

ORIGINAL ARTICLE

Empirical study of hybrid zone movement

RJA Buggs

Church Farm, Capel, Tonbridge, Kent, UK

Hybrid zones are 'natural laboratories' for studying the origin, maintenance and demise of species. Theory predicts that hybrid zones can move in space and time, with significant consequences for both evolutionary and conservation biology, though such movement is often perceived as rare. Here, a review of empirical studies of moving hybrid zones in animals and plants shows 23 examples with observational evidence for movement, and a further 16 where patterns of introgression in molecular markers could be interpreted as signatures of movement. The strengths and weaknesses of methods used for detecting hybrid zone movement are discussed, including long-term replicated sampling, historical surveys, museum/herbarium collections, patterns of relictual populations and introgression of genetic markers into an advancing taxon. Factors governing hybrid zone movement are assessed in the

light of the empirical studies, including environmental selection, competition, asymmetric hybridization, dominance drive, hybrid fitness, human activity and climate change. Hybrid zone movement means that untested assumptions of stability in evolutionary studies on hybrid zone can lead to mistaken conclusions. Movement also means that conservation effort aimed at protecting against introgression could unwittingly favour an invading taxon. Moving hybrid zones are of wide interest as examples of evolution in action and possible indicators of environmental change. More long-term experimental studies are needed that incorporate reciprocal transplants, hybridization experiments and surveys of molecular markers and population densities on a range of scales.

Heredity (2007) **99**, 301–312; doi:10.1038/sj.hdy.6800997; published online 4 July 2007

Keywords: hybrid zone; introgression; hybridization; non-equilibrium; invasion; extinction

Introduction

Hybrid zones occur when the geographic ranges of closely related taxa meet and cross-fertilize to produce hybrids (Barton and Hewitt, 1985, 1989; Harrison, 1993). Such zones have been found in a wide range of both animal and plant groups, and in terrestrial, marine and freshwater systems. They provide 'natural laboratories' for evolutionary biologists investigating the formation (Hewitt, 1988; Howard, 1993; Moore and Price, 1993; Cain *et al.*, 1999; Marshall *et al.*, 2002; Campbell, 2004) and maintenance (Rieseberg and Buerkle, 2002; Lexer *et al.*, 2004) of species differences. Characterization of their spatio-temporal dynamics is essential to such studies, and the movement of a hybrid zone on an ecological time-scale can radically alter evolutionary outcomes.

Case studies of the geographical movement of hybrid zones also provide empirical evidence for conservation biologists investigating the dynamics of species invasions (Endler, 1977; Ellstrand, 1992; Rhymer and Simberloff, 1996; Wolf *et al.*, 2001). Assessing hypotheses of the causes and consequences of hybrid zone movement is critical if their long-term fate, the extinction of one taxon, is to be averted (Ellstrand, 1992; Rhymer and Simberloff, 1996); many threatened species owe their demise at least in part to hybridization with invading relatives (Levin

et al., 1996; Haig, 1998; Allendorf *et al.*, 2001; Wolf *et al.*, 2001; Allendorf and Lundquist, 2003).

A good understanding of the basis for the spatio-temporal dynamics of hybrid zones has been developed from theoretical principles, informed by a number of empirical studies. This initially took place in the context of two evolutionary hypotheses: stasipatric speciation, in which a new chromosomal rearrangement spreads at the expense of parental forms (Key, 1968; White, 1968, 1978), and phase III of Wright's shifting balance model, in which a new adaptive peak spreads to other populations (Wright, 1977, 1982; Barton, 1992; Kondrashov, 1992). The widespread occurrence of natural hybrid zones, the taxonomic questions they pose and the opportunities they present for investigating processes of species isolation make them a research field in their own right (Barton and Hewitt, 1985).

It is recognized that hybrid zones vary greatly in their structures depending on the degree of genetic and ecological differentiation between the two meeting taxa, their rates of dispersal and the fitness of their hybrid offspring (Harrison, 1993). Conditions for movement depend upon these factors. When hybrids have greater fitness than parental taxa, a hybrid zone will be stable if the hybrid's fitness is bounded. In an 'ecotonal' zone, this is in an environment intermediate to that occupied by the parental taxa (Moore, 1977; Moore and Price, 1993; Good *et al.*, 2000). If not thus bounded, the hybrid may expand its range at the expense of parental ranges. Unidirectional expansion might occur if one parental form is of lower fitness than the other and out-competed. Movement in favour of one parental form might appear to occur if hybridization is asymmetric and repeated backcrossing of hybrids with that parental form leads

Correspondence: Dr RJA Buggs, Department of Botany, University of Florida, 220 Bartram Hall, PO Box 118526, Gainesville, FL 32611 USA, E-mail: buggs@ufl.edu

Received 23 February 2007; revised 11 April 2007; accepted 16 April 2007; published online 4 July 2007

to the advance of a hybrid much more closely related to that form. Where hybrids are fitter than their parents, pre-zygotic reproductive isolation is unlikely to evolve, so the only way in which the hybrid zone can cease to exist is by the prevalence of one genotype (Paterson, 1978; Liou and Price, 1994).

When hybrids are of lower fitness than parents, a hybrid zone is usually known as a 'tension zone' (Key, 1968; Barton, 1979; Barton and Hewitt, 1985). The low fitness of hybrids causes spatial mixing of the parental taxa to be minimized, leading to narrow, straight hybrid zones (Key, 1968; Barton, 1979; Barton and Hewitt, 1985). Hewitt (1975) and Endler (1977) suggested, and Barton (1979) showed that tension zones can move due to gradients of population density or asymmetry of hybridization between the parental taxa. Differential adaptation of the parents may also cause movement (Key, 1968; Barton and Hewitt, 1985). However, Barton and Hewitt (1985) argued that tension zones will be stable in troughs of low population density and these would be frequent and deep enough to resist movement due to fitness differences or asymmetry of hybridization. This is one reason for scepticism of models of speciation involving hybrid zone movement (Barton and Hewitt, 1981).

Two further causes of hybrid zone movement can be hypothesized. 'Dominance drive' could occur where a dominant allele displaces a recessive allele (Moran, 1981; Mallet, 1986). Climate change could also play a role as it has been implicated in the movement of species range boundaries generally (Parmesan, 1999; Thomas and Lennon, 1999) and the movement of a (non-hybrid) contact zone between red and arctic foxes (Hersteinsson and MacDonald, 1992).

The considerations above predict that hybrid zones can move under a variety of circumstances. However, such movements may be difficult to find in the present because long-term studies, which might detect gradual movements or rare episodes of rapid movement halted by frequent barriers, are rare (Harrison, 1990; Hairston *et al.*, 1992). In 1985, 14 hybrid zones in the literature could be categorized (five of them tentatively) with respect to their geographical stability and of these, five appeared to be unstable (Barton and Hewitt, 1985). Over the last 20 years, more empirical cases have been observed where a hybrid zone appears to be moving. In addition, development and widespread use of molecular markers in ecological studies has greatly increased our knowledge of genetic patterns at a number of hybrid zones. These patterns are sometimes interpreted in terms of zone movement. Current empirical knowledge of hybrid zone movement is reviewed below with discussion of the strengths and weaknesses of the different lines of evidence. This permits assessment of the factors that are driving movement of hybrid zones in nature.

Identifying hybrid zone movement

Observation over time

Observation of hybrid zones over multiple years is the most reliable method of detecting their movement, and such evidence has been found in several genera of both animals and plants. Twenty-three of the clearest exam-

ples are documented in Table 1. The precise nature of the evidence available in each case differs. The best documented have been subject to long-term studies by single research groups. For example, morphological surveys were carried out twice annually for 18 years over a zone between salamanders *Plethodon glutinosus* and *Plethodon jordani* (Hairston *et al.*, 1992), and annually for 17 years between ticks *Aponomma hydrosauri* and *Aponomma limbatum* (Bull and Burzacott, 2001). Fourteen annual isozyme surveys were conducted on a hybrid zone between crickets *Allonemobius socius* and *Allonemobius fasciatus* (Britch *et al.*, 2001). Such long-term studies are difficult to sustain and in most cases in Table 1 evidence is only available for two or three time points, based on historical evidence.

Information on the position of hybrid zones in the past may be provided by records of an alien introduction (for example, *Solenopsis*, *Orchelimum*, *Orconectes*, *Cervus* and *Pseudorasbora* hybrid zones in Table 1), by historical surveys (for example, *Poecile*, *Hippolais*, *Vermivora*, *Corvus*, *Sceloporus* and *Mercurialis* hybrid zones in Table 1), and by museum or herbarium collections (for example, *Quiscalus* hybrid zone in Table 1). Issues of reliability may accompany such historical evidence and researchers occasionally question the data collected by others (Woodruff, 1981). There is sometimes a lack of precision in details of times and locations, as shown by uncertainties indicated for some of the figures in Table 1. However, there are few reasons to suppose that field naturalists of the past were systematically less reliable than those of today, and there is potential for more widespread use of historical collections in tracing past ecological changes (Sparks, 2007).

Replication in space

Comparative studies in space (as well as time) may be useful in drawing inferences about zone movement. In three of the observed cases of hybrid zone movement in Table 1 (*Plethodon*, *Mercurialis* and *Allonemobius*), researchers have examined more than one replicate area of hybrid zone. In each of these cases, the different areas appear to vary in the speed or direction of putative zone movement, cautioning against the drawing of general conclusions from a single transect. Comparisons of two areas where direction or speed of movement appears to differ may help in the identification of factors governing zone movement; for example, in the case of *Mercurialis annua*, the two hybrid zones differ in the sexual system and population density of the hexaploid plants.

