Bimodal hybrid zones and speciation

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Contact zones exemplify a series of stages in speciation. In unimodal hybrid zones intermediates predominate; in bimodal zones hybrids are rare and parental forms predominate; and finally, species might overlap, but never hybridize. Recent studies show bimodality to be associated strongly with assortative mating or fertilization, and only weakly with overall levels of genetic divergence or intrinsic genomic incompatibility. Ecological divergence across most bimodal hybrid zones suggests that ecology contributes more to speciation than genomic incompatibility. This continuum of stable contact zones provides empirical evidence for a route to speciation, which does not require allopatry.

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Hybrid zones between divergent geographic populations have long been recognized as a means both to assess taxonomic status and to give clues about modes of speciation[1,2]. Here, we review recent hybrid zone research in this light, paying particular attention to the frequency of intermediate genotypes. Hybrid zones are narrow regions of phenotypic or genotypic change, which separate otherwise more or less homogeneous taxa. In 1997, Harrison and Bogdanowicz[3] highlighted a useful classification of hybrid-zone populations depending on the distribution of genotypic classes (see also Ref. 4). Some are 'unimodal' and consist largely of a 'hybrid swarm', and others are 'bimodal' and consist largely of genotypes resembling the parental forms, with few intermediates. A third category, with intermediate or 'flat' genotypic distributions, consists of a more even mixture of parental and hybrid genotypes (Boxes 1 and 2).

Whatever one's preference for species concepts, bimodality within a local population indicates that speciation of parental forms is nearly complete. Under a practical application of the biological species concept, the ability to remain distinct in sympatry is the only objective test of speciation: completely allopatric forms must be somewhat arbitrarily assigned to species or geographic races[2]. In sympatric speciation, the key step occurs when disruptive selection is strong enough to convert a unimodal distribution of genotypes into a bimodal distribution[5]. Bimodal groups of genotypes can continue to diverge in ecology, habitat adaptation and mating behaviour, because recombination does not break up coadapted genetic architecture. They have attained a degree of genetic and evolutionary independence[3], of the kind featured in evolutionary and phylogenetic species concepts, and, under some definitions, speciation is complete[6,7].

Box 1. Glossary

Endogenous selection: postzygotic selection owing to environment-independent interactions between alleles and genes from distinct taxa, such that fitness is primarily determined by an individual's genotype, irrespective of habitat across the hybrid zone[37].

Exogenous selection: postzygotic selection mediated by environmental variation, such that different genotypes are favoured in different geographic areas. Typically, each parent is favoured in its own habitat type, but in some cases hybrids might have higher fitness in intermediate habitats[37].

Heterozygote deficit: a shortage of heterozygotes compared with Hardy–Weinberg expectation, often measured by the inbreeding coefficient:

$$F_{\mathrm{IS}} = 1 - \frac{P_{\mathrm{Aa}}}{2p_{\mathrm{A}}p_{\mathrm{a}}}$$

where $P\mathrm{Aa}$ is the actual frequency, and $2p\mathrm{A}q\mathrm{a}$ is the expected frequency of heterozygotes Aa, given allelic frequencies $p\mathrm{A}$ and $p\mathrm{a}$. Heterozygote deficits can be caused by selection against heterozygotes, assortative mating and migration between divergent populations, as well as by inbreeding.

Hybrid zone: a region where genetically distinct geographic populations meet and mate, resulting in individuals of mixed ancestry[47].

Hybrid zone, bimodal: a hybrid zone in which populations predominantly consist of individuals genetically similar to one or other parental genotype, with few intermediates (see also Ref. 3). The lack of intermediates must be evident both at single loci (heterozygote deficits) and across multiple loci (strong correlations or disequilibria between loci). Samples should comprise single local populations because lumping geographically structured populations will inflate heterozygote deficits (Wahlund effect) and linkage disequilibria.

