Range shifting species reduce phylogenetic diversity in high latitude communities via competition

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Abstract

1. Under anthropogenic climate change, many species are expanding their ranges to higher latitudes and altitudes, resulting in novel species interactions. The consequences of these range shifts for native species, patterns of local biodiversity, and community structure in high latitude ecosystems are largely unknown but critical to understand in light of widespread poleward expansions by many warm-adapted generalists.

2. Using niche modelling, phylogenetic methods, and field and laboratory studies, we investigated how colonisation of Scotland by a range expanding damselfly, *Ischnura elegans*, influences patterns of competition and niche shifts in native damselfly species, and changes in phylogenetic community structure.

3. Colonization by *I. elegans* was associated with reduced population density and niche shifts in the resident species least related to *I. elegans* (*Lestes sponsa*), reflecting enhanced competition. Furthermore, communities colonized by *I. elegans* exhibited phylogenetic underdispersion, reflecting patterns of relatedness and competition.

4. Our results provide a novel example of a potentially general mechanism whereby climate change-mediated range shifts can reduce phylogenetic diversity within high latitude communities, if colonising species are typically competitively superior to members of native communities that are least-closely-related to the coloniser.

Key words: Climate Change, Range Shifts, Competition, Community Assembly, Damselflies, Odonata, Coexistence, Non-analog communities, thermal niche.

Introduction

Many species are shifting their ranges to higher elevations and latitudes in response to climate change (Parmesan & Yohe 2003; Hickling *et al.* 2005). However, rates of range shift are not consistent across species (Hickling et al 2008), thus many ecological communities are experiencing changes in composition in response to novel regional species pools (Moritz *et al.* 2008; Telwala *et al.* 2013; Therry *et al.* 2016). Typically, high latitude communities which have not been colonised by range shifting species are simple, often containing several endemic, keystone species with little local redundancy in ecosystem function (Gaston 2000; Willig, Kaufman & Stevens 2003). Such features make high latitude communities open to invasions and colonization by range-expanding species (Lebouvier *et al.* 2011), but the general consequences of range expansions for high latitude community diversity are largely unknown. Several recent, large-scale analyses suggest that regional (gamma) biodiversity will continue to increase under climate change at high latitudes, which may also be reflected in increases in (alpha) diversity at the local community level (Menéndez *et al.* 2006; Thuiller *et al.* 2011). However, other analyses suggest that colonizing species may typically outcompete and replace native species at high latitudes (Alexander et al. 2015), resulting in irreversible species loss and biotic homogenization along latitudinal gradients (Dornelas *et al.* 2014). Recent work also suggests that colonization by range-shifting species or invaders often reduces phylogenetic diversity of impacted communities (Lessard *et al.* 2009; Selvi, Carrari

& Coppi 2016), but it is unknown whether or how this process results from patterns of competition between colonizing and native species. Understanding of these underlying mechanisms is critical in order to mitigate loss of phylogenetic diversity at high latitudes. Biotic homogenization and reduced phylogenetic diversity could have severe consequences for ecosystem function and future evolutionary potential for high latitude communities to respond to future climatic stressors (Pio *et al.* 2014; Li *et al.* 2015).

Underlying processes affecting community phylogenetic diversity:

Two processes, environmental filtering and competition, are often invoked to explain the makeup of communities (Kraft *et al.* 2007). Environmental filtering represents the process by which the environment acts as a “sieve”, so that species with shared niche requirement or environmental performances are expected to cluster together in space as they colonise shared habitats (Cavender-Bares *et al.* 2004; McGill *et al.* 2006; Kraft *et al.* 2007). Over an environmental gradient, species with similar niche requirements will persist in shared locales to form communities (Wiescher, Pearce-Duvet & Feener 2012; Laliberté, Turner & B.L. 2014). Inversely, competition may result in the exclusion of ecologically similar species from occupying the same geographic space, via limiting niche similarities between species (Cahill *et al.*, 2008, Darwin 1859). Species with similar functional or niche traits are typically expected to compete most strongly for resources, resulting in reduced densities or local exclusion of all but the best performing (i.e., most competitive) species from each functional group (Macarthur & Levins 1967). Under competitive exclusion, and in contrast to environmental filtering, coexistence within a community is therefore often expected to arise from interspecific variation in functional and niche traits (Macarthur & Levins 1967; Chesson 2000). In high-diversity regions, competition may determine coexistence within communities, but if the number of potential competitors is limited, or if spatial environmental variation is extreme, environmental filtering is often the dominant process. In most cases, these processes act in tandem (Chesson 2000; Kraft *et al.* 2007).

These processes of filtering and competition are also influenced by the evolutionary history of species that can potentially coexist. Because multiple traits contribute to an individual or species' ecological niche (Kraft et al, 2015), niches are often less evolutionarily labile than individual traits (Wiens *et al.* 2010). Thus traits which determine a species' environmental niche tend to be conserved among closely related species (Wiens & Graham 2005; Wiens *et al.* 2010). Such phylogenetic niche conservation implies that community assembly processes (such as colonisation of and persistence in a patch) based on niche similarity or differences may generate phylogenetic structure within communities (Webb *et al.* 2002). If ecological niches are highly evolutionarily conserved among closely related taxa within the regional species pool, and competition is an important factor limiting coexistence within communities, phylogenetic overdispersion is expected to arise within communities (Webb *et al.*, 2002). Phylogentic overdispersion occurs in this case because closely related species, with shared community-based niches, are more likely to competitively exclude each other from limited resources and habitats (Burns & Strauss 2011; Violle *et al.* 2011; Peay, Belisle & Fukami 2012). Alternatively, if niche traits are evolutionarily conserved but environmental filtering is more important for ecological processes such as colonisation and persistence, then phylogenetic underdispersion may define local community structure (Webb *et al.*, 2002). This is because, in the absence of strong competition, shared niches among closely related taxa will cause them to cluster in resource and habit space (Cavender-Bares *et al.* 2004). Under these general predictions, many studies have attempted to classify the relative roles of competition versus environmental filtering as drivers of community assembly, based on estimates of phylogenetic structure alone (Webb 2000; Lebrija-Trejos *et* *al.* 2010). However, several key limitations of this approach make inferring the roles of competition and environmental filtering from phylogenetic structure problematic.

The limitations in determining community processes based on phylogenetic clustering within the community are twofold. Firstly, contrasting with the traditional assumptions above, niche traits that determine competition within communities may not be the same traits that are important for habitat filtering, and these traits may experience different levels of phylogenetic conservatism (Silvertown *et al.* 2006; Pigot & Tobias 2013). Second, conserved functional traits, which do not relate to niche occupancy but instead influence a species' competitive ability, may also result in phylogenetic underdispersion within communities dominated by competitive processes (Mayfield & Levine 2010). More recent theory suggests that if functional traits that predict competitive abilities (e.g., body size, aggression levels, boldness, or growth rates) are conserved, coexisting species will be those most similarly matched in competitive ability and thus should be closely related, while distantly related species with lower competitive abilities values will be excluded (The Competitive Trait Conservatism Hypothesis; Chesson, 2000; Mayfield & Levine, 2010). However, the relative influence of competition on phylogenetic dispersion within communities has rarely been empirically tested (Mayfield & Levine 2010; Thuiller *et al.* 2011; Alsos *et al.* 2012) .

Range expansions and phylogenetic diversity of high latitude communities:

Widespread range shifts under climate change create the ideal natural laboratory to understand community assembly dynamics, because changes in the regional species pool are observable over short spatial scales reflecting the colonisation process, where expanding, range edge communities reflect most recent opportunities for coexistence. In Great Britain, several members of the regional damselfly biota have been expanding northward or to greater altitudes under climate change (Hickling *et al.* 2005). We examined patterns of species coexistence in local damselfly guilds in Northeast Scotland with relationship to environmental variables and opportunity for competition between established residents and incoming, range expanding species.

Taking advantage of these well-documented range expansions among British Odonata, we aim to improve understanding of community assembly processes under dynamic regional changes in biodiversity, and to empirically investigate the merits of using phylogenetic community structure to access community assembly processes. In particular we aim to study these effects in a species-poor, high latitude community where the ecological effects of individual range shifting species are likely to be profound. Recent range expansions of potential competitors may pose a conservation risk to high-latitude endemics, compounding stressors due to climate change alone (Lancaster 2016). Thus understanding the mechanisms that influence possible interactions between high-latitude residents and cosmopolitan range shifting species is of high importance. To achieve our aims, we investigated phylogenetic dispersion of species within colonized and uncolonized damselfly communities, whether niche traits are phylogenetically conserved among incoming and resident species, and how patterns of niche shifts related to competition reflect the shared evolutionary history of the species within this study.

