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Dispersal Predicts Hybrid Zone Widths across Animal Diversity: Implications for Species Borders under Incomplete Reproductive Isolation

Jay P. McEntee,[1,*] J. Gordon Burleigh,[1] and Sonal Singhal[2,†]

1. Department of Biology, University of Florida, Gainesville, Florida 32611; 2. Department of Biology, California State University, Dominguez Hills, Carson, California 90747

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abstract: Hybrid zones occur as range boundaries for many animal taxa. One model for how hybrid zones form and stabilize is the tension zone model, a version of which predicts that hybrid zone widths are determined by a balance between random dispersal into hybrid zones and selection against hybrids. Here, we examine whether random dispersal and proxies for selection against hybrids (genetic distances between hybridizing pairs) can explain variation in hybrid zone widths across 131 hybridizing pairs of animals. We show that these factors alone can explain ∼40% of the variation in zone width among animal hybrid zones, with dispersal explaining far more of the variation than genetic distances. Patterns within clades were idiosyncratic. Genetic distances predicted hybrid zone widths particularly well for reptiles, while this relationship was opposite tension zone predictions in birds. Last, the data suggest that dispersal and molecular divergence set lower bounds on hybrid zone widths in animals, indicating that there are geographic restrictions on hybrid zone formation. Overall, our analyses reinforce the fundamental importance of dispersal in hybrid zone formation and more generally in the ecology of range boundaries.

Keywords: cline theory, hybridization, range boundaries, tension zone model, reproductive interference, biotic interactions.

Introduction

The edge of a taxon's geographic range often abuts the edge of the range of another closely related taxon (Case and Taper 2000). If reproductive isolation between these taxa is incomplete, hybrid zones can form. Here, we adopt Harrison's (1990, p. 72) definition of hybrid zones as "zones of interactions between genetically distinct groups of individuals resulting in at least some offspring of mixed ancestry," with genetically pure populations found outside the zone. Hybrid zones often form when previously isolated populations come into secondary contact as a result of changing range boundaries (Remington 1968), but they also may form in place while populations diverge with gene flow (Haldane 1948; Endler 1977; Nosil 2012). Often, these regions of contact are narrow relative to the distributions of pure populations, even when they extend along significant swaths of a species' range (figs. 1, 2).

While hybrid zones have long been the subject of evolutionary inquiry (Endler 1977; Barton and Hewitt 1985; Harrison 1990), they remain underappreciated in ecology, particularly in the study of geographic range limits. Geographic range limits are thought to arise from a number of factors, such as dispersal barriers, abiotic limits, and biotic interactions, including hybridization (Case and Taper 2000; Case et al. 2005; Goldberg and Lande 2007; Hochkirch et al. 2007; Sexton et al. 2009; Jankowski et al. 2013; Weber and Strauss 2016). Few ecological studies, however, have considered the potential for hybridization to set range boundaries. Given the increasing evidence for the prevalence of hybridization across the animal tree of life (Mallet et al. 2016), hybridization is likely to be important in the formation of many range boundaries, even where hybrids have yet to be found (Levin 2006). Thus, the extensive body of empirical and theoretical work on hybrid zones, although largely focused on evolutionary questions, may also yield important ecological lessons about range limits for two reasons. First, because hybrid zone studies typically sample densely at the edges of species' ranges, they provide high-resolution data for the analysis of range boundaries. Second, hybrid zone data are typically analyzed using a fairly small set of standardized approaches, making it possible to compare the spatial scale of range limits across phylogenetically distant relatives, like mammals and insects.

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[*] Present address: Department of Biology, Missouri State University, Springfield, Missouri 65897.

[†] Corresponding author; email: sonal.singhal1@gmail.com.

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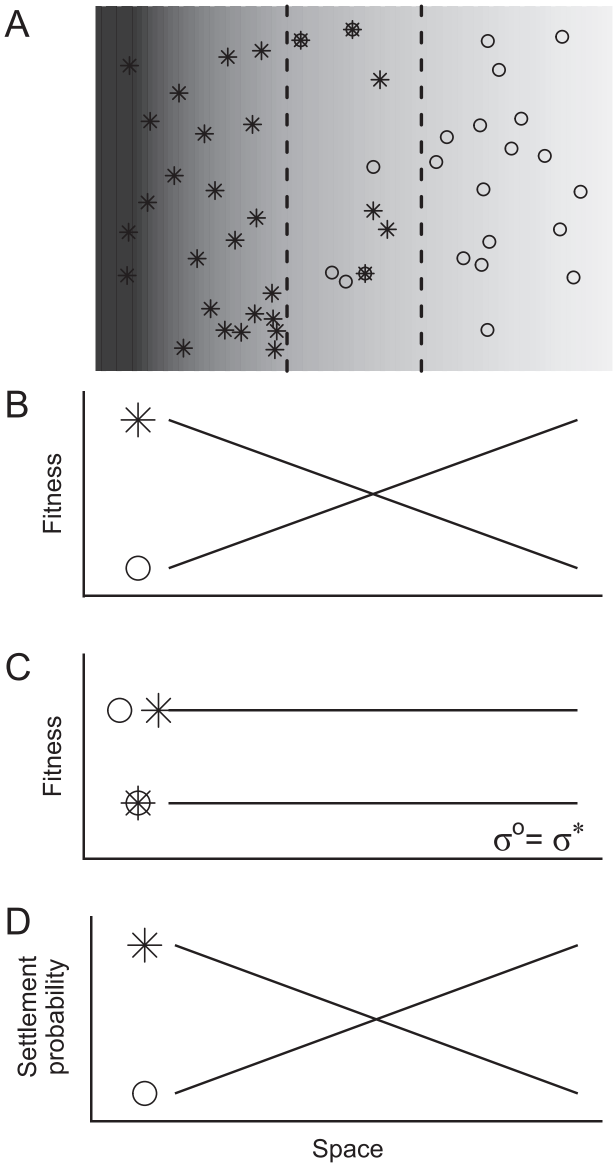

Figure 1: Depictions of hybrid zone models. *A* depicts a clinal hybrid zone, where two differentiated taxa (circles and asterisks) meet and form hybrids (asterisks inside circles, here indicating individuals of mixed ancestry). The dashed lines indicate the approximate boundaries of where hybrids are formed. Models to explain the stabilization of these hybrid zones are not mutually exclusive but invoke different processes. In *B*, the fitness of the two taxa varies inversely along an ecological gradient, with hybrids formed in the area where they have similar fitness. The environmental gradient is indicated by the shading in *A*. *C* depicts the most commonly invoked form of the tension zone model, in which fitness is constant across the hybrid zone but where hybrids always have lower fitness than "pure" individuals. Stabilization occurs as a balance between selection against hybrids and dispersal rate σ, which is generally modeled as being similar between taxa. *D* depicts a habitat selection model where hybridizing taxa differ in habitat preferences, and hybrids are formed where these habitat preferences overlap.

