Climatic niche divergence or conservatism? Environmental niches and range limits in ecologically similar damselflies

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Abstract. The factors that determine species' range limits are of central interest to biologists. One particularly interesting group comprises odonates (dragonflies and damselflies), which show large differences in secondary sexual traits and respond quickly to climatic factors, but often have minor interspecific niche differences, challenging models of niche-based species coexistence. We quantified the environmental niches at two geographic scales to understand the ecological causes of northern range limits and the coexistence of two congeneric damselflies (*Calopteryx splendens* and *C. virgo*). Using environmental niche modeling, we quantified niche divergence first across the whole geographic range in Fennoscandia, and second only in the sympatric part of this range. We found evidence for interspecific divergence along the environmental axes of temperature and precipitation across the northern range in Fennoscandia, suggesting that adaptation to colder and wetter climate might have allowed *C. virgo* to expand farther north than *C. splendens*. However, in the sympatric zone in southern Fennoscandia we found only negligible and nonsignificant niche differences. Minor niche differences in sympatry lead to frequent encounters and intense interspecific sexual interactions at the local scale of populations. Nevertheless, niche differences across Fennoscandia suggest that species differences in physiological tolerances limit range expansions northward, and that current and future climate could have large effects on the distributional ranges of these and ecologically similar insects.

Key words: biogeography; Calopteryx splendens; Calopteryx virgo; *climate; ecological speciation; ectotherms; niche divergence; nonecological speciation; sexual selection; thermal adaptation.*

Introduction

Interest in ecological niches (Hutchinson 1965) is growing among ecologists and evolutionary biologists, largely as the development of novel analytical methods, such as climate niche modeling and geographic information systems proliferate and become widely available (GIS, Wiens 2004, Kozak and Wiens 2006, Wiens et al. 2009, McCormack et al. 2010). As a result, there is growing attention to the interplay between extrinsic factors (e.g., climate) and intrinsic organismal traits (e.g., genetic factors) on the influence of species' geographic range limits (Soberón 2007). Geographic range limits often coincide with major physical barriers, such as water bodies or mountains (Angert and Schemske 2005), suggesting that the external environment might impose a direct physical constraint, even without ecological differences. However, there are many examples of species boundaries where geographic range limits are abrupt, with no obvious external barriers (Kirkpatrick and Barton 1997, Bridle and Vines 2007, Pearman et al. 2008). Theoretical models have shown

that maladaptive and asymmetric gene flow from the center of a species' geographic distribution to the periphery might restrict range limits and might keep marginal populations in a state of local maladaptation (Holt and Gomulkiewicz 1997, Kirkpatrick and Barton 1997). In addition, and certainly not mutually exclusive, low effective population sizes at the range limits (Eckert et al. 2008), or lack of genetic variation (Blows and Hoffmann 2005) might restrain species distributions and determine the geographic location of range limits.

Ecological speciation has been a popular and widely acknowledged process in adaptive radiations during the last decade (Schluter 2000, Rundle and Nosil 2005). However, not all cases of speciation and evolutionary divergence can be attributed to intra- and interspecific differences in ecological niches (Schluter 2009). For instance, in some animal groups, like salamanders and certain avian and insect taxa, adaptive niche diversification appears to play a relatively minor role in speciation and evolutionary divergence (Rundle and Nosil 2005, Sobel et al. 2009). Likewise, in some insect groups such as odonates (damselflies and dragonflies), pre-mating reproductive isolation appears to evolve largely independent of local adaptive niche diversification, and might be more affected by sexual selection, social interactions, and/or learning (McPeek and Brown 2000, Svensson et al. 2004, 2006, 2010, McPeek et al.

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2008). Moreover, ecological intraspecific divergence in some odonates can be swamped by gene flow, as demonstrated in both individual marking studies (Keller et al. 2010) and in the low levels of molecular differentiation found in marker-based genetic studies (Abbott et al. 2008, Keller et al. 2010, Wellenreuther et al. 2011).

These ecological and behavioral attributes of odonate ecologies and mating systems make this insect group interesting for both ecologists and evolutionary biologists, as niche differences within and between closely related odonate species may a priori be expected to be relatively minor. Consequently, most phenotypic differences between taxa are likely to have evolved postspeciation, reflecting ecological divergence after reproductive isolation has been achieved through nonecological mechanisms (McPeek and Brown 2000, Svensson et al. 2010). Consequently, odonates challenge both niche divergence models of species existence and the generality of ecological speciation, since many odonate species might be broadly neutral in their niche use (Siepielski et al. 2010). Speciation in odonates might therefore largely have been driven by sexual selection, sexual conflict, and various nonecological mechanisms (McPeek and Brown 2000, McPeek and Gavrilets 2006, McPeek et al. 2009).

Here we quantified the extent of niche differentiation in relation to allopatry, sympatry, and local coexistence in two closely related odonates (Dumont et al. 2005) that co-exist in Fennoscandia, the banded demoiselle (*Calopteryx splendens*) and beautiful demoiselle (*Calopteryx virgo*; see Plate 1). *Calopteryx splendens* and *C. virgo* closely resemble each other ecologically and phenotypically, but show large differences in secondary sexual traits (Corbet 1999, Askew 2004), and speciation has been argued to be largely driven, or at least be accompanied, by sexual divergence (Rüppel et al. 2005). These characteristics make investigations of niche use particularly interesting because the overall degree of ecological differences are a priori expected to be relatively low, although a certain degree of ecological divergence is always expected even when speciation is largely nonecological (Rundle and Nosil 2005). By quantifying the niches of these two phenotypically similar species at two spatial scales and in different ecological conditions (allopatry vs. sympatry), we aimed to gain a better understanding of the impact of abiotic and climatic factors. We were also interested in quantifying and understanding the ecological causes behind the northern range limits of both these species in Fennoscandia, particularly the role of a classical biogeographic boundary, "Limes Norrlandicus," that has been described in central Sweden (described in Fransson [1965]).

To achieve these goals, we compared the environmental niche models for both species across their overall range and in the area of sympatry in Fennoscandia (Godsoe 2010), and tested for niche divergence vs. conservatism, while accounting for spatial autocorrelation between sampling sites. Incorporating information about spatial autocorrelation is important in partly allopatric species, as apparent niche divergence could result from actual interspecific niche differences or simply from spatial autocorrelation in niche space (McCormack et al. 2010). Evidence for niche divergence requires that two conditions are satisfied: (1) niche characteristics differ significantly between species; and (2) these differences are greater than the divergence in environmental background (McCormack et al. 2010). Conversely, niche conservatism is supported if niche differences are smaller than background environmental divergence. The results in this study shed some light on the role of species-specific environmental tolerances limiting northern range limits in odonates, which are likely to be relevant also to other insects and ectotherms; the phenomenon underscores the importance of quantifying environmental niche differences at different spatial scales and in different ecological settings.

