Article:
Jarillo, J., Jupke, J.F., Sinclair, T. et al. (2026) Predictors of food web resistance to environmental change. Ecology Letters, 29 (6). e70434. ISSN: 1461-023X

https://doi.org/10.1111/ele.70434

Predictors of food web resistance to environmental change

Javier Jarillo[1,2], Jonathan F. Jupke[3], Tom Sinclair[4,†], Lorraine Maltby[4], Ralf B. Schäfer[5,6], Frederik De Laender[1]

[1]Research Unit of Environmental and Evolutionary Biology; Institute of Complex Systems & Institute of Life, Earth & Environment, University of Namur, Belgium

[2]Department of Statistics and Operations Research, Complutense University of Madrid, Spain

[3]iES, Institute of Environmental Sciences, RPTU Kaiserslautern-Landau, Germany

[4]Department of Animal and Plant Sciences, The University of Sheffield, United Kingdom

[5]Faculty of Biology, University of Duisburg–Essen, Essen, Germany

[6]Research Center One Health Ruhr, University Alliance Ruhr, Essen, Germany

[†]Current affiliation: BASF SE, Agricultural Solutions – Ecotoxicology, Limburgerhof, Germany

July 28, 2026

Running title: Predictors of food web resistance.

Key words: Food web stability, environmental change, modeling, biodiversity, community composition.

Type of article: Letter.

Words in Abstract: 152; **Words in main text:** 4359;

Number of figures in main text: 6; **Number of tables in main text:** 0; **Number of references:** 87.

Corresponding author: Frederik De Laender. Research Unit of Environmental and Evolutionary Biology; Institute of Complex Systems & Institute of Life, Earth & Environment, University of Namur, Rue de Bruxelles 61, 5000 Namur, Belgium. e-mail: frederik.delaender@unamur.be.

Author Contributions: RBS, LM and FDL designed the study. JFJ and TS computed the data for the taxon tolerances, and derived the composition of typical macroinvertebrate communities from European river systems. JFJ assembled the macroinvertebrate field data. JJ performed the mathematical deviations and numerical simulations. JJ and FDL wrote the first draft of the manuscript, and all authors contributed substantially to the final version of the manuscript.

Data accessibility statement: All data and code employed to obtain the different results are available at `https://github.com/javjarillo/getreal_model`. The results of the simulations can be accessed via Zenodo (Jarillo et al., 2026).

Abstract

Impacts of environmental change on ecosystems are seemingly highly context-dependent and contingent on details. Here, we provide mathematical and numerical evidence that there is some generality to the resistance of food webs to species loss. To this end, we mathematically analyze simple food web models, run simulations with randomly wired food webs, develop a spatially explicit meta-community model for realistic macroinvertebrate communities inhabiting European streams, and analyze field data. These approaches jointly support three general rules for food web resistance: 1) all else equal, predators are more vulnerable than prey, and predator diversity declines before prey diversity; 2) food webs with higher prey diversity tend to be less resistant to environmental change; and 3) food web resistance decreases with the mean taxon tolerance, and reaches a maximum at an optimal ratio of predator to prey tolerance. Our findings elucidate characteristics that make food webs vulnerable, fostering more effective conservation practices.

1 Introduction

Environmental change such as global warming or pollution alters species' demographic rates, threatening population persistence over time (Johnson et al., 2017; Maxwell et al., 2016; Urban, 2015; Trisos et al., 2020; Barbarossa et al., 2021). This process raises ethical questions (Tilman, 2000; Simaika and Samways, 2010), but will also have major consequences for the functioning of ecological systems (Loreau et al., 2001; Vaughn, 2010; Oliver et al., 2015; Pires et al., 2018). Hence, sustainable strategies aimed at biodiversity protection should understand the mechanisms that connect environmental change to biodiversity change (Lande et al., 1997; Richter et al., 2003; Kremen, 2005).

Predicting how environmental change leads to biodiversity change requires understanding how species tolerances map to resistance of the focal ecological system. A species' tolerance describes how strongly an environmental change alters its demographic rates when considered in isolation, i.e. not embedded in its community. A low tolerance implies a strong effect, and vice versa. This definition is independent of the kind of environmental pressure and is widely used and reported in applied ecology (Deutsch et al., 2008). For example, tolerances underpin regulatory thresholds in ecotoxicology (Jager et al., 2011), but also drive climate-impact assessments in species distribution models (Kearney and Porter, 2009). In contrast, resistance describes the ability of an ecological system to retain its species composition under increasing environmental pressure (Grimm and Wissel, 1997). Technically speaking, resistance is the highest level of environmental change that does not result in species loss. Because interactions among species can amplify or buffer the direct physiological effects captured by tolerance, communities may lose species at stress levels below or above what species responses would suggest. Understanding how tolerance maps to emergent resistance is therefore essential for anticipating biodiversity loss and for designing management actions that target the most vulnerable components of ecological networks.

How specific environmental change drivers affect communities is well documented (Jackson et al., 2001; Boonstra et al., 2015; Barlow et al., 2018; Halpern et al., 2019; Beauchesne et al., 2021). However, predicting these effects and assessing resistance remains challenging. That is because species differ in their tolerances, and species interactions can propagate or transform direct effects, leading to unexpected outcomes (Ockendon et al., 2014; Ratzke et al., 2020). In addition, measuring resistance requires adopting a gradient approach, where one exposes the focal community to ever-increasing environmental

change levels. Mathematical models offer a way to integrate information on species tolerances and interactions, and estimate resistance or related quantities (Rohr et al., 2006; Monte, 2009; Serván et al., 2018; Thompson et al., 2018; Gibbs et al., 2022; van den Berg et al., 2022; De Laender et al., 2023). One obstacle to the use of such models is their high number of parameters, reflecting the complexity of ecological networks (Montoya et al., 2006) and jeopardizing their routine use in applied ecology. An important objective is therefore to seek broad principles that predict resistance from a handful of descriptors, across ecosystems.

Resistance is one of several dimensions of ecological stability (Pimm, 1984; Grimm and Wissel, 1997; McCann, 2000; Donohue et al., 2016; Radchuk et al., 2019). Yet, it has received comparatively less attention than local asymptotic stability, resilience, or invariability. Other stability components may be analyzed, such as resilience (the rate of recovery after a perturbation) or invariability (reciprocal of temporal biomass variance). Here, we decided to focus on the food web resistance because it most directly captures the short-term biodiversity responses to environmental change. For example, the size and architecture of ecological networks, and statistical summaries of growth and interaction rates have established effects on local asymptotic stability (Allesina and Tang, 2015; Grilli et al., 2016; Jordán and Scheuring, 2004; Rao et al., 2024; Srednick and Swearer, 2024; Liu et al., 2024; Gibbs et al., 2024). Another example is the well-established link between (a-)synchronous species responses, population-level temporal variability, and temporal stability of aggregate properties such as total biomass (Loreau and De Mazancourt, 2013; Loreau et al., 2021; Gonzalez et al., 2020; Wang et al., 2019). Similar results are at present not available for resistance. This is problematic because resistance is particularly relevant in applied ecology, as it captures the threshold level of environmental change beyond which species loss becomes unavoidable, and therefore gives direct input to environmental law and regulation.

The objective of this paper is to unveil general principles that predict resistance to environmental change, for the case of food webs. Trophic interactions form one of the fundamental building blocks of ecological communities and can lead to unexpected outcomes for species coexistence (Chesson and Kuang, 2008; Archibald et al., 2023; Talmy et al., 2024). To achieve our objective, we adopt four complementary approaches. We begin with mathematical analyses of simplified Generalized Lotka–Volterra models (Lotka, 1920; Volterra, 1926; Tilman, 2007) to derive explicit predictions about how prey and predator tolerances and food web structure shape food web resistance. These theoretical expectations are then tested through simulations of randomly parameterized food webs, followed by more realistic meta-community simulations using trait-based macroinvertebrate assemblages distributed across spatial river networks. Finally, we analyze field data from European streams to evaluate whether empirical patterns of predator and prey richness across impact gradients align with the model-based predictions.

We identify three general rules that determine the resistance of food webs to environmental change. First, we find that predators are generally less resistant than prey. A consequence is that food web resistance increases as predators have on average higher tolerance. Second, food web resistance declines with the number of prey species, while the number of predators has a smaller effect. We explain this result based on energetic considerations for population growth. Third, resistance decreases with the mean taxon tolerance, and reaches a maximum at an optimal ratio of predator to prey tolerance. These rules are supported by mathematical analyses, and numerical simulations with both randomly parameterized models and detailed trait-based metacommunity models of six representa-

tive macroinvertebrate food web assemblages found across European streams (Jupke et al., 2022). Furthermore, our simulations highlight the specific conditions under which rules 1 and 3 are expected to break down. We finally analyze observed macroinvertebrate communities across three different European freshwater systems, finding that more degraded sites tend to have a smaller number of predator taxa, which provides empirical evidence to our first rule.

2 Model and methods

2.1 Food web model

We modeled a bitrophic food web of n_P predators and n_V prey (or victim) taxa affected by the presence of an environmental driver:

$$\begin{aligned} \frac{\mathrm{d}V_i}{\mathrm{d}t} &= \left[b_i - m_i \left(1 + \frac{\xi}{\tau_i}\right) - \sum_{j=1}^{n_V} \alpha_{ij} V_j - \sum_{k=1}^{n_P} \lambda_{ik} P_k \right] V_i, \qquad i = 1, \ldots, n_V, \\ \frac{\mathrm{d}P_k}{\mathrm{d}t} &= \left[-d_k \left(1 + \frac{\xi}{\tau_k}\right) - \alpha_{kk} P_k + \sum_{i=1}^{n_V} \lambda_{ik} \eta_{ik} V_i \right] P_k, \qquad k = 1, \ldots, n_P. \end{aligned} \tag{1}$$

Here, V_i and P_k denote the abundance densities of prey taxon i and predator taxon k. For each prey taxon, b_i and m_i are the intrinsic birth and death rates, while d_k is the intrinsic death rate of predator taxon k. The parameters α_{ij} represent the interspecific competition strength between prey taxa i and j; intraspecific competition for prey and predators is set to $\alpha_{ii} = 1$ by rescaling population densities. The parameter λ_{ik} is the attack rate of predator k towards prey i, and η_{ik} is the corresponding conversion efficiency of consumed prey biomass into predator biomass. The environmental change level ξ linearly increases taxon-specific death rates, modulated by each taxon's intrinsic tolerance τ_i. This tolerance is an inherent property of each taxon, independent of ecological interactions. Equilibrium densities are found by solving this set of differential equations. Here, we focus on parameter settings for which the equilibrium in absence of environmental change, $\xi = 0$, have all taxa present.

Environmental change multiplies a taxon's death rate in inverse proportion to its tolerance τ (Eq. (A.7) from Supplementary Information A.1): the same environmental change level ξ will increase the death rate more in taxa with lower tolerance.

This increase in the death rate affects population dynamics, possibly leading to the loss of a taxon. One can therefore determine, for a given taxon, the highest environmental change level ξ that does not lead to its extinction. We define this level as the taxon's resistance Ω. We then define the lowest resistance across all predator taxa as the predator-level resistance, Ω_P. Similarly, the prey-level resistance, Ω_V, is the lowest resistance across all prey taxa. Finally, the minimum of the predator-level and prey-level resistances, $\min(\Omega_V, \Omega_P)$ is the resistance of the whole food web. This definition of resistance, which is based on the least resistant taxon within the community, is in line with EU legislation on chemical pollutants that aims to avoid biodiversity loss (European Parliament and Council of the European Union, 2009). Alternative definitions based on the loss of $X\%$ of the taxa can also be established, and lead to similar expressions for resistance (Supplementary Information A.7).

2.2 Mathematical analyses of simplified food webs

We started by simplifying the main equation from the previous subsection, Eq. (1), to make it analytically tractable. We considered two simplifying scenarios.

First, we considered communities of completely equivalent prey taxa (i.e., in which all the taxa have exactly the same parameters) and completely equivalent predator taxa, where predators are all generalists feeding on all the available prey (Supplementary Information A.2). Yet, taxa can have different tolerances. Since all prey and predator taxa share the same parameters, it is easy to check that, in the absence of environmental change ($\xi = 0$), all prey (and predators) would have the same equilibrium prey (and predator) density, Eq. (A.10). However, environmental change ($\xi > 0$) might introduce differences among taxon equilibrium densities, because not all taxa have the same tolerance. In the supplements, we explain how we obtained analytical expressions for taxon, prey-level, predator-level, and food web resistances (Eq. (A.16)).

Second, we considered communities where again all prey are equivalent and all predators are equivalent, but now predators have distinct food sources. That is, we considered specialist predators (each predator feeding on a unique prey) (Supplementary Information A.3). Given the kind of model we considered, the number of prey must be larger than the number of predator taxa for all to persist without environmental change: $n_V \geq n_P$. Thus, this scenario implies that we have three different categories of taxa: prey taxa (attacked by predators); competitor taxa (compete with prey taxa, but are not attacked by the predators); and predator taxa. Also for this scenario we explain in the supplements how we obtained analytical expressions for taxon, trophic levels, and food web resistance (Eqs. (A.19, A.20)).

2.3 Simulations of random food webs

To analyze the robustness of the results obtained for the two simplified scenarios, we generated random communities with random parameters, but making sure that all taxa are able to locally coexist in the absence of environmental change. Taxon parameters and tolerances were sampled from lognormal distributions with a coefficient of variation of 10%, unless otherwise specified. To isolate the effect of community structure from that of tolerance distributions, we fixed the minimum and maximum sampled tolerance values within each trophic level across all communities regardless of species richness. In the absence of environmental change, we computed the equilibrium densities using Eq. (A.6)(Supplementary Information A.1) and verified that all taxa have positive equilibrium densities. If any taxon went extinct, a new set of parameters was sampled. Then, we iteratively increased the environmental change level, increasing the death rates of the taxa, and computed the equilibrium densities of the taxa from the community, and when the different taxa were removed. The detailed simulation protocol is available in `https://github.com/javjarillo/getreal_model`.

Furthermore, to evaluate the robustness of our analytical predictions in food webs where prey trophic-level diversity emerges from predation–competition trade-offs, we simulated communities composed of n_P specialist predators feeding on n_P prey, together with $n_V - n_P$ weaker competitors. These weak competitors exerted only a small competitive effect on the prey species (low mean $\alpha_{\text{eaten prey,weak comp}}$), whereas the reciprocal effect of the eaten prey on the weak competitors is stronger (high mean $\alpha_{\text{weak comp,eaten prey}}$). As in the previous simulations, all dynamical parameters were sampled from lognormal distributions with the same coefficient of variation, and the equilibrium densities and taxa diversities were

computed from increasing levels of environmental change.

2.4 Simulations of realistic food webs in streams

Randomly assembled local communities may overlook key structural features of real ecosystems that influence how taxa tolerances map to resistance. Hence, we also compared the mathematical analysis results with results obtained from numerical simulations of realistic macroinvertebrate communities in streams across Europe, exposed to realistic environmental change drivers. The purpose of these simulations is not to provide a fully accurate reconstruction of any particular real river system but to test whether the qualitative predictions derived from the analytical and random food web models persist when adding complexity in the form of a spatial structure, i.e. a dendritic network, which is a well-established abstraction for riverine systems (Rodriguez-Iturbe and Rinaldo, 1997; Fagan, 2002; Carrara et al., 2012).

To this end, we used a meta-community version of Eq. (1) that explicitly accounts for taxa traits and tracks the populations dynamics across 100 patches that are connected through dispersal on a realistic river network. The equations governing the metacommunity dynamics are shown in Eq. (B.5) from Supplementary Information B. To generate realistic spatial dendritic river networks, we employed the OCNET package (Carraro et al., 2020). This package implements the Optimal Channel Network (OCN) framework (Rinaldo et al., 2014), which produces realistic river-like networks, consisting on a set of local patches connected by streams.

To derive realistic macroinvertebrate assemblages, we used previously compiled data from national monitoring agencies, the scientific community, and available databases (Jupke et al., 2022). We used 9976 records of observed species composition across 6965 sampling sites spread across Europe to derive a list of 7 realistic macroinvertebrate assemblages (Jupke et al., 2022) representative of different European river types as proposed by Lyche Solheim et al. (2019). The taxon composition of these assemblages are listed in Supplementary Information B, and Tables F.2–F.8 from Supplementary Information F. For each assemblage, predator-prey links were established using the Global Interactions (GloBI) database (Poelen et al., 2014), and average interaction strength between taxa across locations were estimated from species traits (Tachet database: Tachet et al. 2000) based on food overlap and body size (Jonsson, 2014; Tsai et al., 2016; Eklöf et al., 2017). For each location, the taxa's local birth and death rates were randomly sampled from normal distributions, while local interaction strengths were also randomly sampled employing the previously computed average interaction strengths across locations. Moreover, we classified the taxa as either 'flying' or 'aquatic' (non-flying), depending on the dispersal traits also available at the Tachet database. Flying taxa were allowed to move between each pair of patches of the spatial network, while aquatic taxa could just move through the connected patches. For each patch x, and each taxon, dispersal rates were randomly sampled from normal distributions, and the specific dispersal rate from x to another node y is modulated by the distance between patches x and y, compared to the distance from x to either all the other patches (flying taxa) or to just all the connected patches (flying taxa) (Eq. (B.4) from Supplementary Information B).

We ran this model at increasing environmental change levels ξ for three pollutants, as examples of real environmental change drivers that river communities are exposed to: atrazine (a herbicide), imidacloprid (an insecticide), and copper (a metal), assuming equal exposure for all local patches. The use of chemical pollutants here is illustrative; the framework extends to any driver producing taxon-specific demographic effects. For each of

the pollutants, the taxon tolerances τ_i were estimated from hierarchical Species Sensitivity Distribution (hSSD) Models that capture true variation of taxa tolerances (Jupke et al., 2024; Jupke, 2024). We calculated food web resistance as in the simulations with random food webs. The detailed simulation protocol of the meta-community model is available at `https://github.com/javjarillo/getreal_model`.

2.5 Field data

We analyzed a data set of macroinvertebrate community composition at 5536 river sites in France (n=1315), UK (n=1228), and Germany (n=2993). Data from France and UK were respectively obtained from the Naïades (`https://naiades.eaufrance.fr`) and Biosys (`https://environment.data.gov.uk/dataset/fa98090d-d715-4d34-80f9-bb7621aa7101`) databases, while data from Germany were provided by German federal state authorities. From each sample, we have a list of macroinvertebrate taxa observed on the sample, that were classified as either prey or predators, employing the GLOBI database (Poelen et al., 2014), that includes the reported trophic links between multiple taxa. Moreover, each site was classified as high, mid, and low impacted, based on the use of their potentially flood-prone area (pfa) (Lemm et al., 2021). For more detailed information, see Supplementary Information C.

3 Results

3.1 Analytical results: Estimators of food web resistance

To understand the factors driving food web resistance, we analyse two simplified versions of the main food web model (Eq. (1)) (see Supplementary Information A). In the first scenario, taxa within trophic levels are ecologically equivalent and all predators are generalists, feeding with equal intensity on all prey. In the second scenario, all prey are equivalent but each predator is unique as it attacks a single prey. Importantly, in both scenarios taxa have different tolerances τ to environmental change, and all taxa coexist when environmental change is absent.

For both scenarios, we obtain analytical expressions for the predator-level resistance (Eqs. (A.12) and (A.20) from Supplementary Information A, respectively). We find that, in both scenarios, predator-level resistance depends on the reciprocal tolerance of the least tolerant predator, i.e. the maximum of all predator reciprocal tolerances ($1/\tau$). To obtain a general estimator applicable even when not all taxa's tolerances are known, we approximate this maximum as the value at κ standard deviations to the right of its mean value. Fig. E.6 shows that a value of $\kappa = 3$ is a reasonable choice, given the number of species and the distribution of the tolerances. For small variability in predators' tolerances, both simplifying scenarios produce similar estimates of predator-level resistance Ω_P, with the difference vanishing as tolerance variability approaches zero. Furthermore, since the resistance estimated under the specialist simplifying scenario consistently exceeds that obtained under the generalist simplifying scenarios (Supplementary Information A.3), we adopt the generalist estimate as a conservative measure of predator-level resistance,

$$\Omega_P = \mathrm{H}\left(\tau_P\right) \frac{\frac{b}{m} - 1 - \frac{d}{m}\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta}}{\frac{\mathrm{H}(\tau_P)}{\mathrm{H}(\tau_V)} + \frac{d}{m}\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta} + \kappa\,\frac{d}{m}\,\mathrm{CV}\left(\frac{1}{\tau_P}\right)\left[\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta} + \lambda\,\frac{n_P}{n_V}\right]}\,, \tag{2}$$

where τ_V and τ_P are respectively the tolerances of prey and predators, $\mathrm{H}(\cdot)$ is the harmonic mean, and $\mathrm{CV}(\cdot)$ is the coefficient of variation. The remaining parameters represent standard parameters of the General Lotka-Volterra model: b (prey birth rate), d and m (prey and predators death rates, respectively), α (interspecific competition among the prey), λ (attack rate), and η (conversion efficiency of prey into predators). (See table F.1 from Supplementary Information F for the definition of the parameters.)

We likewise obtain an estimator for prey-level resistance Ω_V,

$$\Omega_V = \mathrm{H}(\tau_V)\ \frac{\frac{b}{m} - 1}{1 + \kappa\, \frac{1+(n_V-1)\,\alpha}{1-\alpha}\, \mathrm{CV}\left(\frac{1}{\tau_V}\right)}, \tag{3}$$

where again the maximum value $\max\left(\tau_V^{-1}\right)$, corresponding to the least tolerant prey, is estimated as κ standard deviations to the right of the mean, $\mathrm{mean}(\tau_V^{-1}) = 1/\mathrm{H}(\tau_V)$.