Much of our understanding of how hybridization can set range limits derives from theoretical models of hybrid zone stabilization. With respect to ecology, these models can be divided into two classes: those that require ecological gradients (Endler 1977; Goldberg and Lande 2007; Armsworth and Roughgarden 2008; Price and Kirkpatrick 2009) and those that do not (Bazykin 1969; Barton and Hewitt 1985; Case et al. 2005; Goldberg and Lande 2007). In hybrid zone models requiring ecological variation across space, each parental taxon is adapted to its local environment and shows decreased fitness elsewhere (fig. 1). In such hybrid zones, hybrid offspring are typically limited to the ecotone, where their fitness is similar to—or even greater than—that of parental taxa (fig. 1; Moore 1977). In contrast, in models without ecological gradients, fitness does not depend on local environmental conditions. One such model is the tension zone model (Key 1968; Bazykin 1969; Barton and Hewitt 1985), in which hybrids show reduced fitness compared with their parents, either because of intrinsic selection, such as Dobzhansky-Muller incompatibilities (Dobzhansky 1936; Muller 1942), or because hybrid traits have low fitness in all environments (Mallet et al. 1998). Importantly, the location of a tension zone can be random with respect to geographic space and local ecological gradients, although it is predicted to move toward regions of reduced dispersal (Barton and Hewitt 1985; Goldberg and Lande 2007). Of course, both ecological variation and selection against hybrids independent of local ecology can affect a single hybrid zone (Bronson et al. 2003; Taylor et al. 2014).

Ideally, to understand how range boundaries associated with hybridization are typically formed and maintained, we could reconstruct the conditions under which these boundaries are formed. Such an approach would allow us to understand how ecological transitions, taxon fitness across such transitions, and taxon habitat preference—or the lack thereof—interact to structure hybrid zones and enforce range boundaries of hybridizing taxa (fig. 1). However, such an approach is not feasible for most taxa. Absent this more direct approach, we can examine whether variation in hybrid zone widths can be predicted by the factors that stabilize hybrid zones in theoretical models. To make our predictions, we focus on the tension zone model both because it has been extensively applied in the hybrid zone literature (Barton and Gale 1993; Gay et al. 2008) and because the simple form of the model assumes a homogeneous environment, making it a useful null model for how hybrid zones might form and stabilize with respect to local ecology. The simple form of the tension zone model predicts that hybrid zones are stabilized by just two forces, random dispersal and selection against hybrids. The balance between these two forces determines the width of the hybrid zone boundary, which is expected to be stable through time

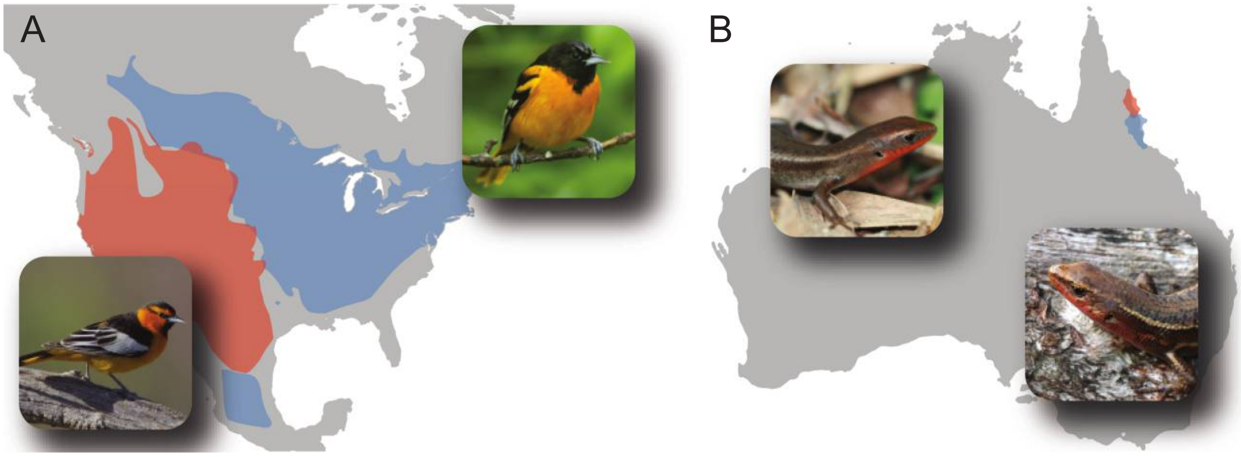

Figure 2: Geographic ranges and species photos for two of the hybrid zones included in this study. *A*, *Icterus bullocki* (red; *left*) and *I. galbula* in North America (blue; *right*). *B*, *Carlia crypta* (red; *left*) and *C. rubrigularis* (blue; *right*) in Australia. The *I. bullocki*/*I. galbula* hybrid zone is geographically extensive and occurs between temperate, high-dispersing, morphologically differentiated species. In contrast, the *C. crypta*/*C. rubrigularis* hybrid zone is geographically narrow and occurs between tropical, low-dispersing, morphologically cryptic species. These two hybrid zones exemplify some of the diversity in hybrid zones. Image credits: *I. bullocki* (photograph by Gregory Smith; distributed under a CC-BY 2.0 license), *I. galbula* (photograph by Laura Gooch; distributed under a CC-BY 2.0 license), *C. crypta* (photograph by Ben Phillips), *C. rubrigularis* (photograph by Sonal Singhal).

under a number of demographic and ecological scenarios (Case et al. 2005; Goldberg and Lande 2007).

In this study, we address a central question in the ecology of hybrid zones: which factors determine the widths of hybrid zones? To answer this question, we conducted a meta-analysis of 131 hybridizing pairs animal taxa. In particular, we explore whether dispersal distance and the strength of selection against hybrids predict hybrid zone width, as in the tension zone model. This study represents the first quantitative synthesis of hybrid zones since Barton and Hewitt (1985) and thus provides a novel summary of patterns from hybrid zones in the DNA sequencing era.

Methods

Literature Review

We identified animal hybrid zones for inclusion in this meta-analysis by using Google Scholar and Web of Knowledge on February 6–8, 2016, and May 1–4, 2017. We reviewed matches to the search term “hybrid zon*” and all articles that cited the four major software programs used to estimate clines: HZAR (Derryberry et al. 2014), Cfit7 (Gay et al. 2008), Analyse 1.3 (Barton and Baird 1995), and ClineFit (Porter et al. 1997). From each study and for each cline we recorded cline width, cline center, and cline type (e.g., morphological, behavioral, genetic; see table A1; tables A1, A2, S1–S22 are available online).

