#### Correlative and comparative approaches

In the absence of experiments, correlative and comparative methods can determine whether data are consistent with theory, but they do not constitute

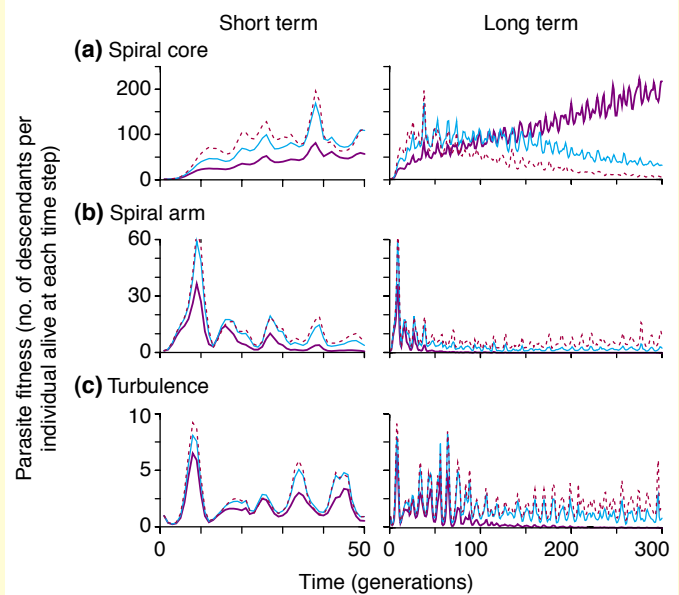
### Box 5. Global patterns of community structure can determine evolutionary attractors

Savill *et al.* [a] extended the host–parasitoid model introduced in Box 4 to examine the evolution of parasitoid dispersal, which they described by the level of parasitoid aggregation in patches of high host density. These models yield a rich variety of spatial self-structuring at the community level, including spirals, spiral chaos and turbulence. In this system, pattern formation at the community level defines the limits for the evolution of aggregation strength.

There is a complex interplay of selection at different levels of biological organization. At both a local scale and in the short term, individual fitness is always higher at higher levels of aggregation strength ( $\mu$ ) (Fig. 1). However, within spirals, where waves of parasitoids track waves of hosts, there is selection for reduced  $\mu$  in the longer term, because strongly aggregating parasitoids migrate away from the core faster than do weakly aggregating ones, so that low- $\mu$  parasitoids come to dominate the core. Because a spiral propagates from the core, low- $\mu$  parasitoids eventually dominate the entire spiral. Because spirals can only form when there are many low- $\mu$  parasitoids, selection within spirals enhances the continuation of spirals. On a longer time scale again, selection among spirals selects for higher- $\mu$  parasitoids because spirals with strongly aggregating parasitoids rotate more quickly than do those with more weakly aggregating parasitoids.

The global pattern also depends on the dispersal of hosts. When the dispersal of hosts is relatively low and aggregation of parasites exceeds a threshold, the self-organizing pattern is turbulent, and turbulence out-competes spirals. Thus, competition between spirals can increase  $\mu$  to a point where turbulence emerges, which creates an attractor for high- $\mu$  parasitoids. In turbulence, the attractor for  $\mu$  is determined by a balance between alternative strategies of aggregating strongly in the back of a host wave, and aggregating weakly in the path of a wave waiting for a new front to arrive.

At higher levels of host dispersal, spirals out-compete turbulence and so there is an attractor for low- $\mu$  parasitoids. Thus, in spite of the fact that short-term local inclusive fitness is always greater for higher  $\mu$  in all areas of spirals and turbulence (Fig. 1), the evolutionary attractor for parasitoid aggregation strength is determined by the global pattern.