Hybrid zone, unimodal: a hybrid zone in which intermediate hybrid genotypes predominate (see also Ref. 3). Unimodality should be considered the null hypothesis, against which the more complex hypothesis of bimodality can be tested. A flat hybrid zone is intermediate between bimodal and unimodal zones (see also Ref. 3).

Linkage disequilibria: gametic associations expressed as a shortage of haplotypes compared with random expectation. For two loci, the disequilibrium coefficient is often used, $D_{\mathrm{AB}} = P_{\mathrm{AB}} - p_{\mathrm{A}}p_{\mathrm{B}}$. Gametic associations are commonly generated by migration of individuals between genetically divergent populations or, within hybrid populations, by assortative mating and/or epistatic selection.

Until recently[3], most of the hybrid-zone literature and theory has concentrated on unimodal examples[1,8]. Bimodality is achieved in populations with extremely strong heterozygote deficits coupled with nearly maximal linkage disequilibria between loci (Box 1), parameters that are central to the genetic theories of hybrid zones, as well as of speciation. Therefore, understanding bimodality represents a logical extension of traditional hybrid-zone theory in the direction of speciation.

The continuum from unimodality to bimodality

Even within unimodal hybrid zones, the influx of individuals from outside the zone will lead to an excess of parental genotypes, which can often be detected as stable associations between loci (linkage disequilibria – see Box 1) and less often as deviations from Hardy–Weinberg proportions within loci (heterozygote deficits – see Box 1). For example, two transects through a hybrid zone between the toads *Bombina variegata* and *Bombina bombina* in Poland show strong linkage disequilibria between unlinked genes, but virtually no evidence for heterozygote deficits[9]. The greater persistence of linkage disequilibria is explained because they decay only at the rate of recombination per generation, whereas heterozygote deficits collapse completely after a single generation of random mating. In another *Bombina* transect studied recently in Croatia[10], there are Hardy–Weinberg deviations and far higher levels of linkage disequilibria than in Poland[9]. In Croatia, active ecological preferences in a patchy habitat lead to mosaic patchiness in genotype frequency. However, despite variation in levels of single locus and linkage disequilibria, most *Bombina* hybrid-zone populations are unimodal in genotype distribution (Box 2).

There are also examples of zones transitional between unimodal and bimodal types, with 'flat' genotypic distributions.

