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## Hybrid Zones: Windows on Climate Change

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### Abstract

Defining the impacts of anthropogenic climate change on biodiversity and species distributions is currently a high priority. Niche models focus primarily on predicted changes in abiotic factors; however, species interactions and adaptive evolution will impact the ability of species to persist in the face of changing climate. Our review focuses on the use of hybrid zones to monitor species' responses to contemporary climate change. Monitoring hybrid zones provides insight into how range boundaries shift in response to climate change by illuminating the combined effects of species interactions and physiological sensitivity. At the same time, the semi-permeable nature of species boundaries allows us to document adaptive introgression of alleles associated with response to climate change.

### Keywords

hybridization; distribution; gene flow; range limits; adaptive introgression

### Climate change and biodiversity

Changes in the distributions of species have been and will continue to be an obvious and important consequence of climate change [1]. Over geological time, and most recently during the Pleistocene, climates have fluctuated greatly, and species distributions have changed in response. In the present day, anthropogenic impacts on global climate have become a major source of concern. Primarily because of the rapidity of the change, anthropogenic contributions to climate change have generally negative impacts on biodiversity.

Over the past decade, the ability to predict the influence of anthropogenic climate change on species' distributions and persistence has improved [2-4]. However, niche models focused on abiotic factors have dominated the literature, and these models rarely incorporate species interactions or adaptive evolution, two major factors that undoubtedly impact the ability of

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species to persist in the face of changing climate [2,5]. Tracking how species respond to climate change should involve a multifaceted approach – one that includes examining changes in distributions and interspecific interactions, together with analysis of adaptive evolution – in order to gain a comprehensive understanding of the impacts of climate change on contemporary biodiversity. Long term monitoring of hybrid zones is one important way to document distributional changes and observe interspecific interactions under dynamic climate scenarios; in addition hybrid zones provide an opportunity to observe and characterize patterns of adaptive introgression [6].

## Hybrid zones as sensitive markers of environmental change

Hybrid zones occur where the ranges of species or other genetically distinct entities overlap; in these areas individuals from two “species” hybridize and produce offspring of mixed ancestry. The locations of many hybrid zones (e.g. black-capped (*Poecile atricapillus*) and Carolina (*P. carolinensis*) chickadees [7-9]; northern (*Glaucomys sabrinus*) and southern (*G. volans*) flying squirrels [10-12]; *Papilio* butterflies, [13,14]; *Allonemobius* crickets [15]) are influenced by climate, and change in climate can lead to hybrid zone movement (e.g., [7]), changes in range overlap, and the origin of new hybrid zones [16] (Table S1, Figure 1). It is important to note that hybrid zones can also move due to factors other than climate. Under the tension zone model [17], in which a hybrid zone is maintained by selection against individuals of mixed ancestry, (see below) hybrid zones are free to move. Tension zone position is influenced by the density of the interacting species, with hybrid zones coming to rest in density troughs. A hybrid zone can, just by chance, experience movement under this model (e.g. *Mus musculus* hybrid zone [18]), which could mistakenly be attributed to climate change or other co-varying environmental factors. When hybrid zone movement is detected, additional evidence is always necessary to support a role for climate-mediated factors [7,19] (see Box 1).

It has long been recognized that hybrid zones are important windows on the evolutionary process, because the outcomes of many generations of hybridization and recombination allow insights into the genetics of local adaptation, reproductive barriers and speciation [17,20-24]. Hybridization can also provide an important source of genetic variation that contributes to the evolution of novel phenotypes or adaptation to new environments [25-32]. Hybrid speciation is well documented in plants [24], but remains controversial in animals [33-36]; adaptive introgression is now a well-established phenomenon in many organisms. Studying how hybrid zones move in response to climate change will allow a more holistic understanding of the influence of both abiotic and biotic factors on range limits and how interacting species respond to climate change. Hybrid zones represent excellent systems for monitoring distributional changes both across continents and along elevational gradients; they also can provide insights into the role of adaptive introgression as a response to changing climate. Thus, hybrid zones have the potential to act as windows on anthropogenic climate change.

Here we discuss the utility of hybrid zone research for determining how species respond to contemporary climate change, either through changes in geographic distributions [7], or through adaptive introgression of alleles that facilitate species persistence [13]. Long-term

monitoring of hybrid zones has enormous potential for informing (1) how species respond to climate change [37], and (2) how climate change might alter patterns of introgression [13]. This potential remains largely unrealized.

