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

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34 Abstract

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

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

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

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

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

55 Introduction

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

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

80 *Underlying processes affecting community phylogenetic diversity:*

81 Two processes, environmental filtering and competition, are often invoked to explain
82 the makeup of communities (Kraft *et al.* 2007). Environmental filtering represents the process
83 by which the environment acts as a “sieve”, so that species with shared niche requirement or
84 environmental performances are expected to cluster together in space as they colonise shared
85 habitats (Cavender-Bares *et al.* 2004; McGill *et al.* 2006; Kraft *et al.* 2007). Over an
86 environmental gradient, species with similar niche requirements will persist in shared locales
87 to form communities (Wiescher, Pearce-Duvet & Feener 2012; Laliberté, Turner & B.L.
88 2014). Inversely, competition may result in the exclusion of ecologically similar species from
89 occupying the same geographic space, via limiting niche similarities between species (Cahill
90 *et al.*, 2008, Darwin 1859). Species with similar functional or niche traits are typically
91 expected to compete most strongly for resources, resulting in reduced densities or local
92 exclusion of all but the best performing (i.e., most competitive) species from each functional
93 group (Macarthur & Levins 1967). Under competitive exclusion, and in contrast to
94 environmental filtering, coexistence within a community is therefore often expected to arise
95 from interspecific variation in functional and niche traits (Macarthur & Levins 1967; Chesson
96 2000). In high-diversity regions, competition may determine coexistence within communities,
97 but if the number of potential competitors is limited, or if spatial environmental variation is

98 extreme, environmental filtering is often the dominant process. In most cases, these processes
99 act in tandem (Chesson 2000; Kraft *et al.* 2007).

100 These processes of filtering and competition are also influenced by the evolutionary
101 history of species that can potentially coexist. Because multiple traits contribute to an
102 individual or species' ecological niche (Kraft *et al.*, 2015), niches are often less evolutionarily
103 labile than individual traits (Wiens *et al.* 2010). Thus traits which determine a species'
104 environmental niche tend to be conserved among closely related species (Wiens & Graham
105 2005; Wiens *et al.* 2010). Such phylogenetic niche conservation implies that community
106 assembly processes (such as colonisation of and persistence in a patch) based on niche
107 similarity or differences may generate phylogenetic structure within communities (Webb *et*
108 *al.* 2002). If ecological niches are highly evolutionarily conserved among closely related taxa
109 within the regional species pool, and competition is an important factor limiting coexistence
110 within communities, phylogenetic overdispersion is expected to arise within communities
111 (Webb *et al.*, 2002). Phylogenetic overdispersion occurs in this case because closely related
112 species, with shared community-based niches, are more likely to competitively exclude each
113 other from limited resources and habitats (Burns & Strauss 2011; Violle *et al.* 2011; Peay,
114 Belisle & Fukami 2012). Alternatively, if niche traits are evolutionarily conserved but
115 environmental filtering is more important for ecological processes such as colonisation and
116 persistence, then phylogenetic underdispersion may define local community structure (Webb
117 *et al.*, 2002). This is because, in the absence of strong competition, shared niches among
118 closely related taxa will cause them to cluster in resource and habit space (Cavender-Bares *et*
119 *al.* 2004). Under these general predictions, many studies have attempted to classify the
120 relative roles of competition versus environmental filtering as drivers of community
121 assembly, based on estimates of phylogenetic structure alone (Webb 2000; Lebrija-Trejos *et*

122 *al.* 2010). However, several key limitations of this approach make inferring the roles of
123 competition and environmental filtering from phylogenetic structure problematic.

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

139 *Range expansions and phylogenetic diversity of high latitude communities:*

140 Widespread range shifts under climate change create the ideal natural laboratory to
141 understand community assembly dynamics, because changes in the regional species pool are
142 observable over short spatial scales reflecting the colonisation process, where expanding,
143 range edge communities reflect most recent opportunities for coexistence. In Great Britain,
144 several members of the regional damselfly biota have been expanding northward or to greater
145 altitudes under climate change (Hickling *et al.* 2005). We examined patterns of species

146 coexistence in local damselfly guilds in Northeast Scotland with relationship to
147 environmental variables and opportunity for competition between established residents and
148 incoming, range expanding species.

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

163 Materials and Methods

164 Study system

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

170 2015). Higher temperatures are also correlated with increased damselfly population densities
171 in high-latitude habitats (Lancaster *et al.* 2015). Levels of interspecific aggression and direct
172 competition are also positively correlated with environmental temperature in damselfly
173 communities from high latitudes (Lancaster, Morrison & Fitt 2017).

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

186 Within our study area of Northeast Scotland (see below), there are six species of co-
187 occurring damselflies, four of which are long-time residents of the region: *Lestes sponsa*
188 (Hansemann, 1823), *Enallagma cyathigerum* (Charpebtier, 1840), *Pyrrhosoma nymphula*
189 (Sulzer, 1776). These are common and widespread species across most of Great Britain as
190 well as much of Europe and Asia (Askew 1988). The northern relict species within Scotland
191 *Coenagrion hastulatum* (Charpentier, 1825) is also a long-time resident of the region. Two
192 additional species are currently range expanding into or within the region: *Coenagrion puella*
193 (Linnaeus, 1758) and *Ischnura elegans* (Vander Linden, 1820). *Ischnura elegans* has recently
194 undergone a northwards range shift in Northeast Scotland, with a 143km northwards range

195 shift between 1985 and 1995, and is currently undergoing an altitudinal range shift to upland
196 sites (Hickling *et al.*, 2005; Cham *et al.*, 2014), while *C. puella* has only recently started
197 colonising Scotland and is found only sporadically through our study area (Hickling *et al.*,
198 2005; Cham *et al.*, 2014). All of these species are members of the family Coenagrionidae
199 (superfamily Coenagrionoidea) except for *L. sponsa*, which belongs to the somewhat
200 distantly related Lestidae (superfamily Lestoidea). Based on 97 occupied sites visited during
201 the summer breeding season across Northeast Scotland (see ‘Field surveys’, below), we
202 identified 56 unique combinations of co-occurrence among these 6 species, with no site
203 occupied by all 6 species.

