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Global change effects on the stability of food-web motifs

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“It's been a long road, getting from there to here. It's been a long time...”

– Diane Warren, Star Trek Enterprise Theme –

Summary

Global change affects ecosystems worldwide and has already caused a massive decline in the world's biodiversity. As the processes behind environmental change continue at ever-accelerating rates, this leads to a severe threat of ecosystem functioning, ecosystem services, and, in the end, human well-being. The most prominent drivers of global biodiversity loss are climate change, increasing nitrogen deposition, land-use change and biotic exchange. Their correlation with species extinctions has been documented in numerous studies some of which have identified the underlying mechanisms they operate on. However, it still remains difficult to predict the exact effects of specific drivers of environmental change on populations. This makes it hard to identify particularly endangered species and to develop adequate conservation strategies.

In my thesis, I focus on small-scale effects of global-change drivers on single individuals or populations. I use bioenergetic modelling to show how these low-level effects scale up to higher levels of ecological organisation and influence the stability of food-web motifs. Finally, I provide experimentally testable hypotheses on environmental-change effects and their compensation. Throughout the research chapters of my thesis, I study the effect of different environmental-change drivers on the stability of different trophic motifs.

In Chapter 2, I focus on single consumer-resource interactions and how environmental warming influences their stability. The relationship between temperature and species' biological rates (metabolism, growth and feeding) is well-known from empirical warming experiments. However, their interactive effects on the stability of consumer-resource systems are still under debate. I show that warming leads to dynamic stabilization of biomass oscillations. These results are based on an extensive literature research about temperature scaling of metabolism, feeding rates and maximum population size. Implementing these relationships into a generalized bioenergetic model yields information on the dynamical consequences of the different scaling relationships. The vast majority of possible parameter combinations predicts a dynamic stabilization of consumer-resource interactions at the risk of predator starvation. Consequently, this is tested in a microcosm experiment using bacterial prey (*Pseudomonas fluorescens*) and a cilliate predator (*Tetrahymena pyriformis*). Time-series analyses of these experiments confirmed the hypothesis of warming leading to an increased population stability while, at the same time, undermining species diversity.

In Chapter 3, I investigate the effect of nutrient enrichment which has been reported to induce unstable dynamics in consumer-resource systems. The resulting oscillations have been shown to endanger species persistence in trophic systems of low complexity.

However, in more complex natural systems this effect seems to be dampened which indicates that some intrinsic properties of complex systems prevent unstable dynamics. Identifying these “ecosystem buffers” is crucial for our understanding of the stability of ecosystems and an important tool for environmental and conservation biologists. Earlier theoretical studies suggested that this stabilization might be caused by so-called “weak interactions”. However, their relevance has rarely been tested experimentally. I use network and allometric theory for an *a-priori* identification of species that buffer against externally induced instability of increased population oscillations via weak interactions. Afterwards, the hypotheses are tested in a microcosm experiment using a soil food-web motif. I show that large-bodied species feeding at the food web's base, so called “trophic whales”, can buffer ecosystems against unstable dynamics induced by nutrient enrichment.

In Chapter 4, I investigate the combined effects of habitat fragmentation and nutrient enrichment as they occur under increasing land-use intensity. Moreover, this chapter tackles the challenges of an integrative ecological theory on how different drivers of global change interact. I thus study the combined effects of habitat isolation and nutrient enrichment on the stability of a tri-trophic food-chain. Therefore, I expand bioenergetic models towards spatially explicit systems of two habitat patches using empirically-derived allometric scaling relationships of animal migration. I find that extinctions that occur at high levels of habitat fragmentation are caused by reduced bottom-up energy supply. Thus, conservation activities that focus only on single species might not prevent biodiversity loss if they ignore the respective lower trophic levels. The starvation effects of isolation are counteracted by nutrient enrichment which increases energy fluxes along the food chains. Thus, habitat isolation stabilizes eutrophic systems but undermines species diversity in oligotrophic systems.

The three research chapters provide good examples of how a generalized bioenergetic modelling approach provides an in-depth understanding and can generate testable hypotheses on the behaviour of simple trophic systems under global change. The general findings are combined and discussed in the Synopsis which also provides a categorization of environmental stressors according to their respective influence on ecosystem stability. The Synopsis elucidates the interplay of multiple environmental stressors and how their combined effects endanger biodiversity. In an ever changing world, our understanding of ecosystem processes and their underlying mechanisms is of striking importance. This conceptual work will foster future research by (1) applying general modelling tools to investigate the effects of different environmental stressors, (2) testing the generated hypotheses in experimental systems, and (3) synthesizing the findings according to their respective influence on systems stability. Furthermore, it will contribute to new and well-founded conservation approaches.

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Ecological stability in response to warming

Katarina E. Fussmann†, Florian Schwarzmüller†, Ulrich Brose, Alexandre Jousset and Björn C. Rall

†These authors contributed equally to this work.

K.E.F., U.B., B.C.R. and A.J. designed the microcosm experiment. K.E.F. conducted the experiments. Statistical procedures on time series and functional responses were carried out by B.C.R. and K.E.F.. B.C.R analysed the database. F.S. wrote and analysed the bioenergetic model. All authors contributed to the manuscript.

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Chapter 3

'Trophic Whales' as Biotic Buffers: Weak Interactions Stabilize Ecosystems against Nutrient Enrichment.

Florian Schwarzmüller, Nico Eisenhauer and Ulrich Brose

F.S., N.E. & U.B designed the experiment; F.S. did the modelling and the experimental work; F.S. & U.B. analysed the data; F.S., N.E. & U.B. wrote the manuscript.

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Chapter 4

Energy fluxes in fragmented ecosystems: dynamic stability of tri-trophic food chains under nutrient enrichment and habitat isolation

Florian Schwarzmüller and Ulrich Brose

F.S. & U.B designed the experiment; F.S. did the modelling and analysed the data;
F.S. & U.B. contributed to the manuscript.

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Part I

General Introduction

Chapter 1

Introduction

1.1 Aims and scope of this thesis

The world's biodiversity is at risk as global change influences ecosystems worldwide (Pimm *et al.* 1995; Sala *et al.* 2000; Dirzo *et al.* 2014). Several reviews over the last two decades reported a massive decline in biodiversity; the so-called sixth wave of mass extinction (Barnosky *et al.* 2011), associated with drivers of environmental change such as climate warming, increased nitrogen deposition, land-use change, biotic exchange and an increased atmospheric CO_2 level. Already 15 years ago, Sala and colleagues (Sala *et al.* 2000) identified these five processes as the main drivers of current and future biodiversity loss. Furthermore, in 2005, the Millennium Ecosystem Assessment (Millenium Ecosystem Assessment 2005) predicted an even more rapidly increasing impact over the next decades. This decrease in species numbers, of course, has a tremendous effect on the stability of ecological communities and yet unknown consequences for the functioning of ecosystems and their services for human well-being (Dirzo *et al.* 2014). The changes within ecological communities might even exceed the predictions as these drivers often occur in combination. Warming, for example, is often associated with a reduction in suitable habitat (Eklöf, Kaneryd & Münger 2012) or the range shift of species leading to the invasion of other ecosystems (Lurgi, López & Montoya 2012a). However, some studies also suggested compensating effects between the different effectors. Increased metabolic demands of a species due to warming might, in some cases, be compensated by an increased nutrient availability via enrichment (Binzer *et al.* 2012).

Although the number of studies on global change effects on ecosystems is high and still increasing, we are still far from a profound knowledge of how environmental stressors endanger biodiversity. This is mainly because of two reasons: first, most studies only report changes in species numbers or their abundances without a mechanistic understanding of how and why they occur; and second, studies that took a more mechanistic approach often look at the level of populations or individuals, and not at the community level. Moreover, despite the urgency of the matter and the expected severe extent to which important ecosystem services might change, studies looking at more than one environmental stressor are still scarce (O'Gorman, Fitch & Crowe 2012). In particular, when it comes to the interactive influence of multiple stressors on ecosystem stability, we are still lacking an integrative ecological theory. This, however, is crucial to estimate the status of ecosystems and, more importantly, to predict what might happen during the next decades (Lurgi, López & Montoya 2012b).

Theoretical Ecology and ecological modelling have often been suggested as stepping stones bridging the gap between small-scale experiments and large-scale observations (Brose 2010). By integrating the knowledge obtained by small-scale experiments into biologically sound models, these can be used to predict the effect of global change on more complex systems (Brose *et al.* 2012).

Throughout this thesis I present a way of conceptualizing the effect of environmental stressors and their interactions on the stability of ecosystems. I thus address the effect of three of the most important drivers of global biodiversity loss: global warming, nutrient enrichment and habitat fragmentation. Additionally, in chapter 3, I also investigate the effect of introducing an additional trophic interaction to a food-web motif. I do this using an integrative model that is parametrised using empirical data, in combination with mesocosm experiments to validate the findings.

In this introduction I first review some of the reported effects of environmental change drivers on ecosystems and the species they contain as well as on between-species interactions. I then introduce the tools I use during this thesis: a bioenergetic model on trophic interactions that is expandable to model environmental changes and the concept of food-web motifs. Finally, I give a short introduction to different aspects of stability which are the response variables throughout this thesis.

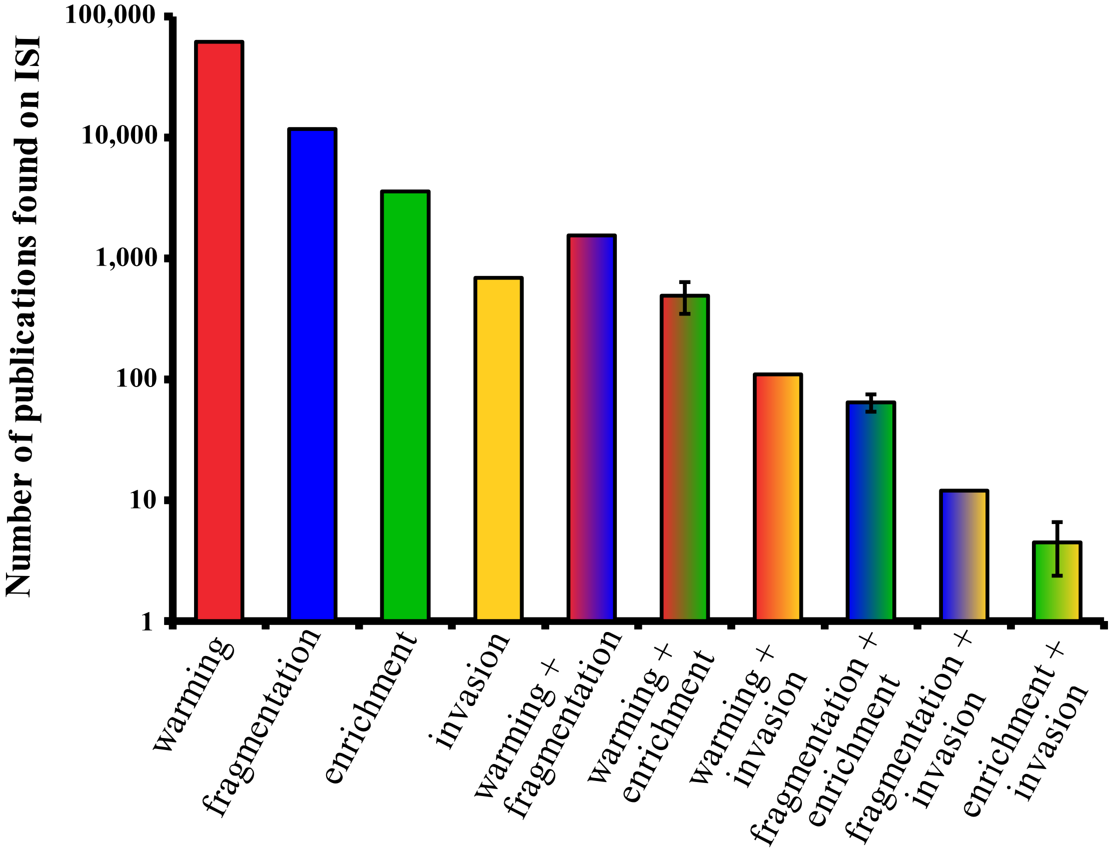

Figure 1.1 *Number of publications on the different drivers of global change published between 2000 and December 2014. Numbers are based on a search in the ISI Web of knowledge database for the research topics "environmental sciences, ecology", "biodiversity, conservation", and "zoology". The respective search terms were:* ***warming:*** *"warming" OR "climate change";* ***fragmentation:*** *"land use change" OR "habitat fragmentation";* ***enrichment:*** *"nutrient enrichment" OR "nitrogen deposition"; and* ***invasion:*** *"species invasion" OR "biotic exchange". Error bars result from an altered order of search terms.*

