



# Historical hybrid zone movement: More pervasive than appreciated

## Abstract

Hybrid zones are established where two divergent populations meet and interbreed, but experience some reproductive isolation. If one population expands its range at the expense of the other, their hybrid zone moves. While hybrid zone movement is generally considered to be uncommon and insignificant, recent studies challenge this idea. The commonality of contemporary hybrid zone movement—with shifts in hybrid zones tracked over years to decennia—cannot be disputed, given the many examples available. Cases of historical hybrid zone movement—covering centuries or millennia of mobility—are accumulating, with movement having been inferred from five lines of evidence: (1) range shifts documented in the fossil/pollen record; (2) distribution dynamics derived from species distribution modelling; (3) enclaves of a displaced population persisting inside the range of an expanding one; (4) a peak of linkage disequilibrium at the leading edge of a moving hybrid zone; and (5) genome-wide genetic traces of a displaced population, left behind in an expanding one. While most of these lines of evidence are not straightforward to interpret and/or broadly applicable, the latter—a genomic footprint of hybrid zone movement—promises to be particularly suitable to determine whether a hybrid zone has been on the move since its inception. I argue that historical hybrid zone movement is likely to be prevalent and deserves wider acknowledgement in historical biogeography.

## 1 | CAN HYBRID ZONES MOVE—AND WHY SHOULD WE CARE?

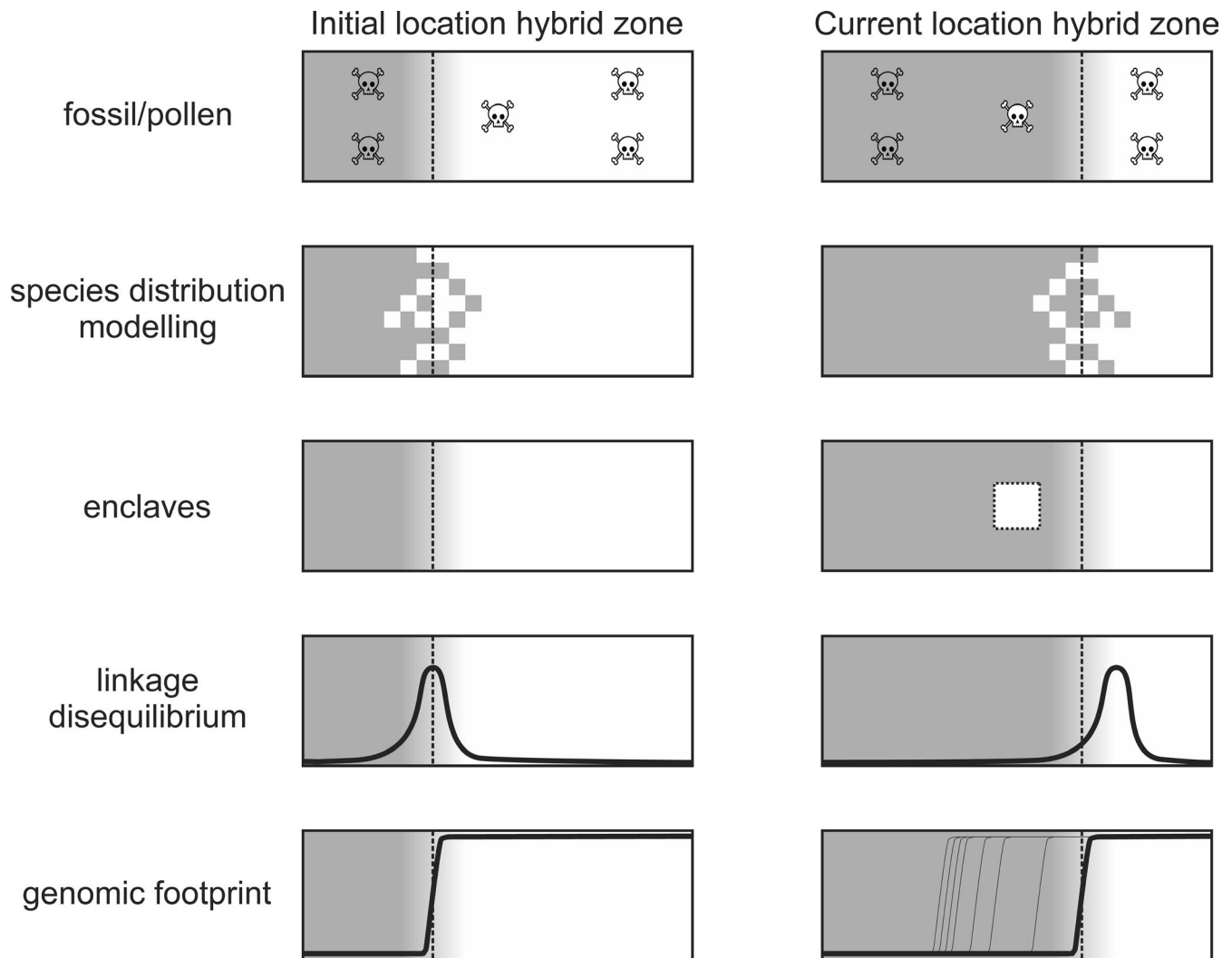
If an ancestral population is divided into two isolated gene pools that start evolving independently, the speciation process is initiated and genetic incompatibilities accumulate (Wu & Ting, 2004). When the genomes of the daughter populations have become too distinct to function together properly, but the fitness of their hybrids is still greater than zero, there is a window of opportunity for alleles of one population to become incorporated in the genomic background of the alternate population: a process known as introgression (Mallet, 2005). If populations with incomplete reproductive isolation were to meet in secondary contact, they can establish a hybrid zone (Barton & Hewitt, 1985). If one population has a competitive edge over, and were to expand its range at the expense of, the other, hybrid zone