Relictual populations

Current patterns of distribution have sometimes been used to draw inferences of past hybrid zone movement. Where relictual populations of one taxon occur in isolated areas within the range of another, it has been invoked as evidence to assess hybrid zone movement in *Mus musculus* (Barton and Hewitt, 1981), *M. annua* (Buggs and Pannell, 2006) and *Limnodynastes tasmaniensis* (Littlejohn and Roberts, 1975). Such patterns can provide useful corroboration for other evidence, but might also be explained by long-range dispersal events.

Table 1 Observed cases of hybrid zone movement

Species (advancing taxa first)	Location	Evidence	Movement (km)	Time (year)	Hybrid fitness	Possible mechanism	References
<i>Plethodon glutinosus</i> – <i>Plethodon jordani</i> (salamanders)	North Carolina	Thirty-six surveys of colour pattern composition	~0.4	18	H?	Human disturbance; superiority of <i>P. glutinosus</i> ?	Hairston <i>et al.</i> (1992)
<i>Aponomma hydrosauri</i> – <i>Aponomma limbatum</i> (Ticks)	S. Australia	Annual morphological surveys	1–2	17	L	Environmental change; differential adaptation	Bull and Burzacott (2001)
<i>Allonemobius socius</i> – <i>Allonemobius fasciatus</i> (crickets)	Appalachian mountains	Annual isozyme surveys	Frequency shift over 300 km wide mosaic	14	Variable	Climate change	Britch <i>et al.</i> (2001)
<i>Solenopsis invicta</i> – <i>Solenopsis richteri</i> (fire ants)	N. America	Surveys after alien introduction; distribution of RAPD markers and cytoplasmic elements	~350	<60	?	Higher fitness of <i>S. invicta</i> , sex differences in migration or selection	Shoemaker <i>et al.</i> (1994, 1996, 2000), Goodisman <i>et al.</i> (1998)
<i>Orchelimum nigripes</i> – <i>Orchelimum pulchellum</i> (katydids)	Potomac River, E. USA	Survey after alien introduction	>25	<100	L	Mate preference	Shapiro (1998, 2000, 2001), Cabrero <i>et al.</i> (1999)
<i>Orconectes rusticus</i> – <i>Orconectes propinquus</i> (crayfish)	Northern Wisconsin lake	Survey after alien introduction; patterns of cytonuclear disequilibrium	~6.3	9	H	Skewed sex ratios	Perry <i>et al.</i> (2001)
<i>Cervus nippon nippon</i> – <i>Cervus elaphus</i> (deer)	Scotland	Surveys after alien introduction; isozymes, microsatellite markers and mtDNA RFLPs	?	~80	=?	Assortative mating, selective advantage of <i>C. n. nippon</i> genotype	Abernethy (1994), Goodman <i>et al.</i> (1999)
<i>Pseudorasbora parva</i> – <i>Pseudorasbora pumila</i> (minnows)	E. Japan	Surveys after alien introduction; 5-year allozyme study and mtDNA survey	?	~30	L	Assortative mating; male–male competition	Konishi and Takata (2003, 2004a, b)
<i>Poecile carolinensis</i> – <i>Poecile atricapillus</i> (chickadees)	Ohio	Three morphological surveys	100	60	L	Male intrasexual dominance or female preference	Bronson <i>et al.</i> (2003a, b), Woodcock <i>et al.</i> (2005), Reudink <i>et al.</i> (2006)
<i>Hippolais polyglotta</i> – <i>Hippolais icterina</i> (warblers)	Western Europe	Three morphological surveys	60–240	70	?	Cross-species learning of song parameters; differential parasite infestation	Faivre (1993), Yeatman-Berthelot and Jarry (1994), Secondi <i>et al.</i> (2003), Reullier <i>et al.</i> (2006)
<i>Vermivora pinus</i> – <i>Vermivora chrysoptera</i> (warblers)	E. N. America	Morphological surveys, patterns of mtDNA distribution	‘Substantial’	~100	?	Mate choice and habitat preference?	Remington (1968), Gill (1997), Shapiro <i>et al.</i> (2004), Dabrowski <i>et al.</i> (2005)
<i>Corvus corone corone</i> – <i>Corvus corone cornix</i> (crows)	Denmark and Germany	Two morphological surveys	19	78	?	<i>C. c. corone</i> more aggressive	Saino and Scatizzi (1991), Rolando and Giachello (1992), Haas and Brodin (2005)
<i>Sceloporus tristichus</i> – <i>Sceloporus cowlesi</i> (lizards)	Arizona	Two chromosome polymorphism surveys	>1.5	~30	?	Overgrazing	Leaché and Cole (2007)
<i>Mercurialis annua</i> diploid–hexaploid (mercuries)	Spain	mtDNA introgression	>8	?	L	Pollen swamping due to sexual system and higher fitness of diploids	Buggs and Pannell (2006, 2007), Dorken and Pannell (2007)
<i>Quiscalus quisculus quiscula</i> – <i>Quiscalus quisculus versicolor</i> (grackles)	Louisiana	Two morphological/cytological surveys	80/200	40	L?	High dispersal ability of species suggests selection is maintaining narrow hybrid zone	Yang and Selander (1968), Moore and Dolbeer (1989)
<i>Pseudophryne bibroni</i> – <i>Pseudophryne semiarimorata</i> (frogs)	S. Australia	Morphological variation of collected specimens	32	~30	L?		Woodruff (1972), McDonnell <i>et al.</i> (1978),
		Five surveys of colour pattern composition; introgression of isozyme marker	<20 (colour pattern)	15	L		Woodruff (1981)
			<75 (isozyme introgression)	?			

Table 1 Continued

Species (advancing taxa first)	Location	Evidence	Movement (km)	Time (year)	Hybrid fitness	Possible mechanism	References
<i>Triturus cristatus</i> – <i>Triturus marmoratus</i> (newts)	France	Two morphological surveys; one allozyme and mtDNA survey	>30	~30	L	Asymmetric mate choice?	Arntzen and Wallis (1991)
<i>Limnaporus dissortis</i> – <i>Limnaporus notabilis</i> (waterstriders)	SW Canada	Two morphological surveys	<10?	~13	=	Almost all hybrids are males, and <i>L. notabilis</i> females prefer <i>L. dissortis</i> or hybrid males	Spence (1990), Sperling and Spence (1991), Klingenberg <i>et al.</i> (2000)
<i>Heliconius erato hydarana</i> (butterflies)	Panama	Two morphological surveys	47	17	L?	Dominance drive; selection by predators	Blum (2002)
<i>Heliconius erato petiverana</i> (butterflies)	Panama	≥4 wing pattern surveys; 1 allozyme survey; 2 mtDNA surveys	50	20	L	Competitive exclusion; deforestation	Dasmahapatra <i>et al.</i> (2002)
<i>Anartia fatima</i> – <i>Anartia amathea</i> (butterflies)	Panama	Two morphological surveys	0.7–0.9	5	?	Competitive superiority of <i>G. aurei</i>	Hafner <i>et al.</i> (1998)
<i>Geomys aeneus</i> – <i>Geomys doerrii</i> (rodents)	New Mexico	Two morphological surveys	≥30	≤12	?	Agricultural activity modifying habitat	Hillis and Simmons (1986)
<i>Pholidobolus montium</i> – <i>Pholidobolus affinis</i> (lizards)	Ecuador	Two morphological surveys	<0.35	55	L	Human disturbance favouring <i>H. annuus</i> ; differential adaptation	Carney <i>et al.</i> (2000)
<i>Helianthus annuus</i> – <i>Helianthus bolanderi</i> (sunflowers)	California	Three morphological surveys					

Hybrid fitness: L, lower than parents; H, higher than parents.

Patterns of molecular markers

Patterns of molecular markers have been hypothesized to provide a signature of hybrid zone movement: a moving zone will leave in its wake a tail of clines of unlinked neutral markers, 'the hybrid zone will thus appear to be asymmetrical with apparent unidirectional introgression across the zone' (Moran, 1981, p 71). Recent modelling has shown that even limited hybridization between two taxa can result in substantial introgression, when one is competitively displacing the other (Currat and Excoffier, 2005). However, these patterns are hard to interpret, as they might also be evidence for introgression of advantageous alleles away from a static hybrid zone due to selection (Moran, 1981). Where a mitochondrial or chloroplast marker has introgressed, cytoplasmic nuclear interactions or selection for nuclear but not cytoplasmic genes may play a role (Rieseberg and Soltis, 1991). Barton and Hewitt (1985) suggested that marker evidence was most unequivocal when many neutral alleles introgressed, all in the same direction. In some of the hybrid zones listed in Table 1, patterns of introgression have been studied, apparently confirming the possible value of introgressed markers in detecting hybrid zone movement.

