

large-scale spatial synchrony because different cities are near different attractors – and, therefore, stochasticity is important for understanding the spatial dynamics of measles.

The success of the description, with relatively simple models, of spatio-temporal dynamics in measles and pertussis suggests that understanding rather complex dynamics in ecology will be possible with careful work. Understanding spatio-temporal data provides intriguing challenges, but should yield rich rewards. The importance of understanding, and using, nonlinear dynamics to understand population dynamics is another theme for ecology in the new millennium. The inseparability of endogenous and exogenous forces in shaping the dynamics we observe is likely to remain the final resolution to

the long-standing debate over the role of density dependent versus density-independent forces in ecology. Incorporation, in a quantitative sense, of both exogenous and endogenous forces will remain a theoretical challenge.

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Ecotone: speciation-prone

Geographic regions where organisms change abruptly have always drawn attention from biologists. Clines, hybrid zones or intergrades (the terminological distinctions have become obscured over the years¹) are fascinating for several reasons. In taxonomy, they can serve to establish the presence of gene flow between two forms, which might be a reason to assign them infraspecific rank. To evolutionary geneticists, they are ‘natural laboratories’ where evolutionary forces and barriers to gene exchange can be studied². Now, a new study³ reveals yet another attraction of clines: they might sometimes be areas where new species evolve in a process known as parapatric speciation.

Cline studies came of age in the early 1980s, when Barton *et al.*^{1,4} successfully modelled hybrid zones as the result of a balance between dispersal and selection. That is, genes flow into the zone from both sides, but hybrid infertility and inviability counteract this process. Under this model, the reduced fitness of hybrids is ‘internal’, rather than the result of a selection pressure imposed by the environment.

In the wake of these studies has come the awareness that, generally, hybrid zones are of secondary origin and are maintained largely independent of the environment. Populations diverge allopatrically; when they expand and meet one another their genetic incompatibilities cause hybrid inferiority. The hybrid

zone then moves about until it is ‘trapped’ by an area of low population density or a barrier to gene flow (a river, an unsuitable habitat, or some other geographic or ecologic feature).

However, at the same time other researchers have pointed out that ecology itself might play a more important role in the origin and maintenance of hybrid zones. Mathematically elaborating the ideas of earlier evolutionary biologists, such as Ronald Fisher⁵ and Julian Huxley⁶, Endler⁷ emphasized that some zones could be caused, or modified, by differently directed selection pressures on either side of an ecological transition, thus showing that clines can build up in the face of considerable gene flow⁷.

The past decade has seen an increase in the recognition of environmental selection influencing the characteristics of clines. Now, even hybrid zones, such as the classic one between the fire-bellied toads *Bombina bombina* and *Bombina variegata* (on which much of Barton’s theoretical work was based), are turning out to be influenced partly by environmental selection^{8,9}.

Plasticine skinks

The new study by Schneider *et al.* on tropical lizards³ goes one step further by showing that environmental selection can be the primary and principal cause for a hybrid zone. This opens the way for parapatric speciation: species might

actually form across an ecotone¹⁰. It firmly links a set of morphological clines with environmental selection. Not only that, the new study includes a field experiment to implicate the agent responsible for selection, and it also shows that simple geographic separation is not likely to have been responsible for the differentiation.

Schneider *et al.* studied *Carlia rubrigularis*, a common leaf-litter skink in the Australian tropics. The species occurs in the belt of closed rainforest on the Cape York peninsula, but also in the adjoining open eucalypt forest further inland. The ecotone between these two habitats can be as narrow as a few hundred metres. Perpendicular to the ecotone – and bisecting the skink’s range – lies the Black Mountain Corridor (BMC), a well known biogeographic barrier of pre-Pleistocene age.

The researchers sampled eight skink populations: four north and four south of the BMC. Of each quartet, two localities were in rainforest and two were in open forest. For every mature individual caught, they measured five morphological traits, after which the animal – minus its tail tip – was released again. Five to ten tail tips were used for each population to sequence a 400-bp portion of the mitochondrial cytochrome *b* gene.