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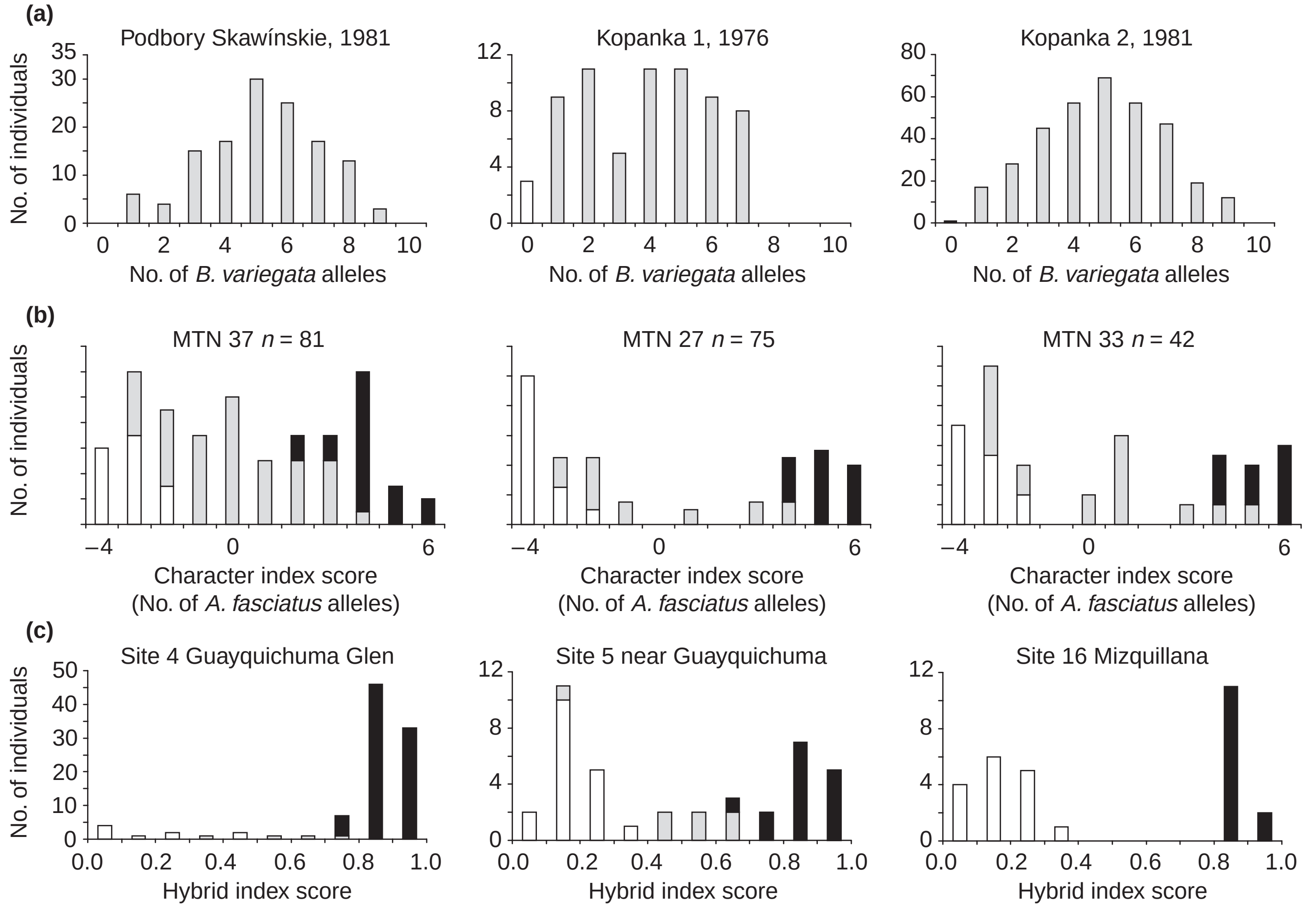
Box 2. Allozyme genotype distributions along a continuum from unimodal to bimodal populations

The figure shows the three types of contact zone: (a) unimodal, *Bombina bombina* × *Bombina variegata*[9]; (b) flat to bimodal, *Allonemobius socius* × *Allonemobius fasciatus*[14], and (c) strongly bimodal, *Heliconius himera* × *Heliconius erato*[16]. Individual genotypes identified as parental are shown in black or white and hybrids are shaded. The distribution of multilocus individual genotypes is an *n*-dimensional matrix, where *n* = the number of loci or characters and is therefore difficult to visualize. A common method of simplifying such data (but which involves considerable loss of information) is to use a hybrid index, three examples of which are given here.



(Online: Fig. I)

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In *Bombina*, alternative alleles are fixed between the species: the index is simply the number of *B. variegata* alleles in each individual. In *Heliconius* and *Allonemobius*, where allelic differences are not fixed, the index scores are either counts of diagnostic alleles in each individual (*Allonemobius*)[14] or are means across all alleles (alleles commonest in *H. erato* score one and those in *H. himera* score zero; the index is expressed as the proportion of *erato* alleles)[16]. Each histogram shows samples collected from a single local population. Although we have not done so here, bimodality can be tested statistically; for example, Feder used a likelihood criterion based on the probabilities that each individual genotype was derived from either parental population[7]. Allonemobius *plots (b) redrawn, with permission, from Ref. 14.*

They occur in organisms such as oaks[11], fishes[12], leopard frogs[13] and crickets[14]. A few *Bombina* populations near the Croatian transect (described above) are flat or even bimodal[15], thus demonstrating that genotype distributions can vary considerably between sites within the same zone (Box 2).