An important implication of these estimators for prey and predator resistance is that, all else equal, predators are less resistant than prey (as shown in Supplementary Information A.4). This substantiates the intuitive result that predators require prey to persist, while prey can persist without predators. Because of the same reason, predator-level resistance depends on both prey and predator parameters and tolerances (Eq. (2)), while prey-level resistance only depends on parameters and tolerances of the prey (Eq. (3)). Thus, one can use the predator-level resistance Ω_P as a proxy for overall food web resistance, and from its estimator we can derive a series of conclusions on what makes a food web resistant.

First, food web resistance increases as predators have on average higher tolerance $\mathrm{H}(\tau_P)$ (Fig. 1, upper panels). We note that this result is general for the case of stressors that only act by increasing mortality. If stressors also act by reducing prey reproduction, we show in Supplementary Information D that the extinction order can reverse (Supplementary Information D and Fig. E.7). Second, for positive inter-specific competition strength α, greater numbers of prey species n_V make for less resistant food webs; whereas the number of predator species has a much smaller effect (Fig. 1, right panels). Increasing both the absolute or the relative number of prey taxa decreases food web resistance (Supplementary Information A.6). In the case of no inter-specific competition, $\alpha \approx 0$, prey richness should not significantly affect food web resistance (Supplementary Information A.6).

A third insight relates to the distribution of tolerances among predator and prey taxa. Specifically, we find that there exists an optimal ratio $\mathrm{H}(\tau_P)/\mathrm{H}(\tau_V)$ that maximizes food web resistance (Eq. (A.26) from the Supplementary Information A.5). Hence, food web resistance may increase or decrease with $\mathrm{H}(\tau_P)/\mathrm{H}(\tau_V)$. Nevertheless, the existence of such an optimum ratio indicates that food web resistance would be lower when there are large differences between predator and prey tolerances.

All these results were obtained for the definition of resistance given by the loss of the 1st species within the trophic levels. In the Supplementary Information A.7, we explore an alternative definition of resistance: the environmental change level required to remove 50% of the taxa within a trophic level. The analytical expressions for this alternative definition (Eqs. (A.33) and (A.34)) are analogous to Eqs. (2) and (3), with the maximum reciprocal tolerances replaced by their medians and the number of taxa rescaled to reflect the 50% loss, so that all previous qualitative conclusions remain valid under this alternative criterion.

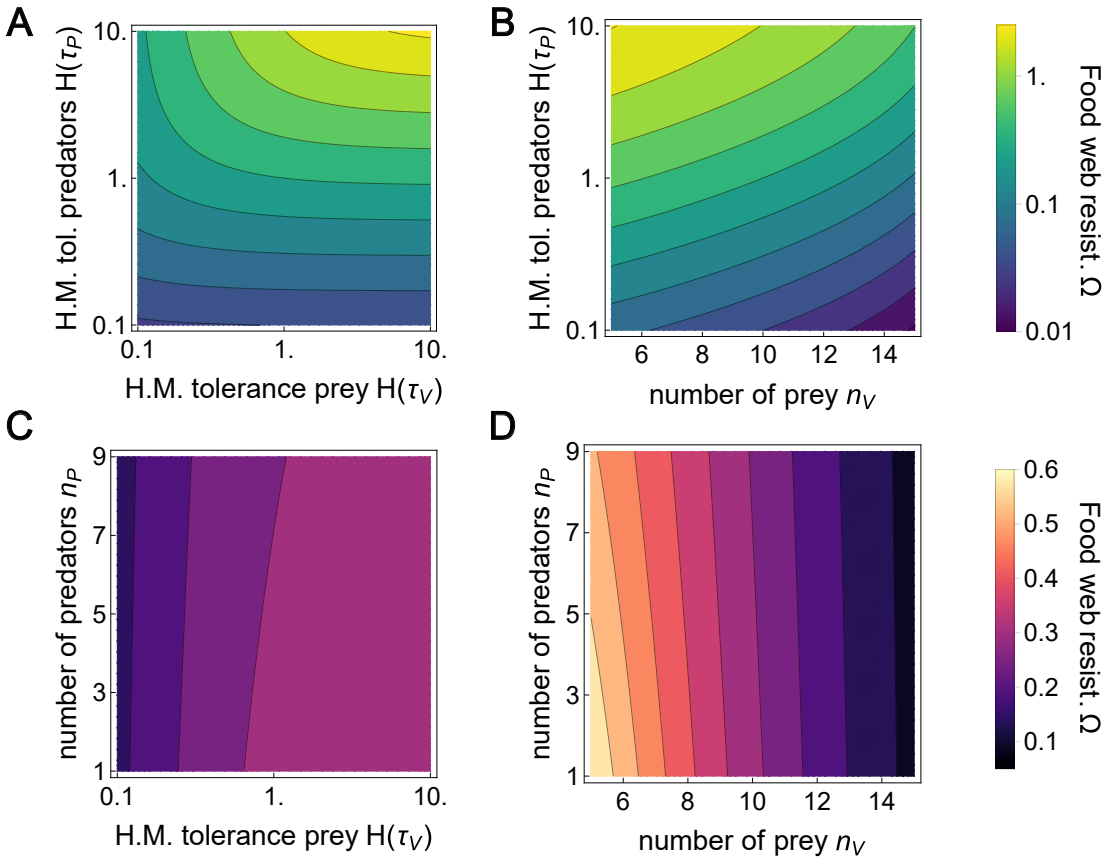

Figure 1: **Effect of taxon tolerances and food web composition on food web resistance.** Food web resistance Ω (obtained from Eq. (2), since predator-level resistance is smaller than prey-level resistance, Supplementary Information A.4) as function of the harmonic mean of tolerances for prey and predators, $\mathrm{H}(\tau_V)$ and $\mathrm{H}(\tau_P)$, and of the number of prey and predator species, n_V and n_P. The harmonic mean of the tolerances of predators (panels A & B, vertical axes) limits this resistance. Moreover, the tolerance of the prey species (panels A & C, horizontal axes), and the number of prey species (panels B & D, horizontal axes), also have a noticeable influence. On the contrary, the number of predators (panels C & D, vertical axes) only plays a minor role. For this plot, we have employed $b = 1$, $m = d = 0.1$, $\lambda = 3$, $\eta = \alpha = 0.1$, $\mathrm{CV}\left(\tau_P^{-1}\right) = 0.1$, and $\kappa = 3$. Moreover, for the different panels, we have employed $n_V = 10$, $n_P = 5$, and $\mathrm{H}(\tau_V) = \mathrm{H}(\tau_P) = 1$ as default values when these parameters are not present in the panel frame axes.

3.2 Numerical simulations: random communities

In real communities, taxa are not equivalent, nor do real predators have perfectly segregated dietary niches. We therefore simulated randomly wired food webs of species with variable parameter values, using Eq. (1). These simulations support the gist of our main analytical results.

First, as found with our analyses, predators are less resistant than prey, and resistances do not differ between generalist and specialist food webs (Fig. 2). In addition, the analytical expressions obtained for the predator-level and prey-level resistances (Eq. (2) and Eq. (3), respectively) provide good estimators for average resistances of the trophic levels (Fig. 2). In particular, this confirms that the variability of taxon tolerances (measured as the coefficient of variation) decreases the resistance. To assess the robustness of this result in more complex food webs, where the diversity at the prey trophic level is mediated by

predation-competition trade-offs, we relaxed two assumptions of our simulation model for specialist food webs. First, we consider food webs with n_P predators feeding on n_P prey, and $n_V - n_P$ weak competitors of the prey taxa. Second, we consider that, caused by interspecific competition, the effect of the prey on the competitors is much stronger than the reciprocal effect (mean $(\alpha_{\text{weak comp, eaten prey}}) = 16 \times$ mean $(\alpha_{\text{eaten prey,weak comp}})$. These modifications to our simulation design did not change the first main result that predators are less resistant than taxa at the lower trophic level, even when predators are up to 18.8 times more tolerant than their prey (Fig. E.1 from Supplementary Information E). However, when there are competitors of the prey taxa not consumed by any predator of the food web, and much less tolerant than both prey and predator taxa (Fig. E.1, lower-right panel), this main result might change, and some competitors might be less resistant than the predators. This only occurs when both conditions are simultaneously met: (i) there are competitors not subject to predation, and (ii) these competitors are less tolerant than both prey and predator taxa.

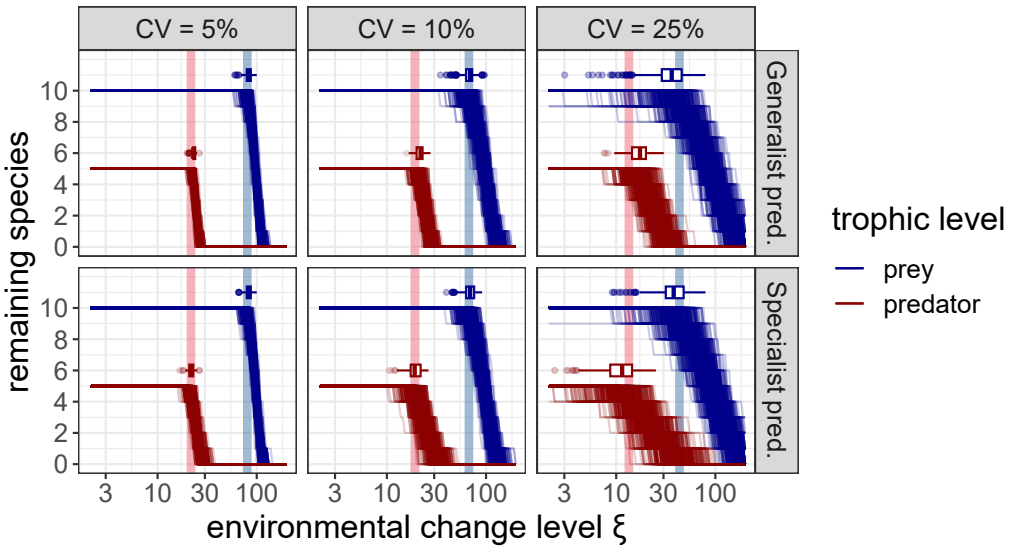

Figure 2: **Predators are less resistant than prey across 500 randomly wired food webs.** Food webs consist of 10 prey and 5 (either generalist or specialist) predators, which can coexist in the absence of environmental change level ξ, and with tolerances, parameters and interaction strengths obtained from random variables with the specified mean values but with 3 different coefficient of variations CV (5%, 10%, 25%). The resistance of a trophic level is the level at which the first taxon from such level is lost. The different realizations show for each of the 500 food webs richness is reduced as we increase the environmental change level, and upper boxplots show, for the 500 food webs, the environmental factor at which the first taxon from each trophic level is removed. Vertical bars in lighter colors are the analytically predicted predator-level and prey-level resistances assuming equivalent taxa, Eqs. (2, 3). Note that this result only changes under specific conditions (Fig. E.1, lower-right panel).

Second, as our analytical results pointed out, predator-level resistance decreases with the number of prey taxa (Eq. (2)), for both scenarios of random food webs with either generalist or specialist predators (Fig. 3, panel A). Moreover, prey-level resistance tended to be higher, and also independent of the number of predators(Eq. (3); Fig. 3, panel A). This negative effect of prey diversity on food web resistance vanishes when interspecific competition among prey is absent ($\alpha = 0$), as the derivative $\frac{\partial \Omega_P}{\partial n_V}$ approaches zero in that

limit (Supplementary Information A.6; and Fig. E.3 from Supplementary Information E). These results also hold under the alternative 50%-loss resistance definition (Figs. E.4 and E.5 from Supplementary Information E).

Third, assuming the mean tolerance is kept constant, the food web resistance is maximal at an optimal ratio of the harmonic means $\mathrm{H}(\tau_P)/\mathrm{H}(\tau_V)$ (Fig. 3, panel B), as predicted by our analytical results. Food web resistance decreases when the differences in the tolerances between trophic levels become large. We obtain this result by computing the derivatives of the food web resistance with respect to this ratio (from Supplementary Information A.5). Again, this rule would break down under the specific condition of having competitors of the prey taxa not consumed by any predator, far less tolerant than both prey and predators. In this case, the food web resistance would be given by the resistance of these competitors, decreasing with a decreasing $H(\tau_V^{\text{competitor}})$.

3.3 Numerical simulations: realistic macro-invertebrate communities

Real prey and predators are not randomly wired, nor do they have random birth and death rates. Instead, predator-prey interactions and parameters are determined by traits, and have well-documented tolerances to specific environmental variables. In addition, taxa are distributed across space, forming metacommunities. We therefore used 9976 records of observed species composition across 6965 sampling sites spread across Europe to reconstruct 7 realistic macroinvertebrate assemblages representative of different European river systems as classified by Lyche Solheim et al. (2019) (see Tables F.2–F.8 from Supplementary Information F; for details of the derivation of the macroinvertebrate assemblages, see Jupke et al. (2022)). We used independent trait data from the GLOBI database (Poelen et al., 2014) to wire and parameterize these food webs, and a probabilistic model of taxon tolerances to each of three chemical pollutants (a metal, copper; a herbicide, atrazine; and a pesticide, imidacloprid) (Sinclair et al., 2024; Jupke, 2024; Jupke et al., 2024) (Methods' Section 2.4). These tolerances show no marked differences between prey and predators (see Fig. E.2, panel A, from Supplementary Information E). In contrast, taxon tolerances were different between assemblages and pollutants (Fig. E.2, panel B).

Simulations of the reconstructed food webs using the metacommunity model (Methods' Section 2.1) confirm most of our main results. First, we find predator resistance to be lower than prey resistance (Fig. E.2, panel C). That is, even though there are no apparent differences in tolerances τ between trophic levels, predators are generally less resistant than prey taxa, echoing our analytical and simulation results.

Second, the number of prey species within the assemblages seems to reduce food web resistance, measured as the smallest concentration leading to the loss of one species (Fig. 4, panel A), as predicted by our analytical estimator, Eq. (2). Moreover, food web resistance seems to increase with the mean taxon tolerance, again as predicted by our estimator (Fig. 4, panel B). Finally, we obtained mixed results for the ratio of mean tolerances of predator and prey species, which did not seem to impact food web resistance in a unimodal way (Fig. 4, panel C). Based on the analytical estimators, we would expect the existence of an optimum ratio of tolerances that maximizes the food web resistance. However, such a conclusion holds assuming that the mean taxon tolerances are not different across the six communities, which, as previously discussed, might not be true for the considered communities (Fig. E.2, panel B).

In conclusion, the general rules obtained from analysing simplified versions of the food

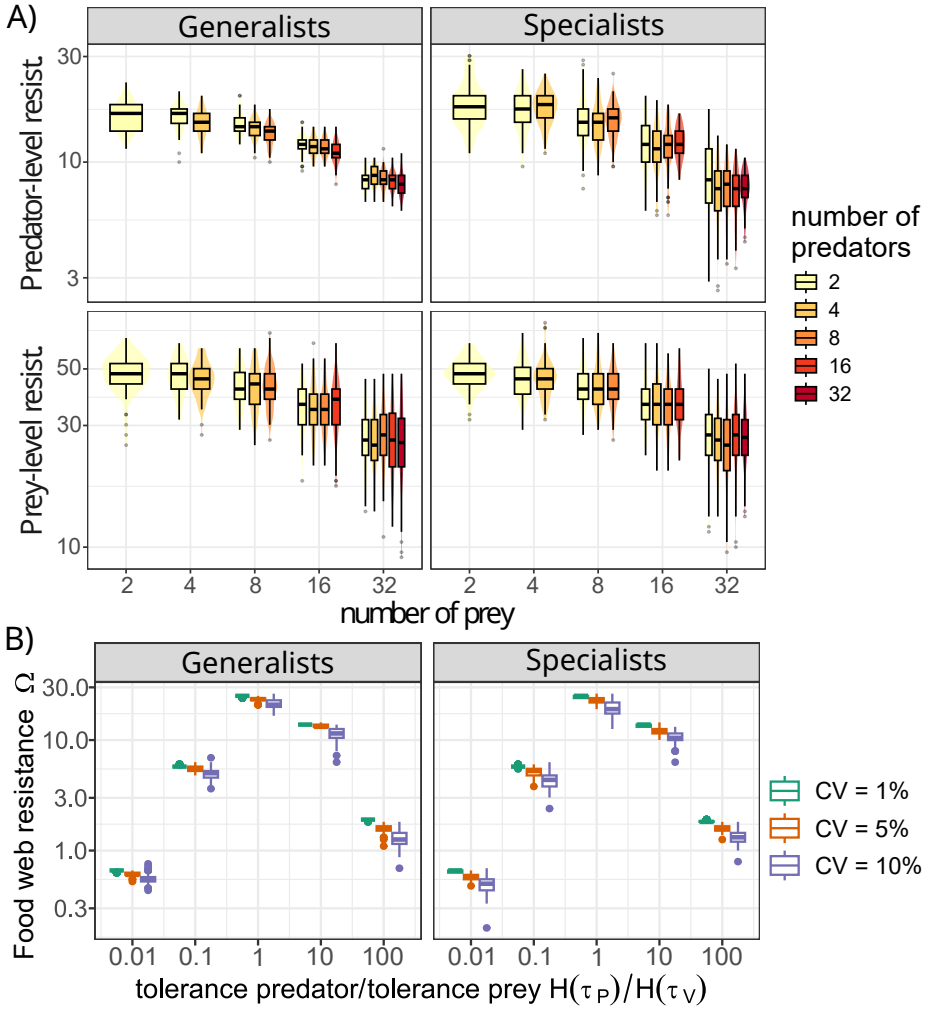

Figure 3: **Panel A) Predator-level resistance decreases with the number of prey in randomly wired food webs.** Trophic-level resistances, defined as the minimum environmental change level required to remove the 1st taxa from the trophic level, as function of the number of prey and predator taxa of the food web. To isolate the effect of food web structure from the distribution of the tolerances, we fixed the minimum and maximum sampled tolerance within each trophic level, so they do not depend on species richness. Predator-level resistance decreases with the number of prey, while does not significantly differ with the number of predators. Prey-level resistance is greater than predator-level resistance. In accordance, it does not depend the number of predator taxa, since predators tend to be lost at lower environmental change levels. **Panel B) Food web resistance is maximal at an optimal ratio of tolerances across trophic levels in randomly wired food webs.** Resistances of random bitrophic food webs with the same mean tolerances $\langle\tau\rangle = \text{mean}\,(\text{H}(\tau_P),\ \text{H}(\tau_V)) = 1$, but different ratios of tolerances across trophic levels $\text{H}(\tau_P)/\text{H}(\tau_V)$, and different coefficients of variations (CV) of the food web parameters and tolerances. Our numerical simulations of these random communities support that the variability tends to decrease the food web resistance, and the existence of an optimal ratio of tolerances across trophic levels that maximizes the food web resistance.

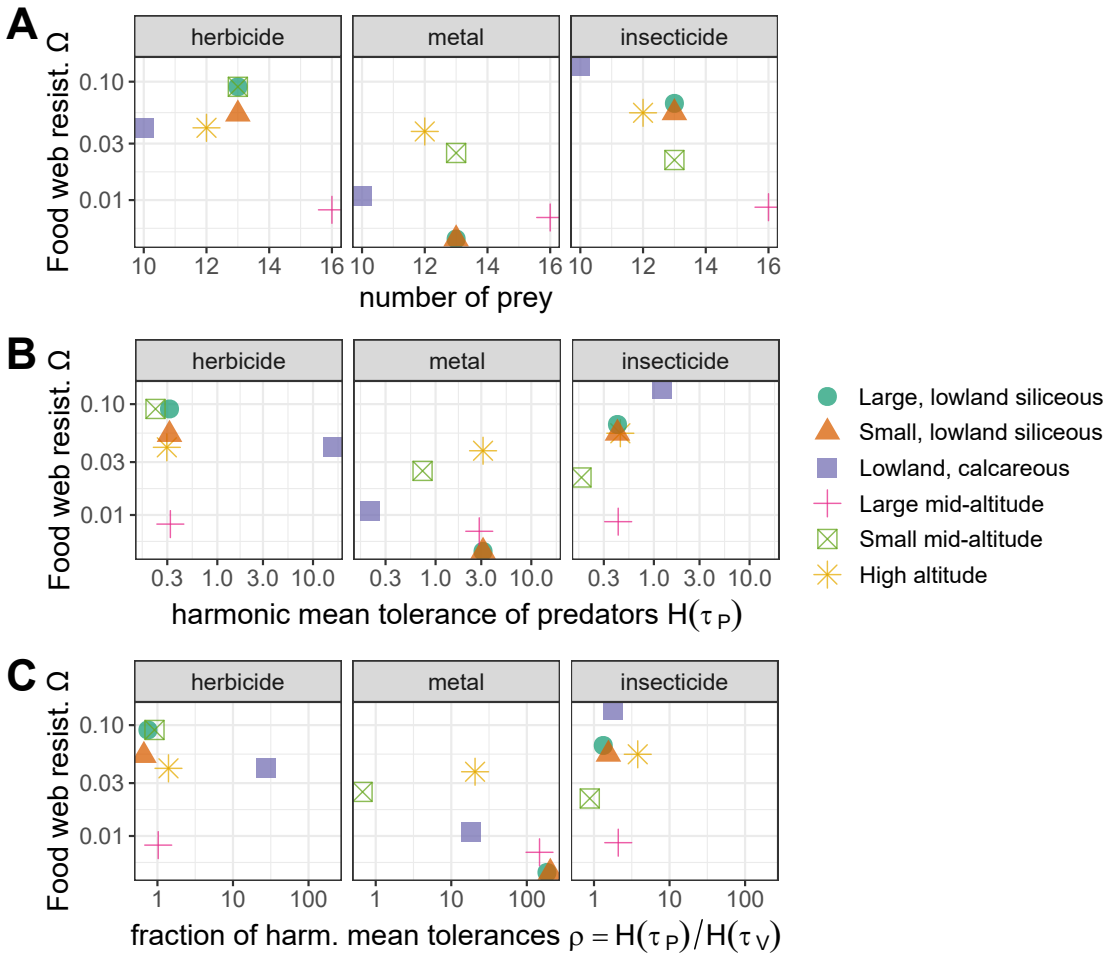

Figure 4: Panel A) **For the six realistic macroinvertebrate assemblages** containing at least one predator, **food web resistance** (measured as the smallest environmental change driver concentration that can remove one taxon) **decreases with the number of prey taxa** within the food web. Panel B) For the same food web assemblages, **resistance increases with the harmonic mean of predator tolerances**. Panel C) For the same food web assemblages, we do not observe a clear optimal ratio of tolerances $\rho = H(\tau_P)/H(\tau_V)$ that maximizes food web resistance; this might be caused by differences in mean taxon tolerances across the communities (Fig. E.2, panel B). To verify these results, we fit a linear model `log(resistance)` $\sim \log H(\tau_P) + n_V + \log\rho + (n_V : \log\rho)$, `obtaining an` $R^2 = 0.7608$, `and these coefficients for the different explanatory variables:` $0.31 \log H(\tau_P)$ $(p = 0.065)$; $-0.21\, n_V$ $(p = 7 \cdot 10^{-4})$; $-1.93 \log\rho$ $(p = 4 \cdot 10^{-3})$; `and` 0.11 $(n_V : \log\rho)$ $(p = 0.02)$.

web model (Eq. (2)) explain the resistance of stream macroinvertebrate assemblages, as obtained with a detailed trait-based metacommunity simulation model.