Additionally, we summarized metadata for each hybridizing pair (table A2). We (1) found estimates of dispersal rates in the literature, (2) measured a morphological proxy for dispersal in birds for bird-specific analyses, and (3) either found or estimated genetic distances of mitochondrial (mtDNA) and nuclear (nDNA) sequences between hybridizing taxa. Details on how we collected these data appear below. Several hybridizing pairs were studied across multiple temporal or geographic transects. For these pairs, we also recorded data by transect. Hybridizing pairs that could not be included because of incomplete metadata are summarized in table S1.

Dispersal Estimates

In the tension zone model, clines are stabilized as a balance between the dispersal of hybridizing taxa into the hybrid zone and selection against hybrids. Accordingly, we identified a dispersal rate estimate for each hybridizing pair either by referencing estimates included in the studies themselves or by culling estimates from the broader literature. We preferentially targeted estimates from the species themselves, then their close relatives (i.e., congenerics), and then related taxa with similar natural history (e.g., temperate-breeding latitudinal migrant passerines). Across hybridizing pairs, dispersal was estimated using a number of methods, including measuring isolation-by-distance relationships from population-genetic data (Rousset 1997) and using mark-recapture studies to estimate movement rates. To ensure that dispersal and cline width estimates were not autocorrelated, we avoided estimates of dispersal rates derived from cline width estimates, for example, using estimates of linkage disequilibrium in the hybrid zone to estimate root-mean-square dispersal (Barton and Gale 1993).

Different methods for measuring dispersal make different assumptions. For example, field-based estimates are typically less than genetic estimates because field-based approaches fail to capture most long-distance dispersal events (Koenig et al. 1996). Additionally, field-based estimates are often given in units proportional to years, whereas genetic estimates are given proportional to generations. While these methodological differences likely introduce error, this error is unlikely to be more than one order of magnitude. For some taxa, we were able to identify multiple estimates of dispersal; these estimates were generally within an order of magnitude. Furthermore, dispersal in our data set varied across more than four orders of magnitude (from .007 to 150 km; fig. S1; figs. S1–S7 are available online). Thus, we do not expect these errors to result in qualitative differences in our results.

As literature-based dispersal estimates are not standardized across studies, we pursued an alternate standardized proxy for a sample of hybrid zones. For avian hybrid zones, we measured a morphological proxy for dispersal, the hand-wing index (HWI; Claramunt et al. 2012), on adult bird study skins in the Florida Museum of Natural History; the Museum of Vertebrate Zoology at the University of California, Berkeley; and the Natural History Museum, London. We measured up to three individuals of each sex per taxon. We averaged HWI by sex, then by taxon, and then by hybridizing pair to estimate a single HWI value per hybridizing pair. The mean numbers of measured specimens per taxon and per hybridizing pair were 4.4 ± 1.9 (SD) and 6.5 ± 3.8, respectively.

Genetic Distance Estimates

As tension zones may be stabilized by selection against hybrids, we estimated mtDNA and nDNA genetic distances between hybridizing taxa as a proxy for selection against hybrids. Increasing genetic divergence tends to result in stronger selection against hybrids (Coyne and Orr 1989; Sasa et al. 1998; Pereira and Wake 2009; Singhal and Moritz 2013), for example via the accumulation of negative epistatic interactions like Dobzhansky-Muller incompatibilities (Fierst and Hansen 2010).

To estimate genetic distance between taxa, we searched GenBank for all available sequence data for hybridizing taxa. We then estimated mtDNA and nDNA distances separately. We aligned sequence data using MUSCLE (Edgar 2004) and then calculated the average genetic distance between hybridizing taxa with the Tamura-Nei model of molecular evolution (Tamura and Nei 1993), using the dist.dna function in the R package ape (Paradis et al. 2004). For species sampled for multiple loci, we averaged distance estimates across loci, weighted by length. For those taxon pairs where we could not find genetic data, we used estimates of genetic divergence from the literature ($n = 11$ mtDNA and 7 nDNA genetic distances).

In total, we were able to estimate or identify mtDNA distances for 131 taxon pairs and nDNA distances for 73 taxon pairs. We performed analyses using either (1) nDNA distance and mtDNA distance as separate predictors of hybrid zone widths (hereafter, "nDNA+mtDNA analyses") or (2) mtDNA distance as the sole proxy for selection against hybrids (hereafter, "mtDNA-only analyses"). These two analyses have distinct advantages. nDNA is likely to serve as a better proxy for selection against hybrids than mtDNA distances (Galtier et al. 2009; Pereira et al. 2011), but the mtDNA-only analyses allow for more inclusive sampling.

Introgression can both decrease estimates of genetic distance and increase estimates of cline width, leading to autocorrelation between these two variables. We inferred the potential prevalence of introgression by identifying cases in which hybridizing pairs were nonmonophyletic in neighbor-joining phylogenies inferred from mtDNA sequences. Eighty-two hybridizing pairs were reciprocally monophyletic, suggesting that these data sets did not include introgressed alleles. For 40 taxa, nonmonophyly could be the result of incomplete lineage sorting, introgression, or both. For 11 taxon pairs, our genetic distance estimates were taken from the literature, so we could not test for reciprocal monophyly. For the nDNA sequences, very few loci showed reciprocal monophyly. Thus, we calculated both mean and maximum pairwise genetic distances for both mtDNA and nDNA sequences. Maximum pairwise genetic distance should be impacted by introgression only in extreme cases; we used these estimates as an alternate predictor for cline width in sensitivity analyses (see below).

For bird-only analyses (see below), we used time to the most recent common ancestor (TMRCA) as an alternate proxy for selection against hybrids using a large, multilocus phylogeny (Burleigh et al. 2015; McEntee et al. 2018). This data set excludes pairs of races or subspecies.

General Modeling Approach

Cline width measures the transition between genotypic or phenotypic traits in the hybrid zone. Hybrid zone studies often estimate multiple clines: across different molecular markers and phenotypic traits, at different time points, and/or for different spatial transects. While variation among cline widths within a hybrid zone can reveal evolutionary processes (Anderson 1953; Bazykin 1969; Singhal and Bi 2017; Schumer et al. 2018), we are primarily interested in variation in hybrid zone width among different hybrid zones instead of variation within hybrid zones. Thus, for each hybridizing pair we calculated the geometric mean of cline widths, which should reflect cline width at the modal geographic center between taxa (fig. S2).

