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Thermal plasticity and evolution shape predator-prey interactions differently in clear and turbid water

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Abstract

1. Warming and eutrophication negatively affect freshwater ecosystems by modifying trophic interactions and increasing water turbidity. We need to consider their joint effects on predator-prey interactions, and how these depend on the thermal evolution of both predator and prey.
2. We quantified how 4°C warming and algae-induced turbidity (that integrates turbidity *per se* and increased food for zooplankton prey) affect functional response parameters and prey population parameters in a common-garden experiment. We did so for all combinations of high- and low-latitude predator (damselfly larvae) and prey (water fleas) populations to assess the potential impact of thermal evolution of predators and/or prey at a high latitude under warming using a space-for-time substitution. We then modelled effects on the system stability (i.e. tendency to oscillate) under different warming, turbidity and evolutionary scenarios.
3. Warming and turbidity had little effect on the functional response parameters of high-latitude predators. In contrast, warming and turbidity reduced the handling times of low-latitude predators. Moreover, warming increased the search rates of low-latitude predators in clear water but instead decreased these in turbid water.
4. Warming increased stability (i.e. prevented oscillations) in turbid water (except for the "high-latitude predator & high-latitude prey" system), mainly by decreasing the prey's carrying capacity and partly also by decreasing search rates, while it did not affect stability in clear water. Algae-induced turbidity generally decreased stability, mainly by increasing the prey's carrying capacity and partly also by increasing search rates. This resembles findings that nutrient enrichment can reduce the stability of trophic systems. The expected stability of the high-latitude trophic system under warming was dependent on the turbidity level: our results suggest that thermal plasticity tends to destabilize the high-latitude trophic system under warming in clear water but not in turbid water, and that thermal evolution of the predator will stabilize the high-latitude system under warming in turbid water but less so in clear water.

5. The extent to which thermal plasticity and evolution shape trophic system stability under warming may strongly differ between clear and turbid water bodies, with their contributions having a more stabilizing role in turbid water.

Keywords: Eutrophication, *Daphnia magna*, predator-prey interactions, space-for-time substitution, thermal evolution, trophic system stability, turbidity, warming

Introduction

Whether global change will threaten the local persistence of populations and the stability of ecosystems will crucially depend on how populations can cope with the increasing co-exposure to stressors (Côté et al., 2016; Orr et al., 2020) and how trophic interactions are modified (Filazzola et al., 2020; Urban et al., 2016). Nevertheless, both important insights have rarely been integrated in a single study. Warming and eutrophication are two major global change-related factors negatively affecting freshwater ecosystems (Moss, 2011; Woodward et al., 2010). Eutrophication increases algae growth, and may thereby cause freshwater systems to switch from a clear to a turbid state that may impair ecosystem functioning (Scheffer et al. 2001). Zooplankton grazers play an important role in the transitions between algae-induced turbidity states given their potential to suppress algae populations (Lampert et al., 1986; Scheffer et al. 2001; Rogers et al., 2020). Interestingly, algae-induced turbidity may also change the interactions of zooplankton grazers with their predators (Jönsson et al., 2011; Kimbell et al. 2016). Warming may not only magnify the effects of eutrophication on algae-induced turbidity (Moss, 2011), but in itself also impair ecosystem functioning (García et al., 2018). While both warming (e.g. Twardochleb et al., 2020) and turbidity (e.g. Shaw et al., 2006; Kimbell et al. 2016) may affect trophic interactions, their combined effects on trophic interactions remain largely unexplored (but see Figueiredo et al. 2019).

Empirical studies have shown that warming may both increase and decrease the short-term trophic interaction strength, which represents the short-term impact of the predator on the prey population density and is often measured as predation rate (Englund et al., 2011;

Sentis et al., 2012; Uiterwaal & DeLong, 2020). Predation rates typically increase and then reach a plateau with increasing prey densities, a relationship described by the functional response model (Holling 1959). Functional responses are characterized by search rates and handling times, which reflect predation rates at low and high prey densities, respectively (Holling, 1959). Thermal effects on functional response parameters obtained in the laboratory have been shown to match patterns in field settings, hence can be used to predict warming effects in natural systems (Archer et al., 2019). The thermal response patterns of search rates and handling times, hence of the resulting predation rates, may be unimodal (Englund et al., 2011; Sentis et al., 2012; Uiterwaal & DeLong, 2020). Hence, depending on what side of the unimodal response curve warming is happening, it can lead to increases or decreases in the functional response parameters. Turbidity is also known to affect the functional response. An increase in turbidity has been found to generally decrease predation rates by lowering search rates for both visual and non-visual aquatic predators (reviewed by Ortega et al., 2020), and less so by increasing handling times (e.g. Allen-Ankins et al., 2012). Yet, also for effects of turbidity, opposite patterns have been observed (e.g. Shaw et al., 2006). For algae-induced turbidity, a positive effect on predation rate could be, for example, a result of a slower swimming speed of the prey under relaxed food stress (Larsson & Kleiven, 1996). Taken together, warming and turbidity have the potential to change short-term interaction strength in the same or opposite directions, asking for empirical studies on their combined effects.

Despite its importance, much less is known about the effects of warming and turbidity on the long-term stability of the predator-prey system, which can be defined as the tendency of the predator and prey population densities to oscillate around the equilibrium densities (Pimm, 1984; Synodinos et al., 2021). These effects will not only depend on changes in the functional response parameters, but also parameters relevant for the population dynamics such as the predator metabolic rate and the prey's carrying capacity. Warming is expected to increase stability (i.e. prevent oscillations) via decreasing the prey's carrying capacity and increasing the predator's metabolic rate (Fussmann et al., 2014; Rall et al., 2010; Sentis et al., 2015), while it can also increase stability via decreasing search rates and increasing handling times (Wang et al., 2021). As an increase in algae-induced turbidity also implies more resources for grazers, it may destabilize the predator-prey system by increasing the carrying capacity of the grazers (Kratina et al., 2012). The few studies on warming and turbidity have never combined them to explicitly investigate how these factors jointly shape the trophic system stability.