The results were clear-cut. The animals in open forest populations were smaller, with relatively shorter limbs and larger heads for their size. However, mitochondrial DNA (mtDNA) showed hardly any difference across the ecotone. Paired open–rainforest populations shared many haplotypes and had a Φ_{st} (a measure of genetic differentiation) of 0.026–0.194, suggesting strong gene-flow.

However, sequence divergence across the BMC was considerable, with Φ_{st} values of 0.968 or more. In other words, the several million years of isolation had not produced any morphological divergence, but the environmental gradient had, in spite of pervasive gene flow.

The fact that open forest animals reached maturity at a smaller size suggested selection for rapid reproduction, possibly as a response to higher predation pressure in this habitat. To test this idea, Schneider *et al.* placed 480 plasticine skink models along transects across the ecotone. After approximately two weeks, 21 of the models in the open forest showed bill-marks from bird attacks, compared with only four in the rainforest – this difference is highly significant.

The study by Schneider *et al.* is the most impressive one in a series of publications on vertebrate clines that have appeared over the past three years. In a 1997 study on the little greenbul (*Andropadus virens*) in Cameroon, Smith *et al.* found that heritable morphological differences had built up across the ecotone between rainforest and savannah¹¹. The savannah birds were larger and had relatively longer wings, which, presumably in response to increased predation by raptors, made them better fliers. They also had relatively deeper beaks. However, microsatellites and mtDNA were similar across the ecotone, suggesting that the morphological differentiation is the result of direct selection on a small number of loci, rather than a secondary intergradation between two broadly differentiated populations.

In two other bird species, the olive sunbird (*Nectarinia olivacea*) and the black-bellied seedcracker (*Pyrenestes ostrinus*), Smith now has found similarly large morphological differentiation across the Cameroon ecotone¹². At the same time, a study of blue tits (*Parus caeruleus*) on the French island of Corsica has revealed morphological and life history adaptations in forest habitats separated by only 25 km (Ref. 13). However, genetic data are still lacking from these situations, thus ongoing gene flow can only be assumed.

Where next?

What do these new studies tell us about speciation? Strictly speaking, the bird studies do not prove that parapatric speciation is in progress. Hybrid zones that are of secondary origin and maintained by hybrid inferiority could become associated with ecotones if these areas are density troughs or barriers to dispersal¹⁴. Even the flow of neutral markers across the ecotone can be expected when a hybrid zone is secondary, but maintained by selection on only a small number of loci. The skink work is more convincing,

because it incorporates direct evidence for different predation pressures in different habitats and demonstration of the same pattern in two unrelated populations (i.e. on either side of the BMC).

A much larger data set will be necessary to make a strong case for parapatric speciation. This will have to await the inflow of molecular data for the sunbird, seedcracker and blue tit cases. Also vital will be the outcome of a large-scale survey of ecotone differentiation, which has just begun, involving many species from different vertebrate classes in tropical habitats in Africa, Australia and South America (T. Smith, pers. commun.).

Even if such circumstantial evidence is supportive of the idea, we still lack a good insight into the second stage of parapatric speciation. How can reproductive isolation evolve? Early models of parapatric speciation relied on reinforcement, where reduced fitness of hybrids selects for improved assortative mating, but this process is not likely to be effective in situations where gene flow is strong¹⁵. However, studies of sympatric speciation are beginning to suggest that assortative mating can evolve easily as a by-product of adaptation. For example, in sticklebacks (*Gasterosteus aculeatus*)¹⁶ and cichlids (Cichlidae)¹⁷ mating takes place within the same size class. In such a case, adaptive size-differences across an ecotone (similar to the skinks) would automatically produce assortative mating as well. Experimental work might help clear up these issues.

Finally, it is important to stress that, if parapatric speciation turns out to be prevalent, it will not be restricted to rainforest edges. Drastic ecotones abound in nature. Coastal zonation, cave entrances and altitudinal gradients are just a few of the many situations where the process might be at work¹⁰. The way things look now, biologists' infatuation with transition zones is by no means over yet.

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Corrigendum

Blount, J.D. *et al.* *Trends Ecol. Evol.* 15, 47–49

The surname of the first author of Ref. 1 should be spelt Olson and not Olsen.

We apologize to Valérie Olson and our readers for this error.