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16

Biotic drift or the shifting balance—did forest islands drive the diversity of warningly coloured butterflies?

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16.1 The problem

According to Stephen Hawking 'God does throw dice'. Our question will be 'When are the dice thrown?' It has been customary to think of Wright's shifting balance as a stochastic theory of evolution and Fisherian natural selection as deterministic; contrariwise both R. A. Fisher and Sewall Wright believed in fundamental stochasticity (Turner 1987, 1992). We propose a different dichotomy: that divergence can take place as an adaptive response either to stochastic changes in the genetic structure of the population, or to stochastic changes in the biotic environment, or of course, both. We will explore this through the spectacular evolutionary divergence of the colour patterns of South American butterflies, particularly *Heliconius*.

16.2 The facts

Geographical variation in South American long-winged butterflies (*Heliconius*, ithomiines, and others) is among the most striking examples of evolutionary radiation. 'In tropical South America, a numerous series of gaily-coloured butterflies and moths are found all to change their hues and markings together, as if by the touch of an enchanter's wand, at every few hundred miles' (Bates 1879). The geographical diversity of colour patterns, coupled with the close similarity of colour patterns between species within any one area led to Bates' (1862) theory of mimicry. Turner (1968, 1976*a*) showed that there has been a pattern of convergent evolution within the Heliconiini, such that individual clades have radiated into many of the mimetic patterns, and each of these patterns in turn is shared by members of separate clades. This pattern of divergence and convergence within the genus is repeated as a pattern of divergence and convergence between races within species: it is a fair conjecture that this racial divergence/convergence is what underlies the pattern at the higher taxonomic level. The most spectacular example is the now well-known parallelism of the mutual Müllerian mimics *Heliconius melpomene* and *H. erato*, which each have around 30 identifiable races and around 10 distinct colour patterns. Each race and pattern of *H. melpomene* is sympatric with a closely similar looking and presumably mimetic race of *H. erato* (there is one exception) (Fig. 16.1).

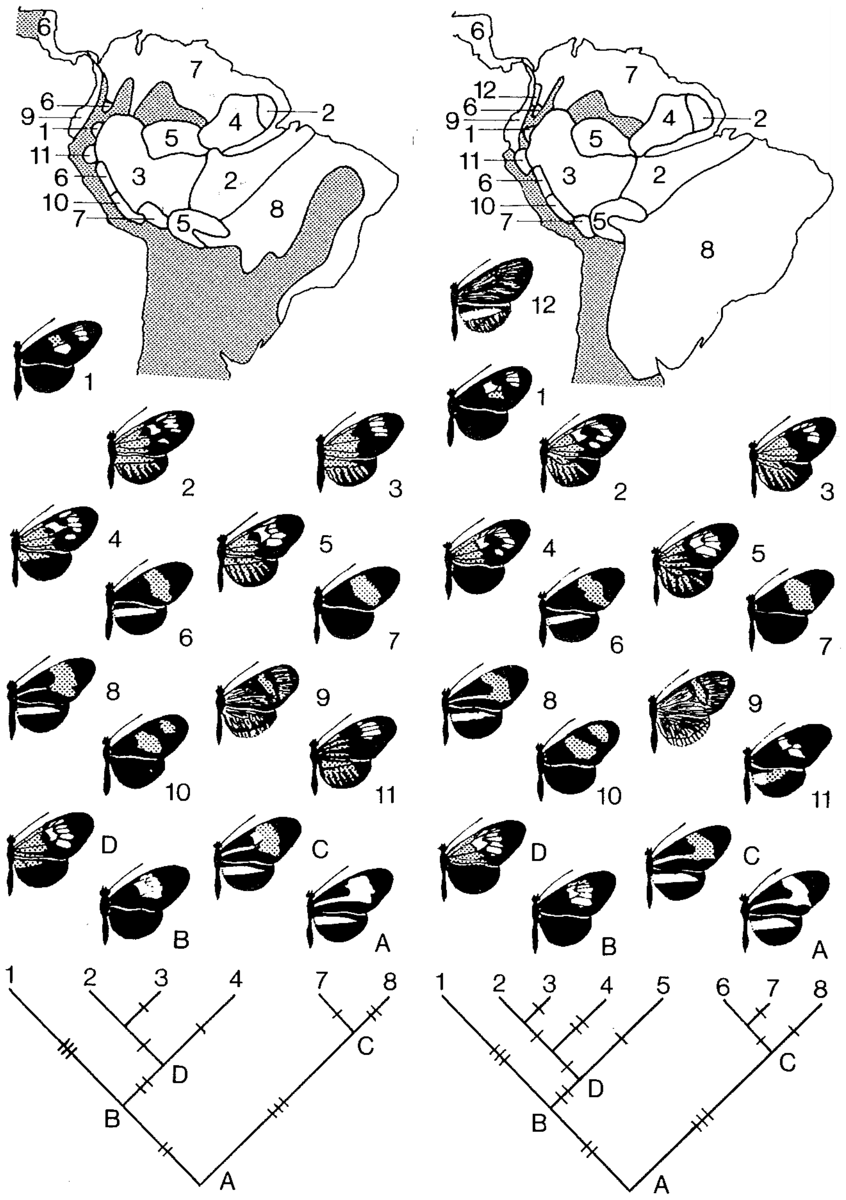


Fig. 16.1 Parallel mimicry and geographical variation between (a) *Heliconius melpomene* and (b) *Heliconius erato*. From Sheppard *et al.* (1985).