1.2 Temperature effects on ecosystems

Climate change and environmental warming are by far the most discussed aspects of global change (see Fig. 1.1). Over the last 100 years, mean annual temperatures have increased between 0.3 and 0.6 °C (McCarty 2001) and they are predicted to increase by another 1.1 to 6.4 °C by the end of this century (IPCC 2007). Along with changes in the mean annual surface temperature, the Intergovernmental Panel on Climate Change (IPCC) predicts changes in precipitation patterns; a global sea-level rise; and an increased frequency of so-called extreme events like wild fires, floods or droughts

(Easterling *et al.* 2000). Though extreme events have been reported to have a striking influence on ecological communities (Ciais *et al.* 2005; Holmgren *et al.* 2006), the increase in global temperature alone will affect species, their interactions and the ecosystems they inhabit (Parmesan 2006). Climate change ecologists have documented three major responses to increasing mean annual surface temperature: latitudinal and altitudinal range shifts of species (Parmesan *et al.* 1999; Walther *et al.* 2002; Parmesan & Yohe 2003; Walther 2010); an advancement of spring events and resulting changes in the demography of species (Root *et al.* 2003; Edwards & Richardson 2004); and selection towards small-bodied species in warmed ecosystems (Daufresne, Lengfellner & Sommer 2009; Gardner, Heinsohn & Joseph 2009; Gardner *et al.* 2011; Sheridan & Bickford 2011).

Current warming, for example, has already caused a latitudinal and altitudinal range shift of species by 6.1 km per decade towards the poles or 6.1 metres per decade upwards in altitude (Parmesan & Yohe 2003). This has dramatically changed ecosystem composition and will, in the long run, lead to lower global biodiversity (Lurgi *et al.* 2012a; Galiana *et al.* 2014). Moreover, increasing temperature, especially in the winter months, has also led to an advancement of spring events in species life cycles (2.3 days per decade according to (Parmesan & Yohe 2003)). Both temporal and spatial shifts have strong impacts on interspecific interactions, especially when there is asynchrony of species responses (Montoya & Raffaelli 2010). This has been shown for most types of interactions including plant-pollinator (Memmott *et al.* 2007), plant-herbivore (Visser, te Marvelde & Lof 2012), and multi-trophic interactions (Edwards & Richardson 2004; Both *et al.* 2009). The third major response, the changes in mean population body sizes, were reported to lead to changes in interaction strengths or even to a complete rewiring of trophic networks if they are associated with changes in prey preference (Petchey, Brose & Rall 2010; Jochum *et al.* 2012; Lurgi *et al.* 2012b).

On top of this, there are additional consequences of environmental warming that affect all species across ecosystem borders and taxonomic groups. Those are changes in their biochemical rates. Especially in ectotherms, increased temperature leads to an increase in cell metabolism (Gillooly *et al.* 2001) which, in turn, influences species traits such as respiration rates, population growth and feeding rates (Savage *et al.* 2004; Brown *et al.* 2004; Ehnes, Rall & Brose 2011; Rall *et al.* 2012). Although these occur on the level of individuals (respiration and feeding) or populations (growth) they ultimately influence species interactions and even ecosystem stability (Vasseur & McCann 2005; Fussmann *et al.* 2014). Increased respiration, for example, will lead to a higher energetic demand and therefore to shrinking population sizes (Meehan 2006). In contrast, recent studies also predicted higher maximum feeding rates, which could result in higher energy uptake and thus growing populations (Vucic-Pestic *et al.* 2011; Rall *et al.* 2012). However, the increase in energy uptake is estimated to be lower than the increase in metabolic demands (Fussmann *et al.* 2014). Ultimately, this will lead to simpler food webs with less trophic levels (Petchey *et al.* 1999) but exact predictions on the food-web level are complicated as warming might take effect gradually and indirectly (Brose *et al.* 2012).

1.3 Nutrient enrichment and its consequences for biodiversity

Studying the relation between a system's biodiversity and its nutrient status goes back to the middle of the 20th century. In 1959, G.E. Hutchinson raised one of the major questions of modern ecological research. He pointed out that till that date, there had been no conceptional explanation of the world's biodiversity, how it evolved and why it should be stable (Hutchinson 1959). It took more than 30 years until Tilman came up with a hypothesis for the diversity of plant communities that was based on the ability to acquire limiting nutrients (Tilman 1982). He argued that with one type of nutrients in the system, the species that will exploit it best will competitively exclude all other species. Therefore, the number of species should be equal to the number of nutrient sources. A few years later, he extended his approach saying that if species have more than one limiting nutrient and if there is a trade-off in the ability of acquiring one nutrient versus the other, the number of coexisting species can be higher if the levels of the respective nutrients is low (Tilman & Pacala 1993). Although other processes like temporal and spatial heterogeneity (Tilman & Pacala 1993) or the presence of shared predators (Brose 2008) have been identified to foster biodiversity, the relationship nutrient limitation and a high biodiversity remains (Vitousek *et al.* 1997; Foster & Gross 1998; Leibold 1999; Suding *et al.* 2005).

Not only do species differ in their ability to obtain nutrients but whole ecosystems are shaped by the relative availability of key resources (Smith, Tilman & Nekola 1999). Terrestrial ecosystems, for example, are mostly limited by the availability of nitrogen (Tilman & Pacala 1993) whereas in aquatic ecosystems phosphorous is the most limiting nutrient (Leibold 1999). These two types of ecosystems also differ in the way they are affected by global change. While terrestrial ecosystems are affected by the direct deposition of fertilizers and an increased fixation rate of atmospheric nitrogen (Bobbink, Hornung & Roelofs 1998), phosphorous levels of aquatic ecosystems are raised by an increased riverine input of fertilizer and by extensive aquaculture (Bonsdorff *et al.* 1997).

Nutrient enrichment undermines biodiversity not only via competitive exclusion (Tilman 1982) but also in various other ways. In aquatic ecosystems, for example, nutrient input causes massive algal blooms which, in turn, lead to hypoxia (Breitburg 2002). Nutrient enrichment has also been reported to alter the relation of bottom-up and top-down processes in multi-trophic systems (Jochum *et al.* 2012; Shurin *et al.* 2012), having dramatic influence on the dynamics of food chains (Otto, Rall & Brose 2007; Binzer 2013) and entire food webs (Binzer *et al.* 2012). This has been extensively studied in predator-prey systems where theoretical and empirical studies have found an increase of predator biomasses along with a decrease in system stability, a process known as the “paradox of enrichment” (Rosenzweig 1971; McCann, Hastings & Huxel 1998; Fussmann *et al.* 2000; Rall, Guill & Brose 2008; Schwarzmüller, Eisenhauer & Brose 2014).

1.4 Land-use change – ecosystem change

Changes in land-use intensity as a consequence of human population growth and an increased need for food, fibre and water will shape our planet's future surface (Foley *et al.* 2005). The conversion of remaining natural habitat and the intensified use of already transformed land will thereby lead to a decline in species diversity (Brooks *et al.* 2002; Foley *et al.* 2005). Although low-intensity agriculture increases habitat variability and, as a consequence, leads to higher biodiversity (Tscharntke *et al.* 2005), the nowadays very common high-intensity use of agricultural land has led to a massive decline in species numbers (Brooks *et al.* 2002). This, in turn, threatens the functioning of important ecosystem services such as plant pollination and biological pest control (Tscharntke *et al.* 2005). Moreover, intensively-used ecosystems show disturbed functioning in terms of energy fluxes as well as lowered resilience (Barnes *et al.* 2014). Various processes in intensively-used ecosystems are responsible for this loss in diversity and functioning: focusing on monocultures and the use of pesticides lower both plant and animal diversity; drainage lowers landscape-level water tables; and expanding agricultural area leads to loss and fragmentation of natural habitats (Tscharntke *et al.* 2005; Leuschner *et al.* 2014). In particular, the latter has recently attracted attention and has been studied in more detail. A remarkable review by Fahrig disentangled the relatively vague concept of habitat fragmentation into the two-fold process of habitat loss and "habitat fragmentation *per se*", which is the breaking-apart of habitats into smaller fragments (Fahrig 2003). The difference lies in the resulting landscape structures: habitat loss decreases the overall habitat size and the number of habitat patches, and increases patch isolation; habitat fragmentation *per se* does not necessarily reduce habitat size but leads to a higher number of smaller patches which decreases landscape-level isolation (Fahrig 2003). Habitat loss is strongly correlated with lower population sizes, a decline in species numbers and simpler interaction networks (Hagen *et al.* 2012). Effects of habitat fragmentation *per se* are generally weaker and can be either negative or positive (Fahrig 2003; Cooper, Li & Montagnes 2012) depending on patch quality, the hostility of the surrounding matrix, as well as species characteristics (Hagen *et al.* 2012).

1.5 Interactions between multiple stressors

Already by looking at the presented single effects of the most prominent stressors, the different ways in which global change influences the world's ecosystems are quite complex. However, the overall picture becomes even more complicated as these stressors only rarely occur in isolation (O'Gorman *et al.* 2012). Despite this, the number of studies that look at combined stressor effects is comparably low. According to a literature search (Fig 1.1), only about 1% of the studies on one stressor consider the influence of a second. The number of studies investigating respective three-way interactions is below 10 for all possible combinations.

There are generally two ways in which multiple stressors might co-occur. First, one of the stressors might cause the other one. Second, they might occur independently from each other but still influence the ecosystem and the species therein interactively. I will hereafter list some examples from the first category.

Global warming and the accompanying changes in precipitation patterns will cause floods and desertification (IPCC 2007). These will destroy natural habitats and lead to increased habitat fragmentation (Easterling *et al.* 2000; Ciais *et al.* 2005). Higher run-off from agricultural fields due to more frequent flodding events will also lead to stronger nutrient input into aquatic systems (Smith *et al.* 1999; Van De Pol *et al.* 2010). Moreover, warming of soil and water surface will increase microbial activity and fixation of airborne nitrogen. Warming also leads to more pronounced stratification of water bodies (O'Reilly *et al.* 2003) and thus strengthens the effects of enrichment-caused hypoxia (Shurin *et al.* 2012). Finally, latitudinal and altitudinal shifts in species ranges due to environmental warming will augment the probability of invasions into ecosystems at higher altitudes and latitudes (Lurgi *et al.* 2012a). Warming thus can have many secondary effects on ecosystems by causing other stressors.

Nutrient enrichment will lead to competitive exclusion of rare species and thus cause their retreat into small and fragmented habitat remnants (Tilman & Pacala 1993). Moreover, changes in nutrient status will amplify invasion success (Davis, Grime & Thompson 2000; Tilman 2004).

Land-use change can have secondary effects on ecosystems by changing habitat structure. This can reduce ground shading and thus alter microclimates (Foley *et al.* 2005), ultimately leading to the opening of ecological niches for possible invasion by exotic species (Tscharntke *et al.* 2005).