movement would ensue (Buggs, 2007). Considering that (a) it is unlikely that both populations have equal fitness at the location where they first establish secondary contact and (b) any position of equal fitness is unlikely to be static for long under environmental change, it would be expected that hybrid zone movement due to population displacement is the rule, rather than the exception (Arntzen, Vries, Canestrelli, & Martínez-Solano, 2017; Wielstra, Burke, Butlin, Avci, et al., 2017).

Hybrid zone movement would entail an important extension of historical biogeography. With many of the hybrid zones observed today having been established thousands of years ago, during periods of major climate upheaval (Hewitt, 1988), there is considerable scope for dynamic hybrid zones. Hybrid zone movement also has implications for conservation biology, as man-made climate and habitat change, as well as the introduction of exotic species, are predicted to cause anthropogenic hybrid zone movement (Taylor, Larson, & Harrison, 2015). Hence, hybrid zone movement could represent an important force in shaping past, present and future distribution patterns. While contemporary hybrid zone movement has now been regularly observed (Buggs, 2007), historical hybrid zone movement is generally considered to be uncommon and insignificant (Barton & Hewitt, 1985; Hewitt, 1988). Recent studies challenge this idea and I argue here that historical hybrid zone movement is likely to be more wide-spread and influential than currently appreciated.

## 2 | OPPORTUNITIES AND LIMITATIONS FOR HYBRID ZONE MOVEMENT ACCORDING TO THE LITERATURE

Most hybrid zones are thought to be tension zones, in which the fitness of the hybrids is lower than that of the parents (Barton & Hewitt, 1985; Hewitt, 1988; Key, 1968). The reduced hybrid fitness prevents, or at least delays, the blending of parental genotypes into a single population and keeps the hybrid zone geographically restricted. Therefore, tension zones can persist over extended periods of time, with a balance between dispersal and interbreeding, on the one hand, and removal of admixed genotypes by selection on the other. Theory predicts that tension zones are able to shift across the landscape in response to gradients in population density,