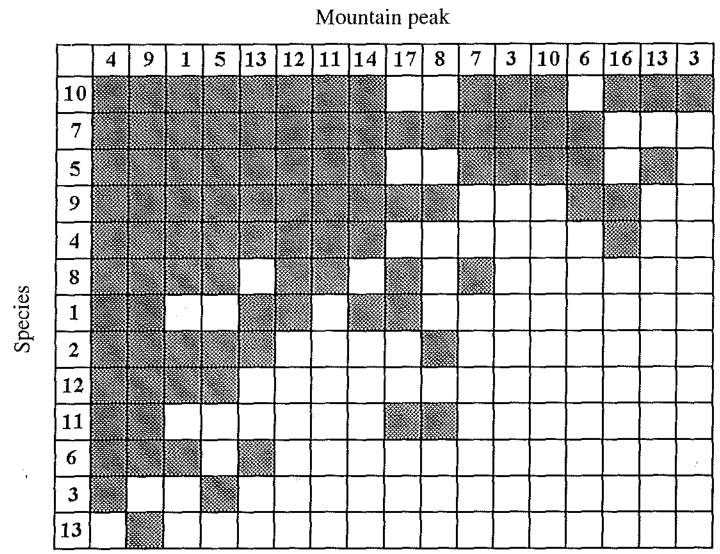
The rampant geographical diversification within these species is paradoxical. Predators' memories ensure that warning patterns are subject to strong frequency-dependent and stabilizing selection: rare patterns are at a disadvantage and a new pattern will be favoured only once it has evolved to a high frequency, selection usually favouring the commoner and best recognized form (e.g. Mallet and Singer 1987; Speed and Turner submitted). The same problem arises with the origin of warning colour itself: a rare pattern may gain little advantage of its own, and may sacrifice fitness by being conspicuous compared with the original cryptic pattern. Hence there are difficulties in explaining how warning colours increase from a low frequency within a population (Fisher 1930; Turner 1971*a*; Harvey and Greenwood 1978) without resorting to a group selectionist argument that aposematism is 'an adaptation involving only a small sacrifice of life' (Poulton 1890). Thus there are three related evolutionary puzzles: the origin of warning colour itself, the origin of new warning colours from old, and the divergence of existing warning patterns, as seen in *Heliconius*.

16.3 The biotic drift model

The Brown–Sheppard–Turner model (Brown *et al.* 1974; Sheppard *et al.* 1985; Turner 1983, 1984*a*) assumes that the conversion of these butterflies from one mimetic pattern to another is brought about by natural selection but driven by stochastic changes in the ecological community; there is no contribution from random genetic drift.

Because species are usually distributed patchily, as now adumbrated in the 'metapopulation model' (Gilpin and Hanski 1991), any small (or indeed large) isolated part of a 'continent' of species contains at any one time only a stochastic subsample of the species which might be present: thus the islets of the Gulf of Finland have sharply differentiated floras as a result of more or less random accidents in their colonization history (Halkka *et al.* 1975). The species composition of the flora and fauna undergoes biotic drift ('faunal' and 'floral drift' are alternatives). The classic case of mammals on the mountain tops that contain the fragments of a previously continuous moist forest now split by the arid conditions of the Great Basin (Brown 1971) shows what happens during biotic drift (Fig. 16.2): there is a significant stochastic element. The pattern is, however, one of 'disorderly extinction' (Turner 1977*a*, 1984*b*) rather than 'random extinction': some islands have a greater loss of species than others, and some species have a higher probability of extinction than others; the variance in the number of mountains occupied by a species is 4.7 times greater than expected if each species had an equal probability of extinction. Such changes must surely have considerable effects on evolution: the form which natural selection takes, for all the constituent species, will differ from island to island or patch to patch. This introduces a strong stochastic element into the process of adaptation itself.

It is suggested that the patterns of warningly coloured butterflies evolve primarily by 'ring switching' (Turner 1976*b*, 1977*b*, 1984*a*, *c*, *passim*; Sheppard *et al.* 1985). Natural selection favours the convergence of the patterns of warningly coloured butterflies onto a common pattern, so that they all become Müllerian mimics: such an assemblage is called a mimicry ring. In the tropics it is normal for around six such rings to coexist within one life-form (bees, long-winged butterflies), indicating that something prevents total convergence on a single ring. This barrier is held to be the considerable differences between the patterns of the rings, such that the cognitive generalization of predators never confuses one ring with another; probably this is enhanced by microhabitat differences between both mimicry rings (Mallet and Gilbert 1995; Beccaloni 1995) and the predatory birds. There is thus an 'adaptive valley' between the rings. Individual species can cross the valley, and thus 'switch rings' or undergo 'mimetic capture' if they generate a mutation that gives a passable resemblance to the pattern of another ring. The resemblance does not have to be perfect, only sufficiently good to confuse enough of the predators enough of the time; higher levels of mimetic resemblance are achieved later through gradual convergent evolution.



Mountain peak

Species

	4	9	1	5	13	12	11	14	17	8	7	3	10	6	16	13	3
10	▨	▨	▨	▨	▨	▨	▨	▨			▨	▨	▨		▨	▨	▨
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Fig. 16.2 Biotic drift or disorderly extinction of the boreal mammal fauna of the Great Basin (western USA) following its fragmentation by desert conditions: each mountain peak contains a subset of the total fauna. Shading indicates presence; numbers are mountain peaks or mammal species. After Brown (1971), redrawn by Turner (1977*a*, 1984*b*). See Brown (1971) for the names of the peaks and the mammals.

