Title: Thermal environment and ecological interactions modulate the importance of evolution in response to warming

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Abstract

Understanding the interaction between evolutionary history, the current abiotic environment, and biotic interactions is critical for a more nuanced understanding of the response of communities to anthropogenic stressors. We leveraged a long term experiment manipulating temperature in mesocosms containing communities of phytoplankton and zooplankton to examine how evolution in response to long-term community warming affects consumer-resource dynamics at different temperatures. We showed that the evolution in response to warming depends on both the current thermal environment, as well as the presence of interactions between consumers and resources. We also demonstrated that evolution influences the outcomes of current ecological dynamics. For each consumer–resource pair, the effects of evolution were temperature-dependent, but both the effects and the temperature dependence itself additionally depended upon the identity of evolving species in each pair. Evolution resulted on a win-win situation for the first resource species: across all temperatures, this resource was more fit and the consumer was less successful, with fitness gains peaking at intermediate temperatures. For this resource species our results supported the "hotter is better" hypothesis, especially at moderate or intermediate temperatures, while "hotter is worse" for the consumer. In the second species pair, patterns were more complex. Warm-origin populations of both the second resource and the consumer generally failed to show improved fitness. Overall, our results show that evolution altered resource and consumer fitness, but these effects were dependent on the current combination of abiotic and biotic conditions.

Key words: consumer-resource interactions, eco-evolutionary dynamics, global climate warming, predator-prey interactions, temperature dependence, thermal adaptation

Introduction

Climate change has emerged as a critical challenge to species and ecological communities (Parmesan 2006, Radchuk et al. 2019). Multiple mechanisms by which species and communities respond to increasing temperatures (e.g., range shifts, plastic changes to behavior, phenology, etc.) interact to determine the degree to which species and communities are affected by climate change (O'Connor et al. 2012, Lurgi et al. 2012, Gaitán-Espitia and Hobday 2021). Because temperature represents a strong selective agent for populations, evolution likely constitutes one important mechanism by which species respond to warming, especially for dispersal-limited populations or species with rapid generation times (O'Donnell et al. 2018). Evolution in response to warming has been experimentally documented in a variety of organisms, including, for instance, green algae (Padfield et al. 2016, Schaum et al. 2017), arthropods (Gilchrist and Huey 1999, Geerts et al. 2015, Hangartner and Hoffmann 2016), and larger organisms, such as lizards (Logan et al. 2014). While less frequently studied, evolution in natural populations in response to warming has been observed as well (Higgins et al. 2014, Geerts et al. 2015, Johansson et al. 2016, Johansson and Laurila 2017, Diamond et al. 2017). Because evolution in response to abiotic factors, like climate warming, is frequently explored in single populations, the implications of evolution in communities responding to warming remain understudied. Nonetheless, given that many of the species most likely to evolve in response to warming—such as plankton with short generation times and larger population sizes—are also critical for ecosystem functioning and services (*e.g.,* water quality, carbon sequestration)(O'Donnell et al. 2018), we can expect that evolutionary responses to warming will have important consequences for both ecological and human systems (Rudman et al. 2017).

Multiple hypotheses exist for how evolution in response to warming may alter the populations' thermal response curves of a number of fitness attributes [e.g., "hotter is better", "biochemical adaptation", and "partial compensation" (Angilletta et al. 2010, Liu et al. 2022)]. Evidence from natural

62 populations, however, demonstrates that the thermal performance of populations can depart from
63 theoretical expectations (DeLong et al. 2018). In some cases responses match anticipated shifts in
64 thermal performance with adaptation under warmer temperatures (Knies et al. 2006, Diamond et al.
65 2017). In other cases they exhibit unexpected results, which can also depend upon the life history
66 parameter measured (Kingsolver and Huey 2008, Johansson et al. 2016). Such unforeseen results may,
67 in part, be explained by life history tradeoffs (Latimer et al. 2011), such as those that can emerge
68 between coping with acute thermal stress and chronic exposure (Rezende et al. 2014). For instance,
69 evolution may favor increased survival under chronic warm temperatures at the expense of critical
70 thermal maximum temperature during acute thermal stress (Johansson and Laurila 2017). Thus, both
71 the type of thermal stress experienced by populations (i.e., increasing mean temperature vs. frequent
72 acute fluctuations), as well as the current thermal environment (e.g., temperature and duration of
73 thermal experiments) may be important for interpreting empirical patterns and understanding the
74 implications of evolution that occurs in response to warming.

75 The presence of additional interacting species introduces additional factors influencing
76 evolutionary outcomes. The effects of evolution can depend on the current ecological conditions of
77 populations experiencing warming. When species are embedded in complex communities, the
78 opportunities for additional costs, constraints, or benefits of evolution can emerge. For instance, there
79 can be trait tradeoffs or novel selective pressures present that arise out of additional ecological (or
80 evolutionary) changes that occur as communities respond to warming. Such trait tradeoffs can drive
81 differences in evolutionary responses compared to evolution in single populations (Van Doorslaer et al.
82 2009a, 2010). Selection that occurs within an ecological community is therefore likely to qualitatively
83 change predictions about thermal adaptation derived from single populations (Angilletta Jr. et al. 2006),
84 such that individual species' responses to temperature can be insufficient to explain changes to
85 community composition (Tabi et al. 2020).

In consequence, we expect that when shifts in thermal performance occur in traits that affect how species interact, such as resource acquisition or metabolism, this could affect overall fitness of populations that interact and respond to warming. Specifically, 1) different life history traits within a species can have different thermal dependencies (Dell et al. 2011, Huey and Kingsolver 2011), 2) consumer and resource species have documented differences in these thermal dependencies (O'Connor et al. 2009, Álvarez-Codesal et al. 2023), and 3) evolutionary potential can differ across trophic levels (Terhorst et al. 2010, Hague and Routman 2016). Therefore, it follows that evolution in response to warming has the potential to alter consumer-resource dynamics, while also being reciprocally influenced by them (Faillace et al. 2021), and that the effects of evolution may additionally depend upon current thermal environment. For example, previous research using a space-for-time substitution demonstrated that locally adapted populations of consumer and resource species from different latitudes had contrasting eco-evolutionary dynamics at two temperatures (De Block et al. 2013). More generally, a variety of altered dynamics are possible. One possibility that emerges is cryptic eco-evolutionary dynamics where evolution in both species yields a "moving target" that mimics purely ecological dynamics. In this case, evolution may alter the thermal performance of the interacting species in similar ways, such that the outcomes of the interaction remain apparently unchanged, but are actually being maintained by the evolutionary response. A second possibility is that the effects of the interaction on species' fitness may depend upon the current thermal environment. This might occur if, for example, their thermal tolerances evolve to different degrees or if only one interacting species evolves. Additionally, although responses are sometimes examined at multiple temperatures, most studies are typically of short duration and do not consider the effects of evolution at longer timescales to quantify changes to fitness.

To examine both the influence of ecological interactions on evolutionary responses to warming as well as understand the long-term effects of evolution on the ecology of interacting species, we used a

110 long-term warming mesocosm experiment in plankton communities. We examined the consequences of
111 evolution in response to long-term warming in communities for consumer-resource interactions. We
112 used populations of two resource species (i.e., freshwater green algae, *Chlamydomonas reinhardtii* and
113 *Desmodesmus* sp.) and a consumer species (i.e., *Daphnia pulex*) differing in thermal origin. We
114 hypothesized that the effects of evolution on species' fitness would be dependent upon current thermal
115 environment and the presence of species interactions. Specifically, we asked, 1) whether biotic
116 interactions affect the importance of evolutionary history across a range of temperatures, and 2)
117 whether temperature affects the importance of evolutionary history.