In the case of the hybrid zone between the birds *Quiscalus quisculus quiscula* and *Quiscalus quisculus versicolor*, populations of the former are only slightly introgressed with genes from the latter, whereas those of the latter are heavily introgressed with genes from *Q. q. versicolor*. This is as we would expect given that *Q. q. quiscula* is advancing (Yang and Selander, 1968). At the frog *Pseudophryne bibroni*–*Pseudophryne semiarmorata* hybrid zone, a tail of asymmetric introgression of an *Ldh* isozyme marker diagnostic of *P. semiarmorata* populations into *P. bibroni* populations to the north of the hybrid zone also fits with the observed zone movement in favour of *P. bibroni* (McDonnell *et al.*, 1978). A hybrid zone between lizards *Sceloporus tristichus* and *Sceloporus cowlesi* has moved over 1.5 km in around 30 years in favour of the former; correspondingly, *S. cowlesi* mitochondrial DNA is found introgressed over 8 km into the current range of *S. tristichus* (Leaché and Cole, 2007). Introgression between newts *Triturus cristatus* and *Triturus marmoratus* is found in the area of recent species replacement, but is absent in other areas (Arntzen and Wallis, 1991). At a hybrid zone between two warbler species, predominantly *Vermivora chrysoptera* mtDNA haplotypes are found in hybrids at the leading edge of a *Vermivora pinus* expansion (Dabrowski *et al.*, 2005) and cytonuclear disequilibrium is also found at a crayfish *Orconectes rustica*–*Orconectes propinquus* hybrid zone. Two studies of deer, *Cervus elaphus* and alien *Cervus nippon nippon*, show introgression in both taxa (Abernethy, 1994; Goodman *et al.*, 1999), but the expanding alien taxon shows higher levels of introgression which are uniform across its range, while introgression is lower in *C. elaphus* and more common near the region of overlap (Goodman *et al.*, 1999).

Interpretation of introgression in terms of hybrid zone movement has consistently generated controversy. Moran's paper (1981) suggesting the idea contained eight possible examples, only two of which had been identified as such by the original investigators. In three of the cases above, where historical observation appears to confirm evidence for movement from genetic markers, alternative

explanations have still been suggested. In the case of *P. bibroni* and *P. semiarmorata*, Woodruff (1981) questioned the colour pattern data of McDonnell *et al.* (1978) and suggested that the distribution of the *Ldh* marker might be a northward introgression due to *P. semiarmorata* male dominance. It has been suggested that the pattern of introgression in *Cervus* could be due to hybridization far into the *C. nippon nippon* range, or an ancestral polymorphism (Goodman *et al.*, 1999). Given the difficulty of interpreting marker evidence in cases like the above, where historical evidence is available, caution is needed in drawing conclusions from genetic marker evidence alone.

Several recent examples of hybrid zones in the literature show patterns of markers that have been discussed by investigators in terms of hybrid zone movement, where confirmatory historical observation does not appear to be available. In some of these cases, factors have been observed which are likely to promote movement. Below, I describe three well-studied cases where zone movement has been postulated and discuss the difficulties involved in interpreting the evidence, then list 13 other possible cases. Details of these 16 hybrid zones can be found in Supplementary Table 1.

A sharp hybrid zone north of Brisbane between 'Moreton' and 'Torresian' chromosomal races of the grasshopper *Caledia captiva* appears to be a tension zone, but 'Moreton' rDNA and mtDNA extend up to 450 km north into the 'Torresian' regions (Shaw and Wilkinson, 1980; Arnold *et al.*, 1987; Marchant, 1988; Marchant *et al.*, 1988; Shaw *et al.*, 1993). While this asymmetrical introgression could be due to selective incorporation of 'Moreton' genes at the hybrid zone, a balance of evidence points to the markers being neutral, and the introgressed genes being the result of southward hybrid zone movement in favour of the 'Torresian' race (Marchant, 1988; Marchant *et al.*, 1988; Shaw *et al.*, 1993) and biased gene conversion (Arnold *et al.*, 1988). Short-term studies of the hybrid zone's dynamics have not shown ongoing movement. Over a 6-year period, the zone appeared to be in stasis (Shaw *et al.*, 1985), and in a 4-year study of four allozyme markers there was a 200 m shift northwards towards an area of reduced gene flow (Kohlmann and Shaw, 1991). It is suggested that the past southward movement was due to climate change (Shaw *et al.*, 1990).

Complex patterns of molecular markers are found in the plant species *Piriqueta caroliniana* in Florida, at a hybrid zone between morphotypes: *caroliniana* (to the north) and *viridis* (to the south). Sharp clines in *caroliniana* markers occur over an ~100-km wide zone, coincident with high levels of gametic disequilibrium indicating ongoing hybridization. Introgression of *viridis* traits is found to the north of this area, extending ~300 km into the *caroliniana* range. To the south, almost all *viridis* populations contain low frequencies of markers associated with *caroliniana*. It is proposed that this pattern has emerged due to the arrival of the *viridis* morphotype in southern Florida since the last Pleistocene glaciation (Maskas and Cruzan, 2000). The sharp clines are thought to indicate a tension zone (Cruzan, 2005). Presence of *caroliniana* alleles in the *viridis* populations (Martin and Cruzan, 1999; Cruzan, 2005) is thought to be due to northwards movement of the tension zone and presence of *viridis* alleles in the *caroliniana* range (Martin

and Cruzan, 1999) due to selective introgression north of the tension zone (Cruzan, 2005). However, to illustrate the ambiguity of introgression data even in such a well-studied system as this, the data might hypothetically also be interpreted in terms of a southward movement of a contact zone initially established in northern Florida. The widespread *viridis* markers to the north of the sharp cline could be due to genetic assimilation by invading *caroliniana* morphotypes. This scenario incorporates two factors: first, a lack of disequilibria among diagnostic genetic markers in the northern hybrid populations, which suggests that introgression of *viridis* alleles into *caroliniana* morphotypes has slowed or stopped (Cruzan, 2005); and second, asymmetric hybridization in favour of the *caroliniana* morphotype in experimental studies (Wang and Cruzan, 1998).

Mouse subspecies *Mus musculus musculus* and *Mus musculus domesticus* meet at a hybrid zone stretching across Europe. Mitochondrial DNA introgression has been studied at five widely spaced transects. In three of these, introgression of *domesticus* mtDNA was found in *musculus* populations, and in two, introgression of *musculus* mtDNA was found in *domesticus* populations (Božíková *et al.*, 2005 and references therein). A study of ten allozyme loci showed asymmetry always in the direction of *domesticus* into *musculus* (Raufaste *et al.*, 2005). Several studies have found that *musculus* females prefer *musculus* males, but *domesticus* females display no breeding preference (Smadja and Ganem, 2002; Smadja *et al.*, 2004; Bimova *et al.*, 2005; Ganem *et al.*, 2005). Hybrids appear to be of low fitness (Britton-Davidian *et al.*, 2005). The hypothesis that the zone could be moving in favour of *musculus*, leaving a trail of *domesticus* markers, was discussed 25 years ago but rejected as the zone appears to have been stable from 1960 to 1980 and the distribution of the subspecies on islands close to the mainland suggest movement in the opposite direction (Barton and Hewitt, 1981). More recently this hypothesis has been raised again (Smadja *et al.*, 2004; Raufaste *et al.*, 2005).

In a further 13 hybrid zones, patterns of introgression might be interpreted as evidence for movement: gulls *Larus glaucescens* and *Larus occidentalis* (Bell, 1996; Gay, 2006); pocket gophers *Thomomys townsendii* and *Thomomys bottae* (Patton, 1993; Patton and Smith, 1993); *Thomomys bottae actuosus* and *Thomomys bottae ruidosae* (Ruedi *et al.*, 1997); fish *Gambusia affinis* and *Gambusia holbrooki* (Reznick, 1981; Scribner, 1993; Scribner and Avise, 1993; Scribner and Avise, 1994a,b); hares *Lepus granatensis*/*Lepus europaeus* and *Lepus timidus* (Thulin and Tegelström, 2002; Melo-Ferreira *et al.*, 2005, 2007); salamander *Chioglossa lusitanica* North and South forms (Sequeira *et al.*, 2005); mussels *Mytilus galloprovincialis* and *Mytilus edulis* (Gardner and Skibinski, 1988; Skibinski and Roderick, 1991; Willis and Skibinski, 1992; Gardner *et al.*, 1993; Wilhelm and Hilbish, 1998; Bierne *et al.*, 2003); beetles *Carabus albrecti* and *Carabus lewisianus* (Takami and Suzuki, 2005); lizard *Sceloporus grammicus* chromosomal races F5 and FM2 (Sites *et al.*, 1996; Marshall and Sites, 2001); warblers *Dendroica townsendii* and *Dendroica occidentalis* (Pearson, 2000; Pearson and Rohwer, 2000; Rohwer *et al.*, 2001; Owen-Ashley and Butler, 2004); plants *Iris innominata* and *Iris douglasiana* (Lenz, 1959; Young, 1996); plants *Ipomopsis aggregata* and *Ipomopsis tenuituba* (Wu and Campbell, 2005);

cottonwoods *Populus angustifolia* and *Populus fremontii* (Keim *et al.*, 1989; Paige *et al.*, 1991; Martinsen *et al.*, 2001).