**Fig. 1.** Effects of individual- and community-level selection in the host–parasitoid model of Savill *et al.* [a] are reflected in the short-term fitness and long-term fitness, respectively, of parasites with high and low aggregation tendency. In the short term, highly aggregating parasites (red line) always have a higher fitness than intermediate- (blue line) or low-aggregation (purple line) parasites in all areas of spatial pattern (left-hand graphs). This reflects individual-level selection. However, in the longer term, the effects of community-level selection become manifest, and lower-aggregating parasites are selected. From the right-hand graph (a) it can be seen that, within the spiral core, the low-aggregation parasites have the most offspring in the long term. Within areas of other spatial patterns [(b) and (c)], selection favours highly aggregating parasites on the longer timescale, but these are far outnumbered by the higher per capita number of offspring from individuals in the spiral core (compare scales of y-axes). These properties hold at any stage of the system.

Although properties of individuals ultimately determine the global pattern, the evolutionary attractor is set by dynamics at the level of spatial pattern.

#### Reference

- a Savill, N.J. *et al.* (1997) Self-reinforcing spatial patterns enslave evolution in a host–parasitoid system. *J. Theor. Biol.* 188, 11–20

critical tests of community-level selection and are open to alternative interpretations. There has been little explicit consideration of spatial structure in this work, in spite of the fact that interpretation usually demands an implicit spatial context.

Some evidence of this type exists from studies of parasite virulence and is in keeping with theoretical predictions of the tradeoffs between individual-level (within-host) and community-level (between-host) selection. Arguably, the best known correlative evidence is the rapid reduction in virulence to intermediate levels in the myxoma virus, a disease of rabbits *Oryctolagus cuniculus* in Australia and (to a lesser extent) Europe [39]. This is consistent with predictions about tradeoffs between selection at the level of the individual and that of the

community, and the spatial effects of reduced host densities on transmission.

Another well-known example is Herre's comparative study of the virulence of nematodes infecting several species of fig wasps [18,40]. This showed increased virulence of nematodes associated with increased levels of co-infection (by unrelated nematodes) and an increased likelihood of horizontal transmission, exactly as predicted from tradeoffs between individual- and community-level selection [12,40]. However, interpretation of his field data is ambiguous, in that either the level of co-infection or relative amounts of horizontal and vertical transmission can explain the observed pattern in virulence.

Comparative data for virulence in human pathogens is also consistent with a balance between

selection at the individual level acting to increase virulence and that at the community level acting to limit it. For example: vector-borne pathogens tend to be more virulent than are nonvector-borne pathogens; there is a significant positive correlation between virulence and the degree of waterborne transmission in diarrhoeal diseases; and, within nonvector-borne pathogens, pathogens able to survive longer in the external environment tend to higher virulence than those with limited ability to survive outside their hosts [17]. These trends are most readily interpreted in terms of spatial effects on transmissibility.

Selection at the community level is predicted to favour prudent predators when prey patches are colonized by single predator clones [22]. Ladybirds *Adalia bipunctata* preying on aphids *Sitobion avenae* show prudent behaviour in that they restrict their egg-laying to the early development of the aphid colony and lay fewer eggs per colony than they are capable of [41]. Laying only at the beginning of colony development can be explained by individual-level selection, because eggs laid later are likely to be cannibalized by early-hatching larvae. However, restricting the number of eggs laid cannot be explained by individual-level selection.

Our final note concerns biocontrol agents, in which the virulence of parasites or predators can be determined (at least initially) by the experimenter. In managing virulence for biocontrol, it is increasingly recognized that the most effective impact of biocontrol agents on large spatial scales might be achieved by less aggressive strains that do not overexploit prey in a patch so rapidly that they reduce the likelihood of spread to other patches [23]. Agents of intermediate 'virulence' are more effective because of spatial effects in epidemiology; predators cannot disperse to all prey patches instantaneously.

### Conclusions

Maynard Smith and Szathmáry [3] argue that ecosystems (and, by implication, communities) do not represent a major transition in evolution because they have 'no individuality and separateness' from other entities of the same kind. However, a variety of spatial models of multispecies systems shows that individuality in time and space of alternative subcommunities is emergent – there is order for free. Spatial self-structuring arises through local interactions between individuals and their neighbours and an element of localized dispersal. It provides for highly nonlinear dynamics, whereby community-level selection can eventually override the selfish interests of the individual. If mutation occurs in traits that affect the fitness of individuals, which in turn influences community dynamics, then spatial self-structuring effectively generates a landscape of many 'experiments' on which selection can act. The subcommunities, which need not be discrete patches in time and space, provide some measure of spatial

and temporal integrity and a substrate for evolution. Spatial systems that include nonlinear genetic interactions (e.g. epistasis) are likely to provide a particularly rich substrate for evolution.