118 **Methods**

119 *Source and maintenance of organisms prior to experimentation*

120 Organisms originated from a long-running mesocosm experiment in Dorset, England. This
121 mesocosm experiment has been the subject of multiple previous publications (e.g., Yvon-Durocher et al.
122 2015, Schaum et al. 2017, Álvarez-Codesal et al. 2023). Briefly, at the time of sampling in 2019, open-air
123 experimental ponds of 1 m^3 water of mixed freshwater phytoplankton and zooplankton had been
124 continuously maintained since 2005 (i.e., approximately 14 years). Half of the mesocosms were kept at
125 ambient temperature conditions, while half experienced a consistent temperature increase of +4 °C
126 above ambient temperatures (n = 8 for both at the time of our sampling). Temperature in all ponds
127 fluctuated seasonally. Mesocosm communities initially contained the same mixture of phytoplankton
128 and zooplankton, but previous work has demonstrated significant changes to community structure in
129 the warmed mesocosms, as well as evolution in thermal tolerance in warmed populations of at least one
130 phytoplankton species, *Chlamydomonas reinhardtii* (Yvon-Durocher et al. 2015, Schaum et al.
131 2017)(Figure 1).

132 We sampled two phytoplankton resource species, the algae *C. reinhardtii* and *Desmodesmus* sp.
133 from each treatment in January 2019, as well as a consumer species, *Daphnia pulex* in October 2019 (for
134 further details see Álvarez-Codesal et al. 2023). The discrepancy in dates occurred because we were
135 unsuccessful in isolating consumers on the first attempt. Sorting flow cytometry isolated single algal
136 cells and PacBio Sequel 2 long-read sequencing using full-length 18S fusion primers (forward: NSF4/18 =
137 CTGGTTGATYCTGCCAGT; reverse: EukR = TGATCCTTCTGCAGGTTCACCTAC) confirmed species identity
138 and genotypic differences between ambient-origin and warm-origin populations of the algae (Comeau
139 et al. 2017). We identified one unique clone for each of the two species, *C. reinhardtii* and
140 *Desmodesmus* sp. The identity of the consumer populations originating from each of 5 individuals
141 isolated from the experiment was confirmed morphologically by a taxonomist (however, genotypic
142 differences were not verified by sequencing for the *Daphnia*). All species reproduced asexually, enabling
143 us to maintain clonal populations of each genotype (algae) or putative clone (*Daphnia*) in semi-
144 continuous laboratory batch cultures until the start of the experiments. To avoid confounding effects of
145 plasticity or maternal effects, we maintained populations of these species in common garden
146 conditions—20 °C with 12:12 light-dark cycle—for over six months (many generations) prior to
147 subsequent experimentation. All organisms grew in autoclave-sterilized COMBO growth medium
148 (Kilham et al. 1998). *Daphnia* grew in modified low-phosphorus COMBO (Kilham et al. 1998) that
149 reduces bacterial load. Aeration maintained culture health and growth, and we aimed to maintain algal
150 populations in the exponential growth phase leading up to the experiment. Additionally, *D. pulex* grew
151 on a laboratory culture of *Ankistrodesmus* sp. (sourced from Sciento UK) to ensure that daphnids were
152 not acclimated to the algal species used in the experiments. *Daphnia* cultures received 50 mL of dense
153 *Ankistrodesmus* once per week as a food source. Periodic filtering of adult and juvenile daphnids into
154 fresh medium removed metabolic waste products and resting eggs.

155 *Experimental design*

156 Our experimental design crossed long-term evolutionary history—either to "ambient" or
157 "warm" temperature conditions— of each consumer–resource pair with 4 growth temperatures (Figure
158 1). In this way, we sought to examine how the effects of evolution in response to warming in a
159 consumer–resource pair depend upon the current thermal environment. The experiment occurred in 4
160 incubators that varied in temperature: 14, 18, 22, and 26 °C. These temperatures encompass much of
161 the observed growing season activity range for the consumer from this system. The presumed
162 approximate thermal optimum of reproduction of the ambient-origin population of 20 °C served as the
163 mid-point across the range (Craddock 1976). Non-consumption controls additionally allowed us to verify
164 the importance of algal evolutionary history in the absence of consumers. We conducted the
165 experiment for each consumer–resource pair in two temporal blocks, across which we swapped
166 incubator temperatures (for tractability and to avoid pseudoreplication at the incubator level). Thus, we
167 had 6 warming evolutionary history–consumption treatments crossed with 4 growth temperatures
168 (Figure 1) in each temporal block for each consumer–resource pair (n = 4 per treatment, yielding a total
169 of 96 microcosms within temporal block). At the start of each experimental block, we estimated
170 abundance of the ambient-origin and warm-origin resources using a hemocytometer to count cells
171 under a compound microscope (NIKON Eclipse Ni). We then standardized approximate starting
172 abundances of the two populations, however starting densities thus differed somewhat between blocks
173 within a resource species and between resource species. We randomized microcosm position within
174 each incubator. The experiment ran a total of 4 times (n = 8 for treatment across 2 temporal blocks,
175 yielding N = 192 per consumer–resource pair and N = 384 across both pairs). The experiment ran for 3
176 weeks, or approximately 42–100 generations of algae and 2–4 generations of *Daphnia*.

177 To each sterile microcosm we added 100 mL of sterile COMBO medium and 100 mL of density-
178 standardized resource from either the ambient-origin or warm-origin population (of either *C. reinhardtii*
179 or *Desmodesmus* sp.). To treatments containing *Daphnia*, we then added 5 daphnids either of ambient-

origin or warm-origin to each microcosm, one from each of 5 isoclonal lineages of ambient-origin or warm-origin populations of *Daphnia*, such that the evolutionary origin of the resource was crossed with that of the consumer. It was infeasible to grow out the number of juveniles that would be needed to ensure precisely aged populations from the 5 isoclonal *Daphnia* lineages from both the ambient- and warm-origin populations. Therefore, we chose from among largest adult daphnids to ensure that we included individuals of the largest instar for each population. This provided a snapshot of the *Daphnia* community at the point at which we initiated the experiment, but the adults may have differed in age, contributing to differences among temporal blocks. The *Daphnia* were previously starved for 24-hours, filtered, and rinsed in sterile water to remove residual *Ankistrodesmus* before addition to the experiment. Thus our evolutionary history–consumption treatments repeated at 4 temperatures were: 1) ambient-origin resource alone, 2) warm-origin resource alone, 3) both ambient-origin resource and consumer, 4) ambient-origin resource + warm-origin consumer, 5) warm-origin resource + ambient-origin consumer, and 6) both warm-origin resource and consumer.

Estimation of equilibrium densities and interaction strength

Responses included equilibrium density (per ml) of the resource species, as well as a census of adult and larval *Daphnia* present in each microcosm. After 3 weeks, we first filtered and preserved all *Daphnia* adults and juveniles from a microcosm in 95% ethanol for later enumeration under a dissecting scope in two size categories, adults and juveniles. Safranin (Sigma-Aldrich) stained the *Daphnia* for simpler visualization of the preserved samples during counting under a stereo microscope (Leica S9i), which ensured that molts were not counted erroneously. We next cryopreserved two 150 µL samples of well-mixed algae suspension from each microcosm using 15 µL of a 1% sorbitol solution in 96-well plates at –80 °C. Flow cytometry (BD FACSCanto II high-throughput sampler) then estimated cell densities (for more details, see Álvarez-Codesal et al. 2023). For *Desmodesmus* sp., because flow cytometry measures particles, we report our results as coenobia (i.e., small colonial cellular aggregates) rather than

204 converting from aggregates to cells. Coenobia are the units with which consumers interact, making them
205 an appropriate unit for this species.

206 We used interaction strength to quantify the effect of consumers on resource abundance. To
207 estimate the population-level interaction strength (IS), we calculated an inverse form of the log-
208 response ratio (also called the Dynamic Index) using Equation 1 (Berlow et al. 2004, Schaum et al. 2017):

209 $$IS = \frac{ln(\frac{\overline{N}}{D_i})}{t}$$ Equation 1

210 where $\overline{N}$ is the final mean algal abundance of the no consumption (algae-alone) controls for each
211 population, ambient-origin or warm-origin, for each resource species, *C. reinhardtii* or *Desmodesmus*
212 sp., D_i is the final algal abundance of replicate i from a given population in the presence of consumers,
213 and t is the length of the experiment (equal to 21 days for our experiment). Larger values of IS indicate
214 stronger effects of consumers on resource abundance. We chose to focus on population-level
215 interaction IS rather than the *per capita* IS because we measured the interaction over a period of 21
216 days (i.e., it was not a short-term measure) during which the consumer population size was not
217 constant. Thus, we might have some consumer individuals dying and others hatching and emerging
218 during the experiment, so that populations are not at equilibrium, making the population-level log-
219 response ratio an appropriate choice for our design (Berlow et al. 2004).

