

**Ecological models provide the first evidence of increased costs for hybrids in a
migratory divide**

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Statement of authorship

JL and KD designed the study; all authors contributed equally to the analyses and writing of
the paper.

Data accessibility

No new data was used in this article, the tracking data was previously published and can be
found in the supplementary material of the original papers. Ecological and locality data used
can be found at the databases indicated in the Methods.

Keywords: migratory divide, hybrid fitness, extrinsic postzygotic isolation, niche models,
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Abstract

Ecological speciation predicts that the fitness of hybrids will be reduced if they exhibit intermediate phenotypes that fall between parental niches. Empirical support for this prediction is sparse and migratory divides may help fill this gap. Divides occur between populations with divergent migratory routes. Hybrids in divides are predicted to take intermediate routes over terrain avoided by pure forms, reducing their fitness. We test this prediction here in a well-characterized divide between Swainson's thrushes using niche models and models of landscape connectivity. These models predicted lower habitat suitability in the intermediate range between the migratory ranges of pure forms and optimal routes that circumvent this area. Birds that took intermediate routes used stopover sites of lower predicted suitability and overlapped less with optimal paths than birds migrating on either side of the divide. Our results have broad implications as migratory divides are common in nature and not limited to birds.

Keywords: migratory divide, hybrid fitness, extrinsic postzygotic isolation, niche models, landscape connectivity, speciation

INTRODUCTION

Divergent ecological selection is important for speciation (Schluter 2000, 2001, 2009; Rundle & Nosil 2005; Nosil 2012), with a growing number of studies showing how adaptation to different ecological niches can reduce interspecific matings (i.e., serve as a premating barriers). However, our understanding of the ways in which ecology reduces hybrid fitness (i.e., postmating barriers) remains limited. It has long been hypothesized that hybrids can exhibit intermediate phenotypes that are maladaptive, falling between the optima of both parental niches. Nevertheless, except for a few case studies, very little information on the actual traits that reduce hybrid fitness is known (Rice & Hodtert 1993; Naisbit Russell E. *et al.* 2001; Jones *et al.* 2006). Migratory behavior may fill this gap (Tsukamoto *et al.* 2002; Bearhop *et al.* 2005; Bolger *et al.* 2008; Bensch *et al.* 2009; Rolshausen *et al.* 2009; Rohwer & Irwin 2011; Delmore & Irwin 2014; Hobson *et al.* 2015). Migratory routes are genetically determined in many animal groups and are thought to involve navigation around unsuitable habitat (Alerstam *et al.* 2008). Migratory divides arise when divergent populations originating in the same region take different migratory routes to circumvent these putative barriers for successful migration (Bensch *et al.* 1999; Irwin & Irwin 2005; Delmore *et al.* 2012; Lyons *et al.* 2012). It has been hypothesized that hybrids in these divides will use intermediate migratory routes and that this behavior will be maladaptive as it will bring them through unsuitable habitat (Helbig 1991; Bensch *et al.* 1999; Irwin & Irwin 2005; Veen Thor *et al.* 2007; Delmore & Irwin 2014).

Existing work on this ‘migratory divide hypothesis’ (hereafter MDH) has largely focused on testing whether hybrids take intermediate routes, with a number of studies providing support for this behavioral pattern (Helbig 1991; Gagnaire *et al.* 2009; Delmore &

Irwin 2014). However, this is only one prediction from the MDH. Intermediate routes are also expected to be maladaptive, or ecologically inferior. This prediction has yet to be tested. Here we integrate direct tracking data with ecological niche models and landscape connectivity analyses to assess the suitability (or lack thereof) of intermediate routes for migration. Ecological niche models use environmental data from known localities to identify environmental variables associated with the presence of a species (i.e., their niche); these data are then used to predict the distribution of suitable habitat for that species across a geographic landscape. Landscape connectivity analyses integrate data on the resistance of moving through different types of landscapes to predict general movement patterns or pathways for a species across a region of interest. Resistance represents how difficult movement through a particular region is, with higher resistance being equivalent to higher difficulty. For example areas of high elevation may be assigned higher resistance values as flight at high altitudes is a energetically costly behavior that usually requires specific physiological adaptations (Bishop *et al.* 2015).