The resulting combined effect of multiple stressors on species in an ecosystem, whether they are caused by one another or occur independently, was subject to some recent studies. There were reports on simple additive, synergistic (more than just additive) and even compensatory effects of multiple stressors (O'Gorman *et al.* 2012). As an example for synergistic effects, Eklöf and colleagues reported that warming increased migration rates in a fragmented system (Eklöf *et al.* 2012). This, in turn, led to a stronger effect of fragmentation and in the end a higher mortality than predicted from single effects of warming and fragmentation alone. Compensatory effects between two stressors, for example, were found in two studies that looked at the combined effect of nutrient enrichment and warming in aquatic systems (Shurin *et al.* 2012) and food-web models (Binzer *et al.* 2012). They both found that a higher nutrient supply could compensate for the stronger need for energy in warmed systems.

However, studies that investigate more than one stressor and their potential interactions are still scarce and we are lacking data as well as a theoretical framework to come up with predictions on their future importance (Lurgi *et al.* 2012b). In the following, I will present a potentially useful tool that might bridge the gap between current ecological theory and the challenges that ecologists face in an ever-changing world.

1.6 Consumer-resource models

The previous paragraphs have shown that global change effects on ecological systems are numerous and diverse, and that they act on different levels of ecological organisation. This yields a lot of challenges for their predictability and consequently also for designing possible management strategies (Tylianakis *et al.* 2008). The presented empirical studies on these effects, however, provided data that can be used to build ecological models which, in turn, lead to a deeper understanding of global change effects. I will now briefly introduce a model that depicts trophic interactions between species, and that can also be parametrised to mimic changes in the environment.

The first ideas

The history of modelling species interactions as pairs of predator and prey or consumer and resource goes back to the beginning of the last century. In the 1920s, Lotka and Volterra (Lotka 1925; Volterra 1926) independently came up with a model that was able to describe the dynamics of predator and prey populations based on three empirically measurable parameters: the birth rate of the prey, the death rate of the predator and the feeding rate of the predator on the prey. Writing the model in a general form yields

$$\dot{R}=G\cdot R-F\cdot CR \qquad \text{(1.1), and}$$

$$\dot{C}=\varepsilon\cdot F\cdot CR-M\cdot C \qquad \text{(1.2),}$$

where $\dot{R}$ and $\dot{C}$ are the changes of the respective resource (*R*) and consumer populations (*C*) over time, *G* is the growth term of the resource (for example a birth rate), *M* is the mortality term of the consumer (death rate), and *F* represents the feeding rate of the consumer on the resource. The factor ε scales between zero and one and gives the efficiency of the predator in converting eaten prey individuals into own biomass.

In the original form, the Lotka-Volterra model looked at changes in numbers of individuals and suggested constant growth, death and feeding rates, which implies consumer-resource dynamics which are called neutrally stable. This means that the densities of the two populations will constantly oscillate with amplitudes that depend not only on the parameter values *G*, *F* and *M* but also on the initial values of *R* and *C*. Small changes in one of the populations will therefore shift the whole system to a new state with different oscillations. This has been regarded as being unrealistic for biological systems that seem to be more or less resilient against small perturbations (May 1972; Holling 1973).

Logistic growth

Since the development of the first models, the level of sophistication of model parameters has been increased quite drastically by incorporating more and more aspects of biological reality (Berryman 1992). The first change suggested to the original model was that the growth term *G* should not be constant but dependent on the resource density. The idea of a population limiting its own growth was already well established in the literature and is known as the logistic growth function (Malthus 2008). Applying it to consumer-resource theory, the growth term of the resource can be written as

$$G=r\left(1-\frac{R}{K}\right) \qquad (1.3),$$

with *r* being the maximum growth rate and *K* the maximum resource density or carrying capacity that is limiting growth. Implementing this self-limitation leads to a resource growth that is maximized at low densities and reaches zero at the carrying capacity. In consequence, the two-equation system becomes what is called non-excitable. Although every increase in consumer population leads to higher feeding (see eqn. 1.1 and 1.2), the consequently reduced resource density again fosters growth. The system therefore reaches a stable equilibrium after small disturbances. Although the assumption of logistic resource growth has been criticised for being too simple (Thomas, Pomerantz & Gilpin 1980), it has good empirical support and captures the dynamics of many single-species populations (Gause 1934; Allee 1949). Nevertheless, there have been suggestions for considering a higher level of complexity by adding explicit nutrient dynamics (Brose, Berlow & Martinez 2005a; b) comparable to those used in theoretical plant ecology (Tilman 1982; Huisman *et al.* 2001).

The functional response

The next step in the history of consumer-resource models was the implementation of a prey-density-dependent feeding rate (Rosenzweig & MacArthur 1963). This was motivated by empirical findings, that the predation risk of a prey individual changes with changing prey density (Holling 1959a). Holling found that changes in prey density influences the feeding of every predator individual via the so-called functional response (Holling 1959a; b). His underlying assumption was that predator individuals spend their time hunting or eating. Thus, the total time budget *T* is either spent searching for prey (T_S) or eating and handling the found prey (T_H)

$$T=T_S+T_H \qquad (1.4).$$

Following this assumption, Holling argued that the number of prey individuals caught

(N) should be a function of the resource species density (R), the time spent searching (T_S) and the success rate of finding prey (a)

$$N = aT_S R \tag{1.5}$$

The total time spent handling prey individuals (subduing and ingesting) is therefore a function of the numbers of prey caught, multiplied by the handling time per prey item (h)

$$T_H = hN = haT_S R \tag{1.6}$$

The per-capita feeding rate F_C ,given by the number of prey caught per unit time, is therefore

$$F_C = \frac{N}{T} = \frac{aT_S R}{T} = \frac{aT_S R}{T_S + T_H} = \frac{aT_S R}{T_S + ahT_S R} = \frac{aR}{1 + ahR} \tag{1.7}$$

which is the so-called Holling Type II functional response (please also see Huang 2010 for the derivation). Holling originally introduced three types of functional responses: Type I has a constant feeding rate (which is the same assumption as in the Lotka-Volterra models; eqn. 1.1 and 1.2) up to a certain threshold where feeding cannot increase anymore. This has often been suggested to be true for filter-feeding organisms, which feed with a constant rate until they are absolutely satiated.

The Type II functional response (eqn. 1.7) was generally suggested for animals hunting in homogeneous environments with a constant encounter rate. It is thus based on the same assumptions and shows the same dynamics as other models of interacting particles, such as the Michaelis-Menten kinetics (Michaelis & Menten 1913). In this model, the per-capita feeding-risk (first derivative of eqn. 1.7) has its maximum at the lowest prey densities and decreases with increasing prey density. The Type III functional response, in contrast, has a prey-density-dependent encounter rate which yields a sigmoidally shaped feeding rate where the per-capita feeding-risk increases at low prey densities. This mimics, for example, environments that offer a shelter or refuge for the prey (Real 1977; Hassell, Lawton & Beddington 1977; Crawley 1992). At low prey densities where there is enough hiding space for all individuals, the feeding rate only increases slightly with prey density. When all of the refuge space is occupied, the feeding rate increases exponentially and the per-capita feeding-risk reaches its maximum when half of the maximum feeding rate is reached. In both Type II and Type III functional responses the feeding rate levels off at higher resource densities and saturates at 1/h. The two types of functional responses can actually be converted into each other by substituting the success rate a with bR^q , its prey-density-dependent form, where b is a scaling factor and q is the so-called Hill exponent that gives the strength of the prey density dependence of the success rate (Real 1977). Inserting this into eqn. 1.7 gives a general form of the functional reponse:

$$F_C = \frac{bR^{q+1}}{1+bhR^{q+1}} \tag{1.8}$$

At $q = 0$ the success rate is not dependent on prey density (Type II) and at $q = 1$ the success rate scales linearly with prey density (classic Type III). Empirical studies suggest a smooth transition between the two functional forms depending on the specific predator-prey pair and even report q-values above one (Vucic-Pestic *et al.* 2010; Kalinkat *et al.* 2013). In some cases, increasing prey density even reduces overall feeding rates. For example, this occurs when prey individuals protect themselves showing group defences such as swarm behaviour (Jeschke & Tollrian 2005). These functional responses are sometimes referred to as Type IV although this does not match the original definition (Holling 1959a). To this date, many empirical studies have used the framework of functional response and added even more empirical realism to it. Several studies, for example, suggested inclusion of predator interference (Beddington 1975; DeAngelis, Goldstein & O’Neill 1975), dependency of functional response parameters (b, h and q) on the dimensionality of the ecosystem (Pawar, Dell & Savage 2012) or their scaling with body mass and temperature (Rall *et al.* 2009, 2012; Vucic-Pestic *et al.* 2010, 2011; Kalinkat *et al.* 2013).

The implementation of a prey-density-dependent feeding rate was first suggested by Rosenzweig and MacArthur (Rosenzweig & MacArthur 1963). In their model, the per-capita feeding rate F_C follows

$$F_C = \frac{a_{max} R}{R_0 + R} \tag{1.9}$$

which is exactly the notation of a standard Michaelis-Menten kinetic (Michaelis & Menten 1913) and thus strongly related to the Holling Type II functional response (eqn 1.7). a_{max} is the maximum feeding rate and R_0 gives the prey density at which half of the maximum feeding is realized (half-saturation density). Real (1977) showed that eqns. 1.7 and 1.9 can be converted into each other by substituting a_{max} by 1/h and R_0 by 1/ah. Note, that the prey-density dependence of the feeding rate now makes the system excitable (McCann 2011).

Towards an empirically-grounded biomass model

Since the early days of ecosystem modelling there have generally been two groups of models: ones that are specifically tailored to model certain species and interactions and others that allow a very wide range of parameters and can thus be applied to a variety of species and communities. While models from the first group are not designed to find general patterns, the latter ones often lack empirical reasoning or natural realism (1992). During the development of those models, evidence was accumulating that the parameters of consumer-resource models (growth , feeding, and death rates) are not arbitrary numbers but depend on species traits. In particular, the scaling of these rates with species body mass (the so-called allometric scaling, Peters 1983; Savage *et al.* 2004; Brown *et al.* 2004), led to improved consumer-resource models. Yodzis and Innes (Yodzis & Innes 1992) formulated a model, deriving all model parameters from species body masses using general scaling relationships (Peters 1983; Savage *et al.* 2004; Brown *et al.* 2004; Vucic-Pestic *et al.* 2010; Ehnes *et al.* 2011; Rall *et al.* 2012; Kalinkat *et al.* 2013). In their model, all rates and the carrying capacity are defined by a rate-specific intercept and the body mass (m_i) of the species to the power of an allometric scaling exponent (a):

$$r_i = r_0 m_i^{a_r} \; ; \; K_i = K_0 m_i^{a_K} \; ; \; y_i = y_0 m_i^{a_y} \; ; \; B_0 = B_{0,0} m_i^{a_{B_0}} \; ; \; x_i = x_0 m_i^{a_x} \qquad (1.10\text{-}1.14).$$

In this model, r_i is species i's maximal growth rate and K_i i's carrying capacity (see eqn. 1.3); the feeding parameters are given by the maximum ingestion rate y_i and the half-saturation density $B_{0,i}$ (compare eqn. 1.9); x_i is the species' metabolic rate. r_0, K_0, y_0, $B_{0,0}$ and x_0 are the rate-specific intercepts whereas a_r, a_K, a_y, a_{B0} and a_x are the respective allometric exponents. It should be noted that this type of model captures changes in biomasses, not in abundances. All rates are therefore parametrised on the basis of population biomass changes. The death rate M in eqn. 1.2, for example, is substituted by the population's metabolic rate x that captures all biomass loss due to respiration. The first model (Yodzis & Innes 1992) used very general scaling laws obtained from metabolic theory (generally ¼ or -¼ Peters 1983; Brown *et al.* 2004), but since then a large amount of studies have provided an empirical basis for slightly different scaling factors. Ehnes and colleagues (Ehnes *et al.* 2011), for example, analysed 3,661 respiration rates of invertebrates and found an exponent of $a_x = -0.31$. Comparably, there is data on the species growth rates (Savage *et al.* 2004) and their carrying capacity (Meehan 2006). A recent study also looked at the feeding rates in 2,564 functional-response experiments and found allometric scaling for prey-density-dependent success rate b, handling time h and scaling exponent q (Kalinkat *et al.* 2013). The parameters obtained by these studies can be used to improve biological realism of consumer-resource models and therefore provide a good empirical basis for generalizable biomass models.