220 *Analyses*

221 We $\log_{10}$-transformed abundances to better meet assumptions of normality in the subsequent
222 analyses. In all models, a block effect and all block interactions accounted for differences related to
223 temporal blocks. In all analyses, we centered the temporal blocking variable to ensure interpretability
224 (Schielzeth 2010). We conducted analyses to examine how current thermal environment and biotic
225 interactions determined the importance of past evolutionary history to warming in governing fitness (as

226 assessed by abundance across multiple generations) of resources and consumers. A single MANOVA
227 including evolutionary history treatments with and without consumers present would obfuscate
228 differences that might occur in the interaction between evolutionary history and temperature when the
229 algae grew alone or with consumers (in part through spurious significance related to the presence or
230 absence of *Daphnia* as a response in the two types of treatments). Therefore, to examine how current
231 biotic interactions impact the importance of evolutionary history, we conducted separate analyses on
232 the $\log_{10}$-transformed abundance per ml of algae when consumers were present or absent. In all
233 models, the interaction between the main effects (evolutionary history and temperature) assessed
234 whether the effects or importance of evolutionary history depend upon current thermal environment.
235 Thus, we first conducted an analysis of variance (ANOVA) for each algal species grown alone (because
236 they were tested independently). These analyses tested whether algal evolutionary history interacted
237 significantly ($\alpha = 0.05$) with temperature when consumers were absent. The model included the
238 evolutionary history (2 levels—ambient-origin or warm-origin resources) and temperature (4 levels—
239 14, 18, 22, and 26 °C test temperature) and the interaction, in addition to the block effect and block
240 interactions, with final algal density as the response.

241 We next conducted a separate multivariate analysis of variance (MANOVA) for each consumer–
242 resource pair. Responses included the $\log_{10}$-transformed abundance per ml of the resource, interaction
243 strength, and the $\log_{10}$-transformed abundances per microcosm of adult and juvenile *Daphnia*. Main
244 effects of the model included evolutionary history treatment (4 levels—ambient-origin resource and
245 consumers, ambient-origin resource + warm-origin consumers, warm-origin resource + ambient-origin
246 consumers, and warm-origin resource and consumers), temperature (4 levels—14, 18, 22, and 26 °C test
247 temperature), and the interaction between temperature and evolutionary history. Univariate tests
248 assessed significance at $\alpha = 0.05$ for individual responses. Planned contrasts further disentangled the
249 drivers underlying the evolutionary history treatment and determined specifically if 1) resource

250 evolution, 2) consumer evolution, or 3) the interaction between evolutionary history of the resource and
251 consumer (i.e., coevolution) affected responses. All analyses were conducted in SAS 9.4 (SAS Institute
252 2011).

253 **Results**

254 Evolutionary history in response to warming in complex communities, current temperature, and
255 their interaction had highly significant effects for both consumer–resource pairs, but the relative
256 importance of resource, consumer, or coevolution differed between the pairs (see Tables 1 and 2 for
257 specific results from algae-alone ANOVAs and consumer–resource MANOVAs). We describe specific
258 effects below using results from ANOVAs and planned contrasts for each response variable.

259 *Current thermal environment influences the importance of prior resource evolution in response to*
260 *warming*

261 Resource evolution in warmed communities affected both algal species when grown alone, but
262 the effects of evolutionary history were opposite in direction and differed in strength (Table 1). Warm-
263 origin *Chlamydomonas reinhardtii* had higher abundance than the ambient-origin genotype at all
264 temperatures with no significant interaction between resource evolutionary history and current thermal
265 environment (effect of evolutionary history in algae-alone ANOVAs: $F_1 = 158.47$, $p < 0.0001$; interaction
266 between evolutionary history and temperature: NS), an effect that appeared to be driven by differences
267 across resource evolutionary history in temporal block 2 (Figure 2A, Figures S1 and S2). For
268 *Desmodesmus* sp., the effect of evolutionary history depended upon temperature, with higher
269 abundance of the warm-origin genotype at 14 °C, but lower abundance than the ambient-adapted
270 genotype at the remaining three temperatures (effect of evolutionary history in algae-alone ANOVAs: F_1
271 $= 7.02$, $p = 0.0109$; interaction between evolutionary history and temperature: $F_3 = 5.86$, $p = 0.0017$)
272 (Figure 2B, Figure S1). Here, higher abundance of the warm genotype at 14 °C was observed in temporal

block 1, while the reduced abundance of warm genotype was more generally observed in temporal block 2 (Figure S2).

Interspecific interactions modulate how current thermal environment interacts with prior evolution in response to warming

Effects of interspecific interactions on resource abundance

The presence of the consumer *Daphnia pulex* altered the effects of resource evolutionary history for both resources, but in opposite directions (Tables 2–4). For *C. reinhardtii*, where no significant interaction between resource evolutionary history and temperature occurred when grown alone, the presence of the consumer resulted in a significant evolutionary history by temperature interaction driven by resource evolution (consumer–resource ANOVA resource evolution contrast: F_1 = 318.47, $p < 0.0001$). Specifically, when consumers were present, the importance of resource evolutionary history was higher at intermediate temperatures (18 and 22 °C) than at the two temperature extremes (14 and 26 °C) (Figure 2C). In other words, temperature did not affect the direction of the response to evolutionary history. It did, however, increase the magnitude of the effect size at intermediate compared to extreme temperatures (effect of evolutionary history in consumer–resource ANOVA: F_3 = 107.54, $p < 0.0001$; interaction between evolutionary history and temperature: F_9 = 4.93, $p < 0.0001$). The temperature dependence of evolutionary history was stronger in the first temporal block (Figure S2). On the other hand, for *Desmodesmus* sp., the presence of consumers rendered the interaction between resource evolutionary history and temperature non-significant (effect of evolutionary history in consumer–resource ANOVA: F_3 = 3.54, $p = 0.0175$; interaction between evolutionary history and temperature: NS) (Figure 2D). Here, when consumers were present, resource evolution decreased algal abundance, reversing the pattern seen at 14 °C in the absence of consumers (consumer–resource ANOVA resource evolution contrast: F_1 = 10.57, $p = 0.0016$) (Figure 2D). The

296 observed negative effects of resource evolution were driven by patterns in the second block, with
297 weaker and somewhat opposite effects in block 1 (Figure S2).

298 *Effects of evolutionary history on interaction strength*

299 The importance of resource evolutionary history on algae abundance was reflected in the
300 changes to interaction strength for each consumer–resource pair (Tables 3 and 4). For the *D. pulex*–*C.*
301 *reinhardtii* pair, resource evolution reduced interaction strength (consumer–resource ANOVA resource
302 evolution contrast: $F_1 = 54.90$, $p < 0.0001$), but primarily at intermediate temperatures (interaction
303 between evolutionary history and temperature: $F_9 = 5.16$, $p < 0.0001$) (Figure 3A) in both blocks (Figure
304 S2). For the *D. pulex*–*Desmodesmus* sp. pair, however, resource evolution increased interaction
305 strength, independent of temperature (consumer–resource ANOVA resource evolution contrast: $F_1 =$
306 5.86, $p = 0.0174$; interaction between evolutionary history and temperature: NS) (Figure 3B). For this
307 species pair, overall trends in interaction strength were driven by patterns in block 2, here again with
308 weaker and somewhat opposite effects in block 1 (Figure S2)

309 *Consumer responses to evolutionary history and temperature*

310 For the consumer, *Daphnia pulex*, the effects of evolutionary history differed depending upon its
311 resource species. When paired with *C. reinhardtii*, resource evolution significantly reduced the
312 abundance of adult and juvenile *D. pulex* (adult resource evolution contrast: $F_1 = 5.50$, $p = 0.0211$;
313 juvenile resource evolution contrast: $F_1 = 5.07$, $p = 0.0266$; Table 2, Figure 4A,B). The observed effect of
314 resource evolution was primarily driven by patterns in block 1 (Figure S3). In this pairing, neither
315 consumer evolution nor coevolution affected the abundance of *D. pulex* and the effects of resource
316 evolution were independent of temperature (consumer–resource ANOVA interaction between
317 evolutionary history and temperature: NS).

