Niche differentiation, reproductive interference, and range expansion

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Abstract

Understanding species distributions and predicting future range shifts requires considering all relevant abiotic factors and biotic interactions. Resource competition has received the most attention, but reproductive interference is another widespread biotic interaction that could influence species ranges. Rubyspot damselflies (*Hetaerina* spp.) exhibit a biogeographic pattern consistent with the hypothesis that reproductive interference has limited range expansion. Here we use ecological niche models to evaluate whether this pattern could have instead been caused by niche differentiation. We found evidence for climatic niche differentiation, but the species that encounters the least reproductive interference has one of the narrowest and most peripheral niches. These findings strengthen the case that reproductive interference has limited range expansion, and also provide a counterexample to the idea that release from negative species interactions triggers niche expansion. We propose that release from reproductive interference enables species to expand in range while specializing on the habitats most suitable for breeding.

Introduction

Understanding how species ranges have been shaped by physiological tolerances and biotic interactions is crucial for predicting how species ranges will shift in the future (Lancaster 2022; Sexton *et al.* 2009). Physiological tolerances can be measured experimentally or inferred statistically from the relationships between environmental variables and occurrence data. While "biotic interactions" is a large and diverse category, the vast majority of theoretical and empirical research has focused on trophic interactions and exploitative resource competition, which are closely related phenomena. Exploitative competition can exclude species from portions of their fundamental niche by reducing resources below the level required for the population to increase when rare (Godsoe *et al.* 2017). Other negative species interactions have often been assumed to have effects similar to exploitative competition, but theoretical and empirical research has shown that not to be the case. Direct interactions, such as aggressive and reproductive interference, can shape species distributions in ways that would not be predicted by niche theory (Grether *et al.* 2017; Grether & Okamoto 2022; Kishi & Nakazawa 2013; Patterson & Drury 2023). Interspecific interference does not consistently favor species with higher intrinsic growth rates and can cause Allee effects that prevent species from persisting at low densities in environments that could support much higher densities (Case *et al.* 2005). If interference is asymmetrical, the species harmed least could prevail even if it has a lower intrinsic growth rate in the absence of interference (Grether & Okamoto 2022; Kishi & Nakazawa 2013; Ribeiro & Spielman 1986). If interference is symmetrical, the first species established in an area could become a barrier to the range expansion of other species (Case *et al.* 2005).

Although progress has been made, empirical research on the real-world consequences of interspecific interference lags far behind theory and laboratory experiments.

Reproductive interference is a widespread form of interspecific interference that occurs in all kinds of sexually reproducing organisms (Gröning & Hochkirch 2008; Takahashi *et al.* 2016; Ting & Cutter 2018). In animals, reproductive interference is typically caused by persistent mate recognition errors, which can be costly for both species and yet impossible for selection to eliminate (Drury *et al.* 2019). Theoretical and experimental work has shown that reproductive interference can cause Allee effects and impede range expansion, particularly in taxa with limited dispersal capabilities (Bargielowski & Lounibos 2016; Case *et al.* 2005; Kishi *et al.* 2009; Kishi & Nakazawa 2013; Kuno 1992; Kyogoku 2015; Kyogoku & Nishida 2012; Kyogoku & Wheatcroft 2020; Noriyuki & Osawa 2016). However, the best evidence that reproductive interference has shaped species ranges comes from studies of invasive species actively displacing other species (Butler and Stein 1985; Söderbäck 1995; Liu et al. 2007; Bargielowski et al. 2013; Sun et al. 2014; Bargielowski and Lounibos 2016). Determining whether reproductive interference has limited species ranges is more challenging.

Rubyspot damselflies (*Hetaerina* spp.; Garrison 1990) are a promising study system in this regard because previous research has revealed a biogeographic pattern consistent with the hypothesis that reproductive interference has limited range expansion in North America (Drury *et al.* 2019, 2015; Grether *et al.* 2020). Briefly, the species that encounters the least reproductive interference has the largest latitudinal range and overlaps with the most congeners, while the species with the largest longitudinal range is allopatric across most of its range, and thus has also largely escaped from reproductive interference. Field experiments and landscape genomic analyses will be required to test this hypothesis directly. Here we use existing data to evaluate whether niche differentiation could account for the same biogeographic pattern. If niche differentiation cannot account for the large differences between species in range size and overlap, the case for reproductive interference limiting species ranges would be strengthened.

A few conceptual and methodological distinctions are needed to clarify our approach to testing predictions of the niche differentiation hypothesis. The various ecological niche concepts all have in common the idea that a species' ecological niche pertains to environmental space (Godsoe *et al.* 2017; Sillero *et al.* 2021; Vandermeer 1972). As such, niche axes are environmental variables, not geographic or geo-environmental dimensions. Niche differentiation refers to changes in the relationship between environmental variables and population growth rates that occurred after two or more species diverged from a common ancestor. Species with broader niches are capable of persisting in a broader range of environments and thus tend to have larger geographic ranges (Brown 1984; Carscadden *et al.* 2020; Kambach *et al.* 2019; Slatyer *et al.* 2013). In taxonomic groups in which niche differentiation has occurred and most species are habitat specialists, a habitat generalist with a relatively broad niche (Figure 1a), or one near the ancestral group centroid (Figure 1b), would be expected to have the largest geographic range and the most geographic overlap with the other species (Suárez-Mota & Villaseñor 2020; Tomašových *et al.* 2017).

Ecological niche modeling is widely used to characterize and compare species' realized niches (i.e., the portions of fundamental niches currently occupied) and to make predictions about species distributions in regions that are incompletely surveyed or in the future based on climate change projections (Ahmadi *et al.* 2018; Boys *et al.* 2021; Buermann *et al.* 2008; Guisan *et al.* 2013; Inman *et al.* 2019; Melo-Merino *et al.* 2020; Novella-Fernandez *et al.* 2021; Pearson

& Dawson 2003; Peterson & Holt 2003). While the focus of such studies is usually on geographic space, ecological niche models (ENMs) can also be used to make inferences about niche differentiation (Ahmadi *et al.* 2018; Evans & Jacquemyn 2022; Warren *et al.* 2019, 2021). To avoid ambiguity, we focus here on ENMs constructed using Maxent (Phillips *et al.* 2017), but the same concepts apply to other correlative ENMs. Maxent is a machine-learning, presence-background method that often outperforms presence-only and presence-absence methods (Elith *et al.* 2011; Merow *et al.* 2013; Valavi *et al.* 2022; Wisz *et al.* 2008) and is widely used for species comparisons (Jaime *et al.* 2015; Namyatova 2020; Wellenreuther *et al.* 2012). The basic output is an equation for predicting the suitability of any combination of values of the environmental variables in the training set. Suitability can be projected to the geographic extent or to an *n*-dimensional environmental hypercube, where *n* is the number of environmental variables (Figure 1c-e; Warren et al. 2019). The environmental hypercube is closely analogous to Hutchinson's (1957) *n*-dimensional hypervolume, except that instead of being the discrete set of environments where the species has a positive intrinsic growth rate, all environments in the hypercube are weighted by their estimated suitability. Statistics commonly referred to as 'niche breadth' and 'niche similarity' (or 'niche overlap') can be calculated using the hypercube or the geographic projection (Figure 1d,e; Warren et al. 2021).