Studies on how global change-related stressors affect trophic interactions in the long term typically only consider acute, plastic responses in predator and prey (Daugaard et al., 2019; Sentis et al., 2015). Nevertheless, there is increasing evidence that evolution also plays an important role in shaping responses to global change (Stoks et al., 2014; Urban et al., 2016, Wang et al. 2021). Thermal evolution can play a crucial role reversing maladaptive thermal responses or enhancing adaptive ones (Diamond & Martin, 2016) but this may not always be the case (Diamond & Martin 2020). One powerful way to test the potential impact of thermal evolution is to apply a "space-for-time substitution", where the current phenotypes of warm-adapted populations at their local high temperature are viewed as the future phenotypes of cold-adapted populations after thermal evolution (De Frenne et al., 2013; Verheyen et al., 2019). Typically, such studies contrast low- and high-latitude populations whose temperature difference matches the predicted temperature increase under a certain IPCC warming scenario at the high latitude. Without difference in turbidity between latitudes (as reported by Dodds et al., 2019; Stephens et al., 2015), latitude-based space-for-time substitutions may inform how thermal evolution can change the trophic system stability, and whether this differs between clear and turbid water bodies. Ideally, such studies should consider evolution in both predator and prey (De Block et al., 2013; Laws, 2017) and use a cross factorial design to disentangle the relative contribution of predator and prey evolution. In a rare example study, it was shown that predation rates between damselfly larvae and water fleas depended on the interplay of thermal evolution of each interacting species (De Block et al. 2013). Yet, no studies assessed the effects of evolution in both predator and prey on predation rates at multiple prey densities, needed to assess effects on system stability, or considered the potential mediating effect of turbidity.

We examined (i) how warming and turbidity in isolation and when combined affect the short-term interaction strength and the long-term stability of a predator-prey system, and

(ii) how thermal evolution in the predator and/or in the prey may modulate these effects. We used the larvae of the damselfly *Ischnura elegans* preying on the water flea *Daphnia magna*, a textbook predator-prey model for the functional response in pond food webs (Begon et al., 2021). *D. magna* is a key zooplankton grazer, thereby playing an important role in suppressing algae-induced turbidity (Lampert et al., 1986; Rogers et al., 2020). The effect of warming and turbidity on the interaction of this grazer with its predators is therefore relevant for the occurrence of algae blooms. To increase realism we studied algae-induced turbidity (as key response to eutrophication in pond food webs) that integrates both turbidity *per se* and an increased food level for zooplankton grazers. As aquatic ectotherms that often occur in shallow water bodies, both predator and prey are vulnerable to warming (Woodward et al., 2010). To apply a space-for-time substitution, we studied predator and prey populations from replicated low- and high-latitude populations in Europe, which show latitude-associated thermal adaptation (De Block et al., 2013; Debecker & Stoks, 2019). As no latitudinal difference in turbidity could be detected between the high- and low-latitude study sites (Appendix A), thereby confirming other studies (Dodds et al., 2019; Stephens et al., 2015), no evolutionary responses to turbidity were to be expected. To investigate the contributions of the thermal evolution of the predator and the prey in shaping the outcome of the high-latitude predator-prey system, we also included latitude-crossed predator-prey combinations in the space-for-time substitution.

Based on previous studies between predatory damselfly larvae and their daphnid prey, we expected warming to result in higher search rates and shorter handling times (Twardochleb et al., 2020, Wang et al. 2021). Following the meta-analysis by Ortega et al. (2020), we expected turbidity *per se* to result in lower predator search rates, potentially due to the lower accuracy of locating the prey, and possibly also in longer handling times. Yet, given that algae-induced turbidity may relax food stress and thereby lower the swimming speed of zooplankton prey, it may also increase search rates by increasing the success rate of predator attacks (Larsson & Kleiven, 1996, Pauwels et al. 2010). Given the above predictions, we expected the effects of warming on these functional response parameters to increase the system stability in clear water, but to increase or decrease the system stability in turbid water. We accordingly expected the plastic and evolutionary effects of warming on system stability to differ between clear and turbid conditions. We also expected warming to result in a lower carrying capacity of the prey, thereby increasing the system stability (Fussmann et al., 2014; Rall et al., 2010). In contrast, we expected algae-induced turbidity to result in a higher carrying capacity of the zooplankton prey (as algae are a resource for this prey; Kratina et al., 2012), thereby decreasing system stability.

Materials and methods

For both predator and prey we cultured three populations from low-latitude (southern France) and three populations from high-latitude (southern Scandinavia) sites (Appendix A). All populations inhabited shallow lakes with both damselflies and water fleas present. To avoid joint adaptation of predator and prey at the population level we sampled different sites for predators and prey. No ethical approval or permit for fieldwork was required in this study.

Experimental design and general procedure

To examine the effects of predator and prey latitude, temperature and turbidity on the short-term predator-prey interaction strength and the long-term system stability, we used a full factorial experiment with 16 treatments: 2 predator latitudes (high or low latitude) × 2 prey latitudes (high or low latitude) × 2 temperatures (20 or 24°C) × 2 turbidity levels (clear or turbid). The rearing temperatures correspond to the mean summer water temperatures of the shallow lakes inhabited by the populations in the high- (20°C) and low- (24°C) latitude regions (De Block et al., 2013; Debecker & Stoks, 2019; Dinh Van et al. 2014). Temperature treatments were maintained in incubators (to rear the damselfly larvae) and in temperature-controlled water baths (to rear the *Daphnia* and to conduct the predation trials). The 4°C temperature difference also represents the predicted temperature increase at the high-latitude sites by 2100 according to IPCC (2013) scenario RCP8.5. This allows for a space-for-time substitution to examine the effects of evolution of high-latitude predators and prey under global warming (De Frenne et al., 2013; Verheyen et al., 2019). We used two turbidity levels, corresponding to clear (0.1 nephelometric turbidity units, NTU) and turbid (6 NTU, corresponding to a Secchi depth of ca. 12 cm, and a Chlorophyll *a* concentration of ~350 µg Chlorophyl *a* L^{-1}) states of the shallow water bodies that serve as habitats for both the prey and the predators (Van de Meutter et al., 2005). Both turbidity levels can be found in water bodies inhabited by the study species in the low- and high-latitude regions (Appendix A). As we were specifically interested in algae-induced turbidity as a consequence of eutrophication we did not manipulate turbidity through sediment addition (as done in other studies, e.g. Allen-Ankins et al., 2012) but by directly manipulating the concentration of algae. Predators may be more sensitive to algae-induced turbidity compared to sediment-induced turbidity (Nieman et al., 2018). Moreover, only by using edible algae we could mimic the realistic double effect of eutrophication on zooplankton grazers: increasing their food level and changing interactions with their predators (here the damselfly larvae). Hence, the algae used to induce turbidity was the same as the food provided to *Daphnia*.