3.4 Empirical support for theoretical predictions

A main prediction of our theory is that predators are less resistant to environmental change than prey, all else being equal. Hence, ecosystems exposed to higher levels of environmental change are expected to contain fewer predators relative to prey.

Macroinvertebrate food webs are well suited to test this prediction, as species can be approximately categorized as competitors for detritus and algae, or predators of said

competitors, reflecting our modeling setup. To test this expectation, we analyzed a data set of macroinvertebrate community composition at 5536 river sites in France, UK, and Germany (Fig. 5; see Supplementary Information C.).

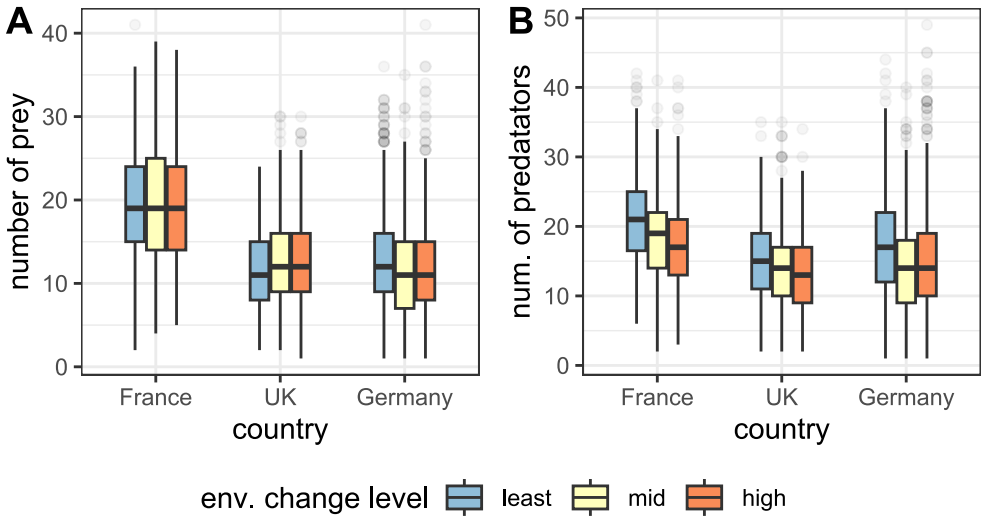

Figure 5: **River sites across France (n=1315), UK (n=1228), and Germany (n=2993) with greater environmental change levels have comparable macroinvertebrate prey richness (panel A) but lower macroinvertebrate predator richness (panel B) than sites with lower environmental change levels.** This result suggests that predators are less resistant than prey taxa, and are among the first to be eliminated following environmental change. For each observation, environmental change level has been defined as 0 for the least impacted sites, $\frac{1}{2}$ for the mid impacted sites, and 1 for the high impacted sites. To estimate the effects of country and environmental change level, type-II anova tests `diversity ~ level * country`, using Anova function from R car package (Fox and Weisberg, 2019), were employed. For the number of prey, we obtain that the p-values associated to the different factors were: 0.019 (env. change level), $< 2.2 \cdot 10^{-16}$ (country), and $5.1 \cdot 10^{-7}$ (env. change level:country). This means that country is the most important factor affecting the prey diversity; whereas the effect of environmental change level was statistically significant but the direction differed among countries. For the number of predators, the associated p-values were: $< 2.2 \cdot 10^{-16}$ (env. change level), $< 2.2 \cdot 10^{-16}$ (country), and $4.2 \cdot 10^{-6}$ (env. change level:country). Hence, both country and environmental change level have highly significant effects on the number of predators.

Employing two-way ANOVAs, we found that environmental change level did not consistently affect prey richness, but significantly reduced predator richness across all countries ($p < 2.2 \cdot 10^{-16}$), consistent with our theoretical results.

4 Discussion

4.1 New insights

We have identified three general predictions of food web resistance. These predictions are supported by multiple lines of evidence, as shown in Table. 1. Mathematical analyses and

numerical simulations indicate that these predictions are valid in any food web characterized by distinct levels of prey taxa and predator taxa. While our results deal with food webs with two trophic levels, we do allow competition among prey species, which could encode an additional trophic level below that is not explicitly modeled. Furthermore, if the dynamics of this lower trophic level are sufficiently faster than those of the two modeled trophic levels, our results should hold for longer food webs as well, as long as effects of environmental change happen at the highest trophic levels. Within these limits, the three rules we uncovered are valid, even when parameterizing our models to specific conditions using trait data, and when accounting for spatial dynamics in a metacommunity context. Despite the fact that traits predict trophic interactions (Gibert and DeLong, 2017, but see Jonsson et al., 2018), we did not find that trait data altered the above-mentioned general predictors of food web resistance, distilled from a simplified food web in which species were largely ecologically equivalent.

In this article, we considered the resistance of a community affected by a single environmental change driver. This reduces the resistance to a single number, which plays the role of a threshold beyond which species loss is inevitable. In real cases, however, ecological communities are challenged by a suite of various drivers occurring at the same time. Such multiple-driver scenarios can lead to unexpected effects that are driven by species interactions (Gilbert et al., 2014; Kroeker et al., 2017; Thompson et al., 2018; Beauchesne et al., 2021; Turschwell et al., 2022). Including response surfaces is one way to anticipate such driver interactions, as it accounts not only for joint effects of multiple environmental change drivers, but also potential covariances among them (Van Moorsel et al., 2023). Doing so would change the equations we found for predator and prey resistance, Eqs. (2) and (3), as resistance to a one driver will depend on that of others. However, most of our predictions on community tolerance would still stand.

A first prediction is that predators dictate the resistance of the whole food web because they are less resistant than prey. That is, the first taxon lost by the action of any environmental factor is expected to be a predator, even if its inherent tolerance τ is the same as that of prey. This highlights the role of species interactions and indirect effects in determining the resistance of taxa (Clements and Rohr, 2009; Säterberg et al., 2013; Ockendon et al., 2014; Kleinhesselink and Adler, 2015; Fleeger, 2020; Beauchesne et al., 2021; Zelnik et al., 2022). This result does not contradict the finding that specific predators are more resistant than specific prey (cf. right panels of Fig. 2). Instead, it shows that predators are, on average, more affected by environmental factors, which indicates that the effect of these factors may be greater at higher trophic levels (Voigt et al., 2003; Binzer et al., 2011; Bracken and Low, 2012). The analysis of macroinvertebrate data confirms this prediction (Fig. 5), even though other predictors (encoded in the country covariate) may intervene and blur this result.

The fact that top predators are more extinction-prone than species at lower trophic levels is a classic observation in empirical studies (Cardillo et al., 2004; Säterberg et al., 2013), and has been shown to have potentially far-reaching implications for ecosystem structure (Estes et al., 2011; Donohue et al., 2017). This greater vulnerability of top predators is often explained in the context of habitat fragmentation (e.g. Layman et al., 2007; Ryser et al., 2019). For example, Bayesian network approaches have found that top predators in spatial networks, all else equal, tend to be more extinction-prone following habitat loss because of their lower metapopulation capacity (Häussler et al., 2020). Our findings show that, even without considering spatial mechanisms, predators are also more sensitive to environmental perturbations than their prey. Because regions subject to environmental

change typically experience multiple perturbations, including habitat loss (Bowler et al., 2020), our findings support calls for greater conservation efforts at higher trophic levels (Säterberg et al., 2013).

The second prediction is that food webs with many different prey taxa are expected to be less resistant towards the loss of one predator (Fig. 3, panel A). The reason for this result is that high competition among the prey leads to lower density per prey species, and thus lower prey consumption. Because predator population growth is the balance between consumption and mortality, the same increase of predator mortality is more likely to result in predator loss when consumption is lower. Additional results illustrate this mechanism by showing that this effect disappears as inter-specific competition among prey gets weaker (Fig. E.3 from Supplemental Material). This result is in line with the classical work of May (1972, 2019), which suggests that more diverse communities might be less stable, a pattern reinforced when interspecific competition (or other non-antisymmetric) interactions are stronger (Allesina and Tang, 2012). This mechanism mainly applies to systems where prey dynamics are dominated by bottom-up control and resource limitation (i.e., high interspecific competition). In more productive systems, where predators exert strong top-down control and prey competition is reduced, the relation might change. Indeed, it has been mathematically proven that the negative effect of prey diversity on food web resistance should be reduced for low interaction strengths (Kokkoris et al., 2002), and that a positive diversity-stability relationship can emerge (McCann, 2000). Overall, the relation between diversity and stability likely depends on the stability component considered (Pennekamp et al., 2018; Jarillo et al., 2022).

Finally, and as one would expect, the food web resistance Ω increases with the tolerances of both prey and predator taxa (see Fig. 1). In particular, it linearly increases with the average of the harmonic means of prey and predator taxa, mean $(\mathrm{H}(\tau_V), \mathrm{H}(\tau_P))$, reflecting earlier results in simplified models (Clark et al., 2021; Jarillo et al., 2022). Our third prediction postulates that, for a given mean tolerance, there exists an optimum ratio of predator and prey tolerance $\mathrm{H}(\tau_P)/\mathrm{H}(\tau_V)$ that maximizes community resistance. That is, due to the taxon interactions, the food web resistance decreases for large differences between the tolerances across trophic levels, which shows that food web resistance might not be an additive property based on the taxon tolerances (Singer et al., 2013). This analytical result was obtained under the assumption of all prey and predators having the same parameters, but confirmed numerically in random communities (Fig. 3, panel B). In more complex systems, a more detailed analysis should be proposed to prove these results. In general, the distribution of taxon tolerances, and particularly the differences between the predators and prey tolerances, would certainly influence the food web resistance, because of the trophic interactions within the community (see Fig. 4, panel B). In particular, this result may have applications in ecotoxicology, where previous studies have proven the existence of differences in tolerances between trophic levels depending on the chemical mode of action (Kienzler et al., 2019).

4.2 Limitations and perspective

One limitation of our mathematical analyses is that we assume predator and prey species are on average equally tolerant. While there is no broad support for a relationship between tolerance and trophic level (da Silva et al., 2023), empirical evidence indicates that for some environmental drivers, such as ocean acidification, top predators may be significantly more tolerant than taxa at lower trophic levels (Hu et al., 2022, 2024). Our simulations illustrate that relaxing this assumption only invalidates our findings when some species compete with

Table 1: **Summary of the evidence for each of the three rules that govern food web resistance to environmental change**. Entries refer to the figures and equations that support each rule. These rules are valid as long as there are no competitors of the prey taxa that are both not consumed by the predators and far less tolerant than the prey and predators. Otherwise, Ω_P might not well represent the food web resistance, potentially breaking rules 1 and 3.

Theory	Random food webs	Spatial metacommunity	Field data
Rule 1. *Predators are more vulnerable to environmental change than their prey.*			
$\Omega_P < \Omega_V$ (Eqs. (2)–(3))	Predators go extinct at lower env. change levels than prey (Fig. 2)	Predators have lower resistances than prey (Fig. E.2, Supplementary Information E)	Predator richness (but not prey richness) declines with env. change level (Fig. 5)
Rule 2. *Food webs with more prey species are less resistant to environmental change.*			
Ω_P decreases monotonically with prey richness (Eq. (2), Fig. 1)	Predator-level resistance declines with prey richness (Fig.3)	Communities with higher prey richness exhibit lower metacommunity-level resistance (Fig. 4)	Not directly testable with observational data
Rule 3. *Food web resistance is maximised at an intermediate predator-to-prey tolerance ratio.*			
Non-monotonic dependence of Ω_P on τ_P/τ_V (Eq. (2), Fig. 1, Supplementary Information A.5)	Hump-shaped relationship between resistance and τ_P/τ_V (Fig. 3)	No linear trends of food web resistance with the tolerance ratios (Fig. 4)	Not directly testable with observational data

the prey (*competitors*, hereafter) and are both (1) not consumed by any predator (specialist scenario) and (2) are less tolerant than predators and prey. In that case, the competitors tend to go extinct before the predators (Fig. E.1, bottom-right panel), violating rules 1 and 3 (Table 1). Conversely, rule 2 continues to hold, since more prey taxa would result in higher competition between the prey and competitors, reducing the resistance of the competitors.

Our mathematical analysis also assumes that taxa within a trophic level share similar dynamical parameters, neglecting potential trade-offs between competitive ability and vulnerability to predators (Leibold, 1996; Chase et al., 2002). If such trade-offs existed, and if prey species less affected by predators are also less tolerant to environmental change, some of these weak competitors might be expected to go extinct before some predators. However, incorporating these trade-offs did not change the conclusion that predators are less resistant, except in the specific case where competitors of the prey are not consumed by predators and are less tolerant than the rest of the taxa (Fig. E.1, right panels).

When analyzing how food web structure modulates resistance, we also did not explicitly

analyze the effect of biomass distribution across trophic levels before the perturbation–the initial biomass pyramid (Galiana et al., 2021). The shape of this pyramid may influence food web resistance, especially for inverted pyramids, for which taxa at lower levels present lower biomass, pushing their predators sooner to extinction because of bottom-up effects.

Finally, even though our numerical results with random communities (considering both generalist and specialist food webs) include many different simulations that confirm the three rules described here under most conditions (Fig. 2), the meta-community simulations of our realistic macroinvertebrate communities include results for only six typical communities. The results obtained from this limited number of realistic metacommunities seem to support rules 1 and 2, while support for rule 3 is mixed (Fig. 3). A more in-depth study involving a larger number of communities would be necessary to provide stronger validation.

Our predictors can be divided into two categories: those that describe the food web's ecology, and those that describe species tolerances. Our results suggest that both are mostly independent, leading to insights on which food webs are less resistant: those with more sensitive predators, with many prey, or with less balanced tolerances of prey and predators. Two of the three predictions relate to species tolerances, suggesting that responses to the environment are more important than ecological mechanisms. However, this suggestion is misleading, because the role of the species tolerances is precisely driven by these ecological mechanisms, which either magnify or dampen taxon tolerances. Our results show that there appears to be regularity in the ways in which they do so, which is an encouraging finding, given the diversity of environmental factors of which global change is composed.

5 Acknowledgments

The authors thank the German federal state authorities for access to biological monitoring data. JJ acknowledges funding from the PR17/24-31947 project.

References

S. Allesina and S. Tang. Stability criteria for complex ecosystems. Nature, 483(7388): 205–208, 2012.

S. Allesina and S. Tang. The stability–complexity relationship at age 40: a random matrix perspective. Population Ecology, 57(1):63–75, 2015.

K. M. Archibald, H. M. Sosik, H. V. Moeller, and M. G. Neubert. Predator switching strength controls stability in diamond-shaped food web models. Journal of Theoretical Biology, 570:111536, 2023.

V. Barbarossa, J. Bosmans, N. Wanders, H. King, M. F. P. Bierkens, M. A. J. Huijbregts, and A. M. Schipper. Threats of global warming to the world's freshwater fishes. Nature Communications, 12:1701, 3 2021. ISSN 2041-1723. doi: 10.1038/s41467-021-21655-w. URL `https://www.nature.com/articles/s41467-021-21655-w`.

J. Barlow, F. França, T. A. Gardner, C. C. Hicks, G. D. Lennox, E. Berenguer, L. Castello, E. P. Economo, J. Ferreira, B. Guénard, C. G. Leal, V. Isaac, A. C. Lees, C. L. Parr, S. K.

Wilson, P. J. Young, and N. A. J. Graham. The future of hyperdiverse tropical ecosystems. Nature, 559:517–526, 7 2018. ISSN 0028-0836. doi: 10.1038/s41586-018-0301-1. URL https://www.nature.com/articles/s41586-018-0301-1.

D. Beauchesne, K. Cazelles, P. Archambault, L. E. Dee, and D. Gravel. On the sensitivity of food webs to multiple stressors. Ecology Letters, 24:2219–2237, 10 2021. ISSN 1461-023X. doi: 10.1111/ele.13841. URL https://onlinelibrary.wiley.com/doi/10.1111/ele.13841.

A. Binzer, U. Brose, A. Curtsdotter, A. Eklöf, B. C. Rall, J. O. Riede, and F. de Castro. The susceptibility of species to extinctions in model communities. Basic and Applied Ecology, 12:590–599, 11 2011. ISSN 14391791. doi: 10.1016/j.baae.2011.09.002.

W. J. Boonstra, K. M. Ottosen, A. S. Ferreira, A. Richter, L. A. Rogers, M. W. Pedersen, A. Kokkalis, H. Bardarson, S. Bonanomi, W. Butler, F. K. Diekert, N. Fouzai, M. Holma, R. E. Holt, K. Kvile, E. Malanski, J. I. Macdonald, E. Nieminen, G. Romagnoni, M. Snickars, B. Weigel, P. Woods, J. Yletyinen, and J. D. Whittington. What are the major global threats and impacts in marine environments? investigating the contours of a shared perception among marine scientists from the bottom-up. Marine Policy, 60:197–201, 10 2015. ISSN 0308597X. doi: 10.1016/j.marpol.2015.06.007.

D. E. Bowler, A. D. Bjorkman, M. Dornelas, I. H. Myers-Smith, L. M. Navarro, A. Niamir, S. R. Supp, C. Waldock, M. Winter, M. Vellend, S. A. Blowes, K. Böhning-Gaese, H. Bruelheide, R. Elahi, L. H. Antão, J. Hines, F. Isbell, H. P. Jones, A. E. Magurran, J. S. Cabral, and A. E. Bates. Mapping human pressures on biodiversity across the planet uncovers anthropogenic threat complexes. People and Nature, 2(2): 380–394, 2020. doi: https://doi.org/10.1002/pan3.10071. URL https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1002/pan3.10071.

M. E. Bracken and N. H. Low. Realistic losses of rare species disproportionately impact higher trophic levels. Ecology Letters, 15:461–467, 5 2012. ISSN 1461023X. doi: 10.1111/j.1461-0248.2012.01758.x.

M. Cardillo, A. Purvis, W. Sechrest, J. L. Gittleman, J. Bielby, and G. M. Mace. Human population density and extinction risk in the world's carnivores. PLoS biology, 2(7): e197, 2004.

F. Carrara, F. Altermatt, I. Rodriguez-Iturbe, and A. Rinaldo. Dendritic connectivity controls biodiversity patterns in experimental metacommunities. Proceedings of the National Academy of Sciences, 109(15):5761–5766, 2012.

L. Carraro, E. Bertuzzo, E. A. Fronhofer, R. Furrer, I. Gounand, A. Rinaldo, and F. Altermatt. Generation and application of river network analogues for use in ecology and evolution. Ecology and Evolution, 10(14):7537–7550, 2020.

J. M. Chase, P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, R. M. Nisbet, and T. J. Case. The interaction between predation and competition: a review and synthesis. Ecology letters, 5(2):302–315, 2002.

P. Chesson and J. J. Kuang. The interaction between predation and competition. Nature, 456(7219):235–238, 2008.

A. T. Clark, J.-F. Arnoldi, Y. R. Zelnik, G. Barabas, D. Hodapp, C. Karakoç, S. Koenig, V. Radchuk, I. Donohue, A. Huth, et al. General statistical scaling laws for stability in ecological systems. Ecology Letters, 24(7):1474–1486, 2021.

W. H. Clements and J. R. Rohr. Community responses to contaminants: using basic ecological principles to predict ecotoxicological effects. Environmental Toxicology and Chemistry: An International Journal, 28(9):1789–1800, 2009.

P. S. Craig. Exploring novel ways of using species sensitivity distributions to establish pnecs for industrial chemicals: Final report to project steering group 3 april 2013. 2013.

C. R. da Silva, J. E. Beaman, J. P. Youngblood, V. Kellermann, and S. E. Diamond. Vulnerability to climate change increases with trophic level in terrestrial organisms. Science of the Total Environment, 865:161049, 2023.

F. De Laender, C. Carpentier, T. Carletti, C. Song, S. L. Rumschlag, M. B. Mahon, M. Simonin, G. Meszéna, and G. Barabás. Mean species responses predict effects of environmental change on coexistence. Ecology Letters, 26(9):1535–1547, 2023.