Importantly, niche metrics based on geographic projections are not suitable for studying niche differentiation because they conflate geography and environment (Figure 1d,e). Consider the question of whether species differences in niche breadth can explain differences in range size. It would be circular to test whether range size correlates with niche breadth calculated using geographic projections that are based on occurrence samples from across the species' ranges. For this question, it only makes sense to use estimates of niche breadth in environmental space.

Likewise, estimates of niche similarity based on geographic projections confound niche overlap with geographic overlap, and thus should not be used to evaluate whether niche similarity predicts geographic overlap. While these points might seem obvious, they have not surfaced in our reading of the niche modeling literature, and most papers with niche statistics based on ENMs use the geographic versions (Evans & Jacquemyn 2022).

To evaluate whether niche differentiation can account for large differences in range size and geographic overlap, we constructed ENMs for 17 of the 18 species of calopterygid damselflies in North America and made several types of niche comparisons in environmental space. Surprisingly, we found that the species with the largest latitudinal range and the most geographic overlap with other species has one of the narrowest ecological niches and is no closer in niche space to the other species than expected by chance. These results strongly suggest that something other than niche differentiation accounts for this species' expansive range, and therefore strengthen the case for reproductive interference limiting species ranges. This study also provides a counterexample to the idea that release from negative species interactions precipitates niche expansion (Herrmann *et al.* 2021; Lancaster 2022).

Materials and methods

Study system

The life cycle of rubyspot damselflies is centered around areas with suitable larval habitat in perennial springs, streams, or rivers (Corbet 1999; Delgado 2002; Johnson 1973; Novelo-Gutiérrez 2000). At the adult stage, females return repeatedly to the larval habitat to oviposit in submerged vegetation, and males compete for perching sites above the water surface and attempt to clasp arriving females (Córdoba-Aguilar & González-Tokman 2014). Most sympatric species experience high levels of reproductive interference because the females are too similar phenotypically for males to reliably distinguish between them, the only striking exception being the smoky rubyspot damselfly, *Hetaerina titia* (Drury) (Drury *et al.* 2019, 2015; Grether *et al.* 2020). Female *H. titia* have darker wings than females of other species and consequently are pursued and clasped at lower rates by heterospecific males (Drury *et al.* 2019, 2015). Release from reproductive interference could explain why *H. titia* has the largest latitudinal range and occurs in sympatry with the most congeners (Figure 2). The species with the largest longitudinal range, *H. americana* (Fabricius), was recently split into two sister species based on genetic data (Standring *et al.* 2022; Vega-Sánchez *et al.* 2019, 2020), but the occurrence records are indistinguishable; we refer to this monophyletic subclade as "*H. americana* spp.". The melanic wing pigmentation that makes *H. titia* distinct from congeners increases its resemblance to *Calopteryx* (Figure 3; Córdoba-Aguilar et al. 2007), a younger genus in the same family (Calopterygidae; Standring et al. 2022). Our niche comparisons include 12 of the 13 species of *Hetaerina* and all five species of *Calopteryx* that occur in North America.

Occurrence data and range overlap

Species occurrence data were obtained from the Global Biodiversity Information Facility in December 2020 (https://doi.org/10.15468/dl.wmxwvj; https://doi.org/10.15468/dl.cd58ag) and trimmed to a rectangular area (in degrees of longitude and latitude) slightly beyond the geographic range of *H. titia* (-130, -60, 0, 55) to encompass the ranges of all species of Calopterygidae with which *H. titia* overlaps. We refer to this area as the 'full extent', to distinguish it from the rectangular areas of overlap between individual species pairs, which we refer to as 'shared extents' (Figure 1c). To estimate species' range sizes, we used R package ‘alphahull’ (Pateiro-López & Rodríguez-Casal 2010; The R Foundation for Statistical Computing, R version 4.1.2).

Environmental variables

Variable selection is a crucial part of ecological niche modeling (Sillero *et al.* 2021; Warren *et al.* 2014). Maxent requires environmental data across the full geographic extent at locations where the species is known to occur and randomly selected background points (Merow *et al.* 2013; Phillips & Dudík 2008). The standard approach for most applications is to use a combination of bioclimatic and land cover layers, but it is important to consider the natural history of the species and the goals of the study (Phillips *et al.* 2006). It might be supposed that aquatic variables would be required to construct ENMs for insects with aquatic larvae, but the abiotic variables that govern aquatic insect assemblages (e.g., light levels, water chemistry, water clarity, water temperature, disturbance regimes, organic matter, sedimentation) are strongly influenced by and therefore covary with climate, elevation, and land cover (Burgherr & Ward 2001; Faria *et al.* 2021; Null *et al.* 2013; Yoshimura 2012). Bioclimatic layers based on air temperature and precipitation have often been used along with elevation and land cover layers to construct ENMs for aquatic plants (Alahuhta *et al.* 2011; Gillard *et al.* 2017; Lumbreras *et al.* 2013), freshwater fish (Comte & Grenouillet 2015), and aquatic insects (Kusch 2015; Megna *et al.* 2021; Shah *et al.* 2015; Sundar *et al.* 2021) including Odonata (Bhowmik & Schäfer 2015; Cancellario *et al.* 2022). Using more proximal environmental variables does not necessarily result in better niche models; e.g., for modeling the distributions of aquatic invasive species in lakes across the US, the WorldClim air temperature layers consistently outperformed a new global dataset of lake surface water temperatures (Burner *et al.* 2023).

Scale is another important consideration (Elith & Leathwick 2009; Phillips *et al.* 2006). Testing the hypothesis that niche differentiation accounts for differences between species' ranges on a continental scale requires environmental variables that could differ between species' ranges on a continental scale. An environmental layer for the presence/absence of flowing water would be useful for generating high-resolution habitat suitability maps but not for studying niche differentiation, because flowing water is a habitat requirement for all calopterygid damselflies in North America (Westfall & May 1996). Syntopic species of rubyspot damselflies often differ in microhabitat use (e.g., current speed, canopy cover, stream width (Anderson & Grether 2011; McEachin *et al.* 2021), which suggests that microhabitat data would be useful for explaining the distributions and relative densities of species within streams, as has been shown in other aquatic insects (Goss *et al.* 2020), but microhabitat differences could not account for species range differences at the continental scale.

Based on the above considerations, we followed the standard approach and constructed ENMs using bioclimatic and land cover layers. Air temperature, precipitation, and elevation data were obtained from WorldClim version 2.1 (Fick & Hijmans 2017) and averaged over the years 1970-2000. Percent tree cover and land cover type (Table S1) were obtained from MODIS Terra data 2008 (Geospatial Information Authority of Japan). Normalized difference vegetation index (NDVI) was obtained from NASA Earthdata using 'MODISstp' (Busetto & Ranghetti 2016). Land cover type was aggregated from 15 to 30 arc-seconds (~ 1 km) to match the spatial resolution of the other variables.