Bimodal hybrid zones also show considerable variation, both in overall frequency of hybrid genotypes, and in the relative abundance of F_1 and backcross types. In a hybrid zone, between the butterflies *Heliconius himera* and *Heliconius erato*, 10% of individuals in mixed populations are hybrids and about half of these are F_1 (Ref. 16) (Box 2). But, hybrid genotypes can be much rarer; for example, only 1.3% in some hybridizing populations of *Triturus* newts[17]. F_1 hybrids are absent in samples from Louisiana iris hybrid zones (*Iris fulva*, *Iris brevicaulis* and *Iris hexagona*), although they must occur occasionally because backcross genotypes are relatively common[18]. Rare hybrids probably exist between many other sibling taxa but they are poorly documented. Finally, at the end point of this series, there are sympatric overlaps between taxa not known to hybridize at all.

Thus, there is a continuum from unimodal to bimodal genotypic distributions in hybrid zones. Unfortunately, multilocus genotypic data are required to assess bimodality and many published studies provide neither data nor hybrid-index plots, such as those given in Box 2. Statements, such as 'hybrid populations consist of 50% hybrid individuals', are difficult to interpret: all hybrids might be close to parental (implying a bimodal pattern) or intermediates (implying a unimodal or flat distribution). To characterize this continuum more fully, future studies should provide individual data or at least some means of visualizing the distribution of genotypes.

Variation within genomes

There can be considerable heterogeneity between loci in levels of bimodality. In one notable example of crickets (*Gryllus*)[19], an early survey based on morphological and allozyme data suggested unimodal distributions within populations. Subsequent studies of nuclear DNA markers with greater differentiation between parental taxa showed a bimodal pattern[3]. In *Gryllus*,

Table 1. Bimodal hybrid zones[a]

Species	Percentage of hybrids in centre of hybrid zone	Type of prezygotic isolation	Postzygotic incompatibilities known	Genetic distance (Nei's *D*)	Level of differentiation between parental taxa[b]	Refs
Allonemobius fasciatus × *socius* (ground cricket)	1–7% F_1 hybrids	Assortative fertilization (0–19% hybrid offspring in population cages)	None	0.19	E	14,23,27
Heliconius himera × *erato* (butterfly)	10% hybrids (F_1 and backcross classes)	Mate choice (5.2% rate of interspecific mating in the field)	None (but probably ecological and mimetic)	0.28	E, M^c, D	16,26,30
Gryllus firmus × *pennsylvanicus* (cricket)		Temporal isolation and mate choice	Complete inviability in one direction of cross	0.02–0.03	E, M^o, N	3,19
Littorina saxatilis 'morphotypes' (periwinkle)	11–29%	Mate choice (10% interform pairs)	None	≈0	E, M^o	33,46
Ficedula hypoleuca × *albicollis* (flycatcher)		Mate choice (2.6% heterospecific mating versus 13.8% exp.)	F_1 fitness = 30%	0.0006	M^c	42
Triturus cristatus × *marmoratus* (newt)	1.3–14.3% hybrids	Mate choice	F_1 male sterile; F_1 female 73% reduction in hatch rate	0.86	E, M^o, C, D	17
Helianthus annus × *petiolaris* (sunflower)	F_1 genotypes rare	Pollen competition (0–17% natural hybridization rate)	F_1 seed set < 1% viability recovered in backcross genotypes	0.88	E, M^o, C, D	20,21
Iris fulva × *brevicaulis* (iris)	F_1 genotypes absent	Divergent flowering time	Reduced seed viability and germination?	0.20	E, M^f	18,48
Iris fulva × *hexagona* (iris)	F_1 genotypes absent	Divergent flowering time?	None	0.29	E, M^f	18,28
Iris chrysophylla × *tenax* (iris)	Hybrids rare	Divergent flowering time and pollen–style incompatibility	None		M^f	49

[a] This table includes most examples known to the authors with information on both pre- and postzygotic isolation. Question marks indicate effects suggested by authors but which have not been demonstrated experimentally.