C. A. Deutsch, J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences, 105(18):6668–6672, 2008.

I. Donohue, H. Hillebrand, J. M. Montoya, O. L. Petchey, S. L. Pimm, M. S. Fowler, K. Healy, A. L. Jackson, M. Lurgi, D. McClean, et al. Navigating the complexity of ecological stability. Ecology letters, 19(9):1172–1185, 2016.

I. Donohue, O. L. Petchey, S. Kéfi, A. Génin, A. L. Jackson, Q. Yang, and N. E. O'Connor. Loss of predator species, not intermediate consumers, triggers rapid and dramatic extinction cascades. Global Change Biology, 23(8):2962–2972, 2017.

J. Eklöf, Å. Austin, U. Bergström, S. Donadi, B. D. Eriksson, J. Hansen, and G. Sundblad. Size matters: relationships between body size and body mass of common coastal, aquatic invertebrates in the baltic sea. PeerJ, 5:e2906, 2017.

J. A. Estes, J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. Trophic downgrading of planet earth. Science, 333:301–306, 7 2011. ISSN 0036-8075. doi: 10.1126/science.1205106. URL `https://www.science.org/doi/10.1126/science.1205106`.

European Parliament and Council of the European Union. Regulation (ec) no 1107/2009 of the european parliament and of the council of 21 october 2009 concerning the placing of plant protection products on the market and repealing council directives 79/117/eec and 91/414/eec. Official Journal of the European Union, L309:1–50, 2009. URL `http://data.europa.eu/eli/reg/2009/1107/oj`.

W. F. Fagan. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. Ecology, 83(12):3243–3249, 2002.

J. W. Fleeger. How do indirect effects of contaminants inform ecotoxicology? a review. Processes, 8(12):1659, 2020. ISSN 2227-9717. doi: 10.3390/pr8121659. URL https://www.mdpi.com/2227-9717/8/12/1659.

J. Fox and S. Weisberg. An R Companion to Applied Regression. Sage, Thousand Oaks CA, third edition, 2019. URL https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

N. Galiana, J.-F. Arnoldi, M. Barbier, A. Acloque, C. de Mazancourt, and M. Loreau. Can biomass distribution across trophic levels predict trophic cascades? Ecology Letters, 24 (3):464–476, 2021.

T. Gibbs, S. A. Levin, and J. M. Levine. Coexistence in diverse communities with higher-order interactions. Proceedings of the National Academy of Sciences, 119(43): e2205063119, 2022.

T. L. Gibbs, G. Gellner, S. A. Levin, K. S. McCann, A. Hastings, and J. M. Levine. When can higher-order interactions produce stable coexistence? Ecology letters, 27(6):e14458, 2024.

J. P. Gibert and J. P. DeLong. Phenotypic variation explains food web structural patterns. Proceedings of the National Academy of Sciences, 114(42):11187–11192, 2017.

B. Gilbert, T. D. Tunney, K. S. McCann, J. P. DeLong, D. A. Vasseur, V. Savage, J. B. Shurin, A. I. Dell, B. T. Barton, C. D. Harley, et al. A bioenergetic framework for the temperature dependence of trophic interactions. Ecology letters, 17(8):902–914, 2014.

A. Gonzalez, R. M. Germain, D. S. Srivastava, E. Filotas, L. E. Dee, D. Gravel, P. L. Thompson, F. Isbell, S. Wang, S. Kéfi, et al. Scaling-up biodiversity-ecosystem functioning research. Ecology Letters, 23(4):757–776, 2020.

J. Grilli, T. Rogers, and S. Allesina. Modularity and stability in ecological communities. Nature communications, 7(1):12031, 2016.

V. Grimm and C. Wissel. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. Oecologia, 109(3):323–334, 1997.

B. S. Halpern, M. Frazier, J. Afflerbach, J. S. Lowndes, F. Micheli, C. O'Hara, C. Scarborough, and K. A. Selkoe. Recent pace of change in human impact on the world's ocean. Scientific Reports, 9, 12 2019. ISSN 20452322. doi: 10.1038/s41598-019-47201-9.

J. Häussler, G. Barabás, and A. Eklöf. A bayesian network approach to trophic metacommunities shows that habitat loss accelerates top species extinctions. Ecology Letters, 23 (12):1849–1861, 2020.

H. Hillebrand. On the generality of the latitudinal diversity gradient. The American Naturalist, 163(2):192–211, 2004.

N. Hu, P. E. Bourdeau, C. Harlos, Y. Liu, and J. Hollander. Meta-analysis reveals variance in tolerance to climate change across marine trophic levels. Science of the Total Environment, 827:154244, 2022.

N. Hu, P. E. Bourdeau, and J. Hollander. Responses of marine trophic levels to the combined effects of ocean acidification and warming. Nature Communications, 15(1): 3400, 2024.

J. B. C. Jackson, M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. Historical overfishing and the recent collapse of coastal ecosystems. Science, 293:629–637, 7 2001. ISSN 0036-8075. doi: 10.1126/science.1059199. URL https://www.science.org/doi/10.1126/science.1059199.

T. Jager, C. Albert, T. G. Preuss, and R. Ashauer. General unified threshold model of survival-a toxicokinetic-toxicodynamic framework for ecotoxicology. Environmental science & technology, 45(7):2529–2540, 2011.

J. Jarillo, F. J. Cao-García, and F. De Laender. Spatial and ecological scaling of stability in spatial community networks. Frontiers in Ecology and Evolution, 10:861537, 2022.

J. Jarillo, J. F. Jupke, T. Sinclair, L. Maltby, R. B. Schäfer, and F. De Laender. Simulations – food-web resistance, 2026. URL https://doi.org/10.5281/zenodo.19110901.

C. N. Johnson, A. Balmford, B. W. Brook, J. C. Buettel, M. Galetti, L. Guangchun, and J. M. Wilmshurst. Biodiversity losses and conservation responses in the anthropocene. Science, 356(6335):270–275, 2017.

T. Jonsson. Trophic links and the relationship between predator and prey body sizes in food webs. Community Ecology, 15(1):54–64, 2014.

T. Jonsson, R. Kaartinen, M. Jonsson, and R. Bommarco. Predictive power of food web models based on body size decreases with trophic complexity. Ecology Letters, 21(5): 702–712, 2018.

F. Jordán and I. Scheuring. Network ecology: topological constraints on ecosystem dynamics. Physics of Life Reviews, 1(3):139–172, 2004.

J. F. Jupke. The capacity of broad-scale aquatic typology systems to capture differences in composition and chemical sensitivity of biological assemblages. PhD thesis, Rheinland-Pfälzische Technische Universität Kaiserslautern-Landau, 2024.

J. F. Jupke, S. Birk, M. Álvarez-Cabria, J. Aroviita, J. Barquín, O. Belmar, N. Bonada, M. Cañedo-Argüelles, G. Chiriac, E. M. Elexová, C. K. Feld, M. T. Ferreira, P. Haase, K.-L. Huttunen, M. Lazaridou, M. Lešťáková, M. Miliša, T. Muotka, R. Paavola, P. Panek, P. Pařil, E. T. Peeters, M. Polášek, L. Sandin, D. Schmera, M. Straka, P. Usseglio-Polatera, and R. B. Schäfer. Evaluating the biological validity of european river typology systems with least disturbed benthic macroinvertebrate communities. Science of the Total Environment, 842:156689, 2022.

J. F. Jupke, T. Sinclair, L. Maltby, J. Aroviita, L. Barešová, N. Bonada, E. M. Elexová, M. T. Ferreira, M. Lazaridou, M. Lešťáková, et al. Europe-wide spatial trends in copper and imidacloprid sensitivity of macroinvertebrate assemblages. Environmental Sciences Europe, 36(1):124, 2024.

M. Kearney and W. Porter. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology letters, 12(4):334–350, 2009.

A. Kienzler, K. A. Connors, M. Bonnell, M. G. Barron, A. Beasley, C. G. Inglis, T. J. Norberg-King, T. Martin, H. Sanderson, N. Vallotton, et al. Mode of action classifications in the envirotox database: Development and implementation of a consensus moa classification. Environmental Toxicology and Chemistry, 38(10):2294–2304, 2019.

G. K. K. King, F. Larras, S. Charles, and M. L. Delignette-Muller. Hierarchical modelling of species sensitivity distribution: development and application to the case of diatoms exposed to several herbicides. Ecotoxicology and Environmental Safety, 114:212–221, 2015.

A. R. Kleinhesselink and P. B. Adler. Indirect effects of environmental change in resource competition models. The American Naturalist, 186(6):766–776, 2015.

G. D. Kokkoris, V. A. Jansen, M. Loreau, and A. Y. Troumbis. Variability in interaction strength and implications for biodiversity. Journal of Animal Ecology, pages 362–371, 2002.

C. Kremen. Managing ecosystem services: what do we need to know about their ecology? Ecology letters, 8(5):468–479, 2005.

K. J. Kroeker, R. L. Kordas, and C. D. Harley. Embracing interactions in ocean acidification research: confronting multiple stressor scenarios and context dependence. Biology Letters, 13(3):20160802, 2017.

R. Lande, B.-E. Sæther, and S. Engen. Threshold harvesting for sustainability of fluctuating resources. Ecology, 78(5):1341–1350, 1997.

C. A. Layman, J. P. Quattrochi, C. M. Peyer, and J. E. Allgeier. Niche width collapse in a resilient top predator following ecosystem fragmentation. Ecology letters, 10(10): 937–944, 2007.

M. A. Leibold. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. The American Naturalist, 147(5):784–812, 1996.

J. U. Lemm, M. Venohr, L. Globevnik, K. Stefanidis, Y. Panagopoulos, J. van Gils, L. Posthuma, P. Kristensen, C. K. Feld, J. Mahnkopf, et al. Multiple stressors determine river ecological status at the european scale: Towards an integrated understanding of river status deterioration. Global Change Biology, 27(9):1962–1975, 2021.

Y. Liu, J. Hu, and J. Gore. Ecosystem stability relies on diversity difference between trophic levels. Proceedings of the National Academy of Sciences, 121(50):e2416740121, 2024.

M. Loreau and C. De Mazancourt. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. Ecology letters, 16:106–115, 2013.

M. Loreau, S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. Science, 294(5543):

804–808, Oct. 2001. ISSN 0036-8075, 1095-9203. doi: 10.1126/science.1064088. URL https://www.science.org/doi/10.1126/science.1064088.

M. Loreau, M. Barbier, E. Filotas, D. Gravel, F. Isbell, S. J. Miller, J. M. Montoya, S. Wang, R. Aussenac, R. Germain, et al. Biodiversity as insurance: from concept to measurement and application. Biological Reviews, 96(5):2333–2354, 2021.

A. J. Lotka. Analytical note on certain rhythmic relations in organic systems. Proceedings of the National Academy of Sciences, 6(7):410–415, 1920.

A. Lyche Solheim, L. Globevnik, K. Austnes, P. Kristensen, S. J. Moe, J. Persson, G. Phillips, S. Poikane, W. van de Bund, and S. Birk. A new broad typology for rivers and lakes in europe: Development and application for large-scale environmental assessments. Science of the Total Environment, 697:134043, 2019.

S. L. Maxwell, R. A. Fuller, T. M. Brooks, and J. E. Watson. Biodiversity: The ravages of guns, nets and bulldozers. Nature, 536(7615):143–145, 2016.

R. M. May. Will a large complex system be stable? Nature, 238(5364):413–414, 1972.

R. M. May. Stability and complexity in model ecosystems. Princeton university press, 2019.

K. S. McCann. The diversity–stability debate. Nature, 405(6783):228–233, 2000.

L. Monte. Predicting the effects of ionising radiation on ecosystems by a generic model based on the lotka–volterra equations. Journal of environmental radioactivity, 100(6): 477–483, 2009.

J. M. Montoya, S. L. Pimm, and R. V. Solé. Ecological networks and their fragility. Nature, 442(7100):259–264, 2006.

N. Ockendon, D. J. Baker, J. A. Carr, E. C. White, R. E. Almond, T. Amano, E. Bertram, R. B. Bradbury, C. Bradley, S. H. Butchart, et al. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. Global change biology, 20(7):2221–2229, 2014.

T. H. Oliver, N. J. B. Isaac, T. A. August, B. A. Woodcock, D. B. Roy, and J. M. Bullock. Declining resilience of ecosystem functions under biodiversity loss. Nature Communications, 6(1):10122, Dec. 2015. ISSN 2041-1723. doi: 10.1038/ncomms10122. URL https://www.nature.com/articles/ncomms10122.

F. Pennekamp, M. Pontarp, A. Tabi, F. Altermatt, R. Alther, Y. Choffat, E. A. Fronhofer, P. Ganesanandamoorthy, A. Garnier, J. I. Griffiths, et al. Biodiversity increases and decreases ecosystem stability. Nature, 563(7729):109–112, 2018.

S. L. Pimm. The complexity and stability of ecosystems. Nature, 307(5949):321–326, 1984.

A. P. F. Pires, D. S. Srivastava, N. A. C. Marino, A. A. M. MacDonald, M. P. Figueiredo-Barros, and V. F. Farjalla. Interactive effects of climate change and biodiversity loss on ecosystem functioning. Ecology, 99(5):1203–1213, May 2018. ISSN 0012-9658, 1939-9170. doi: 10.1002/ecy.2202. URL https://onlinelibrary.wiley.com/doi/10.1002/ecy.2202.

J. H. Poelen, J. D. Simons, and M. C. J. Global biotic interactions: An open infrastructure to share and analyze species-interaction datasets. Ecological Informatics, 24:148–159, 2014. ISSN 15749541. doi: 10.1016/j.ecoinf.2014.08.005.

R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, 2023. URL `https://www.R-project.org/`.

V. Radchuk, F. D. Laender, J. S. Cabral, I. Boulangeat, M. Crawford, F. Bohn, J. D. Raedt, C. Scherer, J. C. Svenning, K. Thonicke, F. M. Schurr, V. Grimm, and S. Kramer-Schadt. The dimensionality of stability depends on disturbance type. Ecology Letters, 22(4):674–684, 2019. ISSN 14610248. doi: 10.1111/ele.13226.

X. Rao, J. Chen, S. Wang, H. Su, Q. Rao, W. Xia, J. Liu, X. Fan, X. Deng, H. Shen, et al. Population asynchrony within and between trophic levels have contrasting effects on consumer community stability in a subtropical lake. Journal of Animal Ecology, 93 (10):1593–1605, 2024.

C. Ratzke, J. Barrere, and J. Gore. Strength of species interactions determines biodiversity and stability in microbial communities. Nature ecology & evolution, 4(3):376–383, 2020.

B. D. Richter, R. Mathews, D. L. Harrison, and R. Wigington. Ecologically sustainable water management: managing river flows for ecological integrity. Ecological applications, 13(1):206–224, 2003.

A. Rinaldo, R. Rigon, J. R. Banavar, A. Maritan, and I. Rodriguez-Iturbe. Evolution and selection of river networks: Statics, dynamics, and complexity. Proceedings of the National Academy of Sciences, 111(7):2417–2424, 2014.

I. Rodriguez-Iturbe and A. Rinaldo. Fractal river basins: chance and self-organization. Cambridge University Press, 1997.

J. R. Rohr, J. L. Kerby, and A. Sih. Community ecology as a framework for predicting contaminant effects. Trends in Ecology & Evolution, 21(11):606–613, 2006.

R. Ryser, J. Häussler, M. Stark, U. Brose, B. C. Rall, and C. Guill. The biggest losers: habitat isolation deconstructs complex food webs from top to bottom. Proceedings of the royal society B, 286(1908):20191177, 2019.

T. Säterberg, S. Sellman, and B. Ebenman. High frequency of functional extinctions in ecological networks. Nature, 499(7459):468–470, 2013.

C. A. Serván, J. A. Capitán, J. Grilli, K. E. Morrison, and S. Allesina. Coexistence of many species in random ecosystems. Nature ecology & evolution, 2(8):1237–1242, 2018.

J. P. Simaika and M. J. Samways. Biophilia as a universal ethic for conserving biodiversity. Conservation Biology, 24(3):903–906, 2010.

T. Sinclair, P. Craig, and L. L. Maltby. Climate warming shifts riverine macroinvertebrate communities to be more sensitive to chemical pollutants. Global Change Biology, 30 (4):e17254, 2024.

A. Singer, J. M. Travis, and K. Johst. Interspecific interactions affect species and community responses to climate shifts. Oikos, 122(3):358–366, 2013.

G. Srednick and S. E. Swearer. Understanding diversity–synchrony–stability relationships in multitrophic communities. Nature Ecology & Evolution, 8(7):1259–1269, 2024.

E. Szöcs, M. Brinke, B. Karaoglan, and R. B. Schäfer. Large scale risks from agricultural pesticides in small streams. Environmental Science & Technology, 51(13):7378–7385, 2017.

H. Tachet, P. Richoux, M. Bournaud, and P. Usseglio-Polatera. Invertébrés d'eau douce. Systématique, biologie, écologie. CNRS éditions, Paris, page 588, 2000.

D. Talmy, E. Carr, H. Rajakaruna, S. Våge, and A. Willem Omta. Killing the predator: impacts of highest-predator mortality on the global-ocean ecosystem structure. Biogeosciences, 21(10):2493–2507, 2024.

P. L. Thompson, M. M. MacLennan, and R. D. Vinebrooke. Species interactions cause non-additive effects of multiple environmental stressors on communities. Ecosphere, 9 (11):e02518, 2018.

D. Tilman. Causes, consequences and ethics of biodiversity. Nature, 405(6783):208–211, 2000.

D. Tilman. Interspecific competition and multispecies coexistence, volume 3, pages 84–97. Oxford University Press, 2007. ISBN 9780199209989. doi: 10.1093/oso/9780199209989.003.0010.

C. H. Trisos, C. Merow, and A. L. Pigot. The projected timing of abrupt ecological disruption from climate change. Nature, 580:496–501, 4 2020. ISSN 0028-0836. doi: 10.1038/s41586-020-2189-9. URL https://www.nature.com/articles/s41586-020-2189-9.

C.-H. Tsai, C.-h. Hsieh, and T. Nakazawa. Predator–prey mass ratio revisited: does preference of relative prey body size depend on individual predator size? Functional Ecology, 30(12):1979–1987, 2016.

M. P. Turschwell, S. R. Connolly, R. B. Schäfer, F. De Laender, M. D. Campbell, C. Mantyka-Pringle, M. C. Jackson, M. Kattwinkel, M. Sievers, R. Ashauer, et al. Interactive effects of multiple stressors vary with consumer interactions, stressor dynamics and magnitude. Ecology Letters, 25(6):1483–1496, 2022.

M. C. Urban. Accelerating extinction risk from climate change. Science, 348:571–573, 5 2015. ISSN 0036-8075. doi: 10.1126/science.aaa4984. URL https://www.science.org/doi/10.1126/science.aaa4984.

N. I. van den Berg, D. Machado, S. Santos, I. Rocha, J. Chacón, W. Harcombe, S. Mitri, and K. R. Patil. Ecological modelling approaches for predicting emergent properties in microbial communities. Nature ecology & evolution, 6(7):855–865, 2022.

S. J. Van Moorsel, E. Thébault, V. Radchuk, A. Narwani, J. M. Montoya, V. Dakos, M. Holmes, F. De Laender, and F. Pennekamp. Predicting effects of multiple interacting global change drivers across trophic levels. Global Change Biology, 29(5):1223–1238, 2023.

C. C. Vaughn. Biodiversity Losses and Ecosystem Function in Freshwaters: Emerging Conclusions and Research Directions. BioScience, 60(1):25–35, Jan. 2010. ISSN 1525-3244, 0006-3568. doi: 10.1525/bio.2010.60.1.7. URL https://academic.oup.com/bioscience/article-lookup/doi/10.1525/bio.2010.60.1.7.

W. Voigt, J. Perner, A. J. Davis, T. Eggers, J. Schumacher, R. Bährmann, B. Fabian, W. Heinrich, G. Köhler, D. Lichter, R. Marstaller, and F. W. Sander. Trophic levels are differentially sensitive to climate. Ecology, 84:2444–2453, 2003. ISSN 00129658. doi: 10.1890/02-0266.

V. Volterra. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. Mem. Acad. Lincei Roma, 2:31–133, 1926.

S. Wang, T. Lamy, L. M. Hallett, and M. Loreau. Stability and synchrony across ecological hierarchies in heterogeneous metacommunities: linking theory to data. Ecography, 42 (6):1200–1211, 2019.

Y. Zelnik, N. Galiana, M. Barbier, M. Loreau, E. Galbraith, and J.-F. Arnoldi. How collectively integrated are ecological communities? bioRxiv, pages 2022–12, 2022.