204 Field surveys

205 Data on damselfly communities throughout Northeast Scotland was obtained by
206 surveying 97 occupied pond sites between 4th of May through 23rd of July 2014. This period
207 covers the peak flight times for all species studied, with *I. elegans*, *P. nymphula*, *C.*
208 *hastulatum*, *C. puella* and *E. cyathigerum* reaching peak adult density in mid-June, while *L.*
209 *sponsa* adult densities peak in mid-July (Cham *et al.*, 2014), and *L. sponsa* emergence is
210 highly synchronized in this period (Powney *et al.* 2014). Furthermore, *L. sponsa* peak
211 emergence occurs earlier in the northern extent of its range than in the south (Sniegula, Golab
212 & Johansson 2016), leading to high interspecific convergence among of flight times among
213 all 6 coexisting species in our study area. Sites ranged from 56.37° to 57.68° Latitude, and -
214 4.13° to -2.11° longitude, and elevation between 3m to 442m, thus covering a large spatial
215 extent and encompassing a range of climatic variation (table S1). Sites were selected to be as
216 similar to each other as possible across the region, and to exhibit mutual suitability for all
217 colonizing and native species. For this reason we limited our surveys to permanent water
218 bodies with open, shallow bottoms and consistent varieties of emergent vegetation.
219 Temporary, flowing, or heavily-shaded water bodies, each of which only support a subset of

220 Scottish species, were avoided in our site selection procedure. We visited sites between
221 8:00am and 6:00pm, when the weather was warm with little or no rain, so that sites were
222 visited when the weather was favourable and all species of damselfly present would be
223 active. We recorded air temperatures during each of our site visits in order to quality control
224 the density data (see below). Sites were surveyed by walking transects around the perimeter
225 of water bodies and capturing damselflies in timed catching bouts. Species present were
226 recorded and a proxy for the density of each species was calculated as the number of
227 individuals of each species caught per minute of capture time; sites were visited multiple
228 times and the per species mean density was averaged over the study period. A species was
229 assumed to not be present at significant density at a site if no individuals were observed
230 within 15 minutes of catching effort during the species' adult flight season, and return trips to
231 most ponds confirmed presumed absences. Co-occurrence at each site does not necessarily
232 imply stable coexistence, as damselflies often exhibit metapopulation dynamics characterized
233 by frequent local extinction and recolonization events (Mcpeck, Brown & Apr 2000;
234 Gibbons, Reed & Chew 2002). Our study design does not encompass long-term dynamics,
235 and thus captures predictors of co-occurrence rather than stable coexistence. However, our
236 study design enables us to capture the dynamics of competitive interactions that are likely to
237 correlate with longer-term patterns of persistence or competitive displacement across the
238 region.

239 Morphology

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

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

255 Statistical analyses of climate and species interactions

256 To identify patterns of competitive displacement from climatically favourable sites
257 arising between range-shifting (i.e., *I. elegans*) and resident species, we compared linear
258 models to explain the log(density) of each of the resident species, averaged over the season at
259 each site. Because mean annual temperature has been shown to be the best abiotic predictor
260 of damselfly field densities (Lancaster *et al.* 2015), we included in these models an effect of
261 climate (georeferenced values of uncorrelated, biologically relevant climate variables from
262 table S1: Hijmans *et al.* 2005), an effect of *I. elegans* presence, and all interactions between *I.*
263 *elegans* presence and temperature. The full model was compared against all reduced models
264 using linear models in the base stats package in R v.3.0.2 (R core development team, 2008).
265 The best model was selected using the corrected Akaike Information Criterion (AICc;
266 Mazerolle 2015) (Table S2). *C. puella* and *C. hastulatum* were not found at sufficient
267 numbers of sites to include in these analyses. Given the high reliance of damselflies on
268 climate (see ‘study system’, above), a significant interaction suggests that the presence of *I.*
269 *elegans* modifies the ability of resident species to persist in preferred sites, and indicates that

270 competition may be an important driver of co-occurrence patterns in recently colonised
271 communities. In the absence of evidence for competition, environmental filtering processes
272 were investigated by examining patterns of niche overlap and coexistence between species
273 (see niche overlap, below). To determine whether site-specific densities were spatially
274 autocorrelated within each species, we ran a Mantel test of species densities in the Ecodist
275 package for R (Goslee & Urban 2007). To determine if daily air temperatures (measured on
276 the day of capture) affected our local density estimates (via effects on individual activity
277 levels and thus detectability), we ran mixed effect linear models in the lmerTest and lme4
278 packages for R (Kuznetsova et al., 2016) regressing daily density estimates on air
279 temperature measurements taken at the time when sampling occurred, and including a
280 random effect for site, since most sites were visited on multiple occasions.

281

282 Phylogenetic community structure

283 Phylogenetic reconstruction of Scottish damselfly evolutionary relationships was
284 obtained from Dumont, Vierstraete & Vanfleteren (2010) and Guan *et al.* (2013), with branch
285 lengths set to 1 because true branch lengths are unknown and are potentially unlikely to
286 accurately reflect rates of divergence in niche traits (Fig. 1). To estimate phylogenetic over-
287 or under-dispersion at each site, phylogenetic relationships were used to construct a pairwise
288 phylogenetic distance matrix of all species within each site using the cophenetic() function in
289 the picante package for R (Kembel *et al.* 2010). Subsequently, mean pairwise distances were
290 calculated for each site, and compared to a null expectation using the ses.mpd() function, also
291 in picante, where the null expectation was generated by randomizing shuffling tip labels on
292 the phylogeny 99 times. Where the observed phylogenetic dispersion of a site was greater
293 than 90% of randomly-generated phylogenies for the site, we classified the site as

294 phylogenetically overdispersed. Similarly, we diagnosed phylogenetic underdispersion where
295 the phylogenetic dispersion at a site was less than 90% of randomly generated phylogenies
296 for that site. If the phylogenetic dispersion of a site was similar to the middle 80% of
297 randomly-generated phylogenies for the site, we classified the site as evenly phylogenetically
298 dispersed. Due to conservative cutoffs for phylogenetic dispersion, we do not attempt to use
299 these data to draw rigorous conclusions about phylogenetic patterns at any particular site.
300 However, such conservative cutoffs give us an appropriate range of values to feed into further
301 analysis. Sites with only one species present were classified as single species communities.
302 These categories were used in linear models to analyse the correlation between phylogenetic
303 structure of communities and climate or the presence of *I. elegans*.