MATERIALS AND METHODS

Study species and ecology: evolutionary history and current ecology

The Eurasian *Calopteryx* group began to radiate around 6.2 Mya (million years ago) and the first product of this radiation, around 5.3 Mya, was the *C. virgo* group, while the *C. splendens* group appeared 3.7 Mya (Dumont et al. 2005). The study species *C. splendens* and *C. virgo* have therefore coexisted in Europe for at least 1.6 Mya, giving ample time for ecological niche divergence. In Fennoscandia, allopatric populations of *C. virgo* in Sweden extend north of the "Limes Norrlandicus" (Askew 2004) and north of 64.85° N latitude in Finland, which is the upper distributional limit of *C. splendens* in Finland (Wellenreuther et al. 2010a). These allopatric *C. virgo* populations in Finland are probably quite young, and appeared after the last Ice Age, as *C. virgo* were able to spread farther north than *C. splendens* following deglaciation (Wellenreuther et al. 2010a). In contrast, in southern Fennoscandia *C. virgo* is largely sympatric with *C. splendens*, although microgeographic "mosaics" of allopatric populations occur, which are often separated by only a few kilometers (Svensson et al. 2010). Both *Calopteryx* species show extensive interspecific interactions in sympatry, with vigorous male–male competition over egg-laying sites (Tynkkynen et al. 2006). Although these two species are strongly sexually isolated from each other across the entire geographic range (Wellenreuther et al. 2010a), heterospecific matings occur in sympatric populations (Svensson et al. 2007, Tynkkynen et al. 2008). Males of the two species differ in secondary sexual wing traits (Rüppel et al. 2005), which are important in both in male–male competition and female mate choice (Tynkkynen et al. 2004, Svensson et al. 2010), as well as in species recognition (Svensson et al. 2007). Males of *C. splendens* have melanized wings that cover ~50% of the wings, whereas *C. virgo* males have almost fully
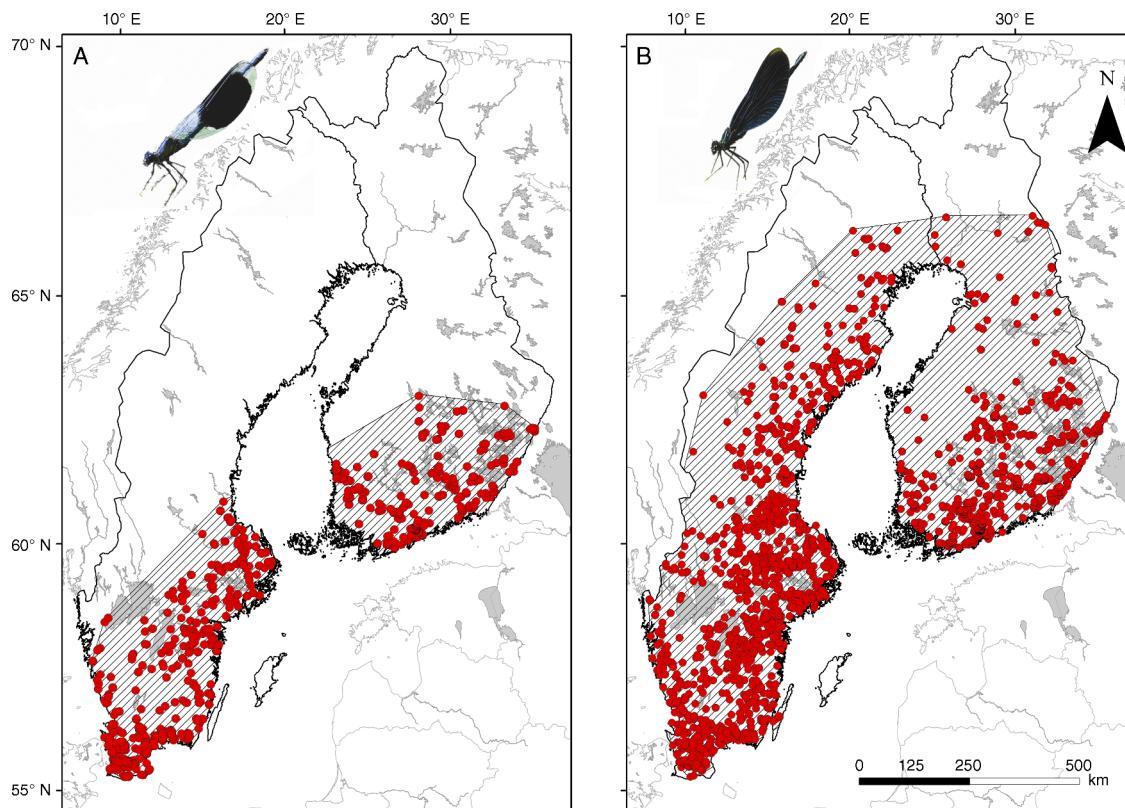
Fig. 1. Species distributions based on all data for the damselflies (A) *Calopteryx splendens* and (B) *C. virgo* in Fennoscandia.

melanized wings, and these species differences in melanic wing coloration have an important function in mediating sexual isolation (Svensson et al. 2007).

Field data

Field observations of adult *C. splendens* and *C. virgo* were conducted during 2007–2009, June–August. The spatial relationship between mature (flying individuals) and immature (aquatic larvae) *Calopteryx* and many other odonates is strong, and adult and larval abundances are therefore typically correlated (McCauley 2006), making it possible to model niche differences of larvae based on adult distribution data. Moreover, comparisons of counts using exuviae vs. adults showed that adult censuses are under many environmental conditions more reliable indicators of odonate abundances (Bried et al., *in press*). In *Calopteryx*, dispersal of adults rarely exceeds 4 km (Stettmer 1996) and adults typically stay within their 300-m home range (Ward and Mill 2007), resulting in relatively high levels of molecular genetic differentiation even among geographically close populations (Svensson et al. 2004). At some of our more intensively studied populations, such as "Klingavälsåns Naturreservat," we typically and regularly find a rich abundance of both adults, larvae caught by netting, and exuviae (E. I. Svensson, M. Verzijden, and M. Wellenreuther, *unpublished data*). In this study,

we visited a total of 131 sites in Sweden and Finland from 13.1–29.6° E longitude and 55.6–66.2° N latitude (Fig. 1). At each site, density (number of individuals per meter) and frequency (relative proportion of the two species) counts were conducted by slowly walking a 100-m stretch of riparian habitat. Whenever possible, population counts were repeated on separate days (332 counts, 2.51 ± 2.17 samples per population, mean ± SE).