## Monitoring changes in geographic distributions using hybrid zones

Understanding factors that limit species' ranges has, for many years, been a focus for ecologists and evolutionary biologists [38-44]. Defining range boundaries is inherently difficult, because population density declines towards range margins, making range boundaries diffuse and difficult to map. When competing species overlap at range edges, the increase in abundance of one species and concomitant decrease in abundance of the other species can occur over large and relatively undefined geographic areas. Only when competition between parapatric species or subspecies is intense will changes in their distributions be relatively straightforward to document. As a consequence, tracking responses to climate change can be difficult. Factors that determine range limits can be abiotic or biotic and include (but are not limited to) temperature, precipitation, and presence or absence of competitors, predators and parasites. Temperature is often implicated as an important abiotic factor determining range boundaries, and many northern and high elevation range boundaries are currently shifting northwards or skywards (in the case of mountain dwelling species) in response to climate change [45-49].

Hybrid zones can be broadly categorized as either clinal or mosaic in structure (Box 2). Clinal hybrid zones can be maintained by several different selection regimes. These include (1) endogenous selection against hybrid genotypes (tension zones) [17], (2) selection favoring different parental types at either end of an environmental gradient [50], or (3) selection in intermediate habitats favoring individuals of mixed ancestry (bounded hybrid superiority model)[51]. When selection against hybrids is strong, changes in the range of one species will be closely tied to the changes in the other species' range [37]. Further, when hybridizing species are distributed along an environmental gradient, hybridization can narrow the region in which both species co-occur, due to ecological and/or reproductive character displacement across the zone of hybridization [52-53]. A narrow zone can facilitate hybrid zone tracking by any method discussed here. In some cases, the hybridizing species will differ in their sensitivity to changing climate, in which case hybrid zone movement will presumably reflect “retreat” of the more vulnerable species.

Mosaic hybrid zones are also useful for monitoring range changes, but for these zones the sampling scheme is critical (Box1)[54]. In mosaic hybrid zones, parental types are distributed on a patchy landscape and hybridization most often occurs across patch boundaries. The distribution of habitat or resource patches can shift with changing climate. To monitor such shifts, mosaic hybrid zones must be sampled at appropriate spatial scales. It is important to note that hybrid zone width can change, which might or might not be related to overall movement, but can also be a result of environmental change (e.g., changes in the underlying habitat mosaic) [55]. The most useful hybrid zones for monitoring range changes in response to climate change will be those that occur between species with broad continental distributions and those that occur along elevational gradients (e.g. [15, 56]).

The utility of hybrid zones for understanding range changes has not gone unnoticed [57,58]. Indeed, the work of Godfrey Hewitt and others clearly shows that we can use the contemporary positions of many hybrid zones in both Europe and North America to better understand historical biogeography and species' responses to climate change throughout the Late Miocene to Late Pleistocene [58]. Post-glacial colonization routes have been mapped for a diversity of animal and plant taxa, using the contemporary distribution of hybrid zones, identified from morphology, genetics, or a combination [22,58,59-63]. Distributional changes in plants have also been inferred from pollen cores (e.g., [64,65]); these cores reveal rapid northward movement of many tree species over the past 10-15K years. Most of the aforementioned work focused on how historical distributions changed in response to changing climate. We propose to use the same approach to examine ongoing range changes and to make predictions about future distributions.

Determining if a hybrid zone is moving can be accomplished using distributional data in combination with phenotypic and/or genetic data (e.g., [66]). Direct measurements of hybrid zone movement require long-term sampling of any of these data types (e.g., [67-69]). Movement can also be inferred indirectly from patterns of allelic variation, but interpreting the genetic signature of hybrid zone movement is complicated (e.g., [55,68,70-72]). Consistent asymmetric introgression of genetic markers has been interpreted as evidence that these markers have been "left behind" as a hybrid zone boundary moved (e.g., [70,71]).

Classic geographic cline analysis allows us to estimate movement by examining allele or phenotype frequency changes across the landscapes at two (or more) time points (See Box 1). For each time point we can estimate the average cline center from a series of locus specific estimates and then determine the difference in cline center between time points to gain an understanding of how far a hybrid zone has moved (e.g., distance moved north [7]). The ideal phenotypes or genotypes used to measure hybrid zone movement will be fixed or nearly fixed for different morphs or alleles between the sampled populations, resulting in stepped clines across the hybrid zone and high power to assign cline parameters (e.g., center and width) (See Box 1). Given that ancestral polymorphism is not expected to leave a biogeographic signature, changes in allele frequencies between non-diagnostic markers are also useful for assessing hybrid zone movement, but power to assign cline parameters in such instances will be low. When available, diagnostic (or nearly diagnostic) differences between species allow us to be confident that alleles that are shared in the hybrid zone are the result of hybridization and introgression, as opposed to shared ancestral polymorphism (see Box 1). In a similar way, we can use distribution data and records of hybrid individuals, or of the overlap between parental species, to determine hybrid zone locations through time (e.g., [66]). This approach can be problematic when identification of hybrids in the field is difficult, or when the parental species have similar morphology.