To effect the capture of a species, the capturing ring has to be better protected than the ring from which the capture occurs: better protection arises either from more effective chemical defence, or from being more numerous. Thus capture is expected to be ongoing, with species exchanged between different rings at different times or even whole rings totally captured, as rings change in their overall abundance or in their composition: a ring which contains a particularly distasteful species or which has become more numerous (as a result of containing a few common species or a very large number of species) is the ring that will effect the captures from other rings. As rings change their abundance over time, species will be captured and maybe recaptured, and if rings differ in their capturing power in different geographical areas, the recaptured species will undergo racial divergence. The theory is thus capable of explaining racial differentiation of the kind seen so spectacularly in *H. melpomene* and *H. erato*.

The Brown–Sheppard–Turner model therefore requires nothing more than changes in the abundance of species in Müllerian mimicry rings that last for a sufficient time to enhance mimetic captures, the time involved being the delay before a suitable mutation occurs, and the time taken to substitute one allele for another. But Turner (1982) argued that although the biotic drift model could indeed generate racial divergence in mimetic *Heliconius* purely by ecological fluctuations in continuous forest, the changes were much more likely and possibly larger during periods when the fauna and flora were fragmented into refuges undergoing extensive and long-term biotic drift. Local extinction of species is universal, but in a continuous habitat is likely to be relatively short-term, as the vacated patches of habitat are recolonized from neighbouring populations. In a habitat fragmented into islands, such an extinction is permanent except through infrequent long-distance recolonization, or until the islands coalesce again. In such island refuges, there is stochastic change in the composition of the flora and fauna which is profound and long lasting. In general, the extinction of species affects the ecology and hence evolution of the remaining species, by removing host plants, predators, parasites, or competitors, and leaving open ecological niches that were previously occupied. Specifically the mimicry rings will change their species composition by the loss of individual species, but also their abundance because of the loss of parasites, competitors, host plants, etc. Such long-term changes would have great power to generate ring capture and geographical divergence in mimetic butterflies.

The biotic drift model has therefore been allied with the 'forest refuge model' for evolution in Amazonia (Fox 1949; Turner 1965; 1976*b*; Haffer 1969; Prance 1973, and Chapter 15; Brown *et al.* 1974; Brown 1979, 1987*a*, *b*), which proposes that the patterns of race formation seen in the biota of much of tropical America are to be explained by a model of allopatric race formation on 'island' refuges; the islands being formed by the shrinkage of the now continuous humid forests during the cool dry periods that accompanied the glacial maxima of the Pleistocene.

16.4 The shifting balance model

The refuge model of divergence is hard to test, in part because of a lack of alternative models. Mallet has therefore suggested random drift as a counter-hypothesis to biotic drift: that the evolution and diversification of warning colours in *Heliconius* might constitute a good example of Wright's (1932, 1977) shifting balance theory occurring in parapatry (Mallet 1986*a*, *b*, 1993; Mallet and Singer 1987). There are three phases:

Phase I: random factors such as mutation, drift, kin-founding, or fluctuations in selection might occasionally cause a novel colour pattern rise to a high frequency in a local population; if by chance this frequency is high enough to exceed the point of unstable equilibrium imposed by the positive frequency-dependent selection on warningly coloured forms (say around 50% in a species which does not belong to a mimicry ring), this will trigger

Phase II: this positive frequency-dependent selection (advantageous when common) raises the frequency of the new colour pattern, until it becomes locally predominant; once it approaches fixation in a local area this leads to

Phase III: the new pattern spreads to other populations at the expense of the older patterns. This might occur by group or interdemic selection via population pressure (see Wright 1977) or by cline movement (Barton 1979; Mallet and Barton 1989*a*; Mallet 1993), or both.

Once a new form has evolved in a local area—whether by drift or by selection—contact with the original form will not lead to swamping: frequency-dependent selection will ensure that the two warning colour patterns remain apart with a sharp cline between them (Mallet and Barton 1989*a*). The cline that forms in this way will be similar to clines formed through selection against heterozygotes, as in chromosomal evolution (Bazykin 1969; Barton 1979); because the spatial location of the cline depends only on predators' labile memories, and is not rooted to any environmental gradient, these clines can move. If there are any asymmetries in selection or migration between the two patterns—for instance, if one form is better at warning away predators—or even if there is genetic dominance for one of the patterns, the clines will move at constant velocity in the direction of the fitter or of the dominant form. Briefly this is because at the centre of the cline the allele frequency will be 0.5 but the frequency of the dominant phenotype at 0.75 will be above the unstable equilibrium point (see Fig. 16.3; also Mallet 1986*a*; Mallet and Barton 1989*a*). In phase III therefore the new form spreads by cline movement in favour of better-adapted or genetically dominant colour patterns. Phase III is perhaps the most important feature of the shifting balance, since it preserves and amplifies the rare events of phases I and II; this is analogous to the natural selection of randomly produced mutations in simple selective processes, except that it can spread novel adaptations even when they are disfavoured at low frequency.