To assess effects on the short-term predation rate and long-term system stability, we conducted a functional response experiment and an experiment to quantify the prey's population dynamics for each of the 16 treatment combinations. We then estimated functional response parameters (search rates and handling times) and carrying capacity, and used these estimated parameters together with prey body mass and predator metabolic rates at 20°C and 24°C that were quantified in a previous study (Wang et al., 2021) to parametrize population dynamic models and predict system stability.

Functional response experiments

We estimated the search rate *a* and the handling time *h* by reconstructing the functional response curve for each of the 16 treatment combinations (details in Appendix B). For each combination, we conducted 6-hour predation trials in daytime (from 10:00 to 16:00) (based on Sentis et al., 2017) with 5-6 prey densities: 6, 12, 15, 30, 48, and 66 *Daphnia* individuals L^{-1}. The highest density of 66 *Daphnia* L^{-1} was only used at 24°C as at 20°C the maximum predation rate of *I. elegans* larvae was reached at 48 *Daphnia* L^{-1} (based on a pilot experiment). The predation trials were replicated 9 times at each prey density, and in total 792 predation trials were conducted with 396 damselfly larvae. We always tested the animals at the temperatures at which they were cultured: animals reared at 20ºC were only tested at 20ºC, while those reared at 24ºC were only tested at 24ºC. Therefore, no additional thermal acclimation step was required.

The predation trials were conducted in white 2 L (18.0 × 13.3 × 12.6 cm) arenas filled with 1 L water at the test (= rearing) temperatures. For the clear water treatment, the medium contained only dechlorinated tap water with a turbidity level of 0.1 NTU, which is close to the turbidity level of the *Daphnia* cultures that were fed daily with algae (< 0.5 NTU). For the turbid water treatment, we also added 15 mL green algal solution (1×10^8 cells mL^{-1}) that was added at the start of the predation trials to obtain a turbidity level of 6 NTU (algal concentration = 1.5×10^6 cells mL^{-1}). In a preliminary test, this turbidity level was kept above 5 NTU after 6 h (at the end of the predation trials) between the treatment temperatures and *Daphnia* densities (all $P > 0.05$), while at longer duration the turbidity level could not be maintained. To account for wasteful killing, the *Daphnia* that had less than 50% of their bodies missing were considered as not consumed (as in Thompson, 1975). Predation rates were expressed as the number of *Daphnia* consumed per damselfly per 6 h. Natural mortality of *Daphnia* was assessed in 5 replicates per prey population × temperature × turbidity treatment at the density of 48 *Daphnia* L^{-1} in predator-free arenas. Mortality was negligible (ranging between 0% and 2% per trial) and thus not accounted for.

Statistical analyses and modelling

Statistical analyses were conducted using R v3.6.3 (R Core Team 2020). To analyze the functional response curves, we followed the procedure by Pritchard et al. (2017, *package frair*). Based on the identified functional response type (Appendix B), we fitted the predation rates of the 16 treatment groups with the type II Rogers' random predator equation accounting for prey depletion (Rogers, 1972) to estimate the search rate a (L day^{-1}) and handling time h (day):

$$N_e = \quad N_0\left(1 - exp^{-a(t-N_e h)}\right) \quad \text{(Equation 1)}$$

where N_e is the number of prey consumed; N_0 is the initial prey density; a is the instantaneous search rate of the predator (L day^{-1}) determined by searching activity and capture success; h

is the handling time the predator spends ingesting and digesting a prey (day); T is the predation time (day). The fitted functional response curves were bootstrapped (n = 999) to obtain 95% confidence bands.

To analyze effects of the treatments (predator and prey source latitudes, temperature and turbidity) on the functional response parameters, we pairwise compared the search rate a and handling time h between treatment combinations using the "indicator variable" approach (as e.g. used in Siepielski et al., 2020). We performed multiple comparisons within and between latitudes, and adjusted P-values with the False Discovery Rate-method (Benjamini & Hochberg, 1995).

To estimate the stability of the predator-prey system, we applied a stability metric that quantifies the tendency of the predator and prey population densities to oscillate around the equilibrium points (Synodinos et al., 2021). The stability metric, $\mathcal{S}$, defines stability in relation to the Hopf bifurcation (i.e. the point at which the population dynamics switch from stable equilibria to limit cycles) (Synodinos et al., 2021)

$$\mathcal{S} = -\frac{(\kappa-\rho-1)}{\rho-1} \quad \text{(Equation 2)}$$

$\mathcal{S} > 0$ corresponds to a stable equilibrium and $\mathcal{S} < 0$ to oscillations. Hence, larger values of $\mathcal{S}$ indicate a more stable system. κ is the ratio of the prey equilibrium density without consumers (carrying capacity) to the prey equilibrium density with consumers, ρ is the energetic gain-to-loss ratio of the predator population at its maximum feeding rate (details described in Appendix C and D).

To assess how turbidity may affect the direction of thermal evolution of the stability metric, we made explicit comparisons for the space-for-time substitution separately in clear and turbid water (Figure. 4).

Results

Functional response parameters

For all 16 combinations of predator latitude, prey latitude, temperature and turbidity treatments, predation rates increased with prey density and then reached a plateau following a type II functional response (Figure 1, Appendix B). Pairwise comparisons using the "indicator variable" approach showed that predator search rates and handling times depended on the combination of predator latitude, prey latitude, temperature and turbidity (Figures 1 and 2, Appendix E).

Warming caused higher (+19%) search rates of low-latitude predators paired with low-latitude prey in clear water ($Z = 3.84$, $P = 0.0076$, Figure 2a), but lower (-19%) search rates for low-latitude predators with both low- ($Z = -4.72$, $P < 0.0001$) and high-latitude ($Z = -6.21$, $P < 0.0001$) prey types in turbid water (Figure 2a and 2c). Instead, warming had no significant effect on search rates of high-latitude predators (Figure 2b and 2d). Turbidity resulted in search rates of low-latitude predators paired with low-latitude prey being higher (+19%) at 20°C ($Z = 3.78$, $P = 0.0102$), yet lower (-17%) at 24°C ($Z = -4.99$, $P < 0.0001$, Figure 2c). As a result, for low-latitude predators, the lowest values of search rate were obtained in turbid warm water. Turbidity caused higher search rates in high-latitude predators at 24°C (+34%) when paired with low-latitude prey ($Z = 6.683$, $P < 0.0001$, Figure 2b). Low-latitude predators had higher (+53%) search rates compared to high-latitude predators when paired with low-latitude prey in clear water at 24°C ($Z = 9.75$, $P < 0.0001$), while high-latitude predators had higher (+38%) search rates compared to low-latitude predators when paired with high-latitude prey at 24°C (clear water: $Z = 19.16$, $P < 0.0001$; turbid water: $Z = 52.77$, $P < 0.0001$).