Integration of global-change drivers into bioenergetic models

Given the empirical basis of recent consumer-resource models (eqn. A1 and A2 in Fig 1.2), the integration of their dependency on environmental variables is just a small step. The most famous example of including such an environmental variable into consumer-resource models was provided by Rosenzweig (1971). He studied the effect of an increasing carrying capacity (K) on the stability of a consumer-resource model with logistic growth (eqn. 1.3 and Fig. 1.2B). He argued that a higher maximum resource density, which mimics nutrient enrichment, should be beneficial for the system. However, he found exactly the opposite: Although, an increasing K led to higher species biomass densities, it reduced system stability by inducing biomass oscillations and, in the end, caused species extinctions. He therefore called this phenomenon the “paradox of enrichment” (Rosenzweig 1971). While it is still debated whether the “paradox of enrichment” can actually be found in natural systems (McAllister *et al.* 1972; Trzcinski, Walde & Taylor 2005), it has been found in lab systems (Fussmann *et al.* 2000; Persson *et al.* 2001; Shertzer *et al.* 2002) and a change in carrying capacity is still widely used in biomass models to alter the nutrient status of the system (McCann *et al.* 1998; Rall *et al.* 2008; Rip *et al.* 2010; Binzer *et al.* 2012; Schwarzmüller *et al.* 2014).

Another strongly empirically-based aspect of modelling the relation between biological systems and abiotic stressors is the dependency of biological rates in a consumer-resource system on the environmental temperature. These can be described by the so-called Arrhenius equations (Fig 1.2A, eqn. A3-A7) where r_0, K_0, y_0, $B_{0,0}$ and x_0 are the rate and body-mass specific normalization constants; E_r, E_K, E_y, E_{B0} and E_x are the so called activation energies; k is Boltzmann's constant; T_0 is the normalization temperature and T is the actual temperature of the system (Gillooly *et al.* 2001). Implementing this into consumer-resource models was primarily done by Vasseur & McCann (2005) who looked at the stability of consumer-resource systems under increasing temperature. However, due to a lack of data, they did not find clear results but narrowed down the parameter space in which certain values of activation energies lead to stable or unstable outcomes, respectively. The growing empirical basis for temperature scaling relationships (Savage *et al.* 2004; Brown *et al.* 2004; Meehan 2006; Ehnes *et al.* 2011; Vucic-Pestic *et al.* 2011; Rall *et al.* 2012) nowadays enables even better predictions (Binzer *et al.* 2012; Fussmann *et al.* 2014; Gilbert *et al.* 2014).

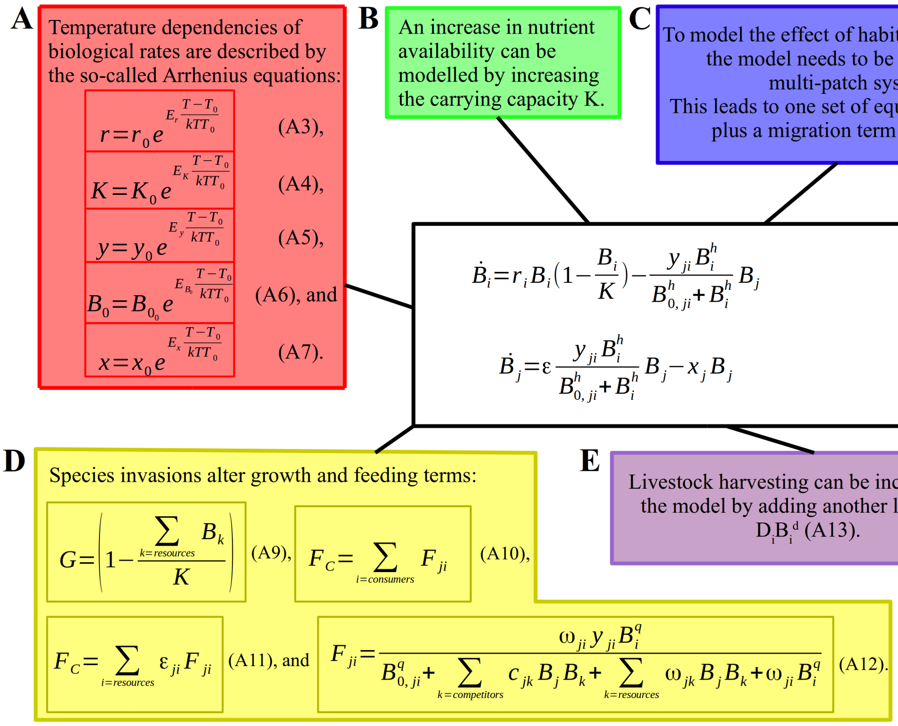

Figure 1.2 *General writing of the consumer-resource biomass-model that is used in this thesis. It consists of two coupled differential equations that describe the changes in biomass densities of resource (A1) and consumer (A2) over time.* ***A-E*** *show possible extensions to the model to mimic environmental changes like* ***(A)*** *warming,* ***(B)*** *nutrient enrichment,* ***(C)*** *habitat fragmentation,* ***(D)*** *the invasion of species or* ***(E)*** *an anthropogenic use of the species via harvesting. For a description of the respective parameters please refer to Chapter 1.6.*

These two examples show that the framework, provided by the types of consumer-resource models described above, is flexible towards the integration of external factors such as the major drivers of global change. Fig 1.2 depicts these and other possible extensions of the model including habitat fragmentation (Fig 1.2 C and Chapter 4), species invasions (Fig. 1.2 D) or harvesting of Livestock (Fig. 1.2 E). Integrating harvesting would be easiest as it just requires the addition of another death term *D* (Bascompte, Melián & Sala 2005) and a scaling factor *d* that gives the density dependency of the harvesting. To model additional species (either for more complex systems or to simulate species invasions) the basic equations have to be extended to a multi-species form (see Fig 1.2 D, eqns. A9 to A12 and Brose *et al.* 2005b) including possible prey preferences (ω) and predator-interference terms (c). Finally, the integration of multiple patches (Fig. 1.2. C) requires an addition of inter-patch dynamics (see Chapter 4).

1.7 Food-web motifs

Consumer-resource models represent, by far, the lowest end on the complexity scale of ecological interaction networks. However, they are well empirically grounded, parametrized and experimentally traceable (see chapter 1.6). Complex ecological systems like food webs, on the other hand, represent a more realistic model of natural ecosystems as they often contain hundreds of species and thousands of interactions (Jacob *et al.* 2011). However, the high complexity counteracts many of the positive aspects of simpler models: manipulating large complex systems experimentally requires a lot of work, both in the lab or in the field, or huge computational power in case of modelling studies; quantifying the effect of experimental manipulations is complicated as there are so many direct and indirect effects; and even the empirical foundation of most interaction webs is weak as most of the interactions are not quantified and some have even never been observed but are based on expert knowledge (Hodkinson & Coulson 2004).

Considering the effects of global-change on ecological systems we have, on the one hand, a huge amount of literature that reports manifold effects on complex systems but lacks predictive power and, on the other hand, relatively well-established and -parametrized systems of low complexity (see Chapter 1.6). Bridging the gap between such small-scale observations and large-scale patterns is one of the challenges of ecological modelling (Brose *et al.* 2005b). Food-web ecologists have therefore established a stepping stone in between the level at which the models are parametrised (individuals, populations, single interactions) and the large systems they want to describe and predict. These levels of intermediate complexity are called “community modules” (Holt 1997) or “network motifs” (Milo *et al.* 2002; Stouffer & Bascompte 2010). They are regarded as smaller trophic entities that consist of two to seven species and are often seen as simple representations of entire food webs (McCann & Yodzis 1994; Bascompte & Melián 2005; Otto *et al.* 2007; Stouffer & Bascompte 2010). However, there is debate that some emergent patterns cannot be predicted without considering the food-web context (Cohen *et al.* 2009).

During the course of this thesis, I do not only study the effect of different drivers of environmental change but I also look at different food-web motifs. In Chapter 2, I focus on a consumer-resource motif (see Chapter 1.6), in Chapter 4, I study a three-species food-chain and in Chapter 3, I investigate the transition from a three-species food-chain to a four-species motif, the “cascade competition motif”.

1.8 Stability

After introducing the general topic and the tools that are used to investigate it, I will finally spend a few words on how to quantify stability. In food-web ecology, there exist a broad variety of stability measures tailored to specific interests. Generally they fall into two categories: (1) resilience and resistance measures and (2) measures of dynamic stability (McCann 2000). The former quantifies a system's response to perturbation (its resistance) as well as whether it will return to its original state and the time that this would take (system resilience). These measures quantify discrete perturbation events on a relatively small time scale (McCann 2011). As the focus of my thesis is the long-term stability of trophic systems under continuous environmental stress, I use the second class of dynamic-stability measures.

In the projects of my thesis I look at two different measures of dynamic stability: persistence and variability. Persistence simply gives the number of species surviving whereas variability gives the amplitudes at which species biomasses are oscillating around the mean, often quantified by the coefficient of variation (variance divided by mean). In the research chapters of this thesis I investigate whether the respective environmental changes applied to the systems (1) increase the variability of the systems and (2) whether they lead to extinctions. Throughout the thesis, I refer to changes in environmental variables that reduce the variability of a system as “dynamically stabilizing” though they might at the same time lead to a lower persistence. On the other hand, processes that increase the variability are referred to as (dynamically) destabilizing though they sometimes increase general stability (i.e. species biomass densities; see “paradox of enrichment”, Rosenzweig 1971).

1.9 Outline of this thesis

The overarching question of how environmental stressors influence the stability of trophic motifs is addressed in various different ways throughout this thesis. In the following research chapters I use a bioenergetic model (presented in Fig 1.2) and its extensions to model the effect of temperature (Chapter 2), nutrient enrichment (Chapters 3 and 4) and habitat fragmentation (Chapter 4) on the stability of different trophic motifs.

In Chapter 2, I look at a simple consumer-resource system undergoing changes in environmental temperature. The temperature dependencies of metabolic rates, carrying capacity, half-saturation density and maximum ingestion rate (see eqn. A1 – A7 in Fig 1.2) are rescaled on the basis of an extensive literature search. This already has implications for the initial hypothesis that warming stabilizes predator-prey interactions by reducing variability in biomass densities. I examine this for all possible parameter combinations and afterwards the results are tested in a microcosm experiment.

In Chapter 3, I revisit the theoretical concept of the “paradox of enrichment” (Rosenzweig 1971), as well as weak-interactions theory (McCann *et al.* 1998). Applying an allometric concept of interaction strengths allows the identification of possibly stabilizing elements in food webs based on their trophic position and their body mass. I refer to them as “trophic whales” and identify examples in natural ecosystems. An exemplary model analysis provides the hypotheses that afterwards are rigorously tested in a microcosm experiment using earthworms as 'trophic whales'.