Prior to niche modeling, we cropped the environmental raster files to the full extent using the 'crop' function in R package 'raster'. To avoid problems with highly correlated predictor variables (Sillero *et al.* 2021), we removed variables with variance inflation factors (VIFs) greater than 2.5 (Hair *et al.* 2019) using the step-wise procedure ‘vifstep’ in R package ‘usdm’ (Naimi *et al.* 2014). The final variable set included ten variables: NDVI, tree cover, elevation, the categorical variable landcover type, and six bioclimatic variables (BIO2, BIO7, BIO8, BIO15, BIO18 and BIO19) (Table S2).

Principal component analysis

To visualize differences between species in environmental space, we carried out a principal component analysis (PCA) of variation among occurrence sites in the continuous environmental variables with the ‘prcomp’ function in R.

Niche models

We constructed ENMs for species with 15 or more occurrence records, after thinning, with Maxent 3.4.1 in R package ‘dismo’ (Phillips et al. 2017; Hijmans et al. 2021). This sample size threshold enabled all ENMs to be based on the same environmental variable transformations, and thus to be directly comparable (Morales *et al.* 2017), but excluded *H. pilula* (Calvert). We thinned the data to one occurrence per km^2 per species using ‘spThin’ (Aiello-Lammens *et al.* 2015) and used the following Maxent settings: 10^4 background points; regularization parameter of 1; 500 iterations; linear, quadratic, product, and hinge features; complementary log-log (cloglog) output; and 10 replicates per model with cross-validation and 30% random test percentage (Fithian *et al.* 2015; Phillips *et al.* 2017; Phillips & Dudík 2008). Model performance can be evaluated by comparing the area under the curve (AUC) to the null AUC (Phillips & Dudík 2008). We computed the null AUC with R package ‘ENMTools’ v1.0.3 and subtracted it from the model AUC to obtain a measure of model performance (ΔAUC).

Niche breadth and similarity

A measure of niche breadth in environmental space (B_{env}) based on Levin's normalized niche breadth (B2) equation was calculated with the 'env.breadth' function in 'ENMTools' (Warren *et al.* 2019). Two measures of niche similarity in environmental space ($D_{env,}$ I_{env}) based on Schoener's *D* and Hellinger's *I* were calculated using the 'identity.test' function (Warren *et al.* 2019). To evaluate whether these metrics are affected by sample size, we carried out a Monte Carlo simulation. Paired samples ranging in size from 10 to 1000 were drawn without replacement from the *H. titia* (*n* = 1080) and *H. americana* (*n* = 3364) occurrence records. With each pair of samples, 'ENMTools' was used to generate empirical estimates and 100 null values of the niche similarity metrics. The empirical and null estimates both increased asymptotically with the number of occurrence records (Figure S1). We explored different ways of adjusting the empirical estimates to reduce their dependence on sample size. Subtracting the null mean was the most effective adjustment (Figure S1), and thus we used this method. The niche breadth metric (B_{env}) was not affected by sample size (Figure S1).

Phylogenetic linear mixed models

To account for phylogenetic nonindependence in comparisons of niche metrics between species pairs (Drury *et al.* 2018; Tobias *et al.* 2014), we fit phylogenetic linear mixed models (PLMMs) with the Markov Chain Monte Carlo (MCMC) algorithm in 'MCMCglmm' 2.3 (Hadfield 2010). We used the fossil-calibrated phylogeny of Standring et al. (2022), appending *C. diminiata* (Burmeister) and *C. amata* (Hagen) based on the topology of Waller & Svensson (2017) (Figure S2). *C. angustipennis* (Selys) could not be included because no phylogenetic data were available for this species. Each PLMM included a species comparison index, patristic distance, and random-effects terms for species identifiers and most recent common ancestors. We ran each model four times and merged the MCMC chains after verifying convergence (Gelman & Rubin 1992).

Shared-extent comparisons

ENMs based on different geographic extents are not comparable (Merow *et al.* 2013), but using large extents for species with small ranges can result in overfitting and AUC inflation (Fourcade *et al.* 2014; Sillero *et al.* 2021). To make pairwise species comparisons, we constructed ENMs using the shared extents of each species pair. This allowed species to be compared in niche breadth (B_{env}) and two additional metrics: mean suitability and proportion of the shared extent occupied. If a geographic area has higher mean suitability for species A than species B, it should be easier for species A to become established in the area. If species A occurs in a larger proportion of a geographic area than species B, it follows that species A has some advantage relative to species B. Making such comparisons in the full extent would be uninformative because mean suitability is affected by range size, and the proportion of the full extent occupied by a species is directly proportional to its range size. In the shared extents, however, these comparisons are valid and could be informative.

We made two types of shared-extent comparisons. First, we compared the niche metrics of *H. titia* to those of the other 16 species using Wilcoxon paired tests. Second, we compared *H. americana* and *H. titia* in their respective shared extents with 10 other species by subtracting the other species' niche metrics from those of *H. americana* and *H. titia* and comparing the two sets of differences with PLMMs.

Results

Principal component space

The first three principal components (PCs) accounted for 68.5% of the variance in the continuous environmental variables (Table S3). The first two PCs separated the species into two clusters, with species with northerly ranges in one cluster and species with southerly ranges in the other; the third PC largely separated species by mean temperature, elevation and tree cover (Figure 4). On the first two PCs, *H. titia* occupied a position between the two clusters but closer to the northern cluster, yet on PC3, *H. titia* occupied a peripheral position, with a mean exceeding that of all species except *H. pilula* (Figure 4). The centroid of *H. titia* was closest to species that occur in the eastern US and farthest from species restricted to Central America (Table S4).

Maxent models

The full-extent ENMs significantly outperformed chance expectations, with ΔAUC in the 0.2 - 0.4 range (Table S4); most shared-extent models also had ΔAUC in the 0.2 - 0.4 range (Tables S5 & S6).

Climatic variables made the largest contributions to the full-extent ENMs, with landcover type perhaps controlling for the relatively recent effects of human activities on damselfly distributions (Table S7). Annual temperature range (BIO7) made the largest contribution to most *Hetaerina* spp. ENMs, while precipitation seasonality (BIO15) or elevation made the largest contribution to *Calopteryx* spp. ENMs. Elevation and precipitation in the coldest quarter (BIO19) made the largest contributions to the ENMs of *H. vulnerata* (Hagen) and *H. fuscoguttata* (Selys), respectively. Landcover type was the second or third most important variable for four *Hetaerina* species and caused the largest decrease in gain when omitted from the *H. miniata* (Selys) model. The vegetation index (NDVI) made the third largest contribution to the *H. americana* spp. ENM. The top three variables for *H. titia* were annual temperature range, elevation, and mean temperature in the warmest quarter (BIO8).

Niche metrics

The hypothesis that *H. titia* overlaps geographically with multiple congeners because it occupies a niche near the genus centroid can be rejected. The ENM of *H. titia* in the full geographic extent was not more similar to that of other calopterygid species than the other species' ENMs were to each other (Figure 5a; Table S4; PLMM, $p \geq 0.24$, 120 species pairs), and the same was true when the analysis was restricted to *Hetaerina* spp. ($p \geq 0.47$, 66 species pairs). The ENM of *H. titia* differed significantly from all other species except *H. sempronia* (Hagen) and *H. fuscoguttata*, and was least similar to species with higher latitudinal or elevational ranges (Table S4).