304 Competitive trials

305 To quantify thermal preference and competition between *I. elegans* and *L. sponsa*,
306 thermal preference trials were conducted in the laboratory using wild-captured damselflies in
307 2016. One hundred and three *I. elegans* and 108 *L. sponsa* from 7 sites (capture dates and
308 locations in Table S3) were assessed for their preferred basking site temperatures in a
309 repeated measures design, where each individual was assessed for its thermal preferences
310 alone, and in the presence of an interspecific ‘competitor’. Treatment order (alone vs. in
311 competition with the other species) was randomised so that repeated exposure to the thermal
312 gradient would have no effect on the damselflies. Thermal preference was assessed by
313 placing the damselfly in a 60cm Tube with a thermal gradient from 60°C to 10°C, achieved
314 by heating the tube at one end using a heat lamp (100W, 50Hz Exoterra ceramic heat emitter)
315 and cooling the opposite end with ice (Fig. S1). Each damselfly was given 5 minutes to settle
316 in their preferred position on the thermal gradient. The thermal environment where the
317 damselfly settled was measured by photographing the damselfly using a Flir Ex Series E6
318 thermal imaging camera and analysing the image using the Flir Tools software package

319 (v5.2.15, Flir systems.). For image analysis, the average temperature was taken of 5 point
320 samples of the temperature surrounding the damselfly (Fig. S2). Points were randomly
321 selected ~5mm from the individual's thorax. Effects of competition were analysed in a
322 mixed-effects linear model where the dependent variable was resting site temperature, and
323 fixed effects were included for species, treatment (alone or in competition), and the
324 interaction (species x treatment). Random effects were included to account for individual ID
325 (repeated measures) and for pair identity (because two individuals share a paired trial). The
326 model was run in lme4 and lmerTest packages for R.

327 Environmental variables and niche model construction

328 Species distributions were modelled over the geographic extent of Scotland using a
329 maximum entropy habitat suitability model implemented in MaxEnt, version 3.3.3k (Phillips,
330 Avenue & Park 2004) and executed through the Dismo package for R (Hijmans *et al.*, 2014).
331 Each species' presence points were obtained from records downloaded from the Global
332 Biodiversity Information Facility (<http://www.gbif.org>), and Odonata records from The
333 British Dragonfly Society (BDS) accessed from the National Biodiversity Network
334 (<http://www.nbn.org.uk/>), with duplicate records removed, leaving 2783 unique presence
335 records for *I. elegans*, 2485 for *L. sponsa*, 5470 for *P. nymphula*, 158 for *C. hastulatum* and
336 4667 for *E. cyathigerum*. Ten thousand randomly selected background points were used as
337 pseudo-absences in each model. The models were constrained to Scotland by using the
338 boundaries dataset available from the Office of National Statistics (Ordnance Survey, 2011).
339 Bioclim climate layers were sampled at 30 arcsecond resolution and clipped to the extent of
340 this region using the Raster package for R (Hijmans *et al.*, 2013); these were used as
341 predictor variables in the models (Table S1). In the case that climatic predictor variables were
342 correlated at > 80% across species presence and background points, the variable considered
343 likely less important to damselfly biology was removed. The MaxEnt model was run 5 times

344 using default parameters, withholding a separate 20% of presence points for model testing on
345 each model run. The final niche model for each species represented the average habitat
346 suitability's calculated across the five model runs. The full model (with all environmental
347 predictor variables) and stepwise-reduced models were compared using AICc, implemented
348 in the ENMeval R package (Muscarella et al., 2016), with a $\Delta AICc$ of 2 denoting significant
349 differences between models. Model fit was also assessed by estimating the area under the
350 Receiver Operating Characteristic (ROC) curve (AUC), which estimates sensitivity versus 1
351 – specificity (positively identified known presences versus the false positive rate). AUC
352 values of 0.5 or less correspond to the model performing similarly or worse than random,
353 while AUC values of $1 - a/2$ (where a is the relative size of the true species range within the
354 study area) indicate a very good fit of the model to the data (Phillips *et al.* 2004).

355 Phylogenetic analysis of niche overlap

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

364 Results

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

368 *cyathigerum* at 82 sites with a mean density of 0.63 ± 1.22 dpm, *I. elegans* at 50 sites with a
369 mean density of 0.34 ± 0.34 dpm, *L. sponosa* from 39 sites with a mean density of
370 0.88 ± 1.59 dpm, and *P. nymphula* from 65 sites with a mean density of 0.13 ± 0.1 dpm.

371 Spatial autocorrelation and abundance responses local to daily temperatures.

372 No species exhibited spatial autocorrelation for site densities except for *I. elegans*,
373 where spatial autocorrelation likely reflects the ongoing range expansion process (spatial
374 autocorrelation for *I. elegans*, $r=0.12$, $P=0.014$; *L. sponosa*, $r=0.01$, $P=0.39$; *P. nymphula*, $r=-$
375 0.9 , $P=0.98$; *E. cyathigerum*, $r=0.02$, $P=0.31$; *C. hastulatum*, $r=0.02$, $P=0.34$; *C. puella*,
376 $r=0.04$, $P=0.21$). Species densities calculated from individual capture bouts were uncorrelated
377 with the air temperature during these capture bouts, confirming that we selected days
378 characterised by favourable weather conditions for sampling, and thus that our density
379 estimates are not confounded by temperature-based detectability issues: *I. elegans* effect of
380 daily temperatures on daily density estimates, Est = -0.005 ± 0.063 , $t= -0.08$, $P= 0.94$; *L.*
381 *sponosa* 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.*
382 *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.*
383 *nymphula* Est= 0.08 ± 0.049 , $t=1.75$, $P=0.09$.