Using a linear model framework, we tested the potential predictors of hybrid zone widths. Predictor variables included genetic distances (nDNA+mtDNA or mtDNA only), dispersal, taxonomic group, and all of their two-way interactions. Prior to modeling, we took the natural log of dispersal, genetic distance, and cline width. We then centered and scaled these variables by subtracting the mean and dividing them by their standard deviations. The two primary variants of our full models were

$$\begin{aligned} Y = \ & a + b_1 \times \log(\text{dispersal}) \\ & + b_2 \times \log(\text{nDNA distance}) \\ & + b_3 \times \log(\text{mtDNA distance}) \\ & + b_4 \times \text{taxonomic group} + \beta X + \epsilon, \end{aligned} \tag{1}$$

$$\begin{aligned} Y = \ & a + b_1 \times \log(\text{dispersal}) \\ & + b_2 \times \log(\text{mtDNA distance}) \\ & + b_3 \times \text{taxonomic group} + \beta X + \epsilon, \end{aligned} \tag{2}$$

where Y is the set of log cline widths, X is the set of two-way interactions, β is the set of interaction coefficients, and the remainder is standard linear model notation. We fit the full models and all simpler variants, with equation (1) fit to the sample of 73 hybrid zones for which we were able to calculate nDNA distances (the nDNA+mtDNA analyses) and equation (2) fit to the sample of 131 hybrid zones for which we had mtDNA distances (the mtDNA-only analyses). We report results from the best-fitting models using the corrected Akaike information criterion (AICc) and model averaging weighted by AICc (Burnham and Anderson 2003). We report model-averaged coefficient estimates with 95% confidence intervals (CIs) calculated from unconditional variances (Buckland et al. 1997) using the R package glmulti (Calcagno and de Mazancourt 2010).

Clade-Specific Analyses

Relationships between hybrid zone width and the predictors might be idiosyncratic across clades. Therefore, we conducted clade-specific analyses for well-sampled clades: amphibians ($n = 20$), birds ($n = 33$), insects ($n = 20$), mammals ($n = 26$), and nonavian reptiles ($n = 17$). We fit linear models for each clade using mtDNA distance as the sole proxy for selection against hybrids (as in linear model eq. [2] but without clade identity as a predictor). We did not conduct clade-level nDNA+mtDNA analyses because of low sample sizes.

Phylogenetic Analyses of Residuals

To account for phylogenetic effects, we either used taxonomic group as a possible predictor (see eqq. [1], [2]) or divided analyses by taxonomic group (see "Clade-Specific Analyses"). We did not perform a fully phylogenetically informed analysis because hybrid zones form independently of each other and their widths cannot reasonably be considered a heritable trait evolving along a phylogeny. Nevertheless, the residuals of our models could be phylogenetically correlated if a latent variable that is heritable at a phylogenetic scale predicted hybrid zone width. Thus, we tested whether the residuals from the best-fitting linear models showed phylogenetic signal, as measured by Pagel's λ (Pagel 1999; Revell 2012) in the R package phytools (Revell 2012). Because our analysis spans corals to mammals, we used the TimeTree of Life, pruned to relevant tips (Kumar et al. 2017). We estimated the phylogenetic signal of model residuals for both the full analyses (both the nDNA+mtDNA and the mtDNA-only analyses) and for the clade-level mtDNA-only analyses.

Sensitivity Analyses

We tested multiple variants of our model fitting to assess the robustness of our results to potential issues (table S2). In all sensitivity analyses, we first filtered the data set to relevant cline estimates and then took the geometric mean of clines within each hybridizing pair. The number of hybrid zones analyzed varies across sensitivity analyses because of this differential filtering.

First, some mean cline widths may be upwardly biased by widths estimated from loci that are nonclinal, either because these loci were never fully differentiated between taxa or because they experienced broad introgression (fig. S2). To address this concern, we fit a set of models to cline widths estimated from molecular hybrid indices only. Because molecular hybrid indices are polygenic, they should reflect the central tendencies for the width of the hybrid zone and thus may be more directly comparable across hybrid zones. Additionally, we estimated the correlation between hybrid index and geometric mean cline width estimates from the same hybrid zones to see whether both approaches yielded similar estimates of cline width.

Second, in our full analyses we sought dispersal estimates that were measured independently of hybrid zone width; occasionally, we discarded a cline-based dispersal estimate that was likely to be more accurate. To ensure that these alternate dispersal estimates do not give qualitatively different results, we repeated our analyses using these "best-available" dispersal estimates instead.

Third, genetic divergence and cline width might be autocorrelated if introgression is common and widespread. Thus, instead of using mean genetic distances between hybridizing pairs in our model, we used maximum genetic distance, which should be affected by introgression only if introgression is complete. We additionally compared our mean and maximum estimates of genetic distance to determine how often introgression might have biased cline estimates.

Fourth, we considered clines for mtDNA data alone. Because they are collected from the same marker type, mtDNA clines may be more directly comparable across hybrid zones and thus allow us to test the robustness of our patterns to variance in widths across cline type.

Last, we performed a set of analyses exclusively on avian hybrid zones. For avian hybrid zones, we measured more standardized alternative proxies for dispersal and selection against hybrids. As an alternative to dispersal estimates from the literature, we used the log of HWI (see "Dispersal Estimates"). As an alternative to genetic distance, we used TMRCA (see "Genetic Distance Estimates"). Thus, birds—which are also the most well-represented taxonomic group in our data set—offer an additional perspective on the robustness of our results.

Software

All analyses were done in R version 3.3.3 using the statistical and graphing packages lme4, glmulti, MuMIn, ggplot2, and cowplot (Bates et al. 2007; Calcagno and de Mazancourt 2010; Jaeger 2016; Wickham 2016; Wilke 2016; Barton and Barton 2018).

Results

Our review of the hybrid zone literature identified 131 hybridizing taxon pairs for which we could find quantitative data on cline widths, dispersal estimates or proxies, and genetic divergence. All data are deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.nvx0k6dnr; McEntee et al. 2020). Across hybridizing taxon pairs, we found data on a median of four clines per pair, across a median of two cline types (fig. S3). The most common cline types measured were for nDNA and mtDNA markers (fig. S3). Hybridizing pairs were fairly evenly split across vertebrate clades, although fish were underrepresented (fig. 3*A*). Hybrid zones occurred globally, although there was a strong bias toward studies from North America and Europe (fig. 3*B*).

The best model from our nDNA+mtDNA analyses had an adjusted R^2 of 0.404 and included three predictors (log dispersal, log nDNA distance, and log mtDNA distance) and a single interaction (log dispersal × log mtDNA distance). Most of the variance explained was attributable to log dispersal; a model including log dispersal as the sole predictor had an adjusted R^2 of 0.36 (table 1). The remaining predictors had lower relative importance (RI), flatter slopes, or both. Model-averaged coefficient estimates were consistent with the tension zone model (tables 1, 2; fig. 4); log dispersal had a strongly positive coefficient (0.63 ± 0.21 [95% CI]; RI = 1), and there was some support for a negative coefficient for log nDNA distance (-0.15 ± 0.25 [95% CI]; RI = 0.78).