**FIGURE 1** The five lines of evidence used to infer historical hybrid zone movement. In this figure a grey and a white population initially establish a hybrid zone upon secondary contact. Subsequently, the grey population has been expanding at the expense of a white one and their current hybrid zone is situated further to the right. Signatures of historical hybrid zone movement may be provided by (1) the fossil/pollen record, if remains of the white population are uncovered inside the range of the grey population; (2) species distribution modelling, if relative habitat suitability in the area of species replacement increased for the grey population and decreased for the white population; (3) enclaves, if a distribution relict of the white population is found nested inside the range of the grey population; (4) a peak in linkage disequilibrium, if linkage disequilibrium is elevated in the direction of movement, so right of the current hybrid zone; and (5) a genomic footprint of hybrid zone movement, if geographical clines (gradients in gene frequency) for individual markers (thin) have their centres (or alternatively their tails) displaced to the left of the current hybrid zone, as defined by the centre of a cline for overall genotype (thick). Note that (1–3) reflect 2-dimensional space, while (4–5) are graphs

asymmetry in hybridization, or differential adaptation of the parents (Barton, 1979; Bazykin, 1969; Key, 1968). Hence, the possibility of hybrid zone movement is firmly embedded in the literature (Buggs, 2007).

However, tension zone theory also predicts that moving hybrid zones easily become trapped at population density troughs or ecological barriers, implying that they could only move short distances before they stabilize (Barton & Hewitt, 1985). Even a considerable fitness advantage of one population over the other is, in theory, insufficient to cause a hybrid zone to move up a population gradient and so escape a density trough (Barton, 1979; Hewitt, 1988). Perhaps for this reason, the predominating idea in

the literature is that hybrid zone movement is short-lived (Buggs, 2007), and studies testing historical hybrid zone movement empirically are few and far between. But is this scepticism warranted? Tension zones are often positioned at an ecotone (Bierne, Welch, Loire, Bonhomme, & David, 2011; Endler, 1977) and it has been argued that hybrid genotypes might actually be favoured at an ecotone (Moore, 1977). The impact of the ecological background on hybrid zone position is particularly evident in mosaic hybrid zones (Harrison, 1990). If a hybrid zone is maintained by an ecotone, and the location of this ecotone shifts position, for example under climate change, the hybrid zone would be expected to follow suit (Taylor et al., 2015).

**TABLE 1** An overview of studies proposing historical hybrid zone movement

Taxon	Region	Evidence	Source
<i>Betula</i> (birch)	Great Britain	1, 5	Wang et al. (2014); Zohren et al. (2016)
<i>Bombina</i> (fire-bellied toads)	Central Europe	3	Arntzen (1978)
<i>Pelophylax</i> (green frogs)	East Asia	2	Komaki et al. (2015)
<i>Lissotriton</i> (smooth newts)	Carpathians	2	Zieliński et al. (2013)
<i>Mercurialis</i> (mercury)	Iberian Peninsula	3	Buggs and Pannell (2006)
<i>Triturus</i> (crested newts)	Balkan Peninsula	2, 3, 5	Wielstra and Arntzen (2012); Wielstra, Burke, Butlin, and Arntzen (2017)
<i>Triturus</i> (marbled newts)	Iberian Peninsula	3	Espregueira Themudo and Arntzen (2007)
<i>Triturus</i> (crested newts)	Turkey	5	Wielstra, Burke, Butlin, Avci, et al. (2017)
<i>Larus</i> (gulls)	Western North America	4	Gay et al. (2008)
<i>Lepus</i> (hares)	Iberian Peninsula	1, 2, 5	Acevedo et al. (2015); Lado et al. (2018); Seixas, Boursot, and Melo-Ferreira (2018)
<i>Lymnodynastes</i> (grass frogs)	Australia	3	Littlejohn and Roberts (1975)
<i>Mus</i> (mice)	Central Europe	3, 4, 5	Barton and Hewitt (1981); Macholán et al. (2011); Wang et al. (2011)

Evidence: historical hybrid zone movement was inferred from (1) the fossil/pollen record; (2) species distribution modelling; (3) enclaves; (4) a peak in linkage disequilibrium; and (5) a genomic footprint of hybrid zone movement. Note that multiple lines of evidence are often presented simultaneously.