Materials and Methods

Study system

Damselflies (Odonata: Zygoptera) are semi-aquatic, predatory insects, which exhibit strong intra- and interspecific competition at both larval (aquatic) and adult (terrestrial) life stages (Convey 1988; Worthen & Patrick 2004). Damselfly performance is highly limited by climate, with higher temperatures shown to increase growth rates (Corbet & May 2008; Nilsson-Ortman *et al.* 2013) and adult flight performance (Okuyama, Samejima & Tsubaki

2015). Higher temperatures are also correlated with increased damselfly population densities in high-latitude habitats (Lancaster *et al.* 2015). Levels of interspecific aggression and direct competition are also positively correlated with environmental temperature in damselfly communities from high latitudes (Lancaster, Morrison & Fitt 2017).

The strong relationship between climate and competitive regimes in damselflies makes dissecting patterns of coexistence easier to characterise than in many other guilds, because both environmental filtering and competitive exclusion are strongly dependent on the same set of (abiotic, thermal) conditions (Saito *et al.* 2016a). Furthermore, most damselfly species in the UK are restricted to still water ponds and lakes, where they have the opportunity to compete for thermally-preferred habitats at all stages of their life cycles (Cham et al., 2014). These shared ecological requirements mean that damselflies are often found in dense guilds around still water ponds, which represent clearly defined, distinct habitat patches (Wilson 1999; Sánchez-Herrera & Ware 2011). Diurnal patterns of flight with damselflies are also highly synchronised (Corbet & May 2008), allowing for accurate sampling of all species within a community. For all of the above reasons, damselflies represent an ideal animal study system for studying coexistence mechanisms on a landscape scale.

Within our study area of Northeast Scotland (see below), there are six species of co-occuring damselflies, four of which are long-time residents of the region: *Lestes sponsa* (Hansemann, 1823), *Enallagma cyathigerum* (Charpebtier, 1840), *Pyrrhosoma nymphula* (Sulzer, 1776). These are common and widespread species across most of Great Britain as well as much of Europe and Asia (Askew 1988). The northern relict species within Scotland *Coenagrion hastulatum* (Charpentier, 1825) is also a long-time resident of the region. Two additional species are currently range expanding into or within the region: *Coenagrion puella* (Linnaeus, 1758) and *Ischnura elegans* (Vander Linden, 1820). *Ischnura elegans* has recently undergone a northwards range shift in Northeast Scotland, with a 143km northwards range shift between 1985 and 1995, and is currently undergoing an altitudinal range shift to upland sites (Hickling *et al.*, 2005; Cham *et al.*, 2014), while *C. puella* has only recently started colonising Scotland and is found only sporadically through our study area (Hickling *et al.*, 2005; Cham *et al.*, 2014). All of these species are members of the family Coenagrionidae (superfamily Coenagrionoidea) except for *L. sponsa*, which belongs to the somewhat distantly related Lestidae (superfamily Lestoidea). Based on 97 occupied sites visited during the summer breeding season across Northeast Scotland (see ‘Field surveys’, below), we identified 56 unique combinations of co-occurance among these 6 species, with no site occupied by all 6 species.

Field surveys

Data on damselfly communities throughout Northeast Scotland was obtained by surveying 97 occupied pond sites between 4th of May through 23rd of July 2014. This period covers the peak flight times for all species studied, with *I. elegans*, *P. nymphula*, *C. hastulatum*, *C. puella* and *E. cyathigerum* reaching peak adult density in mid-June, while *L. sponsa* adult densities peak in mid-July (Cham et al., 2014), and *L. sponsa* emergence is highly synchronized in this period (Powney *et al.* 2014). Furthermore, *L. sponsa* peak emergence occurs earlier in the northern extent of its range than in the south (Sniegula, Golab & Johansson 2016), leading to high interspecific convergence among of flight times among all 6 coexisting species in our study area. Sites ranged from 56.37° to 57.68° Latitude, and -4.13° to -2.11° longitude, and elevation between 3m to 442m, thus covering a large spatial extent and encompassing a range of climatic variation (table S1). Sites were selected to be as similar to each other as possible across the region, and to exhibit mutual suitability for all colonizing and native species. For this reason we limited our surveys to permanent water bodies with open, shallow bottoms and consistent varieties of emergent vegetation. Temporary, flowing, or heavily-shaded water bodies, each of which only support a subset of

Scottish species, were avoided in our site selection procedure. We visited sites between 8:00am and 6:00pm, when the weather was warm with little or no rain, so that sites were visited when the weather was favourable and all species of damselfly present would be active. We recorded air temperatures during each of our site visits in order to quality control the density data (see below). Sites were surveyed by walking transects around the perimeter of water bodies and capturing damselflies in timed catching bouts. Species present were recorded and a proxy for the density of each species was calculated as the number of individuals of each species caught per minute of capture time; sites were visited multiple times and the per species mean density was averaged over the study period. A species was assumed to not be present at significant density at a site if no individuals were observed within 15 minutes of catching effort during the species' adult flight season, and return trips to most ponds confirmed presumed absences. Co-occurrence at each site does not necessarily imply stable coexistence, as damselflies often exhibit metapopulation dynamics characterized by frequent local extinction and recolonization events (Mcpeek, Brown & Apr 2000; Gibbons, Reed & Chew 2002). Our study design does not encompass long-term dynamics, and thus captures predictors of co-occurrence rather than stable coexistence. However, our study design enables us to capture the dynamics of competitive interactions that are likely to correlate with longer-term patterns of persistence or competitive displacement across the region.

Morphology

Morphology has been shown to be a highly variable trait in damselflies, and shifts in morphology may represent either an evolutionary or plastic response to abiotic conditions or altered competitive regimes (Chaput-Bardy *et al.* 2010; Hassall 2013). Thus we investigated effects of climate and altered competitive regimes on body size. A subset of captured damselflies of each species from each site were brought back to lab to assess body size.

Individuals of *C. hastulatum*, which are locally endangered (Cham et al., 2014), were never removed from the field. Scans of each damselfly were taken using an Epson Perfection V37 flatbed scanner, at a resolution of 600 DPI. From these scans, measurements were taken of forewing length, abdomen length and width, thorax length and width and total body length using ImageJ (Schneider, Rasband & Eliceiri 2012). Principal components analysis was conducted in R v.3.0.2 (R core development team, 2008) to account for variation in size across all morphological measurement (Gosden et al., 2011). The first principal component (PC1) accounted for 73.38% of variation in these measurements and was negatively correlated with each. Given the negative relationship, and to make results easier to interpret, inverse PC1 was therefore used to estimate body size.

Statistical analyses of climate and species interactions

To identify patterns of competitive displacement from climatically favourable sites arising between range-shifting (i.e., *I. elegans*) and resident species, we compared linear models to explain the log(density) of each of the resident species, averaged over the season at each site. Because mean annual temperature has been shown to be the best abiotic predictor of damselfly field densities (Lancaster *et al.* 2015), we included in these models an effect of climate (georeferenced values of uncorrelated, biologically relevant climate variables from table S1: Hijmans *et al.* 2005), an effect of *I. elegans* presence, and all interactions between *I. elegans* presence and temperature. The full model was compared against all reduced models using linear models in the base stats package in R v.3.0.2 (R core development team, 2008). The best model was selected using the corrected Akaike Information Criterion (AICc; Mazerolle 2015) (Table S2). *C. puella* and *C. hastulatum* were not found at sufficient numbers of sites to include in these analyses. Given the high reliance of damselflies on climate (see 'study system', above), a significant interaction suggests that the presence of *I. elegans* modifies the ability of resident species to persist in preferred sites, and indicates that competition may be an important driver of co-occurence patterns in recently colonised communities. In the absence of evidence for competition, environmental filtering processes were investigated by examining patterns of niche overlap and coexistence between species (see niche overlap, below). To determine whether site-specific densities were spatially autocorrelated within each species, we ran a Mantel test of species densities in the Ecodist package for R (Goslee & Urban 2007). To determine if daily air temperatures (measured on the day of capture) affected our local density estimates (via effects on individual activity levels and thus detectability), we ran mixed effect linear models in the lmerTest and lme4 packages for R (Kuznetsova et al., 2016) regressing daily density estimates on air temperature measurements taken at the time when sampling occurred, and including a random effect for site, since most sites were visited on multiple occasions.