Warming generally caused shorter (-42%) handling times of low-latitude predators (all Z-values < -7.4, all $P < 0.0001$, Figure 2a and 2c) but had no significant effect on the handling times of high-latitude predators (Figure 2b and 2c). Turbidity in general tended to shorten handling times of low-latitude predators (Figure 1), yet this reduction (-20%) was only significant when paired with high-latitude prey at 24°C ($Z = -4.02$, $P = 0.0038$, Figure 2). Instead, turbidity had no significant effect on the handling time of high-latitude predators. High-latitude predators had overall longer (+73%) handling times compared to low-latitude predators (yet this was not significant in clear water at 20°C, see the last 8 comparisons of handling time in Table S4, Appendix E).

Predator–prey system stability

Based on the 84% CIs, in combinations involving low-latitude predators, warming did not affect stability in clear water but increase it by +76% in turbid water both with low and high latitude prey (Figure 3). In the combinations with high-latitude predators, warming had no effect in most conditions except for an increase (+ 71%) in stability when combined with low-latitude prey in turbid water (Figure 3). Turbidity caused lower (range from -183% to -515%) stability in all combinations with high-latitude prey, while it also caused a lower (-313%) stability for the "high-latitude predator & low-latitude prey" system at 20°C. Warming in combination with turbidity increased stability (+66%) in the "low-latitude predator & low latitude prey" system, while it decreased stability (-431%) in the "high-latitude predator & high latitude prey" system compared to treatments in clear water without warming.

Focusing on the critical comparisons for the space-for-time substitution in clear water, stability tended to be lower (range: -43% to -87%) in most combinations at 24°C compared to the baseline "high-latitude predator & high-latitude prey" system at 20°C, except for the combination "low-latitude predator & high-latitude prey" which tended to have a higher stability (+50%) (Figure 4a). However, none of these patterns reached statistical significance. In contrast, in turbid water, stability was statistically higher (+77% and +83%) in the two combinations with low-latitude predators at 24°C compared to the baseline "high-latitude predator & high-latitude prey" system at 20°C (Figure 4b). Overall, the trends of a decrease in stability with thermal plasticity or thermal evolution (of both predator and prey, or only the prey) observed in clear water were either reversed or cancelled in turbid water, and the trend for an increase in stability for the scenario with predator thermal evolution alone, was magnified and reached significance in turbid water.

Discussion

Our results provide three key insights in the effects of warming and turbidity, and particularly how warming effects may critically depend on turbidity: (1) 4°C warming significantly increased stability for the systems with the low-latitude predator and the system with high-latitude predator and low-latitude prey in turbid water, while it did not significantly affect stability in clear water. The latter contrasts with previous finding showing that warming will stabilize predator-prey dynamics (Fussmann et al., 2014; Sentis et al., 2015; Wang et al., 2021). (2) The general effect of turbidity was to reduce the stability of the predator-prey system, which suggests the effect of turbidity goes in the same direction as the effect of nutrient enrichment in reducing the stability of food webs (Binzer et al., 2012; Kratina et al., 2012). (3) Thermal evolution of predators potentially stabilizes the high-latitude system under warming, and this effect was stronger in turbid water.

Effects of warming and turbidity on the functional response parameters

Consistent with the general patterns identified in previous studies (Englund et al., 2011; Ortega et al., 2020), the functional response parameters (i.e. search rates and handling times) were affected by temperature and turbidity. Notably, the effects of warming on search rates depended on the turbidity level and were only significant for low-latitude predators. The reductions in handling times under warming and turbidity were only detected for low-latitude predators. This highlights the importance to consider latitudinal differentiation of trophic interactions in response to warming and turbidity (for warming: Amarasekare, 2019; De Block et al., 2013; Gauzens et al., 2020; Marino et al., 2018).

In line with two recent studies reporting that the effect of warming on predator biomass may critically depend on turbidity (Symons et al., 2019; van Dorst et al., 2019), the effect of warming on search rates of low-latitude predators reversed from positive in clear water to negative in turbid water. Warming can enhance the speed of sit-and-pursue predators, such as *I. elegans* damselfly larvae (Gyssels & Stoks, 2006), and thereby the encounter rate with prey (Dell et al., 2014; Thompson, 1978; Twardochleb et al., 2020). Instead, turbidity may reduce the rate of prey detection and attack success (Higham et al., 2015; Ortega et al., 2020). This may explain why warming increased search rates of low-latitude predators in clear water, while in turbid water the negative effect of turbidity may have overruled the positive effect of warming on search rates. We hypothesize that in turbid water, predators decreased their search effort at the higher temperature to conserve energy as they faced a lower capture success, though we cannot exclude the possibility that the results were driven by changes in the prey behavior or swimming speed to escape predators. Yet, this assumed negative effect of turbidity on prey detection and attack success (Ortega et al., 2020) cannot explain that turbidity increased search rates for low-latitude prey of low-latitude predators at 20°C and of high-latitude predators. This may instead be explained by the low-latitude prey showing weaker anti-predator responses in turbid water. Turbidity may have weakened the anti-predator responses of the prey as they received less visual predator cues and, as algae-induced turbidity was imposed, they also experienced relaxed food stress (Pauwels et al. 2010) and thereby may have been swimming slower (Larsson & Kleiven, 1996). This is more likely to play a role in low-latitude prey as these have higher intrinsic growth rates compared to high-latitude prey (Appendix D), hence are under stronger pressure to forage. This also highlights the importance of the use of edible algae as turbidity source when testing effects of eutrophication-driven increased turbidity, for the foraging effect could have been overlooked if sediment or non-edible algae would have been used.

