

Testing Range-Limit Hypotheses Using Range-Wide Habitat Suitability and Occupancy for the Scarlet Monkeyflower (*Erythranthe cardinalis*)

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ABSTRACT: Determining the causes of geographic range limits is a fundamental problem in ecology, evolution, and conservation biology. Range limits arise because of fitness and dispersal limitation, which yield contrasting predictions about habitat suitability and occupancy of suitable habitat across geographic ranges. If a range edge is limited primarily by fitness, occupancy of suitable habitat should be high, habitat suitability should decline toward the edge, and no suitable habitat should exist beyond it. In contrast, a range edge limited primarily by dispersal should have unoccupied but suitable habitat at and beyond the edge. We built ecological niche models relating occurrence records for the scarlet monkeyflower (*Erythranthe cardinalis*) to climatic variables and applied these models to independent data from systematic, range-wide surveys of presence and absence to estimate the availability and occupancy of climatically suitable habitat. We found that fitness limitation predominated over dispersal limitation, but dispersal limitation also played a role at the poleward edge. These results are consistent with the hypothesis that dispersal limitation is more important along shallow environmental gradients and also suggest that synergy between dispersal and fitness limitation can contribute to colonization failure. The framework used here is validated by independent data and could be readily applied to inferring causes of range limits in many other species.

Keywords: dispersal limitation, ecological niche model, elevation gradient, latitudinal gradient, species distribution model.

Introduction

Determining why geographic range boundaries arise where they do—sometimes at seemingly arbitrary places along environmental gradients (Kirkpatrick and Barton 1997)—is a fundamental ecological and evolutionary problem. It also

has tremendous applied relevance, given the ubiquity of anthropogenically driven changes in species ranges due to climate change, species introductions, and habitat fragmentation. Hypotheses for range limits fall into two major categories, fitness limitation and dispersal limitation (Sexton et al. 2009). Fitness limitation may arise from many proximate factors, including climatic or other abiotic conditions (Angert 2006; Eckhart et al. 2011), negative biotic interactions such as competition or predation (Bruehlheide and Scheidel 1999; Jankowski et al. 2010), or a lack of mutualist partners (Stanton-Geddes and Anderson 2011; Moeller et al. 2012). Range boundaries arise when the single or combined effects of these limiting variables depress population growth below replacement rates or increase temporal variability in population growth and thus increase extinction probability (Holt et al. 2005). Dispersal limitation can arise if physical barriers or the arrangement of suitable habitat hinders colonization of suitable sites beyond the range edge or by temporal changes in the spatial distribution of limiting environmental variables, such that colonization lags behind creation of newly suitable habitat even in the absence of dispersal barriers (Gavin and Hu 2006; Hara 2010; Pomara et al. 2014). Determining the relative importance of these classes of limitation is important for accurately predicting the ways and rates at which species ranges will shift in response to perturbations such as climate change (Guisan and Thuiller 2005). For example, dispersal limitation is hypothesized to be relatively more important at latitudinal range edges compared with elevational edges because of the steepness of underlying environmental gradients (Kirkpatrick and Barton 1997; Hargreaves et al. 2014). For a given dispersal distance, movement across elevation gradients covers greater environmental distances, resulting in a greater likelihood of populations at or even beyond the species' fitness limit. Yet despite well-established theory and insights from recent syntheses

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(Hargreaves et al. 2014; Lee-Yaw et al. 2016), few studies have simultaneously assessed causes of range limits across elevational and latitudinal gradients for the same species.

Experimental manipulations of the species distribution or putatively limiting environmental variables provide the most definitive tests for fitness and dispersal limitation. For example, if experimentally translocated individuals achieve stable or increasing population growth rates beyond a range boundary, then the range can be inferred to be dispersal limited (Marsico and Hellmann 2009; Van der Veken et al. 2012). On the other hand, if experimental populations have negative population growth rates, then the range boundary is fitness limited (Levin and Clay 1984; Angert and Schemske 2005; Geber and Eckhart 2005). However, inadequate spatial or temporal replication and incomplete representation of the life cycle can yield misleading results (Sexton et al. 2009; Hargreaves et al. 2014; Lee-Yaw et al. 2016). Further, experimental manipulations are impractical or impossible for most organisms. Given these difficulties, approaches that rely on observational data to test for fitness and dispersal limitation would be a broadly applicable alternative to manipulative experiments.

Here we test for fitness and dispersal limitation using spatial variation in modeled habitat suitability and observed occupancy of suitable habitat. In principle, if a range boundary is created primarily by dispersal limitation, habitat suitability should remain high at and beyond the range boundary, but the species will fail to occupy it (table 1). Conversely, if a range boundary is created primarily by fitness limitation, then habitat suitability should decrease toward the range edge and suitable habitat should be greatly reduced beyond it, but the species will occupy suitable habitat where it is available (table 1). Spatial variation in habitat suitability can be inferred from ecological niche models (ENMs; Peterson 2006; Warren 2012), which relate records of occurrence to environmental predictors (Elith and Leathwick 2009). Oc-

cupancy of suitable habitat can then be assessed using independent occurrence data with presence and absence records.

We apply this approach to test the relative importance of fitness and dispersal limitation at elevational and latitudinal range limits of the scarlet monkeyflower (*Erythranthe cardinalis*, formerly *Mimulus cardinalis*; Nesom 2014), a perennial herb of riparian habitats in western North America. *Erythranthe cardinalis* has conspicuous red flowers, making it easily identifiable, so false absences are unlikely when field surveys occur during the flowering season. Riparian habitat is linear and easily surveyed when accessible. The species has been the subject of several other investigations of range-limiting processes across both elevational and latitudinal gradients (Angert and Schemske 2005; Angert 2006; Angert et al. 2008, 2011; Bayly 2015; Sheth and Angert 2016, 2017), which aids interpretation of these results. In this study, we build ENMs, focusing on elements of the climatic niche, and apply these models to powerful independent testing data with true absences from systematic field surveys. Inferences regarding suitable habitat and its occupancy are conducted on the testing data, overcoming many limitations of inferences made from presence-only data (Hastie and Fithian 2013).

Material and Methods

Study System

Erythranthe cardinalis is a perennial herb of riparian habitats ranging from central Oregon, southward throughout California (although it is absent from the Central Valley), and into northern Baja California, Mexico (Thompson 1993). Some herbarium specimens labeled *E. cardinalis* have been collected in Arizona and northern Mexico. Disjunct Arizonan populations have reproductive incompatibilities with Californian populations (Hiesey et al. 1971; Vickery and Wullstein 1987), cluster into well-supported sister clades

Table 1: Conceptual framework and statistical tests for distinguishing dispersal from fitness limitation as primary causes of range edges by examining differences in habitat suitability and occupancy of suitable habitat between the range center (C) and edges (E) and summary of corresponding results for four range edges of *Erythranthe cardinalis*

Variable	Predictions		Tests	Results			
	Dispersal limit	Fitness limit		High edge	Low edge	South edge	North edge
Habitat suitability	C = E	C > E	ANOVA of suitability among central and edge groups	C > E	C > E	C = E	C > E
			Regression of suitability vs. latitude or elevation	C > E	C > E	C > E	C > E
Suitable beyond edge?	Yes	No	Amount of riparian habitat above suitability threshold	No	N/A	No	No
Occupancy of suitable habitat	C > E	C = E	Logistic regressions of presence/absence in suitable sites vs. latitude or elevation	C = E	C = E	C = E	C > E

(Beardsley et al. 2003), and were recently split as *Erythranthe cinnabarina* (Nesom 2014). In addition, putative specimens of *E. cardinalis* from Mexico share morphological characteristics with *Erythranthe verbenaceus* (S. N. Sheth, personal observation) and are frequently misidentified (P. Beardsley, personal communication). Because of this taxonomic uncertainty, and because we could not conduct our own field sampling in Mexico, we focus on the main species range in California and Oregon. Within this geographic range, the species occurs at 0–2,400 m, although maximum elevation declines to the north (Ramsey et al. 2003).