For Chapter 4, I extend the bioenergetic model to a multi-patch version in order to model fragmented habitats. The coupling of patches via migration links between patches is quantified using empirical data of maximum dispersal distances and abundance-body mass relationships. I intensively study the effect of increased habitat isolation on the persistence of a three-species food-chain. Additionally, I look at the interactive influence of an increased nutrient availability in a fragmented system.

Part II
Research chapters

Chapter 2

Ecological stability in response to warming

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That species' biological rates including metabolism, growth and feeding scale with temperature is well established from warming experiments (Brown *et al.* 2004). The interactive influence of these changes on population dynamics however, remains uncertain. As a result uncertainty about stability responses to warming remain correspondingly high. In prior studies, severe consumer extinction waves in warmed microcosms (Petchey *et al.* 1999) were explained in terms of warming-induced destabilization of population oscillations (Vasseur & McCann 2005). Here, we show that warming stabilizes predator-prey dynamics at the risk of predator extinction. Our results are based on meta-analyses of a global database of temperature effects on metabolic and feeding rates and maximum population size that includes species of different phylogenetic groups and ecosystem types. To unravel population-level consequences we parametrised a bioenergetic predator-prey model (Otto *et al.* 2007) and simulated warming effects within ecological, non-evolutionary time scales. In contrast to prior studies (Vasseur & McCann 2005), we find that warming stabilized population oscillations up to a threshold temperature, which is true for the vast majority of possible parameter combinations. Beyond the threshold level, warming caused predator extinction due to starvation. Predictions were tested in a microbial predator-prey system. Together, our results indicate a major change in how we expect climate change to alter natural ecosystems: warming should increase population stability while undermining species diversity.

Ongoing global warming is documented in different ecosystems worldwide (Parmesan 2006; IPCC 2007). Such global warming can lower abundances and lead to extinction, for example, due to habitat loss (Parmesan & Yohe 2003; Thomas *et al.* 2004; Thomas, Franco & Hill 2006; Parmesan 2006). However, specific predictions of consequences for global ecosystems and species are still vague, since warming simultaneously affects multiple levels of ecological organization. This includes simultaneous changes of multiple biological and biochemical rates with temperature (Vasseur & McCann 2005; Rall *et al.* 2009 p. 201; Dell, Pawar & Savage 2011): increased individual metabolic rate (Brown *et al.* 2004) and intrinsic population growth (Savage *et al.* 2004), as well as modified feeding parameters (maximum feeding and half-saturation density) of predator-prey interactions (Rall *et al.* 2009, 2012; Englund *et al.* 2011) (Fig. 2.1a). Traditionally, severe consumer extinction waves in warmed microcosms (Petchey *et al.* 1999) were explained by increased metabolic and feeding rates that destabilize population dynamics by causing stronger oscillations (Vasseur & McCann 2005). However, the lack of systematic empirical data and their integration with generalized models hampered an understanding of their interactive influence on population dynamics and species survival. Hence, predictions of warming effects on ecosystems and their stability remained highly uncertain. To overcome these limitations, we analysed a novel global data base and addressed how warming affects metabolic and feeding rates as well as maximum population size across species of different phylogenetic groups and ecosystem types. Subsequently, we used these empirical physio-ecological scaling relationships and parametrised a bioenergetic model to predict warming effects on population stability and species survival probabilities. We tested these predictions in a microbial microcosm experiment across a temperature gradient. Together, these integrated analyses provide a generalized understanding of how warming affects natural communities.

Temperature dependencies of biological rates (x) are commonly described by the Arrhenius equation (see Fig. 2.1b with metabolic rates as an example):

$$x_c = x_0 e^{E_x \frac{T-T_0}{kTT_0}} \qquad (2.1)$$

where x_0 is a rate- and mass-dependent normalization constant, E_x [eV] is the rate's activation energy, T is the absolute temperature of the system [K], k [eV K^{-1}] is Boltzmann's constant and T_0 [K] the normalization temperature (here: 20°C = 293.15 K).

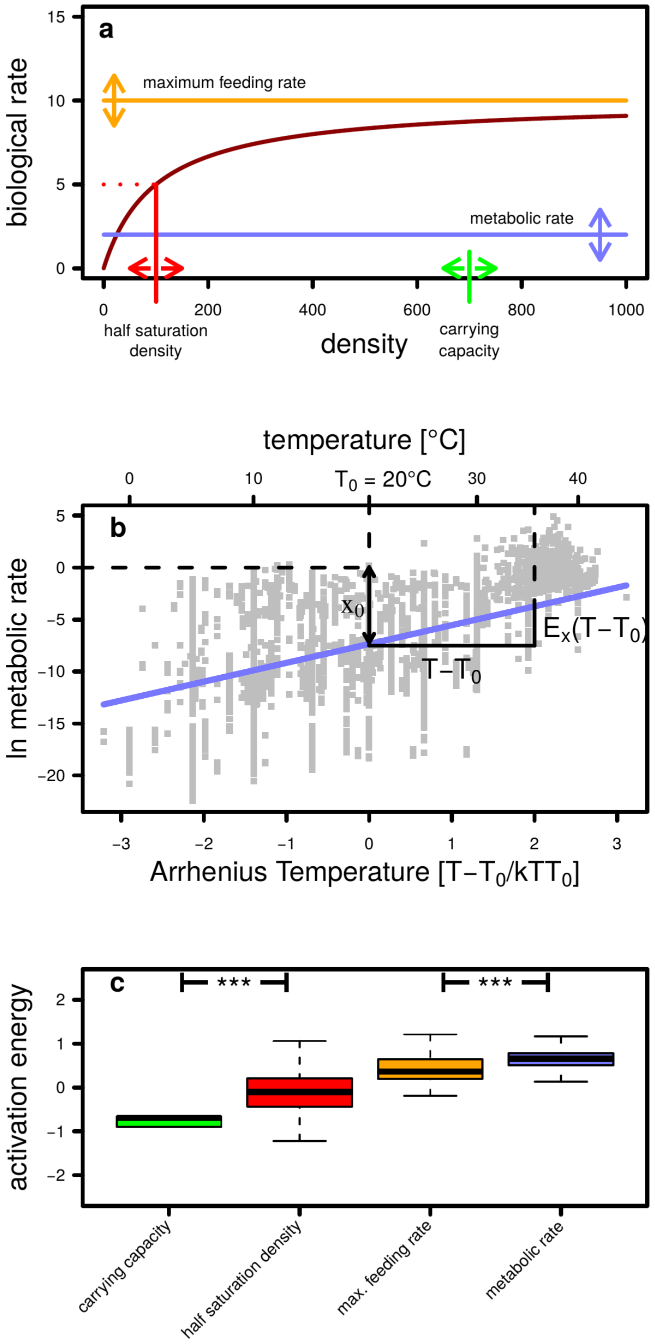

Figure 2.1 a, *Conceptual illustration of how temperature affects the parameters maximum feeding, half saturation density (foraging inefficiency), carrying capacity (maximum prey density) and metabolic rate. The brown line shows the realized feeding rate. The vertical part of the red line shows the half saturation density, and the horizontal dashed part illustrates that at this prey density the half-maximum feeding rate is realized.*

b, *Temperature scaling of metabolic rates as an illustration of activation energies (Ex) in Arrhenius equations.* ***c,*** *Activation energies (E) for carrying capacity (mean = -0.77; s.d. = 0.36), half-saturation density (mean = -0.12; s.d. = 0.53), maximum feeding rate (mean = 0.47; s.d. = 0.44) and metabolic rate (mean = 0.64; s.d. = 0.29) in our empirical databases. Stars denote significant differences (***, p<0.001) between pairs of rates as determined by F-tests (metabolic rate versus maximum feeding; carrying capacity versus half-saturation density).*

Using a global database, we analysed activation energies for metabolic rates, carrying capacities (maximum density of the prey), maximum feeding rates and half-saturation densities (prey density at which half of the maximum feeding rate is realized, see Fig. 2.1a, thus expressing the predator's foraging inefficiency), which are parameters of a bioenergetic population model of previous studies (Otto *et al.* 2007; Schneider, Scheu & Brose 2012; Boit *et al.* 2012). Values for intrinsic growth rate of resource populations were 0.84 eV for multicellular organisms with non-overlapping generations (Savage *et al.* 2004). In our analyses, activation energies of the carrying capacity were generally negative, whereas activation energies of the half-saturation density were close to zero (Fig 2.1c). This significant difference suggests that predators cannot increase their foraging efficiency to cope with scarcer prey in warmer systems. Moreover, maximum feeding increased significantly less with warming than metabolic rate (lower activation energies, Fig 2.1c), which implies that predators in warmer ecosystems suffer from increased energy loss due to metabolism whereas their maximum energy intake cannot increase similarly. Both significant differences (as indicated in Fig. 2.1c) suggest a reduced energy supply for predators in a warmed world.

To investigate the interplay of these warming effects on population dynamics, we used the average activation energies and their standard deviations to parametrise a bioenergetic model (Yodzis & Innes 1992; Brose, Williams & Martinez 2006; Binzer *et al.* 2012) (see Methods). Additionally, we implemented published data for the temperature dependency of resource population growth (Savage *et al.* 2004). Our initial model simulations were based on the average activation energies (see legend of Fig. 2.1 and Supplementary Table S1.1) to predict dynamics along a temperature gradient (0° - 40°C). We found predator extinctions at low temperatures (<11°C) due to unstable population dynamics. Predator and prey persisted along a temperature range between 11°C and 27.5°C, whereas above 27.5°C predators became extinct owing to energy limitations (Fig. 2.2a). Although these temperature thresholds remained specific for the average activation energies, our analyses indicate the general pattern that within the persistence range, increasing temperatures caused decreasing amplitudes of population oscillations - thus stabilizing predator-prey systems from limit cycle (Fig. 2.2b) into equilibrium dynamics (Fig. 2.2d). Although warming increased per unit biomass flux rates, the much stronger metabolic acceleration (Fig. 2.1c) led to lower consumer biomass densities, and eventually reduced population-level fluxes. Furthermore, a decline in prey densities (carrying capacities) that was stronger than the decrease in half saturation densities (Fig. 2.1c) and the associated increase in foraging efficiencies also lowered the population-level fluxes. Consequently, these two main effects caused dampened oscillations due to lower top-down pressure and higher risk of predator starvation as a consequence of lower bottom-up energy supply (Rip & McCann 2011). Thus, warming reduced population energy fluxes and led to dynamics that are similar to an inverse paradox of enrichment (Rosenzweig 1971).