In all models showing the importance of community-level selection, at least some component of dispersal is local, so that individuals of the same species in the same area are more likely to be related by descent. The combined effects of spatial self-structuring and the greater likelihood of relatedness among proximal than among widely separated individuals ensures several features necessary for community-level selection. First, it provides a level of individuality and integrity in subcommunities. Second, there is greater variation in the fitness of individuals of a given species among subcommunities than within subcommunities. Third, there is an amount of heritability in lineages of subcommunities as the individuals in them die and are replaced by others. Because of the high likelihood of relatedness of individuals in the same area, the proximate evolutionary mechanism in most models is ostensibly KIN SELECTION; however, that evolution arises ultimately through differential survival of subcommunities.

The theoretical base for selection at the community level is at least established, if not richly developed. However, given the limited empirical evidence, the question of how important these processes are in nature is, to a large extent, open. If they are important in nature, then communities are a natural and nonarbitrary level of biological organization and represent a major transition in evolution *sensu* Maynard Smith and Szathmáry [3]. It is clear that species and genotypes are not distributed randomly at most spatial scales but manifest a large variety of spatial patterns. It is also clear that spatial structure affects microevolutionary processes [42]. However, it is untested whether spatial structure in real communities provides a sufficient substrate for evolution at the community level. At larger spatial scales, and with macroorganisms, correlative and comparative studies can be used to determine whether patterns are consistent with these ideas. For these kinds of data, interpretations are necessarily limited, and observations of relations among a small subset of species can be obfuscated by interactions with others [18]. Conducting experiments that critically test for the role of spatial structure in community-level selection is a more powerful approach. Those experiments will need to show explicitly that community-level selection can oppose and overcome the effects of individual-level selection. Microbial systems (viruses, bacteria, protozoa) are a promising model for research, because evolution can occur rapidly within them, they can demonstrate spatial self-structuring, and the genetic structure of individuals affects population and community dynamics with attendant feedback from community properties to evolutionary dynamics [43].

### Acknowledgements

We thank Paulien Hogeweg, Katherine Johnson, Maurice Sabelis and Marijn van Ballegoijen for helpful comments on this article, and Paulien Hogeweg for discussion and for Fig. 1 in Box 5. C.R.J. also thanks the Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam. This work was supported by an ARC Large Grant to C.R.J. and by a Fellowship of the Royal Netherlands Academy of Arts and Sciences to M.C.B.

## Glossary

**Community:** two or more interacting species, each with distinctive properties, reproductively isolated from the other, and in which each species interacts directly or indirectly with all others. In this context, 'species' can range from distinct species of molecules to true biological species.

**Competition network:** the nature of competitive interactions among a group of species.

**Emergent property:** a property that arises at one level of organization as a consequence of interactions among entities at a lower level of organization; it is a property unique to the higher level of organization and usually not predictable from knowledge of properties at lower levels.

**Evolutionary attractor:** the properties or state towards which a system tends to evolve, regardless of the starting conditions of the system.

**Horizontal transmission:** transmission of parasites from one host to another, in which the recipient is not the offspring of the initial carrier.

**Integrity:** in this context, persistence of a property or set of properties over a particular time period.

**Intransitive loop:** a circular structure in a competition network, the simplest being where *A* outcompetes *B* outcompetes *C* outcompetes *A*. Intransitive structures are common in subtidal hard-bottom marine systems.

**Kin selection:** a form of natural selection of genes based on the fitness of an individual and its relatives possessing the same genes through common descent.

**Mean-field models:** models without explicit spatial structure, in which homogenous

mixing of all individuals is assumed; typically constructed of differential or difference equations.