The hypothesis that *H. titia* has an unusually broad niche can also be rejected. *H. titia* had the fourth smallest niche breadth in the full extent (Table S4) and a smaller niche breadth than the other species in the shared extents (Wilcoxon paired test $V = 125$, $n = 16$, $p = 0.002$; Figure 6a). *H. titia* did not differ in mean suitability from the other species ($V = 91$, $n = 16$, $p = 0.25$) and yet occupied a larger proportion of the shared extents ($V = 12$, $n = 16$, $p = 0.002$; Figure 6b).

The congener with the largest longitudinal range, *H. americana* spp., had the largest niche breadth in the full extent (Table S4). In their respective shared extents with other species, *H. americana* spp. and *H. titia* did not differ in the proportion of the shared extents occupied

(PLMM, $p = 0.48$, 20 species pairs) or mean suitability ($p = 0.49$), but *H. americana* spp. tended to have greater relative niche breadth ($p = 0.06$).

Sympatric species (67 species pairs) had more similar niches than allopatric species (53 species pairs; PLMM, $p < 0.001$; Figure 5b). Niche similarity was greater between species in the same genus (72 species pairs) than between species in different genera (48 species pairs; Figure 5c), but with only two genera the phylogeny fully accounted for these differences. Across all species, sympatric species were closer in patristic distance than allopatric species (Wilcoxon test, W = 2926, $p < 0.0001$, $n_{allo} = 53$, $n_{sym} = 67$), but with the analysis restricted to *Hetaerina* spp., sympatric and allopatric species did not differ in patristic distance (W = 420, $p = 0.21$, $n_{allo} = 13$, $n_{sym} = 53$). Patristic distance was not a significant predictor of species differences in any niche metric in the full extent (PLMMs, $p \geq 0.21$) or shared extents ($p \geq 0.63$).

Discussion

Modest differences between closely related species in range size might not be predictive of differences in niche breadth, in part simply because some environments are more common than others (Brown 1984). Yet species with exceptionally large geographic ranges are expected to have relatively broad niches (Brown 1984; Carscadden *et al.* 2020; Kambach *et al.* 2019; Slatyer *et al.* 2013). Likewise, species that overlap geographically with large numbers of congeners can be predicted to have niches that, if not unusually broad, are close to the genus centroid (Figure 1). We tested these straightforward predictions in calopterygid damselflies, and while we found evidence for niche differentiation within and between genera, the species with the largest latitudinal range and which overlaps with the most congeners (*H. titia*) has a relatively narrow and peripheral climatic niche. By contrast, the species with the largest longitudinal range (*H.*

americana spp.) has the largest niche breadth in the genus. Both of these species have largely escaped from reproductive interference, *H. titia* by diverging in female coloration (Drury *et al.* 2019, 2015; Grether *et al.* 2020) and *H. americana* spp. by being allopatric to all other congeners across most of its range. Niche differentiation and reproductive interference are not mutually exclusive alternatives – both could have contributed to species differences in range. Nevertheless, finding that the species with the largest latitudinal range, and which encounters the least reproductive interference, has a relatively narrow climatic niche strengthens the hypothesis that reproductive interference has limited the range expansion of other species in this genus.

When a species expands beyond its previous range edge into marginally suitable habitats, ecological and evolutionary responses can broaden the species' niche and facilitate further range expansion (Alexander *et al.* 2022; Case *et al.* 2005; Lancaster 2022). Release from negative species interactions can also lead to niche expansion within a species' existing range (Bolnick *et al.* 2010; Herrmann *et al.* 2021; Sjödin *et al.* 2018). If release from reproductive interference facilitated the range expansion of *H. titia*, why does this species have a relatively narrow climatic niche? In some cases, gene flow from the core of a species' range might prevent adaptation at the edges (Case & Taper 2000; Kirkpatrick & Barton 1997), but *Hetaerina* populations in different river drainages are sufficiently isolated genetically to evolve independently (Drury *et al.* 2019). A better explanation may be that current theory on the effects of species interactions on niche evolution, which is largely based on exploitative resource competition (Alexander *et al.* 2022), does not apply to reproductive interference.

We propose that, instead of triggering niche expansion, release from reproductive interference enables species to expand in range while specializing on the environments most suitable for breeding. The basic argument for why release from interspecific competition leads to niche expansion is that the absence of the competitor frees up resources and converts unsuitable habitat into suitable habitat (Alexander *et al.* 2022; Bolnick *et al.* 2010). Release from reproductive interference would not free up resources, but it would facilitate breeding in areas with high heterospecific densities by eliminating Allee effects. With no barrier to expansion into high-suitability habitats, a species released from reproductive interference would be expected to be concentrated where it reaches the highest population densities, that is, in the core of its fundamental niche. Put simply, release from reproductive interference would enable a species to expand into habitats that support high population densities, resulting in a distribution of suitability values in environmental space that resembles niche contraction (Warren *et al.* 2019). Selection might then strengthen the preference for high suitability habitats, resulting in a narrowing of the species' fundamental niche. This hypothesis is similar to the hypothesis that reductions in pollinator-mediated reproductive interference promote coexistence between plants that specialize on the same pollinators (Katsuhara *et al.* 2021).

We found evidence for niche divergence in the vast majority of congeneric species pairs (Figure 5c), which would seem to differ from what has been found in most other taxa (Peterson 2011), but *Hetaerina* is an ancient genus with estimated species divergence times of 10 to 36 million years (Standring *et al.* 2022). Our finding that sympatric species have more similar climatic niches than allopatric species is not surprising from a statistical standpoint, because the same result would be expected if species ranges overlapped randomly (Warren *et al.* 2014). However, several ecological and evolutionary processes can cause the niches of sympatric species to differ more than those of allopatric species (e.g., competitive displacement, species sorting, character displacement; Pfennig & Pfennig 2012), and negative relationships between niche similarity and geographic overlap have been found in other studies (Novella-Fernandez *et al.* 2021). Perhaps the factors that mediate coexistence in calopterygid damselflies operate on smaller spatial scales than our niche models (Anderson & Grether 2011; McEachin *et al.* 2021). Research on other damselfly clades has shown that predation-mediated trade-offs at the larval stage promote local coexistence in some species assemblages, while in other assemblages the species may be ecologically equivalent and subject to neutral dynamics (Grether *et al.* 2023; Leibold & McPeek 2006; Siepielski *et al.* 2010).

