

Temporal variability and local adaptation

Gene flow is often regarded as a constraining force because it can counteract selective forces that lead to local adaptation¹. Local adaptation (adaptive deme formation) can be studied relatively easily in the context of host–parasite and plant–herbivore interactions through transplant experiments^{2–4}. The presence or absence of local adaptation can then be related to the dispersive ability of the herbivore or parasite. In a recent *TREE* review, Mopper⁴ discussed transplant experiments that have been done with phytophagous insects. Contrary to her expectation, insect mobility seems not to be related to the finding of deme formation (see Table 1 in Ref. 4). In particular, some sessile insects do not present adaptive deme formation, while some highly dispersive species do. We present some arguments that could contribute to explaining this discrepancy, by taking the host's and herbivore's population structure into account.

The main point in Mopper's article is that deme formation of phytophagous insects is adaptive because host populations are highly heterogeneous with respect to their quality as 'insect habitat'. Mopper points out that high levels of migration should prevent the parasite from being locally adapted. Indeed, migration is maladaptive when the environment is variable in space^{5,6} but, when the environment is variable in time this is not necessarily the case.

Environmental variability in time may occur because of various factors. First, host plants are ephemeral and therefore herbivore population extinction would be unavoidable unless migration occurs at sufficiently large rates. As a consequence, herbivore demes must be seen as part of a metapopulation in which each host plant is an ephemeral habitat. Large habitat extinction rates would select for relatively large migration rates⁷. Second, within-host growth of herbivores may lead to a decrease in habitat quality (host-plant saturation) and to competition between close relatives⁸. Therefore, dispersing insects have a chance to find a new under-exploited host plant and to compete against non-relatives. Thus, the rate of habitat loss (resulting from host death and from host-plant saturation) relative to the parasites' generation time and kin competition are important variables to consider when assessing migration. The important point here is that within-host competition selects for local adaptation, since the best competitors are those that are locally adapted. Thus, the evolution of migration rates and of local adaptation depend interactively on each other, but are both dependent on other factors as well, such as host demography and host population structure. In this respect, the absence of deme formation in sessile insects as discussed by Mopper, could be the result of low within-host competition and low host-plant death rates. Deme formation of highly mobile insects could then be the result of strong competition among host plants.

A further factor contributing to environmental variability in time are the natural enemies of the herbivores (entomophagous predators or parasites), as discussed by Mopper⁴. If we assume coevolution between the insect and its enemies, then a given genotype that is selected for in a given site at a given time will be selected

against in the same site at some other time⁹. In particular, if the enemies have large migration rates they will adapt rapidly to their sympatric hosts (the herbivore). Therefore, migration can be adaptive because it enables the herbivore to have the good genes at the right time and to keep up with their rapidly evolving enemies. Such a process could also contribute in the finding of deme formation in mobile herbivores.

The study of deme formation of herbivores or parasites to their long-living hosts represents only one part of a complex picture of coevolution. Within-host competition and between-host dispersal (transmission) have to be considered using a metapopulation approach, which must include measures of habitat survival rates, within-host competition, natural enemies and genetic heterogeneity of the habitats.

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Reply from S. Mopper

The points raised by Gandon *et al.* are valid. To understand the often paradoxical patterns of adaptive deme formation in phytophagous insect populations, we must employ a metapopulation approach¹. A metapopulation can be defined as a collection of demes of common ancestry that influence each other via dispersal². In some systems, each plant is inhabited by an insect deme, more or less adapted to the plant's physical properties³. For insect residents, extinction is inevitable when the plant senesces and dies. So demes continuously arise and dissolve. Without dispersal and colonization of new host plants, the population would vanish. Metapopulation theory predicts a tension between selection for good dispersers and good residents⁴. In the initial stages of host colonization, good dispersers predominate, but eventually diminish in abundance relative to philopatric residents that efficiently exploit host tissue.

As demes adapt, densities approach carrying capacity, host resources degenerate, and intraspecific competition ensues. Decline in resource quality may trigger production of individuals with good disperser phenotypes⁵. Therefore, intra-deme competition may on the one hand select for genotypes best able to exploit the host, and on the other, create environmental cues that elicit facultative production of good dispersers able to escape the declining resource and migrate to higher quality habitat. One point to keep in mind is that new host plants proximal to the resident colony may be more similar by descent to the source pool host than to distant plants. This is particularly true for clonal plant species⁶. Therefore, dispersing insects, being more likely to reach near than far plants, may be partially pre-adapted to their new hosts.

Gandon *et al.* attribute the paradoxical absence of deme formation in some highly sessile insect populations to the lack of intra-deme competition and low plant death rates. But in most studies I reviewed, resident insects occurred at extremely high densities on long-lived plants⁸. In such systems, absence of deme formation may arise from spatial (among branches⁷) or temporal (among years⁸) intra-plant variation. Furthermore, intraspecific competition is not a prerequisite for demic adaptation. The host plant can impose severe selection on developing larvae, regardless of the densities at which they occur⁹.

One final point. Other forms of local extinction beside host plant death are possible, and even probable, and they may have the greatest impact on metapopulation genetic structure. For example, in 1994, Hurricane Andrew hit the north Florida (USA) population of *Stilbosis quadricustatella*, a leafmining insect displaying demic adaptation to individual trees of *Quercus geminata* (sand-live oak)⁶. The enormous volume of precipitation coincided with leafminer pupation, which occurs in the soil and leaf litter. Saturated soils caused heavy leafminer mortality, and the population crashed. This event may have leveled the playing field. Traits that enabled some miners to survive prolonged hydration may be unrelated to ability to disperse or exploit plant tissue. It is likely that pupal mortality was largely stochastic: pupae that by chance occupied drier soil survived. Essentially the adapted demes were 'reset' by the environmental catastrophe, with unknown repercussions for the metapopulation.

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