There are many limits to spread. Moving clines will become trapped at a variety of local barriers. Novel, spreading colour patterns may encounter abiotic conditions under which they are no longer advantageous, whereupon their advance will be halted (Haldane 1948; Slatkin 1973; May *et al.* 1975; Endler 1977). Alternatively, the fronts between invading colour patterns may become trapped in regions of low density (Bazykin 1969; Barton 1979; Hewitt 1988), because more individuals flow into the centre of a density trough than flow out from the low population in the centre. Finally, any actual breaks in the distribution (which are equivalent to extreme density troughs) will also stop clines moving. Density trough trapping could explain why so many hybrid zones between colour pattern races are located at the major Amazonian rivers, in low mountain ranges, and at the isthmus of Panama. The biogeographical result of multiple shifting balances is therefore expected to be a dynamic equilibrium consisting of a patchwork of different colour pattern races exactly like that seen in *Heliconius* today.

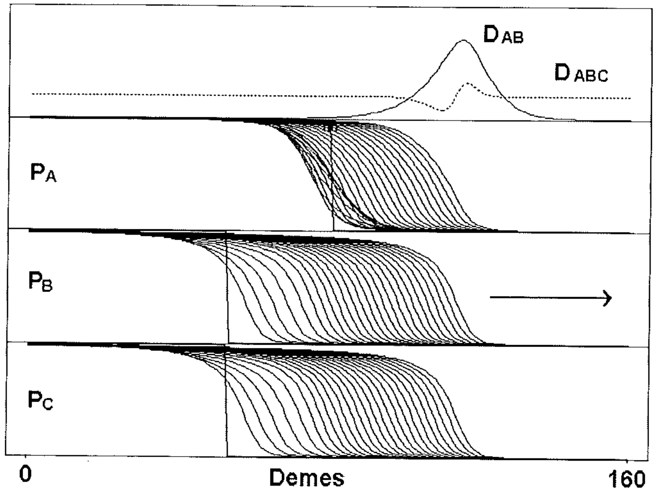

Fig. 16.3 Cline movement as phase III of Wright's shifting balance. The three lower panels show 250 generations of the movement of a three-locus (A, B, C) diploid warning colour cline system (a model of the *Heliconius* three-locus hybrid zone in Tarapoto—see Mallet and Barton (1989*b*) and Mallet *et al.* (1990)) in a linear environment of 160 demes. Each curve represents the gene frequency at ten-generation intervals. These clines are moving to the right under the influence of dominance alone, although adaptive pressures will produce very similar types of cline movement. The simulation starts with two secondary contacts between three patches, a patch on the left fixed for alleles A, B, and C; a central patch fixed for A, b, and c; and a patch on the right fixed for a, b, and c. Initially the identically selected clines at dominant loci B, C move at a constant rate of 0.37 demes per generation towards the symmetrical stationary cline at the codominant locus A. As the dominant clines approach, the A cline is briefly attracted back towards these moving systems. After about 30 generations of cline coalescence, all three clines move off together in the same direction at a reduced velocity of about 0.20 demes per generation. Clines will 'stick together' because of gametic disequilibrium only under conditions of high selection, as here, or if there is epistasis. Selection against foreign phenotypes at each locus is set at 50%, equivalent to heterozygous disadvantage of $s = 0.25$, and is similar to selection observed in *H. erato* of $s \approx 0.23$ per locus (Mallet *et al.* 1990). Gaussian migration is set to $\sigma^2 = 15$ demes^2 per generation. Two-locus gametic disequilibrium under these conditions (top panel) reaches about $D_{AB} \approx +0.09$ (D_{AC} and D_{BC} have similar values), giving a gametic correlation coefficient of $R_{AB} \approx 0.36$ at the centre, and the three-locus disequilibrium varies sigmoidally in the hybrid zone, $D_{ABC} \leq |0.016|$. For further details of the model see Mallet and Barton (1989*a*).

16.5 The evidence

Genetic architecture

Because mimicry produces a highly rugged adaptive surface, ring switching requires mutations of relatively large effect to cross the adaptive trough between two mimicry rings (Turner 1977*b*; Sheppard *et al.* 1985). Phase I of the shifting balance works best with mutations of minor selective effect (Barton and Rouhani 1987, 1991, 1992; Whitlock 1995; see also Chapter 7). Colour patterns in *Heliconius* are inherited at loci of major effect, with measured selection coefficients reaching 0.2 per locus (Sheppard *et al.* 1985; Mallet 1989; Mallet *et al.* 1990). Apparently then the genetic architecture of warning colours in *Heliconius* supports natural selection for mimicry over genetic drift as an initiator of divergence, unless there are initial periods of less intense selection.

Mimetic capture

Brown, Benson, and Sheppard found direct evidence for the capture of a species by a mimetic ring, caught in the act as it were (Brown and Benson 1977; Sheppard *et al.* 1985). *H. hermathena* is confined to isolated colonies in dry, open fields within the Amazonian rainforest. Through almost the whole of its range it has its own distinctive pattern of a red band with yellow bars, resembling none of the mimicry rings which fly with it. But in one small area along the Rio Amazonas it flies with the black and postman race of *H. melpomene* and *H. erato*, which it encounters along the edge where field and forest meet. This postman pattern differs only in lacking the yellow bars and spots of *hermathena*. In one of the half dozen locations where it flies with the postman pattern *H. hermathena* quite accurately mimics the other two species. From Hardy–Weinberg frequencies it is likely that the bars were removed by a single mutation.