Occurrence Points

Training Data: Herbarium Records and Pseudoabsences. We downloaded georeferenced records of occurrence from the Consortium of California Herbaria and the Oregon Flora Project on November 18, 2013. These records were supplemented with 200 additional records from seed and tissue collections made incidentally during other field projects from 1999 to 2009 (A. L. Angert, unpublished data), yielding 880 records. After inspection and cleaning (see app. A; apps. A–D are available online), we retained 432 records (available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.bg15b> [Angert et al. 2018]). To minimize spatial bias, we used OccurrenceThinner v1.0.4 (Verbruggen 2012; Verbruggen et al. 2013) to thin out overly sampled regions (app. A), resulting in 10 pseudoreplicate sets of records ($N = 187$ –204; fig. A1; figs. A1–A3, C1–C4, S1–S7 are available online).

Using the R package *dismo* version 1.0–12 (Hijmans et al. 2015), we generated random pseudoabsences within donut-shaped buffers (outer radius 80 km, inner radius 600 m) surrounding presence records from each set of thinned records. The outer radius constrained pseudoabsences to the vicinity of sampled areas, while the inner radius avoided placing pseudoabsences in occupied areas. In preliminary work, we tested varying outer radii and elimination of inner radii, and results were qualitatively similar. We further constrained the sampling of pseudoabsences by elevation and ecoregion to avoid drawing pseudoabsences from extremely inappropriate habitat, and so the environmental space encompassed by pseudoabsences represented that of true absences (fig. A2). For each set of thinned presence records, we used the same number of pseudoabsences (1:1 ratio) because it is close to actual prevalence observed in the testing data set (40%; Lauzeral et al. 2013), and exploratory analyses showed that higher ratios tended to result in overfitting of the training data (i.e., large drops in metrics of model performance when applied to independent testing data). However, our major conclusions are insensitive to the ratio.

Testing Data: Systematic Surveys of Presence and Absence. We conducted field surveys in June–August 2010 and 2011,

when flowering plants were conspicuous. Survey locations were determined by a stratified, random design, with strata defined by climate and latitude (app. A). We varied the sampling order of strata between years (app. A). At each location, we searched for *E. cardinalis* along two 30-m transects following the waterway. Because environmental predictors were not fine-scaled enough to differ between transects, we combined observations from the two transects into one data point; if *E. cardinalis* was observed along either transect, the site was treated as a presence. At six sites, we observed individuals between transects when there were no recorded individuals along either transect; these sites were analyzed as presences. In total, we visited 240 sites and found *E. cardinalis* at 90 of these (available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.bg15b> [Angert et al. 2018]).

Predictor Variables

We focus on climatic factors for two reasons. First, prior research on this study species has identified growing season temperature as a major determinant of both fitness and distribution (Angert 2006; Angert et al. 2008, 2011). Also, in exploratory analyses, microhabitat variables related to hydrology and topography had undetectable to weak effects on probability of occurrence and were rarely selected for model inclusion, while climatic variables had strong effects and were always selected for model inclusion.

Source of Climatic Variables. We obtained point-specific monthly values of maximum temperature, minimum temperature, and precipitation from ClimateWNA version 5.21 (<http://cfcg.forestry.ubc.ca/projects/climate-data/climatebcwna/>; Wang et al. 2012). Elevation values were derived from the US Geological Survey (USGS) HydroSHEDS digital elevation model with a 90-m resolution (Lehner et al. 2008). For each training presence record and testing data point (presences and true absences), we created a point-specific climatic average for each monthly variable across the 30 years preceding the point's collection date. For the pseudoabsences, which do not have a true date of collection, we calculated climatic averages across the distribution of collection years in the herbarium records. From these data we calculated 19 bioclimatic variables (Hijmans et al. 2005) at a resolution of 90 m using the *biovars* function from the R package *dismo* version 1.0–12 (Hijmans et al. 2015).

Culling of Predictor Variables. We selected a subset of bioclimatic variables with the greatest explanatory power in univariate linear models and without strong collinearity ($r \leq |0.7|$; table B1; tables A1, B1, C1, C2, D1, D2, S1–S4 are available online). This resulted in retention of seven variables: precipitation seasonality (bio15), precipitation of driest month (bio14), annual precipitation (bio12), mean

temperature of coldest quarter (bio11), mean temperature of warmest quarter (bio10), temperature seasonality (bio4), isothermality (bio3), and mean diurnal range (bio2). Bio3, bio10, bio12, and bio14 were natural log transformed before analyses.

Ecological Niche Model Building

We used five widely used ENMs to ensure that results were not sensitive to choice of models and their respective parameterizations. They encompass parametric (generalized linear models [GLMs]), semiparametric (generalized additive models [GAMs]), and nonparametric approaches that incorporate machine learning (random forests [RFs], boosted regression trees [BRTs], and maximum entropy [MAX]). Analyses were conducted in R version 3.0.2 using code generously shared by T. Edwards (Utah State University). Further details on ENM building are available in appendix A.

Model Evaluation

To assess overall model performance, we considered both discrimination (the ability to correctly distinguish between presences and pseudoabsences) and reliability (the agreement between predicted and actual probabilities of occurrence; Pearce and Ferrier 2000). We assessed discrimination with the area under the curve (AUC) of the receiver operator characteristic (Fielding and Bell 1997). To assess reliability, we examined Miller's calibration statistics (Miller et al. 1991) for the calibration curve, which relates observed probabilities of occurrence to model predictions. For example, in a well-calibrated model, sites with predicted values of 0.2 versus 0.8 will be occupied 20% versus 80% of the time, respectively. For a perfectly calibrated model, the logistic regression of observed presence/absence versus the logits of predicted probabilities will have an intercept of 0 and a slope of 1 on the log odds scale. We tested for deviation from perfect calibration by conducting likelihood ratio tests of models with intercept and slope constrained to equal 0 and 1, respectively, versus unconstrained models, using an R function from Wintle et al. (2005). Significant deviations in intercept alone suggest bias in model predictions, meaning observed prevalence in real data is significantly higher (intercept > 0) or lower (intercept < 0) than model predictions across the entire range of predicted values (Pearce and Ferrier 2000). Significant deviations in slope (spread) without bias indicate that the model is overpredicting (slope > 1) or underpredicting (slope < 1) prevalence when predicted values are >0.5 and doing the opposite for predicted values <0.5 (Pearce and Ferrier 2000). Significant deviations in both slope and bias shift the predicted value at which the cross-

over from over- to underprediction occurs. All performance metrics were calculated for both training data (internal validation) and independent testing data (external validation). For GLM, GAM, BRT, and MAX models, internal accuracies were calculated using the entire training data set (resubstitution) and with a fivefold cross-validation procedure. For RF, we report internal accuracy as the out-of-bag estimate from the training data set, which is analogous to a cross-validated estimate.

Hypothesis Testing

We tested whether habitat suitability is lower at range edges in two ways (table 1). First, we divided the testing points into central versus edge groups (defined below; fig. A3) and compared model prediction scores among groups via ANOVA. Second, we conducted second-order polynomial regressions of model predictions versus latitude or versus elevation of each testing data point. We used the former categorical approach because it offered a straightforward contrast between range center and range edges, and we included the latter continuous approach to ensure that the binning of data into categories was not obscuring more complex patterns. Latitudinal groups were assigned on the basis of US Environmental Protection Agency level 3 ecoregions (table A1). Results were not altered by using alternate breakpoints between groups (app. A). Elevational groups were assigned on the basis of a prior reciprocal transplant experiment (Angert and Schemske 2005): <400 m = low margin, 400–1,200 m = center, and >1,200 m = high margin. For regressions, we analyzed presences and absences separately to determine whether average trends were driven by variation across occupied or unoccupied sites.

To test whether suitable habitat is present beyond range edges, we first defined a threshold above which sites could be considered suitable (table 1). We chose the threshold that maximizes the sum of sensitivity and specificity (calculated on the testing data) because this has been demonstrated to perform well compared with others (Liu et al. 2013). However, results are qualitatively similar using a different threshold, maximum kappa (Cohen 1960). We clipped model projections to waterways using the USGS National Hydrography Dataset's stream feature layers for California and the Pacific Northwest (McKay et al. 2012). We also limited the spatial extent to within an 80-km buffer surrounding presence records to avoid summarizing suitable habitat within a rectangle containing obviously unsuitable areas (e.g., ocean). For each model type, we examined histograms of the summed length of climatically suitable stream habitat versus latitude or elevation. Because maximum elevation declines with latitude, we examined latitudinal histograms within low-, mid-, and high-elevation classes; likewise, we examined elevational histograms within south, central, and north regions. Because

the low-elevation range limit is 0 m asl, we could not examine suitable habitat beyond this range edge.