The negative effect of warming on handling times of low-latitude predators was consistent across turbidity levels. This can be explained by the handling times mainly being driven by digestion times (hence physiology) which shorten at higher temperatures (Sentis et al., 2013). Studies in clear water also showed warming to reduce handling times in damselfly larvae feeding on *Daphnia* (Thompson, 1978; Twardochleb et al., 2020) and in other predator-prey systems (Rall et al., 2012; Sentis et al., 2012). In contrast, the effect of turbidity on handling times was generally insignificant. The latter is likely because the main component of handling time (time to digest the prey; Sentis et al., 2013) was not affected by turbidity.

A key finding was that the functional response parameters consistently differed between the two latitudes and were much more affected by warming and turbidity in low-latitude predators. Low-latitude predators had shorter handling times compared to high-latitude predators (not significant in clear water at 20°C). As lower handling times match higher maximal predation rates (Hassell, 2000), this reflects the latitudinal difference in pace-of-life with the fast-paced low-latitude predators having a higher food intake compared to the slowpaced high-latitude predators at *ad libitum* food levels (Debecker & Stoks, 2019). Similar foraging patterns have also been observed in insect and seed consumers whose predation rates increased toward lower latitudes (Hargreaves et al., 2019; Michalko et al., 2019; Roslin, 2017). This selection for high predation rates in the low-latitude populations may also have contributed to their higher responsiveness to warming. Indeed, only low-latitude predators showed higher search rates (in clear water) and shorter handling times under warming. This matches the pattern that low-latitude predators accelerate growth and development more under warming than high-latitude predators (Van Dievel et al., 2019). We hypothesize that the consistent trend of reduced handling times, hence increased maximum predation rates, of low-latitude predators in turbid water is also the result of the faster pace-of-life of the low-latitude predators (Debecker & Stoks, 2019) combined with the reduced anti-predator response of the prey. In addition, there was a signal of latitude-associated adaptation at the higher temperature in terms of search rate. Indeed, at 24°C low-latitude predators had higher search rates compared to high-latitude predators when paired with low-latitude prey, while high-latitude predators had higher search rates compared to low-latitude predators with high-latitude prey. This suggests that predators are more efficient in hunting sympatric prey compared to allopatric prey, and/or, vice versa that prey better cope with allopatric predators compared to sympatric predators, at the higher temperature.

Effects of warming and turbidity on system stability

Previous studies showed that warming may increase predator-prey system stability (Rall et al., 2010; Sentis et al., 2015; Wang et al., 2021). Our current experiment extends these studies by (i) computing stability metrics with all parameters obtained from empirical observations, (ii) considering latitudinal differences (hence thermal evolution) in both predator and prey, and (iii) evaluating the impact of warming in the absence and presence of turbidity, another important global change-related factor. While we also found warming to increase stability, this was only the case in turbid water (except for the "high-latitude predator & high-latitude prey" system) as warming did not affect stability in clear water. The impact of warming on stability thus depended on the combined effects of predator latitude, prey latitude and turbidity. Note that we here simulated 4°C warming (from 20°C to 24 °C) as this is the expected temperature increase by 2100 in the high-latitude populations under IPCC scenario RCP8.5. At even higher temperatures the thermal optimum for the functional response parameters may be exceeded resulting in an even more stable system. Warming increased the system stability in turbid water through the theoretically predicted (Fussmann et al., 2014; Rall et al., 2010) lower carrying capacities at the higher temperature (Appendix C and D), a trend for higher predator metabolic rates (Wang et al., 2021), and lower search rates (for low-latitude predatrs in turbid water). But in clear water, the trend of increased search rates at the higher temperature opposed the effects of warming on the first two factors, resulting in no significant effect of warming on system stability.

In general, turbidity was destabilizing and this was caused by an increased carrying capacity of the zooplankton prey (Appendix D) and by higher search rates in most predator-prey systems. Our results are in line with previous studies suggesting that nutrient enrichment (often correlated to higher turbidity levels) may destabilize trophic systems (as reported in Kratina et al., 2012).

Effects of thermal evolution on stability

We found that the impact of thermal plasticity and thermal evolution on the stability of the high-latitude trophic system under warming is critically dependent on the turbidity level. Indeed, when only assuming thermal plasticity, the high-latitude trophic system became less stable (i.e. more prone to oscillations) under 4°C warming in clear water but not in turbid water. Based on a space-for-time substitution (De Frenne et al., 2013; Verheyen et al., 2019), this tentatively suggest predator thermal evolution could reverse the negative impact of warming through plasticity on the stability of the high-latitude system in clear water, whereas joint thermal evolution of both predator and prey would not. In turbid water, thermal evolution of both predator and prey may stabilize the system under warming and this was entirely explained by thermal evolution of the predator. These space-for-time patterns of the stability metric are mainly contributed by the prey's carrying capacity and partly by the predator search rate (Appendix D, Appendix F), indicating an important contribution of both parameters in mediating effects of warming on stability in our study system. Nevertheless, it should be noted that the contribution of search rate on the stability patterns may be smaller under longer-duration predation trials (Li et al. 2018). Moreover, despite most abiotic/biotic factors being similar in ponds inhabited by the damselflies and water fleas between latitudes (Debecker & Stoks, 2019), factors that differ such as photoperiod may potentially contribute to latitudinal differences in predator/prey performance. Also, the algae-induced turbidity was assumed to be a long-term scenario, reflecting one of the stable states in the shallow lakes (Scheffer et al., 2001). Therefore, our models and predictions are more likely to apply for systems where algae-induced turbidity is loosely related to *Daphnia* density.

The here obtained insights were only possible by also studying the mismatched predator-prey latitude combinations as these allow disentangling the relative contribution of predator and prey evolution. Mismatched combinations may additionally reflect situations where the predator and prey show asymmetrical evolution, for example because of differences in generation time and in genetic constraints. Mismatched combinations may also have field relevance in case of asymmetrical northward migration of predator and prey, for example because of differences in dispersal ability. Our results thereby imply that faster thermal evolution of high-latitude predators (compared to prey) or northward migration of low-latitude predators could help stabilize the high-latitude system under warming.