Advances in DNA sequencing technology allow us to follow changes in hybrid zone positions in real time. The ability to generate molecular markers across the genome for non-model organisms allows detection of divergent genomic regions between closely related species (e.g., [73, 74]). The size and chromosomal distribution of these regions vary across taxa, and mechanisms for their origin and maintenance might vary as well. However, large, multi-locus datasets from broad scale sampling of species ranges and hybrid zones are now

relatively easy to obtain (e.g. see Table 2 in [75]). At the same time, new target enrichment sequencing methods (e.g., exon capture) that are appropriate for the degraded DNA obtained from museum samples can extend our temporal sampling and potentially allow analysis of samples that pre-date human mediated climate change [76]. Finally, the field of citizen science has developed rapidly, and some of the largest citizen science databases are now providing scientists with the raw data necessary to track distributional changes across large geographic regions over relatively short timescales (e.g., a decade) [7] (See Box 2). Combining molecular data from broad geographic sampling with geographic cline analyses allows the close tracking of hybrid zone centers through time. Using these resources, we can record and interpret genetic and distributional changes of hybridizing species in response to climate change.

## Introgression and Adaptation

Natural hybridization has the potential to generate novel genetic combinations, either through hybrid speciation or introgression [16,24,26,34,77]. Compelling evidence for speciation via hybridization remains rare in animals [33] but is more common in plants [24]. In contrast, adaptive introgression is well documented in both plants and animals [78,79]. In fact, recent evidence for genome-wide introgression in the *Anopheles* species complex raises the intriguing possibility that in some cases introgression can be more extensive and more difficult to detect than previously believed [32]. There is growing evidence that introgression can lead to the acquisition of favorable alleles in response to climate change ([77], see *Papilio* example below). Repeated genomic sampling of hybrid zones responding to climate change will be one of the best avenues for determining the importance of adaptive introgression as a response to climate change.

In addition to using hybrid zones to monitor distributional changes of interacting species, we can also use hybrid zone data to document how climate change alters selection pressures. In this context, we must recognize that genomes are not coherent and that genome regions can have independent evolutionary histories. Using this framework, range boundaries might be defined in terms of individual genes or gene regions; that is, introgression represents a (possibly adaptive) range change for a particular genome region. This approach will allow identification of genes that affect thermal tolerances and climate-relevant physiology (i.e., genes that affect phenotypes relevant to climate change), as well as adaptation to altered environments and/or communities. In some cases alleles at these loci are highly diverged between parental species and their patterns of introgression can be tracked using cline analyses (e.g., [7,13] (Box 3). Alternatively, natural variation in hybrid zones can be used to associate particular genotypes with adaptation to climatic niches and to monitor changes in these traits as climate changes [80-83]. Hybrid zones are essentially natural mapping experiments; generations of recombination break down linkage disequilibrium in hybrid genomes and divergent alleles can be associated with environmental variables or phenotypes [84]. This approach will be particularly useful in cases where large, highly admixed or stable hybrid populations exist (e.g. spruce, poplar, house mouse).

## Hybrid zone case studies

Here we describe three case studies that provide insight into the influence of climate change on species distributions and introgression. We recognize that not every hybrid zone will be amenable to this approach, and suggest other avenues of research that will further the role of hybrid zones in the study of climate change.

The widely distributed white spruce (*Picea glauca*), hybridizes with two western spruce species, Engelmann spruce (*P. engelmannii*) [85-88] and Sitka spruce (*P. sitchensis*) [89,90] (Figure 1A). Each spruce species occupies a unique climatic niche and remains genetically, morphologically and ecologically distinct. Yet in areas of contact, there is weak reproductive isolation and extensive gene flow. Species distributions are largely influenced by temperature, precipitation (Sitka and White spruce), continentality and mean winter temperature, all of which have the potential to change rapidly with anthropogenic climate change. Hybrid genotypes appear to form stable populations along environmental gradients between parental habitats, suggesting that combinations of parental alleles can allow hybrids to be locally adapted to conditions at the edge or outside of the parent species range [86,90]. As a result, gene flow among spruce populations might serve as a conduit for adaptive introgression of alleles that enables species to cope with changing environmental conditions [82]. At the same time, monitoring the distribution of hybrid individuals on the landscape will provide insight into the speed with which tree species can respond to climate change. Necessarily, such studies will need to be long-term, given the generation times of these long-lived species.