To test whether occupancy of suitable habitat declines toward range edges, we conducted logistic regressions of presence or absence in suitable sites (i.e., only those sites above the suitability threshold) versus latitude or elevation. We predicted that probability of occurrence would have a hump-shaped relationship with range position if dispersal limitation prevents populations from occupying suitable sites near range edges.

Nonstationarity and Extrapolation

To assess the potential for nonstationarity (i.e., the effects of predictor variables changing across space), we compared results from GLM models with and without terms for climate-by-latitude or climate-by-elevation interactions (app. C). To explore whether projections beyond the range required extrapolation into novel environmental space, we used the ExDet Tool version 1.0 (Mesgaran et al. 2014) to visualize novel environments across the landscape. ExDet reveals whether projections are applied beyond the ranges of individual predictor variables or into places with novel correlation structure among predictor variables, even if still within their univariate ranges. Multivariate novelty is based on Mahalanobis distance to the edge of the multivariate distribution of the reference (background) data (e.g., for two variables, the edge of the ellipse surrounding correlated points); this metric ranges from zero to positive infinity, with values greater than one considered significantly novel.

Results

Model Evaluation

All model projections matched the *Erythranthe cardinalis* distribution well, although models differed in the degree of under- or overprediction in various regions (fig. 1). All models did better than random ($AUC > 0.5$) in discriminating presences from absences, with an average cross-validated AUC of 0.77 across model types. Further description of model accuracy and reliability is in appendix D.

Differences in Climatic Suitability from Range Center to Range Edges

Results for hypothesis tests about climatic suitability and occupancy were qualitatively similar for all models. For simplicity we feature GAM and RF results here because they both performed well (app. D) and represent different model types; GLM, BRT, and MAX results are in the supplemental material, available online.

Latitude. For all model types, average suitability differed among latitudinal regions (table S1). Suitability was significantly lower at the northern range margin compared with the range center but did not differ between the southern range margin and range center (figs. 2, S1; table 1). Although mean suitability of the southern region was high, this was driven in large part by highly suitable sites in the Transverse Mountain Ranges at $\sim 34^\circ\text{N}$ (figs. 3, S2). For all model types, suitability of both occupied and unoccupied sites had a significant quadratic relationship to latitude, although R^2 ranged from only 0.07 to 0.27 (table S2). Predicted suitability of both site types peaked near or just south of the latitudinal range center (table 1). In some models, predicted suitability declined more strongly toward the northern range edge than toward the southern range edge (figs. 3, S2).

Elevation. Average suitability differed among elevational regions for all model types (table S1). Suitability was highest at the mid-elevation range center, significantly lower at the low-elevation range edge, and lowest at the high-elevation range edge (figs. 2, S1; table 1). Suitability of occupied sites had a significant quadratic relationship to elevation, with R^2 ranging from 0.11 to 0.35 (table S2). Predicted suitability of occupied sites peaked near or slightly below the elevational range center and declined strongly toward higher elevations (figs. 3, S2; table 1). Suitability of unoccupied sites tended to decrease more linearly with elevation (table S2; figs. 3, S2).

Suitable Habitat beyond Range Edges

When projections were classified on the basis of the suitability threshold and clipped to appropriate riparian microhabitat, very few climatically suitable stream reaches were detected in the lowest- and highest-latitude bins (figs. 4, S3; table 1). No stream reaches were modeled as suitable above the high-elevation edge (figs. 4, S3; table 1). Suitability was high at low elevations but only in the central latitudinal region (figs. 4, S3; table 1). Visualization of environmental dissimilarity showed that the risk of model extrapolation to novel environments beyond range edges was low (fig. S4).

Spatial Variation in Occupancy of Climatically Suitable Habitat

Latitude. Logistic regressions of presence/absence versus latitude among sites above the suitability threshold suggested decreasing occupancy of suitable sites in the north (figs. 5, S7; tables 1, S4). The probability of presence in suitable sites declined from south to north for all five model types. This inference is supported by calibration curves fit to regional subsets of data (supplemental material; table S3; figs. S5, S6).

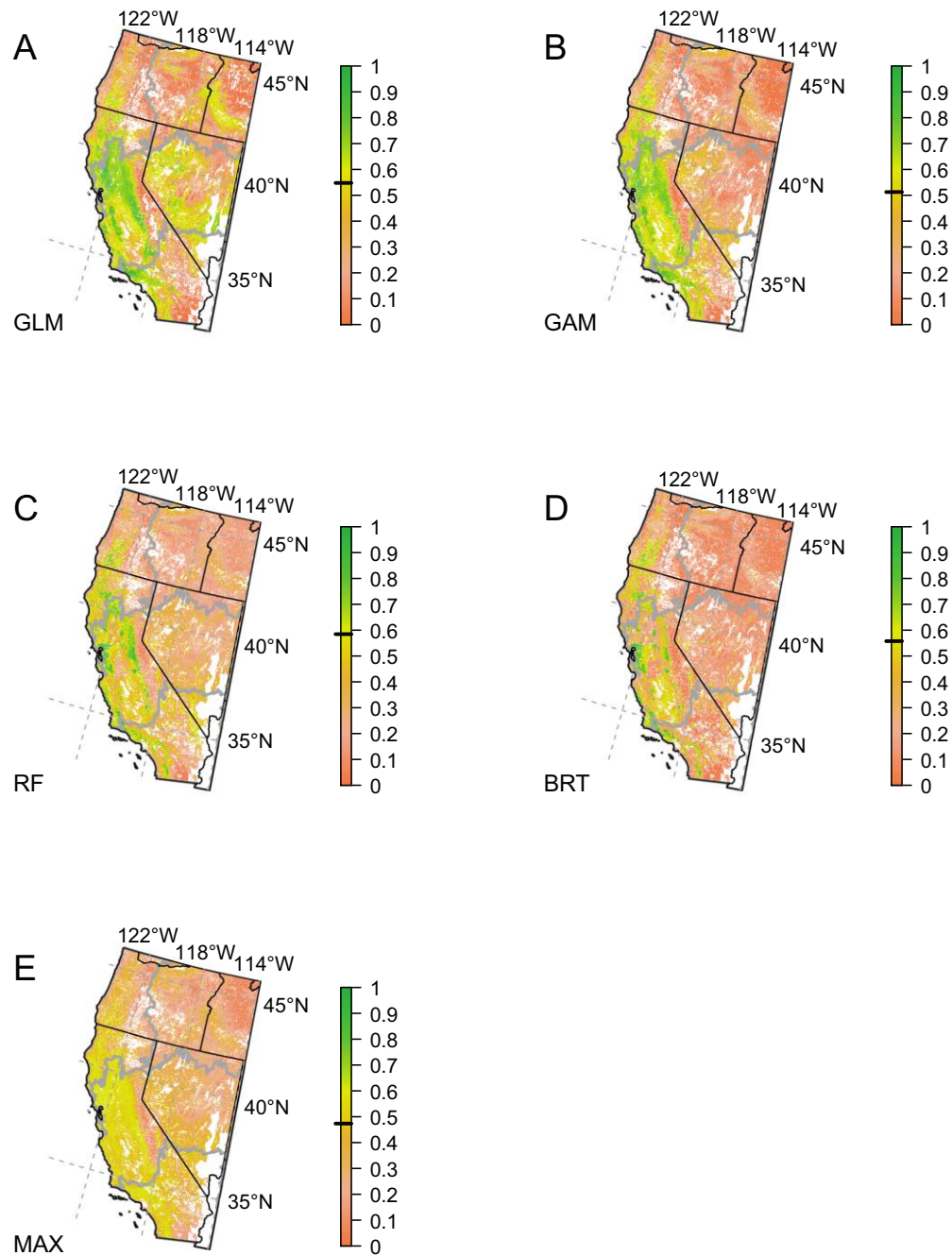


Figure 1: Spatial distribution of habitat suitability based on average predictions from generalized linear models (GLMs; A), generalized additive models (GAMs; B), random forests (RFs; C), boosted regression trees (BRTs; D), and MaxEnt (MAX; E). Green indicates areas of highest suitability.