[b] Abbreviations: E, marked ecological or habitat differences; M^c, colour pattern; M^f, floral morphology; M^o, other morphological characters; C, chromosome structure; D, fixed differences at mtDNA or chloroplast DNA; N, fixed differences at nuclear DNA markers.

the apparent differences between data sets are probably the result of a lack of diagnostic markers at allozymes compared with nuclear DNA. However, heterogeneity between loci might also be a result of differences in levels of selection. Genomic regions under strong disruptive selection should show greater bimodality than weakly selected regions. In perhaps the first study addressing this question, Rieseberg *et al.*[20] used the underrepresentation of genomic regions in *Helianthus* hybrids to infer strong selection acting against those segments.

What differentiates bimodal from unimodal hybrid zones?

Prezygotic barriers to gene flow

Bimodal hybrid zones are invariably coupled with strong assortative mating or assortative fertilization within hybrid populations (Table 1). Three of the best-studied bimodal hybrid zones, in passion-vine butterflies (*Heliconius*), sunflowers (*Helianthus*) and ground crickets (*Allonemobius*), show strong prezygotic isolation as a result of assortative mating, pollen competition and homogamic fertilization, respectively[21–23]. Interestingly, the sunflowers and crickets mate nearly randomly, but show assortative fertilization, which implies that gamete recognition evolves faster than mate recognition in some taxa[21,23].

However, populations within unimodal zones show little assortative mating in a diverse range of taxa (Table 2). In some cases, individuals collected in allopatry do mate assortatively, but this breaks down in the hybrid swarm. For example, the grasshoppers *Chorthippus parallelus parallelus* and *Chorthippus p. erythropus* show marked song differences[24]. When individuals from populations on either side of a hybrid zone in the Pyrenees are mixed, they show significant assortative mating[25]. However, although morphological and song characters change abruptly across the cline in nature, implying strong selection, the clines are unimodal and smooth, and there is little assortative mating locally[25].

Postzygotic barriers to gene flow

By contrast, postzygotic incompatibilities are similar in bimodal and unimodal zones. Both classes of hybrid zone cover the whole spectrum, some showing strong hybrid breakdown and others very little (Box 3, Tables 1 and 2). Bimodal hybrid zones include examples with no hybrid incompatibilities in laboratory crosses, such as in *Heliconius* butterflies[26] and *Allonemobius* crickets[27]. Other bimodal zones even have heterosis, such as in the F_1 hybrids between *I. fulva* and *I. hexagona*, which inherit a propensity for clonal propagation from one parent and high fertility from the other[28]. Despite this heterosis, adult F_1 irises have not been detected in mixed populations[18,28], at least in part because of strong prezygotic isolation.

Table 2. Unimodal hybrid zones[a,b]

Species	Percentage of hybrids in mixed populations	Type of prezygotic isolation	Postzygotic incompatibilities between taxa? (usually less within hybrid populations)	Genetic distance (Nei's *D*)	Level of differentiation between parental taxa	Refs
Bombina variegata × *bombina* Poland (toad)	Little deviation from HW	None?	Yes	0.49	E, M^c, M^o, D	9
Bombina variegata × *bombina* Croatia (toad)	Significant deficit of hybrids	Some owing to habitat choice	Yes	0.49	E, M^c, M^o, D	10
Mercenaria mercenaria × *campachensis* (hard clam)	Significant deficit of hybrids	None?	Yes		E	32
Podisma pedestris chromosomal races (grasshopper)	Little deviation from HW	Weak assortative fertilization	25–30% reduction in F_1 viability	0.009	C	38
Chorthippus parallelus parallelus × *erythropus* (grasshopper)	Little deviation from HW	Assortative mating (allopatry only) and weak assortative fertilization	Sterile F_1 males	0.05	C, M^o	24,25
Heliconius erato colour pattern races (butterfly)	Little deviation from HW	None?	None (but stabilizing selection on colour pattern)	≈0	M^c	30
Chaetodon pelewensis × *punctatofasciatus* (butterflyfish)	Allozymes in HW, 70% colour pattern intermediates	None	None?	≈0	M^c	50

[a] This table includes some examples of well studied unimodal zones but is not intended to be exhaustive.

