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Predicting effects of multiple interacting global change drivers across trophic levels

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Abstract

Global change encompasses many co-occurring anthropogenic drivers, which can act synergistically or antagonistically on ecological systems. Predicting how different global change drivers simultaneously contribute to observed biodiversity change is a key challenge for ecology and conservation. However, we lack the mechanistic understanding of how multiple global change drivers influence the vital rates of multiple interacting species. We propose that reaction norms, the relationships between a driver and vital rates like growth, mortality, and consumption, provide insights to the underlying mechanisms of community responses to multiple drivers. Understanding how multiple drivers interact to affect demographic rates using a reaction-norm perspective can improve our ability to make predictions of interactions at higher levels of organization—that is, community and food web. Building on the framework of consumer–resource interactions and widely studied thermal performance curves, we illustrate how joint driver impacts can be scaled up from the population to the community level. A simple proof-of-concept model demonstrates how reaction norms of vital rates predict the prevalence of driver interactions at the community level. A literature search suggests that our proposed approach is not yet used in multiple driver research. We outline how realistic response surfaces (i.e., multidimensional reaction norms) can be inferred by parametric and non-parametric approaches. Response surfaces have the potential to strengthen our understanding of how multiple drivers affect communities as well as improve our ability to predict when interactive effects emerge, two of the major challenges of ecology today.

1 | INTRODUCTION

Most ecosystems are experiencing a strong increase in the number and intensity of anthropogenic drivers such as climate change, eutrophication, acidification, and chemical pollution (Pörtner et al., 2021). These drivers pressure populations, because their effects are mostly negative (i.e., decreasing growth and reproduction and increasing mortality), although some drivers can have initially positive effects that eventually turn negative (Orr et al., 2020), for example, temperature increasing beyond the optimal growth range (Schaum et al., 2017). Potential interactions between multiple drivers are of particular concern (Brook et al., 2008). Synergies, where the combination has a larger effect than the sum of individual effects, and antagonisms, whose joint effect is smaller than the sum of the individual effects, both complicate predictions and management of multiple driver effects (Crain et al., 2008).

A primary goal of the multiple driver research is to explore and describe the frequency and distribution of multiple driver effects across a wide range of ecological systems. To do so, researchers usually measure a quantity of interest (e.g., population size or community biomass) and estimate the effects of the individual drivers alone and jointly with statistical models that capture the magnitude and sign of the main and interactive effects (Rillig et al., 2019; Suleiman et al., 2022). Meta-analyses have provided important insights on the prevalence of driver interactions across many drivers and domains (Suleiman et al., 2022), demonstrating interactive effects, particularly antagonisms, dominate (Birk et al., 2020; Crain et al., 2008; Darling & Côté, 2008; Harvey et al., 2013; Jackson et al., 2016; Seifert et al., 2020; Tekin et al., 2020). Antagonisms and synergisms may be even more prevalent since current methods do not capture statistical interactions very well (Tekin et al., 2020). Interactions have been identified as a key issue for conservation and management (Côté et al., 2016). Hence, we need to understand and predict how interacting effects of multiple drivers scale up from populations to communities (De Laender, 2018).

Modelling work has shown that the effects of multiple drivers at the community level may not be reliably predicted when multiple populations respond differently to those drivers, even when the effects of those drivers at the population level are additive and species do not interact (Thompson et al., 2018a). Thus, the population response to drivers needs to be known to predict consequences on the community level (Thompson et al., 2018a). Furthermore, even if the effects of drivers on populations may be linear when considering non-interacting species, community responses to the drivers can become non-linear because of species interactions (Thompson et al., 2018b). While pairs of consumers and resources may be differently affected by driver combinations due to the specific sensitivity of their vital rates (Mor et al., 2022), driver effects can also propagate via many direct and indirect pathways in food webs (Beauchesne et al., 2021). Effects of multiple drivers in communities depend jointly on sensitivities of single species to driver combinations and the trophic position of those species in a food web. For instance, whereas top predators can be negatively impacted by drivers, mesopredators may benefit due to their trophic position (Beauchesne et al., 2021). In conclusion, we need to predict both population- and community-level responses to multiple drivers, as well as how these drivers affect trophic interactions between species.

1.1 | Reaction norms provide a mechanistic understanding

We propose that reaction norms, the functional relationships between a driver and key biological rates like growth, mortality, and consumption, provide a mechanistic understanding of population and community responses to multiple drivers. The reaction-norm approach allows (1) identifying how the joint effect of drivers scales up from the population to the community level, (2) predicting when interactions should occur, and (3) obtaining crucial insights into the mechanisms of interactive effects (e.g., Verbeek et al., 2018). Fitting statistical models to community properties like total biomass to estimate effect sizes and signs needs to be complemented with mechanistic knowledge and predictive power. While a statistical model can detect that two drivers have a different effect than their sum on the abundance of an organism, the underlying biological mechanisms remain unknown, hampering our ability to generalize and extrapolate to other systems. For example, we may not know whether an antagonism arises because growth rate, mortality, or attack rate is affected. Hence, we cannot disentangle whether interactive driver effects in communities arise from different species sensitivities to driver combinations, or from trophic interactions. In contrast, these differential effects can be captured by the vital rates of the consumer and resource to driver combinations, which may represent a consistent response across different consumer–resource systems. For instance, plant growth rates can be altered by joint eutrophication and warming, while herbivore consumption may not respond to the drivers (Zhang et al., 2020).

Thermal performance curves (TPCs) describe how rates, like the intrinsic population growth or mortality, change across a temperature gradient (Angilletta, 2009). TPCs have been influential for modelling and predicting food web responses to warming (such as Binzer et al., 2016; Gauzens et al., 2020; Gibert et al., 2022; Uszko et al., 2017). They can easily be extended to include more than one driver, allowing to quantify how additional discrete drivers modulate the TPC or the surface that describes the response (i.e., the growth rate) to joint changes in two or more continuous drivers (Sinclair et al., 2016). They are straightforward to measure

and easily integrated into simple community models, such as those of consumer–resource dynamics (Sinclair et al., 2016; Vasseur & McCann, 2005).

Others have previously proposed reaction norms of vital rates as a starting point to merge physiology with multiple driver research (Collins et al., 2022; Harley et al., 2017; Litchman & Thomas, 2022; Pirotta et al., 2022). Litchman and Thomas (2022) reviewed the literature on phytoplankton growth and found that all reviewed global change drivers can influence the shape of the TPCs. Collins et al. (2022) then made the point that response curves for phytoplankton can only be produced with many driver levels, including unrealistic levels that are not expected to happen in nature. Harley et al. (2017) proposed a theoretical framework based on reaction norms to understand alternative stable states under different multiple driver regimes. Pirotta et al. (2022) reviewed different conceptual frameworks to understand multiple-driver impacts and suggested a continuum of assumptions, ranging from data-driven approaches like generalized additive models to individual-based models, to model the reaction norms of organisms. Here, we integrate these prior calls for action into a coherent process-based approach for consumer–resource systems impacted by multiple drivers, and illustrate how interactions can be predicted when the response surfaces of consumers and resources are known.

2 | MOVING FROM "PATTERNS" TO "PROCESSES"

TPCs have been quantified for a variety of organisms and rates (Angilletta, 2009). At the population level, consistent patterns such as a right-shifted distribution and a drop in the rate after reaching an optimum have been found for population growth rate (see consumer, Figure 1, as well as an exponential increase in mortality; Angilletta, 2009). At the community level, the temperature dependence of attack rate and handling time are often well described by a hump- and U-shaped pattern, respectively (Daugaard et al., 2019; DeLong & Lyon, 2020; Englund et al., 2011; Synodinos et al., 2021; Uszko et al., 2017). Due to interactions between consumers and resources with different TPCs, responses at the community level can become more complex, even in the simplest consumer–resource systems (Dell et al., 2014). Although large datasets on the temperature dependence of rates have become available (Dell et al., 2011), multiple rates are rarely measured for the same population.

We propose that multiple driver effects can be understood by studying how the addition of a focal driver changes the TPC. Measuring the TPC in the presence of this driver for consumer–resource systems allows pinpointing: (1) whether the driver affects the TPC in an additive or non-additive fashion; (2) which rates are most affected by the driver; and (3) how the magnitude and the sign of the effects on both consumer and resource will contribute to the effects at the community level. Response surfaces, that is, changes in the reaction norms with temperature and an additional driver, can be fed into a consumer–resource model to predict community-level properties like composition and biomass in the presence and absence of the two drivers. Importantly, this approach provides understanding at which level of organization and due to which vital rates potential interactions among drivers arise and generate quantitative predictions that can be compared to observations.

We illustrate our approach with an aquatic snail that consumes algae (Figure 1, e.g., Sampaio et al., 2017), exposed to a warming gradient and acidification. The pattern-based approach (path A, Figure 1) evaluates multiple driver effects by fitting a statistical model (i.e., two-factor ANOVA with main effects and interaction term) to a community property such as biomass. In contrast, the process-based approach (path B, Figure 1) would require measuring the vital rates of the consumer–resource system across the relevant temperature and acidification range. If both drivers are continuous and measured jointly across a large number of levels, this would result in response surfaces (not shown). Path B reveals that the additional driver leads to a generally lower growth rate, higher mortality and lower attack rate with a smaller range of critical thermal limits (Figure 1). These rates are subsequently used to parameterize a consumer–resource model to predict the biomass and compare it with the observed biomass under multiple drivers. After validating the predicted biomass with observed data derived from path A, these predictions can be used to inform decision-makers and practitioners. Path A and path B are complementary with different aims: path A addresses the exploration and the generation of hypotheses, whereas path B consequently and simultaneously focuses on the mechanistic understanding of the joint global change drivers with the ultimate aim to be able to make predictions about future global change scenarios (Tredennick et al., 2021). This risk analysis is a key step in the process going from defining management goals to decision-making (Pirotta et al., 2022).