In our mtDNA-only analyses, the best model had log dispersal as its only predictor. The adjusted R^2 of this model was 0.335 (table 3). Across all models, log dispersal was consistently supported as a predictor (model-averaged coefficient: 0.57 ± 0.17 [95% CI]; RI = 1; table 4; fig. 4*A*), and log mtDNA distance had very limited support as a predictor (coefficient: -0.02 ± 0.1 [95% CI]; RI = 0.42; table 4; fig. 4*B*). Taxonomic group and all interactions had even less support (RI < 0.2 for all; table 4).

Our within-clade analyses recovered a positive relationship between dispersal and hybrid zone width across

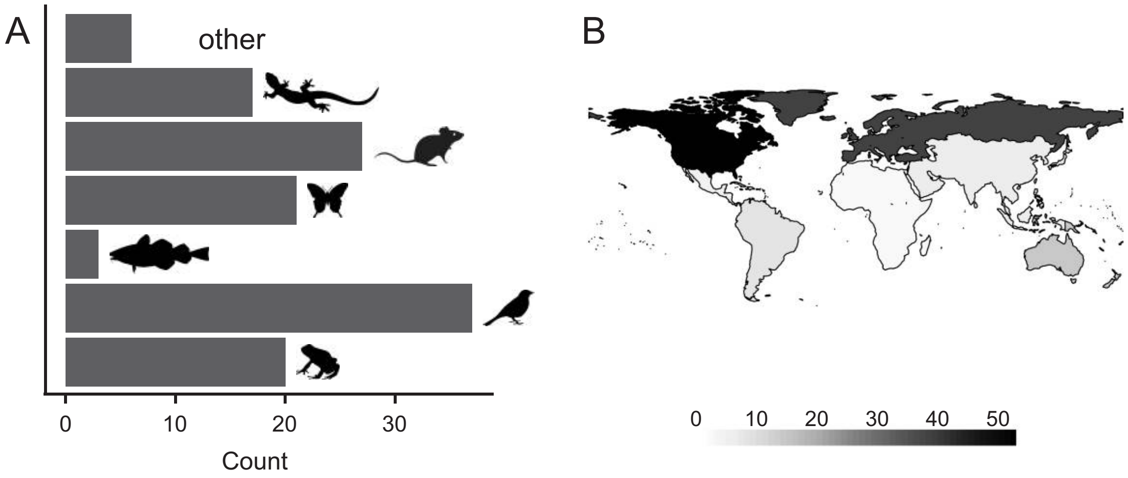

Figure 3: Distribution of hybrid zone studies ($n = 131$) across taxonomic groups (*A*) and geographic regions (*B*).

Table 1: Model fitting for predictors of cline width across hybrid zones

Model	AICc	Weights	Adj. r^2
~ log(dispersal) + log(mtDNA dist) + log(nDNA dist) + log(mtDNA dist) × log(dispersal)	177.4	.224	.404
~ log(dispersal) + log(nDNA dist) + log(nDNA dist) × log(dispersal)	178.5	.131	.385
~ log(dispersal) + log(mtDNA dist) + log(nDNA dist) + log(mtDNA dist) × log(dispersal) + log(nDNA dist) × log(dispersal)	178.5	.129	.406
~ log(dispersal)	178.9	.106	.36
~ log(dispersal) + log(mtDNA dist) + log(nDNA dist) + log(mtDNA dist) × log(dispersal) + log(nDNA dist) × log(mtDNA dist)	179.9	.066	.396

Note: Cline widths were calculated as the log of geometric mean of cline width per hybrid zone ($n = 73$). This model includes as predictors the log of dispersal, the log of mitochondrial DNA (mtDNA) distance, the log of nuclear DNA (nDNA) distance, taxonomic group, and all two-way interactions and is identified as the nDNA+mtDNA model in the text. All variables were scaled and centered before analysis. Shown are the five models with the highest weights. AICc = corrected Akaike information criterion.

all clades but amphibians (fig. 5; table 5). However, the relationship between log mtDNA distance and hybrid zone width varied among clades. The best models for birds and nonavian reptiles included mtDNA distance as a predictor of hybrid zone width. For nonavian reptiles, mtDNA distance scaled negatively with hybrid zone width, as expected in the tension zone model (fig. 5). However, in birds mtDNA distance and hybrid zone width scaled positively, opposite tension zone predictions. Thus, the weak relationship between mtDNA distance and hybrid zone width from analyses across all animal taxa was partly explained by opposing patterns among well-sampled clades.

Phylogenetic Analyses of Residuals

We found no evidence for phylogenetic signal in the full analyses (nDNA+mtDNA analyses: $\lambda = 6.6 \times 10^{-5}$, $P = 1$; mtDNA-only analyses: $\lambda = 5.5 \times 10^{-5}$, $P = 1$). We found evidence for phylogenetic signal in model residuals for our clade-level analyses only in the nonavian reptiles ($\lambda = 0.72$, $P = .037$). These results suggest that the preponderance of the unexplained variance in our linear models is not associated with phylogenetic effects.

Sensitivity Analyses

We tested multiple variants of this basic model to assess the robustness of our results (table S2), recovering similar patterns to our primary analyses (tables S3–S18). Model averaging offered strong support for dispersal as a predictor, with quantitatively consistent coefficient estimates (0.55–0.73) in all but the nDNA+mtDNA analysis of mtDNA clines only, where the slope estimate was much steeper but with a broader CI (1.41 ± 1.84 [95% CI]; RI = 0.98; table S18). Model-averaged coefficient estimates for nDNA distance were consistently negative but weak, with 95% CIs overlapping zero in all but the best-available dispersal analyses (tables S6, S10, S14, S18). For mtDNA distance, model-averaged coefficient estimates were consistently small in magnitude, with 95% CIs always overlapping zero (tables S3–S18).

In addition, we found that cline width estimates from hybrid indices and the geometric mean of clines were strongly correlated in pairwise comparisons (fig. S4; Spearman's $r = 0.87$, $P < 2.2 \times 10^{-16}$), suggesting that our geometric mean estimates were not strongly upwardly biased by outlier loci. Furthermore, mean and maximum genetic distances were strongly correlated for both mtDNA and nDNA (fig. S5; mtDNA: Pearson's $r = 0.93$, $P < 2.2 \times 10^{-16}$; nDNA: Pearson's $r = 0.90$; $P < 2.2 \times 10^{-16}$), suggesting that introgression did not have a significant impact on most of our genetic distance estimates.

For the avian hybrid zones, the alternative proxies for dispersal and selection against hybrids were correlated with the proxies used across all taxa (fig. S6). Models using HWI

Table 2: Model-averaging results for the models shown in table 1

Predictor	Coefficient ± SE	RI
Log(dispersal)	.63 ± .21	1
Log(nDNA dist)	−.15 ± .25	.78
Log(mtDNA dist)	.04 ± .17	.7
Log(dispersal) × log(mtDNA dist)	.15 ± .32	.54
Log(dispersal) × log(nDNA dist)	.06 ± .19	.4

Note: Shown are coefficients and relative importance (RI) for the five predictors with the greatest RI. mtDNA = mitochondrial DNA; nDNA = nuclear DNA.