In some of these, patterns of introgression are accompanied by a putative mechanism (see column 4 in Supplementary Table 1) known to drive hybrid zone movement in other systems (see next section). For example, there is evidence that asymmetrical hybridization may be occurring in eight of the hybrid zones as shown in Supplementary Table 1. When two lines of evidence concur in this way, it seems reasonable to take zone movement as a working hypothesis. Controversy arises because different researchers have different expectations and place more weight on different lines of evidence. Some, like Dasmahapatra *et al.* (2002) set out to look for introgression of neutral markers to test the hypothesis that a zone is moving. Others, such as Gay (2006) find concordant asymmetric introgression at multiple neutral loci but suggest movement in the same direction as the neutral markers due to other lines of evidence such as the distribution of morphological intermediates. Patterns of markers can provide useful information and it is advantageous that data suggesting zone movement can be collected at a single time point by one research group. However, interpretation is difficult and the conclusions drawn may be less reliable than historic observational data.

Identifying causes of hybrid zone movement

As described in Introduction, multiple factors may in theory be implicated in causing hybrid zone movement. The number of empirical studies of moving hybrid zones now available allows some assessment of these factors in nature. The discussion below will mainly draw on studies where there is some observational evidence for movement (Table 1).

In several of these examples, the fitness of hybrids has been assessed: 11 appear to involve hybrids of low fitness, and 3 involve hybrids of equal or greater fitness than their parents. The higher number of zones with low fitness hybrids may reflect a greater propensity of such zones to move, although the observational evidence may be biased because tension zones are easier to detect empirically due to a sharp boundary.

Asymmetrical crossing appears to be playing a role in the movement of zones with both high and low fitness hybrids. In a hybrid zone between chickadees *Poecile atricapillus* and *Poecile carolinensis*, dominance of *P. carolinensis* males, or their preference by *P. atricapillus* females may aid the zone's movement in favour of *P. carolinensis* (Bronson *et al.*, 2003b; Woodcock *et al.*, 2005; Reudink *et al.*, 2006). Katydid *Orchelimum nigripes* females show a conspecific mate preference, whereas *O. pulchellum* females show no clear preference; this may cause movement in favour of *O. nigripes* (Shapiro, 2001). Waterstrider *Limnoporus notabilis* females prefer *Limnoporus dissortis* and hybrid males, giving movement in favour of *L. dissortis* (Spence, 1990; Sperling and Spence, 1991; Klingenberg *et al.*, 2000). In a 5-year allozyme study, all hybrids between the minnows *Pseudorasbora pumila* and *Pseudorasbora parva* have *P. pumila* mtDNA suggesting that this tension zone moves in favour of *P. parva* due to asymmetrical hybridization (Konishi and Takata, 2004a). Sexual system differences between diploid

and hexaploid plants of *M. annua* cause asymmetrical hybridization at their hybrid zone and movement in favour of the diploid (Buggs and Pannell, 2006). Asymmetrical hybridization is suggested in a hybrid zone between butterflies *Anartia fatima* and *Anartia amathea* by deviations from Hardy–Weinberg and linkage disequilibria (Dasmahapatra *et al.*, 2002). These recent findings suggesting a role for asymmetrical hybridization in hybrid zone movement fit well with the predictions of Hewitt (1975), Endler (1977) and Barton (1979).

The apparent role of asymmetrical hybridization in the above moving hybrid zones suggests that movement may well have occurred in the eight hybrid zones as shown in Supplementary Table 1 where such asymmetries occur. Researchers have also discussed the possibility of hybrid zone movement solely on the basis of evidence for asymmetrical hybridization in the species *Eucalyptus risdonii* and *Eucalyptus amygdalina* (Potts, 1986; Potts and Reid, 1985) and *Chorthippus parallelus parallelus* and *Chorthippus parallelus erythropus* (Bella *et al.*, 1992). However, this evidence is not compelling in isolation, as the effect of asymmetric hybridization may be countered by other factors (Barton and Hewitt, 1985).

A role for ecological differentiation between taxa, on which natural selection acts, has been suggested in driving the movement of several of the zones as shown in Table 1, with both high and low hybrid fitness. The most reliable indicator of natural selection at hybrid zones is by reciprocal transplant experiments. These have been used in the case of *M. annua*, where the advancing diploid plants were found to be fitter than the hexaploids in all environments used (Buggs and Pannell, 2007). In other zones, selection has been inferred from observational evidence. The rate of spread of salamanders *P. glutinosus* into the range of *P. jordani* appears too great to be explained by random diffusion, suggesting selection for *P. glutinosus* characters (Hairston *et al.*, 1992). *Heliconius erato hydra* butterflies appear to have a slight advantage over *Heliconius erato petiverana* and selection by predators has been inferred (Blum, 2002). A competitive advantage for the advancing taxon has also been inferred in the movement of hybrid zones between: chickadees *P. atricapillus* and *P. carolinensis* (Bronson *et al.*, 2003b; Woodcock *et al.*, 2005; Reudink *et al.*, 2006), butterflies *A. fatima* and *A. amathea* (Dasmahapatra *et al.*, 2002), lice species *Geomydoecus aurei* and *Geomydoecus centralis* (Hafner *et al.*, 1998), and crows *Corvus corone* and *Corvus corone corone* (Saino and Scatizzi, 1991; Rolando and Giachello, 1992). Differential parasite infestation may play a role in a hybrid zone of warblers *Hippolais polyglotta* and *Hippolais icterina* (Reullier *et al.*, 2006). A strong role for ecological differentiation and natural selection at moving hybrid zones would uphold predictions made by Key (1968), but more experimental evidence is needed in several of the cases above. Also, selection may be slowing some moving hybrid zones: estimates of dispersal in the grackle *Quiscalus quisqualis* suggest that it can occur at 100 km per year, and the much slower movement of the narrow *Q. q. versicolor*–*Q. q. quiscula* hybrid zone has been interpreted as indicating a role for stabilizing selection (Moore and Dolbeer, 1989); and the cricket *A. fasciatus*–*A. socius* hybrid zone appears to be maintained partly by differential adaptation (Howard and Waring, 1991; Britch *et al.*, 2001).

Dominance drive may be assisting the movement of a hybrid zone between butterflies *H. e. hyddara* and *H. e. petiverana*, as the dominant black hindwing allele spreads and replaces the recessive yellow bar allele (Mallet, 1986; Mallet and Barton, 1989; Blum, 2002). The observed rate of movement fits very well with the theoretical expectation (Blum, 2002).

A direct effect of environmental change has been invoked in explaining the movement of five zones. Increased rainfall may have favoured tick species *A. hydrosauri* at a hybrid zone with *A. limbatum* (Bull and Burzacott, 2001) and climate fluctuations may have caused movement in a *T. b. actuosus*–*T. b. ruidosae* hybrid zone (Ruedi *et al.*, 1997). Human-induced climate change appears to have caused movement of the *Pholidobolus montium*–*Pholidobolus affinis* (lizards) hybrid zone, when fields which had been rocky with numerous agaves were cleared of rocks, irrigated and planted with crops (Hillis and Simmons, 1986), and hybridization between salamanders *P. jordani* and *P. glutinosus* may have increased due to intense timbering (Hairston *et al.*, 1992). Ecological changes due to overgrazing may have caused movement in a hybrid zone between lizards *S. cowlesi* and *S. tristichus* (Leaché and Cole, 2007). Global warming was tentatively invoked to explain the movement of a hybrid zone between crickets *A. fasciatus* and *A. socius* (Britch *et al.*, 2001).

Few empirical studies have measured population density in the context of hybrid zone movement. In the case of the diploid–hexaploid hybrid zone in *M. annua*, hexaploid populations were found to be smaller and more scattered than diploid populations (Eppley and Pannell, 2007). This may fit Barton and Hewitt's (1985) prediction that a tension zone will move down a density gradient, although adaptation of the hexaploids sexual system to its population structure may be slowing the movement of the zone (Dorken and Pannell, 2007). It is possible that differences in population density are a proximate cause of some hybrid zone movements, attributed to ecological differentiation or climate change above. More studies are needed that measure this attribute.

Discussion

In 1985, Barton and Hewitt found five hybrid zones in the literature that appeared to be unstable. Publications since then allow a review of 23 hybrid zones in diverse groups that have compelling historical evidence for movement and a further 16 with possible evidence from patterns of molecular markers. This suggests that movement of hybrid zones in the present and recent past could be a widespread phenomenon, deserving more attention in ecological and evolutionary studies. Thus far, empirical approaches have been somewhat disparate. This is to some extent inevitable due to the different types of historical evidence available, and the diversity of taxonomic groups studied, but there is a need for long-term, structured surveys that trace the dynamics of hybrid zones over several decades.

Interpreting patterns of molecular markers

Growth in the use of molecular markers in assessing hybrid zone movement is an exciting development, but caution is needed in its interpretation. This review

identifies 16 studies in animals and plants where patterns of molecular markers might be understood in terms of movement in the absence of firm historical evidence. Barton and Hewitt's (1985) suggestion that marker evidence was most unequivocal when many neutral alleles introgressed in the same direction deserves to be better known, and could prevent some misleading conclusions. However, the patterns in some natural zones are complex, with different markers introgressing in different directions. Sometimes, further light may be shed by comparative studies in space, or locally at different scales, but only repeated sampling over time and use of historical evidence, and manipulative experiments on the processes acting in the hybrid zone can resolve dynamics precisely.

Most of the moving hybrid zones reviewed here are between two taxa with well-defined differences that give rise to well-demarcated hybrid zones. A wide range of related situations may arise where a hybrid zone is harder to define. In some natural zones, different phenotypic characters or regions of the genome may show contrasting spatial patterns and it may be difficult to define a single current hybrid zone location about which introgression may have occurred.