Our study focuses on one of the most thoroughly studied examples of a migratory divide - that between coastal (*Catharus ustulatus swainsoni*) and inland (*C. u. ustulatus*) subspecies groups of Swainson's thrush (hereafter referred to as subspecies for simplicity). These subspecies form a stable hybrid zone where their ranges overlap in western North America (Fig. 1a; Ruegg 2008; Delmore *et al.* 2012) and while they differ in several traits, including song and colour, migratory strategies distinguish them much more clearly than other traits (Delmore & Irwin 2014). Direct tracking of these birds using light-level geolocators has also confirmed a clear migratory divide in this system. Coastal birds migrate along the west coast of North America between British Columbia and Mexico, Guatemala or Honduras, whereas inland birds migrate along more eastern routes between British Columbia

94 and Columbia or Venezuela (Delmore *et al.* 2012). Natural hybrids tracked on migration
95 exhibited a variety of migratory behaviors, but in many cases these birds take intermediate
96 routes (Delmore & Irwin 2014). Intermediate routes cross mountain chains and deserts in
97 southwestern North America suggesting the MDH may explain a large portion of the
98 reproductive isolation between the subspecies (Delmore & Irwin 2014).

99
100 Here, we test the prediction that intermediate routes are inferior to those either side of
101 the divide. Specifically, we use ecological niche models to quantify the migratory niches of
102 pure coastal and inland thrushes and ask whether the intermediate range between the coastal
103 and inland routes is predicted to be less suitable for migration. We then used landscape
104 connectivity models to identify optimal migratory routes between breeding and wintering
105 grounds. Finally, we used data from both pure and hybrid birds tracked on migration to test
106 whether birds migrating in the intermediate range use stopover sites of lower habitat quality
107 and/or intermediate routes that pass through less optimal routes than birds flying in either
108 pure range. Our results support the MDH, showing the intermediate range is inferior and
109 optimal migratory routes avoid this region.

110 111 **MATERIALS AND METHODS**

112 113 **Modelling habitat suitability**

114
115 We used ecological niche models to quantify the migratory niches of the coastal and inland
116 subspecies of the Swainson's thrush. Ecological niche models relate records of occurrence to
117 environmental predictors to determine the set of environmental conditions that are most
118 suitable for species. We defined the migratory ranges of each subspecies using the migratory

119 routes of five pure coastal and four pure inland thrushes that were previously tracked using
120 light-level geolocators (Delmore *et al.* 2012; see Appendix S1 in Supporting Information).
121 Niche models were based on records of Swainson's thrushes maintained by the Bird Banding
122 Laboratory (accessed March 2013 from the USGS Patuxent Wildlife Research Centre). To
123 capture the migratory niche, we restricted locality data to the migratory range of each
124 subspecies in the continental USA and to observations made during both migratory seasons
125 (May and September records for spring and fall migration respectively) from 2006-2011.
126 Duplicate localities within years as well as records with low coordinate precision
127 ("coord_precision" <2 km) were removed resulting in a total of 2940 localities for the coastal
128 and 8044 localities for the inland subspecies (across years and seasons).

129
130 We considered six environmental variables in our niche models. Because climate is
131 positively linked to food availability for migratory birds (Richardson 1990; Jenni & Schaub
132 2003; Tsurim *et al.* 2008), we included precipitation and temperature in our models
133 (specifically, mean precipitation [ppt], mean temperature [tmean], average maximum
134 temperature [tmax], and average minimum temperature [tmin] available from the PRISM
135 time series dataset: <http://www.prism.oregonstate.edu/recent/>; accessed September 2013).
136 Differences in vegetation along migratory routes are also likely to reflect differences in both
137 foraging and sheltering opportunities (Lindstrom 1990; Hutto 1998; Smith & McWilliams
138 2010) and thus we included vegetation in our models (enhanced vegetation index: EVI;
139 NASA MODIS <https://modis.gsfc.nasa.gov/data/dataproduct/mod13.php>; accessed July 2014).
140 Finally, the availability of fresh water is likely important for migrating birds and their insect
141 prey (Tsurim *et al.* 2008; Smith *et al.* 2010), and thus we included a wetness index in our
142 models (compound topographic index: CTI; USGS Hydro1K database
143 <https://www.usgs.gov/centers/eros/science/usgs-eros-archive-products-overview>;