North American tiger swallowtail butterflies in the genus *Papilio* (*P. glaucus* and *P. canadensis*) hybridize in a narrow band that stretches across much of North America [13] (Figure 1B). Decades of research on this hybrid zone in the Great Lakes region of North America (>30 years) have provided unique insights into interspecific gene flow, local selection, ecological divergence, incipient speciation, and hybrid zone movement. The occurrence and movement of this hybrid zone has been attributed to climate change [13,14]. Perhaps more than any other North American hybrid zone, the swallowtail hybrid zone has provided examples of introgression of species-specific alleles in response to climate change. For example, alleles related to the ability of *Papilio* larvae to detoxify host plants have introgressed northwards 200km over the past 15 years, potentially driven by strong selection on novel phenotypes produced within the hybrid zone (Figure 1B). Alleles related to diapause control have also introgressed northwards, but to a lesser extent (Figure 1B). Expanded sampling along this hybrid zone to determine the geographic consistency of these patterns, and using citizen scientists to accurately map the distribution of each species through time, are two natural extensions of the work carried out thus far on *Papilio*.

Black-capped (*Poecile atricapillus*) and Carolina (*P. carolinensis*) chickadees hybridize in a narrow band that stretches from New Jersey to Kansas. The zone of contact appears to be defined by temperature (Figure 1C). A recent examination of the hybrid zone that combined genomic, distributional (from a citizen science database), and climatic data provided clear evidence of hybrid zone movement northwards over the past decade, and showed that the recorded movement was closely tied to warming winter temperatures [7]. This investigation

was limited in geographic scope compared to the extent of the hybrid zone. Additional insight into the influence of climate change on the distribution of both species could be gained by expanding both the genetic and distributional studies. A subset of the loci from the genomic dataset used in this study were fixed for different alleles in the parental species, and preliminary analyses suggest that some of these are located in regions of the genome related to oxidative phosphorylation and metabolism [91]. Additional work on the hybrid zone could provide interesting insight into species barriers and the influence of climate change on the permanence of those barriers, as well as insight into the nature of reproductive isolation as it relates to differences in thermal tolerance in a changing climate.

The highlighted studies are just three examples of species that hybridize where they overlap; these examples are restricted to North America, and for each we already possess significant data. These hybrid zones are easy to map and monitor and have already provided insight into the effects of climate change on species' distributions and the influence of climate on local adaptation and adaptive introgression. Other hybrid zones exist both within North America and elsewhere that have the potential to inform our understanding of the influence of contemporary climate change on species distributions, and on the role of climate change in adaptive introgression (Table S1).

### **Species interactions and climate-driven distributional changes**

Species interactions can confound our interpretation of climate-driven impacts on distribution, but close monitoring of hybrid zones should improve our understanding of these interactions and their influence. Hybrid zone studies have the potential to identify cases in which expansion of one species is limited by biotic interaction with another species; competitive interactions are rarely included as a factor in contemporary climate niche modeling. It is important to note that ecological interactions (but not introgression) can occur in the absence of hybridization. This means that parapatrically distributed species or subspecies will also offer important opportunities for understanding distributional changes in response to climate change.

### **Concluding remarks: The utility of monitoring hybrid zones in a changing world**

For nearly half a century biologists have been using morphological and molecular markers to characterize species interactions within hybrid zones. During that time, the pace of anthropogenic climate change has accelerated with obvious consequences for species' distributions. Range expansions and contractions, and local extinctions are becoming commonplace, but we are not always well prepared to document these changes, or predict them. We are now poised to utilize both historical and current sampling of hybrid zones to understand how species interactions and adaptive responses are being transformed by our changing climate. We emphasize that hybrid zones should be sampled with this change in mind; they should not be viewed as equilibrium situations. We also highlight the utility of new genomic methods (increased genomic and geographic representation, use of historical DNA samples) and public databases (citizen science) that will facilitate studies of hybrid

zone movement. As the approaches we suggest are adopted, hybrid zones will continue to act as windows on evolution and ecology in our changing world.

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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## Glossary

<b>Admixture</b>	The mixing of individuals from two (or more) source populations that have different allele, genotype, or phenotype frequencies
<b>Biogeographic signature</b>	distribution of allelic or haplotypic variation that reflects species distributions in geographic space and through geological time
<b>Clinal hybrid zone</b>	A hybrid zone in which character states change in clinal fashion across the zone. Clinal zones can be “tension zones,” maintained by a balance between dispersal and selection against hybrids, or they can reflect selection along an environmental gradient
<b>Bounded hybrid superiority model</b>	A model that suggests that hybrid zones are maintained by selection for hybrids in intermediate habitats. Hybrids have higher fitness than either parent species in these habitats, but their fitness is lower in either parental species habitat [51]
<b>Hybridization</b>	The interbreeding of individuals from two populations, or groups of populations, which are distinguishable on the basis of one or more heritable characters. [20,99]
<b>Hybrid zones</b>	Regions where genetically distinct groups of individuals meet and mate resulting in at least some offspring of mixed ancestry [19,20]
<b>Hybrid speciation (homoploid)</b>	Origin of new species through the production of a stable population of recombinant individuals that are reproductively isolated from the parent species
<b>Introgression</b>	The incorporation of alleles of one entity into the gene pool of another, typically through hybridization and backcrossing [100]. Adaptive introgression refers to the introgression of advantageous alleles
<b>Mosaic hybrid zone</b>	Hybrid zones that occur when genetically distinct groups of individuals that differ in habitat or resource use interact in a patchy environment [20]