Phylogenetic community structure

Phylogenetic reconstruction of Scottish damselfly evolutionary relationships was obtained from Dumont, Vierstraete & Vanfleteren (2010) and Guan *et al.* (2013), with branch lengths set to 1 because true branch lengths are unknown and are potentially unlikely to accurately reflect rates of divergence in niche traits (Fig. 1). To estimate phylogenetic over- or under-dispersion at each site, phylogenetic relationships were used to construct a pairwise phylogenetic distance matrix of all species within each site using the cophenetic() function in the picante package for R (Kembel *et al.* 2010). Subsequently, mean pairwise distances were calculated for each site, and compared to a null expectation using the ses.mpd() function, also in picante, where the null expectation was generated by randomizing shuffling tip labels on the phylogeny 99 times. Where the observed phylogenetic dispersion of a site was greater than 90% of randomly-generated phylogenies for the site, we classified the site as phylogentically overdispersed. Similarly, we diagnosed phylogenetic underdispersion where the phylogenetic dispersion at a site was less than 90% of randomly generated phylogenies for that site. If the phylogenetic dispersion of a site was similar to the middle 80% of randomly-generated phylogenies for the site, we classified the site as evenly phylogentically dispersed. Due to conservative cutoffs for phylogenetic dispersion, we do not attempt to use these data to draw rigorous conclusions about phylogenetic patterns at any particular site. However, such conservative cutoffs give us an appropriate range of values to feed into further analysis. Sites with only one species present were classified as single species communities. These categories were used in linear models to analyse the correlation between phylogenetic structure of communities and climate or the presence of *I. elegans*.

Competitive trials

To quantify thermal preference and competition between *I. elegans* and *L. sponsa*, thermal preference trails were conducted in the laboratory using wild-captured damselflies in 2016. One hundred and three *I. elegans* and 108 *L. sponsa* from 7 sites (capture dates and locations in Table S3) were assessed for their preferred basking site temperatures in a repeated measures design, where each individual was assessed for its thermal preferences alone, and in the presence of an interspecific ‘competitor’. Treatment order (alone vs. in competition with the other species) was randomised so that repeated exposure to the thermal gradient would have no effect on the damselflies. Thermal preference was assessed by placing the damselfly in a 60cm Tube with a thermal gradient from 60°C to 10°C, achieved by heating the tube at one end using a heat lamp (100W, 50Hz Exoterra ceramic heat emitter) and cooling the opposite end with ice (Fig. S1). Each damselfly was given 5 minutes to settle in their preferred position on the thermal gradient. The thermal environment where the damselfly settled was measured by photographing the damselfly using a Flir Ex Series E6 thermal imaging camera and analysing the image using the Flir Tools software package (v5.2.15, Flir systems.). For image analysis, the average temperature was taken of 5 point samples of the temperature surrounding the damselfly (Fig. S2). Points were randomly selected ~5mm from the individual's thorax. Effects of competition were analysed in a mixed-effects linear model where the dependent variable was resting site temperature, and fixed effects were included for species, treatment (alone or in competition), and the interaction (species x treatment). Random effects were included to account for individual ID (repeated measures) and for pair identity (because two individuals share a paired trial). The model was run in lme4 and lmerTest packages for R.

Environmental variables and niche model construction

Species distributions were modelled over the geographic extent of Scotland using a maximum entropy habitat suitability model implemented in MaxEnt, version 3.3.3k (Phillips, Avenue & Park 2004) and executed through the Dismo package for R (Hijmans *et al.*, 2014). Each species' presence points were obtained from records downloaded from the Global Biodiversity Information Facility (http://www.gbif.org), and Odonata records from The British Dragonfly Society (BDS) accessed from the National Biodiversity Network (http://www.nbn.org.uk/), with duplicate records removed, leaving 2783 unique presence records for *I. elegans*, 2485 for *L. sponsa*, 5470 for *P. nymphula*, 158 for *C. hastulatum* and 4667 for *E. cyathigerum*. Ten thousand randomly selected background points were used as pseudo-absences in each model. The models were constrained to Scotland by using the boundaries dataset available from the Office of National Statistics (Ordinance Survey, 2011). Bioclim climate layers were sampled at 30 arcsecond resolution and clipped to the extent of this region using the Raster package for R (Hijmans *et al.*, 2013); these were used as predictor variables in the models (Table S1). In the case that climatic predictor variables were correlated at > 80% across species presence and background points, the variable considered likely less important to damselfly biology was removed. The MaxEnt model was run 5 times using default parameters, withholding a separate 20% of presence points for model testing on each model run. The final niche model for each species represented the average habitat suitability's calculated across the five model runs. The full model (with all environmental predictor variables) and stepwise-reduced models were compared using AICc, implemented in the ENMeval R package (Muscarella et al., 2016), with a ΔAICc of 2 denoting significant differences between models. Model fit was also assessed by estimating the area under the Receiver Operating Characteristic (ROC) curve (AUC), which estimates sensitivity versus 1 – specificity (positively identified known presences versus the false positive rate). AUC values of 0.5 or less correspond to the model performing similarly or worse than random, while AUC values of 1 – a/2 (where a is the relative size of the true species range within the study area) indicate a very good fit of the model to the data (Phillips *et al.* 2004).

Phylogenetic analysis of niche overlap

Pairwise overlap in habitat suitability of each species was calculated using the D statistic (Warren, Glor & Turelli 2008) based on Schoeners D (Schoener & Schoener 1968), in the Phyloclim package for R (Heibl & Calenge 2013). To test for phylogenetic signal in niche overlap, niche overlap was assessed for correlations with phylogenetic distances between clades at each node of the phylogeny, using the age.range.correlation() tool from the Phyloclim package. The significance of niche overlap across the phylogeny of Scottish damselflies was assessed using a Monte Carlo randomization procedure with 999 permutations of the overlap matrix, with α set to 0.05.

Results

Overall we sampled 4767 individual damselflies over 96 sites, of which *C. hastulatum* occurred at 12 sites with a mean density of 0.3±0.48 damselflies per minute (dpm) (± among-site standard deviation), *C. puella* at 15 sites with a mean density of 0.14±0.19 dpm, *E.*

cyathigerum at 82 sites with a mean density of 0.63±1.22 dpm, *I. elegans* at 50 sites with a mean density of 0.34±0.34 dpm, *L. sponsa* from 39 sites with a mean density of 0.88±1.59dpm, and *P. nymphula* from 65 sites with a mean density of 0.13±0.1dpm.

Spatial autocorrelation and abundance responses local to daily temperatures.

No species exhibited spatial autocorrelation for site densities except for *I. elegans,* where spatial autocorrelation likely reflects the ongoing range expansion process (spatial autocorrelation for I. *elegans,* r=0.12, P=0.014; *L. sponsa*, r=0.01, P=0.39; *P. nymphula*, r =-0.9, P=0.98; *E. cyathigerum,* r=0.02, P=0.31; *C. hastulatum*, r=0.02, P=0.34; *C. puella*, r=0.04, P=0.21). Species densities calculated from individual capture bouts were uncorrelated with the air temperature during these capture bouts, confirming that we selected days characterised by favourable weather conditions for sampling, and thus that our density estimates are not confounded by temperature-based detectability issues: *I. elegans* effect of daily temperatures on daily density estimates, Est = -0.005±0.063, t= -0.08, P= 0.94; *L. sponsa* Est=0.18±0.11, t=1.611,P=0.12; *C. hastulatum* Est=-0.34±0.21, t=-1.67, P=0.15; *E. cyathigerum* Est=0.08± 0.05, t=1.54, P=0.13; *C. puella* Est= -0.27±0.17, t= -1.6, P=0.1;, *P. nymphula* Est=0.08±0.049, t=1.75, P=0.09.

Species interactions and climate

Ischnura elegans density was best explained by a model including only mean annual temperature (Table S2), although the correlation was not significant (effect of bio1=0.55±0.35, t=1.58, *P*=0.12). For *L. sponsa*, the best model included the interaction between mean annual temperature and *I. elegans* presence/absence (Table S2). This interaction effect was a significant predictor of *L. sponsa* densities in the model (effect of bio1 x *I. elegans* presence=-0.21±0.084, t=-2.55, p=0.016; Fig. 2a). In the absence of *I. elegans, L. sponsa* densities were positively correlated with mean annual temperature.