Conclusions

Our study underscores the importance of considering the effects of turbidity in addition to warming in shaping trophic interactions, and suggests that thermal evolution may increase stability under warming depending on the turbidity level. Given that warming and eutrophication are two major global change-related co-occurring factors negatively affecting freshwater ecosystems (Moss, 2011; Woodward et al., 2010) and that evolution may play an important role in shaping responses to global change (Stoks et al., 2014; Urban et al., 2016), our results of contrasting effects of thermal evolution between clear and turbid water highlight the need of integrating evolution and turbidity to improve projections of trophic system stability under warming.

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Conflict of interest

The authors declare no conflict of interest.

Authors' contributions

RS and AS developed the ideas, and together with YJW designed the experiments. YJW performed the experiments and analyses. AS and NT provided analytical advice and modeling support. YJW and RS drafted the manuscript after which all authors contributed and gave final approval.

Data Availability Statement

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.m905qfv32 (Wang et al., 2022).

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Figure legends

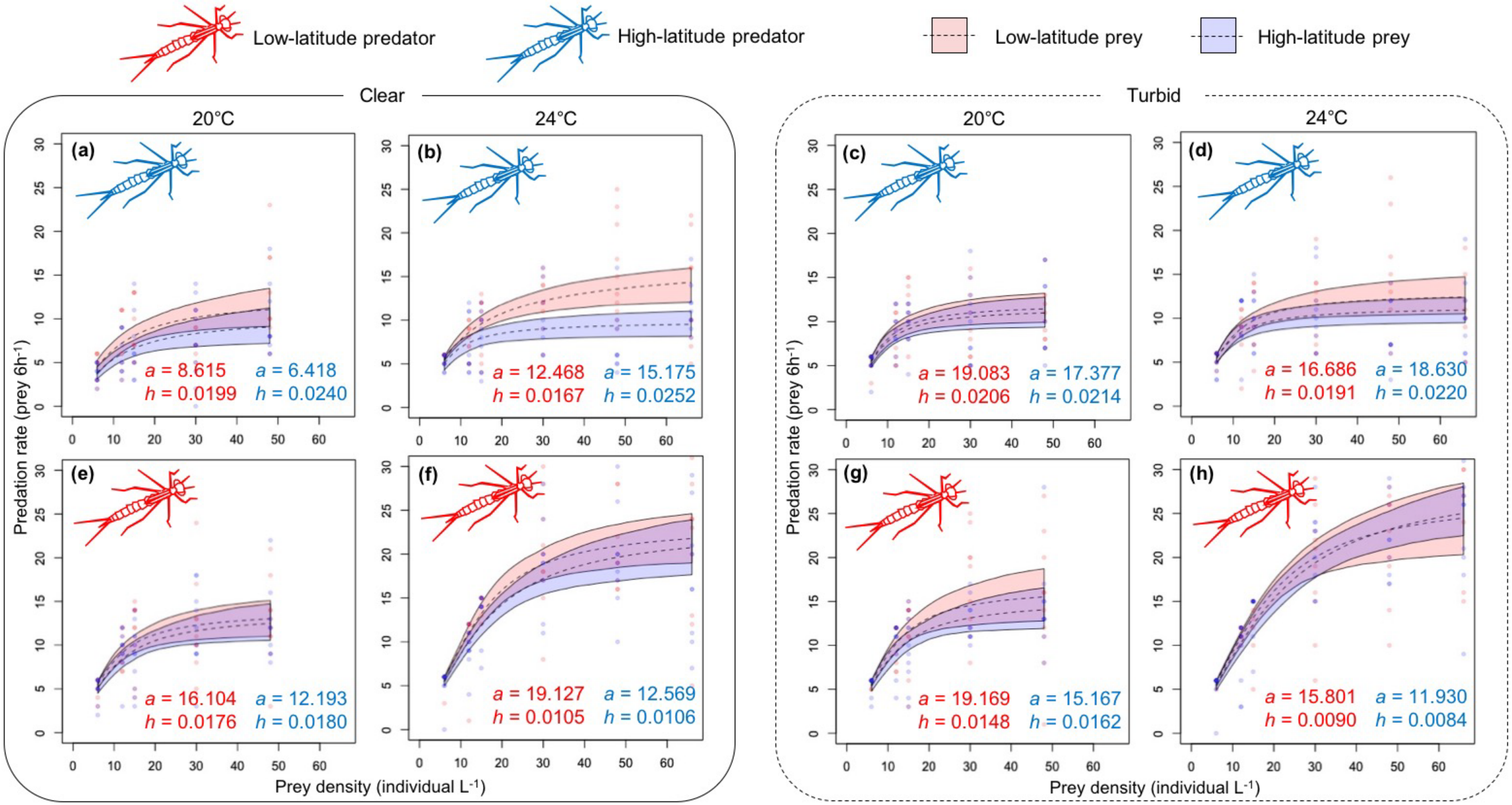
Figure 1. Functional response curves of (a-d) high-latitude and (e-h) low-latitude *Ischnura elegans* damselfly larvae preying on low-latitude (red curves) and high-latitude (blue curves) *Daphnia magna* water fleas under the four combinations of two temperatures (20 and 24°C) crossed with two turbidity levels (clear and turbid water). Shaded areas represent 95% confidence intervals. Parameter a denotes the search rate and h denotes the handling time.

Figure 2. Effects of temperature (20 and 24°C) and turbidity (clear and turbid) on the search rates (a, L day^{-1}) and handling times (h, day) of *Ischnura elegans* damselfly larvae preying on *Daphnia magna* water fleas. Differences in search rates and handling times between treatment combinations are shown next to the bidirectional arrow bars (< or > reflect differences at $\alpha = 0.05$, ≤ and ≥ reflect non-significant trends; False Discovery Rate-corrected comparisons). Asterisks beside the parameters denote significant ($P < 0.05$) higher values compared with the same treatment combination of the other predator latitude ($\alpha = 0.05$, False Discovery Rate-corrected comparisons).

Figure 3. Effects of predator source latitude, prey source latitude, temperature and turbidity on the stability metric S for larvae of the predator *Ischnura elegans* feeding on *Daphnia magna* prey. Values given are estimated means with 84% CI.

Figure 4. Effects of thermal plasticity and thermal evolution on the stability metric S in the high-latitude predator-prey system under warming in (a) clear and (b) turbid water. Given are mean differences in S (%) between each of the four groups at 24°C relevant for the space-for-time substitution (only plasticity and no evolution, evolution of both predator and prey, evolution of only predator, and evolution of only prey) expressed relative to the baseline group representing the current high-latitude trophic system (high-latitude predator & high-latitude prey at 20°C). Positive differences indicate a change toward a more stable system. Asterisks denote significant ($P < 0.05$) differences in S compared with the baseline group at the same turbidity level. Letters above the four groups at 24°C relevant for the space-for-time substitution denote differences between these groups in S.