Digital occurrence records

Field data were complemented with data from the Global Biodiversity Information Facility (*available online*)[4] and The Species Portal (*available onine*; in Swedish).[5] We requested all geo-referenced data for *C. splendens* and *C. virgo* from Sweden and Finland between 1976 and 2009, resulting in 6127 occurrence records (3753 unique localities). Although inaccuracies and differences in reporting locality information likely occur in museum and publicly reported observation data, we found (and removed) three records that were clearly outliers. We further restricted our use of this data to 1-km blocks to reduce spatial inaccuracies. From this data, we created species range maps (Fig. 1) using a

[4] www.gbif.org/
[5] www.artportalen.se/

minimum convex hull polygon with a 4-km buffer (estimated species dispersal distance [Stettmer 1996]) around each set of locality data using ArcMap and Hawth's Tools (*available online*).[6]

Climatic information and environmental data from satellite variables

We compiled a set of climate and satellite remote sensing variables to characterize the environmental heterogeneity across Finland and Sweden (summarized in Appendix A). These included 19 bioclimatic variables derived from the WorldClim database (Hijmans et al. 2005). This database contains estimates of annual means, seasonal extremes, and degrees of seasonality in temperature and precipitation, of relevance both to the adult's environmental requirements (e.g., maximum and minimum temperatures during the warmest quarter) and the larval environmental requirements (e.g., maximum and minimum temperatures during the coldest quarter). From the Shuttle Radar Topography Mission (SRTM), we obtained elevation data, and from remote sensing data collected in 2001, we obtained the surface moisture and roughness, which is a proxy for vegetation heterogeneity (Long et al. 2001), and greenness (Pettorelli et al. 2005, Zhang et al. 2005). In addition, we included both the European soil classification and land cover data sets. All the environmental variables have a spatial resolution of 30 seconds of arc (1 km^2), and all of them have some biological relevance to insect physiological requirements that are likely to explain distributions, particularly the temperature variables. Although the spatial resolution of these data might appear to be broad for mechanistic inferences about niches, we stress that environmental niche modeling is nevertheless an extremely useful tool that should be viewed as a valuable complement for more detailed studies of individuals in the field, some which are ongoing in our laboratory. These more mechanistic approaches include the use of the thermal imaging camera ("IR-camera") to quantify thermal niches of individuals and species under field conditions.

Environmental niche modeling

We used the maximum entropy algorithm in Maxent to develop niche models for species presence data. The Maxent model works by evaluating the environmental suitability of each grid cell in the study area as a function of environmental variables at that cell, and calculates the most important environmental predictors for each species' niche. Niche models were always restricted to one occurrence record/km^2 to eliminate sampling bias and spatial autocorrelation. Niche models were generated using both field and online (GBIF and Artportalen data) data (*C. splendens*, $N = 937$, *C. virgo*, $N = 2999$). Niche models included all the climatic and environmen-

tal data previously described (and summarized in Appendix A), including 19 bioclimatic variables, European soils classification, European CORINE land cover classification, tree cover, surface moisture and roughness, elevation, vegetation greenness, and the distance to the coast for each location.

Seven of 19 climate variables were removed due to high correlations ($R > 0.95$) with other BIOCLIM variables prior to analysis, following the procedures of McCormack et al. (2010). In all cases, the temperature variables removed were correlated with other temperature variables, and precipitation variables were always correlated with other precipitation data. Of the total occurrence data set, 70% was used for model training and 30% for model testing. The "area under the curve" (AUC) metric of the test data was used to evaluate the model fit. Models with an AUC value of 0.7–0.9 are considered to have a very good fit. The jackknife option in Maxent was used to calculate variable importance, the variable with the highest gain (when used in isolation) and the variable that decreases in gain the most (when omitted from the model). The variable with the highest gain contributes the most useful information in itself to the model, whereas the variable that decreases the gain the most contains the most information that is not found in other variables. For each species, we regressed (1) the occurrence records against latitude and longitude to quantify the role of gradients, and (2) the environmental suitability generated by the niche model against latitude and longitude to assess their effects on range differences.

Null models testing niche divergence vs. conservatism in Fennoscandia

First, we tested if the environmental niche models of the two species were more different than expected by chance (identity test; Warren et al. 2008, 2010, McCormack et al. 2010). Second, we used two background tests, one developed by Warren et al. (2008) and one by McCormack et al. (2010), to determine whether the species' ranges were more different from one another than expected based on the environmental background differences. For the identity test, we calculated the similarity of environmental niche models using the niche overlap tool in ENMTools (version 1.2; Warren et al. 2008, 2010), and 100 replicates were used to calculate a pseudoreplicated null distribution. The observed measures of niche overlap values (Schoener's D and Hellinger's I metric), were compared to this null distribution. Schoener's D and Hellinger's I are both similarity metrics, each calculated by comparing the estimates of habitat suitability from the environmental niche models (ENM) generated by Maxent for each grid cell of the study area, after normalizing each ENM, so that all suitability scores sum to 1. Both similarity metrics range from 0 (species' predicted environmental tolerances do not overlap) to 1 (all grid cells are estimated to be equally suitable for both species). The

PLATE 1.   Males of *Calopteryx virgo* (left) and *C. splendens* (right) resting side by side on a branch next to the River Klingavälsån in southern Sweden. Males of the species differ in wing melanization, with *C. virgo* having almost entirely melanized wings and *C. splendens* having partial wing melanization. These species' environmental niches are only weakly differentiated in sympatry, but local coexistence is common, despite strong interspecific competition for male territories. Photo credit: E. I. Svensson.

ecological interpretation of D assumes that the suitability scores are proportional to species abundance, whereas I simply treats the two ENMs as probability distributions (Warren et al. 2010). The null hypothesis of niche identity is rejected when the empirically observed value for I and/or D is significantly different from the pseudoreplicated data sets. For the background test by Warren et al. (2008), we used the randomization procedure in ENMTools, which compares the observed niche overlap values (Schoener's D and Hellinger's I) to a null distribution of 100 replicate overlap values, which were generated by comparing the niche model of one taxon to a model created from random points drawn from the geographic range of the other taxon (Warren et al. 2008). The hypothesis of niche divergence is rejected when the empirically observed value for I and/or D is not significantly different than the values expected from the pseudoreplicated data sets. For the background test by McCormack et al. (2010), we generated 10 000 random points, drawn from a background representing each species' range distributions. Next, we extracted the environmental data for both species occurrence points and 10 000 random background points from within the geographic range of each species. These data were subsequently combined and a Pearson correlation analysis was performed to check for the presence of highly correlated ($R > 95\%$) variables (seven BIOCLIM variables were highly correlated and were thus excluded from further analyses). The pruned data set was subsequently reduced with a Principal Components Analysis (PCA), and the most important axes ($<3\%$) were retained (following examination of the scree plot). On each axis, niche divergence and conservatism were tested against a null model of background divergence by comparing the observed difference (between the two species) in mean niche values for a given PC to the difference in mean background values. The null model of background divergence was created using 1000 jackknife replicates of the random background points for each species by withholding 25% of the points from each run and using sampling without replacement. The null background model of divergence was calculated using the 95% confidence limits from the mean differences of the jackknife results.