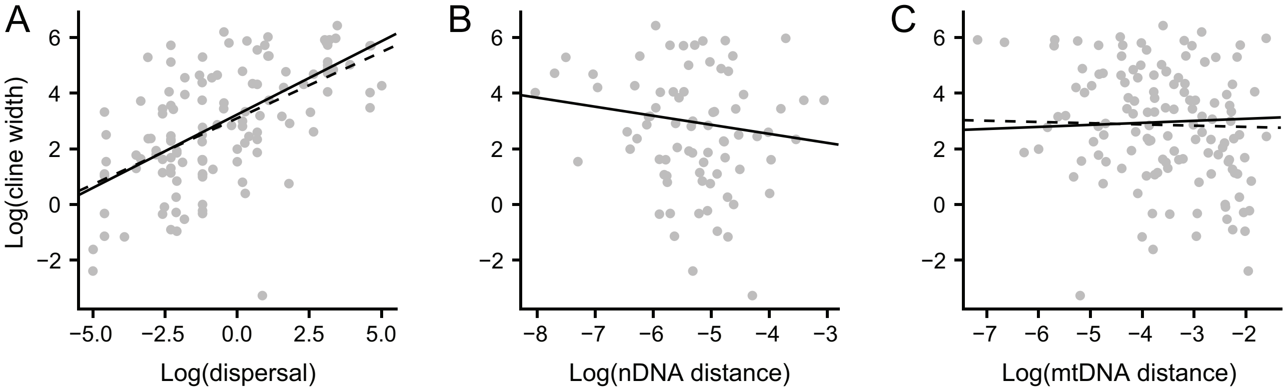

Figure 4: Relationship between mean cline width per hybrid zone in kilometers and the log of dispersal in kilometers (*A*; $n = 125$ hybrid zones), the log of nuclear DNA (nDNA) distance (*B*; $n = 73$), and the log of mitochondrial DNA (mtDNA) distance (*C*; $n = 125$). The solid black line is the model-averaged fit for models that included both nDNA and mtDNA distance as predictors (table 2); the dashed black line is for models that included only mtDNA distance (table 4).

as a proxy for dispersal support were qualitatively similar to analyses using dispersal estimates (tables S19, S20). In models using TMRCA instead of genetic distance as a proxy for selection against hybrids, TMRCA had a negative coefficient (table S22). This pattern is consistent with the tension zone model but opposite that found for genetic distances. Analyses using TMRCA excluded hybrid zone pairs below the species level, which may explain this difference in outcome.

Discussion

Across 131 hybrid zones, we found that random dispersal predicts hybrid zone widths across animals. Dispersal estimates alone explained 33.5% of the variation in hybrid zone widths in our most inclusive analysis. These hybrid zones occur across marine, freshwater, and terrestrial environments and across a wide swath of diversity, including invertebrate and vertebrate taxa. Thus, our results are consistent with random dispersal as a major determinant of hybrid zone width on a global scale across animal diversity.

In the most widely invoked version of the tension zone model (Barton and Hewitt 1985), the shapes of range boundaries are stabilized when selection against hybrids alone counters dispersal across the hybrid zone. To examine support for this proposed balance between dispersal and selection, we tested whether nDNA and/or mtDNA distance, as proxies for selection against hybrids, explained variation in hybrid zone width. We found some support for this hypothesis, albeit limited. As predicted by the tension zone model, we found that cline width scales negatively with nDNA distance. However, the 95% CI for nDNA distance slope estimates often included zero. Thus, our support for selection against hybrids as a structuring force in hybrid zones is limited and particularly weak when we use mtDNA distance as our proxy for selection against hybrids.

Why did we fail to recover stronger evidence that increasing selection against hybrids—here, measured as greater genetic distance—leads to narrower hybrid zones? This could be because our estimates of genetic distance are poor or inconsistent proxies for selection against hybrids. Because we estimated genetic distance using previously published data, the scope of these data varied tremendously across studies,

Table 3: Model fitting for predicting determinants of cline width across hybrid zones

Model	AICc	Weights	Adj. r^2
~ log(dispersal)	307.9	.543	.335
~ log(dispersal) + log(mtDNA dist)	309.6	.227	.332
~ log(dispersal) + log(mtDNA dist) + log(mtDNA dist) × log(dispersal)	310.2	.169	.335
~ log(dispersal) + taxonomic group	314.4	.021	.338
~ log(dispersal) + taxonomic group + taxonomic group × log(dispersal)	314.8	.017	.379

Note: Cline widths were calculated as the log of geometric mean of cline width per hybrid zone ($n = 125$). In contrast to the results presented in table 1, this model does not include the log of nuclear DNA distance as a predictor. Instead, it includes the log of dispersal, the log of mitochondrial DNA (mtDNA) distance, taxonomic group, and all two-way interactions and is identified as the mtDNA-only model in the text. All variables were scaled and centered before analysis. Shown are the five models with the highest weights.

Table 4: Model-averaging results for models shown in table 3

Predictor	Coefficient ± SE	RI
Log(dispersal)	.57 ± .17	1
Log(mtDNA dist)	−.02 ± .1	.42
Log(dispersal) × log(mtDNA dist)	.02 ± .07	.18
Taxonomic group	. . .	.06
Log(dispersal) × taxonomic group	. . .	.02

Note: Shown are coefficients and relative importance (RI) for the five predictors with the greatest RI. Coefficients not reported for predictors including taxonomic group because these are calculated for each one of the seven taxonomic groups. mtDNA = mitochondrial DNA.

from just one individual sequenced per taxon at one gene to tens of individuals sequenced per taxon at tens of genes. This variance in sequencing effort might further explain the relatively weak correlation between mtDNA and nDNA distances (fig. S7; Pearson's $r = 0.26$; $P = .021$; $n = 77$). Future studies may find that better genomic sampling or, more ideally, direct measurements of selection against hybrids might improve our ability to predict hybrid zone width across taxa.

However, possibly selection against hybrids does not structure most hybrid zones and other forces are more important. First, other ecological forces (e.g., competition or pathogens) could play a strong role opposing dispersal across most hybrid zones, with selection against hybrids having relatively limited ecological effect (Case and Taper 2000; Case et al. 2005; Ricklefs 2010). In the absence of ecological gradients, models suggest that these ecological processes would need to have greater intertaxon than intrataxon negative effects in order to stabilize the hybrid zone (Case et al. 2005; Goldberg and Lande 2007). Second, fitness gradients may also have broad importance across hybrid zones (Kruuk et al. 1999), even where it is difficult to detect steep ecological gradients. Fitness differences across ecological gradients should result in hybrid zone transitions that map to fitness gradients (Moore 1977), with widths determined by environments. Such ecological or fitness gradients might contribute to some of the unexplained variation in our models. Future comparative analyses of hybrid zones should ideally incorporate quantitative variation of such gradients.