**Persistence stability:** persistence of all species in an assemblage for >1 turnover of all individuals [a].

**Serial passage experiment:** experiments in which a lineage of parasites are sequentially and repeatedly introduced into populations of uninfected hosts, and their evolved properties are compared with those of the ancestral parasite.

**Soft selection:** selection for a trait in an individual relative to the selection of that trait in others of the same population or the average of that trait in the population. It is frequency dependent, is unconcerned with the absolute phenotype of the trait, and allows inferior individuals in a population a nonzero probability of surviving into future generations.

**Spatial self-structuring:** development of nonrandom spatial patterns in a system as an emergent property.

**Subcommunity:** a collection of individuals in an area within a broader landscape, usually with particular properties of spatial structure, species composition and size; it might contain an identical number of species to, or fewer species than, the community as a whole, and its spatial boundaries might not be discrete.

**Vertical transmission:** transmission of parasites from a host to its offspring.

## Reference

a Johnson, C.R. and Mann, K.H. (1988) Diversity, patterns of adaptation, and stability of Nova Scotian kelp beds. *Ecol. Monogr.* 58, 129–154

## References

- Bourke, A.F.G. and Franks, N.R. (1995) *Social Evolution in Ants*, Princeton University Press
- Keller, L., ed. (1999) *Levels of Selection in Evolution*, Princeton University Press
- Maynard Smith, J. and Szathmáry, E. (1995) *The Major Transitions in Evolution*, W.H. Freeman
- Sober, E. and Wilson, D.S. (1998) *Unto Others: The Evolution and Psychology of Unselfish Behaviour*, Harvard University Press
- Dawkins, R. (1976) *The Selfish Gene*, Oxford University Press
- Leigh, E.G. (1999) Levels of selection, potential conflicts, and their resolution: The role of the 'common good'. In *Levels of Selection in Evolution* (Keller, L., ed.), pp. 15–30, Princeton University Press
- Boerlijst, M.C. (2000) Spirals and spots: novel evolutionary phenomena through spatial self-structuring. In *The Geometry of Ecological Interactions: Simplifying Spatial Complexity* (Dieckmann, U. *et al.*, eds), pp. 171–182, Cambridge University Press
- Dieckmann, U. *et al.*, eds (2000) *The Geometry of Ecological Interactions: Simplifying Spatial Complexity*, Cambridge University Press
- Johnson, C.R. (1997) Self-organizing in spatial competition systems. In *Frontiers in Ecology—Building the Links* (Klomp, N.I. and Lunt, I.D., eds), pp. 245–263, Elsevier Science
- Kaufmann, S. (1995) *At Home in the Universe. The Search for Laws of Self-organization and Complexity*, Viking
- Richards, S.A. *et al.* (1999) Selection for intermediate mortality and reproduction rates in a spatially structured population. *Proc. R. Soc. London B Biol. Sci.* 266, 2383–2388
- Bull, J.J. (1994) Virulence. *Evolution* 48, 1423–1437
- Frank, S.A. (1996) Models of parasite virulence. *Q. Rev. Biol.* 71, 37–78
- Mosquera, J. and Adler, F.R. (1998) Evolution of virulence: a unified framework for coinfection and superinfection. *J. Theor. Biol.* 195, 293–313
- Nowak, M.A. and May, R.M. (1994) Superinfection and the evolution of parasite virulence. *Proc. R. Soc. London B Biol. Sci.* 255, 81–89
- van Baalen, M. and Sabelis, M.W. (1995) The dynamics of multiple infection and the evolution of virulence. *Am. Nat.* 146, 881–910
- Ewald, P.W. (1994). *Evolution of Infectious Disease*, Oxford University Press
- Herre, E.A. (1999) Laws governing species interactions? Encouragement and caution from figs and their associates. In *Levels of Selection in Evolution* (Keller, L., ed.), pp. 209–237, Princeton University Press
