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Book Review

GENETIC STRUCTURE AND LOCAL ADAPTATION IN NATURAL INSECT POPULATIONS.

Edited by Susan Mopper and Sharon Y. Strauss. Chapman and Hall, New York. 1998. Hardback, £65.00. ISBN 0–412–08031–1.

Demes, Hosts and Speciation

I liked the title, which promised broad evolutionary interest. But this is not a general survey of insect population structure and adaptation. Possibly the publishers shortened the title by one long Greek word to make the book sell; the preface makes clear that it is about natural *phytophagous* insect populations. Also, only one kind of adaptation is considered: adaptation to the host plants themselves. I felt somewhat cheated; this book covers a field that is actually a reincarnation of a continuing academic industry: *insect–plant relations*.

For all that, this is an interesting subject, yielding major recent advances. The book contains up-to-date reviews of adaptation to host individuals (chapters by D. Alstad, P. Stiling and A. Rossi, N. Cobb and T. Whitham, W. Boecklen and S. Mopper, S. Mopper, L. Hanks and R. Denno, S. Strauss and R. Karban) and species (S. Gandon *et al*., C. Thomas and M. Singer, J. Itami *et al*., J. Feder *et al*.). All the empirical studies are phenotypic, but phenotypic studies of host adaptation (or any adaptation) are dogged by statistical and quantitative genetic complexities due to genotype/environment correlations and maternal effects (M.-C. Rossiter). It would be best, therefore, if we could identify the biochemical and genetic mechanisms involved. However, although we know a little about unnatural adaptation to insecticides, we still have no idea about natural host adaptations (M. Berenbaum and A. Zangerl). High relatedness within insect broods hatching from single egg-clutches leads to potentially fascinating evolutionary consequences (D. McCauley and P. Goff, J. Costa), but unfortunately no good examples of such consequences were given. Relevant applications, such as the evolution of warning colour and aposematism, were not considered.

Perhaps inevitably, this interdisciplinary subject is in parts limply connected to mainstream evolutionary theory, reflecting weak communication between insect ecologists and evolutionary geneticists (but see theoretical chapter by Gandon *et al*.). For example, the term *deme formation* (Stiling and Rossi, Cobb and Whitham, Boecklen and Mopper, Hanks and Denno) has a curiously 1930s' feel; here, it apparently means 'adaptation to individual hosts, resulting in poor performance on alternative host individuals of the same species'. Sewall Wright introduced the term *deme* somewhat loosely in the 1930s and 1940s, but in population genetics today *deme* is synonymous with *discrete population*, between which a fraction *m* of the deme's *N* individuals may migrate (Strauss and Karban). It would be better to use *local adaptation* (Alstad, Mopper, Strauss and Karban, M. Peterson and R. Denno, Gandon *et al*.) rather than *deme formation*, because that is what is meant, and because local adaptation can also occur in continuous populations on a spatial scale determined by F (gene flow in the sense of diffusion, i.e. standard deviation of parent–offspring distances along a particular axis). Discrete *demes* are completely unnecessary for local adaptation.

This brings me to another gripe, about the confusing term *gene flow* for the combined parameter *Nm*. Drift in discrete populations at equilibrium is controlled by *Nm* through Wright's approximate formula for the standardized variance in gene frequency among demes, $F_{st} \approx 1/(1 + 4Nm)$. Because *Nm* is population size multiplied by the migrating fraction, the term *gene flow* meaning *the number of individuals that migrate* between populations has been popularized by Monty Slatkin. However, this kind of *gene flow* does not control local adaptation at all, in contrast to the thrust of the chapter by Peterson and Denno; it merely measures a tendency towards genetic drift.

It is also invalid to estimate *Nm* from gene frequencies except under the restricted (and often dubious) assumption that gene frequency variance has reached a balance between gene flow and neutral drift. You simply cannot estimate gene flow via allozyme differences between sympatric host-races (as Itami *et al*. suggest) or across a spatial barrier (many examples are published elsewhere), because even if the loci are completely neutral they cannot be both differentiated and at equilibrium at the same time. Feder *et al*. even show that allozyme differences are very likely selected in apple maggot host-races. Even under ideal conditions, one has a circularity, as *Nm* merely indicates how much genetic drift is expected; but the result is already known because F_{st}, from which *Nm* was estimated, is known.

One of the most interesting questions is: 'Does speciation result from host shifts?' *Yes!* – for the tephritids *Eurosta* and *Rhagoletis* according to Itami *et al*. and Feder *et al*.; *No!* – for *Euphydryas* butterflies according to Thomas and Singer. The case for sympatric (incipient) speciation via host shift now seems strong for *Rhagoletis pomonella*, which, only 140 years after shifting to apples in North America, maintains multilocus differences from the ancestral hawthorn race in spite of continuing, though limited gene flow. But whereas sympatric speciation now seems likely, there is little evidence to prove that this is the case, even for congeners such as the blueberry maggot *R. mendax,* which never seems to hybridize with its closest relative *R. pomonella* in the wild. In contrast, Thomas and Singer, who demonstrate a correlation between host choice and performance in rare *Euphydryas editha* populations using multiple hosts (most likely due to multiple locus differences between host-races), show convincingly that host shifts are uncorrelated with speciation in *Euphydryas*. In host-race systems (and potentially for adaptation to individual host trees as well), *local* adaptation can proceed at distance scales $<< \sigma$ because host choice will assort individuals onto the correct host patches. So why no sympatric host-related speciation in *Euphydryas*? In *Euphydryas* there is little tendency for host choice to influence mate choice, so that in mixed populations one host-race almost always out-competes and genetically swamps the other. Thomas and Singer show that such mixed populations are rare and transitory. In *Rhagoletis,* males use the same genetic machinery to select fruits for mating platforms that females use for egg laying. This ensures assortative mating and leads to potentially effective evolutionary segregation and speciation of host-races.

Overall, this book is thought-provoking and well worth a good read, in spite of a lack of evolutionary sophistication in some chapters. With a high content of novel empirical data, I find this book a lot more interesting than *comparative method* meta-analyses or purely theoretical treatments of similar subjects.

James Mallet