Evolutionary implications

Moving hybrid zones provide excellent examples of evolution in action, but much work is needed to characterize the processes responsible for their dynamics. A wide range of both natural and human-induced processes appear to have been involved and no single factor has a universal dominant effect in all zones. When examined, multiple causes are often shown to be involved within a single zone, but few empirical studies have thus far systematically disentangled them. Our knowledge of the interplay of factors is limited and there is a general lack of empirical data on some crucial factors, such as local adaptation and population density. Ideally, long-term, quantitative experimental studies of hybrid zones are needed that incorporate reciprocal transplants (to test hypotheses of local adaptation), hybridization experiments (to test the fitness of hybrids and asymmetries in hybridization dynamics) and regular surveys of population density and molecular and morphological markers at a range of scales.

The study of hybrid zone movement has survived related controversies over stasipatric speciation (Rieseberg, 2001; Navarro and Barton, 2003) and Wright's shifting balance (Coyne *et al.*, 1997, 2000) hypotheses. Most zones discussed here appear to be secondary and so do not necessarily provide support for these hypotheses. The study on the *H. e. hyddara*–*H. e. petiverana* hybrid zone was recently discussed in terms of phase III of Wright's shifting balance model, but does not fully correspond to all the conditions (Blum, 2002). Hybrid zones have also been examined in search for evidence for reinforcement of reproductive isolation (Howard, 1993). In this context, asymmetry of hybridization has sometimes been interpreted as the ongoing evolution of new pre-zygotic reproductive barriers that could end in stable species coexistence. However, conditions for this to occur are stringent (Servedio and Kirkpatrick, 1997; Tiffin *et al.*, 2001) and asymmetry seems more likely to lead to hybrid zone movement and the elimination of one taxon.

Untested assumptions of hybrid zone stasis may lead to mistaken conclusions in evolutionary studies. This is most obviously the case for studies of introgressive hybridization, where failure to detect zone movement, if present, could result in the inference of selection for a gene which is in fact neutral. This could affect the use of hybrid zones as systems in which statistical analysis of genome scans can identify locus-specific selection (Rieseberg and Buerkle, 2002; Lexer *et al.*, 2004; Murray and Hare, 2006) when assumptions about the evolutionary equilibrium or otherwise of the zone affect the models used.

To what extent can recent movements in a hybrid zone be extrapolated to shed light on long-term patterns of migration or genetic exchange? When a currently moving zone shows a trail of introgression over a larger distance than the observed movement, researchers may infer that the movement can be to some extent extrapolated into the past (McDonnell *et al.*, 1978; Leaché and Cole, 2007). In some cases, the limits of the neutral introgression may indicate the location where the initial hybrid zone was formed, but little certainty can be placed on this inference unless multiple neutral markers show a concurrent limit when examined at a range of spatial scales. However, it is likely that many hybrid zones have undergone spatial fluctuations during their history, as illustrated by the case of *Caledia captiva*, where the recent movement of a hybrid zone is in a different direction to past movement inferred from molecular markers (Shaw *et al.*, 1985). Some indication of whether recent hybrid zone movements may be extrapolated into the past may be provided by assessment of the factors causing recent movement. Factors such as deforestation or overgrazing may have started recently, so recent movements will be atypical of the hybrid zone's history. On the other hand, a difference in sexual system between the hybridizing taxa may have a more ancient origin so that recent movements may be representative of those in the past. It is worth noting that it may be unwise to disregard records of movement from the recent past on the assumption that a hybrid zone is many thousands of years old, as the estimated age of a hybrid zone between *T. b. connectens* and *T. b. opulentus* was revised from 10 000 years to 50 years when flood records were examined (Hafner *et al.*, 1998). Overall, while studies of hybrid zone dynamics in the past few decades may help in the modelling of long-term phylogeographic patterns and genetic exchanges, they do not provide a panacea for the difficulties involved in reconstructing past events.

Hybrid zone movement could have the effect of accelerating the rate of evolution in the advancing taxon, in two ways. First, Klopstein *et al.* (2006) show in a simulation study that mutations occurring on the edge of a range expansion can 'surf' on the wave of advance and thus reach a larger spatial distribution and a higher frequency than would be expected in stationary populations. Second, hybrid zone movement may increase introgression of positively selected traits into the advancing taxon from the retreating relative. Traits under positive selection are known to be able to cross hybrid zones (Parsons *et al.*, 1993), and movement may decrease the threshold level of selection needed for introgression to occur (as witnessed by the introgression of neutral markers) and increase the rate at which it occurs. Increased rates of evolution might aid the advancing taxon in overcoming the home-range advantage of the retreating taxon.

Conservation implications

Hybrid zone movements are simultaneous invasions and extinctions, and at times conservation effort may be needed to protect one taxon. The studies above demonstrate some practical difficulties of detecting such movement. This contrasts to the comparative ease with which introgression—a consequence of hybridization which is a conservation concern in its own right (Rhymer and Simberloff, 1996)—may be detected using modern methods. This presents two potential pitfalls. First, if hybrids are of very low fitness, providing an impermeable barrier to gene flow, a survey at a single time point will appear to show the coexistence of two taxa, which have retained their genetic integrity; even if one taxon is being eliminated. Second, in a moving hybrid zone where barriers to gene flow are permeable, the effect of introgression will be most marked in the advancing taxon, with the declining taxon remaining genetically pure. Conservation effort focussed on preventing introgression could inadvertently protect the invading taxon, to the neglect of the declining taxon.

There is some evidence that 11 of the 39 cases of hybrid zone movement reviewed here are to some extent due to local human activity. Hybrid zones seem to have arisen by the human introduction of *C. nippon nippon*, *Solenopsis invicta*, *O. nigripes*, *Orconectes rusticus* and *P. parva* to alien environments. Local, short-term ecological changes to environments by humans via agriculture or forestry may have contributed to the movement of hybrid zones between *P. glutinosus* and *P. jordani*, *P. montium* and *P. affinis*, *L. glaucescens* and *L. o. occidentalis*, *Helianthus annuus* and *Helianthus bolanderi*, *A. fatima* and *A. amathea*, and *S. tristichus* and *S. cowlesi*.

Global warming has been suggested as a 'very preliminary hypothesis' as a cause for the movement of one transect in an *A. socius*–*A. fasciatus* hybrid zone in the recent past (Britch *et al.*, 2001). Past movements evidenced by introgression patterns in the *L. granatensis*–*L. europaeus* (Melo-Ferreira *et al.*, 2007), *T. b. actuosus*–*T. b. ruidosae* (Ruedi *et al.*, 1997) and *Caledia captiva* (Shaw *et al.*, 1993) hybrid zones have been attributed to Pleistocene climate changes. This suggests that hybrid zone movements could provide biological indicators of climate change, an application that could be of public interest in coming years. For a good understanding of where climate change is implicated, development is needed in both the quality and quantity of moving hybrid zone studies. More thorough characterization of hybrid zones than is currently available in many cases is needed, as many factors must be carefully disentangled before firm conclusions can be drawn about the causes of hybrid zone movement. Many studies are needed as multiple species must demonstrate a similar trend before climate change can be reliably identified as a causative factor (Parmesan and Yohe, 2003). At present there is little evidence that climate change is causing current hybrid zone movements, but this may owe more to our ignorance of the latter, rather than lack of the former.

Acknowledgements

I am grateful to JS Parker for first introducing me to moving hybrid zones. I thank JR Pannell, DE Soltis and two anonymous reviewers for helpful comments on earlier versions of this paper.