This case is considered to provide rather strong evidence in support of the theory of ring capture: *H. hermathena* has crossed the gap between two mimicry rings (or been captured by a mimicry ring) only where this gap is narrow enough to be bridged by a single mutation, in this case one that suppresses the extensive yellow bars on the wings. In the remainder of its range, the ancestral pattern of *H. hermathena* is very different from the black, yellow, and red patterns of *Heliconius* species that fly with it (including further races of *H. melpomene* and *H. erato*), and it can reasonably be supposed that more than one large mutation would be required to convert one pattern to the other.

Biotic drift and mimicry in present-day refuges

The evidence for disorderly extinction in heliconiines is still equivocal. As with the mammals (Fig. 16.2), local extinction is often non-random (Mallet 1993, p. 252). In two currently isolated forest refuges, the Serra Negra in north-east Brazil (Sheppard *et al.* 1985, p. 588) and the Serranía de la Macuira, in the Guajira peninsula, Colombia, only *H. erato* remains. *Heliconius erato* is also commonly found, together with *H. melpomene* and one or two other common *Heliconius* species such as *H. sara*, in dry forest and the gallery forest of savannah regions (e.g. in parts of Darién, the Rupununi and coastal savannahs in Guyana, and parts of the Urubamba and Huallaga valleys in Peru), from which the rarer species are absent. In none of these areas are the colour patterns different from those in the adjacent wet forest. In general, when extinctions happen, it is the rarer species that disappear first, not abundant 'weed' species like *H. erato* and *H. melpomene*. It then becomes extremely difficult to explain the geographical divergence of *H. erato* and *H. melpomene*, whose most noticeable feature is that they mimic each other, by means of mimicry of an entirely different set of species in each refuge. Within the heliconiines, there are not enough different species to explain the observed diversification within each species.

Phases I and II: random drift and local change

The shifting balance model would be in severe doubt if the conditions for random drift did not occur in *Heliconius* populations: such conditions can be investigated via studies of population structure, which show that $F_{st} \approx 0.012$–0.025 at allozyme loci in local populations (Silva and Araujo 1994; Jiggins *et al.* 1996) and $F_{st} \approx 0.06$ at colour pattern loci in a hybrid zone (Mallet 1993): a substantial fraction of individuals in a population can be caught, so these values of F_{st} are close to their actual values, rather than depending as is usual on unreliable estimates of gene frequency from much larger populations. Assuming equilibrium between migration and drift, these values imply local effective population sizes of $Nm \approx 4$–21. Shifting balances in underdominant chromosomal rearrangements, which have near-identical dynamics to warning colours (Mallet and Barton 1989a), are likely to occur when $Nm \approx 1$ (Barton and Rouhani 1987, 1992), suggesting that *Heliconius* populations are generally too large; however, most studies of population structure are done where samples are easy to find, and will therefore usually overestimate the true average population size.

It can be argued against this model that because of mimicry the ecological conditions for the operation of phases I and II will only very infrequently be met: the population has to be small for the initial drift of the allele to occur, but if the species is rare, then establishment of a new and by definition non-mimetic pattern (phase II) will be resisted by natural selection imposed by the other species in the mimicry ring, which will strongly favour the old pattern. Thus either (1) the evolving species has to pass through a very brief bottleneck, with the population expanding to the size where it can then overcome selection imposed by the other species (and afterwards, perhaps, capture them) or (2) the species has to be in possession of a unique pattern already, that does not belong to a mimicry ring. This could readily happen if the other species in the ring had become extinct, perhaps as a result of the same forces that reduced the population size of the evolving species. This suggests that both biotic and genetic drift will be required, and perhaps even produced by the same ecological crisis, in order to cause a shifting balance.

Phase III: cline movement

Movement of *Heliconius* hybrid zones would provide good evidence for phase III. Barton and Hewitt (1989) have argued that cline movement will mostly be prevented by trivial population structural fluctuations, and that adaptations will spread much faster by simple natural selection or population spread from refuges than by cline movement; this would constitute a major limitation on the effectiveness of the shifting balance. Indeed chromosomal and warning colour clines are often found at partial barriers to gene flow like Amazonian rivers and the tops of mountains (Nichols and Hewitt 1986; Hewitt 1988; Mallet 1993). But clines will only become associated with such major barriers to gene flow if they can overcome slight perturbations in population density elsewhere in their range. In theory clines can move relatively quickly (Bazykin 1969; Barton 1979; Mallet and Barton 1989*a*; Johnson *et al.* 1990): in *Heliconius*, potential cline movement speeds can be predicted from selection pressures and migration rates using cline theory, assuming that dominance is the only force causing movement. These predicted speeds range from 50–200 km per century (Mallet 1986*a*; Mallet *et al.* 1990).

Many hybrid zones are known to be mobile: the hooded crow/carrion crow zone has moved tens of kilometres in this century (Perrins 1987). Some peculiar disjunct patterns of *Heliconius* and of ithomiine distribution strongly suggest hybrid zone movement in the past (Brown 1979; Lamas 1976; Mallet 1993). Many other hybrid zones in *Heliconius* are apparently stationary, or occur at geographical or environmental barriers from which they are unlikely to move (Turner 1971*b*; Benson 1982; Mallet 1993). But the data on cline stability are very weak; the Guiana hybrid zone studied by Turner (1971*b*, 1976*b*) could have moved 50 km in several hundred years without detection because early data are inaccurate. The only good historical data we know of show major (100 km) changes in the distributions of *H. hecale* and *H. ismenius* races in Panama where accurate locality data were collected in 1916 during the construction of the Panama Canal (G. Small, personal communication; Mallet 1993). Another butterfly hybrid zone, between *Anartia fatima* and *A. amathea*, has moved about 20 km to the east in Darién in the last two decades (Davies *et al.* 1997).