accessed May 2000). All environmental layers were reprojected to a lambert azimuthal equal-area projection and rescaled to 4 km resolution. Climate data and EVI were time-matched such that environmental data for each locality record was extracted for the specific date of the record (CTI was only available as a static data layer).

We constructed ecological niche models using MaxEnt version 3.3.3k (Phillips *et al.* 2004). Separate models were generated for the spring and fall migration of each subspecies and for each of the six years included in our study (i.e. 24 models). Background points for model calibration (1700 per model) were sampled randomly from within the migratory range of the subspecies being modelled. We ran ‘maxent’ (in SWD input format) using the dismo package (Hijmans *et al.* 2017) in R (R Core Team 2013) with a combination of linear, product and quadratic (lpq) features, default settings of the regularization parameter (0.5; Phillips & Dudík 2008), and the maximum number of iterations set to 5000. Models were qualitatively robust to the choice of background and features used during calibration (Fig. S2-3). Model evaluation was based on a temporally independent set of locality records and all models performed well (Fig. S4). Seasonal model projections for each subspecies did not qualitatively differ across years (Fig. S5-S10). We therefore averaged the predicted suitability surfaces for each subspecies (for each season) across years to generate final geographic representations of the spring and fall migratory niches of each subspecies.

We used our niche models to ask if the area between coastal and inland migratory ranges (i.e. the “intermediate migratory range”) is less suitable for migration than coastal or inland ranges. To do so, we extracted estimates of habitat suitability (generated by our niche models) from locations where Swainson’s thrushes and other species closely related to thrushes (Veery [*C. fuscescens*], Gray-cheeked [*C. minimus*] and Hermit thrush [*C. guttatus*],

American robin [*Turdus migratorius*], Western and Mountain bluebirds [*Sialia mexicana*, *S. currucoides*]) have been banded across North America since 2011 (a total of 841 spring records and 349 fall records; data from USGS Patuxent Wildlife Research Centre, accessed June 2015). These sites capture a more expansive set of potential stopover sites on migration and are thus an appropriate set of sites to use in comparisons of the overall suitability of the different migratory ranges (i.e. akin to the use of related species for background selection; Phillips *et al.* 2009). Observations were classified as being within the coastal, intermediate, or inland migratory ranges (see Fig. 1b). Estimates of suitability were not normally distributed and had unequal variance (Shapiro-Wilk test; $p < 0.05$; Levene's test: $p < 0.05$). Thus we used a non-parametric Mann-Whitney U test to compare the average suitability of sites within the intermediate range to each pure migration range. Separate tests were run for each migratory season and subspecies.

Modelling optimal migratory routes

We used Circuitscape version 5.0 (McRae *et al.* 2013) to model landscape connectivity and to identify optimal routes between the breeding and wintering ranges of coastal and inland thrushes. Circuitscape uses electrical circuit theory to predict connectivity across heterogeneous landscapes in which different features of the landscape offer different resistance to the movement of individuals (McRae 2006; McRae & Beier 2007; McRae *et al.* 2013). We ran Circuitscape in the advanced mode allowing raster cells to connect to eight neighbours and provided an input resistance raster that defined the resistance of each grid cell (16 km²) across our study region (North America).