- Lipsitch, M. and Nowak, M. (1995) The evolution of virulence in sexually transmitted HIV/AIDS. *J. Theor. Biol.* 174, 427–440
- Bonhoeffer, S. *et al.* (1996) The curse of the pharaoh: the evolution of virulence in pathogens with long living propagules. *Proc. R. Soc. London B Biol. Sci.* 263, 715–721
- Ebert, D. and Mangin, K.L. (1997) The influence of host demography on the evolution of virulence of a microsporidian gut parasite. *Evolution* 51, 1828–1837
- van Baalen, M. and Sabelis, M.W. (1995) The milker–killer dilemma in spatially structured predator–prey interactions. *Oikos* 74, 391–400
- Elliot, S.L. *et al.* Management of virulence in biocontrol agents. In *The Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management* (Dieckmann, U. *et al.*, eds), Cambridge University Press (in press)
- Sabelis, M.W. *et al.* Evolution of exploitation and defence in plant–herbivore–predator interactions. In *The Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management* (Dieckmann, U. *et al.*, eds), Cambridge University Press (in press)
- Johnson, C. and Seinen, I. Selection for restraint in competitive ability in spatial competition systems. *Proc. R. Soc. London B Biol. Sci.* (in press)
- Mitteldorf, J. and Sloan Wilson, D. (2000) Population viscosity and the evolution of altruism. *J. Theor. Biol.* 204, 481–496
- Ebert, D. (1998) Infectivity, multiple infections, and the genetic correlation between within-host growth and parasite virulence: a reply to Hochberg. *Evolution* 52, 1869–1871
- Ebert, D. (1998) Experimental evolution of parasites. *Science* 282, 1432–1435
- Bull, J.J. *et al.* (1991) Selection of benevolence in a host–parasite system. *Evolution* 45, 875–882
- Mackinnon, M.J. and Read, A.F. (1999) Genetic relationships between parasite virulence and transmission in the rodent malaria *Plasmodium chabaudi*. *Evolution* 53, 689–703
- Messenger, S.L. *et al.* (1999) Virulence evolution obeys a trade-off. *Proc. R. Soc. London B Biol. Sci.* 266, 397–404
- Haraguchi, Y. and Sasaki, A. (2000) The evolution of virulence and transmission rate in a spatially structured population. *J. Theor. Biol.* 203, 85–96
- Chao, L. *et al.* (2000) Kin selection and parasite evolution: higher and lower virulence with hard and soft selection. *Q. Rev. Biol.* 75, 261–275
- Turner, P.E. and Chao, L. (1999) Prisoner's dilemma in an RNA virus. *Nature* 398, 441–443
- Swenson, W. *et al.* (2000) Artificial ecosystem selection. *Proc. Natl. Acad. Sci. U. S. A.* 97, 9110–9114
- Clutton-Brock, T.H. *et al.* (1999) Selfish sentinels in cooperative mammals. *Science* 284, 1640–1644
- Kitchen, D.M. and Packer, C. (1999) Complexity in vertebrate societies. In *Levels of Selection in Evolution* (Keller, L., ed.), pp. 176–196, Princeton University Press
- Boerlijst, M.C. *et al.* (1993) Evolutionary consequences of spiral waves in a host–parasitoid system. *Proc. R. Soc. London B Biol. Sci.* 253, 15–18
- Fenner, F. and Fantini, B. (1999) *Biological Control of Vertebrate Pests: The History of Myxomatosis, an Experiment in Evolution*, CABI Publishing
- Herre, E.A. (1995) Factors affecting the evolution of virulence: Nematode parasites of fig wasps as a case study. *Parasitology* 111 (Suppl.), 179–191
- Hemphill, J.-L. and Dixon, A.F.G. (1997) Are aphidophagous ladybirds (Coccinellidae) prudent predators? *Entomol. Res. Org. Agric.* 15, 151–159
- Thompson, J.N. (1999) Specific hypotheses on the geographic mosaic of coevolution. *Am. Nat.* 153, S1–S14
- Bohannan, B.J. and Lenski, R.E. (2000) Linking genetic change to community evolution: insights from studies of bacteria and bacteriophage. *Ecol. Lett.* 3, 362–377