Centres of endemism

A tight correlation of patterns of endemism between different taxa has always been considered strong evidence for differentiation in refuges. However, the data for most groups have either not been analysed, or are equivocal. Nelson *et al.* (1990) showed that centres of plant endemism discovered by Prance (1973; see also Chapter 15), and used by him as evidence that Pleistocene refuges caused speciation among Amazonian plants, were also areas from which most collections had been taken. It seems that plant centres of endemism may be merely artefacts of poorly documented distributions.

The distribution of some butterflies is much better known. Brown (1979, 1987*a*) collected an enormous data set for Heliconiini and the better-known Ithomiinae in order to find areas with high probabilities for Pleistocene refuges. However, Brown's analysis has a number of problems. Using the data, Brown postulated preliminary areas of endemism. Locally endemic taxa were then assigned to one of these areas. Maps of the taxa assigned to a particular area of endemism were overlaid to produce a contour map of the endemic region. After correction for hybridization and soil types, the centres of such contour maps were assumed to be areas of high probability for the existence of Pleistocene refuges.

There are two inherent circularities in this system. First, some of Brown's earlier taxonomic papers used refuge theory as a justification for naming weakly differentiated taxa as geographical races; these new taxa were then themselves used to identify refuges. Second, the whole analysis depends on the preliminary decisions as to which endemic regions exist where, and on the assignment of taxa to endemic regions. If the races and species that form Brown's data set were actually distributed randomly, it is easy to see that he could have picked areas with weak, randomly produced peaks of endemism and defined them as endemic regions. Any endemic taxa whose distributions centred on this endemic region would be assigned to that region; other taxa with edges running through that endemic region would be assigned to adjacent endemic regions.

The assigned taxa, when overlaid on a map would then produce peaks of endemism near the centre of the endemic region first thought of. Brown's knowledge of the geography and taxa is second to none, and we believe that many of the patterns he has identified may be real; however, his analysis should not be interpreted as an independent statistical test for the existence of non-random peaks in endemism or refuges.

Further, Brown's analysis assumes the distributions of co-mimics to be independent. The geographical races of *H. erato* and *H. melpomene* may have similar patterns of distribution only because the two species are highly mimetic: where one changes its pattern, the other follows. One could even argue that species in different mimicry rings might affect each other in the competition for signalling space, so explaining some correlations between taxa in different rings. We must conclude that there is no clear evidence for refuges from the distribution of centres of endemism, at least without a proper statistical analysis of biogeographical patterns.

Range edges

Beven *et al.* (1984) tested the bird data of Haffer (1981) using simulations and cut-out models of bird distribution data randomly thrown onto maps of the Amazon basin to find how concordance between the edges of randomly distributed taxa compared with actual concordance of range edges: the random distributions were no more discordant than the natural bird distributions except that the natural distributions tended to be broken significantly more often at major rivers. Many of the butterflies studied by Brown (1979) also show distribution edges on major rivers or low mountain ranges. Such correlations between range edges unfortunately do not discriminate clearly between the refuge and parapatric models. Whereas the original zone of contact after expansion from a refuge is not expected to be at a barrier, under both theories hybrid contact zones or tension zones would move to such density troughs. No similar studies have been performed on *Heliconius* but we believe the patterns to be similar.

Fossil evidence of refuges

Much recent work on the Quaternary of South America could have provided support for the refuge theory. There were indeed major climatic disturbances, especially drying, associated with glaciation of temperate regions (Brown 1987*b*; Haffer 1987; Iriondo and Latrubesse 1994). What is unclear is whether these turbulent conditions caused the formation of forest refuges. Pollen studies of cores in the lowlands of Ecuador and Panama suggest that cooling of the order of 5–7 °C occurred in the late Pleistocene. This cooling may have precluded the use of mountainous regions as refuges by lowland forest taxa, and at the same time may have allowed major *friagems* accompanied by killing frosts to sweep throughout much of the lowland Amazon basin where a number of proposed refuges are sited (Bush *et al.* 1990, 1992; Latrubesse and Ramonell 1994). The existence of the Pantepui refuge in the endemic centre of the Guiana Shield is similarly in doubt; recent geological studies indicate that peat deposition under humid conditions started only in the Holocene, and there is evidence for arid conditions of the Pantepui region during the last glacial maximum (Schubert *et al.* 1994). Eastern Ecuador is now home to a variety of endemic taxa, particularly *Heliconius* subspecies, thought to have originated in Pleistocene refuges, yet between 10 000 and 8000 years ago a series of massive volcanic eruptions coated most of the area with ash whose residue is even now 1.5–4 m thick; this would have had a devastating effect on the biota (Iriondo 1994). These studies show that, while there is plenty of evidence for catastrophic environmental changes, these may have been very destructive to all lowland tropical organisms.