A Analytical derivations of food web resistance

A.1 General bitrophic community model

As stated in the main text, we consider a bitrophic community of n_P predators and n_V prey (or victim) taxa, whose dynamics (in the absence of the environmental change) is given by the generalised Lotka-Volterra model (Lotka, 1920; Volterra, 1926; Tilman, 2007),

$$\begin{aligned}\frac{\mathrm{d}V_i}{\mathrm{d}t} &= \left[b_i - m_i - \left(\sum_{j=1}^{n_V} \alpha_{ij}\, V_j\right) - \left(\sum_{k=1}^{n_P} \lambda_{ik}\, P_k\right)\right] V_i\,, \\ \frac{\mathrm{d}P_l}{\mathrm{d}t} &= \left[-d_l - \alpha_{ll}\, P_l + \left(\sum_{i=1}^{n_V} \lambda_{il}\, \eta_{il}\, V_i\right)\right] P_l\,,\end{aligned} \tag{A.1}$$

for $i = 1, \cdots n_V$, $l = 1, \cdots, n_P$, and where the different parameters are defined in Table F.1. This set of equations (A.1) can be written as the matrix equation,

$$\frac{\mathrm{d}\vec{N}}{\mathrm{d}t} = \vec{N} \circ \left[\vec{R} - \mathbf{A}\,\vec{N}\right]\,. \tag{A.2}$$

where "$\circ$" denotes the element-wise (or Hadamard) product of two vectors, $\vec{N}$ and $\vec{R}$ are column vectors containing respectively all taxon abundances and growth rates,

$$\vec{N} = \begin{pmatrix} V_1 \\ V_2 \\ \vdots \\ V_{n_V} \\ \hdashline P_1 \\ P_2 \\ \vdots \\ P_{n_P} \end{pmatrix}\,,\quad \vec{R} = \begin{pmatrix} b_1 - m_1 \\ b_2 - m_2 \\ \vdots \\ b_{n_V} - m_{n_V} \\ \hdashline -d_1 \\ -d_2 \\ \vdots \\ -d_{n_P} \end{pmatrix}\,, \tag{A.3}$$

and $\mathbf{A}$ is the interaction matrix,

$$\mathbf{A} = \left(\begin{array}{cccc:cccc} 1 & \alpha_{1,2} & \cdots & \alpha_{1,n_V} & \lambda_{1,1} & \lambda_{1,2} & \cdots & \lambda_{1,n_P} \\ \alpha_{2,1} & 1 & \cdots & \alpha_{2,n_V} & \lambda_{2,1} & \lambda_{2,2} & \cdots & \lambda_{2,n_P} \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \ddots & \vdots \\ \alpha_{n_V,1} & \alpha_{n_V,2} & \cdots & 1 & \lambda_{n_V,1} & \lambda_{n_V,2} & \cdots & \lambda_{n_V,n_P} \\ \hdashline -\lambda_{1,1}\,\eta_{1,1} & -\lambda_{2,1}\,\eta_{2,1} & \cdots & -\lambda_{n_V,1}\,\eta_{n_V,1} & 1 & 0 & \cdots & 0 \\ -\lambda_{1,2}\,\eta_{1,2} & -\lambda_{2,2}\,\eta_{2,2} & \cdots & -\lambda_{n_V,2}\,\eta_{n_V,2} & 0 & 1 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \ddots & \vdots \\ -\lambda_{1,n_P}\,\eta_{1,n_P} & -\lambda_{2,n_P}\,\eta_{2,n_P} & \cdots & -\lambda_{n_V,n_P}\,\eta_{n_V,n_P} & 0 & 0 & \cdots & 1 \end{array}\right)\,, \tag{A.4}$$

since predators do not have any direct inter-specific competition, see Eq. (A.1). In these expressions, we have introduced the vertical and horizontal dashed lines as visual guides to distinguish the elements corresponding to the prey and to the predators.

To obtain the equilibrium abundances we should solve the matrix equation

$$\vec{0} = \vec{N}^{(\mathrm{eq})} \circ \left[\vec{R} - \mathbf{A}\,\vec{N}^{(\mathrm{eq})}\right]\,. \tag{A.5}$$

Assuming all taxa persist in the habitat, the steady equilibrium densities of the taxa within the community can be computed just from Eq. (A.2)

$$\vec{N}^{(\mathrm{eq})} = \mathbf{A}^{-1}\,\vec{R}\,. \tag{A.6}$$

If on the contrary one or more taxa are removed from the habitat, the new equilibrium densities should be computed directly from Eq. (A.5). Alternatively, the equilibrium densities can also be computed from Eq. (A.6), by removing from the interaction matrix $\mathbf{A}$ and the growth rate vector $\vec{R}$ those rows and columns corresponding to the removed taxa.

In the presence of environmental change, the death rate of all prey and predator taxa can be potentially increased, which might eventually cause the extinction of some of the taxa within the food web. Denoting as ξ the environmental change level, we assume that it linearly increases the death rates of the taxa, with a slope given by the taxon tolerances, τ_i,

$$\vec{R} \longrightarrow \vec{R}^{*} = \begin{pmatrix} b_1 - m_1\left(1+\frac{\xi}{\tau_{V,1}}\right) \\ b_2 - m_2\left(1+\frac{\xi}{\tau_{V,2}}\right) \\ \vdots \\ b_{n_V} - m_{n_V}\left(1+\frac{\xi}{\tau_{V,n_V}}\right) \\ \hdashline -d_1\left(1+\frac{\xi}{\tau_{P,1}}\right) \\ -d_2\left(1+\frac{\xi}{\tau_{P,2}}\right) \\ \vdots \\ -d_{n_P}\left(1+\frac{\xi}{\tau_{P,n_P}}\right) \end{pmatrix}. \tag{A.7}$$

Hence, for a given environmental change level $\xi > 0$, this $\vec{R}^{*}$ should be employed in Eqs. (A.5) or (A.6), causing a change in the equilibrium abundances. From this analysis, we can define the taxon resistance within the community as the minimum environmental change level required to erode such taxon from the community.

Caused by the large number of different parameters, obtaining expressions for the resistances of the taxa in the general scenarios is a too complex task. Because of that, in the following subsections, we will consider simpler scenarios that will let us to derive analytical solutions for such resistances.

A.2 Simple food webs of generalist predators and prey

This simplified model assumes that, in the absence of environmental change (ξ=0), all prey and predator taxa are "equivalent" at each trophic level, in the sense that they have the same parameters. Since here we are considering generalist predators able to feed on all n_V prey taxa within the food webs, this attack rate is normalized by the number of prey taxa (since predators have to split their focus among all the possible prey) ($\frac{\lambda}{n_V}$). However, we would consider that the presence of the environmental change ξ has different effects on the different taxa, represented by different taxon tolerances τ_i.

Hence, for this case of equivalent generalist taxa, the interaction matrix (A.4) and the

growth rate vector (A.7) would read

$$\mathbf{A}_{\text{gen}} = \left(\begin{array}{cccc:cccc} 1 & \alpha & \cdots & \alpha & \frac{\lambda}{n_V} & \frac{\lambda}{n_V} & \cdots & \frac{\lambda}{n_V} \\ \alpha & 1 & \cdots & \alpha & \frac{\lambda}{n_V} & \frac{\lambda}{n_V} & \cdots & \frac{\lambda}{n_V} \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \ddots & \vdots \\ \alpha & \alpha & \cdots & 1 & \frac{\lambda}{n_V} & \frac{\lambda}{n_V} & \cdots & \frac{\lambda}{n_V} \\ \hdashline -\frac{\lambda\,\eta}{n_V} & -\frac{\lambda\,\eta}{n_V} & \cdots & -\frac{\lambda\,\eta}{n_V} & 1 & 0 & \cdots & 0 \\ -\frac{\lambda\,\eta}{n_V} & -\frac{\lambda\,\eta}{n_V} & \cdots & -\frac{\lambda\,\eta}{n_V} & 0 & 1 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \ddots & \vdots \\ -\frac{\lambda\,\eta}{n_V} & -\frac{\lambda\,\eta}{n_V} & \cdots & -\frac{\lambda\,\eta}{n_V} & 0 & 0 & \cdots & 1 \end{array}\right), \; \vec{R}^{*}_{\text{gen}} = \left(\begin{array}{c} b - m\left(1+\frac{\xi}{\tau_{V_1}}\right) \\ b - m\left(1+\frac{\xi}{\tau_{V_2}}\right) \\ \vdots \\ b - m\left(1+\frac{\xi}{\tau_{V_{n_V}}}\right) \\ \hdashline -d\left(1+\frac{\xi}{\tau_{P_1}}\right) \\ -d\left(1+\frac{\xi}{\tau_{P_2}}\right) \\ \vdots \\ -d\left(1+\frac{\xi}{\tau_{P_{n_P}}}\right) \end{array}\right). \tag{A.8}$$

Replacing these expressions in Eq. (A.2), we obtain that for this simplified food web of generalist predators the Lotka-Volterra equations read

$$\begin{aligned} \frac{dV_i}{dt} &= V_i\left[b - m - \alpha\sum_{j=1}^{n_V} V_j - (1-\alpha)\,V_i - \frac{\lambda}{n_V}\sum_{k=1}^{n_P} P_k - m\,\frac{1}{\tau_{V_i}}\,\xi\right], \\ \frac{dP_l}{dt} &= P_l\left[-d + \frac{\lambda}{n_v}\,\eta\sum_{j=1}^{n_V} V_j - P_l - d\,\frac{1}{\tau_{P_l}}\,\xi\right]. \end{aligned} \tag{A.9}$$

From these equations, one can obtain analytical expressions for the equilibrium abundances for prey and predator species (i.e., the abundances for which $\frac{dV_i}{dt} = \frac{dP_l}{dt} = 0$, for $i = \{1, \cdots, n_V\}$, $l = \{1, \cdots, n_P\}$. Such equilibrium abundances read

$$V_i^{(eq)} = \frac{b - m\,\left[1 + \left\langle\frac{1}{\tau_V}\right\rangle\,\xi\right] + \lambda\,\frac{n_P}{n_V}\,d\,\left[1 + \left\langle\frac{1}{\tau_P}\right\rangle\,\xi\right]}{1 + (n_V - 1)\,\alpha + \lambda^2\,\eta\,\frac{n_P}{n_V}} - \frac{m}{1-\alpha}\left[\frac{1}{\tau_{V_i}} - \left\langle\frac{1}{\tau_V}\right\rangle\right]\xi\,, \tag{A.10a}$$

$$\begin{aligned} P_l^{(eq)} =& \frac{\lambda\,\eta\,\left[b - m\,\left(1 + \left\langle\frac{1}{\tau_V}\right\rangle\,\xi\right)\right] - [1 + (n_V - 1)\,\alpha]\;d\,\left[1 + \left\langle\frac{1}{\tau_P}\right\rangle\,\xi\right]}{1 + (n_V - 1)\,\alpha + \lambda^2\,\eta\,\frac{n_P}{n_V}} \\ & - d\,\left[\frac{1}{\tau_{P_l}} - \left\langle\frac{1}{\tau_P}\right\rangle\right]\xi\,, \end{aligned} \tag{A.10b}$$

where $\langle\cdot\rangle$ denotes the arithmetic mean, so $\left\langle\frac{1}{\tau_V}\right\rangle = \frac{1}{n_V}\sum_{i=1}^{n_V}\frac{1}{\tau_{V_i}}$, and a similar expression holds for $\left\langle\frac{1}{\tau_P}\right\rangle$. In particular, this would mean that $\left\langle\frac{1}{\tau_V}\right\rangle$ and $\left\langle\frac{1}{\tau_P}\right\rangle$ are the reciprocals of the harmonic mean of the prey and predator tolerances, respectively. From these expressions, it is easy to check that in the absence of environmental change ($\xi = 0$) all predator and prey taxa have the same equilibrium abundances, as a consequence of the assumption of all having the same parameters. Moreover, if we impose that both trophic levels coexist in the absence of perturbation, so the equilibrium solution (A.10) provides positive abundances, we reach the coexistence condition

$$\frac{b}{m} - 1 > \frac{d}{m}\,\frac{1 + (n_V - 1)\,\alpha}{\lambda\,\eta}\,, \tag{A.11}$$

which ensures that the predators can persist with the given prey availability.

Since predators need the prey species to persist, the first taxon to be removed because of the action of the environmental change ξ would be a predator. And in this model, such predator would be the one with the smallest tolerance $\tau_{P,l}$. This let us to define the resistance of the predator trophic level Ω_P as the minimum environmental change level ξ that leads to the removal of the first predator. This would correspond the the minimum ξ such as the the first predator taxa goes from a positive abundance to a zero abundance. Its inverse is

$$\begin{aligned}\Omega_P^{-1} =& \frac{1}{\frac{b}{m} - 1 - \frac{d}{m}\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta}} \left\{ \left\langle \frac{1}{\tau_V} \right\rangle + \frac{d}{m} \frac{1+(n_V-1)\,\alpha}{\lambda\,\eta} \max\left(\frac{1}{\tau_P}\right) \right. \\ & \left. + \frac{d}{m}\,\lambda\,\frac{n_P}{n_V} \left[\max\left(\frac{1}{\tau_P}\right) - \left\langle \frac{1}{\tau_P} \right\rangle \right] \right\}\end{aligned} \tag{A.12}$$

This expression tells us that the predator resistance depends on the harmonic mean of the tolerance of prey and predator species, and on the minimum tolerance among the predators.

For higher environmental change levels, the more predator taxa would be removed, up to the point that just the prey species persist. Up to this point, the dynamical equation for the prey species would read

$$\frac{dV_i}{dt} = b - m - \alpha \sum_{j=1}^{n_V} V_j - (1-\alpha)\,V_i - m\,\frac{1}{\tau_{V_i}}\,\xi\,. \tag{A.13}$$

And hence, the equilibrium abundance of the prey species i (in the absence of any predator) would read

$$V_i^{(eq)} = \frac{b-m}{1+(n_V-1)\,\alpha} - \frac{1}{1-\alpha}\,m \left\{ \frac{1}{\tau_{V_i}} - \frac{n_V\,\alpha}{1+(n_V-1)\,\alpha} \left\langle \frac{1}{\tau_V} \right\rangle \right\} \xi\,. \tag{A.14}$$

Then, we can obtain the resistance of the prey level from the minimum environmental change level required to remove at least one of the prey,

$$\Omega_V^{-1} = \frac{1}{\frac{b}{m} - 1} \left\{ \max\left(\frac{1}{\tau_V}\right) + \frac{n_V\,\alpha}{1-\alpha} \left[\max\left(\frac{1}{\tau_V}\right) - \left\langle \frac{1}{\tau_V} \right\rangle \right] \right\}. \tag{A.15}$$

Using Eqs. (A.12) and (A.15), and knowing the tolerances of all taxa within the community, analytical estimators for the resistances of the trophic levels of the food web could be derived. However, these estimators depend on knowing exactly the minimum tolerance among the species from each trophic level. Hence, these expressions may result in unreliable estimations if tolerances of some of the taxa are lacking.

To solve this issue, we might try to provide some statistical estimators for $\max(\tau_X^{-1})$, $X = \{V \text{ or } P\}$. Hence, we would assume that the inverse of the taxon tolerances within a trophic level is a random variable following a given distribution, with a given mean $\langle \tau_X^{-1} \rangle$ and standard deviation $\mathrm{std}\left(\tau_X^{-1}\right)$. Then, we replace in Eqs. (A.12) and (A.15) the maximum values of these quantities as the statistics located at κ standard deviations to the right from the sample mean ($\max\left(\tau_X^{-1}\right) \to \langle \tau_X^{-1} \rangle + \kappa\,\mathrm{std}\left(\tau_X^{-1}\right) = \langle \tau_X^{-1} \rangle \left(1 + \kappa\,\mathrm{CV}\left(\tau_X^{-1}\right)\right)$). The factor κ may depend on the sample size, since larger samples are more likely to exhibit more extreme values, and it may also depend on the tail properties of the underlying tolerances. For instance, if τ_X^{-1} were Gaussian, the expected maximum would scale as $\sqrt{2\log n}$ for large sample sizes. In our case, we numerically evaluated the distance between

the empirical sample maximum and the population mean of the reciprocal tolerances. For the typical number of taxa considered here, this distance lies between 0 and 4 standard deviations (Fig. E.6). We therefore take $\kappa = 3$ as a representative value.

This estimation of the maximum reciprocal tolerance let us to obtain the following expressions for the resistances of the trophic levels

$$\Omega_P = \mathrm{H}(\tau_P)\ \frac{\frac{b}{m} - 1 - \frac{d}{m}\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta}}{\frac{\mathrm{H}(\tau_P)}{\mathrm{H}(\tau_V)} + \frac{d}{m}\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta} + \kappa\,\frac{d}{m}\,\mathrm{CV}\left(\frac{1}{\tau_P}\right)\left[\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta} + \lambda\,\frac{n_P}{n_V}\right]}\,, \tag{A.16a}$$

$$\Omega_V = \mathrm{H}(\tau_V)\ \frac{\frac{b}{m} - 1}{1 + \kappa\,\frac{1+(n_V-1)\,\alpha}{1-\alpha}\,\mathrm{CV}\left(\frac{1}{\tau_V}\right)}\,, \tag{A.16b}$$

where $\mathrm{H}(\tau_X) = 1/\left\langle \tau_X^{-1} \right\rangle$ stands for the harmonic mean of the tolerances of the taxa from the specified trophic level (prey or predator).

A.3 Simple food webs of specialist predators and prey

In contrast to the scenarios of all-generalist predators, real ecosystems tend to have more skew interactions, with just few strong trophic relations between predator and prey taxa. To take this fact into account, we consider here the opposite scenario, in which each predator taxon preys upon a single prey. In this scenarios we further assume that each of the prey taxon can be consumed by at most one predator, considering high enough niche differentiation between the predators. Even though this represents just an idealization, since the number of prey taxa is generally bigger than the number of predator taxa, for sufficiently large systems the chances of two coexisting specialist predators feeding on the same prey would be low.

We further assume that all prey and predator taxa have the same parameters (growth rates, interaction strengths ...) as in the previous scenarios. With respect to the tolerances, and to obtain simpler analytical estimators of the resistances of the predator levels, we also assume that all prey taxa are equally tolerant, presenting the same tolerances $\widetilde{\tau_V}$. Under these assumptions, the interaction matrix and growth rate vector read

$$\mathbf{A}_{\mathrm{spec}} = \left(\begin{array}{cccc:ccc:ccc:c} 1 & \alpha & \cdots & \alpha & \alpha & \cdots & \alpha & \lambda & 0 & \cdots & 0 \\ \alpha & 1 & \cdots & \alpha & \alpha & \cdots & \alpha & 0 & \lambda & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \ddots & \vdots \\ \alpha & \alpha & \cdots & 1 & \alpha & \cdots & \alpha & 0 & 0 & \cdots & \lambda \\ \hdashline \alpha & \alpha & \cdots & \alpha & 1 & \cdots & \alpha & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \ddots & \vdots \\ \alpha & \alpha & \cdots & \alpha & \alpha & \cdots & 1 & 0 & 0 & \cdots & 0 \\ \hdashline -\lambda\eta & 0 & \cdots & 0 & 0 & \cdots & 0 & 1 & 0 & \cdots & 0 \\ 0 & -\lambda\eta & \cdots & 0 & 0 & \cdots & 0 & 0 & 1 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & -\lambda\eta & 0 & \cdots & 0 & 0 & 0 & \cdots & 1 \end{array}\right), \quad \vec{R}^{*}_{\mathrm{spec}} = \left(\begin{array}{c} b - m\left(1 + \frac{\xi}{\widetilde{\tau_V}}\right) \\ b - m\left(1 + \frac{\xi}{\widetilde{\tau_V}}\right) \\ \vdots \\ b - m\left(1 + \frac{\xi}{\widetilde{\tau_V}}\right) \\ \hdashline b - m\left(1 + \frac{\xi}{\widetilde{\tau_V}}\right) \\ \vdots \\ b - m\left(1 + \frac{\xi}{\widetilde{\tau_V}}\right) \\ \hdashline -d\left(1 + \frac{\xi}{\tau_{P_1}}\right) \\ -d\left(1 + \frac{\xi}{\tau_{P_2}}\right) \\ \vdots \\ -d\left(1 + \frac{\xi}{\tau_{P_{n_P}}}\right) \end{array}\right). \tag{A.17}$$

Since the number of prey would generally be larger than the number of predator taxa of the food web ($n_V \geq n_P$), this model assumes that we have three different categories of taxa: prey taxa (actually attacked by predators of the food web); competitor taxa (competitors of the prey taxa, but without predation pressure); and predator taxa.