384 Species interactions and climate

385 *Ischnura elegans* density was best explained by a model including only mean annual
386 temperature (Table S2), although the correlation was not significant (effect of
387 $\text{bio1}=0.55 \pm 0.35$, $t=1.58$, $P=0.12$). For *L. sponosa*, the best model included the interaction
388 between mean annual temperature and *I. elegans* presence/absence (Table S2). This
389 interaction effect was a significant predictor of *L. sponosa* densities in the model (effect of
390 $\text{bio1} \times I. elegans$ presence= -0.21 ± 0.084 , $t=-2.55$, $p=0.016$; Fig. 2a). In the absence of *I.*
391 *elegans*, *L. sponosa* densities were positively correlated with mean annual temperature.

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

396 *Ischnura elegans* presence did not show clear-cut patterns of influence on any other
397 species' densities: For *P. nymphula*, *I. elegans* presence and temperature each improve the
398 model fit in comparison to an intercept-only model explaining *P. nymphula* densities (Table
399 S2), but these effects are non-significant, and likely reflect that fact that the *P. nymphula*
400 range, while largely congruent with the range of *I. elegans*, extends to cooler, higher
401 elevation sites within our study region (Cham et al. 2014). For *E. cyathigerum*, a model
402 which included both mean annual temperature and *I. elegans* presence/absence (but not the
403 interaction) best explained local densities (Table S2). *Enallagma cyathigerum* densities were
404 positively associated with *I. elegans* presence, (effect of *I. elegans* presence = 0.89±0.38,
405 $t = 2.32$, $P = 0.02$) and the model also contained a slightly negative but highly non-significant,
406 residual effect of mean annual temperature ($P = 0.93$). Although *I. elegans* presence is weakly
407 correlated with mean annual temperature across our sites, these models did not suffer from
408 collinearity of these effects. No climate variable other than mean annual temperature (bio1)
409 affected the site-specific densities of any species.

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

411 Complementarily to our density data, the presence of *I. elegans* at a site was
412 correlated with larger body sizes in *L. sponso*, in a model that included a covariate for climate
413 and a random effect for site and date (effect of mean annual temperature on *L. sponso* body
414 size = 1.6±1.27, $df = 23.59$, $t = -2.68$, $P = 0.21$; effect of *I. elegans* presence on *L. sponso* body
415 size = -66.85±22.53, $t = -2.97$, $p = 0.007$; Fig. 2c). Similarly, thermal preferences were

416 influenced by competition in ways that are complementary to our density and morphology
417 results. The effect of species x treatment (alone or in competition) on thermal site selection in
418 the laboratory was: $Est=1.97\pm 1.14$, $df=104.19$, $t=1.72$, $P=0.04$ using a 1-tailed hypothesis test
419 to predict that the presence of *I. elegans* would shift *L. sponso* to cooler preferred
420 temperatures; Fig. 3). As predicted, where *I. elegans* was introduced to trials, *L. sponso* shifts
421 to cooler position in comparison to when *L. sponso* is allowed to thermoregulate alone.

422 Phylogenetic community structure

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

429 Niche similarity and phylogenetic signal

430 Variable importance and AUC values for each species' best fit Maxent niche model are
431 presented in table S4. In all cases, the full model (containing all uncorrelated predictor
432 variables) was the best fit, with the lowest AICc. Although individual niche models for each
433 species vary in the relative importance of different climatic variables (Table S4, Fig. 5a),
434 pairwise niche overlap (measured using D; Warren et al. 2008) illustrated that most species
435 occupy similar niche space. *I. elegans*, *E. cyathigerum*, *L. sponso* and *P. nymuphula* showed
436 pairwise overlap values between 0.81 and 0.92 (Fig 5b). Only *C. hastulatum* and to a lesser
437 extent *C. puella* accounted for the majority of niche differences, with *C. hastulatum*
438 demonstrating pairwise overlap values between 0.18–0.25 for all other species (Fig. 5b),
439 while *C. puella* demonstrated values between 0.18–0.65 with all species (Fig. 5b). These

440 patterns of niche similarity showed no phylogenetic signal across the 6 species ($f=0.33$,
441 $p=0.66$). To identify if lack of signal was caused by the relatively large niche differences
442 between the closely related habitat specialist species *C. hastulatum* and *C. puella*, the analysis
443 was repeated with *C. hastulatum* and *C. puella* removed. Again no significant phylogenetic
444 signal was observed ($f=0.3$, $p=0.6$).

445 Discussion

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

465 within communities are more complex than classically expected, raising questions about the
466 utility of phylogenetic signal as a proxy for describing community assembly processes.

467 Evidence for partial competitive displacement

468 We show evidence for incipient competitive displacement of *L. sponsa* by the range-
469 expanding *I. elegans*, where *L. sponsa* is the least related species to *I. elegans* within the
470 regional species pool (Figs. 1, 2a&b, 3). Evidence in support of this includes: (i) *L. sponsa*
471 and *I. elegans* inhabit strongly convergent climatic niche space (Fig. 5a&b). (ii) *L. sponsa*
472 population densities exhibit a negative relationship with *I. elegans* density (Fig 2C). (iii) In
473 the absence of *I. elegans* at a site, *L. sponsa* density is positively correlated with mean annual
474 temperature, but the presence of *I. elegans* disrupts this relationship (Fig. 2b), suggesting that
475 *I. elegans* displaces *L. sponsa* from preferred (warmer) sites. (iv) *L. sponsa* has undergone a
476 morphological shift (to larger body sizes) where *I. elegans* is present (Fig. 2b). (v) *L. sponsa*
477 shifts its thermal preference to cooler temperatures when in competition with *I. elegans* (Fig.
478 3).

479 Patterns of partial competitive displacement between the two least-related species
480 within a guild is consistent with the expectations of the competitive trait conservation
481 hypothesis (Chesson 2000; Mayfield & Levine 2010). Given that *L. sponsa* population
482 densities positively correlate to mean annual temperature, but only in the absence of *I.*
483 *elegans*, it is unlikely that environmental filtering is the primary causal factor explaining the
484 negative relationship between *L. sponsa* density and *I. elegans* density. Moreover, thermal
485 preference trials demonstrate competitive displacement of *L. sponsa* from their preferred
486 thermal regimes in response to the presence of *I. elegans*. This result suggests that
487 behavioural traits, such as aggressive behaviour, might act as the mechanism of competition.
488 At present we lack sufficient evidence to conclude this is the competitive mechanism,

489 although competition for basking sites via aggressive behaviour has been observed in larger
490 territorial odonata species (Lefevre & Muehter 2004; Worthen & Patrick 2004; Byers &
491 Eason 2009). Moreover, it is unlikely that there is only one mechanism by which *I. elegans*
492 and *L. sponsa* compete, as the adult stage represents a relatively short (but critical) period of
493 interaction between these two species. A major component of co-occurrence between these
494 species is during aquatic larval development (see below).