When growing on the resource *Desmodesmus* sp., the effects of consumer evolution became apparent. In this case, warm-origin consumers had overall lower abundance than the ambient-origin population (adult consumer evolution contrast: $F_1 = 15.87$, $p = 0.0001$; juvenile consumer evolution contrast: $F_1 = 9.77$, $p = 0.0024$; Table 4, Figure 4C,D). There was no direct effect of *Desmodesmus* evolution, but coevolution between the resource and consumer affected consumer abundance (adult coevolution contrast: $F_1 = 8.52$, $p = 0.0044$; juvenile coevolution contrast: $F_1 = 12.55$, $p = 0.0006$). The effects on juveniles were driven in a large part by patterns in block 1 (Figure S3). The effects of evolutionary history were also dependent upon current thermal environment when growing on *Desmodesmus* sp. (evolutionary history-temperature interaction for adult and juvenile daphnids respectively: $F_9 = 2.09$, $p = 0.0380$ and $F_9 = 2.21$, $p = 0.0281$; Table 4, Figure 4C,D). For *D. pulex* growing on *Desmodesmus* sp., the effects of consumer evolution were most evident at 14 °C, where evolved *D. pulex* adults ("Evolved consumer" and "Both evolved" treatments in Figure 4) had significantly reduced abundance regardless of *Desmodesmus* evolutionary history compared to the ambient-origin *D. pulex* ("Neither evolved" and "Evolved resource" treatments). The effects of coevolution between the consumer and resource were strongest at 26 °C, with warm-adapted adult *D. pulex* abundance being significantly reduced only in the presence of warm-adapted *Desmodesmus* sp. ("Both evolved" treatment) (Figure 4D). In contrast to the temperature-dependence observed for the resource, *C. reinhardtii*, evolutionary history was less important for consumer abundance at intermediate temperatures.

Robustness of the approach

Although we observed significant effects of temporal block, our planned contrasts examining the overall effects of evolutionary history lend us confidence in interpreting the overall importance of evolutionary history in driving our results. Additionally, because we both centered across temporal

341 blocks, as well as examined patterns within blocks to understand interactions, we feel that our
342 interpretation of our results is robust. The differences across temporal blocks could plausibly have
343 resulted from a number of factors that we were unable to control completely. First, we attempted to
344 maintain all algal source populations in the exponential phase (maximizing population growth rate at
345 start) and standardize starting abundances. Nonetheless, starting populations differed somewhat in
346 abundance within and across blocks. Similarly, some populations may have been in—or closer to—
347 stationary phase than others, despite our efforts to maintain all at exponential growth. Similarly,
348 although we standardized our selection of *Daphnia* by choosing the largest adults, adults may have
349 differed in average age across the temporal blocks, potentially contributing to differences in *Daphnia*
350 population size and growth rate. Finally, we swapped incubators among treatments across the two
351 temporal blocks to avoid incubator pseudoreplication, possibly leading to unmeasured incubator effects.

352 **Discussion**

353 Understanding the interaction between evolutionary history, the current abiotic environment,
354 and biotic interactions is critical for a more nuanced understanding of how communities respond to
355 anthropogenic stressors. Here we showed that both the current thermal environment, as well as the
356 presence of interspecific interactions can affect the importance of prior evolution in response to
357 warming in complex communities, and that this evolution also influences the outcomes of current
358 ecological dynamics. For each consumer–resource pair, the effects of evolution were temperature-
359 dependent, but both the effects and the temperature-dependence itself additionally depended upon
360 the identity of evolving species in each pair.

361 *The importance of evolutionary history depends upon current thermal environment*

362 Evolution in warmed communities had significant effects on the two algal resource species when
363 grown alone, but these effects were opposite in direction and differed in magnitude. In one species,

364 *Chlamydomonas reinhardtii*, prior evolution in warmed communities increased fitness (as assessed by
365 abundance) across all temperatures, a result that is broadly consistent with the "hotter is better"
366 hypothesis (Liu et al. 2022)(Figure S1), although our tested temperature range (determined by the
367 thermal tolerance and activity of the consumer) precluded us from definitively evaluating competing
368 proposed evolutionary responses. The positive direction of change agrees with a previous experiment
369 examining the short-term effects of thermal evolution of *C. reinhardtii* independently isolated from
370 these same mesocosms (Schaum et al. 2017). In the second alga, *Desmodesmus* sp., the effects of
371 evolutionary history were dependent upon the current thermal environment. For this species, fitness
372 was lower in the warm-origin genotype at three of the four tested temperatures, but the pattern was
373 reversed at 14 °C, the lowest temperature in our range. This reversal of direction of effect across
374 temperatures suggests the possibility of a response that is harmful in part of the thermal range, but
375 possibly advantageous in another (Figure S1). The pattern of the result is surprising however, as the
376 expectation is that warm-origin populations would perform better at warm temperatures compared to
377 colder temperatures if the evolutionary response was directly driven by the experimentally imposed
378 temperature treatment.

379 Evaluating the mechanisms underlying this result was impossible given that we only successfully
380 isolated one genotype for each species from each of the ambient and warm mesocosms, however, these
381 results may be consistent with one or more aspects of our system. First, our algal genotypes were
382 isolated from the experimental ponds during the winter season, so this particular genotype may be
383 more successful in the winter conditions experienced by the experimentally warmed ponds. Typical
384 winter conditions in the ponds ranged from approximately 3–10 °C with a mean of around 6 °C (Yvon-
385 Durocher et al. 2015), thus the additional +4 °C of warming experimentally imposed upon these ponds
386 raised the winter temperature to within a few degrees of our 14 °C treatment. We did not examine the
387 effects of evolutionary history at any temperature lower than 14 °C, however, so we are unable to

388 compare the relative fitness of each genotype at typical winter temperatures compared to 14 °C.
389 Conversely, the warm-origin genotype that we isolated may be maladaptive, with lower fitness than the
390 ambient-origin genotype under most conditions. Anthropogenic warming is anticipated to create an
391 extinction debt in many communities (Cotto et al. 2017), with poorly adapted species expected to be
392 lost over time, especially as a result of stochastic processes combined with low dispersal (Kuussaari et al.
393 2009). It is possible that we captured part of this process, with a maladapted genotype "trapped" in the
394 warm mesocosms. Another possibility is that the selection occurred in response to an agent that
395 emerged secondary to the experimentally imposed temperature treatment. Our manipulative approach
396 isolates temperature from other climatic variables that may affect evolutionary trajectory in natural
397 populations, but our populations were nonetheless potentially evolving in response to a number of
398 factors (e.g., community composition) that diverged over the course of this long-running experiment
399 (Yvon-Durocher et al. 2011, 2015, Dossena et al. 2012). Thus, although we can ultimately link our
400 responses to the experimentally-imposed warming treatment, populations are potentially evolving to a
401 number of simultaneous and related stressors (terHorst et al. 2018). While this situation reflects the
402 expectation for natural communities responding to habitat warming—namely that responses will
403 encompass altered biotic interactions as well as direct responses to changed abiotic factors—it is
404 therefore impossible for us to definitively disentangle the most likely mechanism driving the lowered
405 fitness that we observed in warm-origin populations of *Desmodesmus* sp.

406 *Current ecological context modulates the temperature-dependence of the effects of evolutionary history*

407 Our understanding of how evolution is altered in complex communities is still limited. However,
408 previous studies suggest that evolution to environmental stressors, like habitat warming, that occurs in
409 populations embedded within communities can yield different outcomes compared to evolution in
410 single populations (Van Doorslaer et al. 2009b, 2010, terHorst et al. 2018, Hiltunen et al. 2018, De

411 Meester et al. 2019). Our experiment complements a growing body of evidence that shows that
412 evolutionary responses to warming do occur in complex communities (De Meester et al. 2019,
413 McGaughran et al. 2021, Douce et al. 2024), and that such evolution has important consequences for
414 both the direct responses to evolutionary stressors as well as for the interspecific interactions that
415 ultimately shape communities.

