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Predicting effects of multiple interacting global change drivers across trophic levels

Running title: Global change affects 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 – i.e., 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 can be inferred by parametric and nonparametric 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.

KEYWORDS global change, multiple stressors, consumer-resource model, species interactions, reaction norms, thermal performance curves

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), e.g., 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.

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, Fig. 1), as well as an exponential increase of 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, Pawar, 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, i.e. 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 (Fig. 1, e.g. Sampaio et al., 2017), exposed to a warming gradient and acidification. The pattern-based approach (path A, Fig. 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, Fig. 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 (Fig. 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 (Pirodda 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 (Fig. 2). When both drivers have the same effect within a trophic level, e.g., growth rate and attack rate are affected in the same way by both temperature and nutrient availability, antagonisms will occur (Fig. 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 cancelled 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).

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

Studies that focus on “patterns” (path A in Fig. 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 Fig. 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 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 (Jun et al., 2012; e.g. salinity, see 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 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 (Fig. 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, Fig. 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 summarize and 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 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 (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 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 (Fig 4A). The response surface of ingestion across temperature and initial density was generated by fitting the generalized functional response and its parameters attack rate, handling time and attack rate exponent, and the temperature-dependence of the model parameters approximated as a second order polynomial (Fig 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. 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 (2020). To contrast the nonparametric with the parametric approach, we also fitted a GAM to the data from Uszko et al. (2020). Like the generalized function response, the GAM indicated that ingestion rate was temperature and resource density dependent (Fig 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 modelling 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 x 5 levels of driver 1 x 5 levels of driver 2 x 3 replicates). To measure total community biomass with five levels of the two drivers and 3 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 towards 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 towards 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.

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DATA AVAILABILITY STATEMENT

Data sharing not applicable – no new data generated. The R code underlying Figures 1 and S1 is available upon request.

AUTHOR CONTRIBUTIONS

This study was conceived by all authors during a workshop organized by F.D.L. The first draft of the manuscript was written by S.J.V.M. and F.P. with input from all authors. F.D.L. and M.H. developed the model. All authors substantially contributed to revisions of the paper.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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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 driver 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:

$$\begin{aligned}\frac{1}{N_1} \frac{dN_1}{dt} &= f_{11}f_{12}b_1 - f_{21}f_{22}aN_2 - N_1, \\ \frac{1}{N_2} \frac{dN_2}{dt} &= f_{21}f_{22}aN_1 - b_2.\end{aligned}\quad (\text{eq. 1})$$

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

$$r = \frac{\widehat{N_2}}{\widehat{N_1}} = \frac{ab_1f_{11}f_{12}f_{21}f_{22}-b_2}{ab_2f_{21}f_{22}}. \quad (\text{eq. 2})$$

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:

$$\rho = \frac{(b_2 - ab_1)(b_2 - ab_1f_{11}f_{12}f_{21}f_{22})}{(b_2 - ab_1f_{11}f_{21})(b_2 - ab_1f_{12}f_{22})} \quad (\text{eq. 3})$$

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 occurs 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 (Fig. 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 (Fig. 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, e.g., 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): e.g. 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 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 the Supporting Information (Fig. S1).

Figure Legends

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, e.g., 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.

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, $f_1f_2 = 1$, i.e., 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).

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 the Supporting Information (Table S1).

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 red (yellow), low consumption in white (dark purple). Data and functional response parameters are from (Uszko et al., 2020).