Elevation. Logistic regressions of presence/absence versus elevation among only those sites above the suitability threshold had significant quadratic terms for BRT and MAX models, suggesting decreasing occupancy of suitable sites at low- and high-range edges (fig. S7; table S4). However, these models

had among the most severe calibration problems, making them least reliable for inferences about occupancy (app. D). In contrast, logistic regressions showed no changes in occupancy of suitable sites for GLM, GAM, and RF models (figs. 5, S7). The inference that occupancy of highly suitable sites does

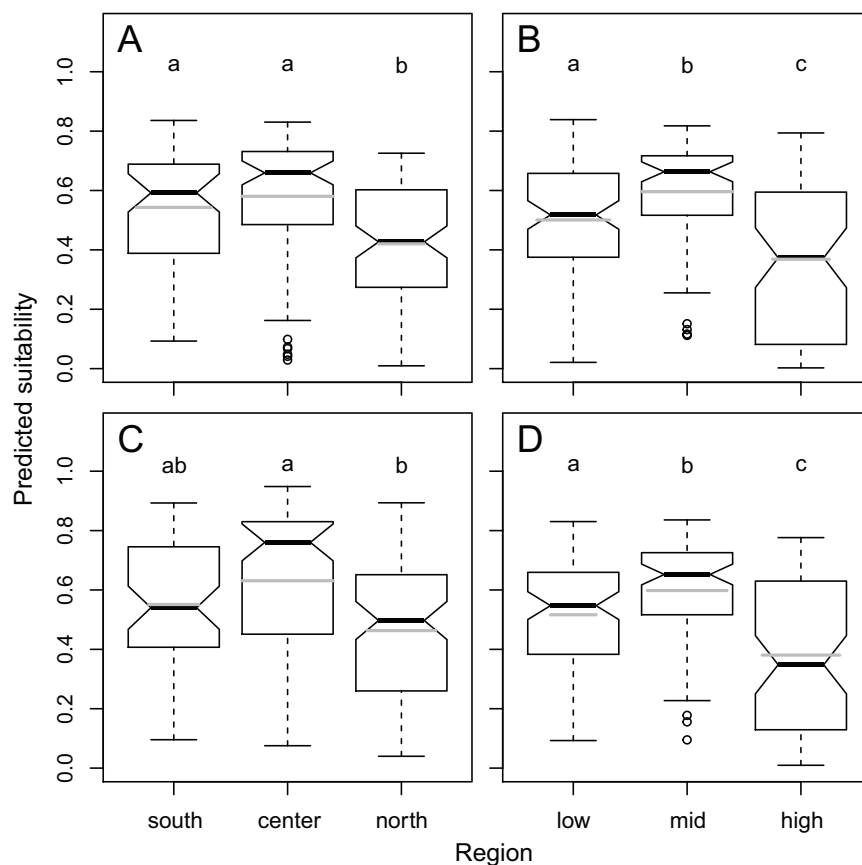


Figure 2: Modeled suitability by latitudinal or elevational region. *A*, Generalized additive model (GAM) by latitudinal region. *B*, GAM by elevational region. *C*, Random forest (RF) model by latitudinal region. *D*, RF by elevational region. Black horizontal lines show medians, gray lines show means, and notches approximate a 95% confidence interval around the median. Boxes give the interquartile range, and whiskers give the most extreme value that is within $\times 1.5$ the interquartile. Regions with different lowercase letters are significantly different in post hoc comparisons of means.

not differ across elevation is supported by calibration curves fit to regional subsets of data ((supplemental material; table S3; figs. S5, S6).

Nonstationarity in Effects of Climatic Variables

We detected many significant interactions between bioclimatic variables and latitude or elevation (app. C), suggesting that the effect of climate on the probability of presence varies across the range. However, GLM models including interactions with latitude or elevation had only slightly higher AUC scores and yielded qualitatively similar patterns of spatial variation in suitability and occupancy (app. C).

Discussion

We used inferences from ENMs (table 1) to examine the relative importance of fitness and dispersal limitation at different spatial scales across the range of the perennial herb

Erythranthe cardinalis. We found a predominant role for fitness limitation, which is in line with recent meta-analyses (Hargreaves et al. 2014; Lee-Yaw et al. 2016). Compared with the range center, modeled climatic suitability was lower at and beyond edges. Nonetheless, there was evidence consistent with dispersal limitation at the northern range edge, where suitable habitat was less likely to be occupied compared with the range center. These results suggest that differences in the steepness of underlying environmental gradients result in greater dispersal limitation at latitudinal range edges (and particularly poleward edges) compared with elevational edges (Kirkpatrick and Barton 1997; Hara 2010; Hargreaves et al. 2014).

Relative Importance of Fitness and Dispersal Limitation Depends on Spatial Scale

Theory predicts that the interplay of dispersal and gradient steepness determines range limits along environmental gra-

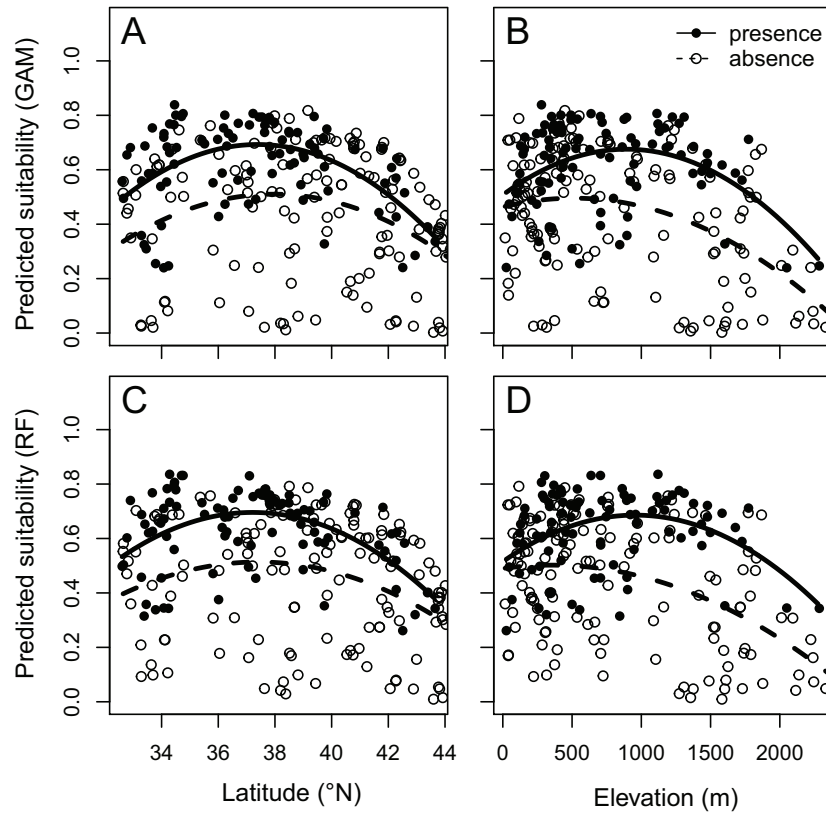


Figure 3: Quadratic regressions of modeled suitability versus latitude ($^{\circ}$ N) and elevation (m). Panels display the average score across 10 replicate training models and best-fit lines for presences (filled symbols, solid lines) and absences (open symbols, dashed lines) from generalized additive models (GAMs) versus latitude (A), GAMs versus elevation (B), random forests (RFs) versus latitude (C), and RFs versus elevation (D).

dients because of their combined effect on environmental distance traversed (Kirkpatrick and Barton 1997; Polechová and Barton 2015). Along steep gradients, dispersal from suitable sites will continually introduce propagules to unsuitable sites, where selection will weed them out or, with high enough migration, they can persist in sink populations. Thus, when gradients are steep relative to dispersal distances, ranges are expected to match or even exceed niches. Conversely, along shallow gradients, ranges are more likely to fall short of niche limits because it takes more dispersal events to reach unsuitable habitat, particularly if temporal environmental changes occur faster than propagules can track. In a meta-analysis of over-the-edge transplant experiments, Hargreaves et al. (2014) found support for these predictions; demographic sinks were more likely beyond elevational than latitudinal edges, and there were no observed cases where latitudinal range edges exceeded niche limits. However, sample sizes for these comparisons were low, and comparisons of latitude and elevation were made across different species, regions, and time periods. This study reinforces these inferences with a systematic comparison of latitude and el-

evation within the same study system. Our comparison is strongest for the northern latitude versus high-elevation contrast, which did not suffer from any of the sampling limitations that affected inferences about the southern latitude versus low-elevation contrast.