416 The inclusion of consumer–resource interactions also introduced an additional layer of
417 complexity necessary to understand how the importance of evolutionary history is affected by
418 temperature. Organisms exhibit a mixture of unimodal and linear responses of traits to temperature,
419 and interacting organisms differ in both the ecological and evolutionary responses of these traits. The
420 interactions themselves may therefore depend upon temperature, influencing the outcomes of
421 evolutionary change evaluated across temperatures (Barton and Yvon-Durocher 2019). For both
422 consumer–resource pairs in our study system, the presence of the consumer altered the interaction
423 between evolutionary history and temperature, indicating that examining the effects of past evolution
424 in response to environmental change can be highly dependent on the current ecological conditions.

425 In the case of the *Daphnia pulex–C. reinhardtii* pair, the importance of evolutionary history was
426 only temperature-dependent when the consumer was present. For this pair, the magnitude of the effect
427 of evolutionary history on algal abundance was higher at intermediate temperatures compared to
428 temperature extremes, adding nuance to the result that "hotter is better", making it instead "hotter is
429 best at moderate or intermediate temperatures". Consumer evolution was unimportant when *D. pulex*
430 was paired with *C. reinhardtii*—warm-origin *C. reinhardtii* significantly reduced the abundance of the
431 consumer regardless of temperature. Thus, "hotter is better" for this resource translates into "hotter is
432 worse" for the consumer in terms of the effects of resource evolution. We noted that the warm-origin
433 genotype exhibited a mucilaginous extra-cellular matrix that might be expected to reduce ingestion

434 rates for filter-feeding consumers like *D. pulex*. These results are also consistent with observations of an
435 increased carbon to phosphorus ratio (i.e., reduced resource quality) observed previously in warm-
436 adapted *C. reinhardtii* independently isolated from these experimental mesocosms (Yvon-Durocher et
437 al. 2017). Such a reduction in resource quality would be expected to negatively affect consumer
438 performance (Leal et al. 2017), but an analysis of nutrient content of the algae was outside the scope of
439 our experiment. It is noteworthy, however, that despite the lack of a significant interaction between
440 evolutionary history and temperature, the importance of resource evolution was strongest at 22 °C, the
441 temperature at which *D. pulex* abundance was highest, and weakest at 26 °C, where the daphnids
442 struggled to persist. The evolution that we observed in *C. reinhardtii* thus appeared to confer a double
443 advantage to the resource, making it both more fit, while simultaneously reducing the success of the
444 consumer, possibly the reason why we observed larger effect sizes for resource evolutionary history in
445 the presence of the consumer, especially at intermediate temperatures (i.e., effect size more than
446 doubled on a $\log_{10}$ scale).

447 The effects of consumer presence for *Desmodesmus* sp. were opposite to those for *C.*
448 *reinhardtii*. Here, the presence of the consumer eliminated the temperature-dependence seen when
449 *Desmodesmus* sp. grew alone, and even reversed the direction of the effect of evolutionary history at 14
450 °C. When paired with the consumer, this subtlety across temperatures was lost, and warm-origin
451 *Desmodesmus* sp. underperformed relative to ambient-origin *Desmodesmus* regardless of temperature.
452 One possible explanation for the apparently reduced fitness of the warm-origin genotype could be that
453 it served as a superior food source for the *Daphnia*. If this were the case, we might expect to see that
454 the *Daphnia* achieved higher abundances when consuming the warm-origin algae. In fact, however,
455 *Desmodesmus* sp. evolutionary history had contrasting effects on the consumer's fitness depending
456 upon consumer thermal origin (i.e., the effect of coevolution on *D. pulex* abundance in this pair).
457 Ambient-origin consumers exhibited a trend towards slightly higher fitness with warm-origin resource,

458 but warm-origin *Daphnia* had lowest fitness when paired with warm-origin *Desmodesmus*. Thus, the
459 effect does not appear to be consistent with increased consumption by the *Daphnia*. Additionally, in this
460 pair, the *Daphnia* experienced temperature-dependent effects of evolutionary history. Here, effects
461 were strongest at the two temperature extremes, with warm-origin *Daphnia* having lowest abundance
462 at these temperatures, and especially at 26 °C and when paired with warm-origin *Desmodesmus* sp.

463 We examined the temperature-dependent consequences of evolution for two consumer–
464 resource pairs over multiple generations of interactions and found evidence for adaptive evolution in
465 response to warming in one of the two species pairs examined. For the *D. pulex*–*C. reinhardtii* pair, we
466 observed adaptive evolution broadly consistent with expectations from the "hotter is better" hypothesis
467 for the resource. While clearly, "hotter is better" did not apply to the consumer in our experiment, we
468 did note a potential—albeit, non-significant—trend better matching "biochemical adaptation" for *D.*
469 *pulex*, at least when paired with *C. reinhardtii*. Specifically, after examining just the performance of the
470 warm-origin consumer relevant to the ambient-origin consumer when paired with the ambient-origin
471 resource (i.e., removing resource evolution from the picture entirely), a trend emerged. The thermal
472 optimum of *D. pulex* seemed to shift from 18 to 22 °C, without any increase in the magnitude of the
473 optimum (Figure S2). Interestingly, however, no such trend is apparent when *D. pulex* is paired with
474 *Desmodesmus* sp., nor does it seem to confer a measurable fitness advantage to the warm-origin
475 consumer. Overall, hotter was worse from the perspective of the consumer, driven both by decreased
476 performance in the presence of warm-origin resources (when paired with *C. reinhardtii*) and as a result
477 of its own evolution (when paired with *Desmodesmus* sp.). These observations should be treated with
478 caution, however, as the experimental design with four temperatures did not enable us to fit thermal
479 performance curves to statistically evaluate these trends in the data. This result may seem surprising,
480 but not only is evolutionary adaptation as a result of warming not expected in all species (Hoffmann and
481 Sgró 2011), it also remains possible that the fitness consequences of the response depend upon the

482 length of the temperature exposure. We focused on the effects of constant temperature over multiple
483 generations, however, the semi-natural mesocosms from which we isolated these genotypes
484 additionally fluctuate in temperature both diurnally and seasonally. These fluctuations may be an
485 important component of the selection imposed by the experimental warming treatment (Diamond
486 2017), and organisms in warmed ponds may experience more frequent and intense, but shorter, periods
487 of thermal stress. A more complete understanding of the interaction between current thermal
488 environment and evolutionary history, therefore, will require an improved understanding of how
489 populations respond to fluctuating temperatures.

490 **Conclusions**

491 Our work demonstrates that local thermal environment and biotic interactions can together
492 modulate the importance of past thermal evolutionary history. In some cases, evolution in response to
493 warming can be beneficial for resources but detrimental for consumers, suggesting that we must
494 account for the effects of warming on ingestion rates (see e.g., Barneche et al. 2021). In other cases, the
495 picture is more complex and changes across a temperature range. This topic deserves further attention
496 to improve our understanding of how populations and communities evolve in response to habitat
497 warming, and how this then feeds back to drive the effects of the evolution. We have built upon
498 previous studies that have primarily used space-for-time latitudinal substitutions in comparisons of
499 different thermally adapted populations (e.g., Sanford et al. 2003, De Block et al. 2013, Dinh Van et al.
500 2013, Tran et al. 2016) and argue that future studies should consider both the current biotic and thermal
501 context of their experiments, while definitely attributing evolutionary response to a manipulated factor
502 of interest. These community properties can affect outcomes, not just in terms of the magnitude of the
503 effect size, but even in direction of the effect. It is therefore of the utmost importance that we account
504 for these interactions in our collective understanding. Evolution can drive responses in unexpected
505 directions, but it is essential that we consider evolutionary responses to anthropogenic change in the

506 context of both the current abiotic and biotic conditions to understand the full extent and direction of
507 its effects.

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512 **Author contributions**

513 CAF and JMM conceived and designed the study. CAF, SAC, AG, and EB isolated organisms and
514 collected data. CAF analyzed the data. CAF wrote the first draft of the manuscript. CAF, JMM, SAC, and
515 EB jointly revised the manuscript. The authors declare no competing financial interests.

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679

680 Table 1. Results from univariate ANOVAs (n = 8) examining the effects of resource evolution when
681 growing alone for *Chlamydomonas reinhardtii* and *Desmodesmus* sp. The models included an evolution
682 treatment and temperature as two main effects, as well as a temporal blocking variable and all
683 interactions. Here, the evolution treatment included just the evolutionary history of the resource
684 species, either ambient-origin or warm-origin. The interaction between evolution treatment and
685 temperature evaluated any temperature-dependence of the effects of evolution. Significant results are
686 in bold.