Data source

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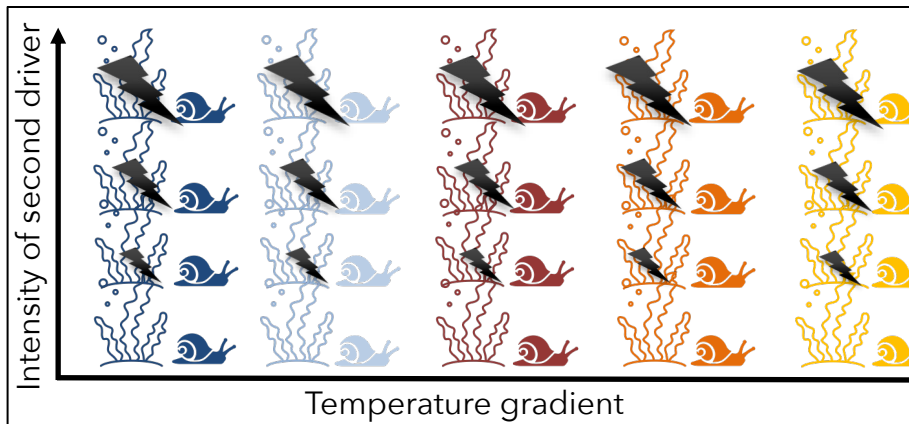
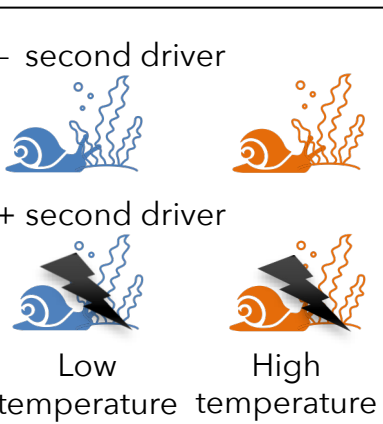
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Table 1 | Research involving acidification as a driver in addition to temperature is the one that most often includes two trophic levels in their experiments. Studies using heavy metal or chemical pollution were mostly measuring responses at several 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 <i>Melita palmata</i> , the gastropod <i>Gibbula umbilicalis</i> / green macroalga <i>Ulva rigida</i> .	Acidification	Consumer mortality, consumption rate	Found significant effects of temperature and acidification, but no interactive effects for any of the grazers.	Sampaio et al., 20
Juvenile crown-of-thorn starfish / coral (<i>Acanthaster</i> spp., <i>Acropora</i> 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., 201
Microzooplankton / phytoplankton	Acidification	Growth rates and grazing rates of MZP	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
<i>Lymnaea stagnalis</i> / submerged plant <i>Vallisneria spiralis</i>	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 (<i>D. magna</i> , <i>D. pulex</i> , <i>C. dubia</i>)	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., 20

Crustacean <i>Amphibalanus amphitrite</i>	Cadmium	Consumer mortality	Found interactive effects of temperature and the pollutant (microplastics or cadmium, respectively) on consumer mortality.	Piazza et al., 2019
Microbial decomposers (<i>Limnephilus sp.</i>)	Cadmium	Consumer mortality	Found interactive effects of temperature and the pollutant (microplastics or cadmium, respectively) on consumer mortality.	Batista et al., 2019
Six phytoplankton species	Nutrients	Resource growth rate	Calculated TPC's for six phytoplankton species in ten nutrient levels to parameterize their model.	Bestion et al., 2019
Six phytoplankton species	Nutrients (and light)	Resource growth rate	Studied the temperature-dependence of Monod parameters for nitrogen and light, again in ten levels, and found that environmental temperature altered growth parameters of six phytoplankton species.	Lewington-Pearce et al., 2019

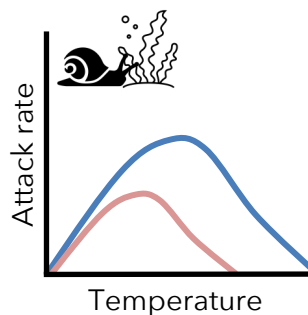
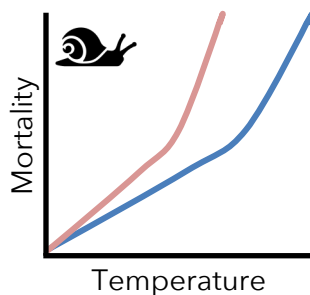
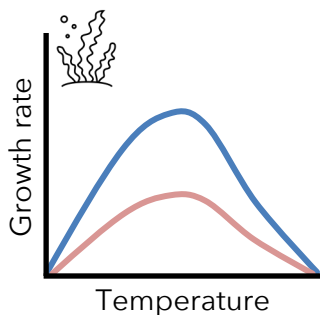