Null models testing niche divergence vs. conservatism in sympatry in Fennoscandia

To obtain quantitative estimates of niche overlap for the area of sympatry in Fennoscandia, we used the identity test and the first background test by Warren et al. (2008) to estimate the degree of niche divergence vs. conservatism. This test allows us to make quantitative comparisons of how much the northern range differences contribute to overall niche divergence between the species.
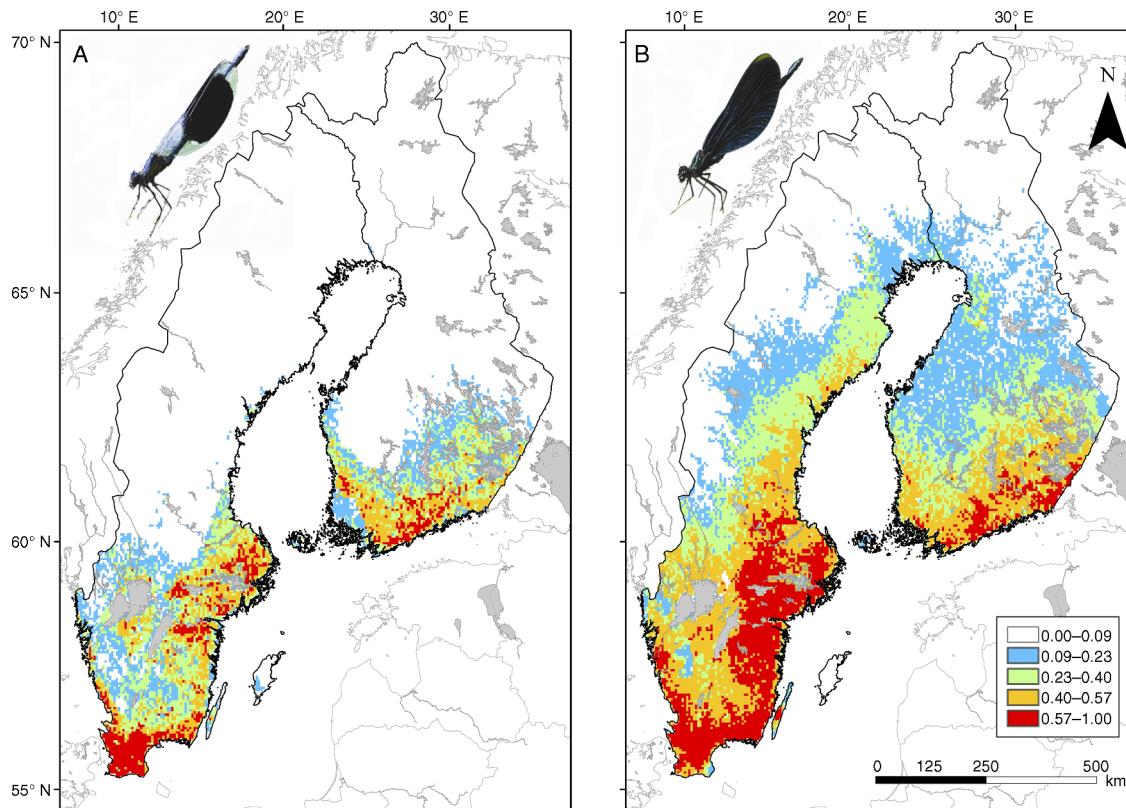
Fig. 2. Maxent distribution maps showing the environmental suitability for (A) *C. splendens* and (B) *C. virgo* in Fennoscandia. Warmer colors depict better environmental suitability.

All analyses in this study were performed with SAS (version 9.2, SAS 2010). Spatial data preparation and analysis were conducted with ArcMap (ESRI, version 9.3, Redlands, California, USA), including the Geospatial and Spatial Analyst extensions and Hawth's Analysis Tools. Environmental niche models were generated with Maxent (version 3.3.3a; Phillips et al. 2006). Niche model tests were conducted using ENM-Tools (version 1.2; Warren et al. 2008).

RESULTS

Visualizing the abundance data of the two species showed that the two *Calopteryx* species have largely overlapping ranges in Fennoscandia, but *C. virgo* occurs farther north than *C. splendens* (Fig. 1). The overall geographic range for *C. splendens* extended from 11.95° to 30.34° E longitude and from 55.38° to 63.05° N latitude, while the range for *C. virgo* extended farther north and spanned from 11.42° to 30.74° E longitude and from 55.39° to 66.74° N latitude.

Niche models were then constructed to quantify differences between species, and both models had a good fit, as indicated by high AUC values (*C. splendens* = 0.915 ± 0.006; *C. virgo* = 0.826 ± 0.006). Fig. 2 shows the predicted niche space for each species, with the range of *C. splendens* in Fennoscandia being entirely nested

within the range of the more northern species, *C. virgo*. Across both the entire range and the sympatric range, the positive correlation between the abundance data of the two species was significant (entire range, $R = 0.50$, $P < 0.0001$; sympatric range, $R = 0.83$, $P < 0.0001$). This indicates similar environmental niches across the entire Fennoscandian range, and that niche similarities might be even more pronounced in the sympatric zone. We modeled the environmental suitability index of both species, which is a proxy for the maximum (potential) abundance (Fig. 2). *Calopteryx virgo* was comparatively rare in southern Sweden, and became more dominant with increasing latitude (Figs. 2 and 3). The abundance of *C. splendens* decreased with increasing latitude ($R^2 = 0.10$, $P < 0.0001$). Regressions of environmental suitability vs. latitude were highly significant (Fig. 3) and highlighted that the relationship between latitude and the environmental suitability index for *C. splendens* is more scattered, indicating lower predictive power (Fig. 3), which was reflected as a lower R value (*C. splendens*, $R^2 = 0.25 \pm 0.14$ [mean ± SE], $P < 0.0001$, intercept = 63.91 ± 0.31; *C. virgo*, $R^2 = 0.52 \pm 0.10$, intercept = 67.70 ± 0.05, $P < 0.0001$). Unlike *C. virgo*, *C. splendens* did not occur at a latitude higher than 63° N (Fig. 3). The correlation between longitude and environmental suitability was less clear, although the

