



## The intersection of specialization and speciation

Related to, but distinct from, the hypothesis that specialization promotes speciation is the hypothesis that speciation in itself generates specialization. Futuyma & Moreno (1988)

The title of his most famous book notwithstanding, Darwin dealt little with how new species come into being (Mayr, 1942, p. 147). His work is a marvel of brilliant induction and insightful examples of adaptation and anagenesis, but cladogenesis was largely ignored. It was into this void that Ernst Mayr stepped. He provided the first lucid explanation of how speciation occurred, an explanation grounded chiefly in geography. The sweeping success of biology's Modern Synthesis assured that the explanation proffered by Mayr (1942), a chief architect of that synthesis, became entrenched for years to come. Indeed, it is a rare biogeographer who does not consider allopatry to be a prerequisite for speciation.

Recent decades have, however, seen a slow and quiet revolution, as more and more researchers studying the phenomenon of speciation have embraced ecological rather than geographical explanations for how new species come into being. A key feature of this 'ecological speciation' revolution is the full invocation of Darwinian natural selection as a means of generating biodiversity and, specifically, reproductive isolation (Rundle & Nosil, 2005). Any classical view of ecological factors, from environment to predator avoidance to competition, falls under this rubric.

Despite the recency of this revolution (some would say 'revival'), over the years various mechanisms by which microevolutionary forces could result in speciation have been formulated. A chief example of such a postulated mechanism is character displacement. When Brown & Wilson (1956) first formalized the concept, it swept through ecological circles like wildfire as it gained near-universal acceptance. Its logic – that competition shaped the extent of morphological, ecological, behavioural, and physiological diversity – seemed beyond reproach. After all, embryonic forms of the argument

dated back at least to Darwin (Schluter 2000). Together with Hutchinson's (1959) concept of limiting similarity, a bedrock ecological principle seemed to be born: interspecific competition for resources leads to a restriction on the number of ways that resource can be acquired, and, consequently, phenotypes (in the broadest Dawkinsian sense) diverge to an extent that no two are similar enough to allow further competition.

The concept soon had its critics, however, with much of the debate focusing on two key points: (1) the provision of alternative explanations for observed patterns, phenotypic plasticity and species sorting, and (2) the lack of clear quantitative results as opposed to the existence of merely qualitative comparisons. These problems were exacerbated by selective publication of positive results and because, in studies of character release or displacement, 'choice of morphological characters determines pattern' (Dayan & Simberloff, 1998). Nonetheless, over time criticism was quelled enough that the notion of character displacement regained its former prominence (Dayan & Simberloff, 1998; Schluter, 2000). Indeed, the detection of character displacement has now achieved a rigorous standard by which six criteria need to be met before the claim can be made confidently (Schluter, 2000):

1. the observed pattern cannot be explained by chance,
2. phenotypic differences between populations under study must have a genetic basis,
3. phenotypic differences must be the result of microevolutionary change (not species sorting),
4. character shifts must reflect acquisition of a primary resource,
5. environments between sites of sympatry and allopatry should be similar, and
6. competition among extant phenotypes must be demonstrated.

Two recent publications in the *Journal of Biogeography* meet, in part, these rigorous standards, and extend our thinking on this subject.

Mammalogists have contributed considerably to the literature on character dis-

placement, but most of this work has focused on the order Carnivora and on morphometric variation, especially cranial or dental characters (Dayan & Simberloff, 1998). By contrast, Russo *et al.* (2007) not only explored patterns in the speciose order Chiroptera, but also focused on divergence in echolocation. They found that call frequency among three species of horseshoe bats (*Rhinolophus* spp.) shifted upwards or downwards when the species occurred in sympatry, the shifts being unrelated to body size. Brown & Wilson (1956) contended from the start that the displaced characters could be behavioural, so work in this area is welcome. Moreover, it emphasizes the role that acoustic and other signals may play in generating biodiversity (see Patten *et al.*, 2004).

A study by Meiri *et al.* (2007) used a more 'standard' data set: canine and skull variation among weasels (Carnivora: Mustelinae) of the Holarctic. The interesting wrinkle is not so much their solid evidence for character displacement as their equally solid lack of evidence for character release. When a species was freed from interspecific competition, it did not revert to some intermediate morphology but instead retained the prevailing characters of its species in sympatric settings. What should be made of this finding? Is it merely a consequence of similar ecological conditions?

A solution may lie in the phylogenetic constraints resulting from evolution towards ecological specialization. Character displacement is, in effect, a type of specialization: a species narrows its niche breadth to avoid competition in a zone of contact with a congener. Just what a species loses or gains by becoming specialized has been a subject of considerable theory and disagreement. Nevertheless, there is a reasonable consensus that, whatever a specialist gains in efficiency of resource use, minimization of competition, or fixation of beneficial alleles (see Whitlock 1996), it loses in future evolutionary potential, meaning a potentially irreversible loss in niche breadth. Or,

as Futuyma & Moreno (1988) put it, 'In many instances the successive evolution of numerous adaptations to a special resource or habitat constitutes an increasing commitment that makes reversion to a generalized habit, or a shift to a very different specialization, increasingly unlikely'. Each step towards specialization is likely to be a step away from having the genetic variation to respond to altered selection pressures in the future.