However, where *I. elegans* was present, *L. sponsa* density no longer correlated with climate. Furthermore, where both of these species co-occurred, densities of *I. elegans* were negatively associated with *L. sponsa* densities (estimate =-0.683±0.28, t =-2.43, *P*=0.03; Fig. 2b). *I. elegans* presence or absence did not influence body sizes of any of the other species.

Ischnura elegans presence did not show clear-cut patterns of influence on any other species' densities: For *P. nymphula*, *I. elegans* presence and temperature each improve the model fit in comparison to an intercept-only model explaining *P.* nymphula densities (Table S2), but these effects are non-significant, and likely reflect that fact that the *P. nymphula* range, while largely congruent with the range of *I. elegans*, extends to cooler, higher elevation sites within our study region (Cham et al. 2014). For *E. cyathigerum*, a model which included both mean annual temperature and *I. elegans* presence/absence (but not the interaction) best explained local densities (Table S2). *Enallagma cyathigerum* densities were positively associated with *I. elegans* presence, (effect of *I. elegans* presence = 0.89±0.38, t=2.32, *P*=0.02) and the model also contained a slightly negative but highly non-significant, residual effect of mean annual temperature (*P*=0.93). Although *I. elegans* presence is weakly correlated with mean annual temperature across our sites, these models did not suffer from collinearity of these effects. No climate variable other than mean annual temperature (bio1) affected the site-specific densities of any species.

Effects of *I. elegans* presence on *L. sponsa* morphology and thermal preferences

Complementarily to our density data, the presence of *I. elegans* at a site was correlated with larger body sizes in *L. sponsa*, in a model that included a covariate for climate and a random effect for site and date (effect of mean annual temperature on *L. sponsa* body size=1.6±1.27, df=23.59, t=-2.68, P=0.21; effect of *I. elegans* presence on *L. sponsa* body size=-66.85±22.53, t=-2.97, p=0.007; Fig. 2c). Similarly, thermal preferences were influenced by competition in ways that are complementary to our density and morphology results. The effect of species x treatment (alone or in competition) on thermal site selection in the laboratory was: Est=1.97±1.14, df=104.19, t=1.72, P=0.04 using a 1-tailed hypothesis test to predict that the presence of *I. elegans* would shift *L. sponsa* to cooler preferred temperatures; Fig. 3). As predicted, where *I. elegans* was introduced to trials, *L. sponsa* shifts to cooler position in comparison to when *L. sponsa* is allowed to thermoregulate alone.

Phylogenetic community structure

Consistent with a decline in *L. sponsa* densities at warmer sites where *I. elegans* is present, warmer sites within our study region exhibited significantly higher levels of phylogenetic underdispersion than cooler sites within this region (effect of mean annual temperature on phylogenetic underdispersion=13.29 ±2.52 , t=5.27 , P <0.01, Fig 4a). In a separate but complementary model, phylogenetic underdispersion was also significantly predicted by the presence of *I. elegans* at a site (9.98±1.39,t=7.19,p<0.001, Fig. 4b).

Niche similarity and phylogenetic signal

Variable importance and AUC values for each species' best fit Maxent niche model are presented in table S4. In all cases, the full model (containing all uncorrelated predictor variables) was the best fit, with the lowest AICc. Although individual niche models for each species vary in the relative importance of different climatic variables (Table S4, Fig. 5a), pairwise niche overlap (measured using D; Warren et al. 2008) illustrated that most species occupy similar niche space. *I. elegans, E. cyathigerum, L. sponsa* and *P. nymuphula* showed pairwise overlap values between 0.81 and 0.92 (Fig 5b). Only *C. hastulatum* and to a lesser extent *C. puella* accounted for the majority of niche differences, with *C. hastulatum* demonstrating pairwise overlap values between 0.18–0.25 for all other species (Fig. 5b), while *C. puella* demonstrated values between 0.18-0.65 with all species (Fig. 5b). These patterns of niche similarity showed no phylogenetic signal across the 6 species (f=0.33, p=0.66). To identify if lack of signal was caused by the relatively large niche differences between the closely related habitat specialist species *C. hastulatum* and *C. puella*, the analysis was repeated with *C. hastulatum* and *C. puella* removed. Again no significant phylogenetic signal was observed (f=0.3, p= 0.6).

Discussion

We show that relatively novel encounters between a range expanding species (*I. elegans*) and a relatively distantly-related species within the native damselfly guild (*L. sponsa*) can generate patterns of phylogenetic underdispersion within high-latitude communities. Phylogenetic underdispersion occurs because *L. sponsa* is displaced from thermally-favourable habitats by *I. elegans*, resulting in lower population densities. Because the other members of the native damselfly guild are much more closely related to *I. elegans* than is *L. sponsa*, invasion by *I. elegans* reduces the overall breadth of phylogenetic representation within these damselfly guilds. This result supports recent conceptual advances suggesting that patterns of competitive exclusion may be common between distantly related species, if traits related to competitive abilities are more strongly phylogenetically conserved than niche traits (Mayfield & Levine 2010). Species' competitive abilities are important predictors of successful range shifts and establishment in novel communities under climate change (Alexander, Diez & Levine 2015), and novel communities produced by environmental change may be subject to high levels of competition (Lancaster *et al.* 2017). Our results suggest that clades with conserved competitive abilities, such as *Coenagrionid* damselflies, may typically dominate novel communities under changing climates, resulting in the loss of phylogenetic diversity, particularly at high latitudes where species richness is low, so the loss of even a single species can significantly impact phylogenetic diversity. Furthermore, our results demonstrate that the processes driving under- and over-dispersion within communities are more complex than classically expected, raising questions about the utility of phylogenetic signal as a proxy for describing community assembly processes.

Evidence for partial competitive displacement

We show evidence for incipient competitive displacement of *L. sponsa* by the range-expanding *I. elegans*, where *L. sponsa* is the least related species to *I. elegans* within the regional species pool (Figs. 1, 2a&b, 3). Evidence in support of this includes: (i) *L. sponsa* and *I. elegans* inhabit strongly convergent climatic niche space (Fig. 5a&b). (ii) *L. sponsa* population densities exhibit a negative relationship with *I. elegans* density (Fig 2C). (iii) In the absence of *I. elegans* at a site, *L. sponsa* density is positively correlated with mean annual temperature, but the presence of *I. elegans* disrupts this relationship (Fig. 2b), suggesting that *I. elegans* displaces *L. sponsa* from preferred (warmer) sites. (iv) *L. sponsa* has undergone a morphological shift (to larger body sizes) where *I. elegans* is present (Fig. 2b). (v) *L. sponsa* shifts its thermal preference to cooler temperatures when in competition with *I. elegans* (Fig. 3).

Patterns of partial competitive displacement between the two least-related species within a guild is consistent with the expectations of the competitive trait conservation hypothesis (Chesson 2000; Mayfield & Levine 2010). Given that *L. sponsa* population densities positively correlate to mean annual temperature, but only in the absence of *I. elegans*, it is unlikely that environmental filtering is the primary causal factor explaining the negative relationship between *L. sponsa* density and *I. elegans* density. Moreover, thermal preference trials demonstrate competitive displacement of *L. sponsa* from their preferred thermal regimes in response to the presence of *I. elegans*. This result suggests that behavioural traits, such as aggressive behaviour, might act as the mechanism of competition. At present we lack sufficient evidence to conclude this is the competitive mechanism, although competition for basking sites via aggressive behaviour has been observed in larger territorial odonata species (Lefevre & Muehter 2004; Worthen & Patrick 2004; Byers & Eason 2009). Moreover, it is unlikely that there is only one mechanism by which *I. elegans* and *L. sponsa* compete, as the adult stage represents a relatively short (but critical) period of interaction between these two species. A major component of co-occurrence between these species is during aquatic larval development (see below).

The consequence of competition for *L. sponsa* is further reflected in changes in *L. sponsa* body size where *I. elegans* is present (Fig. 2c). Competition has widely been demonstrated to result in increased size in invertebrates (Plaistow & Siva-Jothy 1996; Vande Velde & Van Dyck 2013), though the drivers of this morphological shift in this case are unknown. A plastic or evolved response is equally plausible in explaining this result. Slower growth rates through reduced food availability have been shown to delay damselfly emergence, but emergence occurred at a larger size (Pickup, J. and Thompson 1990). Alternatively, competitive interactions have been shown to select for larger body size, which may evolve because they improve competitive ability or facilitate niche divergence from the invader (Plaistow & Siva-Jothy 1996; Vande Velde & Van Dyck 2013). These alternative hypotheses are currently indistinguishable, because the behavioural or resource-use basis for competition between *I. elegans* and *L. sponsa* is unknown. The interactions may revolve around indirect competition for food resources during larval development or reduced adult fitness through direct, competitive interactions (McPeek, Grace & Richardson 2001). The fact that competition appears to be most intense at warmer sites (Fig. 2a) suggests that the *I. elegans* are less competitively dominant at colder sites, or that both species compete most intensively over preferred thermal niches or thermally-mediated resources.