C. reinhardtii			
	d.f.	F-value	p-value
Evolution	1	**158.47**	**< 0.0001**
Temperature	3	**12.56**	**< 0.0001**
Temporal block	1	**54.12**	**< 0.0001**
Evolution–temperature	3	0.67	0.5776
Temperature–block	3	**15.43**	**< 0.0001**
Evolution– block	1	**127.63**	**< 0.0001**
Evolution–temperature–block	3	**5.96**	**0.0015**
Desmodesmus sp.			
	d.f.	F-value	p-value
Evolution	1	**7.02**	**0.0109**
Temperature	3	**47.41**	**< 0.0001**
Temporal block	1	3.94	0.0529
Evolution– temperature	3	**5.86**	**0.0017**
Temperature–block	3	**5.19**	**0.0035**
Evolution–block	1	**42.75**	**< 0.0001**
Evolution–temperature–block	3	**3.10**	**0.0353**

687

688 Table 2. MANOVA (n = 8) results examining the effects of evolution of both the consumer and the
689 resource in complex communities in response to warming for two consumer–resource pairs, *C.*
690 *reinhardtii* and *D. pulex*, and *Desmodesmus* sp. and *D. pulex*. The models included an evolution
691 treatment and temperature as two main effects, as well as a temporal blocking variable and all
692 interactions. Here, the evolution treatment included the four possible combinations crossing the
693 ambient- or warm-origin populations of both resources and consumers, but these analyses did not
694 include algae-alone controls. The interaction between the evolution treatment and temperature
695 evaluated any temperature-dependence of the effects of evolution. Orthogonal contrasts evaluated the
696 effects of 1) resource evolution, 2) consumer evolution, and 3) coevolution between the resource and
697 the consumer. Reported are Wilks' Lambda F-values and associated p-values. Significant results are in
698 bold.

C. reinhardtii–D. pulex			
	d.f.	F-value	p-value
Evolution	12, 243.7	**70495.6**	**< 0.0001**
Temperature	12, 243.7	**45724.4**	**< 0.0001**
Temporal block	4, 92	**1.82E10**	**< 0.0001**
Evolution–temperature	36, 346.5	**1163.05**	**< 0.0001**
Temperature–block	12, 243.7	**51809.9**	**< 0.0001**
Evolution– block	12, 243.7	**63495.4**	**< 0.0001**
Evolution–temperature–block	36, 346.5	**1863.05**	**< 0.0001**
Resource evolution contrast	4, 92	**4.93E10**	**< 0.0001**
Consumer evolution contrast	3, 93	1.72	0.1683
Coevolution contrast	3, 93	1.05	0.3729
Desmodesmus sp.–*D. pulex*			
	d.f.	F-value	p-value
Evolution	12, 243.7	**578.58**	**< 0.0001**
Temperature	12, 243.7	**563.64**	**< 0.0001**
Temporal block	4, 92	**2818757**	**< 0.0001**
Evolution–temperature	36, 346.5	**56.96**	**< 0.0001**
Temperature–block	12, 243.7	**363.01**	**< 0.0001**
Evolution– block	12, 243.7	**633.42**	**< 0.0001**
Evolution–temperature–block	36, 346.5	**61.15**	**< 0.0001**
Resource evolution contrast	4, 92	**55119.7**	**< 0.0001**
Consumer evolution contrast	3, 93	**52771.4**	**< 0.0001**
Coevolution contrast	3, 93	**55945.4**	**< 0.0001**

699

Table 3. *Chlamydomonas reinhardtii* and *Daphnia pulex* univariate ANOVA (n = 8) results examining the effects of evolution of both the consumer and the resource in complex communities in response to warming. The model included an evolution treatment and temperature as two main effects, as well as a temporal blocking variable and all interactions. Here, the evolution treatment included the four possible combinations crossing the ambient- or warm-origin populations of both resources and consumers, but these analyses did not include algae-alone controls. The interaction between the evolution treatment and temperature evaluated any temperature-dependence of the effects of evolution. Orthogonal contrasts evaluated the effects of 1) resource evolution, 2) consumer evolution, and 3) coevolution between the resource and the consumer. Reported are Type III SS F-values and p-values for the model (due to one missing value causing a slightly unbalanced design). Significant results are in bold.

	***C. reinhardtii* $\log_{10}$ abundance**			**Interaction strength**			***D. pulex adult* $\log_{10}$ abundance**			***D. pulex* juvenile $\log_{10}$ abundance**		
	d.f.	F-value	p-value	d.f.	F-value	p-value	d.f.	F-value	p-value	d.f.	F-value	p-value
Evolution	3	**107.54**	**< 0.0001**	3	**19.64**	**< 0.0001**	3	2.35	0.0772	3	1.80	0.1529
Temperature	3	**17.48**	**< 0.0001**	3	**48.61**	**< 0.0001**	3	**6.37**	**0.0006**	3	**7.48**	**0.0001**
Temporal block	1	**162.18**	**< 0.0001**	1	**359.69**	**< 0.0001**	1	0.10	0.7532	1	0.00	0.9543
Evolution–temperature	9	**4.39**	**< 0.0001**	9	**5.16**	**< 0.0001**	9	1.20	0.3067	9	0.53	0.8469
Temperature–block	3	**12.52**	**< 0.0001**	3	**25.83**	**< 0.0001**	3	**5.08**	**0.0026**	3	1.55	0.2062
Evolution–block	3	**4.00**	**0.0099**	3	**11.85**	**< 0.0001**	3	**3.51**	**0.0183**	3	2.31	0.0815
Evolution–temperature–block	9	1.63	0.1170	9	**3.52**	**0.0009**	9	1.40	0.2010	9	1.07	0.3949
Resource evolution contrast	1	**318.47**	**< 0.0001**	1	**54.90**	**< 0.0001**	1	**5.50**	**0.0211**	1	**5.07**	**0.0266**
Consumer evolution contrast	1	1.36	0.2456	1	1.36	0.2456	1	1.48	0.2262	1	0.29	0.5904
Coevolution contrast	1	2.53	0.1150	1	2.53	0.1150	1	0.01	0.9339	1	0.00	0.9740

Table 4. *Desmodesmus* sp. and *Daphnia pulex* univariate ANOVA (n = 8) results examining the effects of evolution of both the consumer and the resource in complex communities in response to warming. The model included an evolution treatment and temperature as two main effects, as well as a temporal blocking variable and all interactions. Here, the evolution treatment included the four possible combinations crossing the ambient- or warm-origin populations of both resources and consumers, but these analyses did not include algae-alone controls. The interaction between the evolution treatment and temperature evaluated any temperature-dependence of the effects of evolution. Orthogonal contrasts evaluated the effects of 1) resource evolution, 2) consumer evolution, and 3) coevolution between the resource and the consumer. Reported are Type III SS F-values and p-values for the model (due to one missing value causing a slightly unbalanced design). Significant results are in bold.

	***Desmodesmus* sp. $\log_{10}$ abundance**			**Interaction strength**			***D. pulex* adult $\log_{10}$ abundance**			***D. pulex* juvenile $\log_{10}$ abundance**		
	d.f.	F-value	p-value	d.f.	F-value	p-value	d.f.	F-value	p-value	d.f.	F-value	p-value
Evolution	3	**3.54**	**0.0175**	3	2.50	0.0645	3	**8.26**	**< 0.0001**	3	**8.66**	**< 0.0001**
Temperature	3	**11.26**	**< 0.0001**	3	**13.15**	**< 0.0001**	3	**14.08**	**< 0.0001**	3	**33.57**	**< 0.0001**
Temporal block	1	**47.32**	**< 0.0001**	1	0.88	0.3513	1	**17.64**	**< 0.0001**	1	**83.67**	**< 0.0001**
Evolution–temperature	9	0.73	0.6804	9	0.77	0.6466	9	**2.09**	**0.0380**	9	**2.21**	**0.0281**
Temperature–block	3	**5.39**	**0.0018**	3	**5.96**	**0.0009**	3	**4.62**	**0.0046**	3	**54.08**	**< 0.0001**
Evolution–block	3	**14.12**	**< 0.0001**	3	**10.25**	**< 0.0001**	3	2.66	0.0528	3	**4.92**	**0.0032**
Evolution–temperature–block	9	0.45	0.9066	9	0.33	0.9636	9	1.33	0.2309	9	**2.10**	**0.0368**
Resource evolution contrast	1	**10.57**	**0.0016**	1	**5.86**	**0.0174**	1	0.51	0.4752	1	3.61	0.0605
Consumer evolution contrast	1	0.07	0.7925	1	1.16	0.2846	1	**15.87**	**0.0001**	1	**9.77**	**0.0024**
Coevolution contrast	1	0.01	0.9385	1	0.58	0.4496	1	**8.52**	**0.0044**	1	**12.55**	**0.0006**

Figure 1. Experimental design in which populations from two resource species and one consumer species were first collected from a long-running warming experiment using communities of plankton in outdoor mesocosms. After isolation and a period of laboratory common garden, for each consumer–resource pair, subsequent experiments examined the interaction between evolutionary history of resources and consumers and current thermal environment on population abundance.