We use a simple consumer–resource model to understand whether the reaction norms of two vital rates (i.e., growth of the resource and the consumer) can help to predict interactive effects for the consumer–resource biomass ratio (Box 1). We find that knowing the overall effects each driver has on species growth and attack rates is sufficient to predict when additive, antagonistic, or synergistic effects on the community-level biomass ratio occur (Figure 2). When both drivers have the same effect within a trophic level, for example, growth rate and attack rate are affected in the same way by both temperature and nutrient availability, antagonisms will occur (Figure 2, scenario 1). When drivers have the opposite effect within a trophic level but exactly offset each other (e.g., the positive effect of temperature on growth is canceled by the negative effect of acidification), the response surface dictates predominantly synergistic effects (scenario 2). When the two trophic levels experience the same effect of the same driver, both interactive and additive effects are possible (scenario 3). Finally, when the two trophic levels experience the opposite effect of the same driver (e.g., temperature stimulates the growth of the resource but reduces the consumer's attack rate), effects will always be additive when these effects offset each other (scenario 4).
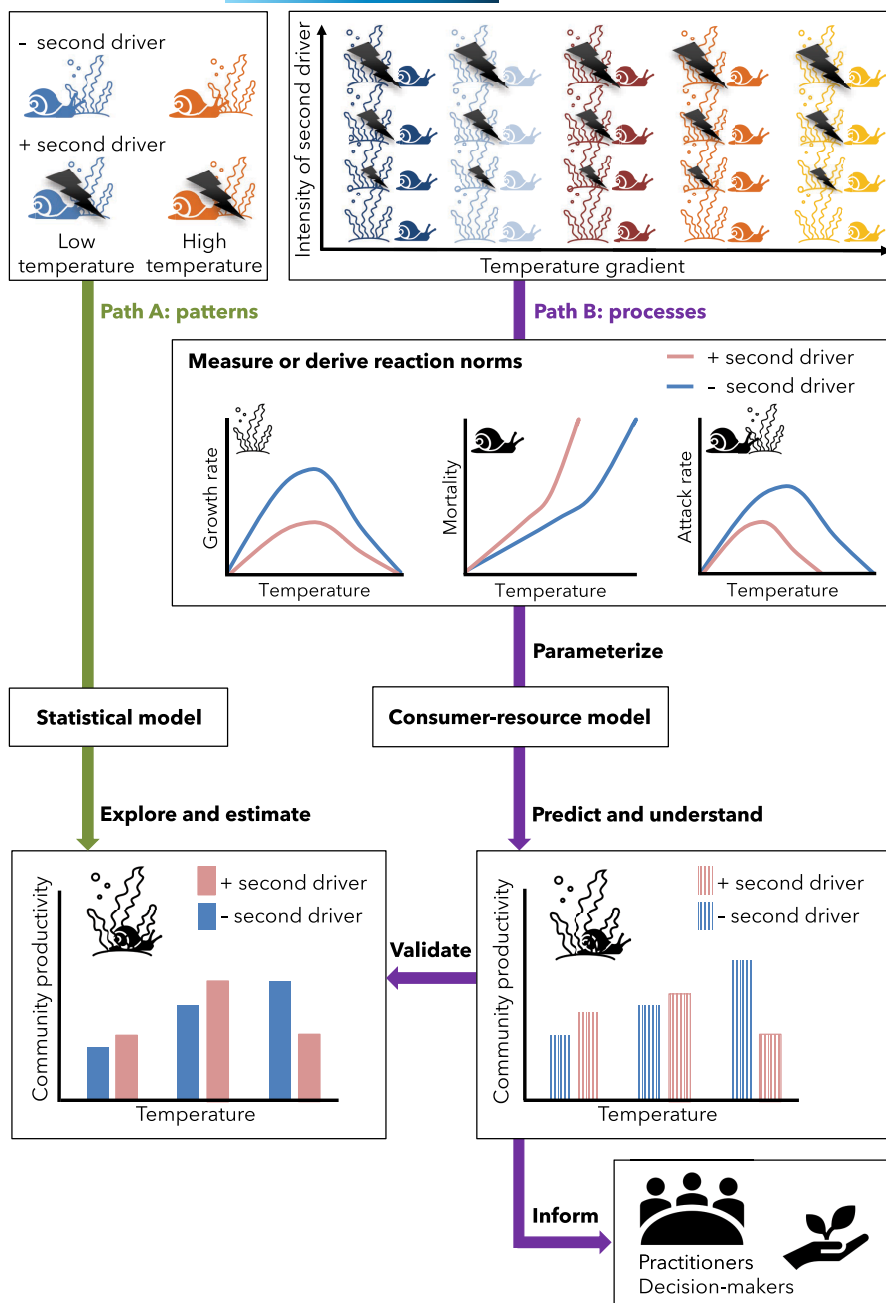
FIGURE 1 Overview of the conceptual framework. A large body of research has focused on estimating the effects of multiple drivers on community properties, such as community productivity by fitting statistical models to experimental data (focus on patterns, path A, green arrow). However, data on rates are rarely being collected. Here, we propose that path B (focus on processes, purple arrow) is a complementary method that would allow understanding of the mechanisms behind the multiple-driver impacts on consumer–resource dynamics. First, reaction norms of model parameters (growth rate, mortality, attack rate) to temperature in the presence (orange lines) and absence (blue lines) of a second driver, for example, acidification, are derived or measured. These reaction norms are consequently used to parameterize consumer–resource models and predict community productivity. The predicted response (right box, graph with the orange and blue line pattern) can then be compared to and validated with measured community productivity (the end of path A, graph with solid blue and orange fill), providing insights about which rates interact to determine the community response.

3 | EFFECTS OF MULTIPLE DRIVERS ON VITAL RATES: EMPIRICAL EVIDENCE

Studies that focus on "patterns" (path A in Figure 1) normally measure a population or community property, such as biomass or abundance. A meta-analysis summarized 88 papers, including 286 responses of freshwater ecosystems to paired drivers (Jackson et al., 2016). For temperature paired with a second driver, they identified 118 responses. Of these, nearly two thirds ($n = 71$) were community-level responses such as biomass, abundance, or diversity. The meta-analysis also identified studies reporting population-level or organism-level responses focusing on growth or survival ($n = 42$ responses or $n = 23$ papers with temperature as one of the two drivers). This seems to suggest that the field

has, to some extent, already started to collect the data needed for the "process-based" approach (path B in Figure 1). Yet, for the implementation of the process-based approach, four criteria must be fulfilled: we need (1) reaction norms (2) for at least two drivers, (3) for different vital rates, (4) for both consumer and resource species (although our approach is more general and also applies to non-trophic communities). None of the 23 studies studying temperature with another driver identified in Jackson et al. (2016) fulfilled all these criteria.

We conducted a literature search to estimate how many studies have focused on the process-based approach. Due to the vast multiple driver literature, we focused on four common drivers that appear in combination with warming: (1) eutrophication, (2) acidification, (3) heavy metal pollution, and (4) chemical pollution. Warming is

BOX 1 A simple proof-of-concept model.

We focus on a consumer–resource pair and three rates: intrinsic growth, consumption, and mortality. These are fundamental parameters of simple consumer–resource models but also of more complex model formulations like trophic networks. We expect higher model complexity (more parameters and state variables) to only increase the potential for non-linearities in community properties (e.g., biomass) to arise when multiple drivers affect multiple rates simultaneously. The resource's (species 1) intrinsic growth rate (b_1) and the consumer's (species 2) attack rate (a) are directly affected by two drivers. We consider the case where driver levels are too low to alter the consumer's death rate (b_2) (Smith et al., 2009). The effects of the drivers can be described by a response surface function f, which quantifies the effect of the driver(s) (≥ 0, where $f = 1$ indicates no effect, $f < 1$ indicates a negative effect, and $f > 1$ indicates a positive effect). We say that f_i is the response surface of species i. For simplicity, we assume the response surface is simply the multiplication of the effects of the two drivers: $f_i = f_{i1}f_{i2}$, where f_{i1} and f_{i2} return the effect of drivers 1 and 2 on species i. This corresponds to two drivers which do not interact: their effects are independent. This leads us to the following equations:

$$\frac{1}{N_1}\frac{dN_1}{dt} = f_{11}f_{12}b_1 - f_{21}f_{22}aN_2 - N_1,$$

$$\frac{1}{N_2}\frac{dN_2}{dt} = f_{21}f_{22}aN_1 - b_2. \tag{1}$$

This model has a point equilibrium, and we can compute the consumer to resource biomass ratio at that equilibrium:

$$r = \frac{\widehat{N_2}}{\widehat{N_1}} = \frac{ab_1f_{11}f_{12}f_{21}f_{22} - b_2}{ab_2f_{21}f_{22}} \tag{2}$$

Given this equation, we can now formalize the prevalence of interactive effects of both drivers on the biomass ratio, using the metric $\rho = \frac{r_{1\&2}/r_0}{r_1r_2/r_0^2}$ from (Turschwell et al., 2022), where $r_{1\&2}$, r_1, and r_2 represent the biomass ratio when both drivers are present, only driver 1 is present, and only driver 2 is present, respectively. r_0 is the biomass ratio when both drivers are absent. When $\rho = 1$, the two drivers act additively (numerator equals denominator in the above equation), while $\rho < 1$ (numerator < denominator) and $\rho > 1$ (numerator > denominator) imply synergism and antagonism, respectively (Turschwell et al., 2022). Note that the absence of a driver j implies $f_{ij} = 1$. Substituting r into the equation for ρ yields:

$$\rho = \frac{(b_2 - ab_1)(b_2 - ab_1f_{11}f_{12}f_{21}f_{22})}{(b_2 - ab_1f_{11}f_{21})(b_2 - ab_1f_{12}f_{22})} \tag{3}$$

Thus, drivers act additively ($\rho = 1$) when $(b_2 - ab_1)(b_2 - ab_1f_{11}f_{12}f_{21}f_{22}) = (b_2 - ab_1f_{11}f_{21})(b_2 - ab_1f_{12}f_{22})$, which can be simplified to $f_{11}f_{12}f_{21}f_{22} + 1 = f_{11}f_{21} + f_{12}f_{22}$, which we rewrite in a more compact form as: $f_1f_2 + 1 = f_1 + f_2$, here $f_1 = f_{11}f_{21}$ is the overall effect exerted by driver 1 on both species and $f_2 = f_{12}f_{22}$ is the overall effect exerted by driver 2 on both species. The product of f_1 and f_2 is then the overall effect of all drivers on all species ($f_{11}f_{12}f_{21}f_{22}$). Consequently, synergism occurs when $f_1f_2 + 1 < f_1 + f_2$, while antagonism occur when $f_1f_2 + 1 > f_1 + f_2$.

This analysis illustrates that the occurrence of driver interactions may be fully determined by the shapes of the response surfaces, which will determine the f_{ij}, and thus f_1 and f_2 (Figure 2). In this example, the ecology of species does not influence the prevalence of driver interactions whether $\rho < 1$, $\rho > 1$, or $\rho = 1$ and ρ does not depend on the consumption rate (a), intrinsic growth rate (b_1), or mortality rate (b_2). Various scenarios on the relative magnitudes of driver effects imply different kinds of driver interactions on the biomass ratio (Figure 2). While the model's assumptions (linear functional responses, reaction surfaces) are admittedly strong, and the chosen response variable simple (consumer to resource ratio at equilibrium), these theoretical results illustrate how the sign and strength of the response surfaces can predispose communities to experiencing unexpected effects of driver mixtures. In more complex models, for example, containing more species and exhibiting more complex (non-point) attractors, we suspect that effects on the biomass ratio and more complex response variables will depend on how a species' ecology (e.g., a consumer's attack rate a) covaries with the driver effects experienced by this species (see also Spaak et al., 2017): for example, species with a higher a could be more sensitive to driver effects. An analysis showing under what conditions we can rely on reaction norms only and when information on the response surface and on the ecology of the community is needed to predict driver interactions on the biomass ratio is presented in Figure S1.

the focal driver since thermal performance curves belong to the best studied reaction norms and hence, we expected warming to be studied frequently in combination with other drivers. Covering other combinations between temperature and all possible drivers (e.g., salinity, see Jun et al., 2012; Rogell et al., 2009) was beyond the scope of the review. We identified studies that included temperature in combination with one of these four drivers, had a minimum of two levels per driver, and measured at least one of three vital

FIGURE 2 Response surface functions predict interactive driver effects on the consumer–resource biomass ratio. These functions determine f_1 (the total effect exerted by driver 1 on both species) and f_2 (the total effect exerted by driver 2 on both species), which in turn together predict driver interactions (blue for additive, orange for antagonistic, yellow for synergistic). We consider four demonstrative scenarios (numbered boxes) which lead to different outcomes. In scenario 1 (dashed diagonal line), the two drivers have identical effects on individual species, regardless of the trophic level: $f_{11} = f_{12}$ and $f_{21} = f_{22}$, implying that $f_1 = f_2$. This scenario implies that antagonisms will occur unless $f_1 = f_2 = 1$ (large black dot), which leads to additive effects. In scenario 2 (solid curve), both drivers have the opposite effect on a trophic level. A simple case is the one where both drivers exactly offset each other's effect (solid line): $f_{11}f_{12} = 1$ and $f_{21}f_{22} = 1$. In that case, $f_1f_2 = 1$, that is, the response surface functions dictate that only values on the solid line are possible, which will lead to predominantly synergistic effects. In scenario 3 (any point in the graph), species in both trophic levels experience the same effect of any particular driver: $f_{11} = f_{21}$ and $f_{12} = f_{22}$. Both interactions and additive effects are possible, hence the labels for this scenario are spread out across the figure. Finally, scenario 4 (large black dot) corresponds to the two trophic levels experiencing the opposite effect (one effect <1, another effect >1) of the same driver. Again, a simple case occurs when $f_{11}f_{21} = 1$ and $f_{12}f_{22} = 1$ (effects offset each other perfectly). In that case, effects will always be additive (large black dot).

rates (growth, mortality, and/or attack rate). We included studies that only considered a single trophic level (e.g., resource only or consumer only). Despite this inclusive search, we only found a total of 63 papers (Figure 3, Table S1), 60 of which were published in the last 10 years (Table S1). More than half of the studies assessed reaction norms of either resource or consumer for more than two temperature levels ($n = 35$), of which the majority had also more than two levels for both drivers simultaneously ($n = 27$).