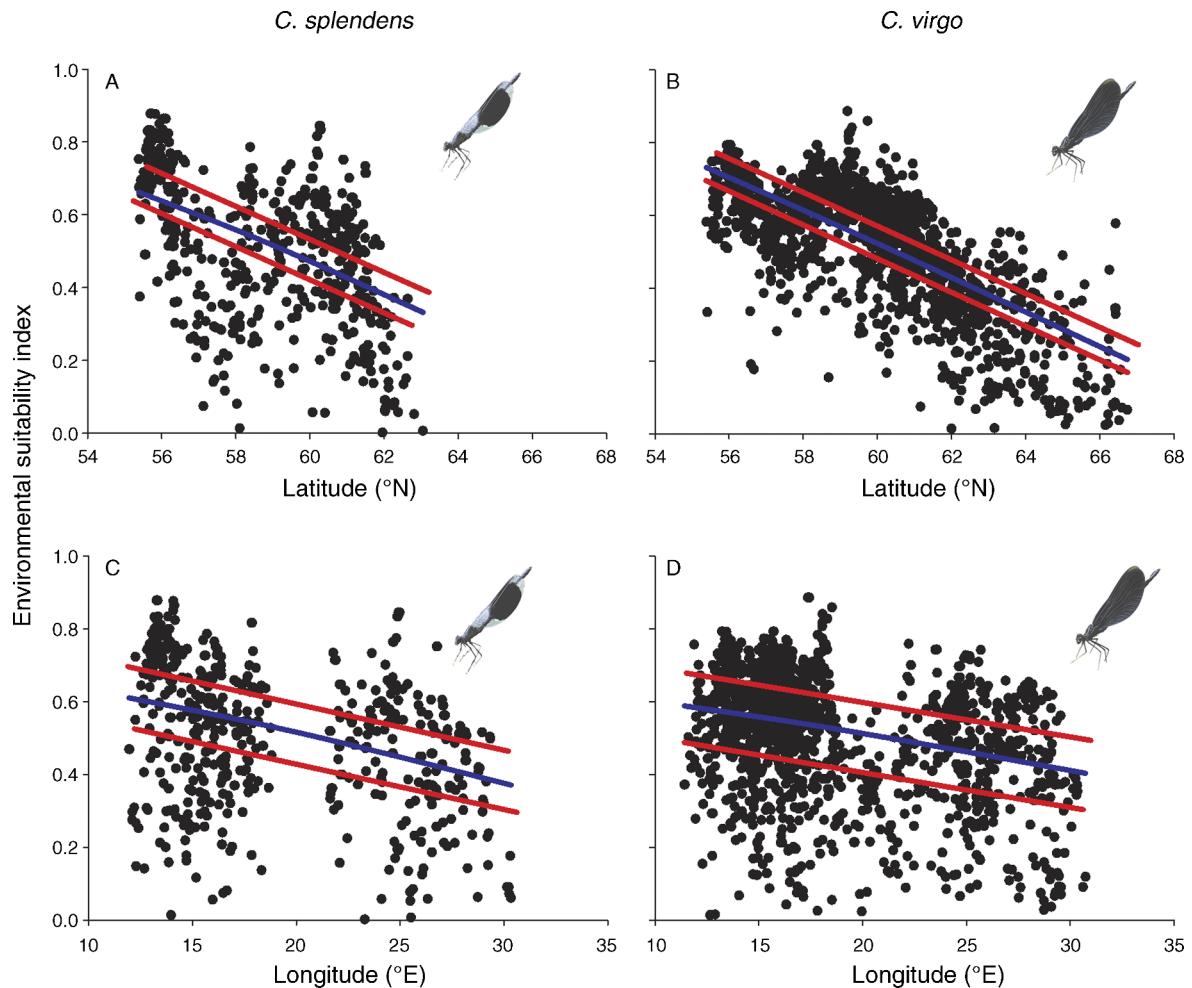*C. splendens*   *C. virgo*

FIG. 3.   Environmental suitability (logistic probability) plotted against latitude across the range for (A) *C. splendens* ($R^2 = 0.25 \pm 0.15$ [mean $\pm$ SE], $P < 0.0001$) and (B) *C. virgo* ($R^2 = 0.52 \pm 0.10$, $P < 0.0001$), and plotted within the zone of sympatry (against longitude) for (C) *C. splendens* ($R^2 = 0.08 \pm 0.15$, $P < 0.0001$) and (D) *C. virgo* ($R^2 = 0.13 \pm 0.18$, $P < 0.0001$).

overall relationship was significant for both species (*C. splendens*, $R^2 = 0.08 \pm 0.15$, intercept = 36.58 $\pm$ 0.31, $P < 0.0001$; *C. virgo*, $R^2 = 0.13 \pm 0.18$, intercept = 36.56 $\pm$ 0.02, $P < 0.0001$). Longitudinal trends are mainly caused by coastal-to-inland gradients, with both species showing a clear preference for coastal environments, where the climate is typically more moderate and temperatures fluctuate less.

Maxent analysis revealed that "mean temperature of the warmest quarter" was the highest ranked variable, and showed the highest gain when used in isolation for both species' models (Table 1 and Appendix C) and also decreased the gain the most for *C. virgo* (Table 1). Vegetation heterogeneity decreased the model gain the most for *C. splendens*. The minimum, maximum, mean, and standard deviations of the top three environmental variables with highest variable importance in Maxent environmental niche models for *C. splendens* and *C. virgo* are shown in Appendix B. To facilitate interpretation and comparisons, we also provide gradient maps

in the Supplementary Material (Appendix E). A large proportion of the remaining highly ranked variables for both species included temperature variables, and to a lesser extent, soil and vegetation-related variables for *C. virgo* (Table 1).

Notably, our niche models also explained a higher fraction of variation in abundances and location of northern range limits of the adult stage (i.e., "Mean Temperature During the Warmest Quarter") than environmental conditions during the larval (nonreproductive) stage (i.e., "Mean Temperature During the Coldest Quarter"; Table 1). The former variable was ranked the highest for both species and explained most of the variation in abundance (>50 % of the total variation explained; Table 1). The latter variable, which only has relevance to the larval stage, as adults do not exist during the winter months, explained considerably less (6.7% and 8.2%), although it is worth emphasizing that this variable was still the second and third most highly ranked factor explaining the distribution of these

TABLE 1. Maxent results showing the most important environmental layers ranked by the amount of variation they explain of the abundance data for the damselflies *Calopteryx splendens* and *C. virgo* in Fennoscandia.

Calopteryx splendens		*Calopteryx virgo*	
Environmental layer	Contribution (%)	Environmental layer	Contribution (%)
Mean temperature of warmest quarter†	58.0	Mean temperature of warmest quarter†, ‡	52.6
Mean temperature of coldest quarter	8.2	Mean temperature of driest quarter	13.9
Soil moisture, surface heterogeneity‡	8.0	Mean temperature of coldest quarter	6.7
Mean temperature of driest quarter	5.7	Growing season productivity	4.7
Mean temperature of wettest quarter	4.8	Soil moisture, surface heterogeneity	4.7
Mean diurnal range	3.4	Soils	2.9
Precipitation of warmest quarter	1.6	Maximum annual productivity	2.8
Evergreen tree cover	1.5	Precipitation of coldest quarter	1.8
Growing season productivity	1.4	Mean temperature of wettest quarter	1.7
Distance to coast	1.2	Distance to coast	1.4
Land cover	1.0	Land cover	1.3
Elevation	1.0	Mean diurnal range	1.3
Total tree cover	1.0	Temperature annual range	1.1
Soils	0.9	Precipitation of wettest quarter	1.0
Precipitation of coldest quarter	0.8	Elevation	0.6
Precipitation of wettest quarter	0.3	Total tree cover	0.3
Mean annual productivity	0.2	Precipitation of wettest month	0.3
Precipitation seasonality	0.2	Deciduous tree cover	0.3
Variation in annual productivity	0.2	Mean annual productivity	0.2
Precipitation of wettest month	0.1	Precipitation seasonality	0.2
Temperature annual range	0.1	Isothermality	0.1
Isothermality	0.1	Precipitation of warmest quarter	0.1
Maximum annual productivity	0.1	Evergreen tree cover	0.1
Deciduous tree cover	0.1	Variation in annual productivity	0.1

Notes: Isothermality is calculated as (mean of monthly [maximum temperature − minimum temperature]) / (temperature annual range) × 100). The variable with the highest gain contributes the most useful information in itself to the model, whereas the variable that decreases the gain the most contains the greatest amount of information that is not found in other variables.