We used Circuitscape with an input resistance raster that accounted for: i) the suitability of each grid cell (inverse of our niche model predictions); ii) the proximity of the cell to high quality habitat (lower resistance was given to cells close to highly suitable sites to avoid penalizing stops in unsuitable cells within a short flying distance to suitable habitat); iii) elevation (flight at high altitudes requires increased energy expenditure and often physiological adaptations; Altshuler & Dudley 2006; Scott Graham R. *et al.* 2009) therefore cells outside the reported elevational range of the birds were given high resistance); and iv) whether or not the cell is on land or in the Gulf of Mexico (i.e. inland birds cross this short stretch of ocean (Delmore *et al.* 2012) but cells in this region were given higher resistance to reflect the lack of stopover opportunities and resulting higher energetic costs of crossing the Gulf). Suitability (including specific scoring of elevation and the Gulf of Mexico) and proximity to suitable sites were combined into a single raster, with inverse suitability and the rescaled proximity index weighted equally. Specific details of the input resistance layer parameterization are provided in the Appendix S2a-d.

We ran separate landscape connectivity analyses for each subspecies and both migratory seasons. Starting regions for the analysis were defined as a) the overlap of the spring coastal and spring inland migratory routes in the wintering grounds in Central and South America for spring migration and b) the overlap of each subspecies' tracked migratory routes with their known breeding grounds in British Columbia, Canada for fall migration. Stopping regions were roughly the reverse of these for each season (Fig. 1b). We used the models generated by Circuitscape to qualitatively assess the distribution of optimal routes during the spring and fall migration and to specifically assess whether these optimal routes tend to avoid the intermediate range.

Evaluating specific hybrid routes

In addition to quantifying the general suitability of the intermediate range between pure migratory ranges and identifying optimal routes, we asked whether actual routes taken by birds through the intermediate range are inferior to those taken through the pure ranges. We used data from birds tracked with geolocators for this comparison: five fitted with tags in the coastal range, four in the inland range and additional 21 from birds in the hybrid zone. For this comparison, we used routes of birds tracked with geolocators, specifically five routes of birds captured in the coastal, four routes of birds captured in the inland range and 21 additional routes of birds captured in the hybrid zone/intermediate range (Delmore *et al.* 2012; Delmore & Irwin 2014). We extracted the suitability scores from stopover sites used by the birds (locations where birds remained stationary for ≥ 2 days based on geocator data; Delmore *et al.* 2012; Delmore & Irwin 2014) and used generalized additive models (or cubic splines) to examine the relationship between mean suitability at stopover sites and the longitude at which the route crossed 30°N (a measure of route intermediacy and the predictor variable in these analyses; Delmore *et al.* 2012; Delmore & Irwin 2014; ‘mgcv’ library of R). Suitability scores were extracted from both the inland and coastal niche models (Fig. S17). Splines were used because while we expect the intermediate routes to be of lower suitability than routes through the range of the subspecies used to build each niche model, we make no specific predictions for the other pure form in this comparison (e.g., these routes could be equally or less suitable). We used the ‘anova’ function in R to compare the fit of these splines to a model incorporating only an intercept (i.e., no slope, or relationship between longitude and habitat suitability).

In addition to comparing the average suitability of stopover sites of different routes, we asked whether intermediate routes make less use of the optimal routes predicted by Circuitscape than birds taking more coastal or inland routes. To do so, we converted the output from Circuitscape into a binary raster, assigning cells with a high amount of predicted flow (or low resistance, >0.75 percentile of connectivity values) a value of 1, and all other cells a value of 0 (Fig. S18). We then overlay the known migratory tracks from above (represented as buffered polygons to account for the standard deviation of the location estimates from the geolocators; Delmore *et al.* 2012; Delmore & Irwin 2014; Fig. S19) on this raster to extract the number of “high-flow” cells that each route incorporates. We used cubic splines to test whether intermediate routes have less overlap with optimal routes than more western or more eastern routes (i.e., pass through fewer cells with high predicted flow).

RESULTS

Predicted habitat suitability is lower in areas between the migratory ranges of pure forms.