Niche differentiation has often been reported to be decoupled from phylogenetic differentiation (Losos 2011; Warren *et al.* 2014), and our study provides another example. Niche similarity was greater within than between genera, but after controlling for tree topology, there was no relationship between niche divergence and patristic distance. This indicates that more closely related congeners are not more similar ecologically. Across all species included in this study, sympatric species were closer in patristic distance than allopatric species, but this appears to be an artifact of the geographic ranges of the genera (*Calopteryx* spp. only occur north of Mexico while most *Hetaerina* spp. occur south of the US-Mexico border; Figures 2 and 3). With the analysis restricted to *Hetaerina*, sympatric and allopatric species did not differ in patristic distance. This might seem to contradict the hypothesis that reproductive interference impedes range expansion, because reproductive interference is generally expected to be stronger between more closely related species (Grether *et al.* 2017; Gröning & Hochkirch 2008), but *Hetaerina* does not appear to conform to that expectation (Drury *et al.* 2015; Grether *et al.* 2020). In any case, a much larger sample of species would be required to robustly test for phylogenetic effects on geographic overlap between species, especially considering that the null expectation is for sympatric species to be less closely related than allopatric species because speciation usually occurs in allopatry (Tobias *et al.* 2014; Warren *et al.* 2014; Weir & Price 2011).

In principle, joint species distribution models (JSDMs) could be used to statistically distinguish species interactions from niche differentiation (Poggiato *et al.* 2021; Wilkinson *et al.* 2019). We opted not to use this approach because species interactions cannot be distinguished from correlated responses to unmeasured environmental variables (Ovaskainen *et al.* 2016; Poggiato *et al.* 2021). With our study system and others, data are not available for all environmental variables that are likely to affect species ranges in similar ways (e.g., dispersal barriers, microhabitat, disturbance). The omission of such variables from a JSDM could result in spurious positive correlations between species that mask negative species interactions (Ovaskainen *et al.* 2016; Poggiato *et al.* 2021). Single-species ENMs (and SDMs) are also limited by the data used to construct them, and niche differentiation could be missed if variables that affect species ranges differently are omitted (Peterson & Nakazawa 2007). We judge this to be a less severe problem than omitting variables that affect species ranges in similar ways from JSDMs, but it is important to consider whether unexplained differences between species ranges could be due to unmeasured variables. We are not aware of any unmeasured variables that might explain continental-scale differences between the species ranges of calopterygid damselflies in North America.

Several other recent studies have drawn inferences about species interactions using ENMs. By comparing the known ranges of Palearctic bat species to those predicted by ENMs, Novella-Fernandez et al. (2021) showed that two pairs of cryptic species with very similar niches exhibit a pattern of geographic avoidance consistent with competitive exclusion. Cavalcante et al. (2022) combined the outputs of ENMs with those of geospatial abundance models and found evidence that the strength of interspecific competition between two endangered Amazonian primates (Atelidae) varies with habitat suitability. Likewise, Braz et al. (2020) found that abundance of a neotropical opossum (*Marmosops incanus*) covaried with the number of potential competitor species at high suitability sites but not at low suitability sites.

In closing we note that niche theory need not be limited to abiotic factors, trophic interactions and resource competition just because Hutchinson (1957) framed it that way. Embracing the full suite of biotic interactions that shape the realized niche would enhance niche theory and its utility for understanding and predicting species distributions. On a methodological note, we encourage niche modelers to pay closer attention to the distinction between geographic and environmental space!

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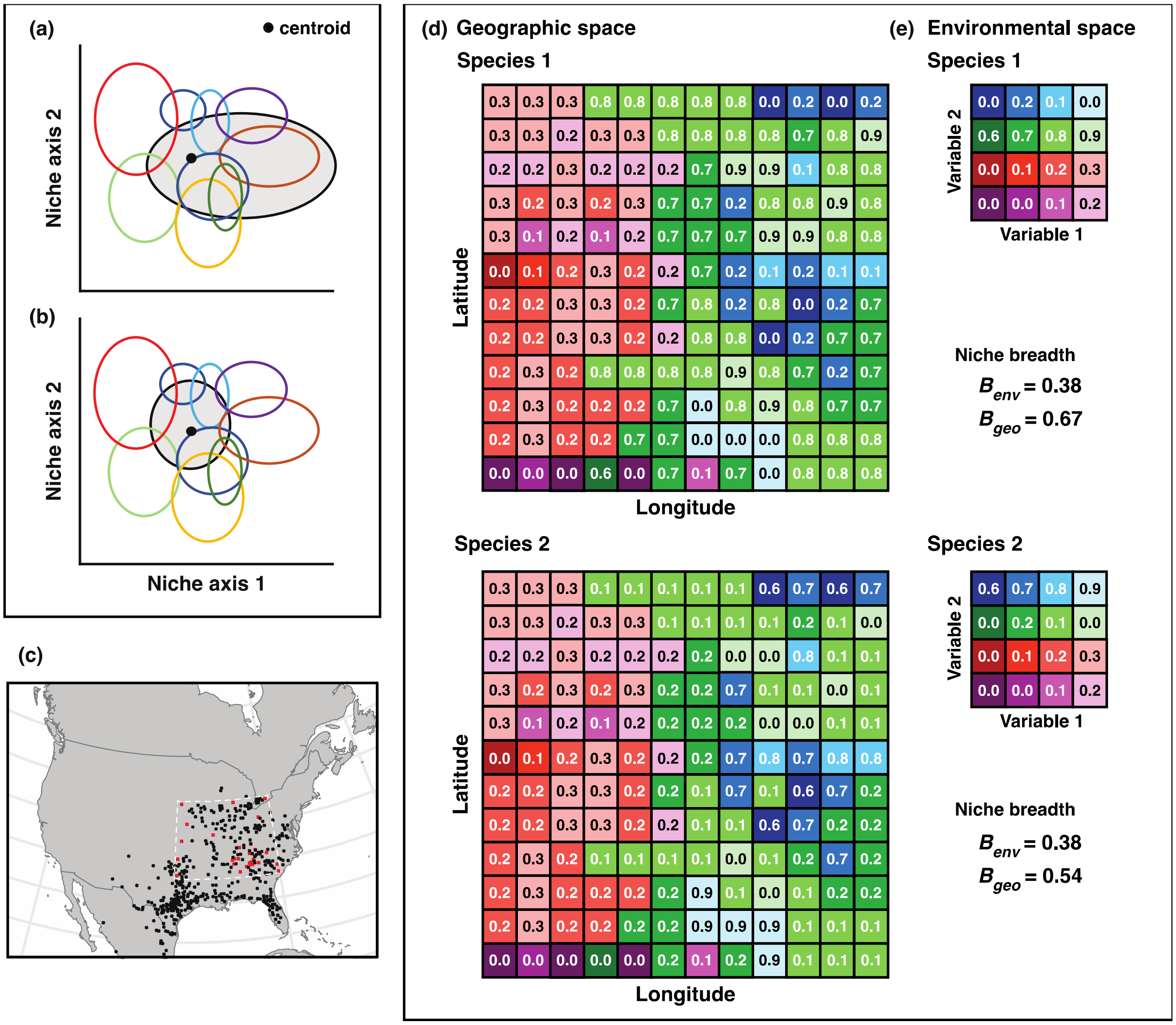

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0.0	0.0	0.1	0.2

0.6	0.7	0.8	0.9
0.0	0.2	0.1	0.0
0.0	0.1	0.2	0.3
0.0	0.0	0.1	0.2

Figure 1. Conceptual diagrams. Upper left: illustration showing that one species' niche (gray ellipse) could overlap the niches of all other species in the group by being (a) especially broad or (b) close to the group centroid (multivariate average). Lower left (c): map depicting the shared geographic extent of two species (within the dashed lines), with red and black symbols representing occurrence records. Right: hypothetical examples of ENM suitability values projected to (d) geographic space and (e) environmental space for two species. For illustration purposes, the environmental space consists of two variables and 16 environments (colors) and

the geographic space consists of 144 locations. Each environment is represented by one cell in environmental space and by multiple cells in geographic space. The numbers in the cells represent suitability values. Green environments have higher suitability for species 1 and blue environments have higher suitability for species 2, but the species have the same distribution of suitability values and therefore the same niche breadth in environmental space (B_{env}). Green environments are more common on the geographic landscape than blue environments, and thus species 1 has greater niche breadth than species 2 in geographic space (B_{geo}). Niche breadth was calculated with Levin's normalized niche breadth equation (B2).