**Species boundaries**

The phenotype, genes or genome regions that remain differentiated in the face of potential hybridization and introgression [75]

**Tension zone**

Clinal hybrid zones maintained by a balance between dispersal into the hybrid zone and selection against hybrids [20]

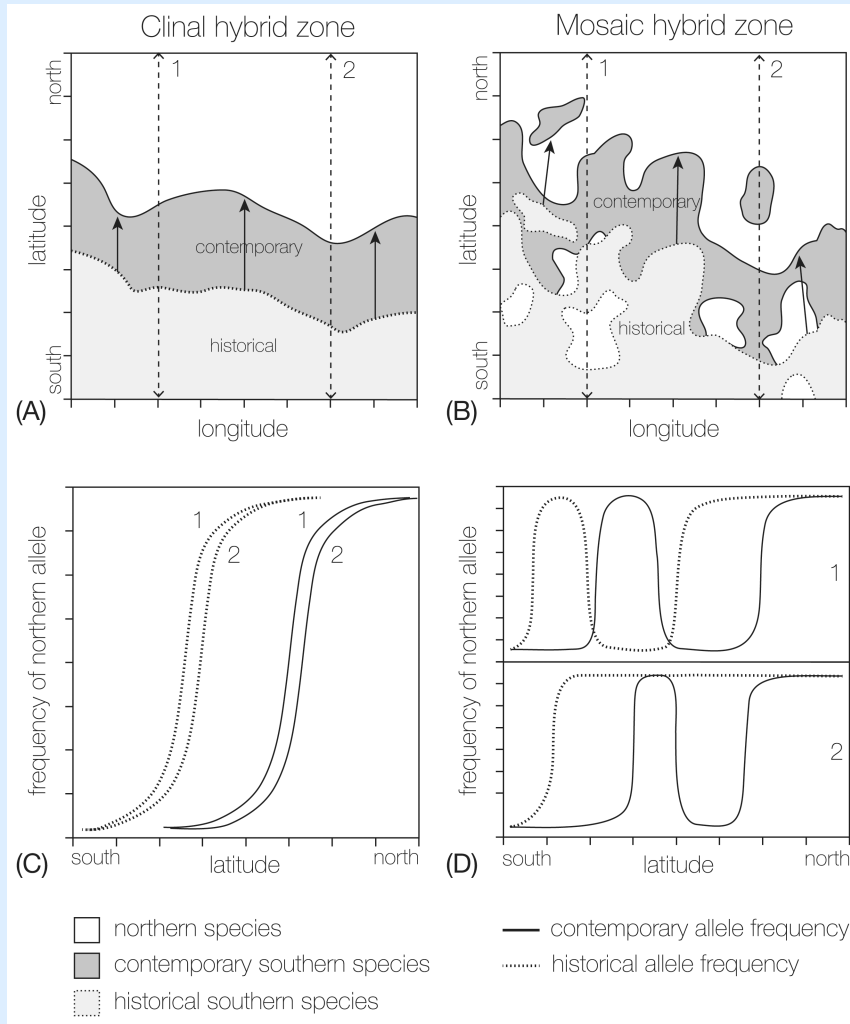
**BOX 1****Sampling hybrid zones in a changing climate**

**TEXT:** Appropriate sampling is critical for understanding patterns of variation within hybrid zones and for inferring ecological and evolutionary processes from those patterns. This is particularly true when species ranges and hybrid zones shift as a result of climate change.

*Markers-* Molecular analyses of hybrid zones tend to focus on regions of the genome that have private alleles or highly differentiated allele frequencies between species. Genome-wide markers are now readily available for any taxon, and diagnostic markers can be identified through genome-wide sequencing of multiple individuals from several allopatric populations. These markers can be used to classify individuals within the hybrid zone as a parental type or as individuals of mixed ancestry (e.g., F<sub>1</sub> hybrid, 1<sup>st</sup> generation backcross etc). With appropriate sampling of allopatric populations, diagnostic markers allow us to be confident that shared alleles within the hybrid zone are a result of hybridization and gene flow as opposed to ancestral polymorphism.