Patterns of suitable habitat predicted by ecological niche models for coastal and inland thrushes varied according to migratory season (Fig. 1c-f). Vegetation and wetness indices made the highest contributions to the coastal models whereas minimum and maximum temperature were more important for inland models (Table S1). The coastal spring model predicted highest suitability in a narrow region along the west coast of North America as well as large areas in the east (Fig. 1c). The inland spring model predicted highest suitability in the eastern United States although there were regions along the west coast that were also predicted to be suitable for this subspecies (Fig. 1d). In line with expectations based on the

MDH, predicted habitat suitability in the intermediate region between the pure migratory ranges was significantly lower in all tests (Mann-Whitney U test, coastal - spring: $W = 14121$, $Z = -7.4$, $p < 0.0001$; inland - spring: $W = 36905$, $Z = -12.9$, $p < 0.0001$; Fig. 2ab; coastal - fall: $W = 1379$, $Z = -5.3$, $p < 0.0001$; inland - fall: $W = 5855$, $Z = -6.5$, $p < 0.0001$; Fig. 2cd).

Models of landscape connectivity predict the migratory divide

Models of landscape connectivity predicted high connectivity west of the Sierra Madres of Mexico, in both migratory seasons (regardless of which species' niche model was used to inform the input for the model; Fig. 3). Areas of high connectivity were also predicted east of the Rocky Mountains and through the central United States, although there were areas of low connectivity in the southern US (e.g., throughout most of Texas). The Mexican plateau in central Mexico showed lower connectivity for both subspecies in both seasons. Visual examination of migratory routes for allopatric coastal and inland birds suggests they coincided well with high connectivity pathways, although inland birds cross the large area of low connectivity in the southern US. Hybrid routes often failed to follow optimal routes, instead going across large areas avoided by the Circuitscape algorithm (e.g. across mountain ranges in the US and less optimal pathways through Mexico and Central America; Fig. 3).

Intermediate routes went through areas of reduced suitability and connectivity

Consistent with the MDH, cubic splines showed a reduction in habitat suitability at stopover sites for more intermediate routes. In other words, estimates of habitat suitability were reduced at intermediate longitudes (Fig. 4a-d). Spline functions provided a better fit to the data than intercept-only models for all but the inland fall model (chi-square test; spring

migration, coastal model $df = 3.23$, $p < 0.0001$, $R^2 = 0.46$, inland model $df = 2.35$, $p < 0.0001$, $R^2 = 0.26$; fall migration, coastal model $df = 5.08$, $p < 0.01$, $R^2 = 0.28$, inland model $df = 1$, $p = 0.075$, $R^2 = 0.07$). Also consistent with the MDH, cubic splines showed a reduction in the use of the optimal routes predicted by Circuitscape for more intermediate routes (Fig. 4e-h). In this case, splines provided a better fit to the data than intercept-only models in all models once again with exception of the inland fall model (chi-square test; spring migration, coastal model $df = 8.78$, $p < 0.0001$, $R^2 = 0.84$; inland model $df = 8.74$, $p < 0.0001$, $R^2 = 0.78$; fall migration, coastal model $df = 1.72$, $p < 0.0001$, $R^2 = 0.34$; inland model, $df = 1.56$, $p = 0.097$, $R^2 = 0.074$).

DICUSSION

Individuals from nearly every animal group migrate. A considerable amount of intraspecific variation has been documented in this behavior, often manifested in the formation of migratory divides between divergent populations. It has long been predicted that hybrids in these divides will take intermediate routes, thus experiencing inferior conditions during migration relative to pure forms. Studies have clearly demonstrated the behavioral component of this hypothesis, the extent to which intermediate routes are ecologically inferior has not been formally assessed. Combining methods from spatial ecology with both banding records and data from geolocators, we assessed the prediction that intermediate routes in a well-established migratory divide are ecologically inferior and provide the first quantitative test of this key prediction from the MDH.

Ecological niche models showed that areas in regions between the migration ranges of pure Swainson's thrushes are less suitable than areas in either pure migratory range. Although there were pockets of elevated suitability in the intermediate range between the pure migratory ranges, these areas were small and less frequent than in pure ranges. Combined with our finding that the suitability of actual landing sites for birds on migration is higher in the coastal and inland ranges than the intermediate range between them, these results suggest that on average birds taking intermediate routes are expected to encounter less suitable habitat on migration. Results from our niche models thus provide clear support for the MDH.