Path A: patterns

Path B: processes

Measure or derive reaction norms

— + second driver
— - second driver



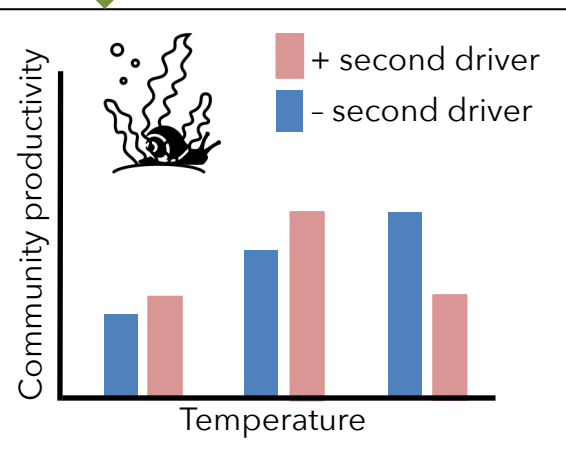
Parameterize

Statistical model

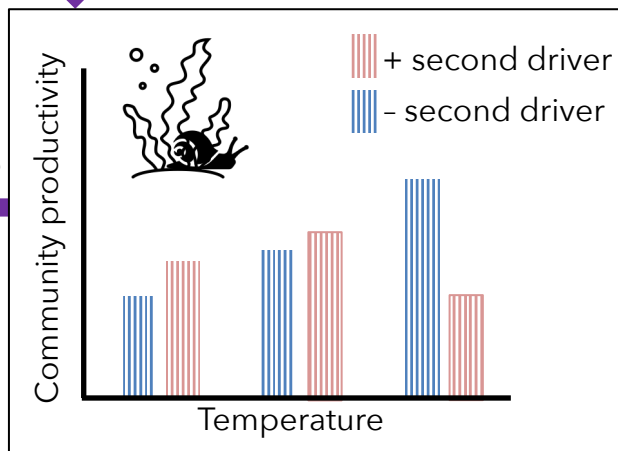
Consumer-resource model

Explore and estimate

Predict and understand



Validate

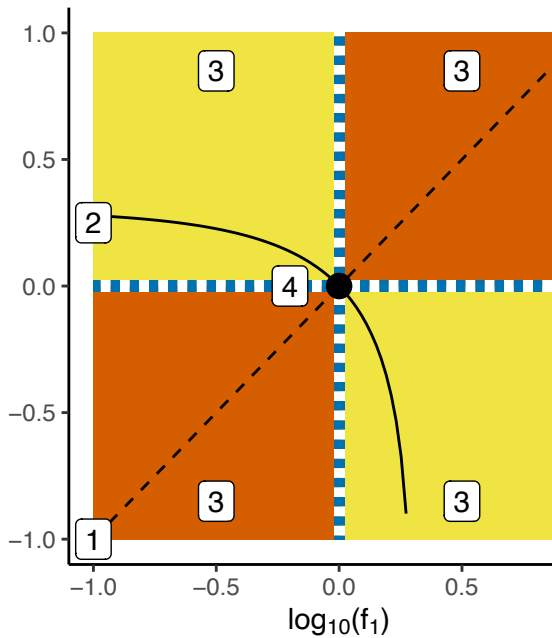


Inform



Practitioners
Decision-makers





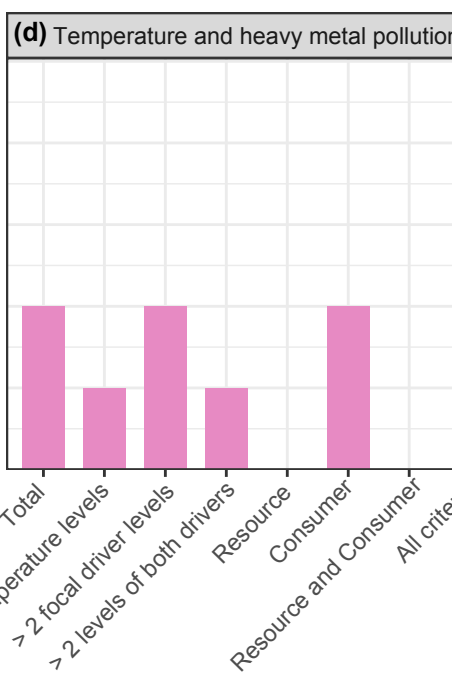
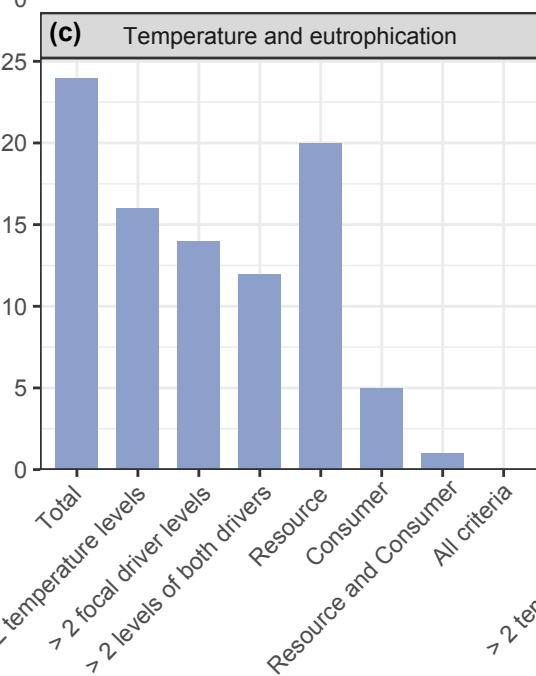
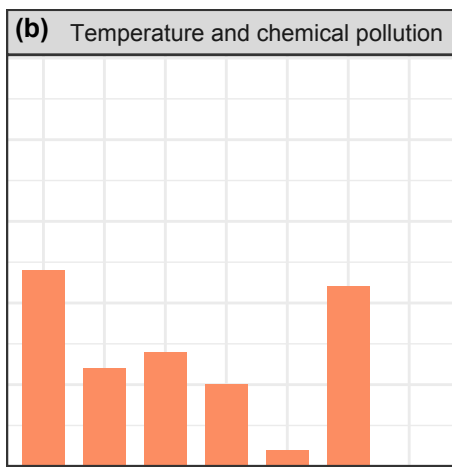
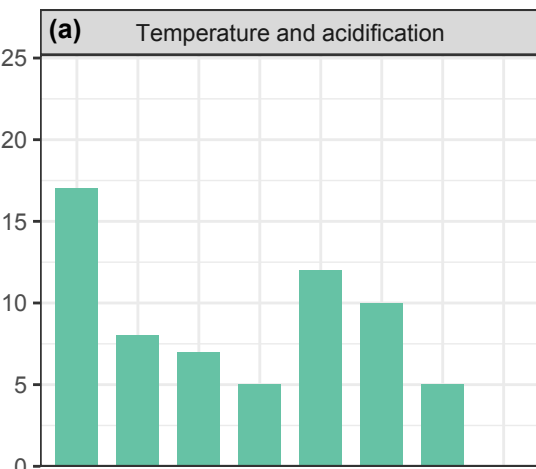
additive