### 3 | CONTEMPORARY AND HISTORICAL HYBRID ZONE MOVEMENT—WHAT DOES THE EVIDENCE SAY?

Unambiguous evidence of hybrid zone movement comes from hybrid zones that have been tracked “live”, as researchers determined their position at multiple points in time, by revisiting a hybrid zone over time, sometimes with the help of survey data or museum collections (see e.g. Arntzen & Wallis, 1991 for an early example). Many examples of such contemporary hybrid zone movement have accumulated (see the review paper by Buggs, 2007), particularly in recent years (e.g. Billerman, Cicero, Bowie, & Carling, 2019; Leaché, Grummer, Harris, & Breckheimer, 2017; Ryan et al., 2018; Taylor et al., 2014). The commonality of contemporary hybrid zone movement seems hard to square with a view that hybrid zones are relatively stable. Yet, the timeframe of proven hybrid zone movement in these cases necessarily only stretches as far back in time as when a study was initiated, on a scale of years to decades (so no more than tens of generations).

As hybrid zones have often been around for millennia (Hewitt, 1988), they could potentially travel hundreds to thousands of kilometres over their lifetime. Is there any evidence for such historical hybrid zone movement? I briefly review the burgeoning literature on the topic and particularly focus on compiling the different lines of evidence that have been used to support the hypothesis of historical hybrid zone movement (Text Box).

Of five lines of evidence, I consider searching for “genomic footprints of hybrid zone movement” the most promising approach to detect historical hybrid zone movement. In the area of species displacement, so in the wake of the moving hybrid zone, a concerted, unidirectional introgression of many physically and functionally unlinked, selectively neutral markers from across the genome is expected. The footprint pattern is (a) unambiguous, because alleles typical for the receding population are left behind in the expanding one; (b) temporally persistent, because the introgression is only subject to genetic drift; and (c) applicable to any moving hybrid zone where introgression between the populations involved occurs. While a large number of markers need to be interrogated to test for a genomic footprint of hybrid zone movement, the necessary datasets can easily be collected nowadays for any system (Gagnaire et al., 2015; Gompert, Mandeville, & Buerkle, 2017; Harrison & Larson, 2014; Twyford & Ennos, 2012).

### 4 | CONCLUDING REMARKS AND FUTURE DIRECTIONS

Many examples of hybrid zones moving in our lifetime have accumulated and often human induced changes in habitat and climate have been interpreted as the driving force (Buggs, 2007; Taylor et al., 2015). It is becoming clear that hybrid zones can move on considerably longer time-scales

### Text Box Inferring historical hybrid zone movement

Past range shifts of hybridizing populations can be deduced from the fossil/pollen record, if remains of one member of a pair of hybridizing populations are found inside the current range of the other population (Figure 1). Even if sufficient material is available, a condition for employing the fossil/pollen record is that the interacting populations can be distinguished, despite their similarity as implied by hybridization. While one study on birch trees succeeded in identification of hybridizing taxa from pollen alone (Wang et al., 2014), another one on hares resorted to sequencing ancient DNA to establish to which taxon fossils belonged (Lado et al., 2018) (Table 1). Given these limitations, the fossil/pollen record is unlikely to be broadly applicable to inferring historical hybrid zone movement.

Range shifts of hybridizing populations have been inferred from species distribution modelling, as predicted habitat suitability for the population presumed to have been replaced decreased over time, while the reverse applies to the supposedly invading population (Figure 1). Climate reconstructions for the mid-Holocene (~6 ka) and Last Glacial Maximum (~22 ka) are publicly available (from the WorldClim database; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Species distribution models based on current climate and distribution data can be projected on these past climate layers (Alvarado-Serrano & Knowles, 2014; Svenning, Fløjgaard, Marske, Nógues-Bravo, & Normand, 2011), thereby providing distribution estimates during the switch from the last glacial to current interglacial period—the most important event in terms of the shaping of present-day hybrid zones (Hewitt, 2011). Distribution shifts have been inferred with species distribution modelling in amphibians and hares (Table 1). While broadly applicable, as only a distribution database for the hybridizing populations need to be assembled, the resolution of species distribution modelling is low and heavily reliant on the assumptions in the model, for example that bioclimatic layers alone can sufficiently reflect a population's ecological niche and that introgression does not alter the niche of the populations involved (Elith, Kearney, & Phillips, 2010).