† The environmental variable with the highest gain when used in isolation, i.e., the most useful information by itself.

‡ The environmental variable that decreases the gain the most when omitted, i.e., the most information that is not present in other variables.

two species (Table 1). Thus, although these data strongly suggest an important role for environmental conditions, particularly temperature, during the adult stage, temperatures during the winter months are clearly also important when explaining the northern range limits of these two species (Table 1).

Null models showed that species niches were not identical across Fennoscandia (Fig. 4A and B), as indicated by the large disparity between the pseudo-replicated null distribution and both niche overlap values (Hellingers $I = 0.84$, Schoener's $D = 0.60$; Fig. 4A, B). Background similarity tests for Hellinger's I showed that the niche overlap for *C. splendens* was lower than expected under the null hypothesis, indicating that *C. splendens* uses a subset of the *C. virgo* habitat (Fig. 4C). Background tests following Warren et al. (2010) for Schoener's D indicate an even stronger disparity between the null distribution and niche overlap values (Fig. 4D). Again, the distribution for *C. splendens* was entirely nested within the background of *C. virgo*. The background tests following McCormack et al. (2010) showed that the first nine principal components (PCs) explained 84% of variation (Table 2; PC values are shown in Appendix D).

The first axis was interpreted as capturing seasonal temperature extremes and showed evidence for niche divergence, explaining a total of 28% variation. (Here

and later in the article, the variables in the axes are explained in detail in Table 2.) Both latitude (−0.88) and longitude (−0.50) were highly and negatively correlated with this axis. The second axis showed evidence of niche divergence and captured 15% of variation, which was predominantly explained by precipitation differences. Again, latitude (−0.31) and longitude (−0.38) were negatively correlated with this axis, indicating environmental gradients along the range of species. The third axis explained 9% of variation, which was mainly captured by differences in vegetation heterogeneity and photosynthetic productivity. Niches did not differ significantly between the species for the third axis, indicating niche conservatism. The remaining six axes (PC 4–9) mainly captured variation in tree cover, mean annual photosynthetic productivity or "greenness," and soil characteristics, and each explained between 8% and 4% of variation. Five were consistent with niche divergence and one with conservatism.

Quantification of niche overlap in sympatry using identity tests showed that niche differences were much smaller compared to the entire Fennoscandian area, and niche use was not significantly different from the null distribution for Hellingers I (0.96, Fig. 4E), and only slightly so for Schoener's D (0.81, Fig. 4F). Most notably, the overall null distribution was close to 1 for both indices, and markedly more uniform compared to
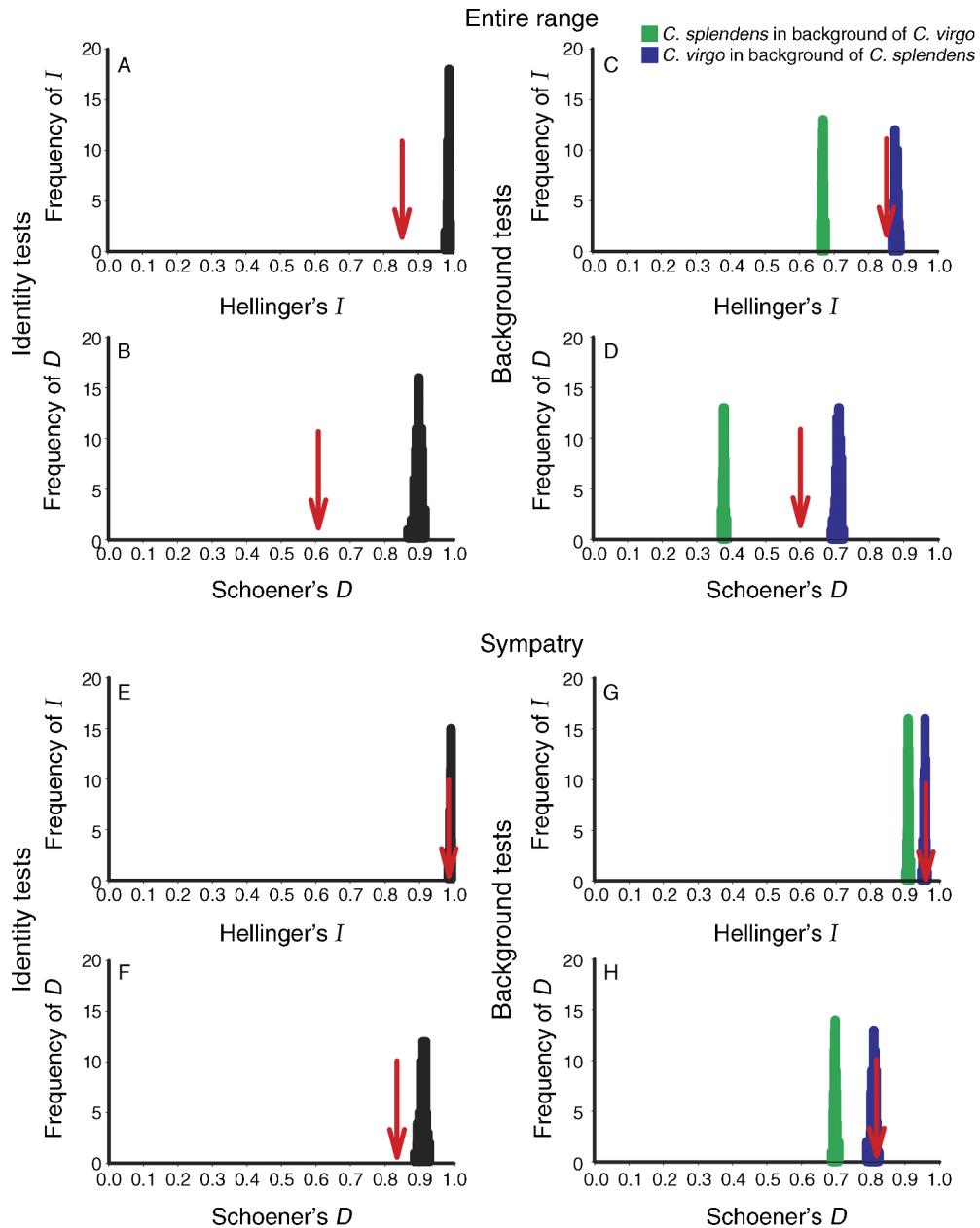
Fig. 4. Niche overlap values (arrows) for Hellinger's *I* and Schoener's *D* are compared to a null distribution. (A) Niche identity tests using Hellinger's *I*. The similarity score (red arrow) is lower than the null hypothesis of niche equivalency, indicating that the environmental niches are not equivalent. (B) Niche identity tests using Schoener's *D*. The similarity score of the two species is lower than the null hypothesis of niche equivalency. (C) Background test for Hellinger's *I*. The observed overlap for *C. splendens* is lower than under the null hypothesis, indicating that *C. splendens* uses a subset of the *C. virgo* habitat. On the contrary, the niche overlap value for *C. virgo* is close to identical with the null hypothesis. (D) Background test for Schoener's *D*. The results are similar to the test shown in (C), with the exception that the results indicate even stronger divergence and conservatism. The same analyses were replicated for the sympatric area (E–F).

the distribution for the entire range. Similarly, background tests showed niche differences between species were again much smaller in sympatry, and niche overlap values obtained with both tests were not different from the null distribution (Fig. 4G–H). Thus, data from the sympatric zone suggested strong niche conservatism and

high ecological similarity between these two phenotypically similar congeners.