Only a handful of studies investigated consumers and resources jointly ($n = 6$), and only one study included both trophic levels and several levels for both drivers (Kamya et al., 2018, Figure 3). However, some researchers either measured vital rates or inferred them from theory for consumer–resource systems. Table 1 lists some of the studies that (partly) collected the data necessary to apply our approach but did not implement it.

What is common to all the studies identified in the literature search is that we currently only have small surface areas within the potential landscape defined by the drivers available for the rates. This is perhaps not surprising because this approach is logistically demanding. To cover the full response surface area, one needs to test a great number of levels while considering physiological limits. Yet, studies measuring vital rates for consumer–resource interactions across highly resolved gradients of two or more drivers are exceedingly rare. Accordingly, none of the studies we found collected all the relevant data to parameterize a consumer–resource model.
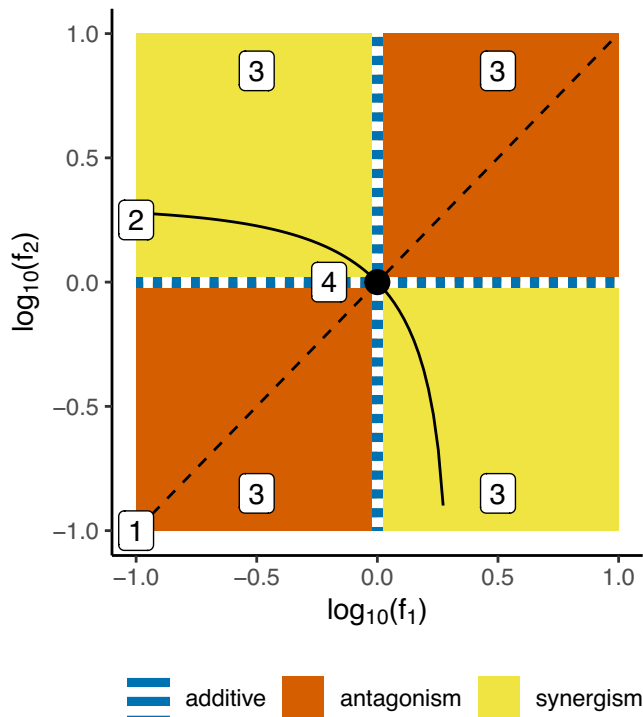
4 | PARAMETRIC AND NONPARAMETRIC APPROACHES TO QUANTIFY RESPONSE SURFACES

The key element of our approach are the response surfaces of vital rates allowing to integrate the response to multiple drivers into consumer–resource models. Response surfaces can be quantified with parametric and nonparametric approaches. To generalize across different consumer–resource systems and be cost and time efficient, we refer readers to the excellent review of experimental methods by Boyd et al. (2018). Both the parametric and nonparametric approaches require experimental designs that measure vital rates across fine-grained environmental gradients. As nonlinear relationships are expected, appropriate experimental designs that maximize information gain should be employed (Boyd et al., 2018). Regression or gradient designs that can identify the underlying relationship between vital rates and gradients of a driver are particularly suited (Boyd et al., 2018; Cottingham et al., 2005; Kreyling et al., 2018). Since the number of driver combinations increases exponentially with the number and levels of multiple drivers, Boyd et al. (2018) suggest reducing the number of drivers by identifying a primary driver with disproportional effect (i.e., warming) and crossing (collapsing) this driver with a series of less important drivers (i.e., pollution, eutrophication). A reduced design in contrast would quantify the impacts of isolated drivers and their three-way combination
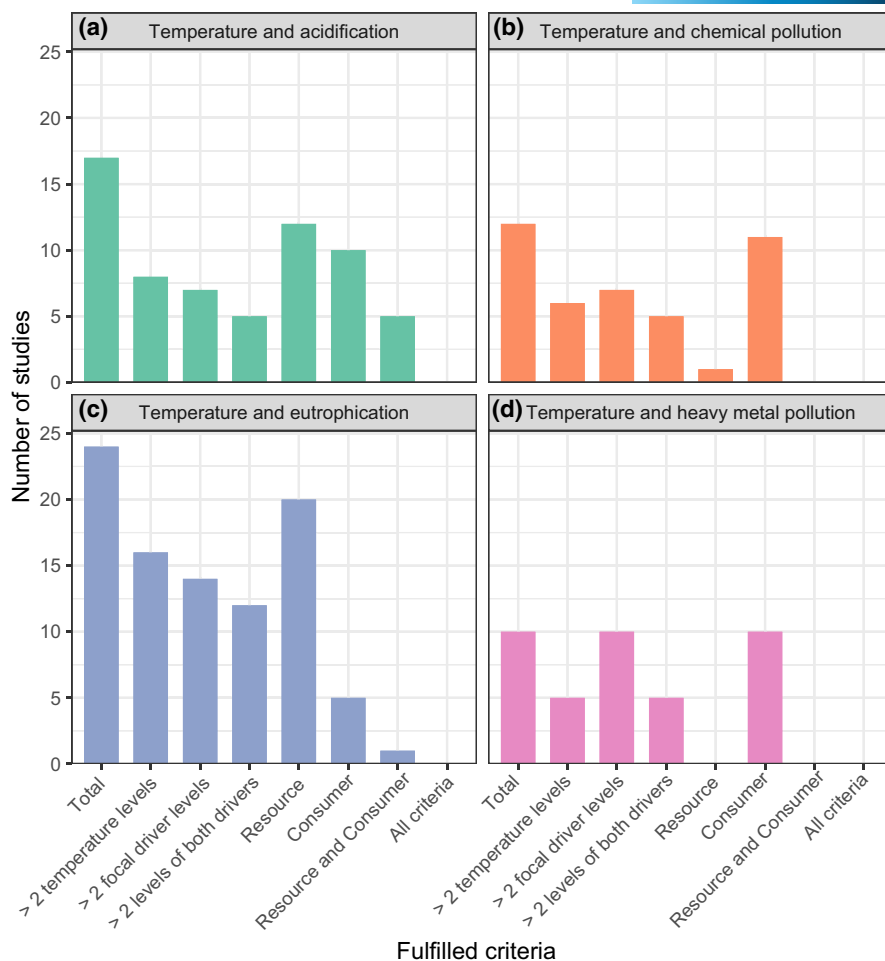
FIGURE 3 Graphic summary of papers identified in the literature review on temperature effects together with a second driver ($n = 63$). (a) Temperature and acidification. (b) Temperature and chemical pollution. (c) Temperature and eutrophication. (d) Temperature and heavy metal pollution. Total: Total number of empirical studies that considered the effects of temperature and a second driver on either a consumer, resource, or both in the same study. Theoretical studies and meta-analyses were excluded. >2 temperature levels: Out of the total studies found, those that used >2 temperature levels. >2 focal driver levels: Out of the total studies, those that used >2 focal driver levels. >2 levels of both drivers: Out of the total studies, those that used >2 levels for both temperature and the second driver. Resource: Out of the total studies, how many looked at the resource. Consumer: Out of the total studies, how many looked at the consumer. Resource and consumer: Out of the total studies, those that assessed both trophic levels in the same experiment. All criteria: Number of studies that fulfil all criteria. Heavy metal pollution includes Cd and As. Chemical pollution includes pyrene, microplastics, insecticides, and pesticides. Out of the total studies found, only one assessed both trophic levels and used >2 temperature levels and >2 levels of the focal driver in the same experiment (Kamya et al., 2018). Albeit both consumer and resource level were included and more than two levels per driver, the rates that were measured in this study do not allow parameterizing a consumer–resource model (Kamya et al., 2018). Neither the survival rate of the predator nor its density-dependent consumption were quantified. The papers underlying the data summarized in this figure are shown in Table S1.

but leaving out all two-way interactions, thus reducing the number of treatment combinations.

The parametric approach employs models of vital rates where the functional forms are expected to match a particular shape (i.e., unimodality). For example, the growth of organisms across a temperature gradient is commonly described by the Arrhenius–Boltzmann equation (in the optimal growth range) or, more realistically across the full temperature range by the Sharpe–Schoolfield equation (Angilletta, 2009). For limiting resources such as nutrients or light, the population-level intrinsic growth rate is well described by the Monod equation (Monod, 1949). Drivers whose univariate reaction norms are well-known can be combined to understand when interactive effects occur. Such efforts will be most valuable

to advance our understanding of multiple drivers if the resulting equations will be thoroughly empirically tested. Bestion et al. (2018) use the Monod equation to model the growth of phytoplankton species. They assumed that the two parameters of the Monod equation (i.e., maximum growth rate and half saturation density) follow the temperature dependence of the Arrhenius–Boltzmann equation in the optimal growth range, hence not allowing for temperature and nutrient treatments to interact. In contrast, Lewington-Pearce et al. (2019) fitted the parameters of the Monod equation independently for each temperature and found that the parameters were temperature dependent and interacted with nitrogen and light supply. The effect of temperature on R* (minimum resource level required for positive population-level growth) was U shaped for