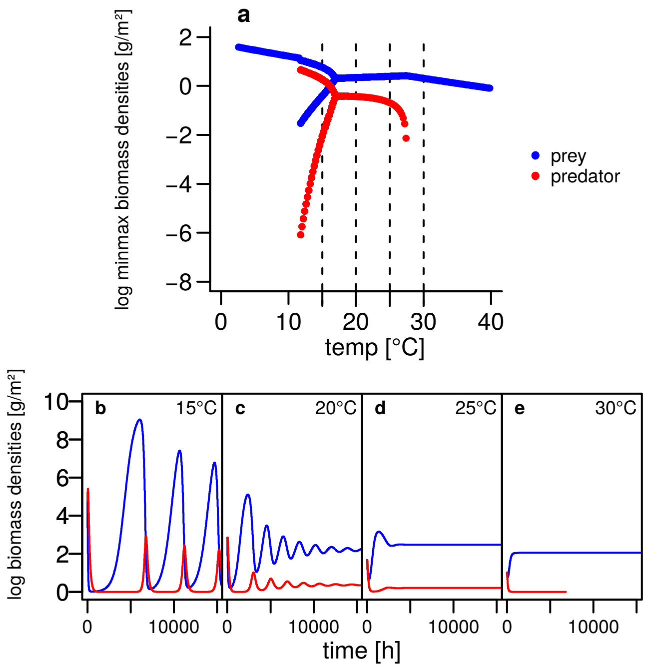

Figure 2.2 Simulated predator-prey dynamics across temperature gradients. ***a,*** *Bifurcation diagram showing the minimum and maximum predator and prey densities within time series across a temperature gradient. Dashed lines indicate the temperatures corresponding to the exemplary time-series.* ***b-e,*** *Exemplary time series at 15°C,20°C,25°C and 30°C. To allow comparisons to empirical data* ***b-e*** *show the first part of the time series including transient dynamics, whereas the bifurcation diagram (a) shows minima and maxima within the last tenth of the simulation representing long-term dynamics. The corresponding longer time series are shown in Supplementary Information 1. Blue: prey densities; red: predator densities.*

To generalize our findings we replicated the simulations with one million random combinations of activation energies (normal distributions with mean values and standard deviations of our meta-analyses, see Fig. 2.1; resource intrinsic growth rate: 0.84 eV ±0.4; Supplementary Table 1.1). *A-posteriori*, we categorized the different outcomes according to the following aspects: whether predator-prey dynamics were stabilized or destabilized in terms of their coefficient of variation in biomass; and whether predators persisted or became extinct with increasing temperature (Fig. 2.3a). The full-factorial combination of these aspects resulted in four categories that were characterized by the distributions of the four activation energies (Fig. 2.3b). In contrast to prior predictions that an increase in temperature should destabilize predator-prey oscillations (Vasseur & McCann 2005), the vast majority of parameter combinations (91,1 %, Fig. 2.3a) led to positive relationships between population stability and warming. Within this group, predators survived at high temperatures, in only 17.5% of all simulations, whereas the combination of stabilizing warming effects and predator extinction at high temperatures occurred in 73.8% - thus highlighting the broad generality of our warming predictions. Notably, only a marginal minority of all simulations (8.9%) supported the present paradigm that warming destabilizes population dynamics (Fig. 2.3; see Supplementary Figures S1.1 to S1.4 for time series and bifurcation diagrams). The varying dynamic consequences of warming (Fig. 2.3a) can be explained by different combinations of activation energies (Fig. 2.3b). If activation energies of half-saturation densities were lower than those of carrying capacities, warming destabilized predator-prey dynamics (Fig. 2.3: both left columns), as predators became more efficient and exerted a stronger top-down pressure. In the opposite case, if activation energies of carrying capacities were lower than those of half-saturation densities, top-down pressure was weakened and energy fluxes were reduced and thus warming stabilized population oscillations (Fig. 2.3: both right columns). In the latter case of stabilized systems, predator extinctions occurred if activation energies of metabolic rates were higher than those of maximum feeding (Fig. 2.3, right column) thus supporting our hypothesis of predator starvation due to energetic mismatch. Despite the strong response of empirical carrying capacities to warming (Fig. 2.1c), our model analyses suggest that they had only marginal effects on population stability and predator persistence, because their distribution was similar across the four stability categories (Fig. 2.3b).

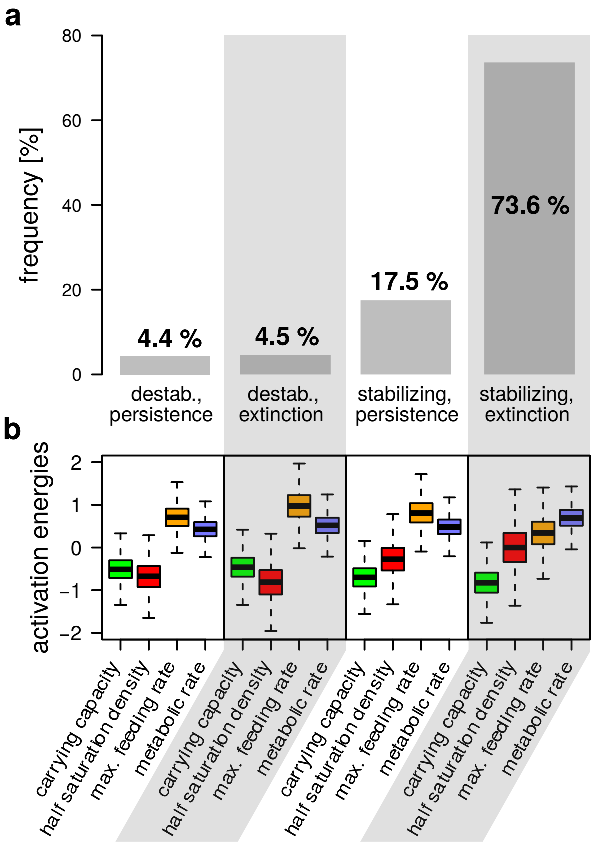

Figure 2.3 Population stability and extinctions in simulated predator-prey systems.
a, *Percentages of possible dynamical outcomes of the simulations. Destabilizing refers to an increase of the coefficient of variation of biomass, stabilizing to a decrease. Persistence and extinction were measured at 40°C for the predator species.* ***b,*** *Boxplot of activation energies corresponding to the categories of the dynamical outcomes shown in a. Outliers were excluded for graphical reasons.*

Overall, our interpretation is consistent with the "principle of energy flux" stating that processes (here, warming) decreasing the energy flux to consumers (here, feeding) relative to their loss rate (here, metabolic rates) will stabilize population dynamics (Rip & McCann 2011). Our results also show that continuing these processes may lead to consumer starvation. Moreover, stability implications of warming may interact with the size structure of the community (Binzer *et al.* 2012; Brose *et al.* 2012) that modifies energy flux patterns (Otto *et al.* 2007). In this context, our results bridge the gap between physiological warming studies and analyses of population stability to provide a mechanistic explanation for possible consequences of warming while stressing population stability and predator extinction as the most likely outcome.

Our approach is based on some limiting assumptions. First, we included only invertebrates (mainly arthropods) in our empirical data bases (Fig. 2.1c) and model analyses (Figs 2.2, 2.3), because they represent most extant species. Although studies of vertebrate activation energies revealed similar patterns in activation energies (Gillooly *et al.* 2001; Brown *et al.* 2004), conclusions for endotherms may differ from our results. Second, we employed random combinations of activation energies in our model analyses (Fig. 2.3 a), because only very few studies measured the activation energies of feeding and metabolic rate for the same species (Vucic-Pestic *et al.* 2011; Rall *et al.* 2012). These studies also documented very small activation energies of half saturation densities and that metabolic rate increases more strongly with temperature than feeding. Accordingly, they represent the fourth category with population stabilization and predator extinction (Fig. 2.3 right-most column), which supports the conclusions of our model analyses. However, our results also indicate the need to further study differences in temperature scaling for biological rates measured for the same species. Third, the empirical data in our databases are founded on short-term experiments excluding evolutionary responses to temperature changes that are beyond the scope here. Here we offer a framework that future studies can use for disentangling evolutionary from ecological consequences of warming. Fourth, we followed prior studies (Gillooly *et al.* 2001; Dell *et al.* 2011) in assuming Arrhenius scaling of the biological processes with temperature, whereas they may systematically break down at critically high temperature thresholds leading to hump-shaped temperature scalings (Pörtner & Knust 2007; Englund *et al.* 2011; Rall *et al.* 2012). Although these hump-shaped relationships should cause extinctions when critically high temperature thresholds are crossed (Pörtner & Knust 2007), our results suggest that extinctions may occur even within the physiologically benign temperature range as a consequence of predator starvation despite abundant resources. Despite these limiting assumptions, our database and model analyses are offering novel testable predictions for how predator-prey systems should respond to warming.

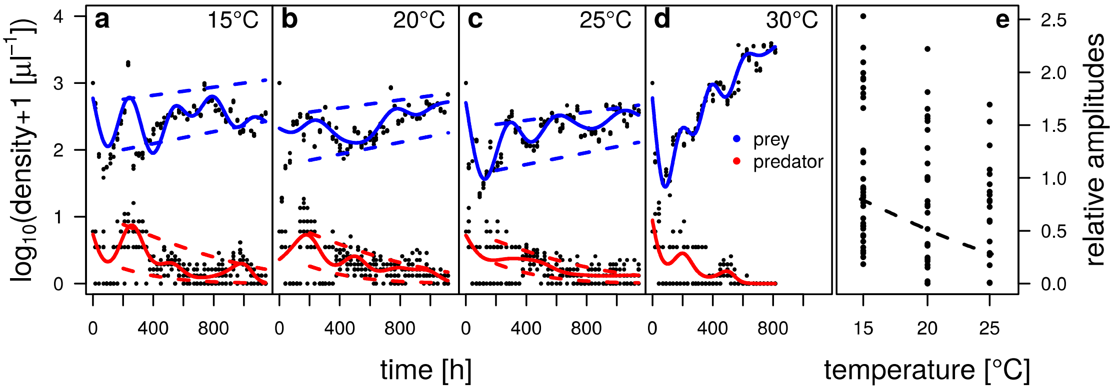

Figure 2.4 Laboratory time series of the predator T. pyriformis (red lines) and its prey P. fluorescens CHA19-GFP (blue lines).

***a-d,** Replicates of the time series at 15°C, 20°C, 25°C and 30°C were fitted with a GAM with a Poisson distribution. Dashed lines in the related colours show quantile regressions indicating the minima and maxima of abundances.* ***e,** Relative amplitudes of both predator and prey time series dependent on temperature. The dashed line denotes the regression line according to an average amplitude sequence number (which is 4); see Supplementary Information 1 for details.*

We tested these predictions by measuring time-series along a temperature gradient from 15°C to 30°C in a microbial predator-prey system with *Tetrahymena pyriformis* preying on *Pseudomonas fluorescens* (see Methods for detailed laboratory and statistical methods) (Zuber *et al.* 2003; Jousset *et al.* 2006). Our model analyses were based on biomass dynamics, whereas we counted abundances in the microbial experiment. As cell sizes were not affected by our temperature treatments (ANOVA, p = 0.7198) the data can be compared. Our results suggest a dampening of population oscillations with warming: although predator and prey populations showed strong oscillations at 15°C (Fig. 2.4a), they were dampened at higher temperatures (20°C, Fig. 2.4b). At 25°C (Fig. 2.4c), two alternative states occurred: in two of three replicates ciliate predators persisted with both species showing lower oscillation amplitudes (Fig. 2.4c, Supplementary Figs S1.5c and g), whereas in the third replicate the predator population became extinct (Supplementary Fig. S1.5k). At this temperature, the fragile predator-prey system was on the verge between persistence and extinction. At 30°C (Fig. 2.4d), predators in all treatments became extinct. Statistically, minima and maxima of bacteria both decreased from 15°C to 25°C with maxima showing a steeper decrease than maxima ($E_{min,t=0}$ = -0.53, p<0.001; $E_{max,t=0}$ = -0.64, p<0.001). Ciliate minima increased and their maxima decreased ($E_{min,t=0}$ = 0.27, p<0.001; $E_{max,t}$ = -0.50, p<=.001). These statistically significant patterns in the activation energies of minima and maxima demonstrated that the amplitudes of the predator and the prey oscillations decreased with warming (Fig. 2.4e). The experimental data thus confirmed the model predictions that warming stabilizes predator-prey dynamics by dampened oscillations, whereas predators become extinct at high temperatures.

Our analyses of global databases, model simulations and empirical microcosm experiments show that warming generally stabilizes population dynamics in predator-prey systems on ecological timescales. This is due to a mismatch between metabolic rate and realized feeding caused by: constant foraging efficiencies (i.e., half saturation densities) while prey densities (i.e., carrying capacities) decrease; and increases in metabolic rate exceeding those of maximum feeding rates. Beyond a threshold temperature, the decreasing energetic efficiency with warming will cause extinction of predators owing to starvation. This contrasts with the present paradigm that warming causes extinctions by increased oscillations (Vasseur & McCann 2005). Our results provide evidence that populations on the verge of extinction are characterized by minimal oscillations or even equilibrium dynamics. Thus, our results increase the predictability of warming effects and illustrate the risk of predator extinction waves in a warmed world.