Fitness and Dispersal Limitation Can Act Synergistically

Mechanisms for range limitation are not mutually exclusive, and there is potential for interesting synergy between them. Likewise, decreasing occupancy of suitable habitat in a metapopulation system could result from gradients in habitat suitability, extinction risk, or colonization rates (Holt and Keitt 2000). For example, deteriorating habitat suitability could contribute to dispersal limitation via a declining number or quality of propagules (Munzbergova and Herben 2005) or increasingly smaller and more isolated habitat patches (Holt and Keitt 2000). In the former case, fitness limitation is arguably the root cause of colonization failure. These interactions could have compounding effects on site occupancy, particularly for species with Allee effects. Svensson (1992) speculated

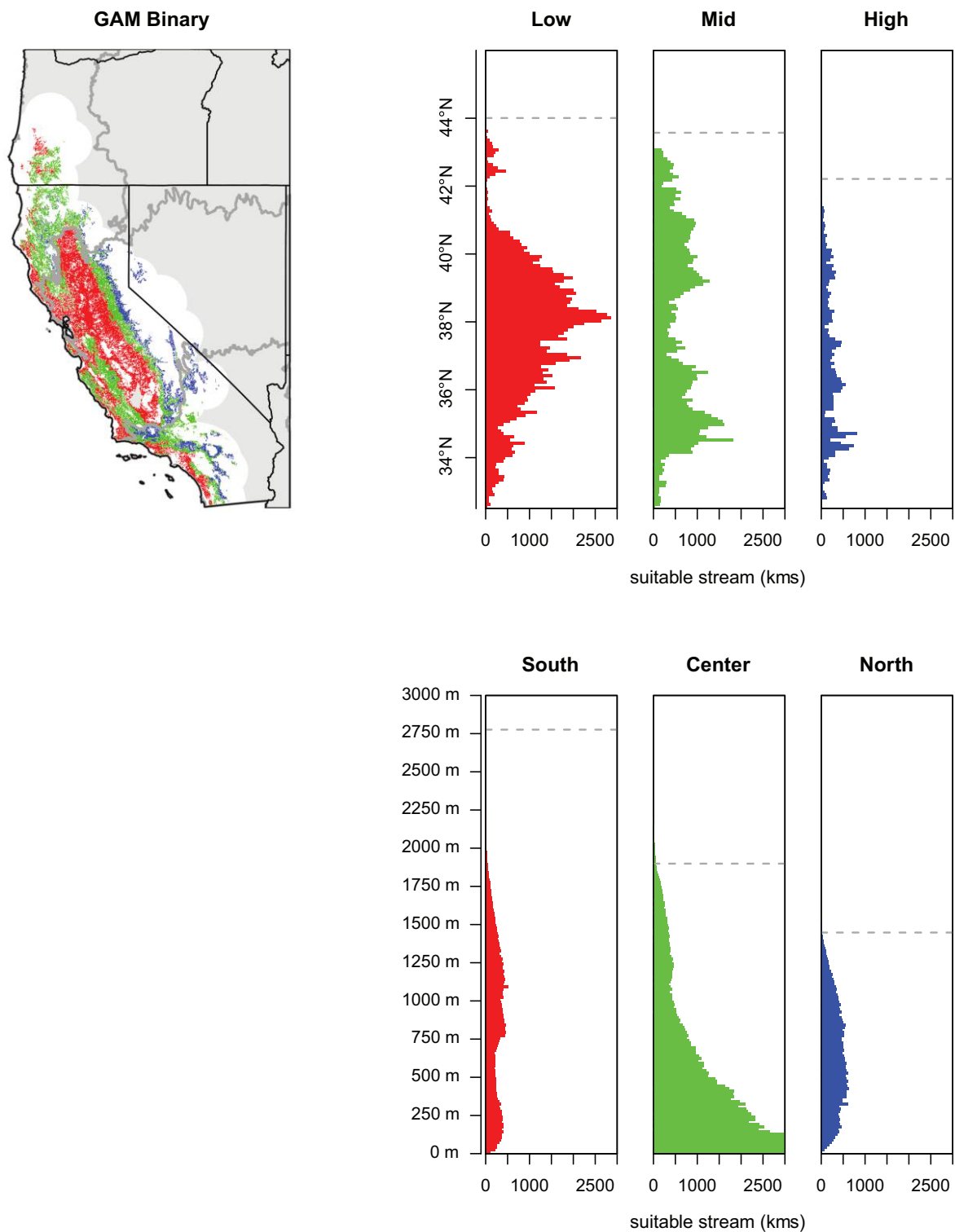


Figure 4: Histograms of climatically suitable stream habitat versus latitude (within each elevational group; *top*) or versus elevation (within each latitudinal group; *bottom*) for the generalized additive model (GAM). Dotted lines in each panel depict the highest or lowest record of occurrence within each group. Map depicts climatically suitable habitat within low- (red), mid- (green), and high- (blue) elevation categories. Mapped projection and sums of suitable habitat are limited to a spatial extent of 80 km from presence records (white polygon).

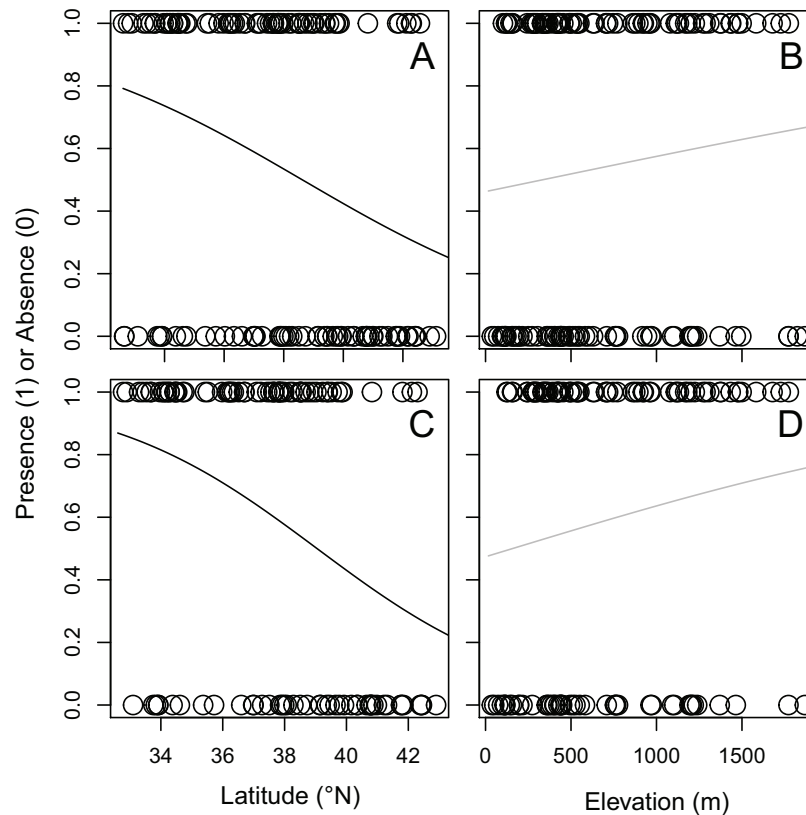


Figure 5: Logistic regressions of occurrence in suitable sites versus range position for generalized additive model (GAM) across latitude (A), GAM across elevation (B), random forest (RF) model across latitude (C), and RF across elevation (D). Circles depict testing data points above the suitability threshold in each model. Fitted lines shows predicted probability of occurrence from best-fit models (black lines, models where linear or quadratic terms had $P < .05$; gray lines, models with nonsignificant terms).

that declining occupancy of three water beetle species at their range edges was due to low abundance and prevalence of source populations for colonization. In this system we found low occupancy of suitable habitat at the northern range edge, which is consistent with dispersal limitation, but ENM also predicted low habitat suitability, as would be expected under fitness limitation. Further study is required to disentangle how reduced occupancy arises from limited dispersal, low habitat quality, and/or low fitness (e.g., that elevates extinction risk). Our results call for increased research emphasis on interactions between fitness and dispersal limitation rather than treating them as a simple dichotomy.