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

512 Lancaster *et al.*(2017) have previously demonstrated that *I. elegans* exhibits
513 increased aggression under experimental warming treatments, suggesting that further

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

528 Temporal dynamics and future directions in our field research

529 A time lag between the colonisation of an antagonistic species in a population and the
530 point at which species displacement become pronounced can radically influence
531 interpretation of how species interact during range shifts. Understanding this temporal lag
532 therefore represents an important avenue for future research. Anecdotally, our data may also
533 suggest that the effect of *I. elegans* presence on *L. sponsa* densities has a temporal
534 component (Fig. 2b). Points circled in green represent sites at the very leading edge of *I.*
535 *elegans*' range, and the point circled in blue represents a newly-created pond (within the last
536 5 years). At these sites, although *I. elegans* is present, patterns of *L. sponsa* densities are
537 similar to those observed at sites in the absence of *I. elegans*. This suggests a temporal lag
538 between *I. elegans*' initial colonisation to a site, and the subsequent decline of *L. sponsa*.

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

543 Niche Overlap and Environmental Filtering

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

559 Phylogenetic patterns

560 Our observed shift in phylogenetic structure within communities as a result of
561 competition (Fig 3A and 3B) has two major implications. Firstly, from a
562 methodological/theoretical perspective, it raises the issue of whether the use of phylogenetic

563 structure can be used as a method for ascertaining community assembly processes (Webb
564 2000; Lessard *et al.* 2009; Lebrija-Trejos *et al.* 2010). Secondly, reduced phylogenetic
565 diversity as a result of climate change-driven range shifts poses a conservation issue.
566 Declines in phylogenetic diversity may be common in regions affected by increased
567 competition from invasive species (Lessard *et al.* 2009), and these diversity losses may be
568 exacerbated under further climatic warming (Willis *et al.* 2008; Zhang *et al.* 2015). Because
569 conservation of phylogenetic diversity is critical for maintaining high levels of biodiversity
570 into the future (Barker 2002), range shifts within regional species pools characterized by
571 conserved competitive abilities may pose a particularly urgent concern, particularly for high
572 latitude ecosystems, which are strongly affected by this colonisation process. Little is known
573 about the factors underpinning range shifts in animals (Angert *et al.* 2011; Comte &
574 Grenouillet 2013) , so we do not know the extent to which species prone to range shifting
575 generally tend to express conserved (i.e., inherited) competitive abilities.

576 Implications

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

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

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603 Data

604 All data used in this study have been deposited in Dryad data repository DOI:
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814 Figure legends:

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816 Figure 1. Phylogeny of Scottish damselfly species constructed using phylogenies from
817 Dumont, Vierstraete & Vanfleteren (2010) and Guan et al. (2013), with branch lengths set to
818 1.

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

820 2a. *Lestes sponsa* density is positively correlated with mean annual temperature at
821 sites where *I. elegans* is absent, but not where *I. elegans* is present (effect of bio1 x *I.*
822 *elegans* presence = -0.21±0.084, t = -2.55, p=0.016). . Green circles represent sites at
823 the current expansion front for *I. elegans*, and blue circles represent ponds less than 5

824 years old. Thus, at all circled sites, the species have only recently co-occurred, and the
825 competitive displacement effect observed at other sites may not have yet developed.

826 2b. *L. sponsa* density is negatively correlated to densities of the invading competitor
827 *I. elegans*. The effect line represents the linear regression effect: -0.683 ± 0.28 , $r^2 = 0.24$
828 $F_{1,19} = 5.89$, $t = -2.43$, $P = 0.03$.

829 2c. *Lestes sponsa* body size at sites where *Ischnura elegans* is present and absent,
830 where body size has been derived from principal components analysis of multiple
831 morphometric measurements (*I. elegans* presence on *L. sponsa* body size =
832 264.52 ± 7.174 , $t = -3.4238$, $p < 0.001$).

833

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

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

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

841 5a. Habitat suitability of each damselfly species using MaxEnt niche modelling.

842 5b. Pairwise niche overlap scores given as Schoeners D (Warren *et al.* 2008).