It is not inconceivable that many of the endemic races we now see scattered around Amazonia have evolved in the last few tens of thousands of years: the island of Marajó is known to have been completely submerged in the Amazon embayment 5000 years ago, yet there are three endemic subspecies of heliconiine and ithomiine butterflies (Brown 1979). In contrast, there are still no examples of forest refuges known to have provided lowland wet forest conditions throughout the late Pleistocene.

Molecular data

Molecular phylogenies have the potential to reveal the historical branching processes of populations, races, and species (Avise 1994). However, there are no fixed allozyme differences between *Heliconius* races (Turner *et al.* 1979; Mallet and Barton 1989*b*), and mtDNA genealogies are uncorrelated with racial boundaries (Brower 1994, 1996). Even the fork in the mtDNA genealogies of both *H. erato* and *H. melpomene* in north-eastern Colombia (Brower 1996) does not coincide with a racial boundary: the mtDNA break occurs within the races *H. erato hydara* and *H. melpomene melpomene* respectively. Brower concludes that mitochondrial data provide little evidence either for or against the refuge theory. The general lack of concordance between mtDNA and colour patterns, and the discordance between mtDNA genealogies of *H. erato* and *H. melpomene*, suggests a lack of vicariance in refuges (Mallet *et al.* 1996)

Brower (1996) has put forward a 'mitochondrial parsimony' hypothesis, which suggests that disjunct red-barred races either side of the Andes are independently derived. In contrast Turner (1981, 1983) and Mallet (1993) had proposed that 'colour pattern parsimony' is more likely since genetics of the similar, although disjunct, colour patterns are nearly identical. But colour pattern parsimony is now problematic; if colour patterns evolved only once, the mtDNA divergence, estimated to be 1–2 Ma old, may be newer than the colour pattern differences. This implies a much older time of divergence for some races than the Quaternary supposed by refuge models (Turner 1976*b*; Brown 1987*a*). However, it is also possible that the evolution of mtDNA and the nuclear genome have become dissociated; this is known in many other species (Avise 1994). Brower's mitochondrial parsimony hypothesis could be tested by sequencing the colour pattern genes themselves. However, this work is unlikely to lead to a resolution of the drift versus selection argument.

Quasi-Batesian mimicry

Recent work by Speed and Turner (1997) suggests a further mechanism for ring switching. Most reasonable models of learning in vertebrate predators suggest that mildly unpalatable mimics do not behave like Müllerian mimics in the way described here, but that at certain population densities they will behave like Batesian mimics, with negative frequency-dependent selection which may cause them to become polymorphic. In this case the butterfly will have forms in two or more mimicry rings. If long-term changes in species density then cause the species to behave more like a conventional Müllerian mimic, it might revert to being monomorphic. Clearly this could result in ring switching via an intermediate stage of stable polymorphism, but it is clear neither how extensive quasi-Batesian mimicry is, nor whether many *Heliconius* species are of weak enough unpalatability: the polymorphic *H. doris* is a likely candidate (Turner 1995).

The problem of novelty

New warning patterns have to arise somehow. The biotic drift model 'under-explains' this novelty of patterns: it can permit only switching between existing patterns, and as it involves extinction, the number of patterns must diminish over time. Ultimately the system will cease to diverge even within species, as more and more patterns become extinct. Mimicry cannot explain novelty.

The shifting balance allows novel colour patterns to arise. The transparent ithomiines, the tiger ithomiines and heliconiines, and the *erato/melpomene* patterns are evolutionary novelties found nowhere else than the Neotropics. Many races of *H. erato* and *H. melpomene* indeed do not seem to mimic anything much but each other, and although similar ancestral patterns can be constructed for each species, it is not clear what selective mechanism caused the two species to co-diversify in the first place. Mallet (1993) suggests that there are no potential models known for most of the Amazonian races. But some of the extra-Amazonian races are apparently ancestral patterns which can plausibly be held to be what these two species evolved from, and the reconstructed intermediate patterns in the cladogram all resemble heliconiine patterns which still exist somewhere in South America, which might have acted as the models for divergence in the past (Turner 1983, 1984*a*). On balance, however, the huge variety and novelty of warning colour patterns is strong evidence for some sort of random initiation of divergence such as shifting balance processes. Alternative ways of explaining novelty are discussed in Turner and Mallet (1996).

16.6 Conclusions

We can summarize the differences between our two models as biotic drift, plus mimetic capture, plus allopatry in refuges on the one hand versus genetic drift, plus shifting balance and cline movement, plus parapatry without refuges on the other. The biotic drift and shifting balance models therefore initially appear diametrically opposed; but it is less surprising than at first thought that they are so difficult to distinguish. The operational distinction between natural selection and genetic drift as a cause of changing gene frequencies is likewise a very fine one (Hodge 1987; Beatty 1992; see also Chapter 7); Wright (1977, p. 455) includes random fluctuations of selection in phase I of the shifting balance.

Most of the components of each model are compatible. In both models, some of the extraordinary geographical diversity is initiated by a stochastic event which involves small population sizes and a depauperate bioton: both genetic and biotic drift are likely to be produced by the same ecological crisis, whether this is continual metapopulation turnover or the result of climatic deterioration. As genes drift so do biota. We have argued that the shifting balance itself will require not only genetic drift but some degree of biotic drift into the bargain: because natural selection on warning colour is number-dependent, a reduction in population density causes not only random genetic drift but a change in the intensity of selection, and the extinction of fellow members of the mimicry ring. We have further argued that the pure biotic drift model does not adequately explain the diversity of patterns, but have suggested that the full conditions for the shifting balance might be met rather seldom. Against this, one needs to ask how many times they need to be met in what span of time to generate the existing diversity: phase III of the shifting balance is a way of magnifying the outcome of a rare event, and in the span of evolutionary time, even an event of low probability may occur frequently enough.