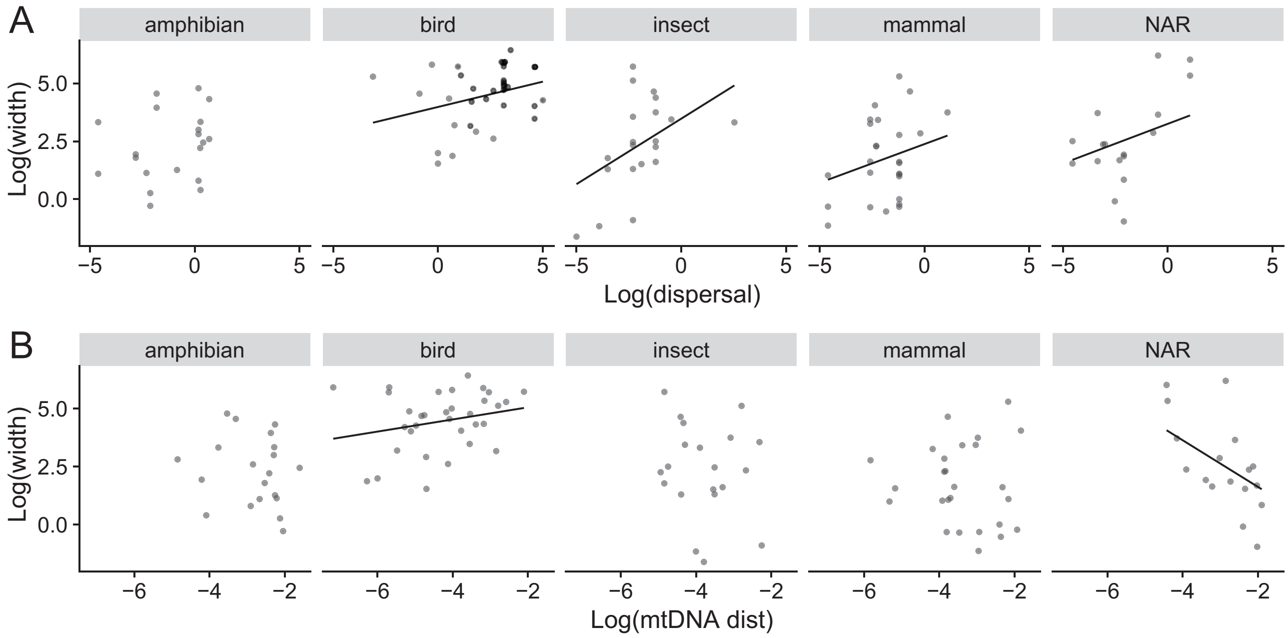

Figure 5: Relationship between mean cline width in kilometers and the log of dispersal in kilometers (*A*) and the log of mtDNA distance (*B*), by taxonomic group. Shown are the five most well-represented taxonomic groups and the linear fits for those variables with a model-averaged relative importance of ≥0.6 (table 5). NAR = nonavian reptiles.

Table 5: Results split by taxonomic group

Taxonomic group	N	Best model	Adj. r^2	Dispersal coefficient	mtDNA distance coefficient	Interaction coefficient	Dispersal RI	mtDNA distance RI	Interaction RI
Amphibians	20	Intercept only	0	.08 ± .32	−.05 ± .24	.03 ± .12	.34	.29	.06
Birds	33	~ log(dispersal) + log(mtDNA dist) + log(mtDNA dist) × log(dispersal)	.24	.31 ± .4	.24 ± .36	−.27 ± .45	.85	.85	.69
Insects	20	~ log(dispersal)	.22	.43 ± .54	−.03 ± .17	0 ± .03	.84	.23	.03
Mammals	26	~ log(dispersal)	.11	.25 ± .49	−.01 ± .12	0 ± .03	.67	.23	.03
NAR	17	~ log(dispersal) + log(mtDNA dist)	.48	.29 ± .59	−.44 ± .59	−.01 ± .05	.66	.82	.07

Note: Within each taxonomic group, we fit linear models that predicted the log of cline width by the log of dispersal, the log of mitochondrial DNA (mtDNA) distance, and their interaction. All variables were scaled and centered before analysis. Shown are the details of the best-fitting model as determined by corrected Akaike information criterion scores. Also shown are the estimated coefficients for all terms and their relative importance (RI), as determined by model averaging across the candidate model set. NAR = nonavian reptiles.

Last, selection against hybrids may be a weak predictor of hybrid zone width because the efficacy of selection against hybrids in stabilizing hybrid zones depends on the rate of hybridization or attempted hybridization. Tension zone models assume random mating under which both taxa suffer negative demographic consequences due to the low fitness of many of their offspring. Assortative mating, however, can lessen these negative demographic effects: the fewer attempts at hybridization, the lesser the demographic consequences of selection against hybrids. Compared with random mating, assortative mating may allow a taxon to expand its range further into the other taxon's range, widening the hybrid zone. Interestingly, we found positive relationships between genetic distances and cline width in clade-level analyses of birds (table 5). This result raises the question of whether assortative mating, in addition to selection against hybrids, scales with genetic distance in some clades.

More generally, our within-clade analyses reinforced that dispersal is a more consistent predictor of hybrid zone width than genetic distance, with four of five clades yielding positive slopes and high RI values in model fitting (table 5). The evidence for a positive association between cline width and dispersal was less strong for amphibians, which may be due to the challenge of characterizing dispersal kernels in species that have spatially (and possibly temporally) clumped dispersal, as is the case for pond-breeding amphibians.

Despite limited evidence that selection against hybrids structures hybrid zones, we argue that the tension zone model necessarily remains a fundamental model in explaining the stabilization of hybrid zones. Most hybrid zones have widths that fall within the predictions of the tension zone under very weak to moderate selection (fig. 6; see also fig. 3 in Barton and Hewitt 1985). Thus, these comparative data collectively continue to support the use of the tension zone as a suitable null model.