*Time points* – To capture hybrid zone movement and species range shifts, populations must be sampled at multiple time points. The time scale for repeated sampling will depend on the strength of selection, generation time and individual dispersal distances. Combining bioclimatic modeling with spatial demographic models can provide insights into expected rates of movement and therefore sampling periodicity. The best strategy will be to simultaneously track environmental and ecological variables (e.g., temperature and precipitation). Hybrid zones can also move stochastically and for reasons other than environmental change [17,21]; therefore, establishing a clear link between climate and hybrid zone movement is critically important.

*Geography* – Hybrid zones should be sampled broadly to characterize the structure (e.g. clinal vs mosaic) and capture the full area of interaction between species. This is particularly true for hybrid zones that are shifting. Sampling allopatric populations of each species is essential for identifying diagnostic markers and localizing the hybrid zone. Sampling of hybrid zones can be in linear transects or over large areas (e.g.[92]). However, linear transects can make clines look broader or sharper depending on the whether the transect is orthogonal to the hybrid zone (see [18]). Restricted geographic sampling of a hybrid zone can obscure patterns of variation, particularly in mosaic hybrid zones where overlap can be extensive and occupied habitat patches can appear and disappear with shifting species distributions. If sampled only at a fine scale, the area of contact or shifts in ranges can be missed. Note: data analyses will differ depending on the type of hybrid zone sampled, see Box 3).



**BOX 1, Figure I. Temporal and geographic sampling of hybrid zones in a changing climate**  
 The top panels represent northward shifts of a southern species (gray) and a northern species (white) for (A) clinal and (B) mosaic hybrid zones. The gray shading represents the northern range edge of the southern species' historical (light gray, dotted line) and contemporary (dark gray, solid line) distributions. Arrows highlight the shift in the species distribution. Lines 1 and 2 represent north-south transects across the hybrid zone. The change in the northern species' allele frequency along each transect for historical (dotted) and contemporary (solid) samples are plotted for the clinal hybrid zone (C) and the mosaic hybrid zone (D). The clinal hybrid zone forms an extensive and narrow zone of contact that extends east and west. In the mosaic hybrid zone, parental forms occupy distinct habitat patches in a heterogeneous landscape and hybridization occurs across patch boundaries. The patterns of variation in allele frequency differ depending on the transect. As the range of the southern species shifts north, habitat patches alter; patches disappear, new patches form and the area of each patch changes.

**BOX 2****Citizen science**

**TEXT:** Citizen science refers to data collection (and sometimes analysis) by members of the general public. These data are often related to natural systems (e.g., wildlife observations) and are collected in collaboration with scientists. A recent review highlighted 56 articles in the primary literature that dealt explicitly with citizen science, but suggested that the field was experiencing rapid growth [93]. Since that time, citizen science and use of citizen generated data has grown exponentially. We suggest that citizen science could be an important avenue of data collection for those interested in following distributional changes in hybrid zones. For example, the data used to generate a distribution map of the contact zone between black-capped and Carolina chickadees in Taylor et al. (2014) came from eBird [94], which is currently the largest citizen science database in the world. From citizen science data the authors were able to generate a high-resolution map of the species distributions and contact zone over a time period that coincided with the authors population sampling. This allowed the authors to combine information on the temporal changes in the chickadee hybrid zone with a genomic dataset and establish the link between hybrid zone movement and climate change. Numerous other citizen science databases exist [93] or are being initiated, that could serve to inform hybrid zone studies and facilitate the tracking of distributional changes over time. Even when hybrids are difficult to identify from morphology (as in the chickadee hybrid zone), participant training and rigorous data filtering will provide data suitable for high-level scientific inquiry. At the same time, citizen science best practices are being developed and made available to those interested in initiating large-scale data collection by public participants [95]. Given that we are suggesting that many hybrid zones should be monitored over the largest geographic region possible, citizen science might be one of the only ways researchers will be able to collect appropriate data. We acknowledge that there are some organisms that might lack public attention, or be inaccessible, but citizen science data collecting programs could generate the necessary involvement in many cases. Public involvement in scientific endeavors, especially when they relate to detecting the impacts of climate change on biodiversity, is increasingly important. Indeed, most scientific granting agencies require that grant proposals indicate how the proposed research will be extended into the public sphere.