Lancaster *et al.*(2017) have previously demonstrated that *I. elegans* exhibits increased aggression under experimental warming treatments, suggesting that further warming at high latitudes could compound the effects of invasions to destabilise high latitude communities (Lancaster *et al.* 2017). Furthermore, Lancaster *et al.* (2017) demonstrated that *I. elegans* is competitively well-matched with *E. cyathigerum*, in terms of larval competitive behaviours, at current water temperatures (these species exhibit highly congruous numbers of aggressive behaviours in laboratory trials to assess interspecific larval competition under different temperature regimes). That *I. elegans* and *E. cyathigerum* are 1) well-matched competitively, 2) closely related phylogenetically, and 3) highly likely to co-occur at sites across NE Scotland (see results section), further supports our conclusions that the Competition-Relatedness hypothesis is a good explanation for drivers of community assembly in high latitude damselfly communities. Under this mechanism, *I. elegans* and *E. cyathigerum* co-occur readily, following the expansion of *I. elegans* into the area, due to their phylogenetically conserved competitive behaviours—in other words, neither can exclude the other. However, as temperatures continue to warm at high latitudes, this balance may shift (Lancaster *et al.* 2017).

Temporal dynamics and future directions in our field research

A time lag between the colonisation of an antagonistic species in a population and the point at which species displacement become pronounced can radically influence interpretation of how species interact during range shifts. Understanding this temporal lag therefore represents an important avenue for future research. Anecdotally, our data may also suggests that the effect of *I. elegans* presence on *L. sponsa* densities has a temporal component (Fig. 2b). Points circled in green represent sites at the very leading edge of *I. elegans'* range, and the point circled in blue represents a newly-created pond (within the last 5 years). At these sites, although *I. elegans* is present, patterns of *L. sponsa* densities are similar to those observed at sites in the absence of I. elegans. This suggests a temporal lag between I. elegans' initial colonisation to a site, and the subsequent decline of *L. sponsa*.

However, given that only 5 ponds in our dataset exhibit this potential lagged effect, the evidence for this is at present is only suggestive. The importance of time lags in competitive displacement, while widely suggested by other researchers (Jackson & Sax 2010), bears further investigation in our study system before firm conclusions can be drawn.

Niche Overlap and Environmental Filtering

Niche overlap among all 6 species exhibited no phylogenetic patterns. Instead, most species exhibited strongly overlapping climatic niche space, with the exception of *C. hastulatum* and *C. puella* (Fig. 5a & 5b). This is unsurprising given that these species represent a guild, using similar resources at similar sites across Scotland. Strong overlap in niche space among each of the interacting species means that environmental filtering based on niche requirements is unlikely to be observed (see also Siepielski *et al.* 2010). The maintenance of a similar niche across a broad phylogenetic scale within damselflies is consistent with earlier studies showing that speciation in damselflies is rarely linked to niche divergence (McPeek *et al.* 2000; Wellenreuther & Sánchez-Guillén 2015). Our results extend these previous findings by demonstrating that, like speciation, competitive displacements in damselflies is also unrelated to levels of niche divergence. The general lack of niche divergence among damselfly species makes this a particularly good system to demonstrate Mayfield and Levine's (2010) hypothesis for how the phylogenetic conservation of traits such as competitive behaviours can produce phylogenetic clustering within communities in the absence of niche trait variation (see also Saito *et al.* 2016) .

Phylogenetic patterns

Our observed shift in phylogenetic structure within communities as a result of competition (Fig 3A and 3B) has two major implications. Firstly, from a methodological/theoretical perspective, it raises the issue of whether the use of phylogenetic structure can be used as a method for ascertaining community assembly processes (Webb 2000; Lessard *et al.* 2009; Lebrija-Trejos *et al.* 2010). Secondly, reduced phylogenetic diversity as a result of climate change-driven range shifts poses a conservation issue. Declines in phylogenetic diversity may be common in regions affected by increased competition from invasive species (Lessard *et al.* 2009), and these diversity losses may be exacerbated under further climatic warming (Willis *et al.* 2008; Zhang *et al.* 2015). Because conservation of phylogenetic diversity is critical for maintaining high levels of biodiversity into the future (Barker 2002), range shifts within regional species pools characterized by conserved competitive abilities may pose a particularly urgent concern, particularly for high latitude ecosystems, which are strongly affected by this colonisation process. Little is known about the factors underpinning range shifts in animals (Angert *et al.* 2011; Comte & Grenouillet 2013) , so we do not know the extent to which species prone to range shifting generally tend to express conserved (i.e., inherited) competitive abilities.

Implications

We find that a climate change-mediated expansion of a warm-adapted, generalist species, *I. elegans*, to a relatively species-poor, high latitude community results in partial competitive displacement of the weakest competitor, *L. sponsa*, resulting in loss of phylogenetic diversity at higher latitudes. Typically, high latitude and high elevation communities exhibit low species diversity, with overrepresentation by endemic or relict species which are locally adapted and exhibit small geographic ranges. Climate change is facilitating the colonization of warm-adapted, widespread generalist species into these communities for the first time, and it is critical to understand how these colonization events alter high latitude community structure and diversity, despite the fact that low levels of native species diversity in these environments can reduce the power of community-phylogenetic analyses.

Our results highlight the importance of evaluating the relative degrees of both niche conservatism and competitive trait conservatism in regional species pools before inferring ecological processes from phylogenetic patterns. Furthermore, our study raises the possibility that competitive trait conservatism may generally be more an important factor in driving community assembly during periods of ecological instability, such as during range expansions, than for stable species pools that have adapted *in situ* to their potential competitors, although this hypothesis remains to be formally tested. Thus competitive displacements or wholesale exclusion by invading or range shifting species may commonly reduce phylogenetic diversity of the invaded community by this mechanism, particularly where ecological niches are similar among native and range-shifting species.

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Data

All data used in this study have been deposited in Dryad data repository DOI: 10.5061/dryad.kp89j

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Figure legends:

Figure 1. Phylogeny of Scottish damselfly species constructed using phylogenies from Dumont, Vierstraete & Vanfleteren (2010) and Guan et al. (2013), with branch lengths set to 1.

Figure 2. Effects of *Ischnua elegans* on *Lestes sponsa* within communities.

2a. *Lestes sponsa* density is positively correlated with mean annual temperature at sites where *I. elegans* is absent, but not where *I. elegans* is present (effect of bio1 x *I. elegans* presence =-0.21±0.084, t =-2.55, p=0.016). . Green circles represent sites at the current expansion front for *I. elegans*, and blue circles represent ponds less than 5 years old. Thus, at all circled sites, the species have only recently co-occurred, and the competitive displacement effect observed at other sites may not have yet developed.

2b. *L. sponsa* density is negatively correlated to densities of the invading competitor *I. elegans*. The effect line represents the linear regression effect:-0.683±0.28, r^2 =0.24 $F_{1,19}$=5.89, t =-2.43, P=0.03.

2c. *Lestes sponsa* body size at sites where *Ischnura elegans* is present and absent, where body size has been derived from principal components analysis of multiple morphometric measurements (*I. elegans* presence on *L. sponsa* body size=-264.52±7.174, t =-3.4238, p <0.001).

Figure 3. Thermal preferences of *Ischnura elegans* and *Lestes sponsa* in the presence and absence of each other. Error bars depict standard errors.

Figure 4. Predictors of phylogenetic structure within Scottish damselfly communities. 4a. Communities are more phylogenetically underdispersed at warmer sites (assessed via mean annual temperature at the site), where letters indicate significant differences. 4b. Effect of *I. elegans* presence vs. absence on patterns of within-community phylogenetic dispersion.

Figure 5. Niche modelling of all damselfly species found in the study region.

5a. Habitat suitability of each damselfly species using MaxEnt niche modelling.

5b. Pairwise niche overlap scores given as Schoeners D (Warren *et al.* 2008).