TABLE 1 Research involving acidification as a driver in addition to temperature is the one that most often includes two trophic levels in their experiments. Studies using heavy metal or chemical pollution were mostly measuring responses at several driver levels, likely because these studies come from the field of ecotoxicology, where response curves are commonly done

| Consumer/resource	Driver	Measured rates	Main findings	Reference
Research focusing on consumer and resource simultaneously				
The amphipod *Melita palmata*, the gastropod *Gibbula umbilicalis*/green macroalga *Ulva rigida*	Acidification	Consumer mortality, consumption rate	Found significant effects of temperature and acidification, but no interactive effects for any of the grazers	Sampaio et al. (2017)
Juvenile crown-of-thorn starfish/coral (*Acanthaster* spp., *Acropora* spp.)	Acidification	Consumer growth, consumption rate	Found a significant effect of temperature, but not of pH on both consumption and coral recovery. They also did not observe any interactive effects between pH and temperature	Kamya et al. (2018)
Microzooplankton/phytoplankton	Acidification	Growth rates and grazing rates of microzooplankton	Found significant interactive effect of temperature and acidification but only for the consumer and not the resource. Found effects of high CO_2 (acidification), warming, and their interactions on growth and grazing rates	Horn et al. (2020)
Lymnaea stagnalis/submerged plant *Vallisneria spiralis*	Acidification	Resource growth rate, plant consumption (feeding) rate	Found no effects of temperature or nutrient treatments on plant consumption rates. But the aquatic plants (resource) grew faster in nutrient-rich than nutrient-poor sediments with rising temperature. Different trophic levels responded differently to the same driver	Zhang et al. (2020)
Research focusing on only one trophic level but with many driver levels				
Daphnids (*Daphnia magna, Daphnia pulex, Ceriodaphnia dubia*)	Microplastics	Consumer mortality	Compared the sensitivity of these species to six concentrations of both primary and secondary microplastics at three different temperatures. Found interactive effects of temperature and microplastics on consumer mortality	Jaikumar et al. (2018)
Crustacean *Amphibalanus amphitrite*	Cadmium	Consumer mortality	Found interactive effects of temperature and the pollutant (microplastics or cadmium, respectively) on consumer mortality	Piazza et al. (2016)
Microbial decomposers (*Limnephilus* sp.)	Cadmium	Consumer mortality	Found interactive effects of temperature and the pollutant (microplastics or cadmium, respectively) on consumer mortality	Batista et al. (2012)
Six phytoplankton species	Nutrients	Resource growth rate	Calculated TPCs for six phytoplankton species in 10 nutrient levels to parameterize their model	Bestion et al. (2018)
Six phytoplankton species	Nutrients (and light)	Resource growth rate	Studied the temperature dependence of Monod parameters for nitrogen and light, again in 10 levels, and found that environmental temperature altered growth parameters of six phytoplankton species	Lewington-Pearce et al. (2019)
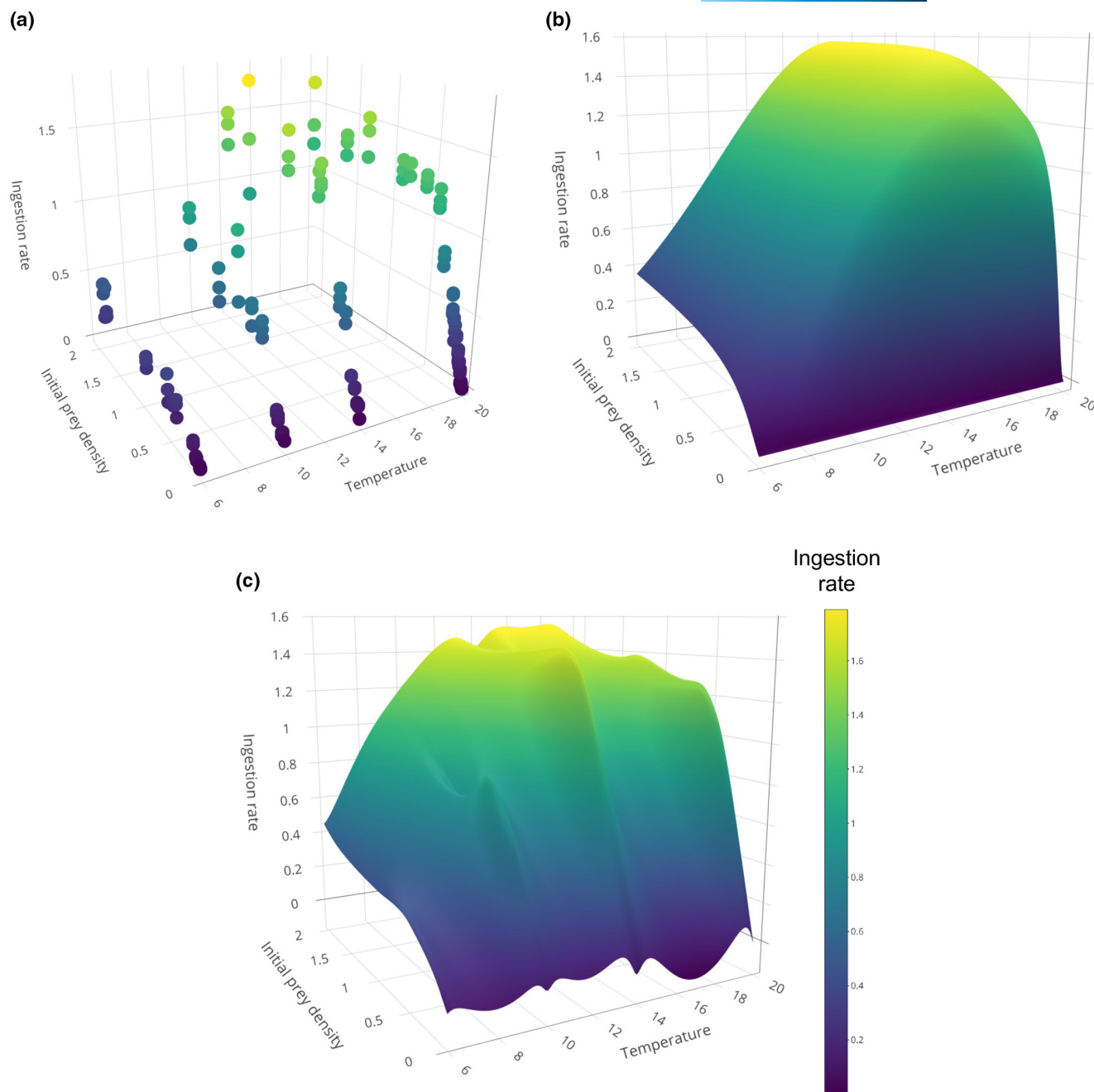
FIGURE 4 Illustration of parametric and nonparametric response surfaces between the effect of temperature and changes in prey density on the ingestion rate of a predator. (a) Experimental measures of ingestion rate across initial prey density and temperature. (b) Response surface of ingestion rate across temperature and prey density with the parametric generalized functional response model. (c) Response surface of ingestion rate across temperature and prey density with a nonparametric generalized additive model (GAM). High ingestion rates are shown in yellow, low consumption in dark purple. Data and functional response parameters are from Uszko et al. (2020).

nitrogen and light, when standardized and compared across species. Thomas et al. (2017) combined the Monod equation with a temperature-dependent reproduction term of the double exponential model, predicting a resource-dependent change in the optimal growth temperature. Subsequent tests of the model using a globally distributed phytoplankton species across a range of temperatures, as well as nutrient concentrations, supported the prediction of nutrient-dependent optimal growth (Thomas et al., 2017). To illustrate the parametric approach, we used the data and model fits from

Uszko et al. (2020) who investigated the effect of temperature and prey density on the ingestion rate of *Daphnia* (Uszko et al., 2020). Ingestion rate was measured across four temperatures and a gradient of initial algae densities (Figure 4a). The response surface of ingestion across temperature and initial density was generated by fitting the generalized functional response and its parameters (i.e., attack rate, handling time and attack rate exponent), and the temperature dependence of the model parameters approximated by a second-order polynomial (Figure 4b).

The nonparametric empirical approach approximates response surfaces of vital rates across fine-grained environmental gradients with flexible, data-driven methods such as generalized additive models (GAMs, Wood, 2017), Gaussian processes (Thorson et al., 2014), or polynomial regression (James et al., 2021), which can deal with both the non-monotonic nature of the data and the inherent noise due to measurement error. Thomas et al. (2017) used GAMs to approximate the underlying response surface of growth across temperature and nutrient concentration. Bestion et al. (2018) fitted GAMs to growth rates across five temperature and 13 phosphate concentrations. Optimal growth temperature was then estimated as the temperature where the GAM prediction was maximized. Morel-Journel et al. (2020) exposed the ciliate *Tetrahymena thermophila*, a heterotrophic consumer, to 25 combinations of temperature and nutrient concentration. Rather than GAMs, they used polynomial regression with quadratic terms showing that abundance responded to both drivers simultaneously. To contrast the nonparametric with the parametric approach, we also fitted a GAM to the data from Uszko et al. (2020). Like the generalized functional response, the GAM indicated that ingestion rate was temperature and resource density dependent (Figure 4c). However, the GAM and the parametric functional response also showed deviations in ingestion rates that could be due to the stochastic nature of the ingestion measurements or point to unknown processes affecting the functional response.

But can these nonparametric functional forms be used in consumer–resource models? Griffiths et al. (2018) show how to achieve this not for multiple drivers but with trait changes in tri-trophic communities. The authors integrated response surfaces approximated with GAMs into an intra-guild predation model. The GAMs revealed similar shapes, for instance saturating consumption rates at high resource densities, as expected by theory. This hybrid modeling approach could be extended to multiple drivers, by studying the response surface of vital rates across temperature and resource availability (i.e., the functional response of the consumer) and directly use the surface to predict the dynamics of the consumer–resource system.

5 | IMPLICATIONS FOR FUTURE RESEARCH AND CONCLUSIONS

We have argued that, for predicting interactions between multiple drivers, there is a need to know how vital rates of consumer–resource systems respond to multiple drivers. Measuring response surfaces for all the rates of consumer–resource systems is logistically more demanding than studying a single community property under the influence of two drivers with two levels each. A response surface with two drivers and five levels will require 25 measurements for each of the three rates (i.e., growth rate of the resource, attack rate, and mortality of the consumer) required to parameterize a consumer–resource model, resulting in 225 measurements with modest replication (3 rates × 5 levels of driver 1 × 5 levels of driver 2 × 3 replicates). To measure total community biomass with five levels of the two drivers and

three replicates, only 75 measurements are needed. While the process-based approach requires both experiments when the consumer–resource model should be validated (300 measurements total), the pattern-based approach can be done with only 75 measurements. Some of these issues can be addressed by more efficient experimental designs (Boyd et al., 2018) and the increasing availability of high-throughput approaches in community ecology (Besson et al., 2022; Dell, Bender, et al., 2014). As we have argued, the expected gain are models that allow predicting multiple driver effects on communities. Measuring response surfaces for species with disproportional effects on communities (e.g., large growth rates for resources or large attack rates for consumers) such as keystone or invasive species may be particularly valuable (Carignan & Villard, 2002) given the larger efforts required by the response surface design. Furthermore, testing our approach across many different consumer–resource systems will allow to test for generalizable effects of multiple drivers on vital rates. Body size is a key trait in consumer–resource systems (Brose et al., 2006) and used by the allometric trophic network model that builds on the allometric relationships between body size and vital rates, and hence may allow to generalize across particular consumer–resource pairs (Simmons et al., 2021).

As not all consumer–resource interactions are amenable to experimental manipulation, we also require new tools that allow us to infer response surfaces from observational data. Time-series data may be suitable to this end, when consumer and resource abundance can be measured under the joint influence of two or more drivers. Trosvik et al. (2008) provide an example where the effects of pH and the biochemical environment were studied on the community dynamics of three competing bacterial species, considering both species interactions and the effect of the environment with GAMs. Whenever response surfaces are quantified from observational data, driver correlations need to be considered. Strong positive or negative correlations among drivers, so called threat complexes (Bowler et al., 2020), limit the extent of the response surface that can be quantified. On the other hand, this reduces the number of relevant driver combinations, hence reducing the logistical burden of our approach. In contrast, we can design experiments that break such intrinsic driver correlations.