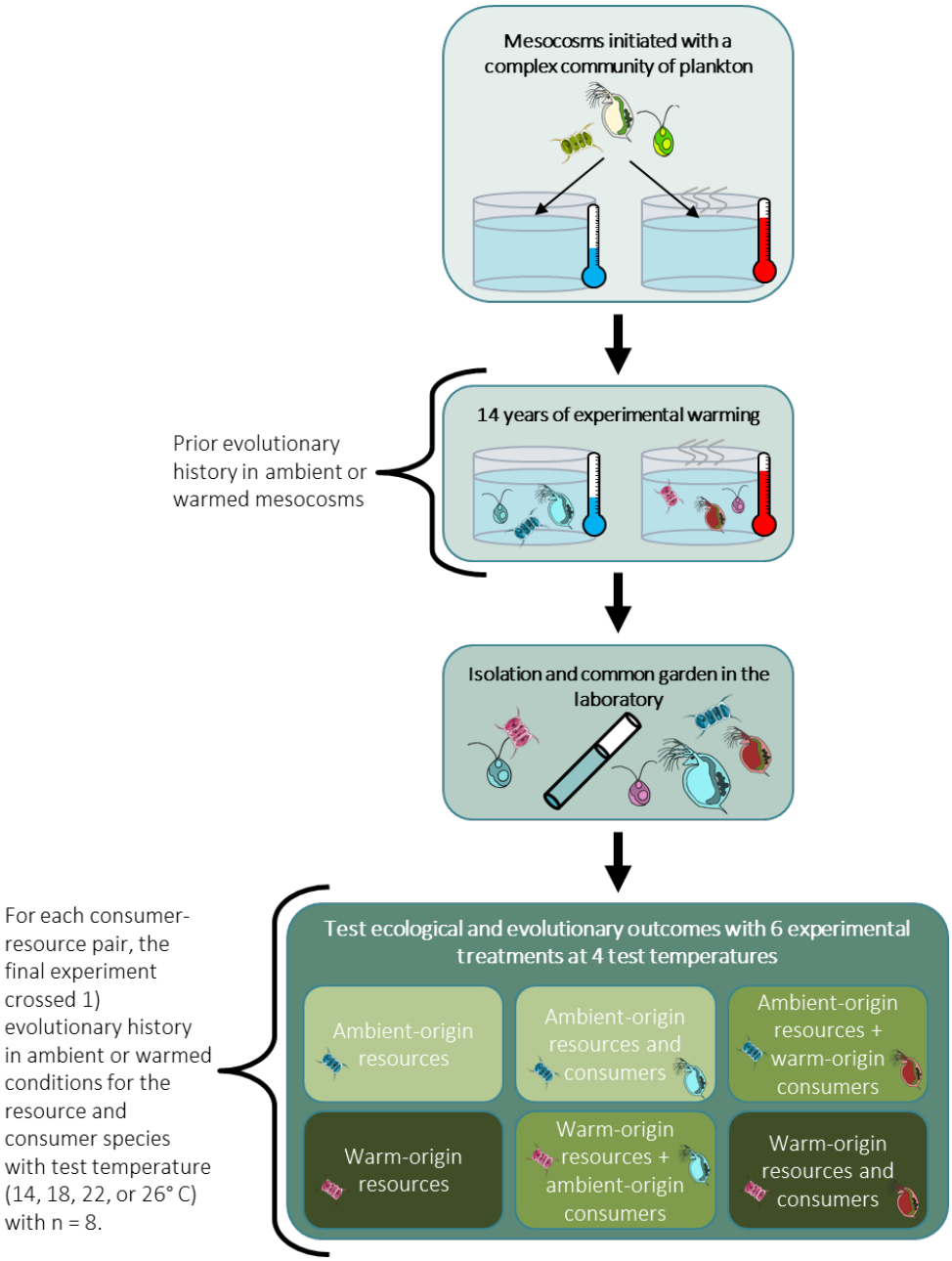

Figure 2A–D. The effects of evolution in warmed communities on the $\log_{10}$-abundance of *C. reinhardtii* and *Desmodesmus* sp. depend upon current thermal environment and whether consumers are absent (A, B) or present (C, D), with related effects to the consumer–resource interaction strength (E, F). Evolutionary history treatments (where "evolved" refers to evolution in the warmed communities) are shown on the x-axis. Circles are the means (n = 8) of each treatment with the error bars showing ± the SEM. Colors correspond to temperature (dark blue = 14, light blue = 18, light pink = 22, and dark pink = 26 °C).