Methods

Database

We used published databases on metabolic rates (White, Phillips & Seymour 2006; Ehnes *et al.* 2011) and functional response parameters (Rall *et al.* 2012) and extended them by protozoan metabolic rates and maximum population densities (Supplementary Information 1). Only data sets containing three or more temperature levels differing by two or more degrees Kelvin were included. To analyse data only within the biological relevant temperature range (Savage *et al.* 2004) we deleted the lowest and/or highest measurements in cases where hump-shaped deviations occurred. We carried out an ordinary least-squares regression on each data set to obtain activation energies (see Supplementary Information 1 for details).

Simulations

Consistent with previous model studies (Yodzis & Innes 1992; Vasseur & McCann 2005; Brose *et al.* 2006; Otto *et al.* 2007; Binzer *et al.* 2012), we used a bioenergetic population model for the simulations where the biomass changes (B'_{prey} and $B'_{predator}$) follow

$$B'_{prey} = GB_{prey} - B_{predator}F \tag{2.2}$$

and

$$B'_{predator} = \varepsilon B_{predator}F - xB_{predator} \tag{2.3},$$

where B_{prey} and $B_{predator}$ are the biomass densities of the prey and the predator species, respectively. G is the resource's logistic growth term, F is the feeding term, ε is the assimilation efficiency and x the predator's metabolic rate (see Supplementary Information 1 for details). As in previous biomass models, biomass loss due to metabolic rate (biomass loss of individuals) or mortality (loss of individuals) is not differentiated.

Laboratory methods

Organisms and culture conditions

We used as bacterial prey *Pseudomonas fluorescens* CHA19, an gacS-isogenic mutant of *P. fluorescens* CHA0, chromosomally tagged with green flourescent protein (GFP) (Jousset *et al.* 2006). This strain does not produce secondary metabolites, which allows monitoring of trophic interactions without toxin-related interferences. Bacterial stocks were kept frozen at -80°C. Before the experiment, bacteria were grown on lysogeny broth plates supplemented with 25 µg ml^{-1} kanamycin. One single colony was picked and cultured overnight at 20°C in liquid lysogeny broth, collected by centrifugation (13000 r.p.m, 10,00 g for one minute) and washed three times in 1:10 modified Ornston and Stanier minimal medium supplemented with 1mM glycerol as sole carbon source.

As predators we used the bacterivorous protozoa *Tetrahymena pyriformis* CCAP 1630/1W. Protozoa were kept in axenic cultures in proteose peptone yeast extract medium containing 20 g proteose peptone and 2.5 g yeast extract per litre at 14 °C for at least five days until reaching sufficient concentrations. Before the experiments, protozoa were collected by gentle centrifugation for three times (300 r.p.m, 400 g, 0 °C, for seven minutes) and resuspended in 1:10 OS 1mM glycerol medium.

Time-series experiments

Time-series experiments were conducted in 100 ml Ornston and Stanier 1:10 0.1 mM glycerol in 250 ml Erlenmeyer borosilicat glass flasks closed with aluminium caps. Flasks were incubated in thermostatic cabinets (Lovibond, Tintometer GmbH, Dortmund) with agitation (200 r.p.m.) at 15°C, 20°C, 25°C and 30°C. Start concentrations of *P. fluorescens* CHA19-GFP were 1000 cells per microlitre whereas *T. pyriformis* concentrations were 5 cells per microlitre in each treatment. Every day, 10 ml of the culture were removed for analysis and replaced with fresh medium. Bacterial counts were determined in a C6 flow cytometer (Accuri, Ann Harbor, USA) from three 150µl aliquots. Bacteria were gated on the base of their SSC-A x FL1-A signal; 50,000 events per sample were recorded. If counts exceeded 5,000 events per second, samples were diluted accordingly. *T. pyriformis* were counted in an improved Neubauer (> 10 cells per microlitre) or a Fuchs-Rosenthal (< 10 cells per microlitre) counting chamber.

Time series analysis

We analysed each time series through generalized additive models (GAMs) (Wood 2011) and generalized linear models to analyse both the amplitude and general average trend of the times series. As populations are integers and our data showed overdispersion, we used quasipoisson models. Subsequently, we simulated 1,000 data points for each time series according to the single model results via the predict function in R. We divided the results of the GAM model by the results of the generalized linear model model to calculate the normalized time-series values. We subsequently analysed at what time-step extrema of the population densities occurred (Kim & Oh 2013) and calculated the resulting normalized amplitudes. We added the corresponding sequence number of the amplitude within a independent time series for further analyses (that is, amplitude 1, amplitude 2). Amplitude strength was analysed using ln-transformed normalized amplitudes as a function of sequence number, Arrhenius temperature and squared Arrhenius temperature and the interaction between both temperature terms with the amplitude sequence number. To ensure independence of data, we used linear mixed effects models (Pinheiro *et al.* 2013) with time-series identity and nested taxonomic group as random effects as well as a temporal correlation of the dependence of amplitudes to amplitude sequence number (corAR1()) (Zuur 2009). We selected models according to the penalized log-likelihood (Akaike's Information Criterion) using Maximum Likelihood (method=”ML”) while subsequently testing the resulting model again with the Restricted Estimates Maximum Likelihood Method (method = “REML”) (Zuur 2009). Furthermore, we analysed how minima and maxima of these predicted average time series behave with temperature and time for systems where the predator survived and systems where the predator went extinct by using the quantile regression at a level of 0.05 and 0.95 (function “qr” in R). To avoid transient dynamic effects, we deleted the first 200 h from the predicted values.

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Chapter 3

'Trophic Whales' as Biotic Buffers

Weak Interactions Stabilize Ecosystems against Nutrient Enrichment.

Florian Schwarzmüller, Nico Eisenhauer, Ulrich Brose

Summary

1. Human activities may compromise biodiversity if external stressors, such as nutrient enrichment, endanger overall network stability by inducing unstable dynamics. However, some ecosystems maintain relatively high diversity levels despite experiencing continuing disturbances.

2. This indicates that some intrinsic properties prevent unstable dynamics and resulting extinctions. Identifying these 'ecosystem buffers' is crucial for our understanding of the stability of ecosystems and an important tool for environmental and conservation biologists. In this vein, weak interactions have been suggested as stabilizing elements of complex systems, but their relevance has rarely been tested experimentally.

3. Here, using network and allometric theory, we present a novel concept for *a-priori* identification of species that buffer against externally induced instability of increased population oscillations via weak interactions. We tested our model in a microcosm experiment using a soil food-web motif.

4. Our results show that large-bodied species feeding at the food web's base, so called 'trophic whales', can buffer ecosystems against unstable dynamics induced by nutrient enrichment. Similar to the functionality of chemical or mechanical buffers, they serve as 'biotic buffers' that take up stressor effects and thus protect fragile systems from instability.

5. We discuss trophic whales as common functional building blocks across ecosystems. Considering increasing stressor effects under anthropogenic global change, conservation of these network-intrinsic biotic buffers may help maintain the stability and diversity of natural ecosystems.

keywords: consumer-resource interactions, food-web motifs, nutrient enrichment, stability, time series, weak interactions, biodiversity, cul-de-sac, anthropogenic stressors

Introduction

Human activities impose external stressors on natural communities, such as species invasions, global warming, habitat destruction or nutrient enrichment (Sala *et al.* 2000). These effects are threatening the biodiversity and functioning of ecosystems either immediately or via lagged dynamical responses in terms of increased population oscillations within complex food webs (Sala *et al.* 2000; Hooper *et al.* 2005; Montoya, Pimm & Solé 2006; Tylianakis *et al.* 2008). A recent review of consumer-resource theory (Rip & McCann 2011) stated that, in a consumer-resource system, all processes that increase net energy flux to the consumer increase the variability of species populations and in the end reduce system stability (Rip & McCann 2011). Hereafter, we follow this approach and refer to factors that increase temporal variability in population densities as destabilizing and to those that decrease the variability as stabilizing or dampening while addressing how natural ecosystems avoid dynamic instability and which intrinsic properties of food-web structure can prevent resulting extinctions (McCann 2000; Montoya *et al.* 2006).

A well-known theory concerning induced instability is the 'paradox of enrichment' (Rosenzweig 1971), which predicts that increased nutrient availability can drive consumer-resource interactions into severely unstable dynamics. Many empirical and theoretical studies have identified effects that stabilize against induced instability (Rooney *et al.* 2006; Brose *et al.* 2006; Otto *et al.* 2007), and the concept of 'weak interactions' balancing unstable dynamics remains centrally important (McCann *et al.* 1998; O'Gorman & Emmerson 2009). Although weak interactions can stabilize simple food-web motifs (McCann *et al.* 1998), they do not necessarily stabilize complex webs when distributed randomly across trophic links (Gross *et al.* 2009). In natural food webs, however, the strengths of trophic interactions are not randomly distributed as they depend on consumer and resource body masses (Brose *et al.* 2008; Rall *et al.* 2011) that are tightly correlated with the trophic position and the linkage density of the species (Riede *et al.* 2011; Digel, Riede & Brose 2011). Here, we expand weak interactions theory (McCann *et al.* 1998) by systematically relating interaction strengths (IS) to species body masses (Box 3.1). Specifically, empirically supported decreases in per unit biomass metabolic and relative feeding rates with individual body masses (Yodzis & Innes 1992; Brown *et al.* 2004; Brose *et al.* 2008; Ehnes *et al.* 2011; Rall *et al.* 2011, 2012) imply that per unit biomass IS decrease with the body-mass ratio between the consumer and its resource. Hence, the largest consumers impose the weakest per unit biomass interactions on a resource (see also Box 3.1).

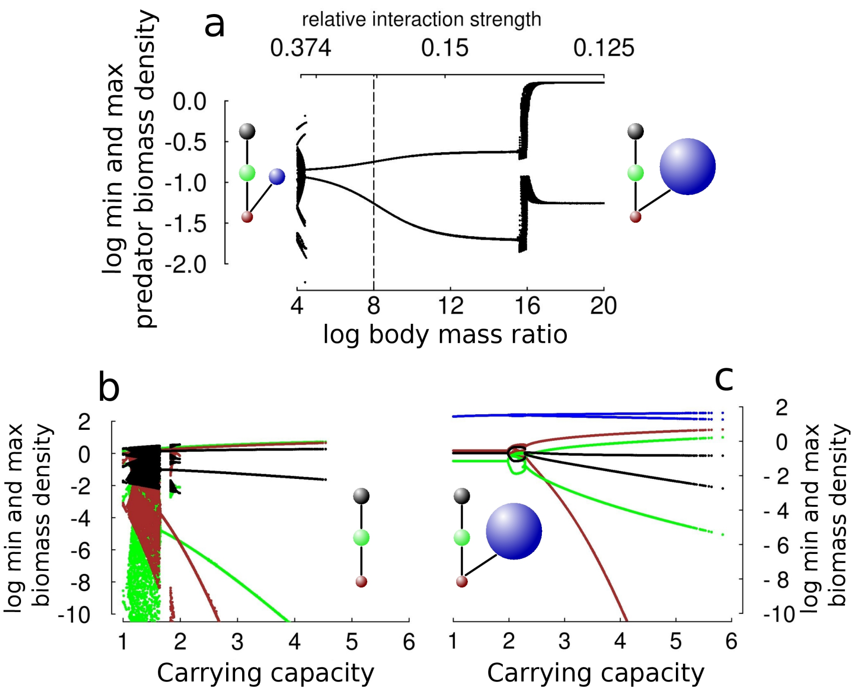

Figure 3.1 Allometric concept of weak interactions.