[b] Abbreviations: HW, Hardy–Weinberg equilibrium; E, marked ecological or habitat differences; M^c, colour pattern; M^o, other morphological characters; C, chromosome structure; D, fixed differences at mtDNA or chloroplast DNA; N, fixed differences at nuclear DNA markers.

In the small sample of well studied hybrid zones considered here, strong prezygotic barriers to gene flow are associated with bimodality, but postzygotic barriers show no clear pattern. How can we explain this? Suppose two populations diverge in allopatry: there are several possible outcomes if secondary contact occurs. If there is hybridization and only postzygotic isolation has evolved, a unimodal hybrid zone will form. Even if there is some prezygotic isolation, populations might still collapse into unimodal hybrid swarms, as has perhaps occurred between *C. p. parallelus* and *C. p. erythropus*, where assortative mating between allopatric populations breaks down in sympatry. Once this has occurred it might be impossible for prezygotic barriers to evolve *in situ* (reinforcement) owing to recombination[29].

Alternatively, assortative mating might be strong enough to allow interacting populations to remain bimodal after contact. Incomplete assortative mating must be stabilized by some postzygotic selection against hybrids or recombination will eventually destroy associations between mate-choice loci. For example, in a *Heliconius* hybrid zone with strong assortative mating and no hybrid inviability[26], the almost complete lack of mtDNA introgression between hybridizing populations[16] is hard to explain given the estimated 5% rate of interspecific matings in nature[22]. Selection most likely acts against hybrids because of maladapted warning colour and other ecological traits[30], and maintains almost complete linkage disequilibrium between mate choice and other differentiated loci. It is the assortative mating that distinguishes the bimodal hybrid zone between *H. himera* and *H. erato* from unimodal hybrid zones between races of *H. erato*. Strong postzygotic ecological selection, particularly on warning colour, is common to both[30].

Paterson argued that premating compatibility is a key factor preventing speciation[31]. Our finding that premating barriers are correlated with bimodality is consistent with this view, although some form of postzygotic disruptive selection will also be necessary to prevent the collapse of divergent mate recognition systems owing to recombination[29].

Types of selection

Recently, the nature of selection acting in several hybrid zones has been studied[27,28,30,32–34]. This work was stimulated by theoretical models of hybrid zones, which invoked either endogenous selection, such as genomic incompatibilities that are independent of the environment[35], or exogenous selection, where fitness depends on the environment (Box 1)[36,37]. In many cases both exogenous and endogenous selection are important[10,32,34]. This is unsurprising because models invoking each are not mutually exclusive. However, in many bimodal zones endogenous selection appears to play a lesser role, implying that exogenous selection, combined with assortative mating, is the primary factor maintaining hybrid-zone stability[26–28,33].

Level of divergence

The overall level of genetic divergence is a poor predictor of the ability to coexist. Unimodal hybrid zones occur between taxa that differ radically at multiple characters, such as chromosome structure, calling song, allozyme and DNA markers; for example, *Bombina* toads[9], and *Chorthippus*[24,25] and *Podisma* grasshoppers[38]. By contrast, bimodal hybrid zones can separate taxa that are morphologically indistinguishable[14] or no more divergent than ecological morphs within parental species[39].