antagonism

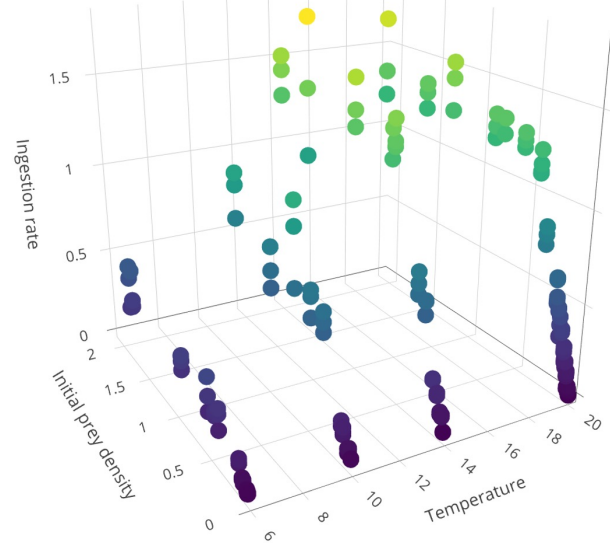


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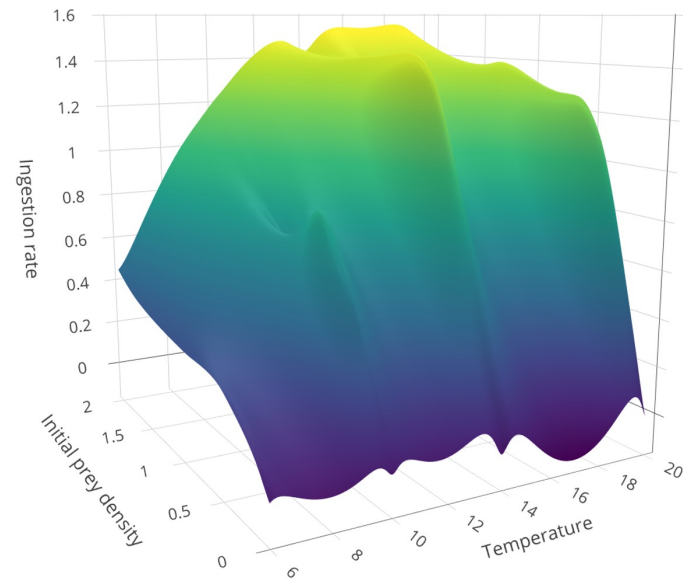


Fulfilled criteria

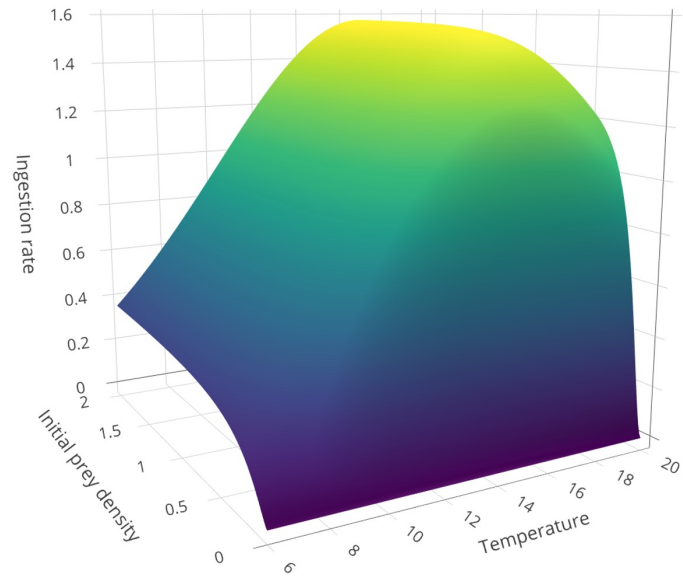
)



(b)



(c)



Inges
rat