Likelihoods of Fitness and Dispersal Limitation

Our results support the hypothesis that fitness limitation is most likely when dispersal has allowed a species to sample many environments and reach the edges of its niche. This likelihood is determined by dispersal ability, which is positively related to range size across many taxa (Lester et al.

2007; Strona et al. 2012), and time. For example, recently introduced species are unlikely to have reached niche limits, and in many groups exotic range extent increases with time since introduction (e.g., Dyer et al. 2016). Over evolutionary timescales, range size increases with species age (Paul et al. 2009), suggesting that older native species are more likely to have reached the limits of their potential distributions. Conversely, dispersal limitation is most likely when environmental fluctuations exceed a species' time and ability to track them via dispersal. In the Northern Hemisphere, dispersal limitation is more likely for species whose ranges extend further northward into areas that have been most impacted by both past glaciation (Svenning et al. 2008) and recent rapid warming (IPCC 2013). Dispersal limitation could be compounded by physical geography. For example, the east-west orientation of major Eurasian mountain ranges could pose a greater dispersal barrier to northward range expansion than in North America, where major ranges are oriented north-south (Brown 1995). Nonetheless, we found a role for dispersal limitation even for a species of midlatitudes

in western North America, suggesting that dispersal limitation could play a pervasive role even when fitness limitation is also operating.

Applying Niche Models to Infer Causes of Range Limits

ENMs can be highly sensitive to methodological choices, such as how pseudoabsences are selected (Hertzog et al. 2014), their spatial extent (Barve et al. 2011), and their ratio to presences (Barbet-Massin et al. 2012). We examined the sensitivity of our results to these choices and found that downstream conclusions about habitat suitability and occupancy were unaffected. We also employed an array of different ENM types with contrasting strengths and weaknesses, and our conclusions were robust to the underlying model type. An independent testing data set with constant detection probability and true absences enabled us to evaluate overfitting and conduct strong hypothesis tests, which is rare in most niche and distribution modeling applications.

Nonetheless, ENM inferences rely on obtaining ecologically relevant predictor variables at an appropriate spatial resolution. For example, if fitness at a range edge is limited by a biotic interaction such as competition, then ENMs built with only climatic variables could yield erroneous conclusions, unless the outcome of biotic interactions covaries reliably with climatic predictors (Taniguchi and Nakano 2000; Lee-Yaw et al. 2016; Godsoe et al. 2017). Biotic interactions are posited to have greater importance at low-latitude and low-elevation range edges, although empirical evidence is sparse (Louthan et al. 2015). Alternatively, biotic interactions might exclude species from local patches idiosyncratically (i.e., Eltonian noise hypothesis; Soberón and Nakamura 2009). However, Lee-Yaw et al. (2016) suggested that climatic suitability predicts fitness limitation for most species and that if climate is operating indirectly via biotic interactions, then it is doing so at a coarse scale. Despite the overwhelming focus in the ENM literature on climatic predictor variables, it is possible to incorporate biotic interactions (Kissling et al. 2012; Anderson 2017). Previous studies have investigated the influence of key competitors (e.g., Meineri et al. 2012), facilitators (e.g., Heikkinen et al. 2007), resources (e.g., Freeman and Mason 2015), or predators (e.g., Kosicki et al. 2016) on ENM predictions, often finding substantial model improvement from their inclusion. Logistically, this is implemented by constraining ENM predictions to the range of the key interactor or adding as predictors their presence/absence, abundance, or probability of occurrence (Kissling et al. 2012; Anderson 2017). The latter is generalizable to entire assemblages (e.g., competitors: Meier et al. 2010; insects and host plants: Pellissier et al. 2013; plants and soil microbes: Bueno de Mesquita et al. 2015). Similarly, it is also possible to include microhabitat characteristics such as chem-

ical and physical characteristics of the local substrate (e.g., Gies et al. 2015). Thus, the framework used in this article can be extended to species whose natural history dictates the inclusion of nonclimatic predictor variables.

For *E. cardinalis*, other lines of evidence bolster inferences about fitness and dispersal limitation. Prior work suggests an overriding effect of temperature and no role for competition with a parapatrically distributed relative, at least with respect to elevation range limits (Angert and Schemske 2005; Angert 2006). Fitness limitation at the high-elevation edge is validated by three independent field translocations (Hiesey et al. 1971; Angert and Schemske 2005; Angert et al. 2008). Similarly, dispersal limitation at the northern edge is validated by a transplant experiment in which experimental populations beyond the northern edge had projected population growth rates >1 (Bayly 2015). Population genetic data show that northern populations are on average younger and have lower heterozygosity than central and southern populations (J. R. Paul, T. Parchman, A. Buerkle, and A. L. Angert, unpublished manuscript), as expected for an expanding range edge (Excoffier 2004). Finally, demographic observations of natural populations reveal that southern populations have low mean fitness ($\lambda < 1$) while northern populations are stable or increasing ($\lambda \geq 1$; Sheth and Angert 2017).

Genetic differentiation and local adaptation across a geographic range can lead to intraspecific variation in climate relationships (e.g., Angert et al. 2011). Also, some species become habitat specialists at the range edge, leading to narrower niche breadth (Svensson 1992; Avila-Flores et al. 2010). Failure to account for such variation (i.e., nonstationarity) could lead to poor model fit at the range edge, particularly if records are more sparse, leading to false inferences of declining suitability or low occupancy. In this study, suitability scores spanned a similar range of variation in the north as at the range center (fig. 3). Also, we compared results for models with and without interactions between climatic variables and latitude or elevation. Critically, although significant interactions often existed, their incorporation did not change inferences about decreases in climatic suitability and occupancy toward range edges. This is especially important given our truncated sampling at the southern range edge; for the lack of sampling there to bias our interpretations, one would have to invoke a sudden spike in nonstationarity in Baja California, departing from that observed across much larger spatial and environmental differences. Hothorn et al. (2010) proposed a method for integrating estimation of nonstationarity into traditional distribution models, which could be a promising avenue for future studies.

ENMs have been used previously to infer nonclimatic limitation of geographic ranges. Approaches include identifying areas where models predict high suitability yet the

species is not observed (e.g., Graham et al. 2010), relating range filling to dispersal ability or the presence of congeners (Laube et al. 2013), relating model fit to dispersal ability (Kharouba et al. 2013), and testing whether adding spatial filters (Cardador et al. 2014) or dispersal costs (Algar et al. 2013) improves model fit. Species that will be most amenable to future investigations of habitat suitability and occupancy are those for which systematic, range-wide field surveys are possible, that occur in regions with high-resolution environmental layers, and whose natural history is known well enough to identify key nonclimatic variables (e.g., edaphic characteristics or interacting species). For mobile, cryptic, or ephemeral species, an important additional consideration is detectability, which influences false absences and might require temporally replicated sampling. Systematic surveying and modeling efforts will help account for spatial heterogeneity in limiting factors and reveal potential interactions between fitness and dispersal limitation. Ultimately, this will improve our understanding of range limitation and aid projections of climate-induced range shifts.

