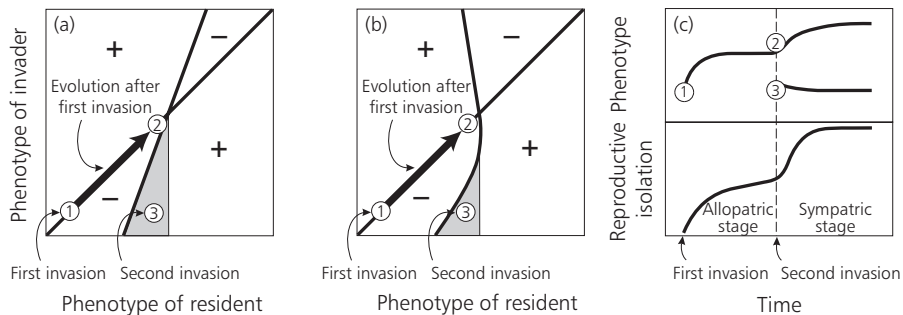


**Box 9.5** Double invasion and frequency-dependent selection

H.D. Rundle, D. Schluter, U. Dieckmann, J.A.J. Metz, and M. Doebeli

The double-invasion scenario described in Box 9.3, which includes an initial allopatric phase and a later sympatric phase, requires that selection be frequency dependent. That is, the fitness landscape of the second invader is dependent on the presence and the phenotype of the first invader. Without frequency dependence, the two forms (depicted by a square and a star in Box 9.3) would not have persisted as competitors in sympatry following the second invasion. Instead, one of the two morphs would have been driven to extinction by the other. Moreover, ecological character displacement can only occur under frequency-dependent selection: in its absence, the second invader is forced to pursue the same evolutionary course as did the first one initially. Below we use the adaptive dynamics framework to depict the possible role of frequency dependence in a simple scenario. We consider a single trait axis along which the two stickleback phenotypes are differentiated. A low value along this axis represents the zooplanktivore phenotype. Greater values indicate more benthic-feeding phenotypes.

The linear pairwise invasibility plot in panel (a) below represents one scenario of events that might have led from a single marine stickleback ancestor to two sympatric species within a lake. The signs (+, -) indicate, for each value of the resident phenotype, the invader phenotypes that can (+) and cannot (-) invade when there is competition for resources. The crossed lines delimit regions of different sign.



The hypothetical sequence of events begins at (1) when the marine form, a zooplanktivore, first invades the lake. Subsequently, adaptation to the new environment [arrow from (1) to (2)] causes this first invader to evolve toward an intermediate phenotype that represents an evolutionary branching point (intersection of the two thick lines). A lake with a single intermediate population at the branching point can be invaded by nearby phenotypes larger or smaller (i.e., the population experiences disruptive selection). The area shaded in gray indicates the trait values of zooplanktivore-like phenotypes permitted to invade once the resident population is close to the branching point. In the scenario in panel (a), the marine form invades a second time (3) before the first population has reached the branching point, which

*continued*

**Box 9.5** *continued*

results in two phenotypes within the lake. Although the new marine invader and the evolved lake form now reside on the same side of the branching point, they can coexist and continue to evolve. Ecological character displacement, driven by frequency-dependent competition for resources, causes further divergence between the two populations until they eventually reach an evolutionarily stable combination of phenotypes [top section of panel (c)].

Under this simple scenario, competitive exclusion precludes a second invasion until the phenotype of the first invader approaches the branching point. Insufficient reproductive isolation may also preclude a second invasion that is too soon after the first. Thus, the timing of the second invasion is dependent not only on favorable geologic events that allow the movement of individuals from the sea into the lake, but also on the evolution of the resident within the lake. As shown in the bottom section of panel (c), partial premating isolation is assumed to build prior to the second invasion (the allopatric phase) as a by-product of phenotypic divergence. After the second invasion (the sympatric phase), natural selection directly on premating isolation (i.e., reinforcement) or on correlated traits might further strengthen premating isolation.

Alternative invasion scenarios that involve more complicated forms of interaction between phenotypes are possible, and lead to nonlinear pairwise invasibilities as in panel (b) above. For example, the first invader might evolve not to a branching point, but instead to an evolutionarily stable attractor that permits no invasion by nearby phenotypes [intersection of the two thick lines in panel (b)]. In this case the intermediate population is under stabilizing selection, not disruptive selection. Such stabilizing selection might occur if zooplankton and benthic resources in the lake peak at different times in the season, such that a generalist intermediate phenotype can exploit both of them in sequence when more specialized zooplanktivore or benthic phenotypes cannot.

In this scenario, the line that delimits (+) and (−) regions in the lower part of the plot is curved to the left. In this case a second invasion is possible if the invading zooplanktivore morph is sufficiently different in phenotype from the resident morph, as the latter population evolves toward an intermediate phenotype. This might happen if a portion of the zooplankton resource base cannot be exploited by an intermediate phenotype. Following a successful invasion, ecological character displacement and reinforcement might cause further divergence between the two populations, as in the previous scenario.

We do not know which of the two above scenarios, intermediate branching point or intermediate stable attractor, best describes the double invasion process in sticklebacks. Distinguishing them would require determining whether the intermediate form in single-species lakes most often experiences stabilizing or disruptive selection. A series of future experiments could also compare the fitnesses of different invading phenotypes in the presence of alternative resident phenotypes.