An interesting aspect of the loss of genetic variation is the tendency for the same loss to occur during speciation. Viewed broadly, the cleaving of one lineage into two would seem necessarily to entail a reduction in genetic variance in each daughter lineage relative to the parent one. If true, then speciation and specialization, long studied as distinct disciplines, one evolutionary, the other ecological, could well be the same phenomenon. It is not that specialization promotes speciation and that speciation generates specialization (see Futuyma & Moreno, 1988) – they are one and the same thing.

Ramifications of this recognition of equivalency are great. Certainly the field of ecological speciation (Rundle & Nosil, 2005) would gain primacy in studies of how populations diverge and how biodiversity is generated. Furthermore, we would then have a clearer explanation for why tropical clades tend to be more species-rich and contain more specialists than their temperate counterparts (e.g. Dyer *et al.*, 2007). More crucially, however, researchers studying speciation would start to see with different eyes. A simple geographic barrier becomes inadequate to 'explain' divergence between populations. We would need to discover how such a barrier led to different selective regimes and how resource use matches resource availability in the different areas. For instance, perhaps subtle differences in climate lead to subtle differences in vegetation structure, which in turn select for subtle differences in a mating signal. It is not hard to see reproductive isolation evolving under such conditions, even in parapatry, and there is empirical evidence in, for example, birds, lizards, and fish (Patten *et al.*, 2004, Rundle & Nosil, 2005) to infer that such mechanistic processes occurs in nature.

Lowered genetic variance associated with specialization may also lead to extended periods during which generalists beget specialists and specialists beget more specialists but during which few generalists evolve. In this vein, character displacement ('specializing') may evolve more readily than character release ('generalizing'). All else being equal, short of outside input, for example from hybridization or macromutation, there may be little 'choice' for a lineage but increasing levels of specialization (Whitlock, 1996). Accordingly, over time populations will edge steadily towards the specialist pole of the generalist–specialist continuum.

As niches narrow so too might the chances of the long-term survival of a lineage. It remains unclear to what extent specialized species are more susceptible than generalized species to extinction (Futuyma & Moreno, 1988), although this idea has been with us since at least the time of the venerable George Gaylord Simpson. If it holds, barring catastrophic events, there should be a net accumulation of specialists over time . . . to a point. Because of their reduced ability to evolve, specialists are more likely than generalists to pay the price when, say, climate or habitat changes rapidly. Periodic mass extinctions may therefore be an inevitable consequence of the accumulation of specialists in an ecosystem, just as huge conflagrations are inevitable when fuel wood is allowed to accumulate unchecked. This is not a call to cull specialists. Rather, it is a call to wed the study of ecological specialization to the study of speciation and therefore to the study of speciation–extinction dynamics. In a world facing potentially devastating near-term effects of global climate change, such a wedding would come none too soon.

#### ACKNOWLEDGEMENTS

My thanks to John Lambshead, Shai Meiri, and Danilo Russo for feedback on a draft of this paper.

MICHAEL A. PATTEN\*

*Oklahoma Biological Survey and Sutton Avian Research Center, University of Oklahoma, Norman, OK, USA*

\*Correspondence: Michael A. Patten, Oklahoma Biological Survey, University of Oklahoma, 111 E.

*Chesapeake Street, Norman, OK 73019, USA.  
E-mail: mpatten@ou.edu*

#### REFERENCES

- Brown, W.L., Jr & Wilson, E.O. (1956) Character displacement. *Systematic Zoology*, **5**, 49–64.
- Dayan, T. & Simberloff, D. (1998) Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mammal Review*, **28**, 99–124.
- Dyer, L.A., Singer, M.S., Lill, J.T., Stireman, J.O., Gentry, G.L., Marquis, R.J., Ricklefs, R.E., Greeney, H.F., Wagner, D.L., Morris, H.C., Diniz, I.R., Kursar, T.A. & Coley, R.D. (2007) Host specificity of Lepidoptera in tropical and temperate forests. *Nature*, **448**, 696–699.
- Futuyma, D.J. & Moreno, G. (1988) The evolution of ecological specialization. *Annual Review of Ecology and Systematics*, **19**, 207–233.
- Hutchinson, G.E. (1959) Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist*, **93**, 145–159.
- Mayr, E. (1942) *Systematics and the origin of species*. Columbia University Press, New York, NY.
- Meiri, S., Dayan, T. & Simberloff, D. (2007) Guild composition and mustelid morphology – character displacement but no character release. *Journal of Biogeography*, **34**, 2148–2158.
- Patten, M.A., Rotenberry, J.T. & Zuk, M. (2004) Habitat selection, acoustic adaptation, and the evolution of reproductive isolation. *Evolution*, **58**, 2144–2155.
- Rundle, H.D. & Nosil, P. (2005) Ecological speciation. *Ecology Letters*, **8**, 336–352.
- Russo, D., Mucedda, M., Bello, M., Biscardi, S., Pidinchedda, E. & Jones, G. (2007) Divergent echolocation call frequencies in insular rhinolophids (Chiroptera): a case of character displacement? *Journal of Biogeography*, **34**, 2129–2138.
- Schluter, D. (2000) Ecological character displacement in adaptive radiation. *The American Naturalist*, **156**, S4–S16.
- Whitlock, M.C. (1996) The Red Queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. *The American Naturalist*, **148**, S65–S77.