Finally, we believe that our framework is also well suited to include the role of rapid evolution and adaptation. The available evidence is mixed, suggesting that some species may be able to adapt to multi-driver environments, reverting to their ancestral states after long-term exposure (Brennan et al., 2017). On the other hand, it was also found that rapid evolution can create novel synergisms between multiple drivers (Orr et al., 2022). Besides evolutionary processes, phenotypic plasticity may influence the response to multiple drivers over shorter time scales and hence the duration of the exposure is an important consideration (King et al., 2022). However, given that both evolution and phenotypic plasticity will shape the reaction norms of vital rates, our approach readily allows us to account for these processes occurring over time.

Currently, our framework does not consider the spatial dimension since the effects of multiple drivers on dispersal are incompletely

understood (Lopez et al., 2021). However, a distributed experiment across a range of model organisms has shown that top-down (i.e., predator cues) and bottom-up effects (i.e., resource availability) will modulate dispersal (Fronhofer et al., 2018). Incorporating dispersal responses into our framework would be an exciting avenue to understand how meta-communities respond to multiple drivers.

Clearly, even with our framework in place, there is still a gap between simple consumer–resource interactions and whole community dynamics and responses. However, apart from the fact that an intermediate step is oftentimes necessary, we believe that a risk analysis for two-species interactions can be of high value. There are many situations where decision-makers are interested in the interactions between only a few species for their management practices, such as keystone species or key invasive species (Carignan & Villard, 2002). One example for the latter is a study by Kamya et al. (2018), which shows that the invasive Crown-of-Thorns starfish, *Acanthaster planci*, increases consumption of coral under further ocean acidification and warming. Their findings are thus directly relevant for decision-makers aiming to manage and monitor the starfish. In conclusion, experiments with a subset of species present in an ecosystem can already yield meaningful information.

The prevalence of interacting multiple drivers in increasingly human-dominated ecosystems is a major global concern. While there is a push toward understanding how many drivers interactively affect ecosystem functions (Rillig et al., 2019), we urge that, besides characterizing the patterns, it is crucial to additionally predict when interactions occur at the population and community level. Implementing the proposed reaction-norm based framework is a major step toward this goal, relying on well-established ecological theory and consumer–resource models, as well as targeted efforts to measure the sensitivity of vital rates of entire consumer–resource systems to multiple drivers.

AUTHOR CONTRIBUTIONS

This study was conceived by all authors during a workshop organized by Frederik De Laender. The first draft of the manuscript was written by Sofia J. van Moorsel and Frank Pennekamp with input from all authors. Frederik De Laender and Mark Holmes developed the model. All authors substantially contributed to revisions of the paper.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable–no new data generated. Code to reproduce the proof-of-concept model is available on Zenodo: https://doi.org/10.5281/zenodo.7428947.

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REFERENCES

Angilletta, M. J. (2009). *Thermal adaptation: A theoretical and empirical synthesis*. OUP Oxford.

Batista, D., Pascoal, C., & Cássio, F. (2012). Impacts of warming on aquatic decomposers along a gradient of cadmium stress. *Environmental Pollution*, *169*, 35–41. https://doi.org/10.1016/j.envpol.2012.05.021

Beauchesne, D., Cazelles, K., Archambault, P., Dee, L. E., & Gravel, D. (2021). On the sensitivity of food webs to multiple stressors. *Ecology Letters*, *24*(10), 2219–2237. https://doi.org/10.1111/ele.13841

Besson, M., Alison, J., Bjerge, K., Gorochowski, T. E., Høye, T. T., Jucker, T., Mann, H. M. R., & Clements, C. F. (2022). Towards the fully automated monitoring of ecological communities. *Ecology Letters*, *25*, 2753–2775. https://doi.org/10.1111/ele.14123

Bestion, E., García-Carreras, B., Schaum, C.-E., Pawar, S., & Yvon-Durocher, G. (2018). Metabolic traits predict the effects of warming on phytoplankton competition. *Ecology Letters*, *21*(5), 655–664. https://doi.org/10.1111/ele.12932

Binzer, A., Guill, C., Rall, B. C., & Brose, U. (2016). Interactive effects of warming, eutrophication and size structure: Impacts on biodiversity and food-web structure. *Global Change Biology*, *22*(1), 220–227. https://doi.org/10.1111/gcb.13086

Birk, S., Chapman, D., Carvalho, L., Spears, B. M., Andersen, H. E., Argillier, C., Auer, S., Baattrup-Pedersen, A., Banin, L., Beklioğlu, M., Bondar-Kunze, E., Borja, A., Branco, P., Bucak, T., Buijse, A. D., Cardoso, A. C., Couture, R.-M., Cremona, F., de Zwart, D., … Hering, D. (2020). Impacts of multiple stressors on freshwater biota across spatial scales and ecosystems. *Nature Ecology & Evolution*, *1–8*, 1060–1068. https://doi.org/10.1038/s41559-020-1216-4

Bowler, D. E., Bjorkman, A. D., Dornelas, M., Myers-Smith, I. H., Navarro, L. M., Niamir, A., Supp, S. R., Waldock, C., Winter, M., Vellend, M., Blowes, S. A., Böhning-Gaese, K., Bruelheide, H., Elahi, R., Antão, L. H., Hines, J., Isbell, F., Jones, H. P., Magurran, A. E., … Bates, A. E. (2020). Mapping human pressures on biodiversity across the planet

uncovers anthropogenic threat complexes. *People and Nature*, 2(2), 380–394. https://doi.org/10.1002/pan3.10071

Boyd, P. W., Collins, S., Dupont, S., Fabricius, K., Gattuso, J.-P., Havenhand, J., Hutchins, D. A., Riebesell, U., Rintoul, M. S., Vichi, M., Biswas, H., Ciotti, A., Gao, K., Gehlen, M., Hurd, C. L., Kurihara, H., McGraw, C. M., Navarro, J. M., Nilsson, G. E., ... Pörtner, H.-O. (2018). Experimental strategies to assess the biological ramifications of multiple drivers of global ocean change—A review. *Global Change Biology*, 24(6), 2239–2261. https://doi.org/10.1111/gcb.14102

Brennan, G. L., Colegrave, N., & Collins, S. (2017). Evolutionary consequences of multidriver environmental change in an aquatic primary producer. *Proceedings of the National Academy of Sciences of the United States of America*, 114(37), 9930–9935. https://doi.org/10.1073/pnas.1703375114

Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, 23(8), 453–460. https://doi.org/10.1016/j.tree.2008.03.011

Brose, U., Jonsson, T., Berlow, E. L., Warren, P., Banasek-Richter, C., Bersier, L.-F., Blanchard, J. L., Brey, T., Carpenter, S. R., Blandenier, M.-F. C., Cushing, L., Dawah, H. A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M. E., Martinez, N. D., Memmott, J., ... Cohen, J. E. (2006). Consumer–resource body-size relationships in natural food webs. *Ecology*, 87(10), 2411–2417. https://doi.org/10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CO;2

Carignan, V., & Villard, M.-A. (2002). Selecting indicator species to monitor ecological integrity: A review. *Environmental Monitoring and Assessment*, 78(1), 45–61. https://doi.org/10.1023/A:1016136723584

Collins, S., Whittaker, H., & Thomas, M. K. (2022). The need for unrealistic experiments in global change biology. *Current Opinion in Microbiology*, 68, 102151. https://doi.org/10.1016/j.mib.2022.102151

Côté, I. M., Darling, E. S., & Brown, C. J. (2016). Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences*, 283(1824), 20152592. https://doi.org/10.1098/rspb.2015.2592

Cottingham, K. L., Lennon, J. T., & Brown, B. L. (2005). Knowing when to draw the line: Designing more informative ecological experiments. *Frontiers in Ecology and the Environment*, 3, 145–152. https://doi.org/10.1890/1540-9295(2005)003[0145:KWTDTL]2.0.CO;2

Crain, C. M., Kroeker, K., & Halpern, B. S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, 11(12), 1304–1315. https://doi.org/10.1111/j.1461-0248.2008.01253.x

Darling, E. S., & Côté, I. M. (2008). Quantifying the evidence for ecological synergies. *Ecology Letters*, 11(12), 1278–1286. https://doi.org/10.1111/j.1461-0248.2008.01243.x

Daugaard, U., Petchey, O. L., & Pennekamp, F. (2019). Warming can destabilize predator–prey interactions by shifting the functional response from type III to type II. *Journal of Animal Ecology*, 88(10), 1575–1586. https://doi.org/10.1111/1365-2656.13053

De Laender, F. (2018). Community- and ecosystem-level effects of multiple environmental change drivers: Beyond null model testing. *Global Change Biology*, 24(11), 5021–5030. https://doi.org/10.1111/gcb.14382

Dell, A. I., Bender, J. A., Branson, K., Couzin, I. D., de Polavieja, G. G., Noldus, L. P. J. J., Pérez-Escudero, A., Perona, P., Straw, A. D., Wikelski, M., & Brose, U. (2014). Automated image-based tracking and its application in ecology. *Trends in Ecology & Evolution*, 29(7), 417–428. https://doi.org/10.1016/j.tree.2014.05.004

Dell, A. I., Pawar, S., & Savage, V. M. (2011). Systematic variation in the temperature dependence of physiological and ecological traits. *Proceedings of the National Academy of Sciences of the United States of America*, 108(26), 10591–10596. https://doi.org/10.1073/pnas.1015178108

Dell, A. I., Pawar, S., & Savage, V. M. (2014). Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *Journal of Animal Ecology*, 83(1), 70–84. https://doi.org/10.1111/1365-2656.12081

DeLong, J. P., & Lyon, S. (2020). Temperature alters the shape of predator–prey cycles through effects on underlying mechanisms. *PeerJ*, 8, e9377. https://doi.org/10.7717/peerj.9377

Englund, G., Öhlund, G., Hein, C. L., & Diehl, S. (2011). Temperature dependence of the functional response. *Ecology Letters*, 14(9), 914–921. https://doi.org/10.1111/j.1461-0248.2011.01661.x

Fronhofer, E. A., Legrand, D., Altermatt, F., Ansart, A., Blanchet, S., Bonte, D., Chaine, A., Dahirel, M., De Laender, F., De Raedt, J., di Gesu, L., Jacob, S., Kaltz, O., Laurent, E., Little, C. J., Madec, L., Manzi, F., Masier, S., Pellerin, F., ... Cote, J. (2018). Bottom-up and top-down control of dispersal across major organismal groups. *Nature Ecology & Evolution*, 2(12), 1859–1863, Article 12. https://doi.org/10.1038/s41559-018-0686-0

Gauzens, B., Rall, B. C., Mendonça, V., Vinagre, C., & Brose, U. (2020). Biodiversity of intertidal food webs in response to warming across latitudes. *Nature Climate Change*, 10(3), 264–269. https://doi.org/10.1038/s41558-020-0698-z

Gibert, J. P., Grady, J. M., & Dell, A. I. (2022). Food web consequences of thermal asymmetries. *Functional Ecology*, 36(8), 1887–1899. https://doi.org/10.1111/1365-2435.14091

Griffiths, J. I., Petchey, O. L., Pennekamp, F., & Childs, D. Z. (2018). Linking intraspecific trait variation to community abundance dynamics improves ecological predictability by revealing a growth–defence trade-off. *Functional Ecology*, 32(2), 496–508. https://doi.org/10.1111/1365-2435.12997

Harley, C. D. G., Connell, S. D., Doubleday, Z. A., Kelaher, B., Russell, B. D., Sarà, G., & Helmuth, B. (2017). Conceptualizing ecosystem tipping points within a physiological framework. *Ecology and Evolution*, 7(15), 6035–6045. https://doi.org/10.1002/ece3.3164

Harvey, B. P., Gwynn-Jones, D., & Moore, P. J. (2013). Meta-analysis reveals complex marine biological responses to the interactive effects of ocean acidification and warming. *Ecology and Evolution*, 3(4), 1016–1030. https://doi.org/10.1002/ece3.516

Horn, H. G., Boersma, M., Garzke, J., Sommer, U., & Aberle, N. (2020). High CO_2 and warming affect microzooplankton food web dynamics in a Baltic Sea summer plankton community. *Marine Biology*, 167(5), 69. https://doi.org/10.1007/s00227-020-03683-0

Jackson, M. C., Loewen, C. J. G., Vinebrooke, R. D., & Chimimba, C. T. (2016). Net effects of multiple stressors in freshwater ecosystems: A meta-analysis. *Global Change Biology*, 22(1), 180–189. https://doi.org/10.1111/gcb.13028

Jaikumar, G., Baas, J., Brun, N. R., Vijver, M. G., & Bosker, T. (2018). Acute sensitivity of three Cladoceran species to different types of microplastics in combination with thermal stress. *Environmental Pollution*, 239, 733–740. https://doi.org/10.1016/j.envpol.2018.04.069

James, G., Witten, D., Hastie, T., & Tibshirani, R. (2021). *An introduction to statistical learning: With applications in R* (2nd ed.). Springer.