DISCUSSION

Here we have quantified environmental niches of two closely related congeneric damselfly species, *C. splendens*

TABLE 2. Test of niche divergence vs. conservatism over the entire range in Fennoscandia for *Calopteryx splendens* and *C. virgo*.

Pairwise comparison	Niche axes			
	PC1	PC2	PC3	PC4
Cs vs. Cv†	1.1469	0.2266	−0.1074	0.1894
95% CI null distribution	−0.6077, −0.6054	0.0077, 0.0096	0.0870, 0.0886	−0.0548, −0.0535
Niche	divergence	divergence	conservatism	divergence
Explained (%)	28	15	9	8
Variable loading 1‡	mean temperature coldest quarter	precipitation wettest quarter	maximum productivity	*variation productivity*
Variable loading 2‡	minimum temperature coldest month	precipitation warmest quarter	soil moisture, roughness	maximum temperature warmest month
Variable loading 3‡	mean temperature warmest quarter	precipitation coldest quarter	mean productivity	(isothermality)
Variable loading 4‡	(precipitation seasonality)	precipitation wettest month	soils	(mean productivity)
Interpretation	seasonal temperature extremes	precipitation extremes	productivity, soil moisture	variation productivity, temperature extremes
Longitude correlation	−0.50	−0.38	0.03	0.47
Latitude correlation	−0.88	−0.31	0.21	0.02

Notes: To be significantly divergent, niche values must differ between the two species. The cumulative eigenvalue for nine PCs in PCA is 0.84.

† Observed differences between the species.

‡ Variable loadings indicate the contributions to the individual PCs, beginning with the highest, in order, 1–4. Parentheses indicate negative values. Values in italics reflect variables with particularly high contributions to a given PC axis (last eigenvector is 0.1 greater than next).

and *C. virgo*, both across their overall northern distribution and in sympatry. Quantifying niche differences between closely related and partly sympatric species is of fundamental interest in ecology, since the differences provide a solid basis for further experimental or observational work, and raise questions about mechanistic underpinnings of broad-scale geographic patterns (Underwood et al. 2000). Environmental niche modeling is certainly a powerful tool in ecological and evolutionary studies, as it can address differences at broad geographic scales and can make use of large data sets, which is otherwise not possible in population biological, behavioral, and mechanistic studies of individuals. The data presented in this study should therefore be interpreted in the light of our ongoing and previous studies of these two species and their ecological differences, which we discuss in the following paragraphs.

Niche differences in *Calopteryx* spp. and other damselfly genera are of interest because these insects have been put forward as examples where speciation has largely been driven by sexual rather than natural selection for niche divergence (McPeek and Brown 2000, Svensson et al. 2006, McPeek et al. 2008). Under this scenario, niche differences are expected to be relatively low, although some degree of divergence is always expected (Rundle and Nosil 2005). The key question is therefore: Is it likely that reproductive isolation in *Calopteryx* has been achieved as a direct or indirect result of different ecological conditions and selection for niche divergence, or has reproductive isolation largely been achieved independently of such differences (Rundell and Price 2009)? The analyses in this study suggest that these two species are ecologically

very similar in the sympatric zone of overlap in southern Fennoscandia, as revealed by nonsignificant niche differentiation and a high correlation between the presence of the two species ($R = 0.84$, see *Results*). Although the spatial scale from which we obtained our environmental data is quite large (1 km^2) and limits, in part, our ability to make further mechanistic inferences, we would like to emphasize that this conclusion about limited niche divergence between *C. splendens* and *C. virgo* is further supported by more detailed mechanistic studies at a smaller spatial scale. For instance, thermal niche differences between these two species have been quantified at one of our most intensively studied sympatric sites ("Klingavälsåns Naturreservat") using thermal imaging (infrared camera, or "IR-camera" [E. I. Svensson, *unpublished manuscript*]). Interestingly, there was no evidence of significant niche differentiation between *C. splendens* and *C. virgo* at this sympatric site for three temperature variables (air temperature, minimum and maximum substrate temperature) in spite of a large data set (>100 individuals [E. I. Svensson, *unpublished manuscript*]). As the thermal niche is obviously a very important component of the total environmental niche (Table 1), the findings from this more detailed mechanistic field study of individuals therefore supports the conclusion in this study that the two species have overlapping niches when they are sympatric. Interspecific niche differences were almost absent in sympatry (Fig. 4E–G), revealing a high degree of niche conservatism. In three out of four null model tests, niches did not differ significantly, suggesting that the species occupy similar, if not identical, environments in the sympatric region (Fig. 4E–H).

Table 2. Extended.

	Niche axes			
PC5	PC6	PC7	PC8	PC9
0.9582	−0.1534	0.1071	0.1028	0.1985
0.088, 0.0892	0.0459, 0.0471	−0.0026, −0.0016	−0.0285, −0.0275	−0.0004, 0.0005
divergence	conservatism	divergence	divergence	divergence
6	6	4	4	4
evergreen tree cover	*mean productivity*	*broadleaf tree cover*	*land cover*	tree cover
(soils)	maximum productivity	iso-thermality	soils	(maximum temperature warmest month)
(soil moisture, roughness)	(tree cover)	(land cover)	(mean temperature wettest quarter)	land cover
iso-thermality	(isothermality)	mean diurnal range	tree cover	mean temperature wettest quarter
evergreen tree cover, soils	productivity, tree cover	broadleaf tree cover, land cover	land cover, soil type	tree cover, summer temperatures
−0.15	0.28	−0.25	−0.08	−0.14
−0.06	0.03	−0.01	0.01	−0.08

In contrast to the lack of niche differences in sympatry, looking across their overall northern range, interspecific niche use differed significantly, resulting in niche divergence. The variables that were associated with these niche differences (Figs. 1 and 2) were mainly temperature and precipitation. For example, we found strong indications for a sharp geographic range limit in the more southern species, *C. splendens* (Fig. 1), which largely coincides with the biogeographic limit "Limes Norrlandicus," where many plant and animal taxa in Sweden have their southward or northward distributional limits (Fransson 1965). This ecotone reflects the marked change in temperatures in western and central Sweden (Table 2), which is further supported by the strong ecotone for temperature and precipitation (Appendix D, PC1 and PC2). Niche modeling identified summer temperatures ('mean temperature of the warmest quarter') as the most important factor determining the abundance of *C. virgo* (52%), and this variable was also a key determinant for *C. splendens* (58%; see also Appendices B and E for details on variable ranges). Null models showed that the best-supported cases of niche divergence (e.g., axes 1 and 2) were always based on temperature and precipitation patterns, and that these axes were strongly linked to both latitude and longitude (Fig. 2, Table 2). The overriding effect of temperature on the distribution of these two species suggests that even though *C. virgo* appears to have diverged in climate tolerance from *C. splendens*, physiological limits to cold temperatures might currently restrict its farther range extension in the north (Fig. 2, Table 2). This inference from the niche results is supported by more mechanistic and experimental physiological studies by Zahner (1959), which showed that the larvae of *C. virgo* were indeed more cold tolerant than the larvae of *C. splendens*. Again, the results from environmental niche modeling should preferably be compared to the results of mechanistic and experimental studies of larvae and/or adults and the different environmental requirements of the two life stages.