References

- Abernethy K (1994). The establishment of a hybrid zone between red and sika deer (genus *Cervus*). *Mol Ecol* 3: 551–562.
- Allendorf FW, Lundquist LL (2003). Introduction: population biology, evolution, and control of invasive species. *Conserv Biol* 17: 24–30.
- Allendorf FW, Leary RF, Spruell P, Wenburg JK (2001). The problems with hybrids: setting conservation guidelines. *Trends Ecol Evol* 16: 613–622.
- Arnold ML, Contreras N, Shaw DD (1988). Biased gene conversion and asymmetrical introgression between subspecies. *Chromosoma* 96: 368–371.
- Arnold ML, Shaw DD, Contreras N (1987). Ribosomal RNA-encoding DNA introgression across a narrow hybrid zone between two subspecies of grasshopper. *Proc Natl Acad Sci USA* 84: 3946–3950.
- Arntzen JW, Wallis GP (1991). Restricted gene flow in a moving hybrid zone of the newts *Triturus cristatus* and *T. marmoratus* in western France. *Evolution* 45: 805–826.
- Barton N (1979). The dynamics of hybrid zones. *Heredity* 43: 341–359.
- Barton N, Hewitt G (1981). Hybrid zones and speciation. In: Atchley WR, Woodruff DS (eds). *Evolution and Speciation*. Cambridge University Press: New York. pp 109–145.
- Barton NH (1992). On the spread of new gene combinations in the 3rd phase of Wright's shifting-balance. *Evolution* 46: 551–557.
- Barton NH, Hewitt GM (1985). Analysis of hybrid zones. *Annu Rev Ecol Syst* 16: 113–148.
- Barton NH, Hewitt GM (1989). Adaptation, speciation and hybrid zones. *Nature* 341: 497–503.
- Bell D (1996). Genetic differentiation, geographic variation and hybridization in gulls of the *Larus glaucescens-occidentalis* complex. *Condor* 98: 527–546.
- Bella JL, Butlin RK, Ferris C, Hewitt GM (1992). Asymmetrical homogamy and unequal sex ratio from reciprocal mating-order crosses between *Chortippus parallelus* subspecies. *Heredity* 68: 345–352.
- Bierne N, Borsa P, Daguin C, Jollivet D, Viard F, Bonhomme F et al. (2003). Introgression patterns in the mosaic hybrid zone between *Mytilus edulis* and *M. galloprovincialis*. *Mol Ecol* 12: 447–461.
- Bimova B, Karn R, Pialek J (2005). The role of salivary androgen-binding protein in reproductive isolation between two subspecies of house mouse: *Mus musculus musculus* and *Mus musculus domesticus*. *Biol J Linn Soc* 84: 349–361.
- Blum MJ (2002). Rapid movement of a *Heliconius* hybrid zone: evidence for phase III of Wright's shifting balance theory? *Evolution* 56: 1992–1998.
- Božiková E, Munchlinger P, Teeter KC, Tucker PK, Macholán M, Pialek J (2005). Mitochondrial DNA in the hybrid zone between *Mus musculus musculus* and *Mus musculus domesticus*: a comparison of two transects. *Biol J Linn Soc* 84: 363–378.
- Britch SC, Cain ML, Howard DJ (2001). Spatio-temporal dynamics of the *Allonemobius fasciatus*-*A. socius* mosaic hybrid zone: a 14-year perspective. *Mol Ecol* 10: 627–638.
- Britton-Davidian J, Fel-Clair F, Lopez J, Alibert P, Boursot P (2005). Postzygotic isolation between the two European subspecies of the house mouse: estimates from fertility patterns in wild and laboratory-bred hybrids. *Biol J Linn Soc* 84: 379–393.
- Bronson CL, Grubb TC, Braun MJ (2003a). A test of the endogenous and exogenous selection hypotheses for the maintenance of a narrow avian hybrid zone. *Evolution* 57: 630–637.
- Bronson CL, Grubb TC, Sattler GD, Braun MJ (2003b). Mate preference: a possible causal mechanism for a moving hybrid zone. *Anim Behav* 65: 489–500.
- Buggs RJA, Pannell JR (2006). Rapid displacement of a monoecious plant lineage is due to pollen swamping by a dioecious relative. *Curr Biol* 16: 996–1000.
- Buggs RJA, Pannell JR (2007). Ecological differentiation and diploid superiority across a moving ploidy contact zone. *Evolution* 61: 125–140.
- Bull CM, Burzacott D (2001). Temporal and spatial dynamics of a parapatric boundary between two Australian reptile ticks. *Mol Ecol* 10: 639–648.
- Cabrero J, Shapiro LH, Camacho JPM (1999). Male sterility in interspecific Meadow Katydid hybrids. *Heredity* 131: 79–82.
- Cain ML, Andreasen V, Howard DJ (1999). Reinforcing selection is effective under a relatively broad set of conditions in a mosaic hybrid zone. *Evolution* 53: 1343–1353.
- Campbell DR (2004). Natural selection in *Ipomopsis* hybrid zones: implications for ecological speciation. *New Phytol* 161: 83–90.
- Carney SE, Gardner KA, Rieseberg LH (2000). Evolutionary changes over the fifty-year history of a hybrid population of sunflowers (*Helianthus*). *Evolution* 54: 462–474.
- Coyne JA, Barton NH, Turelli M (1997). Perspective: a critique of Sewall Wright's shifting balance theory of evolution. *Evolution* 51: 643–671.
- Coyne JA, Barton NH, Turelli M (2000). Is Wright's shifting balance process important in evolution? *Evolution* 54: 306–317.
- Cruzan MB (2005). Patterns of introgression across an expanding hybrid zone: analysing historical patterns of gene flow using nonequilibrium approaches. *New Phytol* 167: 267–278.
- Curat M, Excoffier L (2005). The effect of the Neolithic expansion on European molecular diversity. *Proc R Soc Lond B Biol Sci* 272: 679–688.
- Dabrowski A, Fraser R, Confer J, Lovette I (2005). Geographic variability in mitochondrial introgression among hybridizing populations of Golden-winged (*Vermivora chrysoptera*) and Blue-winged (*V. pinus*) Warblers. *Conserv Genet* 6: 843–853.
- Dasmahapatra KK, Blum MJ, Aiello A, Hackwell S, Davies N, Eldredge P et al. (2002). Inferences from a rapidly moving hybrid zone. *Evolution* 56: 741–753.
- Dorken ME, Pannell JR (2007). The maintenance of hybrid zones along a disturbance gradient. *Heredity* (in press).
- Ellstrand NC (1992). Gene flow by pollen—implications for plant conservation genetics. *Oikos* 63: 77–86.
- Endler JA (1977). *Geographic Variation, Speciation and Clines*. Princeton University Press: Princeton, NJ.
- Eppley SM, Pannell JR (2007). Sexual systems and measures of occupancy and abundance in an annual plant: testing the metapopulation model. *Am Nat* 169: 20–28.
- Faivre B (1993). La prédation joue-t-elle un rôle dans la régression de l'Hypolaïs icterine *Hippolaïs icterina*? *Rev Ecol* 48: 399–420.
- Ganem G, Ginane C, Ostrowski M, Orth A (2005). Assessment of mate preference in the house mouse with reference to investigations on assortative mating. *Biol J Linn Soc* 84: 461–471.
- Gardner J, Skibinski D (1988). Historical and size-dependent genetic variation in hybrid mussel populations. *Heredity* 61: 93–105.
- Gardner J, Skibinski D, Bajdik CD (1993). Shell growth and viability differences between the marine mussels *Mytilus edulis* (L.), *Mytilus galloprovincialis* (Lmk.), and their hybrids from two sympatric populations in S.W. England. *Biol Bull* 185: 405–416.
- Gay L (2006). Impact de l'introgression et de la sélection sur la diversité phénotypique dans deux zones de contact secondaire entre grands goélands. PhD Thesis, Université Montpellier II: Montpellier.
- Gill FB (1997). Local cytonuclear extinction of the golden-winged warbler. *Evolution* 51: 519–525.