Figure 1

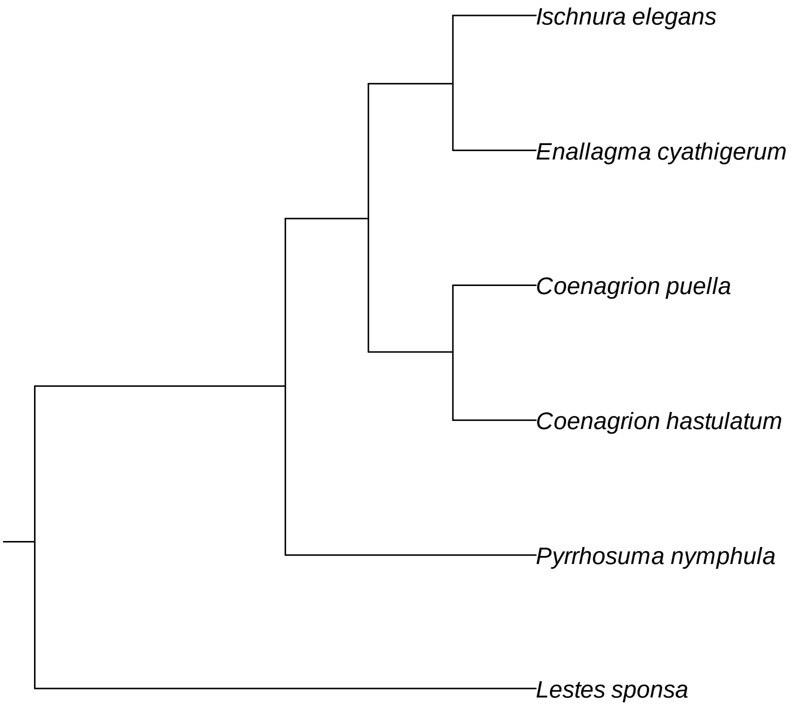

Ischnura elegans
Enallagma cyathigerum
Coenagrion puella
Coenagrion hastulatum
Pyrrhosuma nymphula
Lestes sponsa

Figure 2

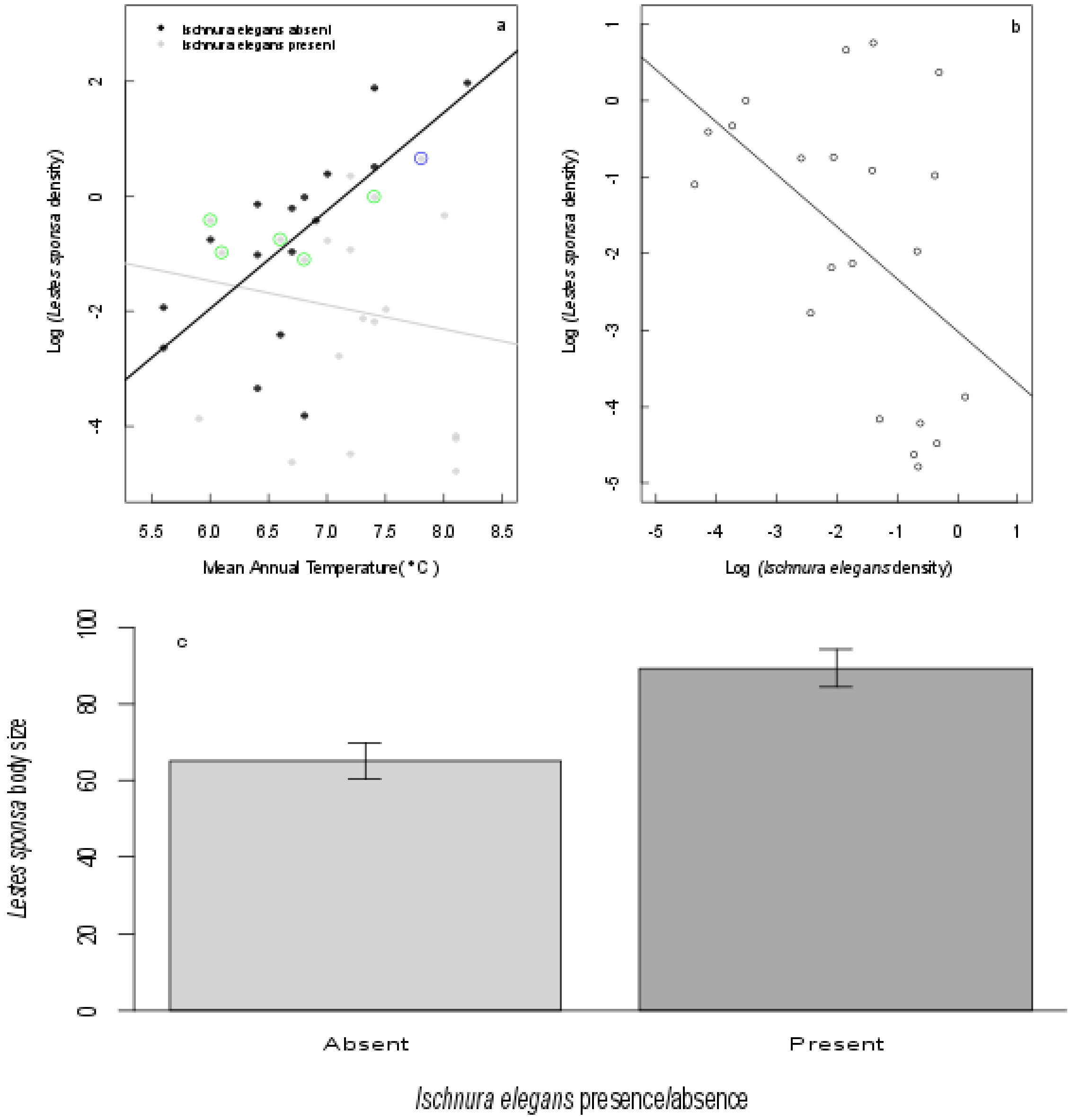

Ischnura elegans absent
Ischnura elegans present
a
Log (*Lestes sponsa* density)
2
0
-2
-4
5.5
6.0
6.5
7.0
7.5
8.0
8.5
Mean Annual Temperature (°C)
b
Log (*Lestes sponsa* density)
1
0
-1
-2
-3
-4
-5
-5
-4
-3
-2
-1
0
1
Log (*Ischnura elegans* density)
c
Lestes sponsa body size
100
80
60
40
20
0
Absent
Present
Ischnura elegans presence/absence