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Literature Cited

- Algar, A. C., D. L. Mahler, R. E. Glor, and J. B. Losos. 2013. Niche incumbency, dispersal limitation and climate shape geographical distributions in a species-rich island adaptive radiation. *Global Ecology and Biogeography* 22:391–402.
- Anderson, R. P. 2017. When and how should biotic interactions be considered in models of species niches and distributions? *Journal of Biogeography* 44:8–17.
- Angert, A. L. 2006. Growth and leaf physiology of monkeyflowers with different altitude ranges. *Oecologia* (Berlin) 148:183–194.
- Angert, A. L., M. Bayly, S. N. Sheth, and J. R. Paul. 2018. Data from: Testing range-limit hypotheses using range-wide habitat suitability and occupancy for the scarlet monkeyflower (*Erythranthe cardinalis*). American Naturalist, Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.bg15b>.
- Angert, A. L., H. D. Bradshaw Jr., and D. W. Schemske. 2008. Using experimental evolution to investigate geographic range limits in monkeyflowers. *Evolution* 62:2660–2675.
- Angert, A. L., and D. W. Schemske. 2005. The evolution of species' distributions: reciprocal transplants across the elevation ranges of *Mimulus cardinalis* and *M. lewisii*. *Evolution* 59:222–235.
- Angert, A. L., S. N. Sheth, and J. R. Paul. 2011. Incorporating population-level variation in thermal performance into predictions of geographic range shifts. *Integrative and Comparative Biology* 51:733–750.
- Avila-Flores, R., M. S. Boyce, and S. Boutin. 2010. Habitat selection by prairie dogs in a disturbed landscape at the edge of their geographic range. *Journal of Wildlife Management* 74:945–953.
- Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution* 3:327–338.
- Barve, N., V. Barve, A. Jiménez-Valverde, A. Lira-Noriega, S. P. Maher, A. T. Peterson, J. Soberón, et al. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modelling* 222:1810–1819.
- Bayly, M. 2015. Translocations of *Mimulus cardinalis* beyond the northern range limit show that dispersal limitation can invalidate ecological niche models. MS thesis. University of British Columbia, Vancouver. <https://open.library.ubc.ca/cIRcle/collections/24/items/1.0223357>, doi:10.14288/1.0223357.
- Beardsley, P. M., A. Yen, and R. G. Olmstead. 2003. AFLP phylogeny of *Mimulus* section *Erythranthe* and the evolution of hummingbird pollination. *Evolution* 57:1397–1410.
- Brown, J. H. 1995. *Macroecology*. University of Chicago Press, Chicago.
- Bruelheide, H., and U. Scheidel. 1999. Slug herbivory as a limiting factor for the geographical range of *Arnica montana*. *Journal of Ecology* 87:839–848.
- Bueno de Mesquita, C. P., A. J. King, S. K. Schmidt, E. C. Farrer, and K. N. Suding. 2015. Incorporating biotic factors in species distribution modeling: are interactions with soil microbes important? *Ecography* 39:970–980.
- Cardador, L., F. Sarda-Palamera, M. Carrete, and S. Manosa. 2014. Incorporating spatial constraints in different periods of the annual cycle improves species distribution model performance for a highly mobile bird species. *Diversity and Distributions* 20:515–528.
- Cohen, J. 1960. A coefficient of agreement of nominal scales. *Educational and Psychological Measurement* 20:37–46.
- Dyer, E. E., V. Franks, P. Cassey, B. Collen, R. C. Cope, K. E. Jones, Ç. H. Şekercioğlu, et al. 2016. A global analysis of the determinants of alien geographical range size in birds. *Global Ecology and Biogeography* 25:1346–1355.
- Eckhart, V. M., M. A. Geber, W. F. Morris, E. S. Fabio, P. Tiffin, and D. A. Moeller. 2011. The geography of demography: long-term demographic studies and species distribution models reveal a species border limited by adaptation. *American Naturalist* 178(suppl.):S26–S43.
- Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40:677–697.
- Excoffier, L. 2004. Patterns of DNA sequence diversity and genetic structure after a range expansion: lessons from the infinite-island model. *Molecular Ecology* 13:853–864.
- Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24:38–49.
- Freeman, B. G., and N. A. Mason. 2015. The geographic distribution of a tropical montane bird is limited by a tree: acorn woodpeckers (*Melanerpes formicivorus*) and Colombian oaks (*Quercus humboldtii*) in the Northern Andes. *PLoS ONE* 10:e0128675.
- Gavin, D. G., and F. S. Hu. 2006. Spatial variation of climatic and non-climatic controls on species distribution: the range limit of *Tsuga heterophylla*. *Journal of Biogeography* 33:1384–1396.
- Geber, M. A., and V. M. Eckhart. 2005. Experimental studies of adaptation in *Clarkia xantiana*. II. Fitness variation across a subspecies border. *Evolution* 59:521–531.

- Gies, M., M. Sondermann, D. Hering, and C. K. Feld. 2015. Are species distribution models based on broad-scale environmental variables transferable across adjacent watersheds? a case study with eleven macroinvertebrate species. *Fundamental and Applied Limnology* 186:63–97.
- Godsoe, W., J. Franklin, and F. Guillaume Blanchet. 2017. Effects of biotic interactions on modeled species' distribution can be masked by environmental gradients. *Ecology and Evolution* 7:654–664.
- Graham, C. H., N. Silva, and J. Velasquez-Tibata. 2010. Evaluating the potential causes of range limits of birds of the Colombian Andes. *Journal of Biogeography* 37:1863–1875.
- Guisan, A., and W. Thuiller. 2005. Predicting species distributions: offering more than simple habitat models. *Ecology Letters* 8:993–1009.
- Hara, M. 2010. Climatic and historical factors controlling horizontal and vertical distribution patterns of two sympatric beech species, *Fagus crenata* Blume and *Fagus japonica* Maxim., in eastern Japan. *Flora* 205:161–170.
- Hargreaves, A. L., K. E. Samis, and C. G. Eckert. 2014. Are species' range limits simply niche limits writ large? a review of transplant experiments beyond the range. *American Naturalist* 183:157–173.
- Hastie, T., and W. Fithian. 2013. Inference from presence-only data; the ongoing controversy. *Ecography* 36:864–867.
- Heikkinen, R. K., M. Luoto, R. Virkkala, R. G. Pearson, and J. H. Korber. 2007. Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Global Ecology and Biogeography* 16:754–763.
- Hertzog, L. R., A. Besnard, and P. Jay-Robert. 2014. Field validation shows bias-corrected pseudo-absence selection is the best method for predictive species-distribution modelling. *Diversity and Distributions* 20:1403–1413.
- Hiesey, W. M., M. A. Nobs, and O. Björkman. 1971. Experimental studies on the nature of species. V. Biosystematics, genetics, and physiological ecology of the *Erythranthe* section of *Mimulus*. Carnegie Institute of Washington no. 628.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965–1978.
- Hijmans, R. J., S. Phillips, J. Leathwick, and J. Elith. 2015. dismo: species distribution modeling. R package, version 1.0–12. <https://cran.r-project.org/web/packages/dismo/index.html>.
- Holt, R. D., and T. H. Keitt. 2000. Alternative causes for range limits: a metapopulation perspective. *Ecology Letters* 3:41–47.
- Holt, R. D., T. H. Keitt, M. A. Lewis, B. A. Maurer, and M. L. Taper. 2005. Theoretical models of species' borders: single species approaches. *Oikos* 108:18–27.
- Hothorn, T., J. Müller, B. Schröder, T. Kneib, and R. Brandl. 2010. Decomposing environmental, spatial, and spatiotemporal components of species distributions. *Ecological Monographs* 81:329–347.
- IPCC (Intergovernmental Panel on Climate Change). 2013. Climate Change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, eds. Cambridge University Press, New York.
- Jankowski, J. E., S. K. Robinson, and D. J. Levey. 2010. Squeezed at the top: interspecific aggression may constrain elevational ranges in tropical birds. *Ecology* 91:1877–1884.
- Kharouba, H. M., J. L. McCune, W. Thuiller, and B. Huntley. 2013. Do ecological differences between taxonomic groups influence the relationship between species' distributions and climate? a global meta-analysis using species distribution models. *Ecography* 36:657–664.
- Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a species range. *American Naturalist* 150:1–23.
- Kissling, W. D., C. F. Dormann, J. Groeneveld, T. Hickler, I. Kuhn, G. J. McNerny, J. M. Montoya, et al. 2012. Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *Journal of Biogeography* 2163–2178.
- Kosicki, J. Z., P. Zduniak, M. Ostrowska, and M. Hromada. 2016. Are predators negative or positive predictors of farmland bird species community on a large geographical scale? *Ecological Indicators* 62:259–270.
- Laube, I., C. H. Graham, and K. Boehning-Gaese. 2013. Intra-generic species richness and dispersal ability interact to determine geographic ranges of birds. *Global Ecology and Biogeography* 22: 223–232.
- Lauzeral, C., G. Grenouillet, and S. Brosse. 2013. Spatial range shape drives the grain size effects in species distribution models. *Ecography* 36:778–787.
- Lee-Yaw, J., H. M. Kharouba, C. Mahoney, M. G. Bontrager, A. M. Csergo, A. M. E. Noreen, Q. Li, et al. 2016. A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. *Ecology Letters* 19:710–722.
- Lehner, B., K. Verdin, and A. Jarvis. 2008. New global hydrography derived from spaceborne elevation data. *Eos* 89:93–94.
- Lester, S. E., B. I. Ruttenberg, S. D. Gaines, and B. P. Kinlan. 2007. The relationship between dispersal ability and geographic range size. *Ecology Letters* 10:745–758.
- Levin, D. A., and K. Clay. 1984. Dynamics of synthetic *Phlox drummondii* populations at the species margin. *American Journal of Botany* 71:1040–1050.
- Liu, C., M. White, and G. Newell. 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography* 40:778–789.
- Louthan, A. M., D. F. Doak, and A. L. Angert. 2015. Where and when do species interactions set range limits? *Trends in Ecology and Evolution* 30:780–792.
- Marsico, T. D., and J. J. Hellmann. 2009. Dispersal limitation inferred from an experimental translocation of *Lomatium* (Apiaceae) species outside their geographic ranges. *Oikos* 118:1783–1792.
- McKay, L., T. Bondelid, T. Dewald, J. Johnston, R. Moore, and A. Rea. 2012. NHDPlus version 2: user guide. US Environmental Protection Agency, Washington, DC.
- Meier, E. S., F. Kienast, P. B. Pearman, J. Svenning, W. Thuiller, M. B. Arau, A. Guisan, et al. 2010. Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography* 33:1038–1048.
- Meineri, E., O. Skarpaas, and V. Vandvik. 2012. Modeling alpine plant distributions at the landscape scale: do biotic interactions matter? *Ecological Modelling* 231:1–10.
- Mesgaran, M. B., R. D. Cousens, and B. L. Webber. 2014. Here be dragons: a tool for quantifying novelty due to covariate range and correlation change when projecting species distribution models. *Diversity and Distributions* 20:1147–1159.
- Miller, M. E., S. L. Hui, and W. M. Tierney. 1991. Validation techniques for logistic regression models. *Statistics in Medicine* 10: 1213–1226.
- Moeller, D. A., M. A. Geber, V. M. Eckhart, and P. Tiffin. 2012. Reduced pollinator service and elevated pollen limitation at the geographic range limit of an annual plant. *Ecology* 93:1036–1048.
- Munzbergova, Z., and T. Herben. 2005. Seed, dispersal, microsite, habitat and recruitment limitation: identification of terms and concepts in studies of limitations. *Oecologia (Berlin)* 145:1–8.