Using allozyme differentiation as a measure of time since divergence, it is clear that both prezygotic isolation and genomic incompatibility can evolve rapidly. Of species pairs with little genetic differentiation (Nei's genetic distance, $D \leqslant 0.05$), three bimodal cases show strong prezygotic isolation (*Ficedula*, *Littorina* and *Gryllus* – Table 1) and four show significant postzygotic effects, including sterility of males and a 30% reduction in hybrid fitness (*Ficedula* and *Gryllus* – Table 1; *Podisma* and *Chorthippus* – Table 2). Although there is a broad correlation between overall reproductive isolation and Nei's *D*, similar to that shown in *Drosophila*[40], this could mostly be explained by genetic divergence

Box 3. Postzygotic isolation in natural hybrid-zone populations

Environmental gradients across many hybrid zones offer a useful means to unravel the contributions of endogenous (i.e. genomic incompatibilities) and exogenous selection (i.e. environmental adaptation). The precise method will depend on the study organism. In species where age cohorts can be identified, changes in genotype frequency can be measured over time and space, giving a direct estimate of selection[27]. Ideally, a single cohort should be sampled through time, but where this is not possible static cohort analysis can be used (i.e. sampling the age cohorts present at a single time). The main (and often limiting) assumption of this method is that recruitment of different genotypes is constant for each cohort[32]. Transplant experiments offer an alternative approach and have been used in diverse organisms, such as *Heliconius* butterflies, periwinkles (*Littorina*) and irises (*Iris* spp.)[28,33,51].

Box 4. Prezygotic isolation in natural populations

Prezygotic isolation is commonly studied by means of laboratory choice tests, but these might not reflect rates of hybridization in nature. Estimating levels of assortative mating in wild populations is relatively easy in many taxa, but it has only been attempted rarely. Two recent studies in a plant and a butterfly hybrid zone demonstrate some useful procedures. In *Helianthus* sunflowers, Rieseberg *et al.*[21] collected families of seeds from known mothers in three hybrid populations. Information on maternal and offspring allozyme genotypes was then used to determine the probable paternal genotype. Population genotype frequencies must also be estimated for each study site, to determine the expected mating frequency under random mating. In the hybrid zone between *Heliconius himera* and *Heliconius erato*, genotyping individuals is easier because each species has a distinct colour pattern, the genetic basis of which is known. Within the hybrid zone, colour pattern is a good predictor of mitochondrial and allozyme genotype[16]. In both *Heliconius* and *Helianthus*, maximum likelihood methods provided a powerful means to integrate information on assortative mating across populations.

after speciation has occurred, given that strong bimodality can evolve so rapidly.

Implications for speciation

Ecological postmating isolation

The nature of selection in bimodal hybrid zones has important implications for our understanding of speciation. Exogenous selection requires deterministic forces, in the shape of habitat adaptation, to have played a primary role in divergence. However, endogenous selection requires either stochastic factors, such as allopatric genomic reorganization and/or founder events, or pleiotropic effects owing to adaptive evolution of other traits[40]. On balance, the ubiquity of exogenous selection in both bimodal and unimodal hybrid zones argues for a driving role of adaptive ecological processes in speciation. These conclusions parallel those reached on adaptive ecological races in other contexts[41].

Reinforcement and the origin of prezygotic isolation

We have argued that assortative mating and fertilization have a primary role in speciation, but so far have not considered how it arises. Initially, prezygotic isolation can be a by-product of changes in habitat use or can be a result of geographically divergent patterns of sexual selection. Premating barriers can also arise via reinforcement, in which natural selection acts to reduce the production of unfit hybrids. There are now several good examples of reinforcement[42,43]. For example, pied and collared flycatchers from sympatric populations pair more assortatively than those from allopatric populations, and phylogenetic evidence suggests that this results from *in situ* divergence in plumage. There is selection against hybrids, and sympatric shifts in both mate preference and sexual plumage reduce hybrid matings, as expected under reinforcement[42].