Replacing Eq. (A.17) in (A.2), we obtain Lotka-Volterra equations for this simple model of specialist predators,

$$\begin{aligned}
\frac{dV_i}{dt} &= V_i \left[b - m - \alpha \left(\sum_{j=1}^{n_P} V_j + \sum_{j=1}^{n_V - n_P} C_j \right) - (1-\alpha)\, V_i - \lambda\, P_i - m\, \frac{1}{\widetilde{\widetilde{\tau_V}}}\, \xi \right] , \\
\frac{dC_i}{dt} &= C_i \left[b - m - \alpha \left(\sum_{j=1}^{n_P} V_j + \sum_{j=1}^{n_V - n_P} C_j \right) - (1-\alpha)\, C_i - m\, \frac{1}{\widetilde{\widetilde{\tau_V}}}\, \xi \right] , \\
\frac{dP_i}{dt} &= P_i \left[-d + \lambda\, \eta\, V_i - P_i - d\, \frac{1}{\tau_{P_i}}\, \xi \right] .
\end{aligned} \tag{A.18}$$

Imposing all these derivatives to be equal to zero, we can obtain equilibrium abundances when all the taxa persist

$$\begin{aligned}
V_i^{eq} =& \frac{b - m\, \left(1 + \frac{1}{\widetilde{\widetilde{\tau_V}}}\, \xi \right) + \lambda\, d\, \frac{1 + (n_V - n_P - 1)\, \alpha}{1-\alpha}\, \left(1 + \frac{1}{\tau_{P_i}}\, \xi \right)}{1 + (n_V - 1)\, \alpha + \lambda^2\, \eta\, \frac{1 + (n_V - n_P - 1)\, \alpha}{1-\alpha}} \\
&+ \frac{\lambda\, d\, \frac{n_P\, \alpha}{1 - \alpha + \lambda^2\, \eta}\, \left(\frac{1}{\tau_{P_i}} - \left\langle \frac{1}{\tau_P} \right\rangle \right) \xi}{1 + (n_V - 1)\, \alpha + \lambda^2\, \eta\, \frac{1 + (n_V - n_P - 1)\, \alpha}{1-\alpha}} ,
\end{aligned} \tag{A.19a}$$

$$C_i^{eq} = \frac{1}{1-\alpha}\, \frac{\left[b - m\, \left(1 + \frac{1}{\widetilde{\widetilde{\tau_V}}}\, \xi \right) \right]\, (1 - \alpha + \lambda^2\, \eta) - \lambda\, d\, \frac{n_P\, \alpha}{1-\alpha}\, \left(1 + \left\langle \frac{1}{\tau_P} \right\rangle \xi \right)}{1 + (n_V - 1)\, \alpha + \lambda^2\, \eta\, \frac{1 + (n_V - n_P - 1)\, \alpha}{1-\alpha}} , \tag{A.19b}$$

$$\begin{aligned}
P_i^{eq} =& \frac{\lambda\, \eta\, \left(1 + \frac{1}{\widetilde{\widetilde{\tau_V}}}\, \xi \right) - [1 + (n_V - 1)\, \alpha]\, d\, \left(1 + \frac{1}{\tau_{P_i}}\, \xi \right)}{1 + (n_V - 1)\, \alpha + \lambda^2\, \eta\, \frac{1 + (n_V - n_P - 1)\, \alpha}{1-\alpha}} \\
&+ \frac{\lambda^2\, \eta\, d\, \frac{n_P\, \alpha}{1 - \alpha + \lambda^2\, \eta}\, \left(\frac{1}{\tau_{P_i}} - \left\langle \frac{1}{\tau_P} \right\rangle \right) \xi}{1 + (n_V - 1)\, \alpha + \lambda^2\, \eta\, \frac{1 + (n_V - n_P - 1)\, \alpha}{1-\alpha}} .
\end{aligned} \tag{A.19c}$$

As before, the condition for all taxa to coexist in the absence of environmental change ($\xi = 0$) coincides with Eq. (A.11). Moreover, since predators need the prey to persist, in this case the first species removed because of the action of ξ is again the predator with the smallest tolerance τ_{P_i}. This lets us to define the resistance of the trophic level as the minimum environmental change ξ required to lose the first predator, and in this scenarios its inverse reads

$$\begin{aligned}
\Omega_P^{-1} = & \frac{1}{\frac{b}{m} - 1 - \frac{d}{m}\, \frac{1 + (n_V - 1)\, \alpha}{\lambda\, \eta}} \left\{ \frac{1}{\widetilde{\widetilde{\tau_V}}} + \frac{d}{m}\, \frac{1 + (n_V - 1)\, \alpha}{\lambda\, \eta}\, \max\left(\frac{1}{\tau_P} \right) \right. \\
& \left. - \frac{d}{m}\, \lambda\, \frac{n_P\, \alpha}{1 - \alpha + \lambda^2\, \eta} \left[\max\left(\frac{1}{\tau_P} \right) - \left\langle \frac{1}{\tau_P} \right\rangle \right] \right\} .
\end{aligned} \tag{A.20}$$

If all predators had the same tolerance τ_P (i.e., $\mathrm{CV}\left(\frac{1}{\tau_P} \right) = 0$), the resistance of the predator level in this model with specialist predators, Eq. (A.20), coincides with the expressions obtained in the case of generalist predators, Eq. (A.12). Conversely, if predators

had different tolerances, the resistance estimated in this model with specialist predators is higher than in the model with generalist predators. Hence, for a general case in which we may have both generalist or specialist predators, or predators that feed on some but not all prey, a conservative estimation of the tolerance of the predator level would be the one obtained with the assumption of generalist predators, Eq. (A.12).

With respect to the resistance of the prey level, since predators need the prey to persist, we can assume that before the first prey species is removed from the habitat because of the action of the environmental change ξ, all predators were previously eradicated. Hence, for studying the resistance of the prey level we would have to analyze a model with just n_V prey, as we did in the previous subsection. Hence, the resistance of the prey can be estimated in this case also employing the expressions obtained for the generalist case, Eq. (A.15).

A.4 Comparing trophic-level resistances: predators are less resistant than their prey

For both cases of simple bi-trophic communities of either generalist or specialist predators, we have obtained analytical expressions for the resistances of the predator and prey level. If tolerances vary among the predators, the predator-level resistance would be slightly lower for specialist bi-trophic communities than for the generalist case. However, such difference would be small, and actually the resistances of both scenarios coincide if the coefficient of variation of the taxa' tolerances is neglected,

$$\Omega_P|_{\mathrm{CV}=0} = \tau_P \, \frac{\frac{b}{m} - 1 - \frac{d}{m}\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta}}{\frac{\tau_P}{\tau_V} + \frac{d}{m}\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta}} \, . \tag{A.21}$$

Moreover, the prey-level resistance is also the same for both simple community models, and when the coefficient of variation of the tolerances is neglected its expression simplifies to

$$\Omega_V|_{\mathrm{CV}=0} = \tau_V \left(\frac{b}{m} - 1\right) . \tag{A.22}$$

We can compute the ratio between these trophic-level resistances,

$$\frac{\Omega_P|_{\mathrm{CV}=0}}{\Omega_V|_{\mathrm{CV}=0}} = \frac{\frac{b}{m} - 1 - \frac{d}{m}\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta}}{\frac{b}{m} - 1} \, \frac{1}{1 + \frac{d}{m}\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta}\frac{\tau_V}{\tau_P}} \, , \tag{A.23}$$

which, taking into account the required condition for all taxa to coexist in the absence of environmental change (Eq. (A.11)), is positive and smaller than 1, proving that predators would generally be less resistant than their prey. This substantiates the intuitive result that predators require prey to persist, while prey can persist without predators. Because of the same reason, predator-level resistance depends on both prey and predator parameters and tolerances, while prey-level resistance only depends on parameters and tolerances of prey.

A.5 Effect of the distribution of taxon tolerances in the food web resistance

Since predators tend to be less resistant than the prey, we can employ the predator-level resistance (Eq. (A.16)) as a proxy for the food web resistance. This resistance increases

with both $\mathrm{H}(\tau_P)$ and $\mathrm{H}(\tau_V)$, which illustrates that those more-tolerant communities would also be more resistant. However, the difference of tolerances between the trophic levels may affect the resistance of the food web.

To examine this, we rewrite the food web resistance, Eq. (A.21), in terms of the mean tolerance across trophic levels, $\langle\tau\rangle = \frac{\mathrm{H}(\tau_V)+\mathrm{H}(\tau_P)}{2}$, and the ratio of the harmonic mean tolerances of the predator vs prey taxa, $\rho = \frac{\mathrm{H}(\tau_P)}{\mathrm{H}(\tau_V)}$,

$$\Omega_P = \langle\tau\rangle \, \frac{2\rho}{1+\rho} \, \frac{\frac{b}{m} - 1 - \frac{d}{m}\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta}}{\rho + \frac{d}{m}\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta} + \kappa\,\frac{d}{m}\,\mathrm{CV}\left(\tau_P^{-1}\right)\,\left(\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta} + \frac{n_P}{n_V}\,\lambda\right)} \,. \tag{A.24}$$

Based on Eq. (A.24), the food web resistance increases with the mean of the tolerances, so communities composed by more tolerant taxa would be more resistant. However, the response to the ratio of tolerances seems less obvious.

To clarify this, we compute the derivative of the resistance with respect to ρ,

$$\begin{aligned}\frac{\mathrm{d}\Omega_P}{\mathrm{d}\rho} = &- \frac{\Omega_P}{\left[\rho + \frac{d}{m}\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta} + \kappa\,\frac{d}{m}\,\mathrm{CV}\left(\tau_P^{-1}\right)\,\left(\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta} + \lambda\,\frac{n_P}{n_V}\right)\right]\,\rho\,(1+\rho)} \times \\ &\times \left[\rho^2 - \frac{d}{m}\,\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta} - \kappa\,\frac{d}{m}\,\mathrm{CV}\left(\tau_P^{-1}\right)\,\left(\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta} + \lambda\,\frac{n_P}{n_V}\right)\right] \,.\end{aligned} \tag{A.25}$$

This derivative is zero if

$$\rho = \rho_{\mathrm{optim}} = \sqrt{\frac{\frac{d}{m}}{\frac{b}{m}-1}\,\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta}}\,\sqrt{\left(\frac{b}{m}-1\right)\,\left[1+\kappa\,\mathrm{CV}\left(\tau_P^{-1}\right)\,\left(1+\frac{\frac{n_P}{n_V}\,\lambda}{\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta}}\right)\right]}\,, \tag{A.26}$$

while the derivative is positive if the ratio of tolerance is smaller than this optimal value, and negative if it is higher. Hence, this proves the existence of an optimal value of the ratio of tolerances of predators vs prey that maximizes the food web resistance.

That is, the food web resistance presents a maximum value for a given optimal ratio of tolerances of predators vs prey taxa, Eq. (A.26). The food web resistance would tend to be reduced when the differences between the tolerances of the trophic levels become large.

A.6 Effect of food web structure on food web resistance

We next examine how food web composition (the number of prey and predator taxa) affects food web resistance. Following the reasoning of the previous subsections, we use the resistance of the predator trophic level Ω_P as a proxy for total food web resistance. We consider the two simplified cases already introduced: food webs formed by equivalent generalist predators Eq. (A.12) and communities formed by equivalent specialist predators Eq. (A.20). Moreover, through this section we will assume that there exist just a small variation in the predators' tolerances, so $1 - \frac{\min\tau_P}{H(\tau_P)} \to 0$ (the relative distance between the minimum tolerance of the predators, and the harmonic mean of tolerances among the predator taxa, is approximately zero).

Depending on the scenarios (of generalist or specialist predators), the derivative of the

food web resistance with respect to the number of prey taxa reads

$$\left(\frac{\partial \Omega_P}{\partial n_V}\right)_{\text{gen.}} = -\frac{\Omega_P}{\frac{b}{m} - 1 - \frac{\frac{d}{m}}{\lambda\,\eta}(1 + (n_V - 1)\alpha)} \frac{\frac{d}{m}}{\lambda\,\eta}\,\alpha \left\{1 + \frac{\Omega_P}{\min \tau_P} \cdot \right. \\ \left. \cdot \left[1 - \frac{1}{n_V\,\alpha}\,\lambda^2 \eta\,\frac{n_P}{n_V}\left(1 - \frac{\min \tau_P}{H(\tau_P)}\right)\right]\right\}, \tag{A.27}$$

$$\left(\frac{\partial \Omega_P}{\partial n_V}\right)_{\text{spec.}} = -\frac{\Omega_P}{\frac{b}{m} - 1 - \frac{\frac{d}{m}}{\lambda\,\eta}\,(1 + (n_V - 1)\,\alpha)} \frac{\frac{d}{m}}{\lambda\,\eta}\,\alpha \left\{1 + \frac{\Omega_P}{\min \tau_P}\right\}.$$

In both generalist or specialist scenarios, the derivative is generally negative for positive enough competition strengths $\alpha > 0$, indicating that increasing prey diversity reduces food web resistance. For weak enough competition strength (in the limit of $\alpha \to 0$), the sign of the derivatives can change, and it will be either positive (for the generalist predators), or negative (for specialist predators). The condition for both scenarios to have a negative derivative are that

$$\alpha > \alpha_{crit} = \frac{\lambda^2 \eta}{n_V}\,\frac{n_P}{n_V}\,\frac{\frac{\Omega_P}{\min \tau_P}}{1 + \frac{\Omega_P}{\min \tau_P}}\,\left(1 - \frac{\min \tau_P}{H(\tau_P)}\right)$$

This critical value α_{crit} goes to zero if the predator richness is much smaller than the prey richness, or if the variation in predators' tolerances is small enough. Hence, $\alpha_{crit} \approx 0$, and in general for positive values of α we would generally expect the derivative to be negative. Only when $\alpha \approx 0$ the sign can be positive, but its absolute value would be small, and the prey diversity should just play a minor effect on the food web resistance.

Analogously, taking the derivative with respect to the number of predators n_P,

$$\left(\frac{\partial \Omega_P}{\partial n_P}\right)_{\text{gen.}} = -\frac{\Omega_P}{\frac{b}{m} - 1 - \frac{\frac{d}{m}}{\lambda\eta}(1 + (n_V - 1)\alpha)} \frac{\frac{d}{m}}{\lambda\,\eta}\,\lambda^2 \eta\,\frac{1}{n_V}\,\frac{\Omega_P}{\min \tau_P}\left(1 - \frac{\min \tau_P}{H(\tau_P)}\right), \\ \left(\frac{\partial \Omega_P}{\partial n_P}\right)_{\text{spec.}} = \frac{\Omega_P}{\frac{b}{m} - 1 - \frac{\frac{d}{m}}{\lambda\,\eta}\,(1 + (n_V - 1)\,\alpha)} \frac{\frac{d}{m}}{\lambda\,\eta}\,\lambda^2\,\eta\,\frac{\alpha}{1 - \alpha + \lambda^2\,\eta}\,\frac{\Omega_P}{\min \tau_P}\,\left(1 - \frac{\min \tau_P}{H(\tau_P)}\right). \tag{A.28}$$

This derivative would be small and negative for the generalist predators scenarios, while for specialist predators it would be small and positive. In both cases, under the assumption that there is small variation in the predators' tolerances, the predator diversity should just have a negligible effect on food web resistance, smaller than the effect of prey diversity.

The above conclusions were obtained by varying the number of prey and predator taxa, n_V and n_P, independently. We now explore how the predator-to-prey ratio ($f_{PV} = n_P/n_V$) affects food web resistance when the total number of taxa ($N = n_V + n_P$) is kept constant. Substituting $n_V = N/(1 + f_{PV})$ and $P = f_{PV}\,N/(1 + f_{PV})$ into Eqs. (A.12) and (A.20),

and differentiating with respect to f_{PV}, we obtain

$$\begin{aligned}
\left(\frac{\partial \Omega_P}{\partial f_{PV}}\right)_{\text{gen.}} =& \frac{\Omega_P}{\frac{b}{m} - 1 - \frac{\frac{d}{m}}{\lambda\,\eta}\left(1 + (n_V - 1)\,\alpha\right)} \frac{\frac{d}{m}}{\lambda\,\eta} \frac{n_V\,\alpha}{1 + f_{PV}} \cdot \\
& \cdot \left\{1 + \frac{\Omega_P}{\min \tau_P}\left[1 - \frac{\lambda^2\,\eta}{n_V\,\alpha}\,(1 + f_{PV})\left(1 - \frac{\min \tau_P}{H(\tau_P)}\right)\right]\right\}, \\
\left(\frac{\partial \Omega_P}{\partial f_{PV}}\right)_{\text{spec.}} =& \frac{\Omega_P}{\frac{b}{m} - 1 - \frac{\frac{d}{m}}{\lambda\,\eta}\left(1 + (n_V - 1)\,\alpha\right)} \frac{\frac{d}{m}}{\lambda\,\eta} \frac{n_V\,\alpha}{1 + f_{PV}} \cdot \\
& \cdot \left\{1 + \frac{\Omega_P}{\min \tau_P}\left[1 + \frac{\lambda^2\,\eta}{1 - \alpha + \lambda^2\,\eta}\left(1 - \frac{\min \tau_P}{H(\tau_P)}\right)\right]\right\}.
\end{aligned} \tag{A.29}$$

For positive competition strength, $\alpha > 0$, the derivative is generally positive for both generalist or specialist scenarios, indicating that, for a fixed total number of species, increasing the relative predator diversity enhances food web resistance, whereas a higher proportion of prey reduces it. Moreover, under the assumption of really weak competition, $\alpha \approx 0$, the derivative is either small and negative (generalist), or small and positive (specialist). But in both cases, under the assumption of $\alpha \approx 0$, the predator-to-prey ratio is not expected to have a big influence on the food web resistance.

Finally, differentiating Ω_P with respect to the total number of taxa, N, allows us to assess how overall diversity influences food web resistance, irrespective of the predator-to-prey ratio:

$$\begin{aligned}
\left(\frac{\partial \Omega_P}{\partial N}\right)_{\text{gen}} =& -\frac{\Omega_P}{\frac{b}{m} - 1 - \frac{\frac{d}{m}}{\lambda\,\eta}\left(1 + (n_V - 1)\,\alpha\right)} \frac{\frac{d}{m}}{\lambda\,\eta}\,\alpha\,\frac{1}{1 + \frac{n_P}{n_V}}\left\{1 + \frac{\Omega_P}{\min \tau_P}\right\}, \\
\left(\frac{\partial \Omega_P}{\partial N}\right)_{\text{spec.}} =& -\frac{\Omega_P}{\frac{b}{m} - 1 - \frac{\frac{d}{m}}{\lambda\,\eta}\left(1 + (n_V - 1)\,\alpha\right)} \frac{\frac{d}{m}}{\lambda\,\eta}\,\alpha\,\frac{1}{1 + \frac{n_P}{n_V}}\left\{1 + \frac{\Omega_P}{\min \tau_P} \cdot \right. \\
& \left. \cdot \left[1 - \frac{\lambda^2\,\eta}{1 - \alpha + \lambda^2\,\eta}\,\frac{n_P}{n_V}\left(1 - \frac{\min \tau_P}{H(\tau_P)}\right)\right]\right\}.
\end{aligned} \tag{A.30}$$

For positive competition strengths these derivatives are negative, provided that the number of predators is not greater than the number of prey species. Hence, the total taxon diversity has a negative effect on food web resistance. For the case of really weak competition, $\alpha \approx 0$, both derivatives go to zero, indicating that under this condition of weak competition, the total diversity does not significantly affect food web resistance.

A.7 Alternative definition of resistance: 50% taxa lost

We defined the trophic-level resistances as the environmental change level at which the first taxon for such trophic level is removed. Hence, the trophic-level resistance would coincide with the minimum taxon resistance across the trophic level.

This definition of resistance can be hence employed to establish conservative thresholds for the communities, ensuring that the species richness is not altered by the action of the environmental change. However, it may depend too much on outlier data, such us taxon with abnormally low tolerances.

An alternative definition of resistance, less influenced by the presence of extreme values, could then be environmental change level at which $x\%$ of the taxa are lost. For example, 50% of the taxa within a trophic level.

The usual predator-level resistance, corresponding to the less resistant predator, is (Eq. (A.12))

$$\begin{aligned}\left(\Omega_P^{-1}\right)_{(1)} =& \frac{1}{\frac{b}{m} - 1 - \frac{d}{m}\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta}} \left\{ \left\langle \frac{1}{\tau_V} \right\rangle + \frac{d}{m} \frac{1+(n_V-1)\,\alpha}{\lambda\,\eta} \left(\frac{1}{\tau_P}\right)_{(n_P)} \right. \\ & \left. + \frac{d}{m}\,\lambda\,\frac{n_P}{n_V} \left[\left(\frac{1}{\tau_P}\right)_{(n_P)} - \left\langle \frac{1}{\tau_P} \right\rangle \right] \right\}\end{aligned} \tag{A.31}$$

where the subindex (1) in $\left(\Omega_P^{-1}\right)_{(1)}$ represents that this is the resistance of the first predator affected, and the subindex (n_p) in $\left(\frac{1}{\tau_P}\right)_{(n_P)}$ denotes that this is the maximum reciprocal tolerance, so the last reciprocal tolerance if we ordered them in increasing order.

For higher stressor intensities, we would have a community of $n_P - 1$ predators and n_V prey (since predators are lost at smaller environmental change levels; Appendix A.4). From this point, the next species removed would be a also predator, so we can also use Eq. (A.12) for the remaining community,

$$\begin{aligned}\left(\Omega_P^{-1}\right)_{(2)} =& \frac{1}{\frac{b}{m} - 1 - \frac{d}{m}\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta}} \left\{ \left\langle \frac{1}{\tau_V} \right\rangle + \frac{d}{m} \frac{1+(n_V-1)\,\alpha}{\lambda\,\eta} \left(\frac{1}{\tau_P}\right)_{(n_P-1)} \right. \\ & \left. + \frac{d}{m}\,\lambda\,\frac{n_P-1}{n_V} \left[\left(\frac{1}{\tau_P}\right)_{(n_P-1)} - \left\langle \frac{1}{\tau_P} \right\rangle \right] \right\}.\end{aligned} \tag{A.32}$$

We can recursively employ the same algorithm until obtaining the environmental change level that removes 50% of the predator taxa

$$\begin{aligned}\left(\Omega_P^{-1}\right)_{50\%} \equiv \left(\Omega_P^{-1}\right)_{(n_P/2)} =& \frac{1}{\frac{b}{m} - 1 - \frac{d}{m}\frac{1+(n_V-1)\,\alpha}{\lambda\,\eta}} \left\{ \left\langle \frac{1}{\tau_V} \right\rangle + \frac{d}{m} \frac{1+(n_V-1)\,\alpha}{\lambda\,\eta} \left(\frac{1}{\tau_P}\right)_{(n_P/2)} \right. \\ & \left. - \frac{d}{m}\,\lambda\,\frac{1}{2}\frac{n_P}{n_V} \left[\left\langle \frac{1}{\tau_P} \right\rangle - \left(\frac{1}{\tau_P}\right)_{(n_P/2)} \right] \right\}.\end{aligned} \tag{A.33}$$

This 50% predator resistance depends on the average reciprocal prey tolerance, $\left\langle \tau_V^{-1} \right\rangle$, in the median of the reciprocal predator tolerances, $\left(\tau_P^{-1}\right)_{(n_P/2)} = \text{med}\left(\tau_P^{-1}\right)$, and in the bias of the predator recirpocal tolerances (the difference between the mean and the median).

A similar argument can be also employed to obtain the 50% prey resistance from Eq. (A.15),

$$\left(\Omega_V^{-1}\right)_{50\%} = \frac{1}{\frac{b}{m} - 1} \left\{ \left(\frac{1}{\tau_V}\right)_{(n_V/2)} - \frac{1}{2}\frac{n_V\,\alpha}{1-\alpha} \left[\left\langle \frac{1}{\tau_V} \right\rangle - \left(\frac{1}{\tau_V}\right)_{(n_V/2)} \right] \right\}. \tag{A.34}$$

This 50% prey resistance depends on the median of the reciprocal prey tolerances, and also on its bias.