- Nesom, G. L. 2014. Taxonomy of *Erythranthe* sect. *Erythranthe* (Phrymaceae). *Phytoneuron* 31:1–41.
- Paul, J. R., C. Morton, C. M. Taylor, and S. J. Tonsor. 2009. Evolutionary time for dispersal limits the extent, but not the occupancy of species' potential ranges in the tropical plant genus *Psychotria* (Rubiaceae). *American Naturalist* 173:188–199.
- Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* 133:225–245.
- Pellissier, L., R. P. Rohr, C. Ndiribe, J.-N. Pradervand, N. Salamin, A. Guisan, and M. Wisz. 2013. Combining food web and species distribution models for improved community projections. *Ecology and Evolution* 3:4572–4583.
- Peterson, A. T. 2006. Uses and requirements of ecological niche models and related distributional models. *Biodiversity Informatics* 3:59–72.
- Polechová, J., and N. H. Barton. 2015. Limits to adaptation along environmental gradients. *Proceedings of the National Academy of Sciences of the USA* 112:6401–6406.
- Pomara, L. Y., K. Ruokolainen, and K. R. Young. 2014. Avian species composition across the Amazon River: the roles of dispersal limitation and environmental heterogeneity. *Journal of Biogeography* 41:784–796.
- Ramsey, J., H. D. Bradshaw, and D. W. Schemske. 2003. Components of reproductive isolation between the monkeyflowers *Mimulus lewisii* and *M. cardinalis* (Phrymaceae). *Evolution* 57:1520–1534.
- Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. The evolution and ecology of geographic range limits. *Annual Review of Ecology, Evolution, and Systematics* 40:415–436.
- Sheth, S. N., and A. L. Angert. 2016. Artificial selection reveals high genetic variation in phenology at the trailing edge of a species range. *American Naturalist* 187:182–193.
- . 2017. Demographic compensation does not rescue populations at a trailing range edge. *bioRxiv*, doi:10.1101/117606.
- Soberón, J., and M. Nakamura. 2009. Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences of the USA* 106:19644–19650.
- Stanton-Geddes, J., and C. G. Anderson. 2011. Does a facultative mutualism limit species range expansion? *Oecologia* (Berlin) 167:149–155.
- Strona, G., P. Galli, S. Montano, D. Seveso, and S. Fattorini. 2012. Global-scale relationships between colonization ability and range size in marine and freshwater fish. *PLoS ONE* 7:e49465.
- Svenning, J. C., S. Normand, and F. Skov. 2008. Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. *Ecography* 31:316–326.
- Svensson, B. W. 1992. Changes in occupancy, niche breadth and abundance of 3 *Gyrinus* species as their respective range limits are approached. *Oikos* 63:147–156.
- Taniguchi, Y., and S. Nakano. 2000. Condition-specific competition: implications for the altitudinal distribution of stream fishes. *Ecology* 81:2027–2039.
- Thompson, D. M. 1993. *Mimulus*. Pages 1037–1046 in J. C. Hickman, ed. *The Jepson manual: higher plants of California*. University of California Press, Berkeley.
- US Environmental Protection Agency. 2013. Level III and IV ecoregions of the continental United States. US Environmental Protection Agency, Washington, DC.
- Van der Veken, S., P. De Frenne, L. Baeten, E. Van Beek, K. Verheyen, and M. Hermy. 2012. Experimental assessment of the survival and performance of forest herbs transplanted beyond their range limit. *Basic and Applied Ecology* 13:10–19.
- Verbruggen, H. 2012. OccurrenceThinner, version 1.04. <http://www.phycoweb.net/software>.
- Verbruggen, H., L. Tyberghien, G. S. Belton, F. Mineur, A. Jueterbock, G. Hoarau, C. F. D. Gurgel, et al. 2013. Improving transferability of introduced species' distribution models: new tools to forecast the spread of a highly invasive seaweed. *PLoS ONE* 8:e68337.
- Vickery, R. K., and B. M. Wullstein. 1987. Comparison of 6 approaches to the classification of *Mimulus* sect. *Erythranthe* (Scrophulariaceae). *Systematic Botany* 12:339–364.
- Wang, T., A. Hamann, D. L. Spittlehouse, and T. Q. Murdock. 2012. ClimateWNA: high-resolution spatial climate data for western North America. *Journal of Applied Meteorology and Climatology* 61:16–29.
- Warren, D. L. 2012. In defense of 'niche modeling'. *Trends in Ecology and Evolution* 27:497–500.
- Wintle, B. A., J. Elith, and J. M. Potts. 2005. Fauna habitat modelling and mapping: a review and case study in the Lower Hunter Central Coast region of NSW. *Austral Ecology* 30:719–738.

References Cited Only in the Online Appendixes

- Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS. <http://www.spatalecolology.com/htools>.
- Cutler, D. R., T. C. Edwards, K. H. Beard, A. Cutler, K. T. Hess, J. Gibson, and J. J. Lawler. 2007. Random forests for classification in ecology. *Ecology* 88:2783–2792.
- De'ath, G. 2007. Boosted trees for ecological modeling and prediction. *Ecology* 88:243–251.
- De'Ath, G., and K. E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81:3178–3192.
- Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. *Journal of Animal Ecology* 77:802–813.
- Hastie, T. 2013. *gam: generalized additive models*. Pages 814–815 in W. Dubitzky, O. Wolkenhauer, K.-H. Cho, and H. Yokota, eds. *Encyclopedia of systems biology*. Springer, New York.
- Levine, N. 2010. *CrimeStat: a spatial statistics program for the analysis of crime incident locations*. Springer, New York.
- Liaw, A., and M. Wiener. 2002. Classification and regression by randomForest. *R News* 2:18–22.
- Muscarella, R., P. J. Galante, M. Soley-Guardia, R. A. Boria, J. Kass, M. Uriarte, and R. P. Anderson. 2014. ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for ecological niche models. *Methods in Ecology and Evolution* 5:1198–1205.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.
- Ridgeway, G., with contributions from others. 2013. *gbm: generalized boosted regression models*. <https://cran.r-project.org/web/packages/gbm/index.html>.

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