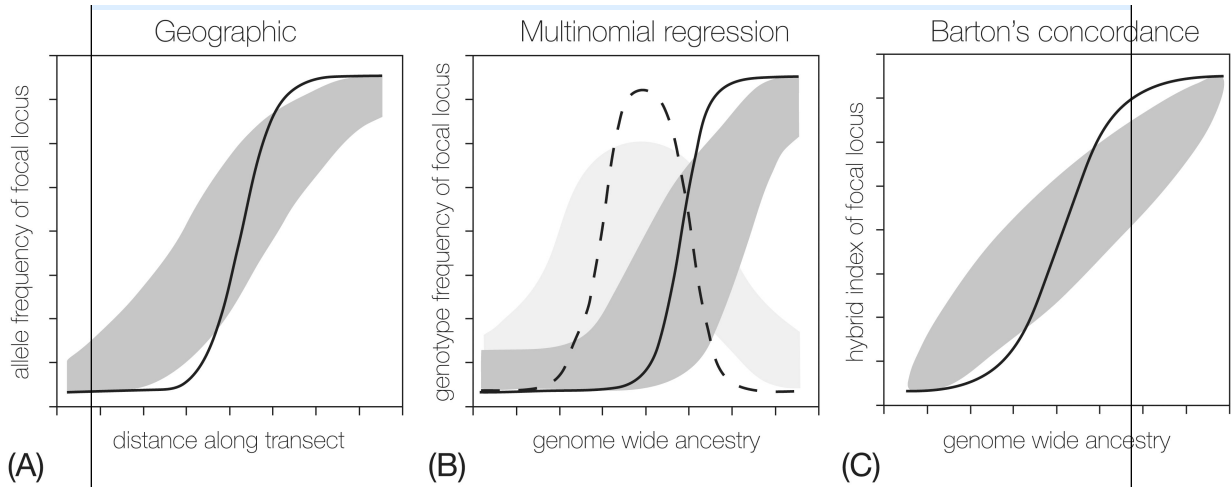
**BOX 3****Detecting admixture and introgression**

**TEXT:** Hybridization and recombination shuffle divergent genomes, thereby allowing regions of the genome to behave independently, depending on linkage relationships and functional interactions (epistasis). Genes or gene regions that function in the genomic background of both of the hybridizing species can be exchanged (introgress). In contrast, regions that contribute to local adaptation, premating barriers, or hybrid unfitness will exhibit restricted introgression. Therefore, patterns of introgression can help identify genomic regions that affect these phenotypes.

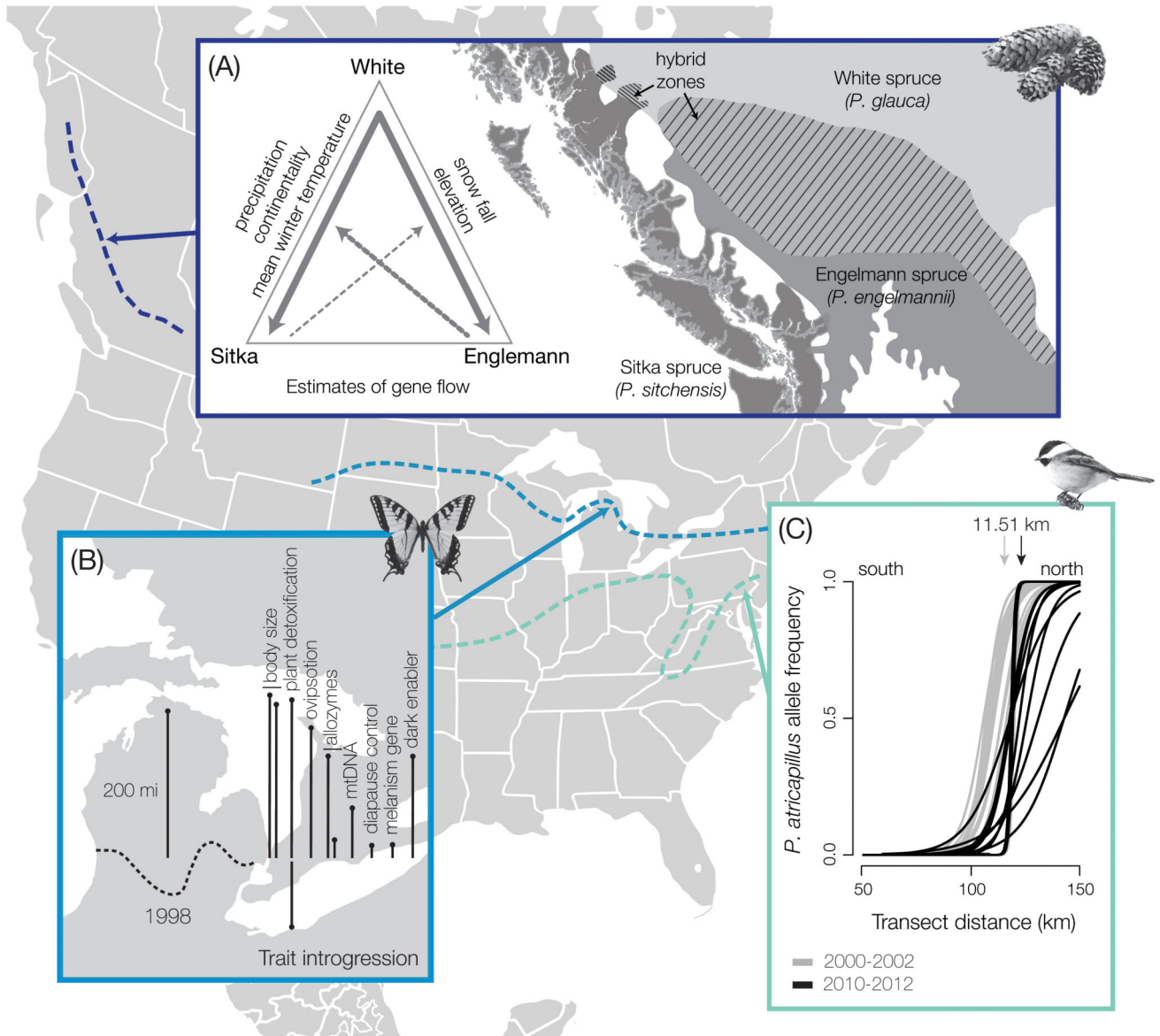
A classic approach to estimating introgression is to plot the change in allele frequencies along a transect across the hybrid zone (geographic cline) (Figure IA). Alleles that contribute to species boundaries or local adaptation will show abrupt changes in frequency across the zone, whereas alleles that introgress will show more gradual changes. Geography is a proxy for admixture; the center of the zone has the greatest admixture and hybrid individuals become less common away from the center. Geographic clines perform well when a hybrid zone is independent of the environment or occurs along an environmental gradient, but in cases where species have patchy distributions allele frequencies can change abruptly between adjacent habitat patches (see Box 1). Mosaic hybrid zones can be characterized using geographic clines but must be sampled appropriately (i.e., across single habitat patch boundaries [54,92]).