Jun, Q., Pao, X., Haizhen, W., Ruiwei, L., & Hui, W. (2012). Combined effect of temperature, salinity and density on the growth and feed utilization of Nile tilapia juveniles (*Oreochromis niloticus*). *Aquaculture Research*, 43(9), 1344–1356. https://doi.org/10.1111/j.1365-2109.2011.02938.x

Kamya, P. Z., Byrne, M., Mos, B., & Dworjanyn, S. A. (2018). Enhanced performance of juvenile crown of thorns starfish in a warm-high CO_2 ocean exacerbates poor growth and survival of their coral prey. *Coral Reefs*, 37(3), 751–762. https://doi.org/10.1007/s00338-018-1699-5

King, O. C., van de Merwe, J. P., Campbell, M. D., Smith, R. A., Warne, M. S. J., & Brown, C. J. (2022). Interactions among multiple stressors vary with exposure duration and biological response. *Proceedings of the Royal Society B: Biological Sciences*, 289(1974). https://doi.org/10.1098/rspb.2022.0348

Kreyling, J., Schweiger, A. H., Bahn, M., Ineson, P., Migliavacca, M., Morel-Journel, T., Christiansen, J. R., Schtickzelle, N., & Larsen, K. S. (2018). To replicate, or not to replicate – That is the question: How to tackle nonlinear responses in ecological experiments. *Ecology Letters*, 21(11), 1629–1638. https://doi.org/10.1111/ele.13134

Lewington-Pearce, L., Narwani, A., Thomas, M. K., Kremer, C. T., Vogler, H., & Kratina, P. (2019). Temperature-dependence of minimum resource requirements alters competitive hierarchies in phytoplankton. *Oikos*, 128(8), 1194–1205. https://doi.org/10.1111/oik.06060

Litchman, E., & Thomas, M. K. (2022). Are we underestimating the ecological and evolutionary effects of warming? Interactions with other environmental drivers may increase species vulnerability to high temperatures. *Oikos*, e09155. https://doi.org/10.1111/oik.09155

Lopez, L., Gil, M., Crowley, P., Trimmer, P., Munson, A., Ligocki, I., Michelangeli, M., & Sih, A. (2021). Integrating animal behaviour into research on multiple environmental stressors: A conceptual framework [preprint]. https://doi.org/10.22541/au.161217752.23254903/v1

Monod, J. (1949). The growth of bacterial cultures. *Annual Review of Microbiology*, 3(1), 371–394. https://doi.org/10.1146/annurev.mi.03.100149.002103

Mor, J.-R., Muñoz, I., Sabater, S., Zamora, L., & Ruhi, A. (2022). Energy limitation or sensitive predators? Trophic and non-trophic impacts of wastewater pollution on stream food webs. *Ecology*, 103(2), e03587. https://doi.org/10.1002/ecy.3587

Morel-Journel, T., Thuillier, V., Pennekamp, F., Laurent, E., Legrand, D., Chaine, A. S., & Schtickzelle, N. (2020). A multidimensional approach to the expression of phenotypic plasticity. *Functional Ecology*, 34(11), 2338–2349. https://doi.org/10.1111/1365-2435.13667

Orr, J. A., Luijckx, P., Arnoldi, J.-F., Jackson, A. L., & Piggott, J. J. (2022). Rapid evolution generates synergism between multiple stressors: Linking theory and an evolution experiment. *Global Change Biology*, 28(5), 1740–1752. https://doi.org/10.1111/gcb.15633

Orr, J. A., Vinebrooke, R. D., Jackson, M. C., Kroeker, K. J., Kordas, R. L., Mantyka-Pringle, C., Van den Brink, P. J., De Laender, F., Stoks, R., Holmstrup, M., Matthaei, C. D., Monk, W. A., Penk, M. R., Leuzinger, S., Schäfer, R. B., & Piggott, J. J. (2020). Towards a unified study of multiple stressors: Divisions and common goals across research disciplines. *Proceedings of the Royal Society B: Biological Sciences*, 287(1926), 1740–1752. https://doi.org/10.1098/rspb.2020.0421

Piazza, V., Gambardella, C., Canepa, S., Costa, E., Faimali, M., & Garaventa, F. (2016). Temperature and salinity effects on cadmium toxicity on lethal and sublethal responses of *Amphibalanus amphitrite nauplii*. *Ecotoxicology and Environmental Safety*, 123, 8–17. https://doi.org/10.1016/j.ecoenv.2015.09.023

Pirotta, E., Thomas, L., Costa, D. P., Hall, A. J., Harris, C. M., Harwood, J., Kraus, S. D., Miller, P. J. O., Moore, M. J., Photopoulou, T., Rolland, R. M., Schwacke, L., Simmons, S. E., Southall, B. L., & Tyack, P. L. (2022). Understanding the combined effects of multiple stressors: A new perspective on a longstanding challenge. *Science of the Total Environment*, 821, 153322. https://doi.org/10.1016/j.scitotenv.2022.153322

Pörtner, H.-O., Scholes, R. J., Agard, J., Archer, E., Arneth, A., Bai, X., Barnes, D., Burrows, M., Chan, L., Cheung, W. L., Diamond, S., Donatti, C., Duarte, C., Eisenhauer, N., Foden, W., Gasalla, M. A., Handa, C., Hickler, T., Hoegh-Guldberg, O., … Ngo, H. (2021). Scientific outcome of the IPBES-IPCC co-sponsored workshop on biodiversity and climate change. *Zenodo*, 1–252. https://doi.org/10.5281/zenodo.5101125

Rillig, M. C., Ryo, M., Lehmann, A., Aguilar-Trigueros, C. A., Buchert, S., Wulf, A., Iwasaki, A., Roy, J., & Yang, G. (2019). The role of multiple global change factors in driving soil functions and microbial biodiversity. *Science*, 366(6467), 886–890. https://doi.org/10.1126/science.aay2832

Rogell, B., Hofman, M., Eklund, M., Laurila, A., & Höglund, J. (2009). The interaction of multiple environmental stressors affects adaptation to a novel habitat in the natterjack toad *Bufo calamita*. *Journal of Evolutionary Biology*, 22(11), 2267–2277. https://doi.org/10.1111/j.1420-9101.2009.01842.x

Sampaio, E., Rodil, I. F., Vaz-Pinto, F., Fernández, A., & Arenas, F. (2017). Interaction strength between different grazers and macroalgae mediated by ocean acidification over warming gradients. *Marine Environmental Research*, 125, 25–33. https://doi.org/10.1016/j.marenvres.2017.01.001

Schaum, C.-E., Barton, S., Bestion, E., Buckling, A., Garcia-Carreras, B., Lopez, P., Lowe, C., Pawar, S., Smirnoff, N., Trimmer, M., & Yvon-Durocher, G. (2017). Adaptation of phytoplankton to a decade of experimental warming linked to increased photosynthesis. *Nature Ecology & Evolution*, 1, 94. https://doi.org/10.1038/s41559-017-0094

Seifert, M., Rost, B., Trimborn, S., & Hauck, J. (2020). Meta-analysis of multiple driver effects on marine phytoplankton highlights modulating role of pCO_2. *Global Change Biology*, 26(12), 6787–6804. https://doi.org/10.1111/gcb.15341

Simmons, B. I., Blyth, P. S. A., Blanchard, J. L., Clegg, T., Delmas, E., Garnier, A., Griffiths, C. A., Jacob, U., Pennekamp, F., Petchey, O. L., Poisot, T., Webb, T. J., & Beckerman, A. P. (2021). Refocusing multiple stressor research around the targets and scales of ecological impacts. *Nature Ecology & Evolution*, 5(11), 1478–1489. https://doi.org/10.1038/s41559-021-01547-4

Sinclair, B. J., Marshall, K. E., Sewell, M. A., Levesque, D. L., Willett, C. S., Slotsbo, S., Dong, Y., Harley, C. D. G., Marshall, D. J., Helmuth, B. S., & Huey, R. B. (2016). Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecology Letters*, 19(11), 1372–1385. https://doi.org/10.1111/ele.12686

Smith, M. D., Knapp, A. K., & Collins, S. L. (2009). A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology*, 90(12), 3279–3289. https://doi.org/10.1890/08-1815.1

Spaak, J. W., Baert, J. M., Baird, D. J., Eisenhauer, N., Maltby, L., Pomati, F., Radchuk, V., Rohr, J. R., Van den Brink, P. J., & De Laender, F. (2017). Shifts of community composition and population density substantially affect ecosystem function despite invariant richness. *Ecology Letters*, 20(10), 1315–1324. https://doi.org/10.1111/ele.12828

Suleiman, M., Daugaard, U., Choffat, Y., Zheng, X., & Petchey, O. L. (2022). Predicting the effects of multiple global change drivers on microbial communities remains challenging. *Global Change Biology*, 28(18), 5575–5586. https://doi.org/10.1111/gcb.16303

Synodinos, A. D., Haegeman, B., Sentis, A., & Montoya, J. M. (2021). Theory of temperature-dependent consumer–resource interactions. *Ecology Letters*, 24(8), 1539–1555. https://doi.org/10.1111/ele.13780

Tekin, E., Diamant, E. S., Cruz-Loya, M., Enriquez, V., Singh, N., Savage, V. M., & Yeh, P. J. (2020). Using a newly introduced framework to measure ecological stressor interactions. *Ecology Letters*, 23(9), 1391–1403. https://doi.org/10.1111/ele.13533

Thomas, M. K., Aranguren-Gassis, M., Kremer, C. T., Gould, M. R., Anderson, K., Klausmeier, C. A., & Litchman, E. (2017). Temperature–nutrient interactions exacerbate sensitivity to warming in phytoplankton. *Global Change Biology*, 23(8), 3269–3280. https://doi.org/10.1111/gcb.13641