Figure 1



Low-latitude predator
High-latitude predator
Low-latitude prey
High-latitude prey
Clear
Turbid
20°C
24°C
20°C
24°C
(a)
a = 8.615
h = 0.0199
a = 6.418
h = 0.0240
(b)
a = 12.468
h = 0.0167
a = 15.175
h = 0.0252
(c)
a = 19.083
h = 0.0206
a = 17.377
h = 0.0214
(d)
a = 16.686
h = 0.0191
a = 18.630
h = 0.0220
(e)
a = 16.104
h = 0.0176
a = 12.193
h = 0.0180
(f)
a = 19.127
h = 0.0105
a = 12.569
h = 0.0106
(g)
a = 19.169
h = 0.0148
a = 15.167
h = 0.0162
(h)
a = 15.801
h = 0.0090
a = 11.930
h = 0.0084
Predation rate (prey 6h-1)
Prey density (individual L-1)
0 5 10 15 20 25 30
0 10 20 30 40 50 60

Figure 2

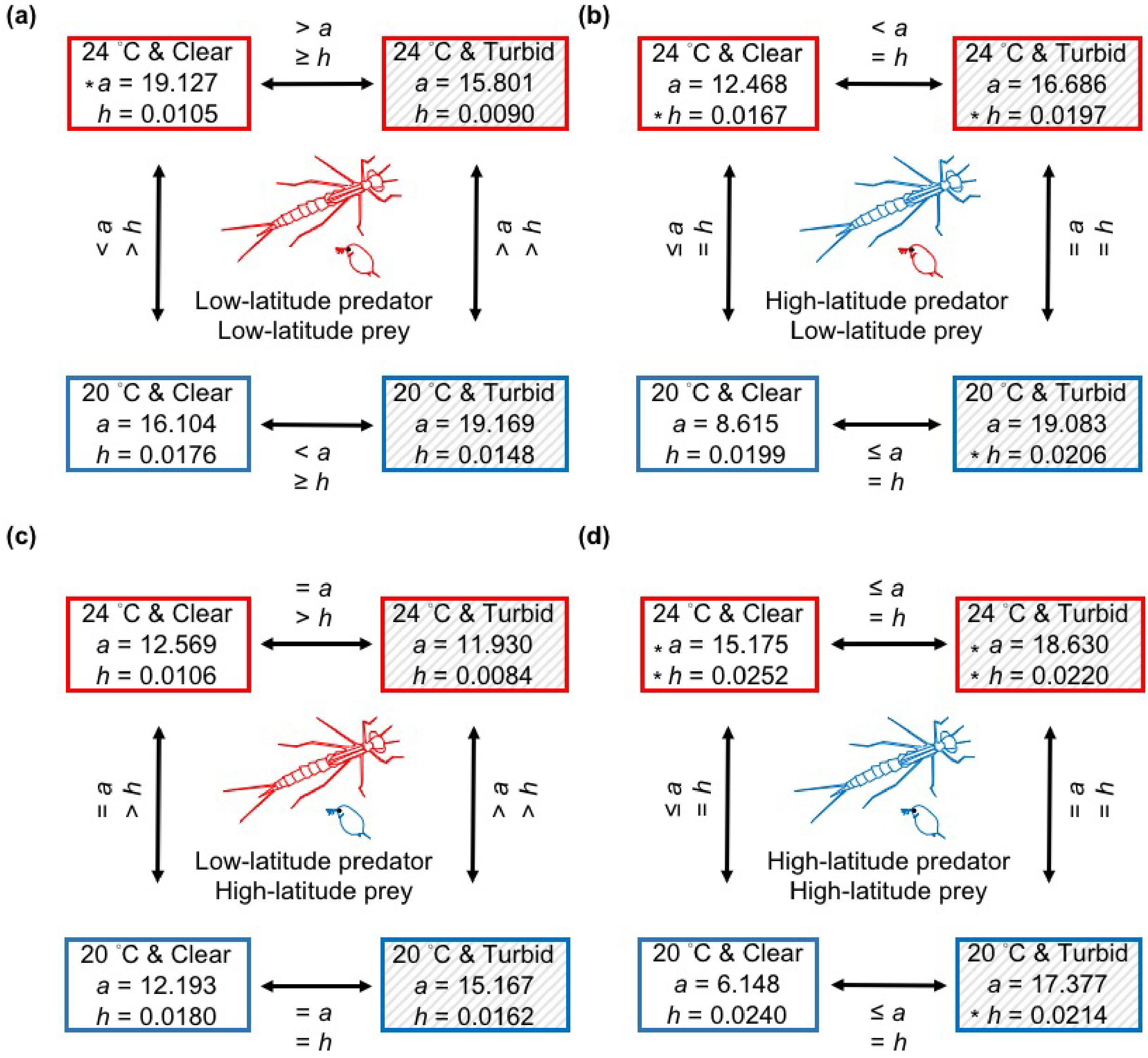

(a)
24 ˚C & Clear
* a = 19.127
h = 0.0105
> a
≥ h
24 ˚C & Turbid
a = 15.801
h = 0.0090
< a
> h
> a
> h
Low-latitude predator
Low-latitude prey
20 ˚C & Clear
a = 16.104
h = 0.0176
< a
≥ h
20 ˚C & Turbid
a = 19.169
h = 0.0148
(b)
24 ˚C & Clear
a = 12.468
* h = 0.0167
< a
= h
24 ˚C & Turbid
a = 16.686
* h = 0.0197
≤ a
= h
= a
= h
High-latitude predator
Low-latitude prey
20 ˚C & Clear
a = 8.615
h = 0.0199
≤ a
= h
20 ˚C & Turbid
a = 19.083
* h = 0.0206
(c)
24 ˚C & Clear
a = 12.569
h = 0.0106
= a
> h
24 ˚C & Turbid
a = 11.930
h = 0.0084
= a
> h
> a
> h
Low-latitude predator
High-latitude prey
20 ˚C & Clear
a = 12.193
h = 0.0180
= a
= h
20 ˚C & Turbid
a = 15.167
h = 0.0162
(d)
24 ˚C & Clear
* a = 15.175
* h = 0.0252
≤ a
= h
24 ˚C & Turbid
* a = 18.630
* h = 0.0220
≤ a
= h
= a
= h
High-latitude predator
High-latitude prey
20 ˚C & Clear
a = 6.148
h = 0.0240
≤ a
= h
20 ˚C & Turbid
a = 17.377
* h = 0.0214

Figure 3.

