Patch selection, benefactors, and a revitalization of ecology

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This book[1] is a major conceptual advance, almost revolutionary, and should reorient research in the evolutionary half of biology for the next decade or more. Perhaps for this reason it is also controversial and has even had some difficulty reaching print.

The central argument is very simple but is unfortunately nowhere stated in the way I find clearest: There is commonly variation, random or otherwise, among very local groups of organisms. Such variation can cause differential productivity of the groups. Phenotypes and genotypes present in positively selected groups at more than average relative frequency will then tend to be more common overall, after the selection.

This conclusion doesn't depend much on such variables as dispersal among groups (even complete mixing each generation is easily included), discreteness of groups, or degree of relatedness. In fact the components of the groups can even be of very different species. If earthworms improve the soil for plant growth (as they do), and if plants provide food for earthworms (as they do), we have a suitable model. For instance, one earthworm genotype may help the plants grow better than another earthworm genotype does. Even if the genotypes occur randomly, some parts of a field will have more good earthworms than will other parts. The plants in good patches tend to grow better and thereby produce more earthworms around them. The good patches thereby expand. Of course one can reverse the argument and use variation among the plants, with the same result.

Such a result, selection for what may be called a benefactor (an organism which increases the fitness of another), does not generally follow from received theory. In received theory, which ignores spatial heterogeneity, the action of good earthworms would benefit good and bad earthworms equally and therefore good earthworms would not oust bad ones. In fact Williams (1966) used the example in that way, to argue that adaptations beyond the individual are implausible. Such an argument was healthy then, in the absence of a reasonable mechanism for group adaptations. Now that there are such mechanisms, Wilson's being the most generally useful, such arguments can be relegated to the residuum where the models fail.

For the model can fail. The good earthworm may happen to be a poor competitor against other earthworms, or easier for birds to catch, or more sensitive to cold. Expansion of, or from, what may be called the patch (a region where individuals affect each other, with its contained individuals) provides a selective vector but doesn't guarantee its strength.

The model can be looked at as a generalized version of the kind of group selection Wright developed. Wright was concerned with the breakup of advantageous epistatic genotypes, a major disadvantage of sexual reproduction. Given a small area where the genotype was fixed, it can under suitable conditions expand to include the whole species. The wave of advance of an advantageous genotype, or set of genotypes, can also occur with patch selection, but it need not because patch selection works even with random mixing. Patch selection also does not require local fixation before the selection works; in fact it produces fixation itself

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[1]The Natural Selection of Populations and Communities, by David Sloan Wilson. Menlo Park, California: Benjamin/Cummings. 1980. xv + 186pp. $12.95.

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without need of auxiliary help.

Patch selection also generalizes mutualism, the latter occurring when the patches consist of single individuals of one or both species.

Wilson sees altruism as a minor and overinterpreted phenomenon, with which I agree. Most benefactors are not altruists, and neutral and selfish benefactors are common. Nevertheless, patch selection does give a useful way for existing altruists to increase although, like Wright's model above, it needs marginal help in this case.

Some benefactors are clearly so by accident or by selection on their beneficiaries, and this is not made clear. A flea doesn't benefit its host species in any evident way, and animal egesta and excreta must go somewhere even though they may help other species wherever they do go. (Which species they help may, however, be affected by patch selection, and this can affect the benefactor and the nature of its wastes.) It will be a difficult but important task to disentangle such accidental benefactors (both types just mentioned are accidental from the perspective of the benefactor) from adaptive benefactors, so that we may have some idea of the relative, and absolute, importance of the two classes. Of course the origin of a beneficiary relationship may be accidental and it may then become adaptive to the benefactor; origin and maintenance are both important but have different significance.

How wide is the domain of patch selection? Apparently very wide but not wide enough to solve everything. Homogeneous regions where all patches are identical must be rare. Variation in patch productivity because of differences among the inhabitants of different patches is presumably common, if less obvious because we haven't looked for it. The main restriction on patch selection would seem to be the requirement that when feedback is involved in the differential productivity of patches, the feedback should be on a time-scale short enough that the patch still exists. How much more than one generation of feedback delay is compatible with patch selection is unknown, but it will depend on the relation between the delay and strength of the feedback and the rate of randomization of patches over time.