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846 Figure 1

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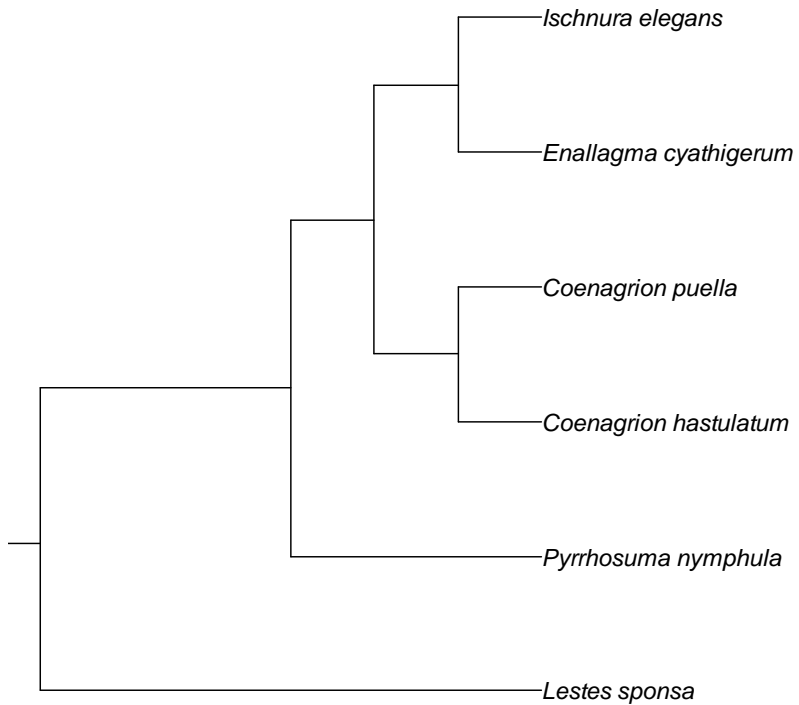
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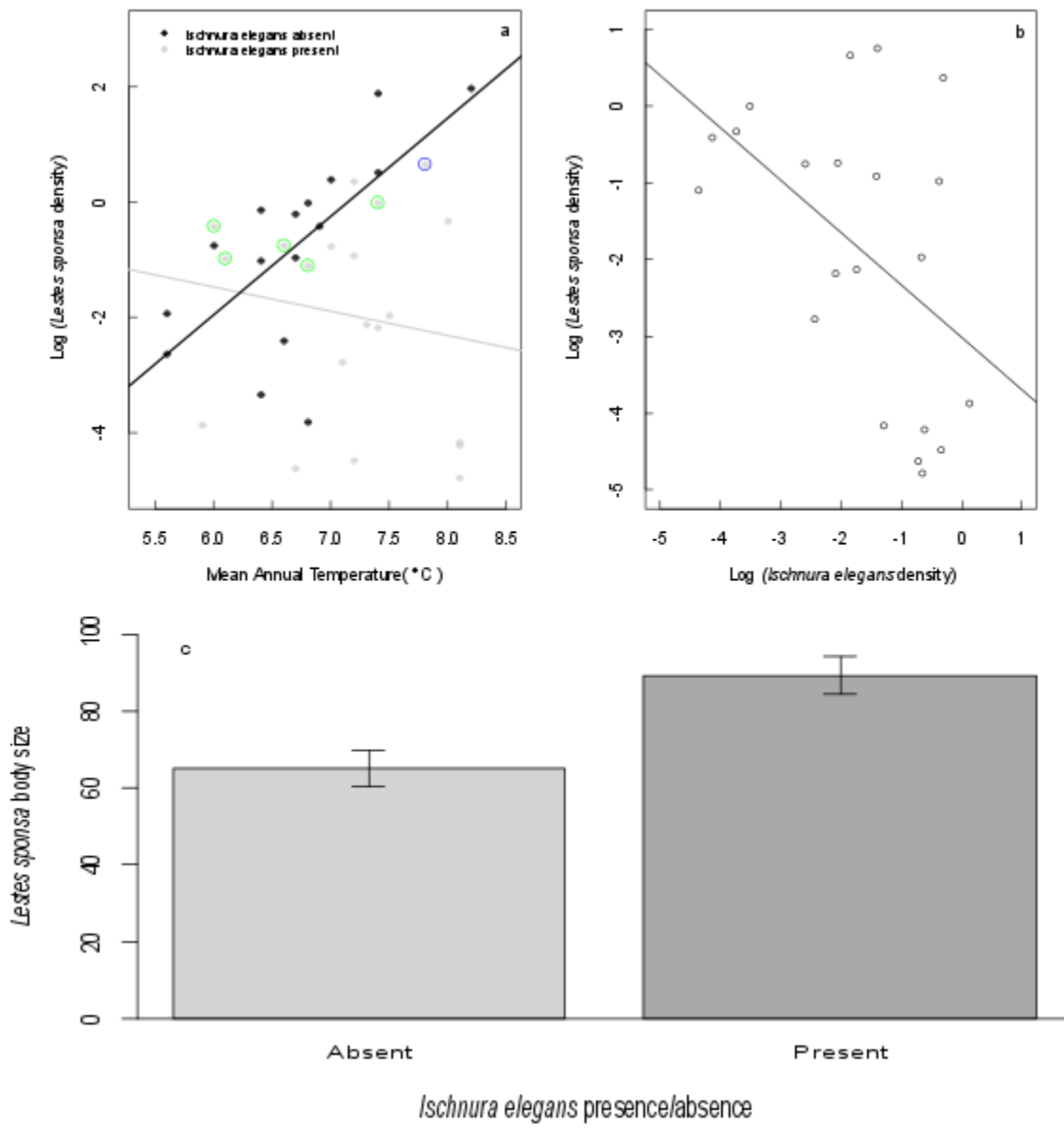
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873 Figure 2