Figure 3

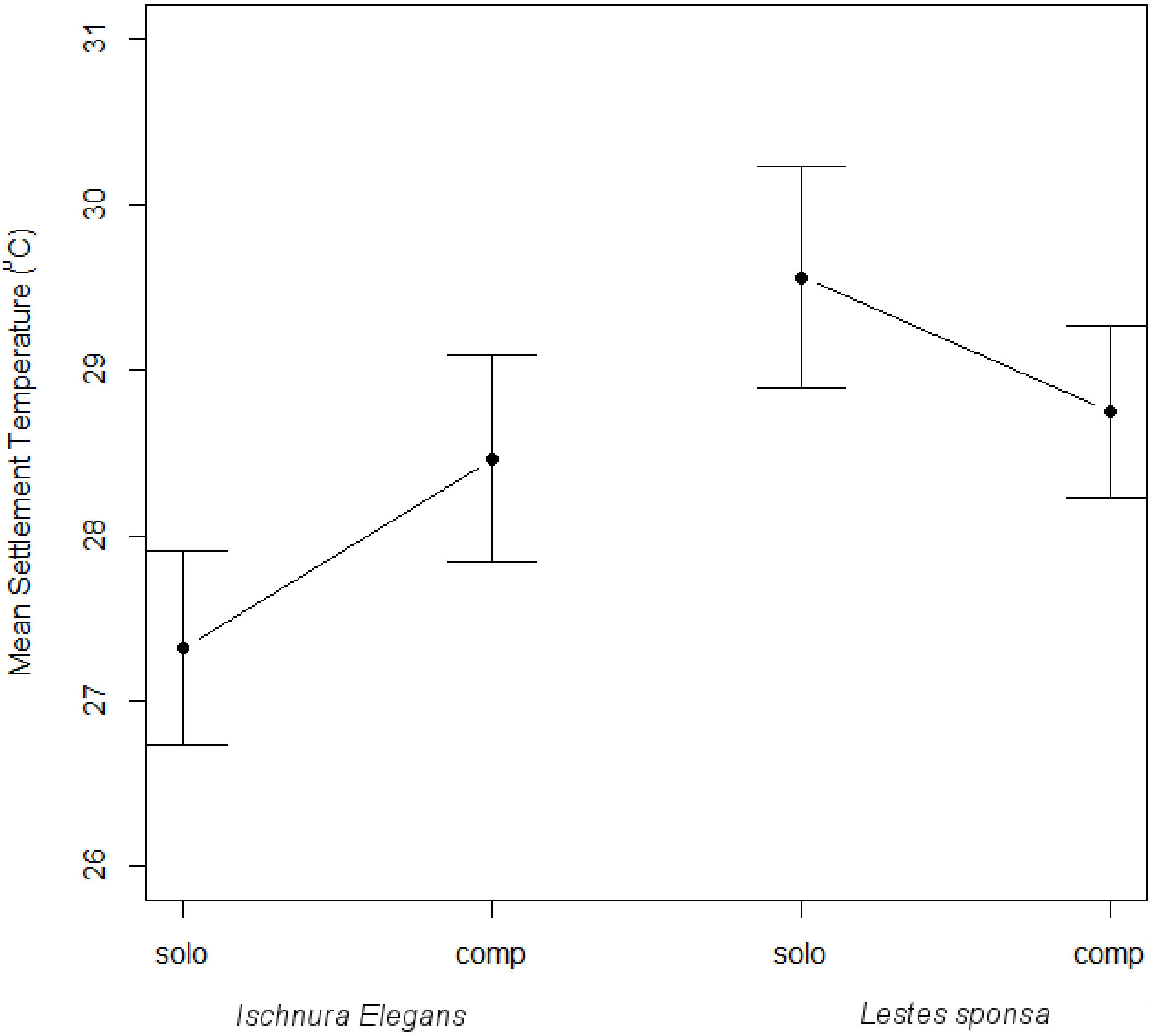

Mean Settlement Temperature (°C)
26
27
28
29
30
31
solo
comp
solo
comp
Ischnura Elegans
Lestes sponsa

Figure 4

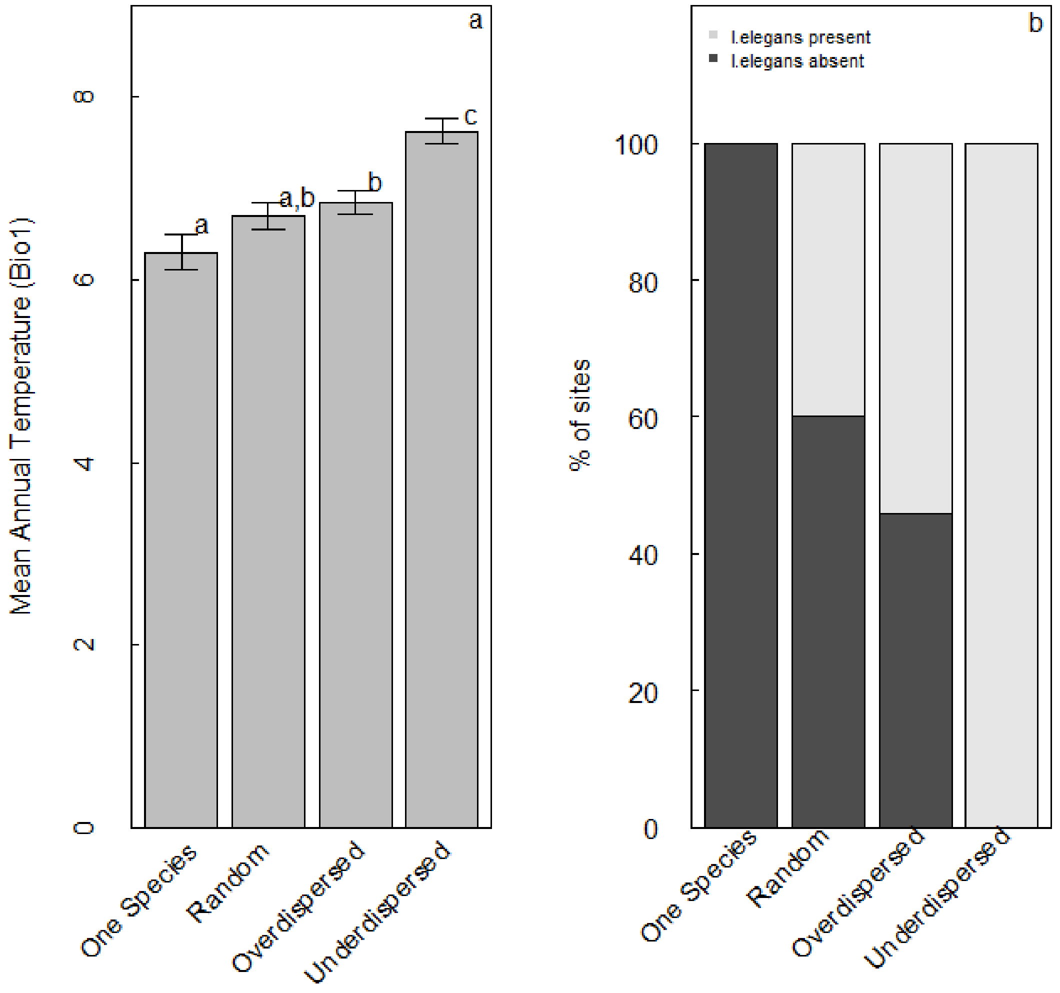
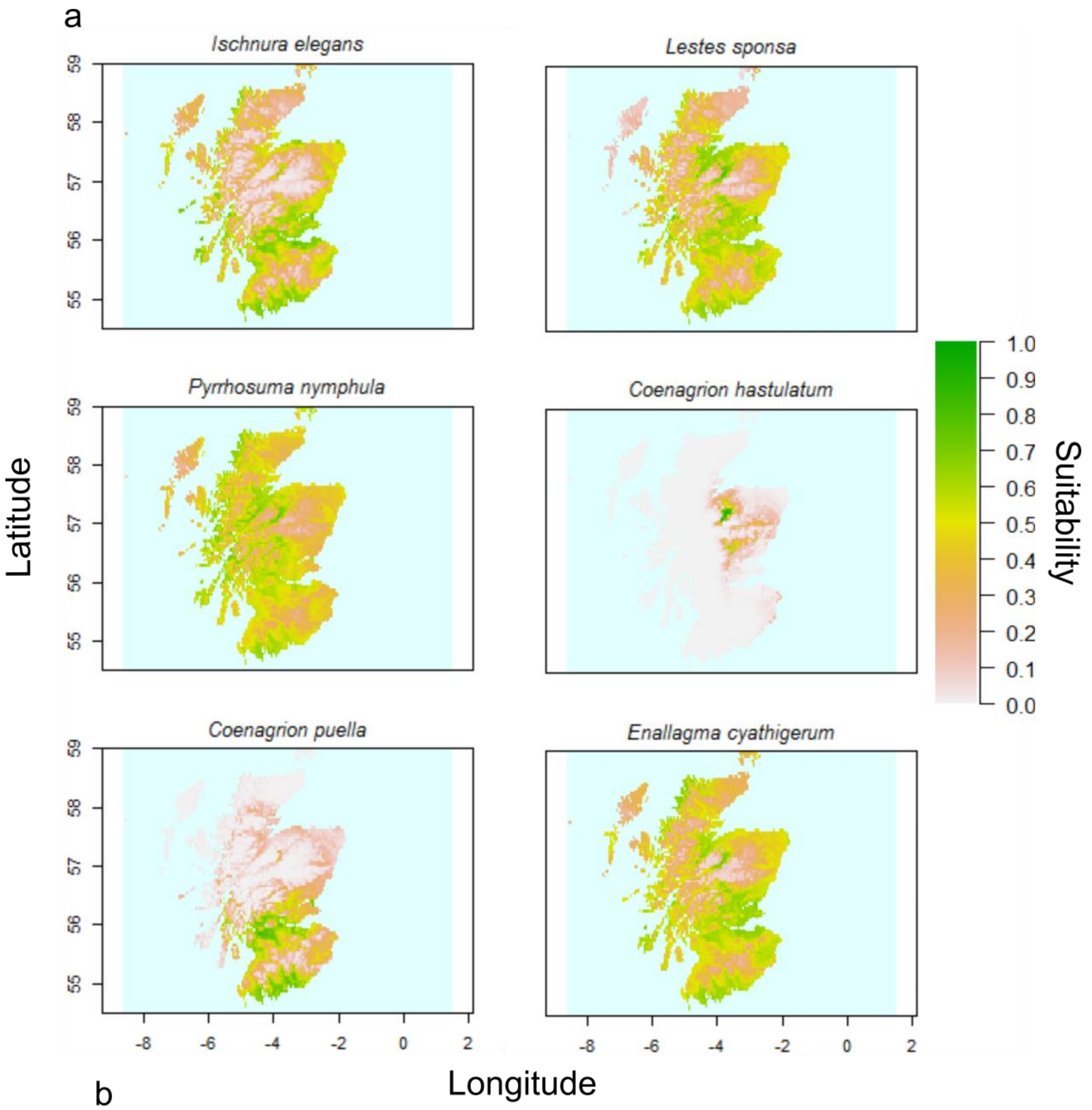

a
Mean Annual Temperature (Bio1)
0
2
4
6
8
a
a,b
b
c
One Species
Random
Overdispersed
Underdispersed
b
■ I.elegans present
■ I.elegans absent
% of sites
0
20
40
60
80
100
One Species
Random
Overdispersed
Underdispersed