If population displacement is incomplete, and the expanding population moves around and past resilient distribution pockets of the receding one, this would result in a characteristic distribution pattern of enclaves of the overall receding population, enveloped by the range of the expanding population (Arntzen, 1978; Littlejohn & Roberts, 1975) (Figure 1). An alternative explanation of long distance colonization would be considered unlikely if the enclave-to-main range distance is high and species vagility is low. Enclaves have been documented in several hybrid zones, particularly for amphibians (Table 1). However, given their presumed rarity, enclaves are probably of limited help in ascertaining hybrid zone movement (Wielstra, Burke, Butlin, & Arntzen, 2017).

Admixture-induced linkage disequilibrium is the association between alleles derived from each parental population in early-generation hybrids and is gradually broken down by recombination over generations of backcrossing (Barton & Hewitt, 1985). Linkage disequilibrium is expected to be elevated ahead of a moving hybrid zone, due to a concentration of early-generation hybrids at its leading edge, where hybrid genomes start recombining with the un-admixed receding population (Figure 1). Empirical evidence is provided by gulls and mice (Table 1). A difficulty with this approach is that it is not straightforward to determine when secondary contact was established and hence how long the hybrid zone has been on the move, and that the signal soon disappears after a zone stops moving (Gay, Crochet, Bell, & Lenormand, 2008; Wang et al., 2011).

Introgression across a moving hybrid zone is predicted to be asymmetric, as selectively neutral alleles from the displaced population introgress into the expanding one, in the wake of a moving hybrid zone (Currat, Ruedi, Petit, & Excoffier, 2008; Quilodrán, Nussberger, Montoya-Burgos, & Currat, 2019). Introgression of a single marker such as mitochondrial DNA could be (and regularly has been) interpreted as resulting from hybrid zone movement (Buggs, 2007), but excluding other potential causes for introgression of single markers is not straightforward (Dasmahapatra et al., 2002; Toews & Brelsford, 2012), making such data insufficient to infer historical hybrid zone movement. However, the case would be much stronger if many unlinked markers have introgressed in the same direction (Barton & Hewitt, 1985). Such a “genomic footprint of hybrid zone movement” has been documented in amphibians and mammals (Table 1). The most straightforward approach is to determine the geographical transition between SNP variants diagnostic for the two populations involved (Figure 1). Diagnostic SNPs can be inferred from localities positioned away from the hybrid zone and presumed to be unaffected by gene flow between the two populations involved. The geographical extent of introgression in relation to the dispersal distance of the taxon under study gives a rough indication of the time a hybrid zone would have been moving and, if information on the position of introgressed markers on the genome is available, time of secondary contact could be inferred from the size of introgressed genome blocks (Baird, 1995).

as well, in response to natural processes. Hence, the notion that hybrid zone movement is rare and short-lived conflicts with empirical data, which suggests hybrid zone movement is common, can be persistent and may cover large distances. Perhaps the most likely explanation is that many of the density troughs that trap hybrid zones conform to ecotones that

are themselves mobile under climate dynamics. Furthermore, on longer time-scales, geological processes can reroute or erase physical barriers such as rocky outcrops or rivers. This could dislodge hybrid zones and allows them to successively skip from one temporary barrier to the next, as suggested long ago (Barton & Hewitt, 1985).

Although historical hybrid zone movement evidently can occur, its frequency is still unclear. I predict that the limited examples published so far will turn out to be unexceptional, and that long-term hybrid zone movement will prove to be more common than currently appreciated. This prediction can be tested by hybrid zone studies inspecting genome-wide gene flow. The plethora of single-marker studies that have revealed asymmetric introgression (Toews & Brelsford, 2012) illustrates that there is a rich testing ground, in which the statistical power of genome-wide datasets can be employed to test for hybrid zone movement, and distinguish it from alternative hypotheses of single-marker introgression, such as adaptive introgression.

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## Keywords

climate change, competition, enclave, fossil record, genomic footprint, historical biogeography, introgression, linkage disequilibrium, pollen record, species distribution modelling

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## BIOSKETCH

**Ben Wielstra** is an assistant professor, interested in the evolutionary history of closely related species—how such species originated and obtained their current distribution and how they interact during the course of their evolution, as ecological divergence drives them apart and gene flow pulls them together.

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