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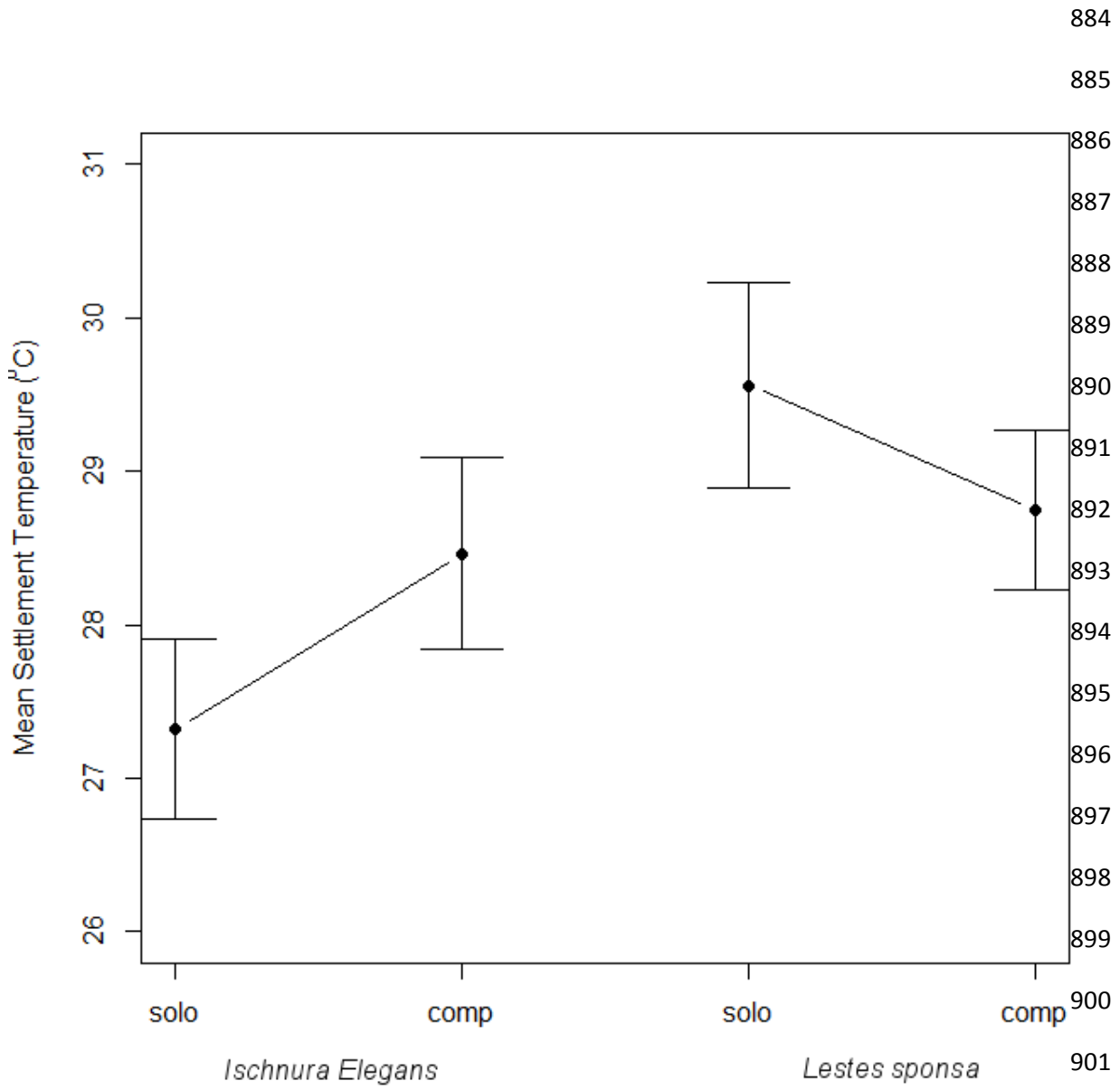
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882 Figure 3

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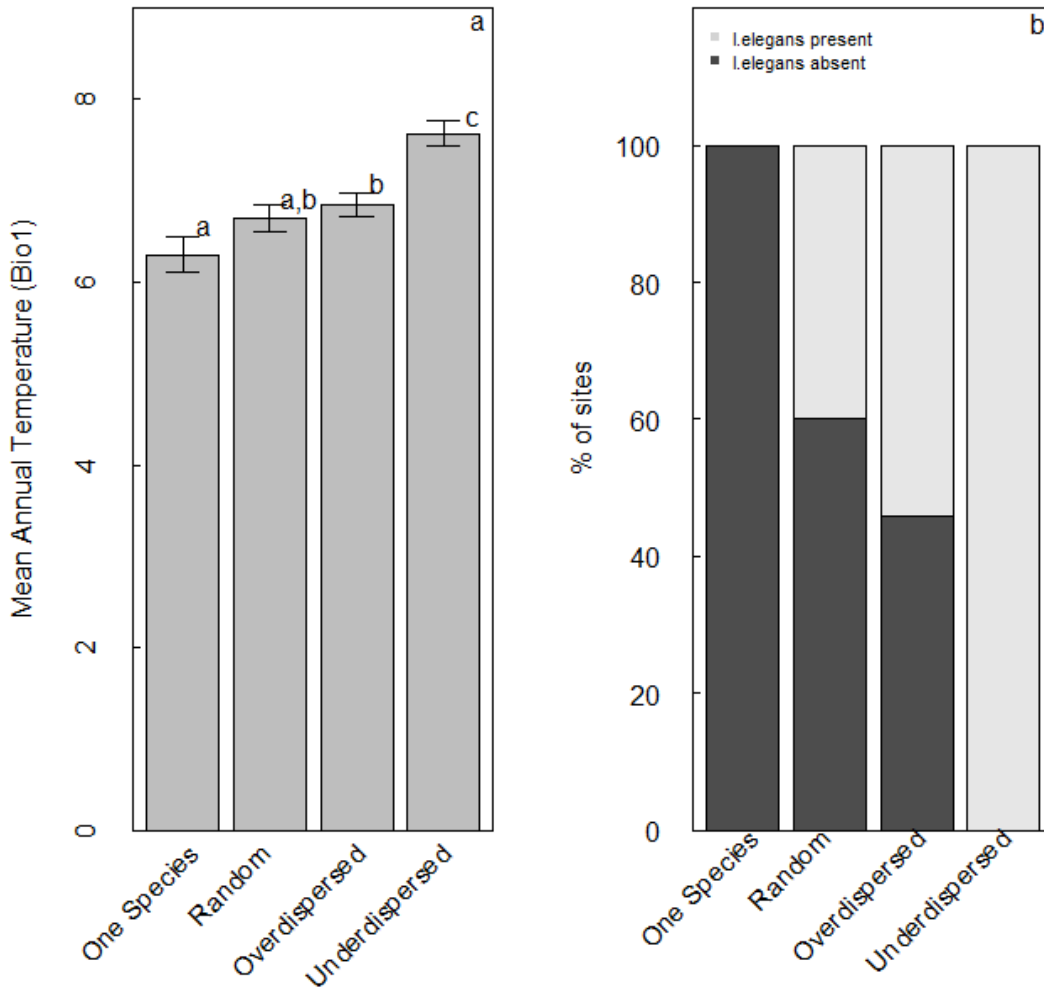
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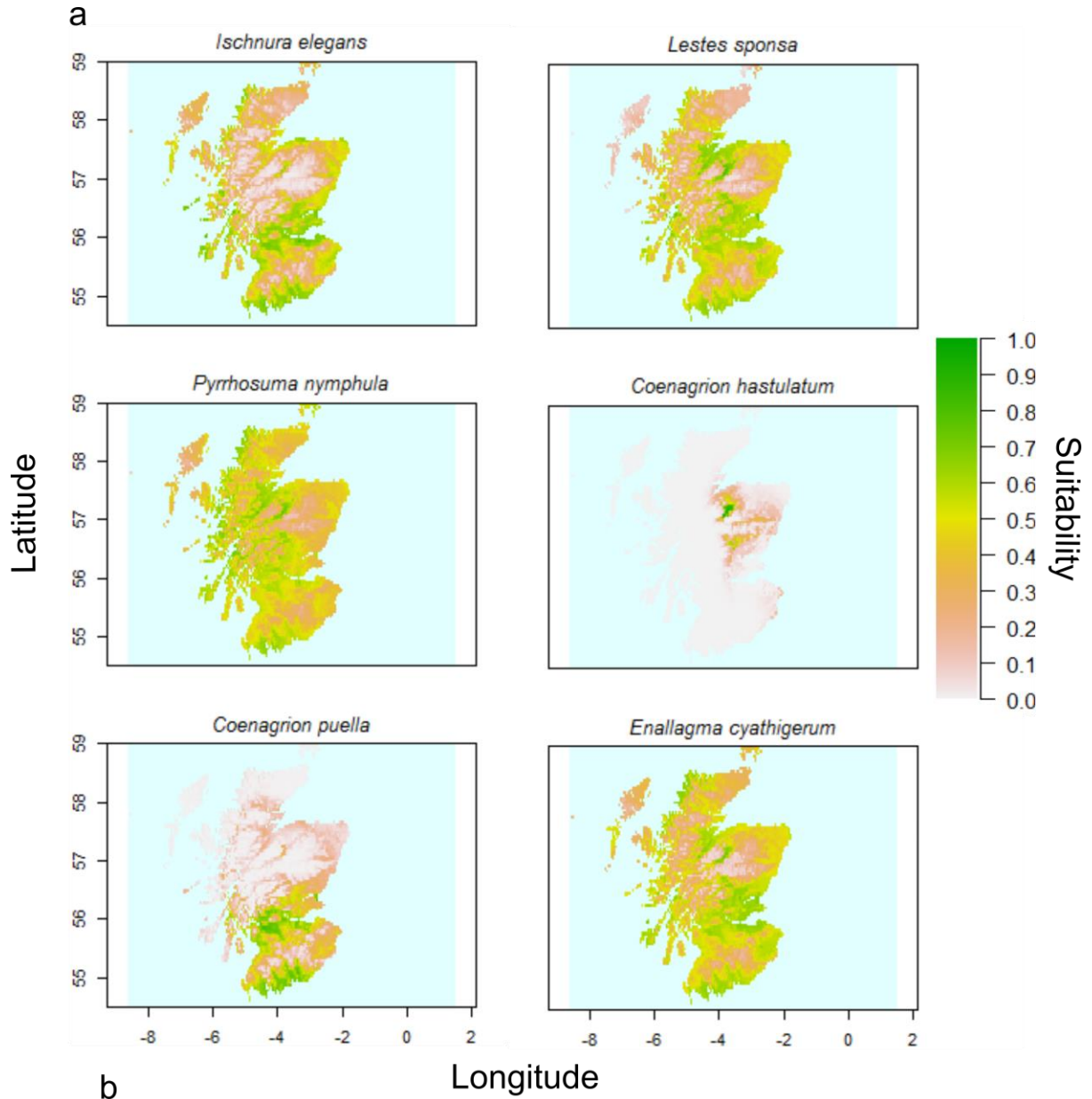