It is worth emphasizing that although the larval stage is considerably longer than the adult stage in odonates such as in the *Calopteryx* genus (where it lasts between one and two years), it is unclear which stage is more important in explaining the current distributions of the genus. From an evolutionary perspective, the most important life stage is where most genetic variation in fitness is available for natural or sexual selection to act upon. In other insects, such as *Drosophila melanogaster*, most genetic variation for fitness is actually expressed during the adult stage, as a result of competition for mates and reproductive opportunities (Chippindale et al. 2001). Thus, although there is plenty of variation in fitness between individuals during the relatively long larval stage, most of which is likely environmentally induced, it is by no means certain that this variation is evolutionarily as important as the variation during the adult stage. The short life stage of adult *Calopteryx* damselflies makes it likely that variation in adult fitness is highly influenced by genetic variation, as well as environmental conditions during the summer months (mainly temperature; Table 1), resulting in extensive genotype-by-environment interactions in how males and females deal with multiple and challenging environmental stressors.

The nonsignificant niche differences in sympatry lead to large local overlap between these two species, resulting in many sympatric populations across the geographic range of *C. splendens* in Fennoscandia (Wellenreuther et al. 2010*a*, *b*). Because of the shared niche space over most of the species' range, frequent local encounters provide ample opportunity for frequent interspecific interactions (e.g., Tynkkynen et al. 2006). These interspecific interactions are presumably key selective factors that account for the evolution and maintenance of the large differences in secondary sexual traits between these species, and also lead to extensive

spatial sexual selection between populations (Svensson et al. 2006, Tynkkynen et al. 2006, Wellenreuther et al. 2010b). In contrast to the diversifying role of locally varying and spatially variable sexual selection, long-term stabilizing natural selection toward some shared niche features of the two species has preserved their overall similarities in nonsexual morphology. This has resulted in a relative stasis of nonsexual morphology and physiology at the phenotypic level (Hansen 1997), except for the secondary sexual traits, which differ markedly between species (Rüppel et al. 2005, Bryde-gaard et al. 2009, Guan et al. 2010).

The high sensitivity of both species to temperature and precipitation suggests that changing climatic conditions will have a large effect on their distribution. Changes in the distributional patterns of species commonly lead to novel species interactions, for example, due to an increasing overlap in species ranges. Recent work on the two *Calopteryx* species in Fennoscandia has shown that a likely future range expansion of *C. splendens* into the allopatric areas occupied by *C. virgo* might potentially lead to increased heterospecific matings and hybridization (Wellenreuther et al. 2010a). This is because species barriers are thought to have largely been driven by sexual selection on species recognition characters, and allopatric *C. virgo* males in northern Fennoscandia have partly lost their ability to discriminate against heterospecific females of *C. splendens*, resulting in a high rate of mate-recognition mistakes when encountering each other in simulated experiments connected with the future range expansion (Wellenreuther et al. 2010a). Recent modeling work by McPeek and Gavrilets (2006) suggests that high rates of differentiation are likely to have heightened speciation rates of odonates during Quaternary climatic oscillations. The results in this study are largely consistent with the general notion that speciation in odonates in general (McPeek et al. 2008), and in the genus *Calopteryx* in particular (Svensson et al. 2006), is a result of sexual selection, and with a more modest role for natural selection and niche divergence. Natural selection might therefore play a primarily conservative role in odonates, keeping species adapted to their current environments, with sexual selection causing much or most phenotypic divergence between populations and incipient species. Evidence for a key role of sexual selection in the divergence of courtship signals in other radiations (e.g., Seehausen 2006) suggests that sexual selection might also be important in the speciation of other animal groups (Allender et al. 2003, Ritchie 2007).

In conclusion, we have found evidence for niche divergence across the entire northern range of both *Calopteryx* species, which is consistent with the pattern found in many closely related species (Knowles et al. 2007, Wellenreuther et al. 2007, Wellenreuther and Clements 2008; Kalkvik et al., *in press*). Such ecological niche divergence has often been interpreted as evidence for, or at least consistent with, ecological speciation

theory (Schluter 2000, 2009, Rundle and Nosil 2005). However, the results in this study underscore the importance of quantifying niche differences across different geographic scales and in different ecological conditions (i.e., both in sympatry and allopatry). When we quantified interspecific niche differences in only the sympatric area within the Fennoscandian range, we found weak and nonsignificant interspecific differences and evidence for niche conservatism (Figs. 2 and 4, Table 3). The contrast between the niche comparison across the entire Fennoscandian range and the sympatric region suggests that niche differences can largely be attributed to latitudinal changes in temperature and precipitation (Table 3 and Appendix D).

Although environmental niche modeling is a correlative approach, and should ideally be complemented with more mechanistic and experimental studies of individuals in the field or in the laboratory, our results suggest several possible future experimental validations of the observed patterns. Such experiments include reciprocal transplant experiments in the field (to establish if nonsuitable conditions during the summer prevent *C. splendens* from expanding northward, beyond its current northern range limit in central Sweden; Fig. 2), more detailed studies of larval environmental tolerances, and further quantification of thermal niches of adults at allopatric and sympatric sites. The results in this study suggest that divergence in physiological temperature and precipitation optima are the most likely factors that can explain the interspecific differences in northern range limits of these two species. This pattern corroborates the view that niche divergence between damselfly species is often limited and affects only some aspects of niche use, and that reproductive isolation is more likely to be linked with diversification in secondary sexual characters (Brown et al. 2000, McPeek and Brown 2000, McPeek et al. 2009, 2011).

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SUPPLEMENTAL MATERIAL

Appendix A

Overview of climate and remote sensing data sets used in this study (*Ecological Archives* E093-119-A1).

Appendix B

Minimum, maximum, mean, and standard deviations for the top three variables in Maxent environmental niche models for *C. splendens* and *C. virgo* (*Ecological Archives* E093-119-A2).

Appendix C

The jackknife test of variable importance for *C. splendens* and *C. virgo* in Sweden and Finland (*Ecological Archives* E093-119-A3).

Appendix D

Graphical representation of principal components from the second background test (*Ecological Archives* E093-119-A4).

Appendix E

Figures depicting the top three variables in Maxent environmental niche models for *C. splendens* and *C. virgo* across Sweden and Finland (*Ecological Archives* E093-119-A5).