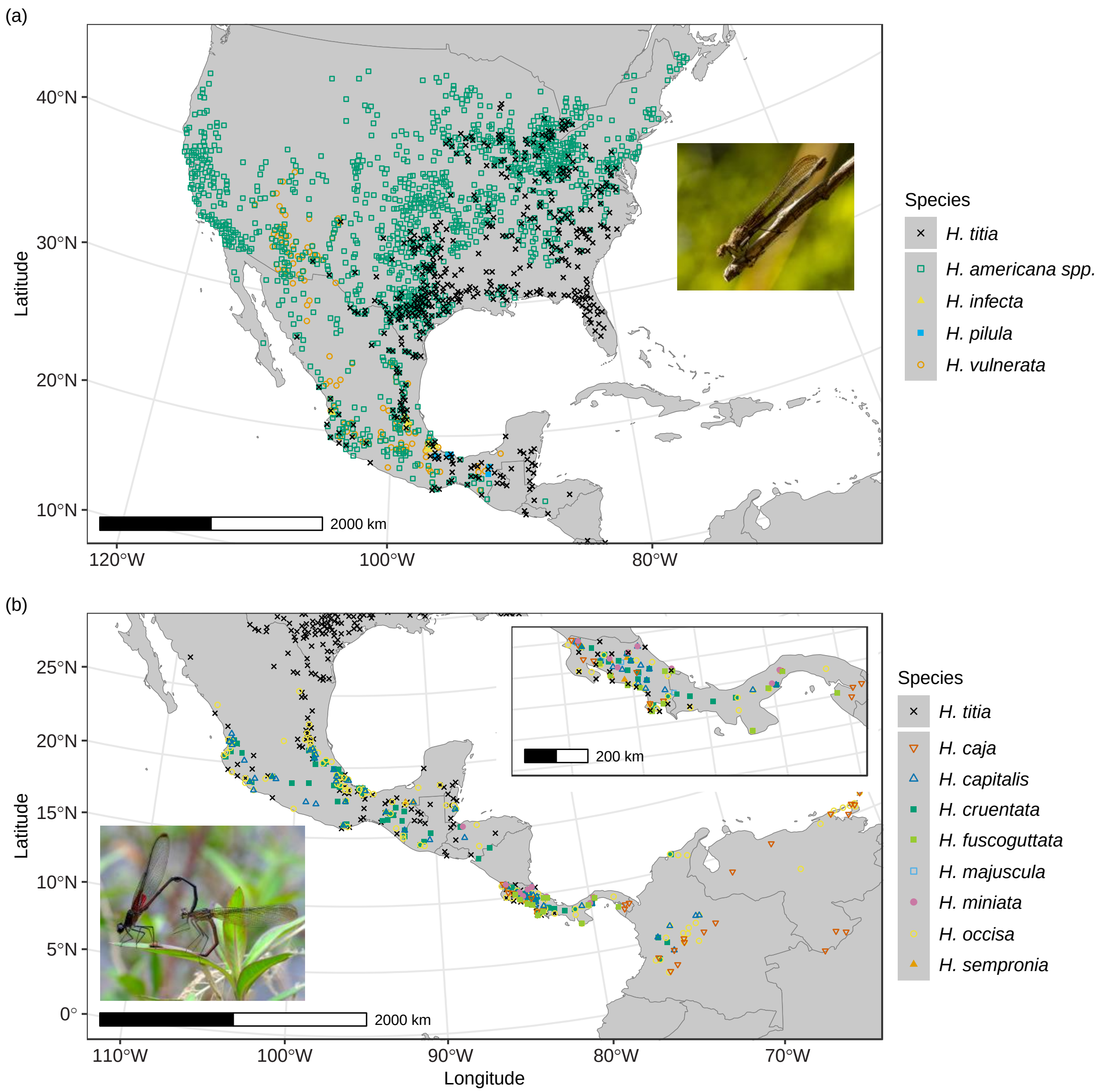

Figure 2. Occurrence maps for all species of rubyspot damselflies (*Hetaerina* spp.) within the range of *H. titia*, separated into (a) northern and (b) southern groups to facilitate viewing. The inset map in (b) is a close-up view of Costa Rica and Panama. Points for *H. titia* were plotted on top of the other species' points in (a) and the inset map. Occurrence records were thinned to a minimum separation distance of 25 km for plotting. Inset photos: (a) female *H. americana* hunting; (b) mating pair of *H. cruentata*. Mapped with Albers equal-area conic projection for North America using R package 'sf' version 1.0-13. Photo credits: G.F. Grether.