In both models natural selection is extremely important, and even when a novel pattern has arisen by drift, mimetic capture must be playing a major role in further evolution: in the Amazon basin, ten or so *Heliconius* species have the same rayed pattern, which must represent mimetic capture by one or two of the species of the rest.

Likewise while the island mimicry model invokes allopatry, to which the shifting balance model was framed as a parapatric alternative, mimetic capture could perfectly well take place in parapatry (Turner 1982) and genetic drift could occur in allopatry or within quaternary refuges. While moving hybrid zones form the important phase III of the shifting balance, the junction boundaries of races originally formed in refuges by mimetic capture or other means, should move in the same way.

If it is hard to disentangle the components of biotic drift and the shifting balance, it will be hard to devise a crucial test to distinguish them. It seems very unlikely that we will find a direct historical record that shows whether genetic or biotic drift actually initiated mimetic divergence. Genetic drift in small, isolated populations might leave a signature of reduced genetic diversity in a founder population; however, expansion during phase III will quickly mop up variation from surrounding populations. We suggest that it will be more fruitful to find intermediate cases of divergence, since both hypotheses predict that local processes causing divergence occur only transitorily. It would be particularly worthwhile to record the species in many more modern-day refuges and metapopulations, and to find whether and how they have diverged: both models imply that initial, perhaps failed, divergences should be common. Studies of the dynamics of actual contact zones and invasions would produce evidence for cline movement.

Finally, perhaps it is only a lack of imagination which has led us both to propose random or chaotic causes of an apparently haphazard diversity of colour patterns. Maybe a deterministic explanation has eluded us; but we doubt it!

16.7 Summary

Species of the South American butterfly genus *Heliconius* have undergone remarkably wide racial divergence in their patterns, and most of the resulting races are Müllerian mimics. As warning coloration normally imposes stabilizing selection on the pattern, this divergence is much in need of explanation. Two models have been suggested. Brown, Sheppard, and Turner proposed that the divergence results from 'mimetic capture', the switching of patterns between adaptive peaks generated by changes in the overall composition of the local biota ('biotic drift') and hence of the mimicry rings to which each species belongs. These changes have in turn been generated by long-term patterns of species extinction in island refuges as biota became progressively isolated and contiguous during contraction and expansion of the rainforest during the Pleistocene. An alternative model, proposed by Mallet, is that truly novel colour patterns became established by mutation and random drift, becoming predominant in local areas; subsequently the novel patterns spread over wide areas by the migration of clines. Under this application of Wright's 'shifting balance', refuges are not necessary for divergence, and Müllerian mimicry evolves after divergence rather than being the driving force for race formation. Although the respective models appear diametrically opposed, there are broad areas of agreement and the hypotheses are difficult to distinguish; in both models there is an initial stochastic event, followed by natural selection for mimicry, and both will operate either in parapatry or allopatry. The novelty and diversity of warning patterns are better explained by the shifting balance.

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17

Adaptive plant evolution on islands: classical patterns, molecular data, new insights

Thomas J. Givnish

17.1 Introduction

The nature of plant life on oceanic islands is shaped by the remoteness of such islands, the resulting selection on plant dispersal mechanisms before arrival, and the ensuing pressures on plant ecology caused by an impoverished set of competitors, predators, pollinators, and frugivores after arrival. Island plants are thus often marked by unusually effective means of long-distance dispersal, the evolution of arborescence, extensive speciation coupled with adaptive radiation in habit and habitat, possession of unspecialized flowers, and loss of anti-herbivore defences (Darwin 1859; Wallace 1878, 1880; Guppy 1906; Rock 1919; Ridley 1930; Docters van Leeuwen 1936; Skottsberg 1956; Fosberg 1963; Carlquist 1965, 1967, 1970, 1974; van Balgooy 1971; Robichaux *et al.* 1990). These classical phenomena are widely thought to provide some of the most striking evidence for the role of ecology and natural selection in shaping life on earth.

Yet the scientific support for some of these phenomena may need re-examination. Many island plants have diverged so dramatically from putative ancestral groups that it is difficult to ascertain their relationships and, thus, to trace the pattern of their evolution (Knox *et al.* 1993; Givnish *et al.* 1994, 1995,1997; Sang *et al.* 1994; Baldwin and Robichaux 1995; Böhle *et al.* 1996; Kim *et al.* 1996; Francisco-Ortega *et al.* 1997; see also Chapter 2). Phylogenies inferred from morphology may be skewed by convergent and/or divergent evolution of selectively important traits; such skewing might be substantial in organisms undergoing 'concerted convergence', in which similar environments select for convergence in several traits simultaneously (Givnish and Sytsma 1997). Such problems may be especially severe for adaptive radiations on islands, in which phenotypic variation among species can be concentrated in the relatively few characters that underlie a specific radiation (e.g. see Grant 1986; Baldwin and Robichaux 1995; Givnish *et al.* 1995).

Molecular systematics provides an important way of circumventing these problems. Recently, several researchers have begun to use molecular techniques to infer phylogeny independently of morphological traits of interest (Givnish and Sytsma 1997), and to