Reinforcement should occur most readily in bimodal hybrid zones. The major theoretical problem for reinforcement is recombination, which breaks down associations between loci affecting mate choice and hybrid fitness[29]. In bimodal hybrid zones this problem has already been overcome because bimodality ensures near-complete association between species-specific traits, in spite of incomplete reproductive isolation. Indeed, theory shows that reinforcement is much more probable when initial levels of assortative mating are high[44]. The patchiness in genotype frequency found in mosaic hybrid zones might further facilitate reinforcement by providing an initial level of pleiotropic assortative mating as a result of divergent habitat use[45]. The idea that speciation in unimodal zones can involve reinforcement has rightly been treated with skepticism, but in bimodal populations the likelihood is greatly enhanced and reinforcement might not be uncommon.

Likelihood of parapatric speciation

Hybrid zones are traditionally assumed to form via secondary contact after geographic divergence in allopatry[2]. However, parapatric divergence *in situ* is virtually impossible to rule out in many cases[35,36]. In some examples, there is good evidence to support secondary contact. For example, *Chorthippus* hybrid zones in the Pyrenees lie at the ridges of cols, exactly where contact was probable as the glaciers retreated after the last Ice Age. Indeed, these hybrid zones could not have existed in their current location before about 9000 BP, certainly too recent for the *in situ* divergence of the morphological and genetic differences between *C. parallelus* races[24].

In other cases, *in situ* parapatric speciation seems highly likely. A good example is a bimodal contact zone between morphs of the rough periwinkle, *Littorina saxatilis*, on the wave-exposed shores of Galicia in northern Spain. The upper shore morph is large, with heavily ridged and banded shells, while on the lower shore snails are smaller, smooth and unbanded. Abrupt changes in allozyme frequency show that the forms are genetically isolated on a microgeographic scale[33], but over a broader scale there is no evidence for parallel genetic divergence between morphs, as expected if different populations of the same morph share a common allopatric origin. In Sweden, similar morphological types are found, also associated with upper and lower shores, but without reproductive isolation[46]. Given that these ecological forms are in contact in many different areas, it seems most parsimonious to explain the evolution of reproductive isolation in Galicia as a process that has occurred via ecological adaptation, followed by *in situ* evolution of assortative mating. Therefore, this is at least one probable example of parapatric speciation.

Furthermore, the existence of unimodal clines, through flat and bimodal hybrid zones to sympatric overlap without hybridization, demonstrates a continuum of stable intermediates between clinal differentiation and good species. Of course, particular taxa cited here could have evolved in parapatry or allopatry. However, their stable hybrid zones, whether bimodal, flat or unimodal (Tables 1 and 2), demonstrate intermediate stages along the evolutionary route that must be taken during parapatric speciation. Parapatric speciation is at least possible and, we argue, not improbable.

Conclusions and prospects

In nature, hybrid zones vary in the degree to which parental genomes maintain cohesion when in contact and a continuum exists from unimodal to bimodal zones. Along this continuum, multiple intermediate stages imply that speciation is a gradual, cumulative process. However, relatively few well documented examples exist. To explore this continuum further, future workers are encouraged to provide actual genotypic data or, at the least, hybrid-index plots (Box 2).

Bimodal zones seem to be characterized by strong mating or fertilization barriers. However, more knowledge about mating and fertilization patterns in nature (Box 4) is needed to assess the generality of this pattern. For example, recent studies in birds, butterflies, crickets and sunflowers demonstrate that rates of hybridization in the wild are relatively easy to estimate[21–23,42].

The frequent occurrence of bimodality also suggests that adaptive evolution of assortative mating is more likely than generally supposed, because almost complete linkage disequilibria between mate choice and trait loci already exists in many such zones. However, reinforcement might play its most significant role in the closing stages of speciation, once bimodality has been achieved by other means. In any case, the relatively frequent occurrence of stable, bimodal hybrid zones demonstrates intermediates along a route for parapatric evolution, thus suggesting that parapatric speciation is not unlikely.

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