Landscape connectivity between wintering and breeding grounds in both migratory seasons was likewise predicted to be higher along the coast and in the interior range than in intermediate range. Connectivity was especially high along the western coast of North America regardless of which model (subspecies and leg of migration) was considered, likely reflecting shorter distances between western breeding grounds and southern overwintering sites through this region (Delmore *et al.* 2012). Nevertheless, all models also predicted additional high flow through most of the interior of the USA, consistent with the migratory range of pure inland thrushes. Connectivity through this area was generally predicted to be as high as movement along the coast with the exception of a large area of low connectivity in the south-central United States. The latter area includes plains (e.g., the South Texas and Rolling Plains ecoregions of Texas), prairies (e.g., Gulf and Blackland Prairie ecoregions of Texas) and savannahs (e.g., the Post Oak Plains ecoregion of Texas) - habitats that are likely unsuitable for thrushes. Much of this area has also been converted for agricultural use and may thus provide fewer resources for stopover (Bonter *et al.* 2009). Given that areas to the north of this gap are predicted to be optimal for migratory flights, it seems likely that the total costs of taking an inland route are still lower than the costs of flying a more direct but

intermediate route (i.e. defined by the true migratory ranges). Here, a key point is that, in addition to landscape heterogeneity, Circuitscape accounts for the distance between starting and stopping regions (in the absence of any landscape differences, Circuitscape would predict highest connectivity along the shortest path between starting and stopping sites). That the optimal flight paths recovered by Circuitscape tended to avoid the most direct path between starting and stopping regions thus suggests that the cumulative costs of taking intermediate migratory routes are greater than the costs of flying along slightly longer coastal or inland routes.

Analyses integrating data on habitat suitability and landscape connectivity with the actual routes of thrushes supported the MDH in most cases, with intermediate routes having lower levels of habitat suitability at stopover sites and overlapping less with optimal routes from our analyses of landscape connectivity. The one exception was a lack of association between either habitat suitability or landscape connectivity and longitude in the inland fall models, likely reflecting the fact that birds migrating further east pass through a large area of reduced connectivity over Texas and Louisiana where plains, prairies and savannahs dominate the landscape.

The estimates of habitat suitability and landscape connectivity we obtained are interesting to consider in light of migratory patterns observed in western North America more generally. Areas of high connectivity recovered east and west of the Rocky Mountains coincide well with the migratory tracks of other *Catharus* species, including Hermit thrushes that form a migratory divide further north (Alvarado *et al.* 2014) and Veeries whose breeding distribution matches the inland subspecies of Swainson's thrushes (Hobson & Kardynal 2015). The Coast and Rocky Mountains also occur at phylogenetic breaks between many

(sub)species and at least eight pairs form strong migratory divides (evidence for reproductive isolation, a lack of hybrids or narrow hybrid zones; Rohwer & Irwin 2011). The intermediate area we identified in our study with low connectivity likely contributes to the existence of the former divides. In most cases the easternmost (sub)species is often taking a longer route between its breeding and winter grounds. Results from our models suggest that in the case of thrushes at least, coastal routes are equally suited to inland thrushes. Genetic constraints likely prevent inland birds from using coastal routes, as they and other eastern groups are believed to retrace the routes they used to expand out of eastern glacial refugia following the last glacial maximum (Ruegg *et al.* 2006). Sub(species) of birds that form divides are not the only individuals to avoid the intermediate area we identified here; other birds (Doren & Horton 2018) and migrants from additional animal groups including insects and bats also appear to circumvent this area (Cryan 2003) suggesting this area of low connectivity may account for the broad scale movement of migrants in North America more generally.