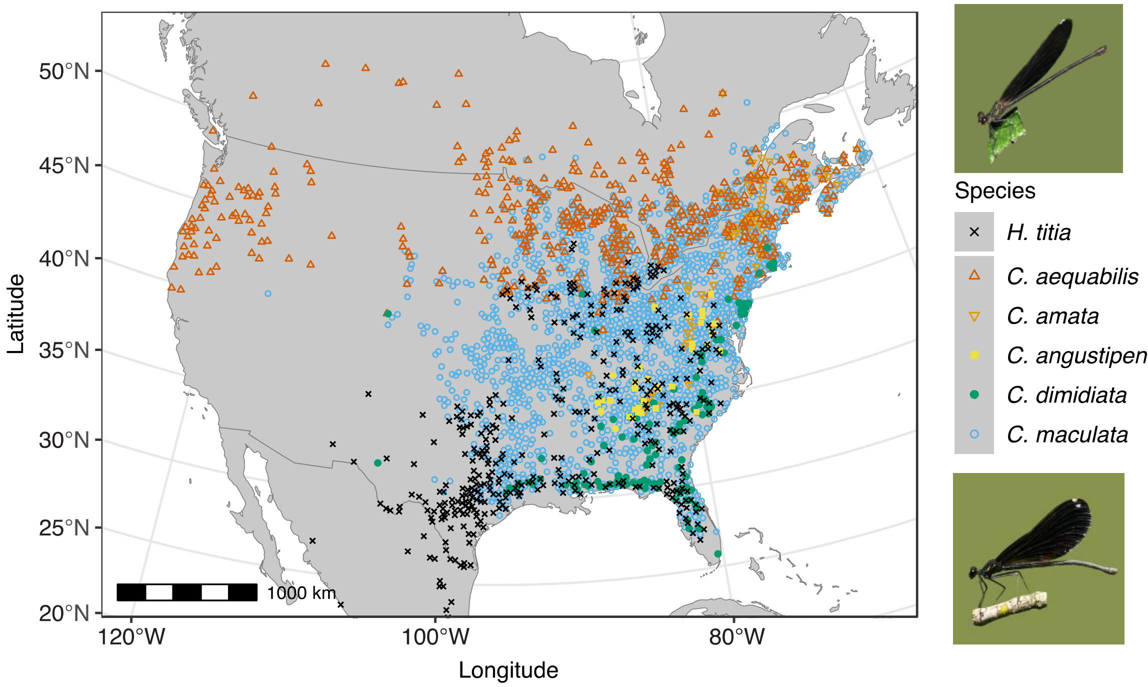

Figure 3. Occurrence maps for all species of *Calopteryx* within the range of *H. titia*. Points for *H. titia* were plotted on top of the other species' points. Upper photo: female *H. titia*. Lower photo: female *C. maculata*. Photo credits: G.F. Grether. For mapping details, see Figure 1.

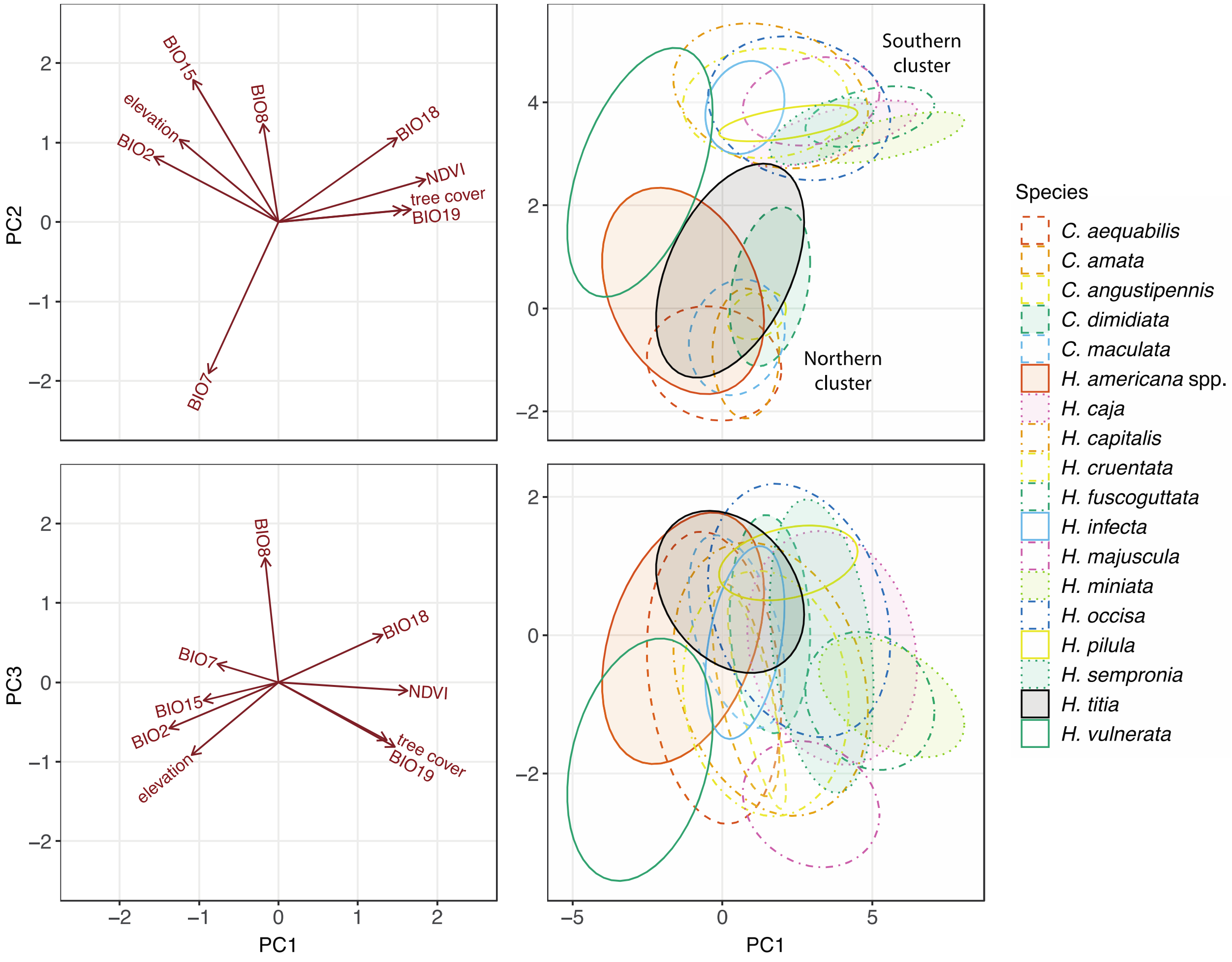

Figure 4. Principal component analysis of environmental variation among the occurrence records of 18 species of calopterygid damselflies within the geographic range of *H. titia*. Left panels: arrows representing the principal component loadings of the environmental variables. Right panels: probability ellipses encompassing 68% (1 standard deviation) of the occurrence records. Key to variable names: diurnal temperature range (BIO2), annual temperature range (BIO7), mean temperature of wettest quarter (BIO8), precipitation seasonality (BIO15), precipitation of warmest quarter (BIO18), precipitation of coldest quarter (BIO19), normalized difference vegetation index (NDVI).