Thompson, P. L., MacLennan, M. M., & Vinebrooke, R. D. (2018a). An improved null model for assessing the net effects of multiple stressors on communities. *Global Change Biology*, 24(1), 517–525. https://doi.org/10.1111/gcb.13852

Thompson, P. L., MacLennan, M. M., & Vinebrooke, R. D. (2018b). Species interactions cause non-additive effects of multiple environmental stressors on communities. *Ecosphere*, 9(11), e02518. https://doi.org/10.1002/ecs2.2518

Thorson, J. T., Ono, K., & Munch, S. B. (2014). A Bayesian approach to identifying and compensating for model misspecification in population models. *Ecology*, *95*(2), 329–341. https://doi.org/10.1890/13-0187.1

Tredennick, A. T., Hooker, G., Ellner, S. P., & Adler, P. B. (2021). A practical guide to selecting models for exploration, inference, and prediction in ecology. *Ecology*, *102*(6), e03336. https://doi.org/10.1002/ecy.3336

Trosvik, P., Rudi, K., Næs, T., Kohler, A., Chan, K.-S., Jakobsen, K. S., & Stenseth, N. C. (2008). Characterizing mixed microbial population dynamics using time-series analysis. *The ISME Journal*, *2*(7), 707–715. https://doi.org/10.1038/ismej.2008.36

Turschwell, M. P., Connolly, S. R., Schäfer, R. B., De Laender, F., Campbell, M. D., Mantyka-Pringle, C., Jackson, M. C., Kattwinkel, M., Sievers, M., Ashauer, R., Côté, I. M., Connolly, R. M., van den Brink, P. J., & Brown, C. J. (2022). Interactive effects of multiple stressors vary with consumer interactions, stressor dynamics and magnitude. *Ecology Letters*, *25*, 1483–1496. https://doi.org/10.1111/ele.14013

Uszko, W., Diehl, S., Englund, G., & Amarasekare, P. (2017). Effects of warming on predator–prey interactions – A resource-based approach and a theoretical synthesis. *Ecology Letters*, *20*(4), 513–523. https://doi.org/10.1111/ele.12755

Uszko, W., Diehl, S., & Wickman, J. (2020). Fitting functional response surfaces to data: A best practice guide. *Ecosphere*, *11*(4), e03051. https://doi.org/10.1002/ecs2.3051

Vasseur, D. A., & McCann, K. S. (2005). A mechanistic approach for modeling temperature-dependent consumer-resource dynamics. *The American Naturalist*, *166*(2), 184–198. https://doi.org/10.1086/an.2005.166.issue-2

Verbeek, L., Gall, A., Hillebrand, H., & Striebel, M. (2018). Warming and oligotrophication cause shifts in freshwater phytoplankton communities. *Global Change Biology*, *24*(10), 4532–4543. https://doi.org/10.1111/gcb.14337

Wood, S. N. (2017). *Generalized additive models: An introduction with R* (2nd ed.). Chapman and Hall/CRC.

Zhang, P., Kuramae, A., van Leeuwen, C. H. A., Velthuis, M., van Donk, E., Xu, J., & Bakker, E. S. (2020). Interactive effects of rising temperature and nutrient enrichment on aquatic plant growth, stoichiometry, and palatability. *Frontiers in Plant Science*, *11*, 58. https://doi.org/10.3389/fpls.2020.00058

DATA SOURCES

Allan, B. J. M., Domenici, P., Watson, S. A., Munday, P. L., & McCormick, M. I. (2017). Warming has a greater effect than elevated CO_2 on predator–prey interactions in coral reef fish. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1857), 20170784. https://doi.org/10.1098/rspb.2017.0784

Alsterberg, C., Eklof, J. S., Gamfeldt, L., Havenhand, J. N., & Sundback, K. (2013). Consumers mediate the effects of experimental ocean acidification and warming on primary producers. *Proceedings of the National Academy of Sciences*, *110*(21), 8603–8608. https://doi.org/10.1073/pnas.1303797110

Aranguren-Gassis, M., Kremer, C. T., Klausmeier, C. A., & Litchman, E. (2019). Nitrogen limitation inhibits marine diatom adaptation to high temperatures. *Ecology Letters*, *22*(11), 1860–1869. https://doi.org/10.1111/ele.13378

Arreguin Rebolledo, U., Nandini, S., Sarma, S. S. S., & Escobar-Sánchez, O. (2020). Effect of salinity and temperature on the acute and chronic toxicity of arsenic to the marine rotifers *Proales similis* and *Brachionus ibericus*. *Marine Pollution Bulletin*, *157*, 111341. https://doi.org/10.1016/j.marpolbul.2020.111341

Batista, D., Pascoal, C., & Cássio, F. (2012). Impacts of warming on aquatic decomposers along a gradient of cadmium stress. *Environmental Pollution*, *169*, 35–41. https://doi.org/10.1016/j.envpol.2012.05.021

Bestion, E., García-Carreras, B., Schaum, C.-E., Pawar, S., & Yvon-Durocher, G. (2018). Metabolic traits predict the effects of warming on phytoplankton competition. *Ecology Letters*, *21*(5), 655–664. https://doi.org/10.1111/ele.12932

Bi, R., Ismar, S. M. H., Sommer, U., & Zhao, M. (2018). Simultaneous shifts in elemental stoichiometry and fatty acids of *Emiliania huxleyi*; in response to environmental changes. *Biogeosciences*, *15*(4), 1029–1045. https://doi.org/10.5194/bg-15-1029-2018

Boyd, P. W., Dillingham, P. W., McGraw, C. M., Armstrong, E. A., Cornwall, C. E., Feng, Y.-Y., Hurd, C. L., Gault-Ringold, M., Roleda, M. Y., Timmins-Schiffman, E., & Nunn, B. L. (2016). Physiological responses of a Southern Ocean diatom to complex future ocean conditions. *Nature Climate Change*, *6*(2), 207–213. https://doi.org/10.1038/nclimate2811

Cardoso, P. G., Grilo, T. F., Dionísio, G., Aurélio, M., Lopes, A. R., Pereira, R., Pacheco, M., & Rosa, R. (2017). Short-term effects of increased temperature and lowered pH on a temperate grazer-seaweed interaction (*Littorina obtusata/Ascophyllum nodosum*). *Estuarine, Coastal and Shelf Science*, *197*, 35–44. https://doi.org/10.1016/j.ecss.2017.08.007

Cuenca Cambronero, M., Marshall, H., De Meester, L., Davidson, T. A., Beckerman, A. P., & Orsini, L. (2018). Predictability of the impact of multiple stressors on the keystone species Daphnia. *Scientific Reports*, *8*(1), 17572. https://doi.org/10.1038/s41598-018-35861-y

Delnat, V., Janssens, L., & Stoks, R. (2019). Whether warming magnifies the toxicity of a pesticide is strongly dependent on the concentration and the null model. *Aquatic Toxicology*, *211*, 38–45. https://doi.org/10.1016/j.aquatox.2019.03.010

Dinh Van, K., Janssens, L., Debecker, S., De Jonge, M., Lambret, P., Nilsson-Örtman, V., Bervoets, L., & Stoks, R. (2013). Susceptibility to a metal under global warming is shaped by thermal adaptation along a latitudinal gradient. *Global Change Biology*, *19*(9), 2625–2633. https://doi.org/10.1111/gcb.12243

Doyle, S. A., Saros, J. E., & Williamson, C. E. (2005). Interactive effects of temperature and nutrient limitation on the response of alpine phytoplankton growth to ultraviolet radiation. *Limnology and Oceanography*, *50*(5), 1362–1367. https://doi.org/10.4319/lo.2005.50.5.1362

Fournier-Level, A., Neumann-Mondlak, A., Good, R. T., Green, L. M., Schmidt, J. M., & Robin, C. (2016). Behavioural response to combined insecticide and temperature stress in natural populations of *Drosophila melanogaster*. *Journal of Evolutionary Biology*, *29*(5), 1030–1044. https://doi.org/10.1111/jeb.12844

Garzke, J., Sommer, U., & Ismar-Rebitz, S. M. H. (2020). Zooplankton growth and survival differentially respond to interactive warming and acidification effects. *Journal of Plankton Research*, *42*(2), 189–202. https://doi.org/10.1093/plankt/fbaa005

Gerhard, M., Koussoroplis, A. M., Hillebrand, H., & Striebel, M. (2019). Phytoplankton community responses to temperature fluctuations under different nutrient concentrations and stoichiometry. *Ecology*, *100*(11), e02834. https://doi.org/10.1002/ecy.2834

Guilhermino, L., Martins, A., Cunha, S., & Fernandes, J. O. (2021). Long-term adverse effects of microplastics on *Daphnia magna* reproduction and population growth rate at increased water temperature and light intensity: Combined effects of stressors and interactions. *Science of the Total Environment*, *784*, 147082. https://doi.org/10.1016/j.scitotenv.2021.147082

Hallare, A. V., Schirling, M., Luckenbach, T., Köhler, H.-R., & Triebskorn, R. (2005). Combined effects of temperature and cadmium on developmental parameters and biomarker responses in zebrafish (*Danio rerio*) embryos. *Journal of Thermal Biology*, *30*(1), 7–17. https://doi.org/10.1016/j.jtherbio.2004.06.002

Hessen, D. O., Hafslund, O. T., Andersen, T., Broch, C., Shala, N. K., & Wojewodzic, M. W. (2017). Changes in stoichiometry, cellular RNA, and alkaline phosphatase activity of chlamydomonas in response

to temperature and nutrients. *Frontiers in Microbiology*, *8*, 476–489. https://doi.org/10.3389/fmicb.2017.00018

Heugens, E. H. W., Tokkie, L. T. B., Kraak, M. H. S., Hendriks, A. J., van Straalen, N. M., & Admiraal, W. (2006). Population growth of *Daphnia magna* under multiple stress conditions: Joint effects of temperature, food, and cadmium. *Environmental Toxicology and Chemistry*, *25*(5), 1399–1407. https://doi.org/10.1897/05-294R.1

Hofmann, P., Chatzinotas, A., Harpole, W. S., & Dunker, S. (2019). Temperature and stoichiometric dependence of phytoplankton traits. *Ecology*, *100*(12). https://doi.org/10.1002/ecy.2875

Horn, H. G., Boersma, M., Garzke, J., Sommer, U., & Aberle, N. (2020). High CO_2 and warming affect microzooplankton food web dynamics in a Baltic Sea summer plankton community. *Marine Biology*, *167*(5), 69. https://doi.org/10.1007/s00227-020-03683-0

Jaikumar, G., Baas, J., Brun, N. R., Vijver, M. G., & Bosker, T. (2018). Acute sensitivity of three Cladoceran species to different types of microplastics in combination with thermal stress. *Environmental Pollution*, *239*, 733–740. https://doi.org/10.1016/j.envpol.2018.04.069

Kamya, P. Z., Byrne, M., Mos, B., & Dworjanyn, S. A. (2018). Enhanced performance of juvenile crown of thorns starfish in a warm-high CO_2 ocean exacerbates poor growth and survival of their coral prey. *Coral Reefs*, *37*(3), 751–762. https://doi.org/10.1007/s00338-018-1699-5

Kavousi, J., Parkinson, J. E., & Nakamura, T. (2016). Combined ocean acidification and low temperature stressors cause coral mortality. *Coral Reefs*, *35*(3), 903–907. https://doi.org/10.1007/s00338-016-1459-3