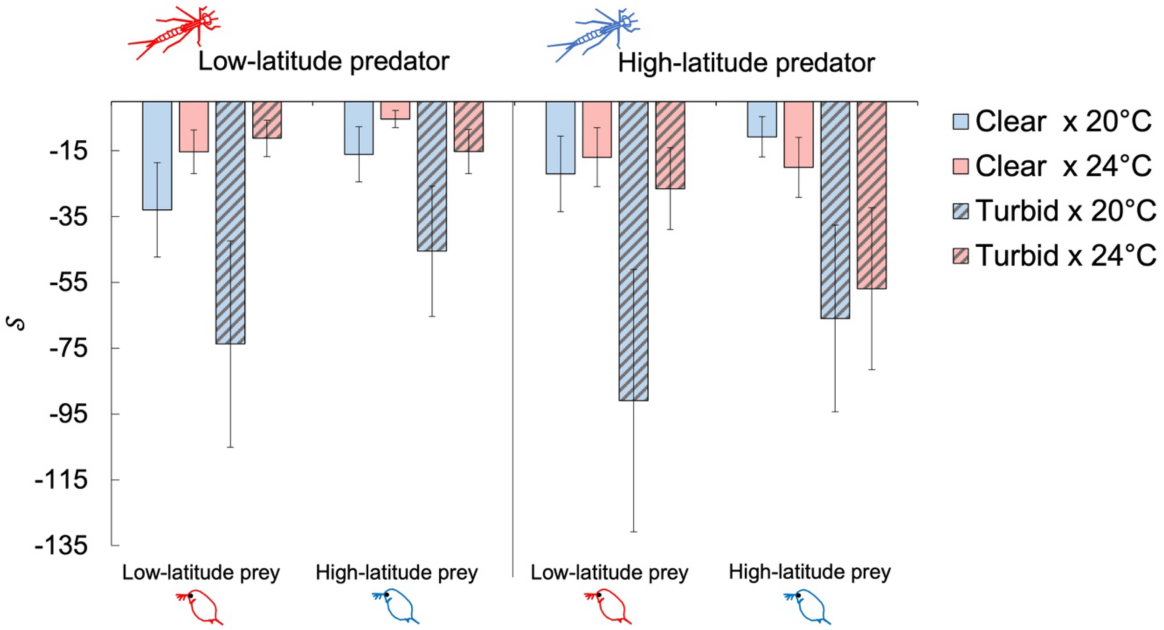
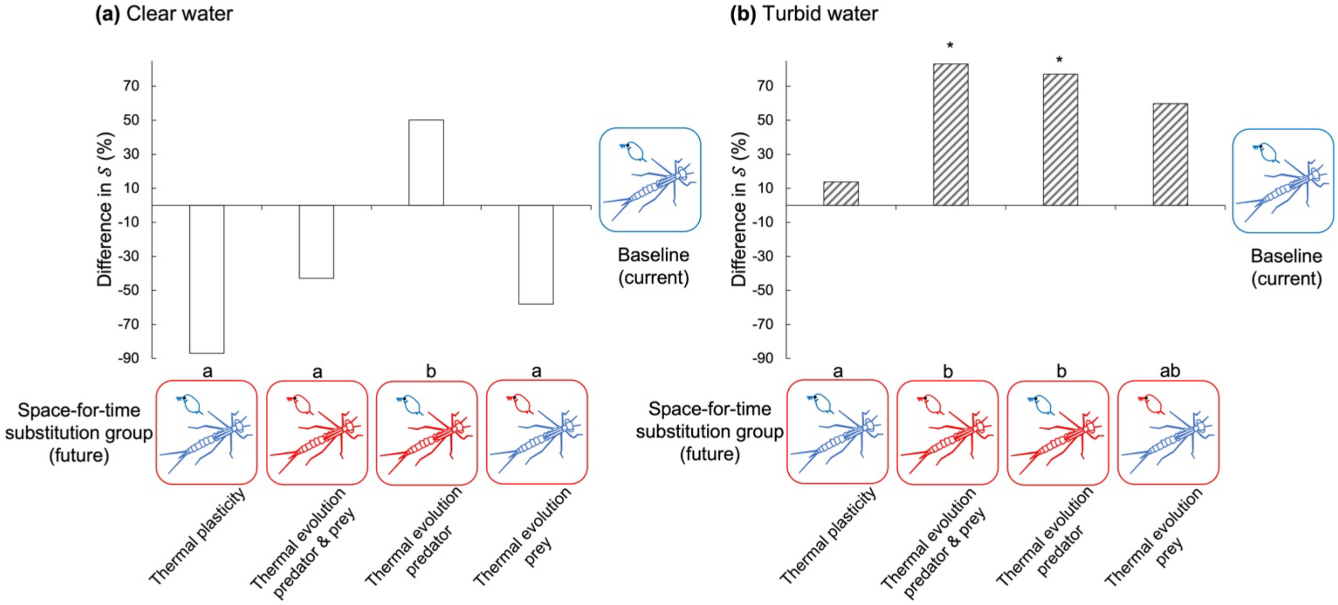

Low-latitude predator
High-latitude predator
Clear x 20°C
Clear x 24°C
Turbid x 20°C
Turbid x 24°C
S
-15
-35
-55
-75
-95
-115
-135
Low-latitude prey
High-latitude prey
Low-latitude prey
High-latitude prey

Figure 4.


(a) Clear water
Difference in S (%)
70
50
30
10
-10
-30
-50
-70
-90
a
a
b
a
Baseline (current)
Space-for-time substitution group (future)
Thermal plasticity
Thermal evolution predator & prey
Thermal evolution predator
Thermal evolution prey
(b) Turbid water
*
*
Difference in S (%)
70
50
30
10
-10
-30
-50
-70
-90
a
b
b
ab
Baseline (current)
Space-for-time substitution group (future)
Thermal plasticity
Thermal evolution predator & prey
Thermal evolution predator
Thermal evolution prey