An alternative is a “genomic cline” approach that plots the change in allele frequency for a locus against an estimate of genome-wide admixture. Individuals within a hybrid zone are each evaluated for the proportion of their genome derived from one parental species (hybrid index). The observed change in allele frequency at the focal locus is then plotted against an expected change based on the mean hybrid index. Significant deviations suggest genes are experiencing selection. This approach, originally introduced by Szymura and Barton (1986), has been implemented in several new forms (see [74,96], Figures IB and IC).

Geographic and genomic cline analyses are complimentary, and each has its own application. However, in cases where hybrid zones are shifting as a result of climate change, the implementation of these approaches is critical. Geographic clines are an obvious way to document shifting species distributions, and as long as care is taken in sampling the hybrid zone (See Box 1), they can be very informative (See [7]). Genomic clines can also be used to document shifting species distributions. In this case, the change in species ranges can be evaluated by comparing the proportion of individuals with different hybrid indices at different time points or geographic locations (see [91]).

**BOX 3, Figure I.**

Clinal analyses for estimating introgression across a hybrid zone. Each panel depicts expected clines for a hybrid zone that is maintained by local adaptation, premating barriers that prevent the formation of hybrids, or selection against hybrids. The black lines depict a locus under selection; one that contributes to local adaptation or reproductive barriers. The gray represents the expected range of cline shapes for unlinked neutral markers. A) Classic geographic clines. B) Genomic clines modeled using multinomial regression [80, 96]. C) Genomic clines modeled using either Barton's concordance method [97], Bayesian genomic clines [98] or the log-logistic method [74].



### Figure 1. Hybrid zone case studies

(A) Spruce hybrid zones (*Picea glauca* × *P. engelmannii* and *P. glauca* × *P. sitchensis*) [90]. The map to the right shows species distributions (indicated by dark gray (*P. sitchensis*), medium gray (*P. engelmannii*) and light gray (*P. glauca*)) and locations of the two hybrid zones. The triangle on the left summarizes estimated gene flow between the three species. Line width roughly corresponds to the percentage of shared alleles. Dashed lines indicate potential gene flow between two parental species and admixed individuals from the other hybrid zone. Climatic variables that are associated with each hybrid zone are indicated on the outside of the triangle. (B) Swallowtail butterfly hybrid zone (*Papilio glaucus* and *P. canadensis*) [13]. The map indicates the hybrid zone (dashed line) running east to west across Wisconsin. Lines represent the extent and direction (north or south) of species-specific trait introgression from 1998 to 2011. (C) Chickadee hybrid zone (*Poecile*

*atricapillus* and *P. carolinensis*) [7]. Locus specific allele frequencies are plotted against distance along a linear transect (geographic clines) from historical (gray) and contemporary (black) sampling. Average shift north of 11.5 km in 10 years.