Figure 5



b

	Ischnura elegans	*Lestes sponsa*	*Pyrrhosoma nymphula*	*Coenagrion hastulatum*	*Coenagrion puella*	*Enallagma cyathigerum*
Ischnura elegans	NA	0.87	0.82	0.22	0.65	0.87
Lestes sponsa		NA	0.87	0.26	0.61	0.91
Pyrrhosoma nymphula			NA	0.23	0.52	0.92
Coenagrion hastulatum				NA	0.18	0.23
Coenagrion puella					NA	0.57
Enallagma cyathigerum						NA

Supplementary material for:

Range shifting species reduce phylogenetic diversity in high latitude communities via competition

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Table S1. Variation in georeferenced climate variables across the study sites in northeast Scotland. Climatic values for each site were bioclimatic variables obtained from (Hijmans et al., 2005).

Climatic variables		*Maximum value*	*Minimum Value*
Bio1	Mean annual temperature	4.8°C	8.2°C
Bio2	Mean diurnal Range	7°C	7.3°C
Bio3	Iscothermality	3	3.9
Bio4	Temperature seasonality	400.9	548.4
Bio8	Mean temperature of wettest Quarter	0.2°C	11.6°C
Bio9	Mean temperature of driest quarter	3.6°C	10.3°C
Bio10	Mean Temperature of Warmest	10.9°C	14.6°C

	Quarter		
Bio15	Precipitation Seasonality	14	26
Bio18	Precipitation of Warmest Quarter	174mm	270mm

Table S2. AICc scores for the different models predicting site-specific density of each species. A ΛAICc of greater than 2 was assumed to be significantly different.

Model	AICc			
	Lestes sponsa	*Ischnura elegans*	*Pyrrhosuma nymphula*	*Enellagma cyathigerum*
~1	153.2	178.9	188.6	266.9
~I.elegan presence/absence (I.E)	152.1	-	183.9	362.5
~Bio1	150.7	167.2	182.6	256.4
~I.E+Bio1	147.5	-	182.3	253.0
~I.E*Bio1	142.9	-	183.6	255.0

Table S3

Sites and dates of damselfly capture for thermal preference trials

Site	Latitude	Longitude	Dates visited		
31	56 38.880	-2 46.185	18/07/2016		
34	57 4.133	-2 30.245	18/07/2016		
51	57 11.174	-3 50.224	07/07/2016	21/07/2016	
84	56 44.537	-2 57.551	05/07/2016	13/07/2016	18/07/2016
87	56 32.503	-2 37.293	13/07/2016	18/07/2016	
90	57 31.311	-3 12.473	07/07/2016	21/07/2016	
91	57 40.562	-3 7.647	07/07/2016	21/07/2016	

Table S4. Permutation importance of climatic predictor variables included within best-fit niche models for each species. AUC from ROC analysis scores are given to assess the fit of each model to the data. More widespread species tend to have lower AUC values for a given model quality; AUC > 0.5 indicates a better-than-random fit to the data. The variable with the highest permutation importance for each species is depicted in bold.

Climatic variables		Permutation importance					
		I.elegans	*L.sponsa*	*C.puella*	*C.hastulatum*	*P.nymphula*	*E.cyathigerum*
Bio1	Mean annual temperature	**54**	11.9	**30.8**	1.5	14.6	12.3
Bio2	Mean diurnal Range	11	12.1	30	36.2	16.9	9.4
Bio3	Iscothermality	2.7	7.7	0.9	3	9.8	1
Bio4	Temperature seasonality	1.5	6.2	13	2.9	1.9	6.9
Bio8	Mean temperature of wettest Quarter	0.3	2.2	2.4	0.8	0.4	5.5
Bio9	Mean temperature of driest quarter	0.5	0.7	0.4	0.2	0.4	0.6
Bio10	Mean Temperature of Warmest Quarter	15.5	**40.4**	8.7	0.1	10.4	**32.8**
Bio15	Precipitation Seasonality	9.1	6.7	10.2	1.1	**28.4**	15
Bio18	Precipitation of Warmest Quarter	5.4	12.1	3.7	**54.2**	17.2	16.6
AUC		0.739±0.009	0.703±0.009	0.873±0.01	0.977±0.012	0.646±0.02	0.666±0.01

Figure S1:

Depiction of the thermal gradient of used for thermal preference trials, where temperature decreased gradually from ~60°C to ~10°C over 1 metre.

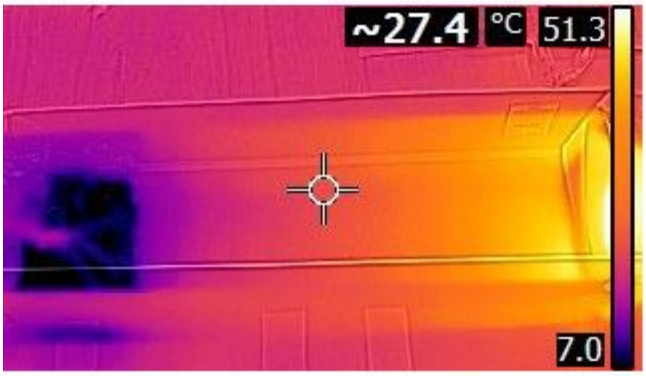
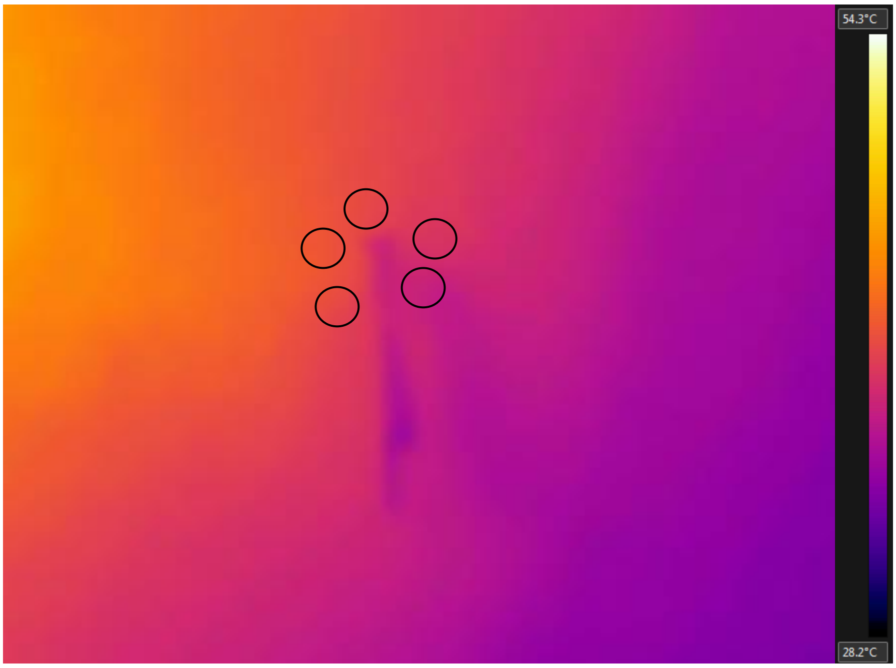


Figure S2:

Example of a thermal image of where a damselfly settled within the thermal gradient. Circles represent locations around the damselfly where environmental temperature was recorded.


54.3°C
28.2°C

972