- Good TP, Ellis JC, Annett CA, Pierotti R (2000). Bounded hybrid superiority in an avian hybrid zone: effects of mate, diet, and habitat choice. *Evolution* **54**: 1774–1783.
- Goodisman MAD, Shoemaker DD, Asmussen MA (1998). Cytoneuclear theory for haplodiploid species and X-linked genes. II. Stepping-stone models of gene flow and application to a fire ant hybrid zone. *Evolution* **52**: 1423–1440.
- Goodman SJ, Barton NH, Swanson G, Abernethy K, Pemberton JM (1999). Introgression through rare hybridization: a genetic study of a hybrid zone between red and sika deer (genus *Cervus*) in Argyll, Scotland. *Genetics* **152**: 355–371.
- Haas F, Brodin A (2005). The crow *Corvus corone* hybrid zone in southern Denmark and northern Germany. *Ibis* **147**: 649–656.
- Hafner MS, Demastes JW, Hafner DJ, Spradling TA, Sudman PD, Nadler SA (1998). Age and movement of a hybrid zone: implications for dispersal distance in pocket gophers and their chewing lice. *Evolution* **52**: 278–282.
- Haig SM (1998). Molecular contributions to conservation. *Ecology* **79**: 413–425.
- Hairston NG, Wiley RH, Smith CK, Kneidel KA (1992). The dynamics of two hybrid zones in Appalachian salamanders of the genus *Plethodon*. *Evolution* **46**: 930–938.
- Harrison RG (1990). Hybrid zones: windows on evolutionary processes. *Oxf Surv Evol Biol* **7**: 129–156.
- Harrison RG (1993). *Hybrid Zones and the Evolutionary Process*. Oxford University Press: Oxford.
- Hersteinsson P, MacDonald DW (1992). Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos* **64**: 505–515.
- Hewitt G (1975). A sex-chromosome hybrid zone in the grasshopper *Podisma pedestris* (Orthoptera: Acrididae). *Heredity* **35**: 375–387.
- Hewitt GM (1988). Hybrid zones—natural laboratories for evolutionary studies. *Trends Ecol Evol* **3**: 158–167.
- Hillis D, Simmons J (1986). Dynamic change of a zone of parapatry between two species of *Pholidobolus* (Sauria: Gymnophthalmidae). *J Herpetol* **20**: 85–87.
- Howard DJ (1993). Reinforcement: origin, dynamics, and fate of an evolutionary hypothesis. In: Harrison R (ed). *Hybrid Zones and the Evolutionary Process*. Oxford University Press: Oxford. pp 46–69.
- Howard DJ, Waring GL (1991). Topographic diversity, zone width, and the strength of reproductive isolation in a zone of overlap and hybridization. *Evolution* **45**: 1120–1135.
- Keim P, Paige KN, Whitham TG, Lark KG (1989). Genetic analysis of an interspecific hybrid swarm of *Populus*: occurrence of unidirectional introgression. *Genetics* **123**: 557–565.
- Key KHL (1968). The concept of stasipatric speciation. *Syst Zool* **17**: 14–22.
- Klingenberg C, Spence J, Mirth C (2000). Introgressive hybridization between two species of waterstriders (Hemiptera: Gerridae: *Limnoporus*): geographical structure and temporal change of a hybrid zone. *J Evol Biol* **13**: 756–765.
- Klopfstein S, Currat M, Excoffier L (2006). The fate of mutations surfing on the wave of a range expansion. *Mol Biol Evol* **23**: 482–490.
- Kohlmann B, Shaw D (1991). The effect of a partial barrier on the movement of a hybrid zone. *Evolution* **45**: 1606–1617.
- Kondrashov AS (1992). The third phase of Wright's shifting-balance: a simple analysis of the extreme case. *Evolution* **46**: 1972–1975.
- Konishi M, Takata K (2004a). Impact of asymmetrical hybridization followed by sterile F-1 hybrids on species replacement in *Pseudorasbora*. *Cons Genet* **5**: 463–474.
- Konishi M, Takata K (2004b). Size-dependent male–male competition for a spawning substrate between *Pseudorasbora parva* and *Pseudorasbora pumila*. *Ichthyol Res* **51**: 184–187.
- Konishi M, Hosoya K, Takata K (2003). Natural hybridization between endangered and introduced species of *Pseudorasbora*, with their genetic relationships and characteristics inferred from allozyme analyses. *J Fish Biol* **63**: 213–231.
- Leaché AD, Cole CJ (2007). Hybridization between multiple fence lizard lineages in an ecotone: locally discordant variation in mitochondrial DNA, chromosomes, and morphology. *Mol Ecol* **16**: 1035–1054.
- Lenz L (1959). Hybridization and speciation in the Pacific Coast irises. *Aliso* **4**: 237–309.
- Levin DA, Francisco-Ortega J, Jansen RK (1996). Hybridization and the extinction of rare plant species. *Conserv Biol* **10**: 10–16.
- Lexer C, Heinze B, Alia R, Rieseberg LH (2004). Hybrid zones as a tool for identifying adaptive genetic variation in outbreeding forest trees: lessons from wild annual sunflowers (*Helianthus* spp.). *J Forest Ecol* **197**: 49–64.
- Liou LW, Price TD (1994). Speciation by reinforcement of premating isolation. *Evolution* **48**: 1451–1459.
- Littlejohn M, Roberts J (1975). Acoustic analysis of an intergrade zone between two call races of the *Limnodynastes tasmaniensis* complex (Anura: Leptodactylidae) in south-eastern Australia. *Aust J Zool* **23**: 113–122.
- Mallet J (1986). Hybrid zones of *Heliconius* butterflies in Panama and the stability and movement of warning color clines. *Heredity* **56**: 191–202.
- Mallet J, Barton N (1989). Inference from clines stabilized by frequency-dependent selection. *Genetics* **122**: 967–976.
- Marchant A (1988). Apparent introgression of mitochondrial DNA across a narrow hybrid zone in the *Caledonia captiva* species-complex. *Heredity* **60**: 39–46.
- Marchant AD, Arnold ML, Wilkinson P (1988). Gene flow across a chromosomal tension zone 1. Relicts of ancient hybridization. *Heredity* **61**: 321–328.
- Marshall JC, Sites JW (2001). A comparison of nuclear and mitochondrial cline shapes in a hybrid zone in the *Sceloporus grammicus* complex (Squamata; Phrynosomatidae). *Mol Ecol* **10**: 435–449.
- Marshall JL, Arnold ML, Howard DJ (2002). Reinforcement: the road not taken. *Trends Ecol Evol* **17**: 558–563.
- Martin LJ, Cruzan MB (1999). Patterns of hybridization in the *Piriqueta caroliniana* complex in central Florida: evidence for an expanding hybrid zone. *Evolution* **53**: 1037–1049.
- Martinsen G, Whitham T, Turek R, Keim P (2001). Hybrid populations selectively filter gene introgression between species. *Evolution* **55**: 1325–1335.
- Maskas SD, Cruzan MB (2000). Patterns of intraspecific diversification in the *Piriqueta caroliniana* complex in southeastern North America and the Bahamas. *Evolution* **54**: 815–827.
- McDonnell LJ, Gartside DE, Littlejohn MJ (1978). Analysis of a narrow hybrid zone between two species of *Pseudophryne* (Anura: Leptodactylidae) in south-eastern Australia. *Evolution* **32**: 602–612.
- Melo-Ferreira J, Boursot P, Randi E, Kryukov A, Suchentrunk F, Ferrand N et al. (2007). The rise and fall of the mountain hare (*Lepus timidus*) during Pleistocene glaciations: expansion and retreat with hybridization in the Iberian Peninsula. *Mol Ecol* **16**: 605–618.
- Melo-Ferreira J, Boursot P, Suchentrunk F, Ferrand N, Alves PC (2005). Invasion from the cold past: extensive introgression of mountain hare (*Lepus timidus*) mitochondrial DNA into three other hare species in northern Iberia. *Mol Ecol* **14**: 2459–2464.
- Moore WS (1977). An analysis of narrow hybrid zones in vertebrates. *Q Rev Biol* **52**: 263–277.
- Moore WS, Dolbeer RA (1989). The use of banding recovery data to estimate dispersal rates and gene flow in avian species: case studies in the Red-Winged Blackbird and Common Grackle. *Condor* **91**: 242–253.
- Moore WS, Price JT (1993). Nature of selection in the northern flicker hybrid zone and its implications for speciation theory. In: Harrison RG (ed). *Hybrid Zones and the Evolutionary Process*. Oxford University Press: Oxford. pp 196–225.