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921 Figure 5

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b

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

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926 Supplementary material for:

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

929 competition

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933 Aberdeen, United Kingdom.

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937 Table S1. Variation in georeferenced climate variables across the study sites in northeast

938 Scotland. Climatic values for each site were bioclimatic variables obtained from (Hijmans et

939 al., 2005).

Climatic variables		<i>Maximum value</i>	<i>Minimum Value</i>
Bio1	Mean annual temperature	4.8°C	8.2°C
Bio2	Mean diurnal Range	7°C	7.3°C
Bio3	Isothermality	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	14	26
	Seasonality		
Bio18	Precipitation of Warmest Quarter	174mm	270mm

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

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

943

944 Table S3

945 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

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

952

Climatic variables		Permutation importance					
		<i>I.elegans</i>	<i>L.sponsa</i>	<i>C.puella</i>	<i>C.hastulatum</i>	<i>P.nymphula</i>	<i>E.cyathigerum</i>
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	Isothermality	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

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958 Figure S1:

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



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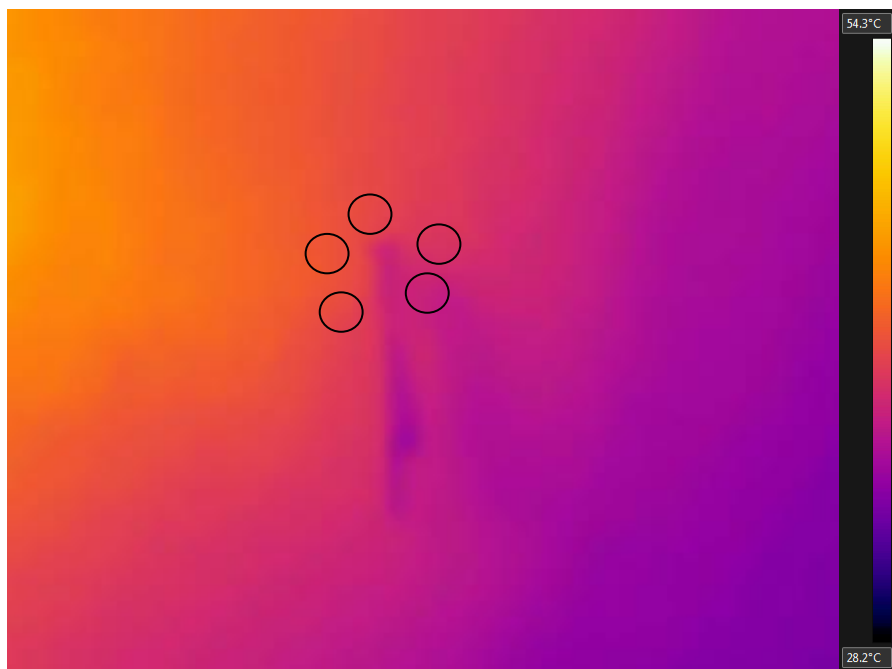
964 Figure S2:

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

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