Our analyses also provide insight into the conditions under which animal hybrid zones deviate from tension zone expectations. Hybrid zones with strongly negative residuals with respect to dispersal (fig. 4*A*) may include instances where ecological gradients are steep, corresponding to fitness differences, and/or where there is habitat selection. For example, the largest outlier in our mean-widths analysis is from an extremely narrow hybrid zone between two lineages of the coral *Eunicea flexuosa*, which illustrates at least one, and perhaps both, of these scenarios (Prada and Hellberg 2014). *Eunicea flexuosa* has broadcast dispersal, with population genetic dispersal rate estimates ranging from 2.9 to 55.52 km per square-root generation. However, the hybrid zone is less than 100 m in width. This zone spans an extremely steep environmental gradient in depth and light availability, resulting in a steep selective gradient (Prada and Hellberg 2013; Prada and Hellberg 2014). Furthermore, despite their strong dispersal capacity, few *E. flexuosa* larvae settle in areas that poorly match their phenotypes (fig. 1 in Prada and Hellberg 2014), such that habitat selection might complement selection in narrowing the hybrid zone (fig. 1). Thus, a combination of strong selection against immigrants and habitat selection likely yields the most potent departures toward narrowness from the pattern found for other hybrid zones. Importantly, unlike most other species included in our analysis, the dominant life stage of corals is sessile. Sessile organisms like plants may be more prone to forming especially narrow hybrid zones relative to expectations from dispersal (Freeman et al. 1991; Cruzan and Arnold 1993), given the potential for fine-scale local adaptation.

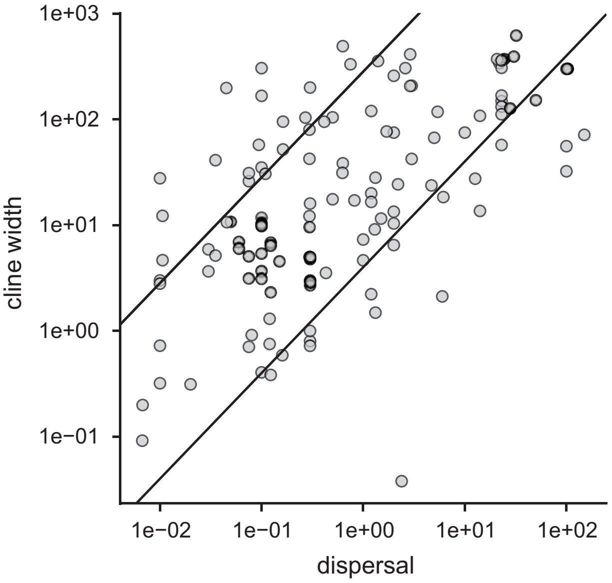

Figure 6: Dispersal and hybrid zone width in kilometers. The two black lines show tension zone predictions for single-locus cline widths under moderate selection against hybrids ($s = 0.5$; lower line) and very weak selection ($s = 0.0001$; upper line). For most hybrid zones, hybrid zone widths fall within expectations generated from a simple tension model based on selection against hybrids and random dispersal only. The outlier with a highly negative residual is a hybrid zone between lineages of the coral species *Eunicea flexuosa*. Outside this outlier, divergence from tension zone expectations is relatively modest. Note that predictions for cline width under a single-locus and multilocus model are similar when selection is moderate to weak (Kruuk et al. 1999). Strong selection can lead to significantly narrower widths than predicted under the single-locus model, possibly explaining the hybrid zones that fall below the lower line.

On the other end of the spectrum, hybrid zones with strongly positive residuals in our full analyses (fig. 4) may correspond with nonequilibrium hybrid zones undergoing neutral diffusion, which ultimately may not be stable (Endler 1977). Positive residuals may alternatively correspond with mosaic hybrid zones, where habitats are substantially interdigitated but which may appear clinal at larger scales (Ross and Harrison 2002). In such cases, patches of habitat favorable to the locally rare taxon can stretch the width of the hybrid zone by supporting peripheral populations. Alternatively, large positive residuals from our analyses may correspond with hybrid zones exhibiting bounded hybrid superiority (Moore 1977), in which hybrids are equally or more fit than their parents. In this scenario, hybrid zone width should be determined by the width of the region in which hybrids have superior fitness.

Finally, while we report evidence for linear relationships, additional patterns may be important. If we exclude the outlier *E. flexuosa* hybrid zone, the relationship between hybrid zone width and dispersal is roughly triangular in shape, with an apparent lower bound (fig. 4*A*). This shape underscores the rarity of narrow hybrid zones in dispersive taxa (Prada and Hellberg 2014). While hybrid zones are often narrow relative to taxon ranges, dispersal may impose limits on how narrow animal hybrid zones can be. This pattern is also somewhat evident in the genetic distance plots, which could suggest a similar limit on hybrid zone width based on recency of divergence. If so, geography should limit where hybrid zones can form, particularly for dispersive taxa. For example, a hybrid zone between highly dispersive species is unlikely to stabilize on a small island simply because space does not permit it. Rather, one taxon in a diverging pair is likely to outlast the other before a hybrid zone can form. Relatively few hybrid zones should stabilize where suitable habitat area is small relative to dispersal. In evolutionary terms, our results reinforce the idea that there is a spatial scale of speciation (Kisel and Barraclough 2010), which may limit how divergence proceeds. While extremely strong ecological gradients and habitat selection could lessen this restriction, the triangular shape of our data imply either that these conditions are rarely met or that researchers have not interpreted existing instances as hybrid zones.

Caveats of This Work

The hybrid zones included in this study may be a biased sample of all likely hybridizing species pairs. The hybridizing pairs included here are disproportionately temperate, morphologically well defined, and common enough to be sampled at a fine scale. Better sampling of hybrid zones between nontemperate, morphologically cryptic, or low-density lineages taxa might reveal different patterns. Additionally, in interpreting our results we assume that the hybrid zones we have analyzed are at dynamic equilibrium, which presumes that time since formation is not an important factor in determining hybrid zone structure (Endler 1977).

Conclusions

Our results emphasize how narrow range limits set by hybridization—and thus geographic transitions between species—can be (fig. 4), especially given that many of these hybrid zones form in the absence of an apparent environmental gradient (Brumfield et al. 2001; Singhal and Moritz 2013; McEntee et al. 2016). Across these studies, we find that cline width for a hybrid zone is, at the median, 18.6 times greater than dispersal length. The narrowness of hybrid zones relative to dispersal suggests that many abrupt range boundaries might be explained in part by hybridization where other explanations, such as competition, habitat transitions, strong gradients, or biogeographic boundaries, have been invoked. Furthermore, the importance of hybridization in setting range boundaries extends beyond hybrid zones. Reproductive interference arising from hybridization—whether via a hybrid zone or not—can limit a species range (Case et al. 2005; Levin 2006). Given the increasing appreciation for the prevalence of hybridization across the tree of life, hybridization is likely an important, and perhaps underappreciated, force constraining the evolution of range limits.

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Statement of Authorship

J.P.M. and S.S. designed the study; collected, analyzed, and visualized the data; and wrote the manuscript. J.G.B. designed the study, helped fund the study, and reviewed and edited the manuscript.

Data and Code Availability

Cline data and metadata from hybrid zones are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.nvx0k6dnr; McEntee et al. 2020). Code used for data analysis and visualization are available from GitHub (https://github.com/singhal/hz_metaanalysis).

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