B Estimation of model parameters of Typical Macroinvertebrate Food Web Assemblages

In section 2.4, we state that we derived typical macroinvertebrate communities from European river systems, based on the river types proposed by Lyche Solheim et al. (2019).

The details of the derivation of the composition of the typical communities are shown in (Jupke et al., 2022). We focused on those river types best represented by our samples. These were the river types R01–R05, R08–R11, R14–R16 and R18 from Lyche Solheim et al. (2019); and all other types were omitted from the analysis.

Furthermore, for each river type we defined typical assemblages (TA) of macroinvertebrates that consist of the taxa that occur frequently in the ecosystems of the respective river type. Moreover, we merged the TAs sharing more than 75% of their taxa, considering them as redundant. This resulted in 7 different TAs for stream macroinvertebrate communities in Europe (Tables F.2–F.8 from Appendix F; for further details of the derivation of these TAs, see Jupke et al., 2022).

Using this list of taxa belonging to each TA, we checked the GloBI database (Poelen et al., 2014) to assign trophic links between the taxa of the community assemblages. This also enabled us to classify the taxa as either prey (taxa not known to feed on other taxa of the community) or predators. To establish the strength of the interaction between taxa, we employed information about their traits, using the Tachet database (Tachet et al., 2000).

We set the interaction strength of two prey taxa to zero (i.e. absence of competition) if they were known to have clearly different food resources. To evaluate this, we computed for each pair of prey taxa the overlap of their food resources,

$$(\text{food overlap})_{i,j} \equiv \frac{\sum_k \mathcal{R}_{i,k}\,\mathcal{R}_{j,k}}{\sqrt{\left(\sum_k \mathcal{R}_{i,k}^2\right)\,\left(\sum_k \mathcal{R}_{j,k}^2\right)}}\,, \tag{B.1}$$

where $\mathcal{R}_{i,k}$ was obtained from the Tachet database, and represents the importance of each food resource k assigned to taxon i. When the food overlap of a pair of taxa is smaller than $\frac{1}{2}$, we considered them to feed on different enough resources, that they do not compete.

Then, among the pair of prey taxa that feed on similar resources, and hence compete, we estimated the competition strength from the difference in body size,

$$\alpha_{ij} = \frac{\omega_{\text{size}}}{\sqrt{2\,\sigma_{\text{size},i}^2 + 2\,\sigma_{\text{size},j}^2 + \omega_{\text{size}}^2}}\,\exp\left[-\frac{\left(\mu_{\text{size},i} - \mu_{\text{size},j}\right)^2}{2\,\sigma_{\text{size},i}^2 + 2\,\sigma_{\text{size},j}^2 + \omega_{\text{size}}^2}\right]\,, \tag{B.2}$$

with $\mu_{\text{size},i}$ the mean of the body size trait for prey taxon i, $\sigma_{\text{size},i}^2$ its variance, and ω_{size} was taken as $\frac{1}{2}$. Following this expression, the competition among two prey taxa decreases with difference in body sizes.

Regarding the trophic interactions, we only let λ_{ij} to be different from zero if in the GLOBI database prey taxon j is reported to be eaten by predator taxon i. In such cases, the attack rate is modulated considering the body size ratio of the prey and the predator taxa. Previous studies have shown an optimum ratio between the predator and prey body masses (Tsai et al., 2016), and since taxon body masses are related to their body size (Eklöf et al., 2017), there would be an optimum size ratio between prey and predators (Jonsson, 2014). For predator-prey relations between taxa with such an optimum body size ratio, we set an attack rate of $\lambda_{\text{opt}} = \frac{1}{2}$. However, for prey-predator pairs without an optimum body size ratio, we modulate the attack rate as

$$\lambda_{ij} = \lambda_{\text{opt}}\,\left[\frac{\mu_{\text{size},i}/\mu_{\text{size},j}}{\left(\text{size}_{\text{predator}}/\text{size}_{\text{prey}}\right)_{\text{opt}}}\,\exp\left(1 - \frac{\mu_{\text{size},i}/\mu_{\text{size},j}}{\left(\text{size}_{\text{predator}}/\text{size}_{\text{prey}}\right)_{\text{opt}}}\right)\right]^2\,. \tag{B.3}$$

In our numerical computations, we have set the optimal body size ratio as $\left(\text{size}_{\text{predator}}/\text{size}_{\text{prey}}\right)_{\text{opt}} = 4$.

Furthermore, since the analyzed TAs are located in river systems, we simulated the spatial dynamics within river-like spatial networks. With the OCNET package (Carraro et al., 2020) we generated random dendritic networks representing the rivers. These networks consist of a series of local nodes or patches, and links representing the water streams. In each patch we simulated the local dynamics employing the model and parameters already described, an we let the taxa disperse between patches. To model this dispersion, using the Tachet database (Tachet et al., 2000) we distinguished between flying and non-flying taxa. Flying taxa were able to move between each pair of nodes of the network, while non-flying taxa solely moved between connected nodes of the dendritic network. For all taxa, the dispersal rate from an initial node to another node was modulated by the inverse of the distance between them,

$$\mathrm{d}_{x\to y} = \mathrm{d}_0 \, \frac{\frac{1}{|x-y|}}{\sum_z \frac{1}{|x-z|}} \,, \tag{B.4}$$

where $|x-y|$ denotes the distance between the nodes x and y, d_0 is set to $\mathrm{d}_0 = \frac{1}{10}$. In this expression, the sum in the denominator represents either the sum across all nodes, for flying taxa; or the sum across all nodes connected to x, for non-flying taxa. Hence, the total dynamics equation for prey and predator species would read

$$\begin{aligned}
\frac{dV_i(x,t)}{dt} =& V_i(x,t) \left[b_i(x) - m_i(x) \left(1 + \frac{\xi}{\tau_{V_i}}\right) - \sum_{j=1}^{n_V} \alpha_{ij}(x)\, V_j(x,t) - \sum_{k=1}^{n_P} \lambda_{ik}(x)\, P_k(x,t) \right] \\
& - \sum_{y\neq x} d_{i,x\to y}\, V_i(x,t) + \sum_{z\neq x} d_{i,z\to x} V_i(z,t)\,, \\
\frac{dP_l(x,t)}{dt} =& P_l(x,t) \left[-d_l(x) \left(1 + \frac{\xi}{\tau_{P_l}}\right) + \sum_{j=1}^{n_V} \lambda_{jl}(x)\, \eta_{jl}(x)\, V_j(x,t) \right] \\
& - \sum_{y\neq x} d_{l,x\to y}\, P_l(x,t) + \sum_{z\neq x} d_{l,z\to x} P_l(z,t)\,.
\end{aligned} \tag{B.5}$$

Finally, since we want to study the effect of environmental change in these food web assemblages, we performed simulations with three different types of environmental change drivers: atrazine (as an example of a herbicide), imidacloprid (as an example of an insecticide), and copper (as an example of a metal). In the absence of any interaction between taxa, we assume that with higher environmental change level the taxon death rates increase, with a slope given by the inverse of the tolerances of the taxa. We obtained such taxon tolerances from hierarchical Species Sensitivity Distribution (hSSD) Models (for copper and imidacloprid: Jupke et al., 2024; for atrazine: Jupke, 2024).

C Analysis of sample data: differences across countries and environmental change levels

To analyze the effect of the environmental change intensity on the biodiversity of real data, we have analyzed 1315 samples of macroinvertebrates from France (Naïades database: `https://naiades.eaufrance.fr`), 1228 samples from UK (Freshwater river macroinvertebrate surveys (Biosys), `https://environment.data.gov.uk/ecology`), and 2993 samples from Germany (monitoring data from German federal states), from sites with different

impact levels of environmental change pressures. The classification of impact level of the different sampling sites was based on the use of their potentially flood-prone area (pfa) (Szöcs et al., 2017):

- we defined least impacted places as those sites with less than 10% of their pfa in agricultural or urban land use;
- sites with a medium impact level as those for which between 10% and 20% of the pfa are used agriculturally or as urban areas;
- and highly impacted sites as those with more than 50% of the pfa under agricultural or urban land use.

Samples from sites with 20–30% of their pfa under agricultural or urban land use were intentionally excluded to enhance the contrast between moderately and highly impacted areas. The data on land use were obtained from Lemm et al. (2021). For each of the sites, we have samples consisiting on records of the different macroinvertebrate taxa forming the community.

Moreover, again using the GLOBI database (Poelen et al., 2014), we classified the taxa present in each sites as prey or predator taxa. This allowed us to compare the diversity at each trophic level for sites with different environmental change levels.

Country was the most important predictor of richness within each trophic level (employing anovas Fox and Weisberg, 2019, $p < 2.2 \cdot 10^{-16}$ for both number of prey and predators). Richness was slightly higher in France than in the UK or Germany, possibly reflecting the latitudinal diversity gradient (Hillebrand, 2004), although differences in sampling protocols and analysis methods cannot be excluded. The level of estimated impact did not consistently affect prey richness ($p = 0.019$, but effects were either positive or negative depending on the country) but did decrease predator richness across all countries ($p < 2.2 \cdot 10^{-16}$). Sites with mid or high levels of environmental change contained 11% or 16% fewer predator species than least impacted sites, respectively. While these results are no empirical proof of our theoretical results, they do offer evidence of selection against communities with many predators.

D Prey extinction first

We consider a system with two prey species V_1, V_2 and one predator P governed by

$$\dot{V}_1 = \left[b_1 - \beta_1\xi - m_1\left(1 + \frac{\xi}{\tau_1}\right) - V_1 - \alpha_{12}V_2 - \lambda_1 P\right]V_1, \tag{D.1}$$

$$\dot{V}_2 = \left[b_2 - m_2\left(1 + \frac{\xi}{\tau_2}\right) - \alpha_{21}V_1 - V_2 - \lambda_2 P\right]V_2, \tag{D.2}$$

$$\dot{P} = \left[-d\left(1 + \frac{\xi}{\tau_P}\right) - P + \lambda_1 V_1 + \lambda_2 V_2\right]P. \tag{D.3}$$

Here V_i and P denote species densities, b_i are prey birth rates, m_i and d are baseline mortality rates, ξ is environmental stress intensity, τ_i and τ_P measure tolerance to stress, β_i controls stress sensitivity of prey birth rates, α_{ij} are interspecific competition coefficients, and λ_i are predator attack rates. Intraspecific competition coefficients have been scaled to one.

We first set $\beta_1 = \beta_2 = 0$, so stress acts only by increasing mortality, as in the main text. In this case, prey per-capita growth rates retain a positive constant term (b_i), whereas the predator has no intrinsic positive term and relies entirely on prey densities. As ξ increases, predator mortality grows linearly, while prey densities remain bounded by self-limitation. Therefore, there exists a finite threshold ξ_P^* at which the predator per-capita growth rate is negative for all feasible prey densities, implying predator extinction. At the same time, declining predator density relaxes predation pressure on prey, preventing prey extinction prior to predator loss.

We next set $\beta_2 = 0$ and allow $\beta_1 > 0$. Stress now reduces the intrinsic birth rate of prey 1 according to $b_1(\xi) = b_1 - \beta_1 \xi$. The per-capita growth rate of prey 1 at low density is approximately

$$g_1(\xi) \approx b_1 - \beta_1 \xi - m_1 \left(1 + \frac{\xi}{\tau_1}\right),$$

up to competition and predation terms. If β_1 is sufficiently large, $g_1(\xi)$ becomes negative at a stress level $\xi_1^* < \xi_P^*$, even accounting for predation release. In this regime, prey 1 goes extinct before the predator.

A sufficient condition for prey-first extinction is

$$\beta_1 > \frac{b_1 - m_1(1 + \xi_P^*/\tau_1)}{\xi_P^*},$$

where ξ_P^* is the predator extinction threshold when $\beta_1 = 0$. Thus, predator-first extinction is structurally enforced when stress affects mortality alone, whereas sufficiently strong stress sensitivity of prey birth rates can reverse the extinction order.

Fig. E.7 illustrates this result. As we increase the effect on one prey species' reproduction, that prey is lost at lower levels of stress. Note that we have made the other prey more competitive to highlight this effect.

E Supplementary Figures

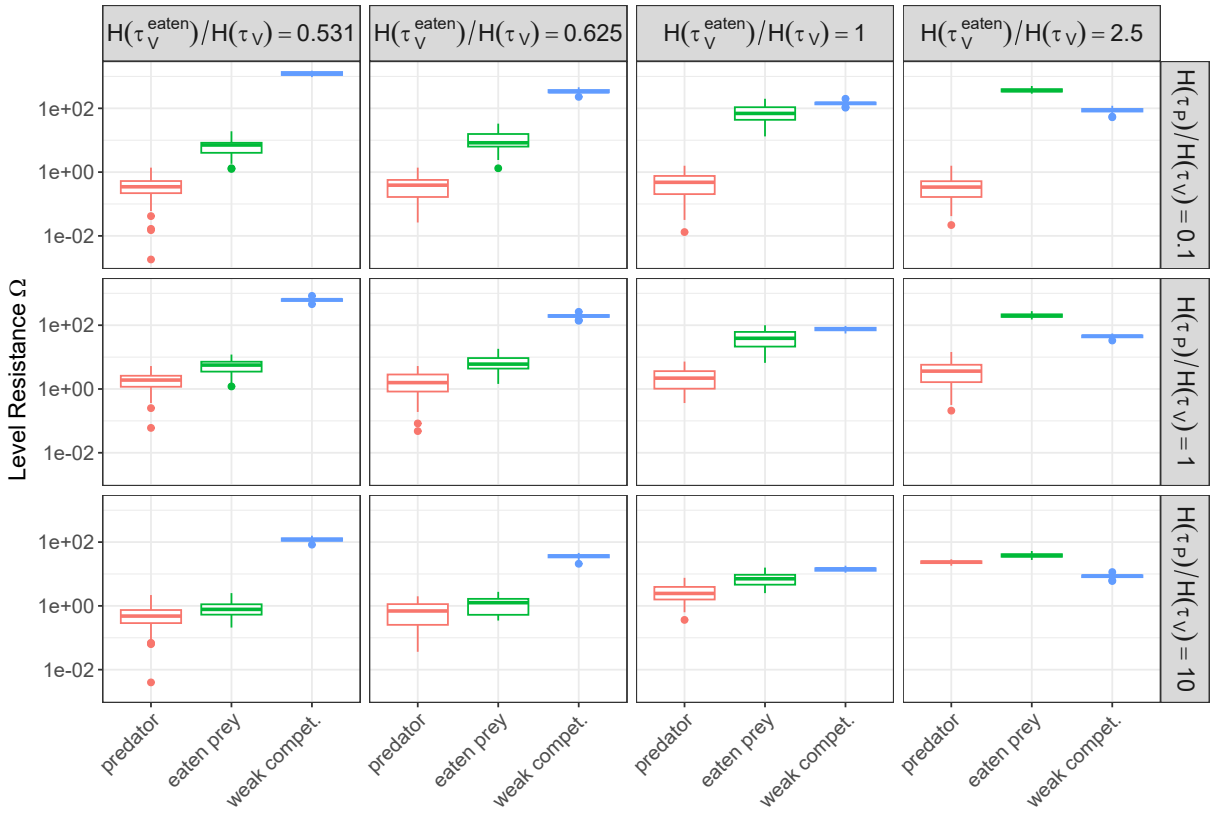

Figure E.1: Resistances of predators, prey and competitor taxa for food webs taxa within random communities with a predation–competition trade-offs. In these food webs, 5 specialist predators feed on 5 prey taxa. These 5 prey exert a high negative effect on 5 weaker competitors via inter-specific competition, while the effect of the weak competitors on the eaten prey is much smaller (mean $(\alpha_{\text{eaten prey,weak comp}}) = 16 \times \text{mean}\,(\alpha_{\text{eaten prey,weak comp}})$). Even if the predators are much more tolerant than their prey ($H(\tau_P)/H(\tau_V^{\text{eaten}}) = 10/0.531 \approx 18.8$, lower-left panel), predators are less resistant than either their prey or other taxa at the prey trophic level. However, when the weak competitors are much less tolerant than both the actually eaten prey and the predators (lower right panel), some of these weak competitors may be less resistant than the predators.

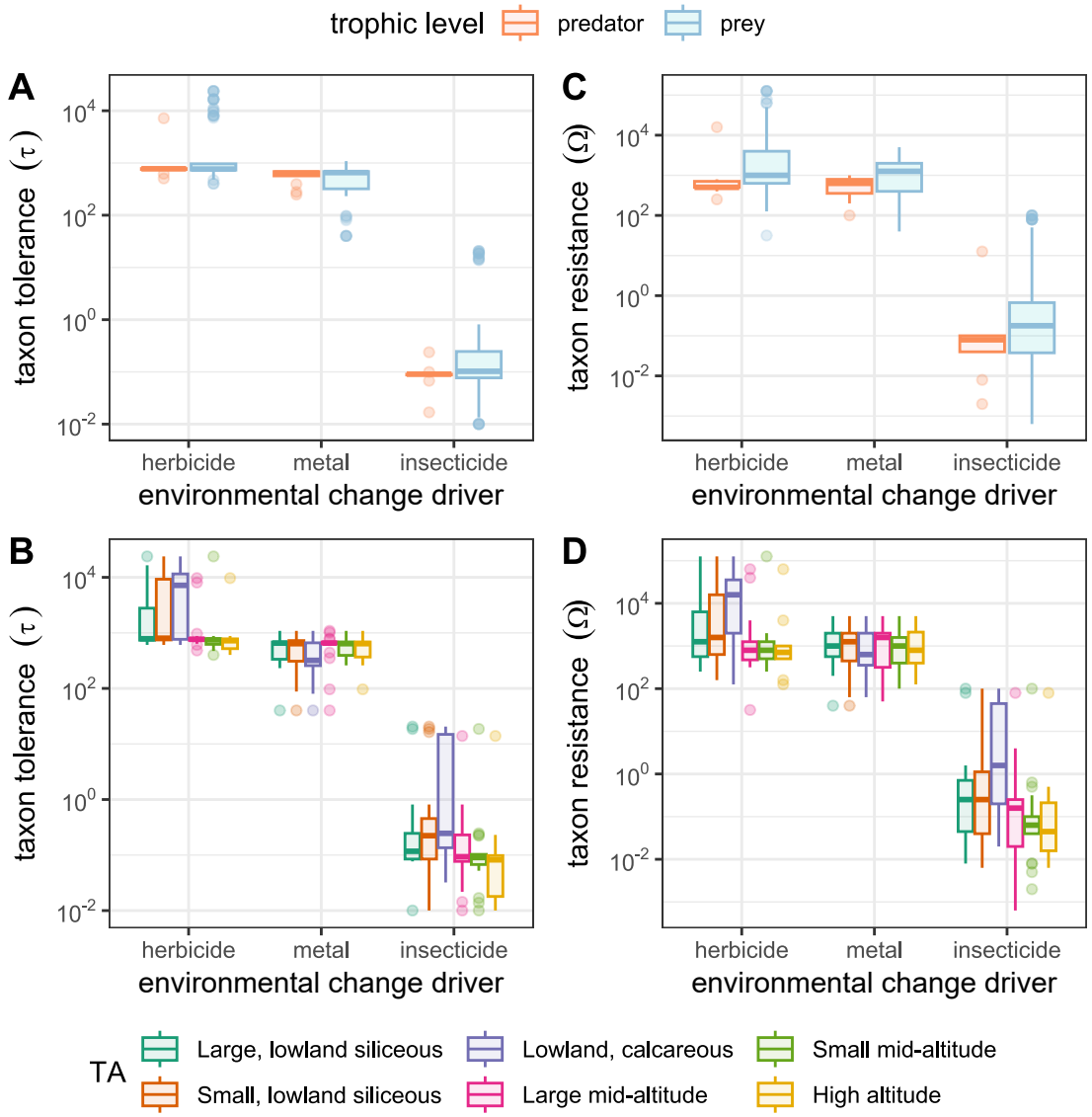

Figure E.2: **Taxon tolerances and resistances towards three different environmental change drivers of taxa from 6 typical food webs representative of macroinvertebrate riverine communities.** The selected typical food web assemblages (TA) were the derived assemblages containing at least one predator. Panel A) Tolerances as predicted by the hSSD models (King et al., 2015; Craig, 2013; Jupke et al., 2024) (that do not take into account taxon interactions) are similar between prey and predator taxa. For confirmation, we realized a type-II two-way ANOVA test `log(tolerance) ~ EnvChangeDriver * TrophicLevel`, using Anova function from car package (Fox and Weisberg, 2019) in R (R Core Team, 2023). The associated p-values were $< 2 \cdot 10^{-16}$ (driver), 0.131 (trophic level) and 0.242 (interaction driver:trophic level). I.e., taxon tolerances were not significantly affected by the predator level. Panel B) However, there exist significant differences in the taxon tolerances among the considered typical food web assemblages (after performing an analogous ANOVA test, the p-values were $< 2 \cdot 10^{-16}$ (driver), $2.2 \cdot 10^{-3}$ (TA) and 0.043 (interaction driver:TA)). Panel C) When taxon interactions are taken into account, our simulations suggest that predators tend to be less resistant than prey, confirming our analytical derivations (Eqs. (2, 3)). (p-values: $< 2 \cdot 10^{-16}$ (driver), 0.011 (trophic level) and 0.69 (interaction change driver:trophic level)). Panel D) There are also significant differences in the taxon resistances belonging to different assemblages (p-values: $< 2 \cdot 10^{-16}$ (driver), $2.0 \cdot 10^{-3}$ (TA) and 0.21 (interaction driver:TA)).