- Moran C (1981). Genetic demarcation of geographical distribution by hybrid zones. *Proc Ecol Soc Aust* **11**: 67–73.
- Murray MC, Hare MP (2006). A genomic scan for divergent selection in a secondary contact zone between Atlantic and Gulf of Mexico oysters, *Crassostrea virginica*. *Mol Ecol* **15**: 4229–4242.
- Navarro A, Barton NH (2003). Accumulating postzygotic isolation genes in parapatry: a new twist on chromosomal speciation. *Evolution* **57**: 447–459.
- Owen-Ashley N, Butler L (2004). Androgens, interspecific competition and species replacement in hybridizing warblers. *Proc R Soc Lond B Biol Sci* **271**: S498–S500.
- Paige KN, Capman WC, Jenneten P (1991). Mitochondrial inheritance patterns across a cottonwood hybrid zone: cytonuclear disequilibria and hybrid zone dynamics. *Evolution* **45**: 1360–1369.
- Parmesan C (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**: 579–583.
- Parmesan C, Yohe G (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.
- Parsons TJ, Olson SL, Braun MJ (1993). Unidirectional spread of secondary sexual plumage traits across an avian hybrid zone. *Science* **260**: 1643–1646.
- Paterson H (1978). More evidence against speciation by reinforcement. *S Afr J Sci* **74**: 369–371.
- Patton J (1993). Hybridization and hybrid zones in pocket gophers (Rodentia: Geomyidae). In: Harrison R (ed). *Hybrid Zones and the Evolutionary Process*. Oxford University Press: Oxford. pp 290–308.
- Patton J, Smith M (1993). Molecular evidence for mating asymmetry and female choice in a pocket gopher (*Thomomys*) hybrid zone. *Mol Ecol* **2**: 3–8.
- Pearson SF (2000). Behavioral asymmetries in a moving hybrid zone. *Behav Ecol* **11**: 84–92.
- Pearson SF, Rohwer S (2000). Asymmetries in male aggression across an avian hybrid zone. *Behav Ecol* **11**: 93–101.
- Perry WL, Feder JL, Dwyer G, Lodge DM (2001). Hybrid zone dynamics and species replacement between *Orconectes* crayfishes in a northern Wisconsin lake. *Evolution* **55**: 1153–1166.
- Potts B, Reid J (1985). Analysis of a hybrid swarm between *Eucalyptus risdonii* Hook-F. and *E. amygdalina* Labill. *Aust J Bot* **33**: 543–562.
- Potts BM (1986). Population dynamics and regeneration of a hybrid zone between *Eucalyptus risdonii* Hook-F and *E. amygdalina* Labill. *Aust J Bot* **34**: 305–329.
- Raufaste N, Orth A, Belkhir K, Senet D, Smadja C, Baird S et al. (2005). Inferences of selection and migration in the Danish house mouse hybrid zone. *Biol J Linn Soc* **84**: 593–616.
- Remington C (1968). Suture-zones of hybrid interaction between recently joined biotas. *Evol Biol* **2**: 321–428.
- Reudink MW, Mech SG, Curry RL (2006). Extrapair paternity and mate choice in a chickadee hybrid zone. *Behav Ecol* **17**: 56–62.
- Reullier J, Perez-Tris J, Bensch S, Secondi J (2006). Diversity, distribution and exchange of blood parasites meeting at an avian moving contact zone. *Mol Ecol* **15**: 753–763.
- Reznick D (1981). Grandfather effects: the genetics of inter-population differences in offspring size in the mosquito fish. *Evolution* **35**: 941–953.
- Rhymer JM, Simberloff D (1996). Extinction by hybridization and introgression. *Annu Rev Ecol Syst* **27**: 83–109.
- Rieseberg LH (2001). Chromosomal rearrangements and speciation. *Trends Ecol Evol* **16**: 351–358.
- Rieseberg LH, Buerkle CA (2002). Genetic mapping in hybrid zones. *Am Nat* **159**: S36–S50.
- Rieseberg LH, Soltis DE (1991). Phylogenetic consequences of cytoplasmic gene flow in plants. *Evol Trends Plants* **5**: 65–84.
- Rohwer S, Bermingham E, Wood C (2001). Plumage and mitochondrial DNA haplotype variation across a moving hybrid zone. *Evolution* **55**: 405–422.
- Rolando A, Giachello P (1992). Interspecific coexistence in corvids in an alpine valley of northwestern Italy. *Boll Zool* **59**: 281–288.
- Ruedi M, Smith MF, Patton JL (1997). Phylogenetic evidence of mitochondrial DNA introgression among pocket gophers in New Mexico (family Geomyidae). *Mol Ecol* **6**: 453–462.
- Saino S, Scatizzi L (1991). Selective aggressiveness and dominance among Carrion Crows, Hooded Crows and hybrids. *Boll Zool* **58**: 255–260.
- Scribner K, Avise J (1994a). Population cage experiments with a vertebrate: the temporal demography and cytonuclear genetics of hybridization in *Gambusia* fishes. *Evolution* **48**: 155–171.
- Scribner K, Avise JC (1994b). Cytonuclear genetics of experimental fish hybrid zones inside Biosphere 2. *Proc Nat Acad Sci USA* **91**: 5066–5069.
- Scribner KT (1993). Hybrid zone dynamics are influenced by genotype-specific variation in life-history traits: experimental evidence from hybridizing *Gambusia* species. *Evolution* **47**: 632–646.
- Scribner KT, Avise JC (1993). Cytonuclear genetic architecture in Mosquito fish populations and the possible roles of introgressive hybridization. *Mol Ecol* **2**: 139–149.
- Secondi J, Bretagnolle V, Compagnon C, Faivre B (2003). Species-specific song convergence in a moving hybrid zone between two passerines. *Biol J Linn Soc* **80**: 507–517.
- Sequeira F, Alexandrino J, Rocha S, Arntzen JW, Ferrand N (2005). Genetic exchange across a hybrid zone within the Iberian endemic golden-striped salamander, *Chioglossa lusitana*. *Mol Ecol* **14**: 245–254.
- Servedio MR, Kirkpatrick M (1997). The effects of gene flow on reinforcement. *Evolution* **51**: 1764–1772.
- Shapiro LH (1998). Hybridization and geographic variation in two meadow katydid contact zones. *Evolution* **52**: 784–796.
- Shapiro LH (2000). Reproductive costs to heterospecific mating between two hybridizing katydids (Orthoptera: Tettigoniidae). *Ann Entom Soc Am* **93**: 440–446.
- Shapiro LH (2001). Asymmetric assortative mating between two hybridizing *Orchelimum* Katydids (Orthoptera: Tettigoniidae). *Am Midl Nat* **145**: 423–427.
- Shapiro LH, Canterbury RA, Stover DM, Fleischer RC (2004). Reciprocal introgression between golden-winged warblers (*Vermivora chrysoptera*) and blue-winged warblers (*V. pinus*) in eastern North America. *Auk* **2004**: 1019–1030.
- Shaw D, Wilkinson P (1980). Chromosome differentiation, hybrid breakdown and the maintenance of a narrow hybrid zone in *Caledia*. *Chromosoma* **80**: 1–31.
- Shaw DD, Coates DJ, Arnold ML, Wilkinson P (1985). Temporal variation in the chromosomal structure of a hybrid zone and its relationship to karyotypic repatterning. *Heredity* **55**: 293–306.
- Shaw DD, Marchant AD, Arnold ML, Contreras N, Kohlmann B (1990). The control of gene flow across a narrow hybrid zone: a selective role for a chromosomal rearrangement? *Can J Zool* **68**: 1761–1769.
- Shaw DD, Marchant AD, Contreras N, Arnold ML, Groeters F, Kohlmann B (1993). Genomic and environmental determinants of a narrow hybrid zone: cause or coincidence? In: Harrison RG (ed). *Hybrid Zones and the Evolutionary Process*. Oxford University Press: New York. pp 165–195.
- Shoemaker D, Ross K, Arnold M (1994). Development of RAPD markers in two introduced fire ants, *Solenopsis invicta* and *S. richteri*, and their application to the study of a hybrid zone. *Mol Ecol* **3**: 531–539.
- Shoemaker DD, Ross KG, Arnold ML (1996). Genetic structure and evolution of a fire ant hybrid zone. *Evolution* **50**: 1958–1976.

- Shoemaker DD, Ross KG, Keller L, Vargo EL, Werren JH (2000). *Wolbachia* infections in native and introduced populations of fire ants (*Solenopsis* spp.). *Insect Mol Biol* **9**: 661–673.
- Sites JW, Basten CJ, Asmussen MA (1996). Cytonuclear genetic structure of a hybrid zone in lizards of the *Sceloporus grammicus* complex (Sauria, Phrynosomatidae). *Mol Ecol* **5**: 379–392.
- Skibinski DOF, Roderick EE (1991). Evidence of selective mortality in favour of the *Mytilus galloprovincialis* Lmk phenotype in British mussel populations. *Biol J Linn Soc* **42**: 351–366.
- Smadja C, Ganem G (2002). Subspecies recognition in the house mouse: a study of two populations from the border of a hybrid zone. *Behav Ecol* **13**: 312–320.
- Smadja C, Catalan J, Ganem G (2004). Strong premating divergence in a unimodal hybrid zone between two subspecies of the house mouse. *J Evol Biol* **17**: 165–176.
- Sparks TH (2007). Lateral thinking on data to identify climate impacts. *Trends Ecol Evol* **22**: 169–171.
- Spence JR (1990). Introgressive hybridization in Heteroptera: the example of *Limnopus* Stal (Gerridae) species in western Canada. *Can J Zool* **68**: 1770–1782.
- Sperling FAH, Spence JR (1991). Structure of an asymmetric hybrid zone between two water strider species (Hemiptera: Gerridae: *Limnopus*). *Evolution* **45**: 1370–1383.
- Takami Y, Suzuki H (2005). Morphological, genetic and behavioural analyses of a hybrid zone between the ground beetles *Carabus lewisianus* and *C. albrechti* (Coleoptera, Carabidae): asymmetrical introgression caused by movement of the zone?. *Biol J Linn Soc* **86**: 79–94.
- Thomas CD, Lennon JJ (1999). Birds extend their ranges northwards. *Nature* **399**: 213.
- Thulin C-G, Tegelström H (2002). Biased geographical distribution of mitochondrial DNA that passed the species barrier from mountain hares to brown hares (genus *Lepus*): an effect of genetic incompatibility and mating behaviour? *J Zool* **258**: 299–306.
- Tiffin P, Olson MS, Moyle LC (2001). Asymmetrical crossing barriers in angiosperms. *Proc R Soc Lond Ser B Biol Sci* **268**: 861–867.
- Wang J, Cruzan M (1998). Interspecific mating in the *Piriqueta caroliniana* (Turneraceae) complex: effects of pollen load size and composition. *Am J Bot* **85**: 1172–1179.
- White MJD (1968). Models of speciation. *Science* **159**: 1065–1070.
- White MJD (1978). Chain processes in chromosomal speciation. *Syst Zool* **27**: 285–298.
- Wilhelm R, Hilbish TJ (1998). Assessment of natural selection in a hybrid population of mussels: evaluation of exogenous vs endogenous selection models. *Mar Biol* **131**: 505–514.
- Willis GL, Skibinski DOF (1992). Variation in strength of attachment to the substrate explains differential mortality in hybrid mussel (*Mytilus galloprovincialis* and *M. edulis*) populations. *Mar Biol* **112**: 403–408.
- Wolf DE, Takebayashi N, Rieseberg LH (2001). Predicting the risk of extinction through hybridization. *Conserv Biol* **15**: 1039–1053.
- Woodcock EA, Rathburn MK, Ratcliffe LM (2005). Achromatic plumage reflectance, social dominance and female mate preference in black-capped Chickadees (*Poecile atricapillus*). *Ethology* **111**: 891–900.
- Woodruff DS (1972). *The Evolutionary Significance of Hybrid Zones in Pseudophyrne (Anura: Leptodactylidae)*, PhD Thesis, University of Melbourne.
- Woodruff DS (1981). Genodynamics of hybrid zones. In: Atchley WR, Woodruff DS (eds). *Evolution and Speciation*. Cambridge University Press: Cambridge. pp 171–200.
- Wright S (1977). *Evolution and the Genetics of Populations*, Vol. 3. University of Chicago Press: Chicago, IL.
- Wright S (1982). The shifting balance theory and macroevolution. *Annu Rev Genet* **16**: 1–20.
- Wu CA, Campbell DR (2005). Cytoplasmic and nuclear markers reveal contrasting patterns of spatial genetic structure in a natural *Ipomopsis* hybrid zone. *Mol Ecol* **14**: 781–792.
- Yang SY, Selander RK (1968). Hybridization in the Grackle *Quiscalus quiscula* in Louisiana. *Syst Zool* **17**: 107–143.
- Yeatman-Berthelot D, Jarry G (1994). *Nouvel atlas des oiseaux nicheurs de France*. SOF: Paris.
- Young ND (1996). Concordance and discordance: a tale of two hybrid zones in the Pacific coast Irises (Iridaceae). *Am J Bot* **83**: 1623–1629.

Supplementary Information accompanies the paper on Heredity website (<http://www.nature.com/hdy>)