To the extent that an altruistic action (reducing the performer's expected fitness) is required for a phenomenon, the phenomenon will be more difficult for patch selection to deal with effectively. Thus regulation of population density below carrying capacity, near a level maximizing population productivity, is almost impossible to select without some sort of mitigating factor. And the fact that the world is green is also not explained. This remains a serious problem despite dogmatic (and mutually contradictory) assertions to the contrary by various authors. The difficulty for patch selection here probably involves both altruism and time-scale of feedback.

I mention these examples because they are unusual. An extraordinary variety of phenomena do fall in the domain of patch selection, many of them (such as biogeochemical cycling) previously considered epiphenomena when considered at all in a causal context. The book has much natural history and should be read carefully. Because the mechanism explains so very much there is a danger of reverting to what Haldane called Pangloss's Theorem, that all is for the best in this best of all possible worlds. Patch selection brings us closer to Pangloss's Theorem, but the domain of patch selection does have limits.

The core of evolutionary theory is a deductive argument, not a predictive argument (Van Valen, 1976). Another name for a valid deductive argument is a proof. The conclusion of a proof is true whenever the assumptions are true. The argument for patch selection is also a proof, which I sketched in the second paragraph of this review. A full derivation (Wilson gives only a restricted formal derivation on pp.23-27) would make explicit all the conditions sufficient for patch selection. The necessary conditions, which bound the domain, may be broader.

The first matter of interest in a scientific proof is whether the assumptions are correct. As far as I can tell the assumptions for patch selection are correct.

The second matter of interest is the domain, how broadly they are correct. And the domain seems about as wide as in my informal derivation. Predictions of the conclusion of a proof are unnecessary, but they may be useful in refining the domain or in detecting a hidden flaw in an inadequately explicit deduction. Wilson makes many fewer predictions at variance with received theory than Darwin did, probably because his theory is less of a departure. Nevertheless he makes several, and the natural history supports them.

Darwin believed that his theory would be disproved if any character of one species could be shown to exist for the benefit of another. Patch selection creates such characters wholesale but it no more disagrees with Darwin's intent than does the special case of mutualism, which Darwin studied extensively. Each species benefits, directly or indirectly, and in a formal but quite artificial way one can model the process by individual selection within each species. Similarly, despite the emphasis on cooperation and community function which patch selection brings, there need be no decrease in the importance we give to competition. Patch selection operates by competition; it is merely that the competitive units are unfamiliar.

Wilson's theory is controversial. I don't really see why. It has been claimed to be only kin selection, which is silly. Dawkins (1979) has claimed that an important part collapses when we remove the effect of an individual experiencing itself. An example (p.27) would seem to, although it doesn't because what is "experienced" is the effect of a frequency. Multiplying all the numbers by 10 changes nothing and removes even the appearance of triviality. Patch selection looks familiar enough for us to say that we knew it all along, but we didn't. It is a radical departure from received theory, and its results are sufficiently uncomfortable that most evolutionary biologists will probably wish the results would just go away. To say that there must be something wrong with a simple proof, even if we can't see just where, is bigotry. I hope that those comfortable critics who are sure the received theory is right will point out exactly where they think patch selection is wrong. Such an effort is as beneficial when it fails as when it succeeds.

"It seems as if ecology is divided into two schools, each inspecting a different side of the same coin and each claiming that its side is all that exists. The evolutionary ecologist advocates self-interest to the exclusion of function, and the ecosystem ecologist advocates function to the exclusion of self-interest. I hope that the theory developed here may help to reconcile these two schools of thought." (Wilson, p.4)

As Huxley is reported to have said when he heard Darwin's theory, "How stupid not to have thought of that myself."

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Literature Cited

Dawkins, R. 1979. Twelve misunderstandings of kin selection. Zeitschrift für Tierpsychologie 51:184-200.

Van Valen, L. 1976. Domains, deduction, the predictive method, and Darwin. Evolutionary Theory 1:231-245.

Williams, G. C. 1966. Adaptation and Natural Selection. Princeton: Princeton Univ. Press. 307pp.