Kendrick, M. R., & Benstead, J. P. (2013). Temperature and nutrient availability interact to mediate growth and body stoichiometry in a detritivorous stream insect. *Freshwater Biology*, *58*(9), 1820–1830. https://doi.org/10.1111/fwb.12170

Kimberly, D. A., & Salice, C. J. (2014). Complex interactions between climate change and toxicants: Evidence that temperature variability increases sensitivity to cadmium. *Ecotoxicology (London, England)*, *23*(5), 809–817. https://doi.org/10.1007/s10646-014-1221-y

Kratina, P., Watts, T. J., Green, D. S., Kordas, R. L., & O'Gorman, E. J. (2019). Interactive effects of warming and microplastics on metabolism but not feeding rates of a key freshwater detritivore. *Environmental Pollution*, *255*, 113259. https://doi.org/10.1016/j.envpol.2019.113259

Lewington-Pearce, L., Narwani, A., Thomas, M. K., Kremer, C. T., Vogler, H., & Kratina, P. (2019). Temperature-dependence of minimum resource requirements alters competitive hierarchies in phytoplankton. *Oikos*, *128*(8), 1194–1205. https://doi.org/10.1111/oik.06060

Li, F., Beardall, J., & Gao, K. (2018). Diatom performance in a future ocean: Interactions between nitrogen limitation, temperature, and CO_2-induced seawater acidification. *ICES Journal of Marine Science*, *75*(4), 1451–1464. https://doi.org/10.1093/icesjms/fsx239

Li, H., Xu, T., Ma, J., Li, F., & Xu, J. (2021). Physiological responses of *Skeletonema costatum* to the interactions of seawater acidification and the combination of photoperiod and temperature. *Biogeosciences*, *18*(4), 1439–1449. https://doi.org/10.5194/bg-18-1439-2021

Malzahn, A. M., Doerfler, D., & Boersma, M. (2016). Junk food gets healthier when it's warm: Temperature and Food quality interactions on *A. tonsa*. *Limnology and Oceanography*, *61*(5), 1677–1685. https://doi.org/10.1002/lno.10330

Marañón, E., Lorenzo, M. P., Cermeño, P., & Mouriño-Carballido, B. (2018). Nutrient limitation suppresses the temperature dependence of phytoplankton metabolic rates. *The ISME Journal*, *12*(7), 1836–1845. https://doi.org/10.1038/s41396-018-0105-1

Nørhave, N. J., Spurgeon, D., Svendsen, C., & Cedergreen, N. (2012). How does growth temperature affect cadmium toxicity measured on different life history traits in the soil nematode *Caenorhabditis elegans*? *Environmental Toxicology and Chemistry*, *31*(4), 787–793. https://doi.org/10.1002/etc.1746

Piazza, V., Gambardella, C., Canepa, S., Costa, E., Faimali, M., & Garaventa, F. (2016). Temperature and salinity effects on cadmium toxicity on lethal and sublethal responses of *Amphibalanus amphitrite nauplii*. *Ecotoxicology and Environmental Safety*, *123*, 8–17. https://doi.org/10.1016/j.ecoenv.2015.09.023

Pistevos, J. C. A., Nagelkerken, I., Rossi, T., Olmos, M., & Connell, S. D. (2015). Ocean acidification and global warming impair shark hunting behaviour and growth. *Scientific Reports*, *5*(1), 16293 10.1038/srep16293.

Poore, A. G. B., Graba-Landry, A., Favret, M., Sheppard Brennand, H., Byrne, M., & Dworjanyn, S. A. (2013). Direct and indirect effects of ocean acidification and warming on a marine plant–herbivore interaction. *Oecologia*, *173*(3), 1113–1124. https://doi.org/10.1007/s00442-013-2683-y

Poore, A. G. B., Graham, S. E., Byrne, M., & Dworjanyn, S. A. (2016). Effects of ocean warming and lowered pH on algal growth and palatability to a grazing gastropod. *Marine Biology*, *163*(5), 99. https://doi.org/10.1007/s00227-016-2878-y

Prada, F., Caroselli, E., Mengoli, S., Brizi, L., Fantazzini, P., Capaccioni, B., Pasquini, L., Fabricius, K. E., Dubinsky, Z., Falini, G., & Goffredo, S. (2017). Ocean warming and acidification synergistically increase coral mortality. *Scientific Reports*, *7*(1), 40842. https://doi.org/10.1038/srep40842

Qu, P., Fu, F., & Hutchins, D. A. (2018). Responses of the large centric diatom *Coscinodiscus* sp. to interactions between warming, elevated CO_2, and nitrate availability. *Limnology and Oceanography*, *63*(3), 1407–1424. https://doi.org/10.1002/lno.10781

Qu, P., Fu, F.-X., Kling, J. D., Huh, M., Wang, X., & Hutchins, D. A. (2019). Distinct responses of the nitrogen-fixing marine Cyanobacterium Trichodesmium to a thermally variable environment as a function of phosphorus availability. *Frontiers in Microbiology*, *10*, 1282. https://doi.org/10.3389/fmicb.2019.01282

Rumschlag, S. L., Boone, M. D., & Fellers, G. (2014). The effects of the amphibian chytrid fungus, insecticide exposure, and temperature on larval anuran development and survival: Chytrid fungus, insecticides, and temperature. *Environmental Toxicology and Chemistry*, *33*(11), 2545–2550. https://doi.org/10.1002/etc.2707

Sadler, D. E., Brunner, F. S., & Plaistow, S. J. (2019). Temperature and clone-dependent effects of microplastics on immunity and life history in *Daphnia magna*. *Environmental Pollution*, *255*, 113178. https://doi.org/10.1016/j.envpol.2019.113178

Sampaio, E., Rodil, I. F., Vaz-Pinto, F., Fernández, A., & Arenas, F. (2017). Interaction strength between different grazers and macroalgae mediated by ocean acidification over warming gradients. *Marine Environmental Research*, *125*, 25–33. https://doi.org/10.1016/j.marenvres.2017.01.001

Seeland, A., Albrand, J., Oehlmann, J., & Müller, R. (2013). Life stage-specific effects of the fungicide pyrimethanil and temperature on the snail *Physella acuta* (Draparnaud, 1805) disclose the pitfalls for the aquatic risk assessment under global climate change. *Environmental Pollution*, *174*, 1–9. https://doi.org/10.1016/j.envpol.2012.10.020

Serra, T., Barcelona, A., Pous, N., Salvadó, V., & Colomer, J. (2020). Synergistic effects of water temperature, microplastics and ammonium as second and third order stressors on *Daphnia magna*. *Environmental Pollution*, *267*, 115439. https://doi.org/10.1016/j.envpol.2020.115439

Shatwell, T., Köhler, J., & Nicklisch, A. (2013). Temperature and photoperiod interactions with silicon-limited growth and competition of two diatoms. *Journal of Plankton Research*, *35*(5), 957–971. https://doi.org/10.1093/plankt/fbt058

Shatwell, T., Köhler, J., & Nicklisch, A. (2014). Temperature and photoperiod interactions with phosphorus-limited growth and competition of two diatoms. *PLoS ONE*, *9*(7), e102367. https://doi.org/10.1371/journal.pone.0102367

Skau, L. F., Andersen, T., Thrane, J.-E., & Hessen, D. O. (2017). Growth, stoichiometry and cell size; temperature and nutrient responses in haptophytes. *PeerJ*, *5*, e3743. https://doi.org/10.7717/peerj.3743

Spilling, K., Ylöstalo, P., Simis, S., & Seppälä, J. (2015). Interaction effects of light, temperature and nutrient limitations (N, P and Si) on growth, stoichiometry and photosynthetic parameters of the cold-water diatom *Chaetoceros wighamii*. *PLOS ONE*, *10*(5), e0126308. https://doi.org/10.1371/journal.pone.0126308

Tasmin, R., Shimasaki, Y., Tsuyama, M., Qiu, X., Khalil, F., Okino, N., Yamada, N., Fukuda, S., Kang, I.-J., & Oshima, Y. (2014). Elevated water temperature reduces the acute toxicity of the widely used herbicide diuron to a green alga, *Pseudokirchneriella subcapitata*. *Environmental Science and Pollution Research International*, *21*(2), 1064–1070. https://doi.org/10.1007/s11356-013-1989-y

Theys, C., Verheyen, J., Tüzün, N., & Stoks, R. (2021). Higher mean and fluctuating temperatures jointly determine the impact of the pesticide chlorpyrifos on the growth rate and leaf consumption of a freshwater isopod. *Chemosphere*, *273*, 128528. https://doi.org/10.1016/j.chemosphere.2020.128528

Thomas, M. K., Aranguren-Gassis, M., Kremer, C. T., Gould, M. R., Anderson, K., Klausmeier, C. A., & Litchman, E. (2017). Temperature–nutrient interactions exacerbate sensitivity to warming in phytoplankton. *Global Change Biology*, *23*(8), 3269–3280. https://doi.org/10.1111/gcb.13641

Ullah, H., Nagelkerken, I., Goldenberg, S. U., & Fordham, D. A. (2018). Climate change could drive marine food web collapse through altered trophic flows and cyanobacterial proliferation. *PLOS Biology*, *16*(1), e2003446. https://doi.org/10.1371/journal.pbio.2003446

Urionabarrenetxea, E., Garcia-Velasco, N., Marigómez, I., & Soto, M. (2020). Effects of elevated temperatures and cadmium exposure on stress biomarkers at different biological complexity levels in *Eisenia fetida* earthworms. *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology*, *231*, 108735. https://doi.org/10.1016/j.cbpc.2020.108735

Vellinger, C., Felten, V., Sornom, P., Rousselle, P., Beisel, J.-N., & Usseglio-Polatera, P. (2012). Behavioural and physiological responses of *Gammarus pulex* exposed to cadmium and arsenate at three temperatures: Individual and combined effects. *PLoS ONE*, *7*(6), e39153. https://doi.org/10.1371/journal.pone.0039153

Weisse, T., Laufenstein, N., & Weithoff, G. (2013). Multiple environmental stressors confine the ecological niche of the rotifer *Cephalodella acidophila*. *Freshwater Biology*, *58*(5), 1008–1015. https://doi.org/10.1111/fwb.12104

Wojewodzic, M. W., Kyle, M., Elser, J. J., Hessen, D. O., & Andersen, T. (2011). Joint effect of phosphorus limitation and temperature on alkaline phosphatase activity and somatic growth in *Daphnia magna. Oecologia*, *165*(4), 837–846. https://doi.org/10.1007/s00442-010-1863-2

Xu, M., Dick, J. T. A., Ricciardi, A., Fang, M., Zhang, C., Gu, D., Mu, X., Luo, D., Wei, H., & Hu, Y. (2016). Warming mediates the relationship between plant nutritional properties and herbivore functional responses. *Ecology and Evolution*, *6*(24), 8777–8784. https://doi.org/10.1002/ece3.2602

Zhang, P., Kuramae, A., van Leeuwen, C. H. A., Velthuis, M., van Donk, E., Xu, J., & Bakker, E. S. (2020). Interactive effects of rising temperature and nutrient enrichment on aquatic plant growth, stoichiometry, and palatability. *Frontiers in Plant Science*, *11*, 58. https://doi.org/10.3389/fpls.2020.00058

SUPPORTING INFORMATION

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