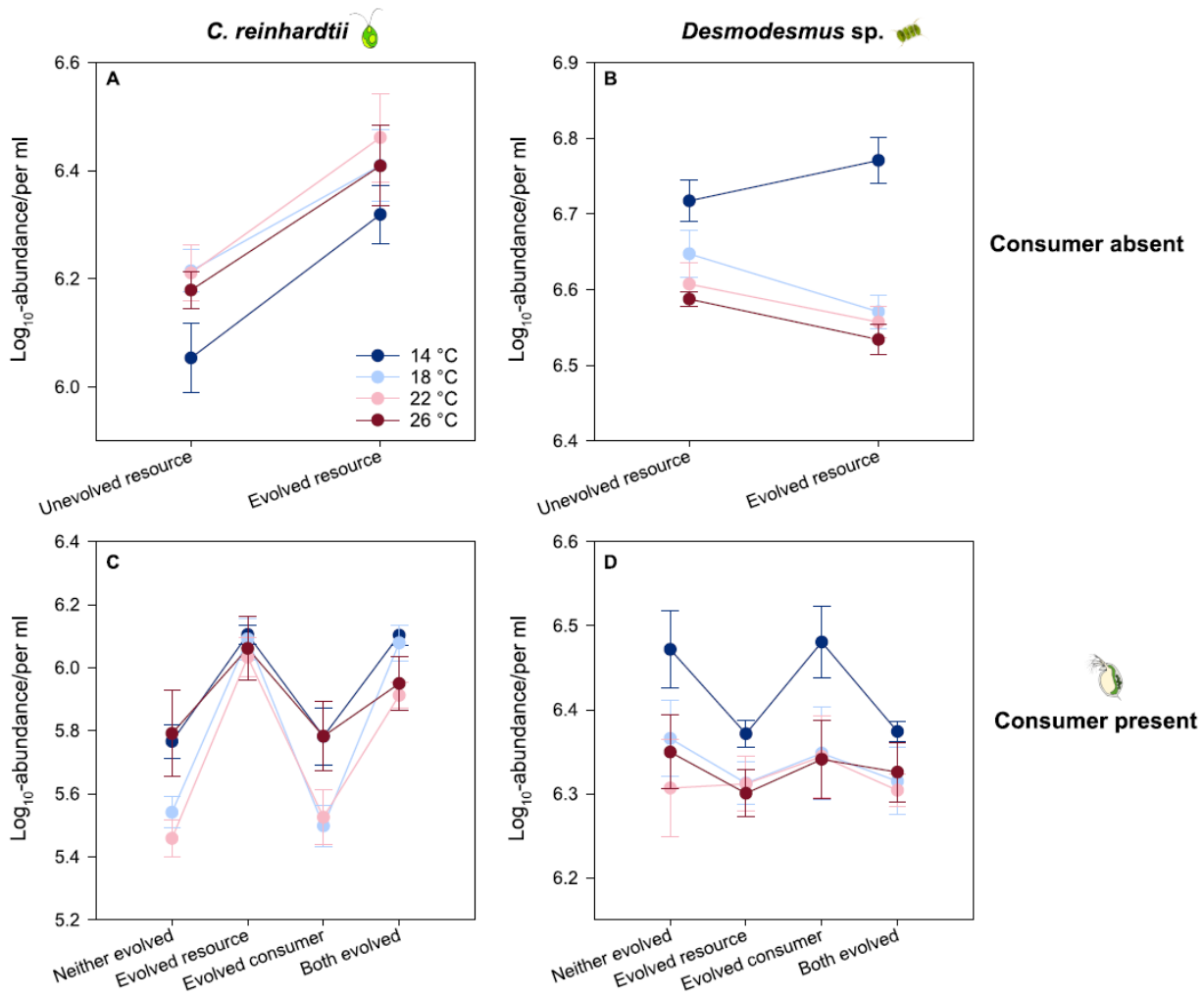

Figure 3A, B. The effects of evolution in warmed communities on interaction strength of *C. reinhardtii* (A) and *Desmodesmus* sp. (B) with *D. pulex* depend upon current thermal. Evolutionary history treatments (where "evolved" refers to evolution in the warmed communities) are shown on the x-axis. Circles are the means (n = 8) of each treatment with the error bars showing ± the SEM. Colors correspond to temperature (dark blue = 14, light blue = 18, light pink = 22, and dark pink = 26 °C).

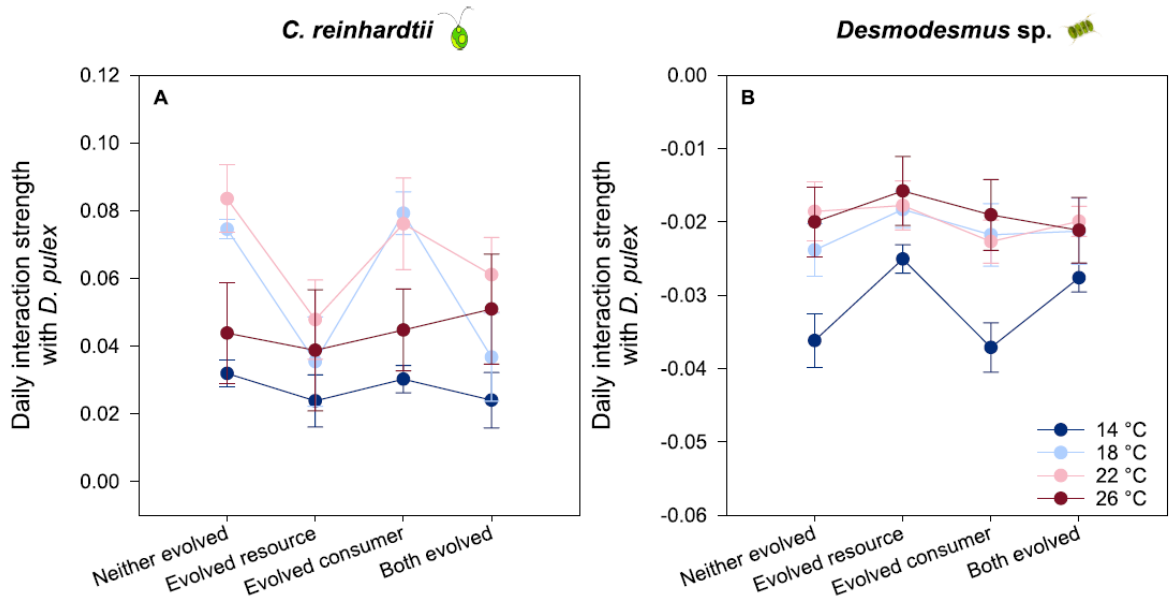
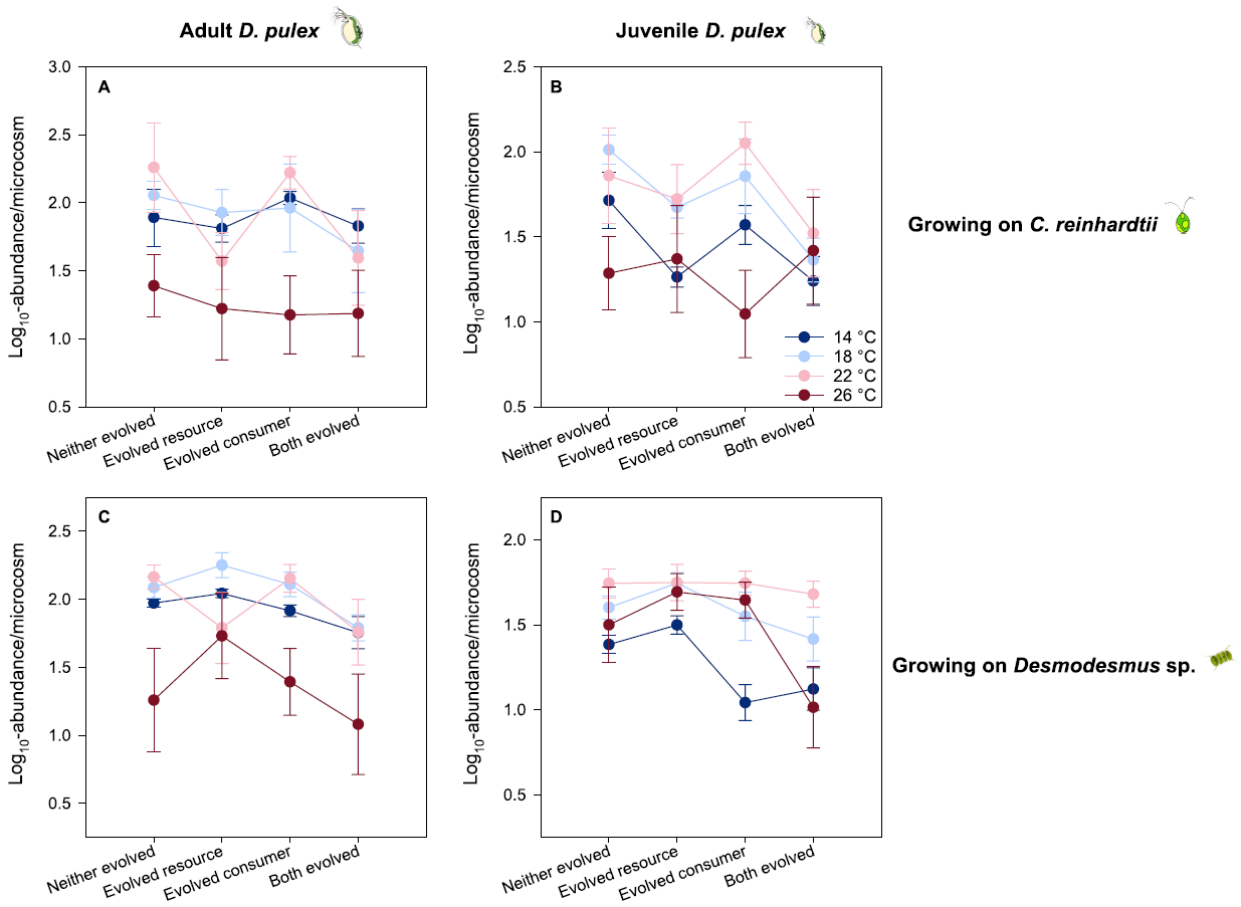
Figure 4A–D. The effects of evolution in warmed communities on the $\log_{10}$-abundance of *D. pulex* juveniles (A) and adults (B) growing on *C. reinhardtii* and on *Desmodesmus* sp. (C, D) depend upon current thermal environment. In all plots, evolutionary history treatments (where "evolved" refers to evolution in the warmed communities) are shown on the x-axis. Circles are the means (n = 8) of each treatment with the error bars showing ± the SEM. Colors correspond to temperature (dark blue = 14, light blue = 18, light pink = 22, and dark pink = 26 °C.