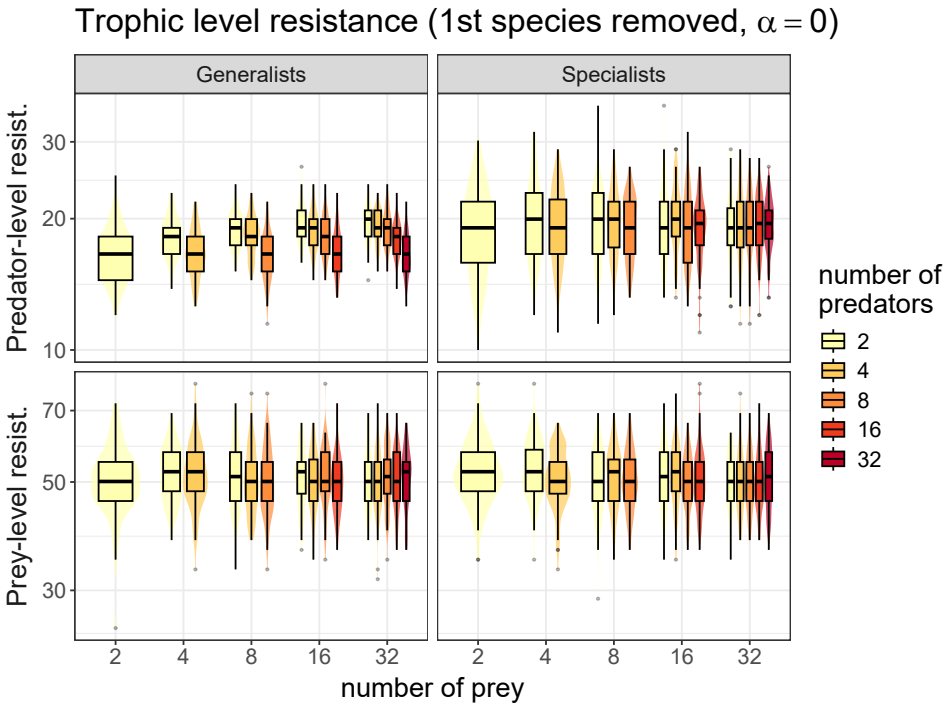

Figure E.3: **Predator-level and prey-level resistances for random communities, as function of the number of prey and predator taxa of the community, for the case without inter-specific competition among the prey** ($\alpha = 0$). The minimum and maximum tolerances within the trophic levels of the communities has been set as fixed, so they will not scale with the community size.

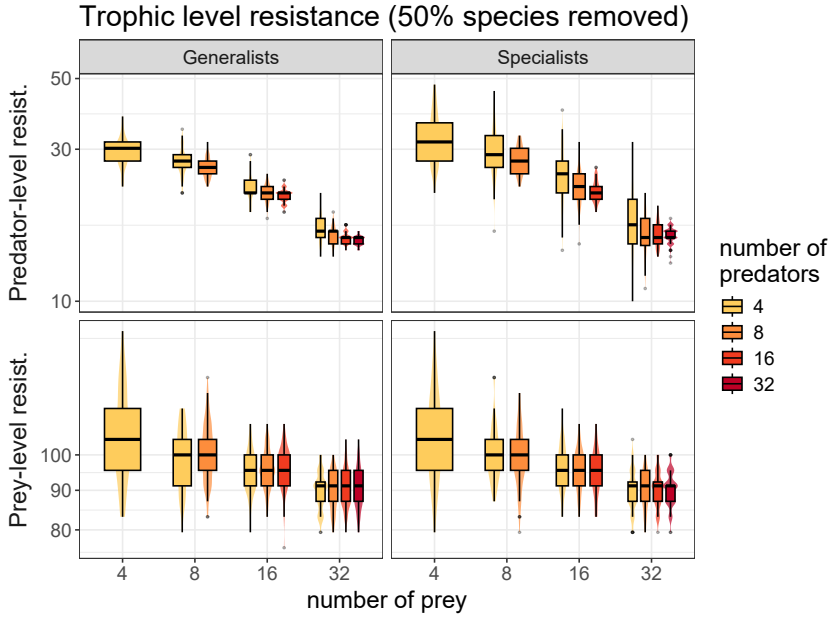

Figure E.4: **Predator-level and prey-level resistances for random communities, defined as the environmental change required to remove 50% of the taxa within the trophic level, as function of the number of prey and predator taxa of the community**. The minimum and maximum tolerances within the trophic levels of the communities has been set as fixed, so they will not scale with the community size.

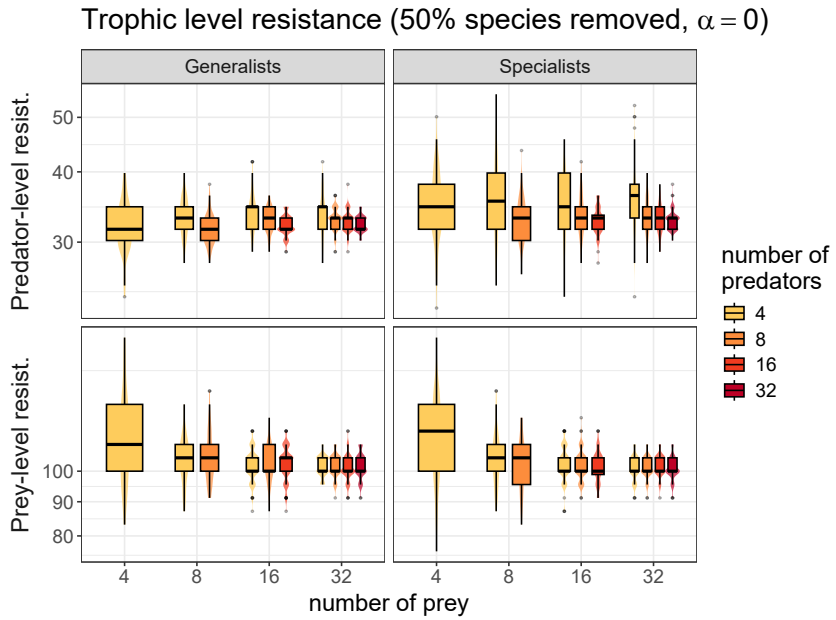

Figure E.5: **Predator-level and prey-level resistances for random communities, defined as the environmental change required to remove 50% of the taxa within the trophic level, as function of the number of prey and predator taxa of the community, for the case without inter-specific competition among the prey** ($\alpha = 0$). The minimum and maximum tolerances within the trophic levels of the communities has been set as fixed, so they will not scale with the community size.

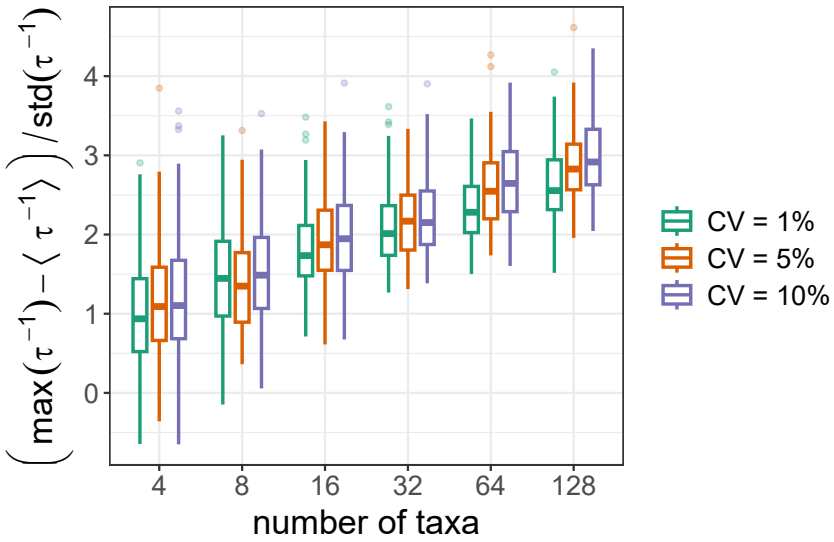

Figure E.6: Distance (in standard deviations) between the maximum reciprocal tolerance among n taxa and its population mean. The distance between the sample maximum and the population mean increases approximately with the logarithm of the sample size $\log n$, although substantial variability is observed. For the characteristic number of taxa considered in our analysis, this distance generally ranges between 0 and 4 standard deviations. We therefore adopt $\kappa = 3$ as as a representative value.

F Supplementary Tables

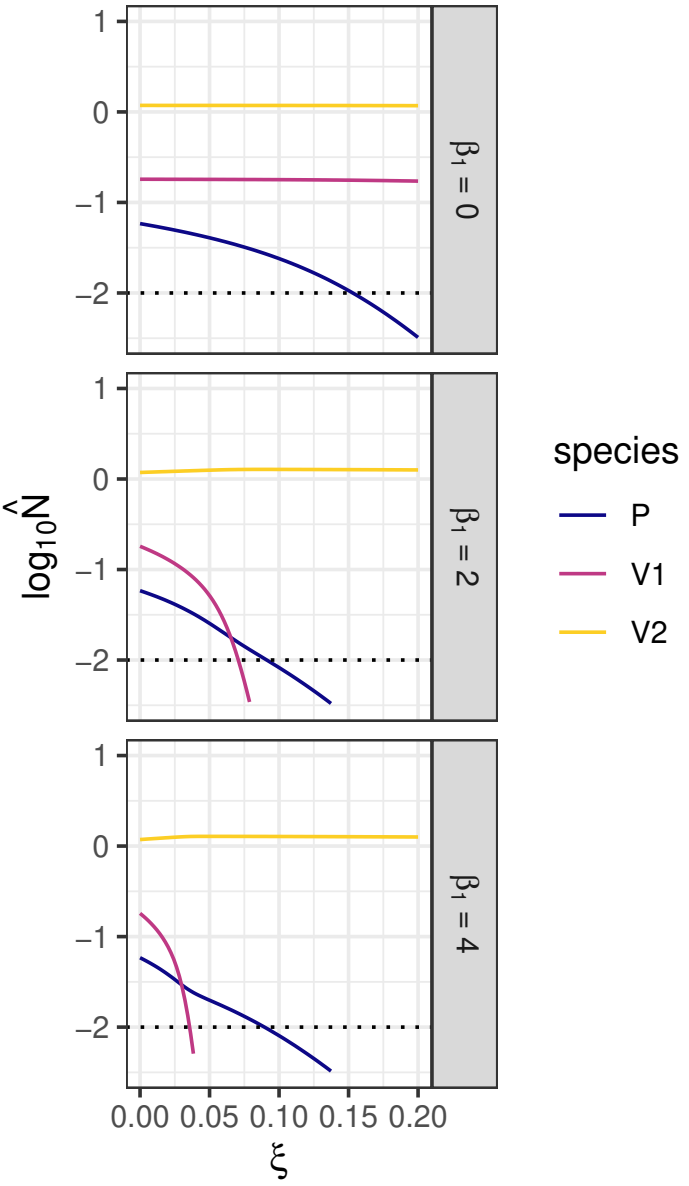

Figure E.7: Equilibrium log-abundances as a function of environmental stress ξ for a two-prey–one-predator system. Parameters are $b_1 = 1$, $b_2 = 1.5$, $m_1 = m_2 = 0.2$, $d = 0.35$, $\tau_1 = \tau_2 = \tau_P = 1$, $\alpha_{12} = \alpha_{21} = 0.5$, $\lambda_1 = \lambda_2 = 0.5$, with $\beta_2 = 0$ and $\beta_1 \in \{0, 2, 4\}$ (panels from top to bottom). When $\beta_1 = 0$, stress acts only through mortality and the predator is lost first. Increasing sensitivity of prey 1 birth rate to stress ($\beta_1 > 0$) reverses the extinction order, leading to prey 1 loss before predator extinction at sufficiently large β_1.

Parameter	Interpretation
n_V	Number of prey taxa.
n_P	Number of predator taxa.
V_i	Abundance of prey taxon i.
P_k	Abundance of predator taxon k.
b_i	Birth rate of prey i, in the absence of the environmental change.
m_i	Death rate of prey i, in the absence of the environmental change.
d_k	Death rate of predator k, in the absence of the environmental change.
α_{ij}	Interspecific competition strength between prey taxa i and j. By re-normalizing taxon abundances, we set $\alpha_{ii} = 1$ for all prey i.
λ_{ik}	Attack rate of predator k towards prey i.
η_{ik}	Efficiency of conversion of consumed biomass from prey i into new individuals of predator k.
τ_i	Tolerance of taxon i (either prey or predator). For equivalent taxa, τ_V and τ_P would represent the tolerance of prey and predators, respectively.
ξ	Environmental change level, which linearly increases the death rate of the taxa.

Table F.1: Parameters of the model.

Family	Genus	Taxa	Predator	Flying
Baetidae	Baetis	Baetis	FALSE	TRUE
Caenidae	Caenis	Caenis	FALSE	TRUE
Chironomidae	Average	Chironomidae	FALSE	TRUE
Heptageniidae	Heptagenia	Heptagenia	FALSE	TRUE
Hydropsychidae	Hydropsyche	Hydropsyche	FALSE	TRUE
Hydroptilidae	Hydroptila	Hydroptila	FALSE	TRUE
Average	Average	Jaera	FALSE	TRUE
Hydrobiidae	Potamopyrgus	Potamopyrgus	FALSE	TRUE
Corophiidae	Corophium	Chelicorophium	FALSE	FALSE
Gammaridae	Average	Dikerogammarus	FALSE	FALSE
Dreissenidae	Dreissena	Dreissena Polymorpha	FALSE	FALSE
Gammaridae	Echinogammarus	Echinogammarus	FALSE	FALSE
Gammaridae	Gammarus	Gammarus	FALSE	FALSE

Table F.2: Typical macro-invertebrate food web assemblage from very large rivers (river type R-01 from Lyche Solheim et al. (2019)).

Family	Genus	Taxa	Predator	Flying
Polycentropodidae	Polycentropus	Polycentropus	TRUE	TRUE
Rhyacophilidae	Rhyacophila	Rhyacophila	TRUE	TRUE
Planorbidae	Ancylus	Ancylus Fluviatilis	FALSE	TRUE
Baetidae	Baetis	Baetis	FALSE	TRUE
Chironomidae	Average	Chironomidae	FALSE	TRUE
Elmidae	Elmis	Elmis	FALSE	TRUE
Ephemerellidae	Ephemerella / Serratella	Ephemerella	FALSE	TRUE
Elmidae	Esolus	Esolus	FALSE	TRUE
Hydropsychidae	Hydropsyche	Hydropsyche	FALSE	TRUE
Lepidostomatidae	Lepidostoma	Lepidostoma Hirtum	FALSE	TRUE
Leuctridae	Leuctra	Leuctra	FALSE	TRUE
Elmidae	Limnius	Limnius	FALSE	TRUE
Hydrobiidae	Potamopyrgus	Potamopyrgus	FALSE	TRUE
Gammaridae	Gammarus	Gammarus	FALSE	FALSE
Lumbriculidae	Stylodrilus	Stylodrilus Heringianus	FALSE	FALSE

Table F.3: Typical macro-invertebrate food web assemblage from large, lowland siliceous rivers (river type R-02 from Lyche Solheim et al. (2019)).

Family	Genus	Taxa	Predator	Flying
Polycentropodidae	Polycentropus	Polycentropus	TRUE	TRUE
Rhyacophilidae	Rhyacophila	Rhyacophila	TRUE	TRUE
Planorbidae	Ancylus	Ancylus Fluviatilis	FALSE	TRUE
Baetidae	Baetis	Baetis	FALSE	TRUE
Chironomidae	Average	Chironomidae	FALSE	TRUE
Elmidae	Elmis	Elmis	FALSE	TRUE
Ephemerellidae	Ephemerella / Serratella	Ephemerella	FALSE	TRUE
Hydropsychidae	Hydropsyche	Hydropsyche	FALSE	TRUE
Elmidae	Limnius	Limnius	FALSE	TRUE
Hydrobiidae	Potamopyrgus	Potamopyrgus	FALSE	TRUE
Sericostomatidae	Sericostoma	Sericostoma	FALSE	TRUE
Simuliidae	Average	Simuliidae	FALSE	TRUE
Gammaridae	Gammarus	Gammarus	FALSE	FALSE
Physidae	Physa	Physa Fontinalis	FALSE	FALSE
Piscicolidae	Piscicola	Piscicola Geometra	FALSE	FALSE

Table F.4: Typical macro-invertebrate food web assemblage from small, lowland siliceous rivers (river type R-03 from Lyche Solheim et al. (2019)).

Family	Genus	Taxa	Predator	Flying
Glossiphoniidae	Glossiphonia	Glossiphonia	TRUE	FALSE
Planorbidae	Ancylus	Ancylus Fluviatilis	FALSE	TRUE
Baetidae	Baetis	Baetis	FALSE	TRUE
Caenidae	Caenis	Caenis	FALSE	TRUE
Elmidae	Elmis	Elmis	FALSE	TRUE
Ephemerellidae	Ephemerella / Serratella	Ephemerella	FALSE	TRUE
Elmidae	Limnius	Limnius	FALSE	TRUE
Hydrobiidae	Potamopyrgus	Potamopyrgus	FALSE	TRUE
Gammaridae	Gammarus	Gammarus	FALSE	FALSE
Tubificidae	Potamothrix	Potamothrix	FALSE	FALSE
Neritidae	Theodoxus	Theodoxus Fluviatilis	FALSE	FALSE

Table F.5: Typical macro-invertebrate food web assemblage from lowland, calcareous rivers (river types R-04 and R-05 from Lyche Solheim et al. (2019)).

Family	Genus	Taxa	Predator	Flying
Rhyacophilidae	Rhyacophila	Rhyacophila	TRUE	TRUE
Baetidae	Baetis	Baetis	FALSE	TRUE
Caenidae	Caenis	Caenis	FALSE	TRUE
Chironomidae	Average	Chironomidae	FALSE	TRUE
Heptageniidae	Ecdyonurus	Ecdyonurus	FALSE	TRUE
Elmidae	Elmis	Elmis	FALSE	TRUE
Ephemerellidae	Ephemerella / Serratella	Ephemerella	FALSE	TRUE
Elmidae	Esolus	Esolus	FALSE	TRUE
Hydropsychidae	Hydropsyche	Hydropsyche	FALSE	TRUE
Hydroptilidae	Hydroptila	Hydroptila	FALSE	TRUE
Leuctridae	Leuctra	Leuctra	FALSE	TRUE
Elmidae	Limnius	Limnius	FALSE	TRUE
Limoniidae	Limoniini	Limoniidae	FALSE	TRUE
Elmidae	Riolus	Riolus	FALSE	TRUE
Simuliidae	Average	Simuliidae	FALSE	TRUE
Gammaridae	Gammarus	Gammarus	FALSE	FALSE
Average	Average	Oligochaeta	FALSE	FALSE

Table F.6: Typical macro-invertebrate food web assemblage from large, mid-altitude rivers (river types R-08, R-10, R-11 and R-18 from Lyche Solheim et al. (2019)).

Family	Genus	Taxa	Predator	Flying
Limnephilidae	Halesus	Halesus	TRUE	TRUE
Perlodidae	Isoperla	Isoperla	TRUE	TRUE
Polycentropodidae	Polycentropus	Polycentropus	TRUE	TRUE
Rhyacophilidae	Rhyacophila	Rhyacophila	TRUE	TRUE
Glossosomatidae	Agapetus	Agapetus	FALSE	TRUE
Planorbidae	Ancylus	Ancylus Fluviatilis	FALSE	TRUE
Baetidae	Baetis	Baetis	FALSE	TRUE
Chironomidae	Average	Chironomidae	FALSE	TRUE
Elmidae	Elmis	Elmis	FALSE	TRUE
Heptageniidae	Heptagenia	Heptagenia	FALSE	TRUE
Hydraenidae	Hydraena	Hydraena	FALSE	TRUE
Hydropsychidae	Hydropsyche	Hydropsyche	FALSE	TRUE
Hydroptilidae	Ithytrichia	Ithytrichia	FALSE	TRUE
Leuctridae	Leuctra	Leuctra	FALSE	TRUE
Elmidae	Limnius	Limnius	FALSE	TRUE
Nemouridae	Protonemura	Protonemura	FALSE	TRUE
Sericostomatidae	Sericostoma	Sericostoma	FALSE	TRUE

Table F.7: Typical macro-invertebrate food web assemblage from small, mid-altitude rivers (river type R-09 from Lyche Solheim et al. (2019)).

Family	Genus	Taxa	Predator	Flying
Empididae	Average	Empididae	TRUE	TRUE
Rhyacophilidae	Rhyacophila	Rhyacophila	TRUE	TRUE
Baetidae	Baetis	Baetis	FALSE	TRUE
Chironomidae	Average	Chironomidae	FALSE	TRUE
Heptageniidae	Ecdyonurus	Ecdyonurus	FALSE	TRUE
Elmidae	Elmis	Elmis	FALSE	TRUE
Hydropsychidae	Hydropsyche	Hydropsyche	FALSE	TRUE
Leuctridae	Leuctra	Leuctra	FALSE	TRUE
Limnephilidae	Average	Limnephilidae	FALSE	TRUE
Limoniidae	Limoniini	Limoniidae	FALSE	TRUE
Nemouridae	Protonemura	Protonemura	FALSE	TRUE
Heptageniidae	Rhithrogena	Rhithrogena	FALSE	TRUE
Simuliidae	Average	Simuliidae	FALSE	TRUE
Average	Average	Oligochaeta	FALSE	FALSE

Table F.8: Typical macro-invertebrate food web assemblage from high-altitude rivers (river types R-14, R-15 and R-16 from Lyche Solheim et al. (2019)).