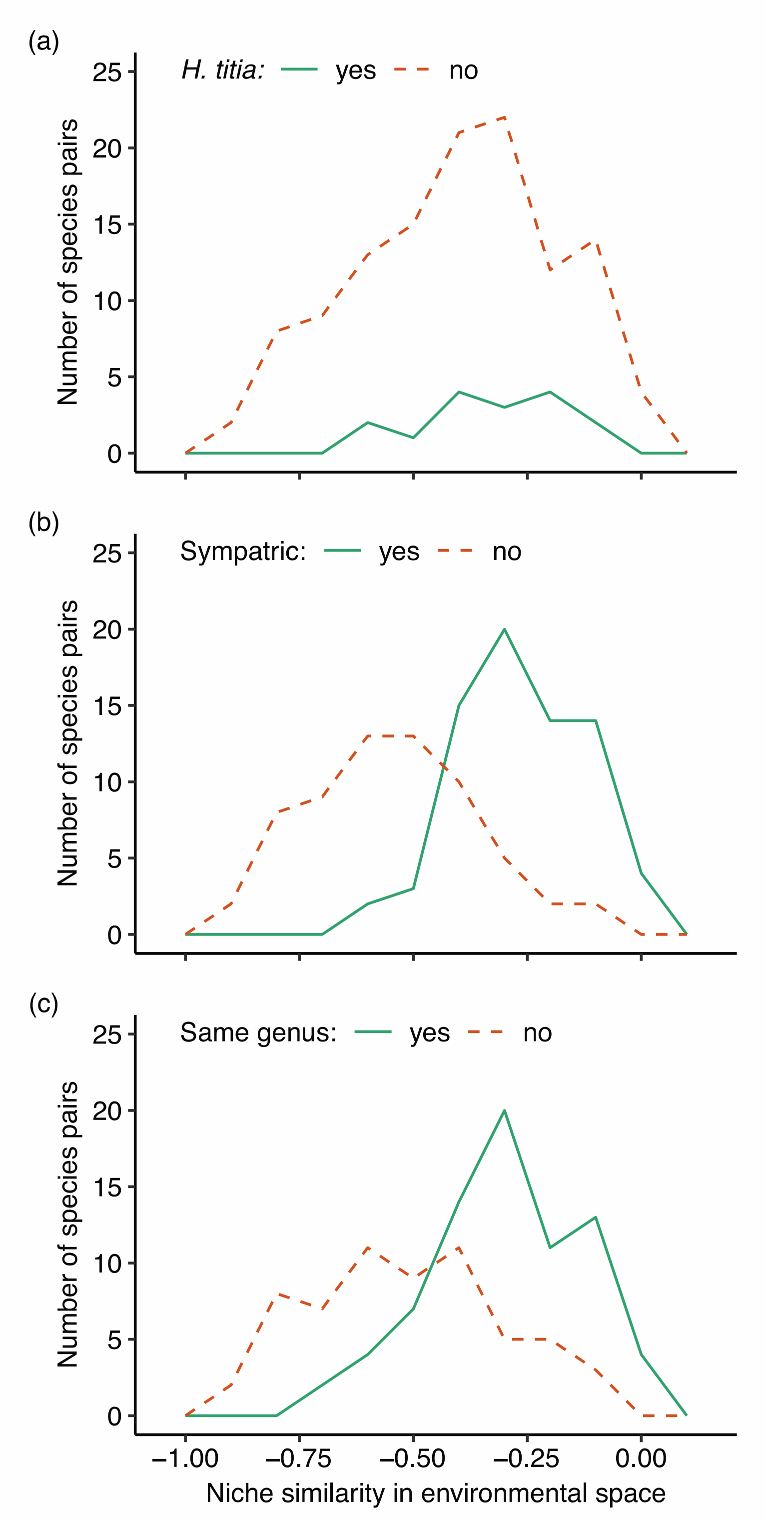

Figure 5. Frequency polygons of niche similarity in environmental space for different groupings of calopterygid damselfly species. (a) Species pairs that include *H. titia* versus all other species pairs. (b) Sympatric species pairs versus allopatric species pairs. (c) Species in the same genus

versus species in different genera (i.e., *Hetaerina* and *Calopteryx*). Niche similarity was estimated from Maxent ENMs in the full geographic extent using index I_{env} (results for index D_{env} were similar). To remove sample-size effects, the null mean I_{env} was subtracted from the observed I_{env}, and thus values farther below 0 on the horizontal axis represent species pairs with lower niche similarity. Differences less than ~ –0.15 were significant with the identity test (Table S4).

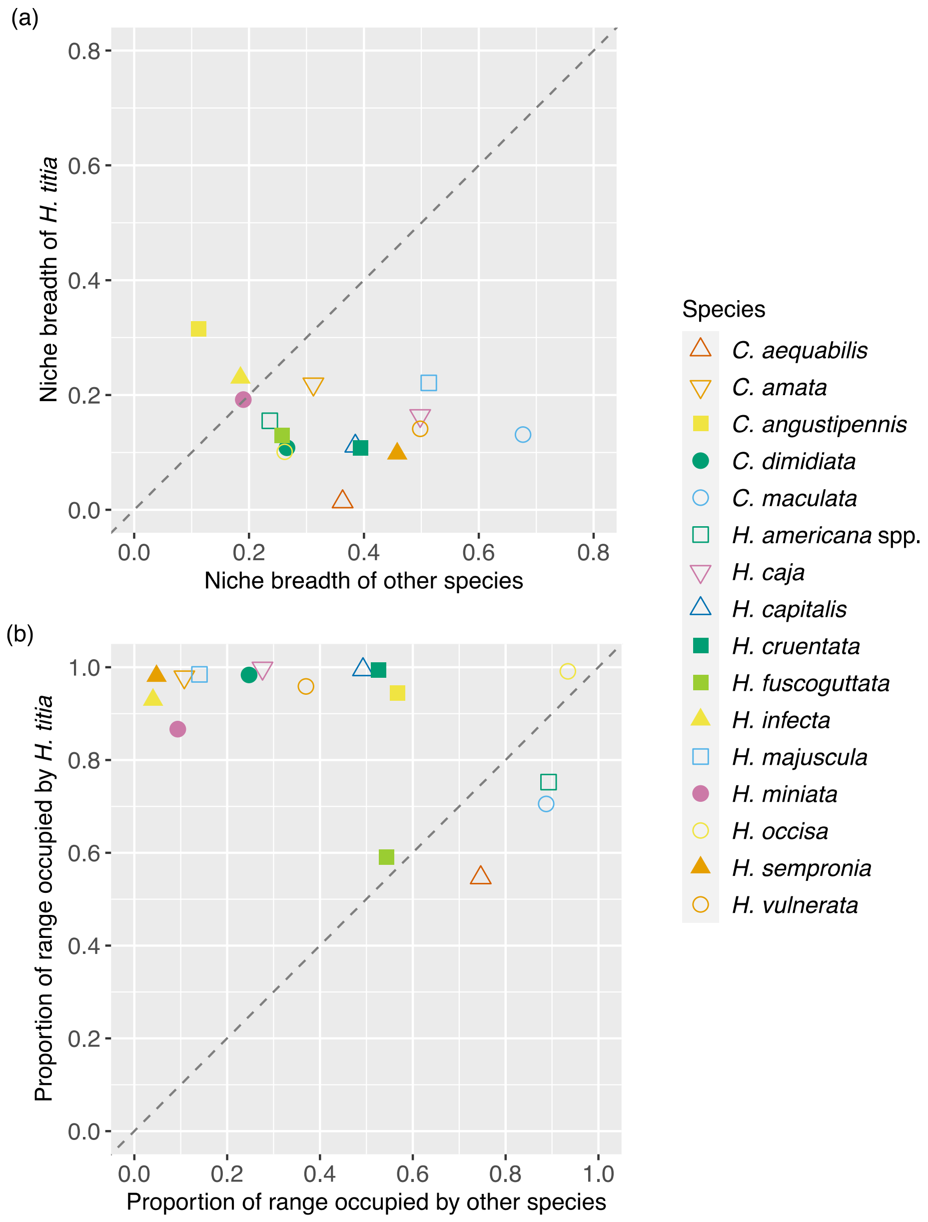

Figure 6. Comparisons between *H. titia* and other species of calopterygid damselflies in the shared extents (i.e., rectangular areas of geographic overlap). (a) Niche breadth in environmental space (B_{env}) estimated from separate Maxent models for each shared extent. (b) Proportion of the shared extents occupied (1 km^2 resolution). The dashed lines have a slope of 1, and thus points above (below) the lines are cases in which *H. titia* had a larger (smaller) value than the other species.

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