On average, birds following a random route through the intermediate range will stop at sites of less suitable habitat and encounter more resistance to movement. Some of the actual observed intermediate routes included isolated pockets of high habitat quality and incorporated some parts of the optimal paths predicted by Circuitscape suggesting migration may not serve as a complete barrier to gene flow. Indeed, we know that some birds taking intermediate routes do return or we would not have tracking data for them (light-level geolocators must be retrieved to download their data). Nevertheless, even a small reduction in gene flow is sufficient to maintain stability in hybrid zones (Irwin 2019). Other aspects of migration that we did not test here may lead to further reductions in gene flow. For example, birds time their migration to coincide with peaks in resources and it is possible hybrids do not do this. In addition, it has been shown that coastal birds arrive on the breeding grounds before

inland birds. If mating is assortative based on arrival time this pattern could reduce gene flow, representing another way differences in migration contribute to reproductive isolation in this system. Finally, while our tracking data suggest some hybrids survived migration, we have no information on if they were able to find mates and produce offspring. Carry-over effects where the condition of birds on the wintering grounds affects their reproductive success on the breeding grounds are common in migratory birds (Marra & Holmes 2001).

CONCLUSION

Overall our results support the key prediction from the MDH that intermediate migratory areas are inferior to those of pure forms in migratory divides. Our findings for Swainson's thrushes in North America may only be the tip of the iceberg. Hundreds of migratory divides have been documented worldwide and in all of the main migratory systems (see reviews for the western (Møller *et al.* 2011) and eastern (Irwin & Irwin 2005) Palearctic). These divides are easy to understand where migratory routes circumvent extreme landscape features like the Tibetan Plateau and Gobi Desert (Irwin & Irwin 2005) or the Mediterranean Sea, Alps and Saharan Desert (Møller *et al.* 2011). Landscape features encountered by migrating birds in North America are not as extreme as those in other migratory systems yet still predict the observed divide between coastal and inland Swainson's thrushes in our models. These results suggest that even seemingly subtle ecological differences across space may be sufficient for generating divides and contributing to reproductive isolation, thus raising the possibility that such divides are more common and important to ecological speciation than currently appreciated.

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562

FIGURE LEGENDS

Figure 1. (a) geographic distribution of coastal (blue) and inland (green) Swainson's thrushes and (b) migratory ranges used in the present study for each subspecies. Crosses within migratory ranges indicate locality points that were used to construct ecological niche models. Start and stop polygons for connectivity models are shown by black boxes. (c-f) Patterns of habitat suitability predicted by ecological niche models constructed for coastal and inland Swainson's thrushes on spring and fall migration. Darker colours indicate higher habitat suitability.

Figure 2. Comparison of the predicted suitability of sites from the pure and intermediate migratory ranges of Swainson's thrushes based on niche models calibrated with data on climate, vegetation, and a wetness index. Grey dots represent the suitability of sites where Swainson's thrushes and related species have been observed within each migratory range. Group mean values and confidence intervals are presented. Significance of results from Mann-Whitney U comparisons is indicated above the boxplots (* 0.05, ** 0.01, *** 0.001).

Figure 3. Regions predicted to have high migratory flow based on models of landscape connectivity in the Swainson's thrush. Colours indicate the cells with flow values $\geq 75^{\text{th}}$ percentile of all cell flow values, with warmer colours indicating higher flow. Grey areas fall below this cut-off. Oceans (and areas outside the study region) are shown in white for clarity even though movement across the Gulf of Mexico was permitted (all values in the Gulf were <75). Migratory routes of the focal group for each model are indicated by solid black lines; hybrid tracks are indicated by red dashed lines. The dashed black line shows 30°N , the measure used for intermediacy of migratory routes in cubic splines.

588

589 **Figure 4.** Relationship between the longitude at which birds cross 30°N and (a-d) habitat
590 suitability of stopover sites and (e-h) the proportion of high connectivity cells areas
591 incorporated in the specific migratory routes of individual Swainson's thrushes. Values for
592 birds captured in the coastal and inland ranges are denoted by blue and dark green symbols,
593 birds captured in the hybrid zone by light green symbols (Delmore *et al.* 2012; Delmore &
594 Irwin 2014).