*(**a**) An increasing body-mass ratio (lower x-axis) of the additional consumer (blue) affects population dynamics of the top predator (black). This is the same as a decreasing relative interaction strength between both consumers (blue and green) on the shared resource (upper x-axis). We show the logarithmic minimal and maximal values of top-predator biomass. The vertical dashed line shows the body-mass ratio values used in (b) and (c).*

*(**b**) and (**c**) show the effect of increasing enrichment (carrying capacity) in absence (b) and presence (c) of an additional consumer with a logarithmic body-mass ratio to its resource of 8 (dashed line in a). The values shown are the logarithmic minima and maxima of species biomasses.*

The colours correspond to the trophic position of the species (brown= resource, green= consumer, black= predator, blue= additional consumer; see also Fig. 2) and the size of the blue nodes indicate the body size of the additional consumer.

In this study, we use a food-web motif that is known as the cascade-competition motif (Grover 1997), where the manipulated species (C_2) competes with the species on the same trophic level (C_1) via a common resource (R) and this competition effect cascades up to the predator level (P) (see motif in Fig. 3.1a and Fig. 3.2). We use this model as it is also employed by the classic weak-interaction theory (McCann *et al.* 1998; Hulot & Loreau 2006) and illustrates the effect of adding a new interaction to a food chain. In contrast to these prior studies, however, we add an allometric approach of IS (Box 3.1) converting changes in interaction strengths via, for example, assuming skewed feeding preferences (McCann *et al.* 1998), into changes in species body-masses. The cascade-competition motif consisting of a food-chain of strong interactions and an additional consumer with a weak interaction therefore translates into a food-chain with small predator-prey body-mass ratios and an additional consumer with a large body-mass ratio to the shared resource.

Box 3.1. Interaction strengths

Interaction strengths (IS) quantify the impact of one species presence on one or multiple other species. In terms of biomasses, the strength of an interaction of species i on species j is calculated as the logarithmic ratio of j's biomass in presence of i to its biomass in absence of i (Otto *et al.* 2008)

$$IS_{ij,N,M} = log_{10}\left(\frac{B_j^{+i}}{B_j^{-i}}\right) \qquad \text{B1.}$$

This is called a **population level** interaction strength ($IS_{N,M}$) as it gives the effect of a whole population of the species on another. The effect of one individual of species i is called **per-capita** interaction strength (IS_M) and can be obtained by dividing the population level IS by the species abundance (N) (Berlow 1999)

$$IS_{ij,M} = \frac{IS_{ij,N,M}}{N} \qquad \text{B2.}$$

The same value of population level IS can thus result from two different scenarios. A large bodied predator, for example, exerts a strong per-capita IS on its prey. However, its abundance is relatively low. The population level IS is the product of per-capita IS and abundance. This means, the same value is given by a small species, exerting a low per-capita IS but having a high abundance (Schneider *et al.* 2012).

For biomass models, it is often more useful to calculate a biomass based IS. We can calculate the **per unit biomass** interaction strengths (IS) by dividing the per-capita IS by the body mass of the species or by dividing the population level IS by the total biomass of the species:

$$IS_{ij} = \frac{IS_{ij,M}}{M} \text{ or } IS_{ij} = \frac{IS_{ij,N,M}}{N \cdot M} \qquad \text{B3 and B4.}$$

With this, we can predict per capita and population-level IS from biomass-level processes like growth and feeding. Following metabolic theory (Brown *et al.* 2004), we assume a stronger per-capita IS but a lower per unit biomass for larger bodied species. This is due to the fact that biological rates like feeding and metabolism increase with body mass with a slope lower than 1 (see model description).

The concept of 'trophic whales'

In order to identify these possibly stabilizing elements of natural systems, we have to bare in mind three nested concepts: (1) species that have no predators are generally referred to as 'top species'. This includes top-predator species as well as large herbivores or toxic or unpalatable animals or plants. (2) The recently developed concept of trophic 'cul-de-sac' species (Bishop *et al.* 2007) addresses species that (i) are top species and (ii) additionally drain away energy from the rest of the food-web. This does restrict the set of top species to those that are in a direct resource competition with a food-web or a sub-part of a food web. However, whether they impose a stabilizing or a destabilizing effect on the community will largely depend on the relative interaction strengths (Fig. 1a and (McCann *et al.* 1998). (3) Following the allometric concept of weak interactions (Box 3.1), stabilizing effects are associated with high individual body-masses. Nesting these three approaches, we end up with species that (i) have a high individual body mass and thus a low per unit biomass feeding rate, (ii) consume basal resources of the food webs, and (iii) are almost invulnerable to predation. By this, we mean that they are not consumed by species within the same food web or sub-web, at least not to an extent that feeds back on their own biomass (top-down control) or the biomass of their competitors (via apparent competition). We will subsequently refer to this class of species as 'trophic whales' as the most incisive example for this class of species are the baleen or whalebone whales feeding on zooplankton that is representing the resource for nearly all other species within the marine pelagic ecosystem (Hop *et al.* 2002). The energy provided by low trophic levels therefore benefits either the whales or the rest of the food web. The fact that whales have much higher body masses than other species also leads to an invulnerability to predation in their adult life stage. In other ecosystems, the trophic and allometric niche of whales corresponds to those of earthworms competing with small microarthropods (Maraun *et al.* 2001; Eisenhauer 2010), planktivorous ducks competing with fish (White, Veit & Perry 2009) or herbivorous mammals that share their resource with a web of small arthropods (Elia *et al.* 2010), just to name a few examples.

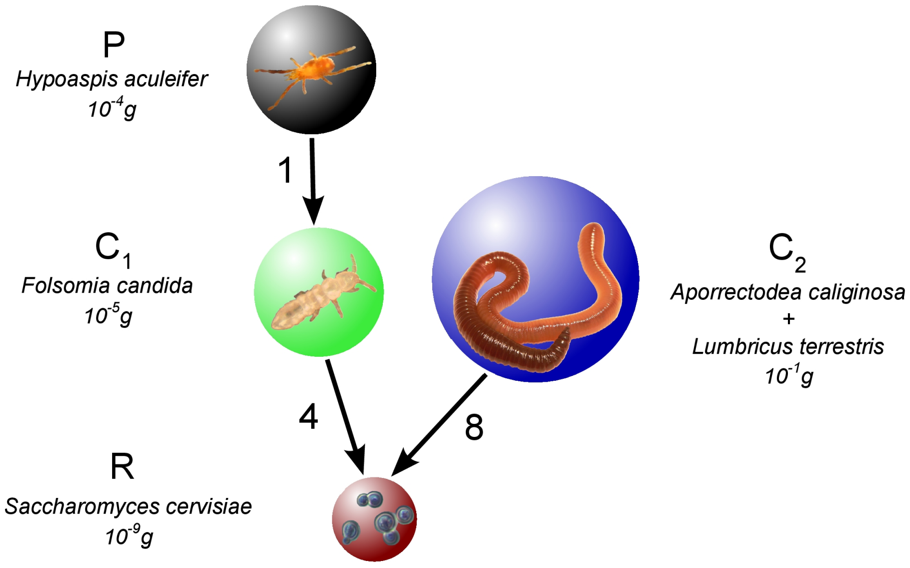

Figure 3.2 Experimental setup. *The soil food-web motif we chose contains a cascade competition between a food chain (R-C_1-P) and a trophic whale (C_2). Species body masses were rounded from empirical data to the next order of magnitude. The arrows indicate feeding interactions with the numbers showing the corresponding consumer-resource log body-mass ratio.*

Hypotheses

In this study, we hypothesized that trophic whales represent biotic buffers against external stressors such as nutrient enrichment. Their large body mass yields weak per-unit biomass IS that have previously been shown to stabilize oscillating cascade-competition motifs (McCann *et al.* 1998). We quantify this effect using exemplary model analyses and identify ranges of trophic whale body masses that prevent unstable dynamics and species loss due to nutrient enrichment. To provide an empirical test of this concept, we studied two different soil food-web motifs composed of soil microorganisms as the basal resource: a food chain of microarthropods (springtails and mites) and the cascade competition motif including earthworms as trophic whales (Fig. 3.2). We explored the effects of (1) enrichment and (2) the presence of earthworms on biomass densities and population dynamics. We hypothesized that (H 1) enrichment increases (1a) species biomasses and (1b) the amplitude of consumer-resource dynamics, and (H 2) earthworms (2a) reduce biomasses and (2b) dampen oscillations in the food chain.

Materials and methods

Model derivation and simulation

Following McCann, Hastings & Huxel (1998), maximal per capita IS, I_{ji}, of a consumer j on a resource i is defined as:

$$I_{\mathrm{ji}} = \frac{\Omega_{\mathrm{ji}} X_j Y_j}{B_0} \qquad (3.1),$$

where Ω_{ji} is the preference of consumer j for the resource i; X_j is the mass-specific metabolic rate of species j; Y_j is a measure of ingestion rate per unit metabolic rate of species j; and B_0 is the half saturation density of the functional response. The strength of an exploitative competition between two consumer species, C_1 and C_2, can therefore be expressed as the quotient of their interaction strength on the shared resource R:

$$\frac{I_{C_2R}}{I_{C_1R}} = \frac{\Omega_{C_2R} X_{C_2} Y_{C_2}}{B_{0_2}} \cdot \frac{B_{0_1}}{\Omega_{C_1R} X_{C_1} Y_{C_1}} \qquad (3.2).$$

We used a simple model without assuming additional parameters for which we don't have empirical evidence. Thus, we used a model without active preferences

$$\Omega_{C_1R} = \Omega_{C_2R} \qquad (3.3),$$

but with equal ingestion rates

$$Y_{C_1} = Y_{C_2} \qquad (3.4),$$

and negative quarter power-law scaling of metabolic rates with body masses (Brown *et al.* 2004)

$$X_{C_1} = X_0 \cdot M_{C_1}^{-\frac{1}{4}}; \quad X_{C_2} = X_0 \cdot M_{C_2}^{-\frac{1}{4}} \qquad (3.5), \text{ and } (3.6),$$

where the metabolic rate of a species (X_j) is dependent on an intercept (X_0) and its bodymass (M_j).

Relative IS as a measurement of a competition strength therefore only depends on the competing species' body masses,

$$\frac{I_{C_2R}}{I_{C_1R}} \propto \left(\frac{M_{C_2}}{M_{C_1}} \right)^{-\frac{1}{4}} \qquad (3.7).$$

With M_{C1} held constant the only changing factor during the simulation was the body size of C_2 (M_{C2}). To model population dynamics, we used a consumer-resource model (Yodzis & Innes 1992) with new allometric coefficients (Ernest *et al.* 2003; Brown *et al.* 2004) which we extended to a multi-species system (Brose *et al.* 2005b, 2006; Heckmann *et al.* 2012). General simulation parameters were chosen according to previous modelling studies (Otto *et al.* 2007; Rall *et al.* 2008): Maximum consumption rate was held constant at y=8, the feeding rates followed a type II functional response and the half-saturation densities were B_0= 0.5 for the top-predator (P) and the intermediate consumer species within the food chain (C_1) and B_0= 2 for the additional consumer (C_2) (for the exact formulas used within the model, see Supplementary Information S2). The extinction threshold was set to 10^{-30} g/m² (Otto *et al.* 2007; Rall *et al.* 2008). Simulations were run for 100,000 time steps (one time step is one generation time of the basal species), they were replicated 10 times, and for each time series 20 extreme values (minimal and maximal biomass values) were calculated. For the calculation, how top-predator (P) biomasses were influenced by the body size of an additional consumer (C_2), we held the carrying capacity constant (K= 3) and only varied the body size of C_2 (Fig. 3.1a). When all other parameters are kept constant, an increasing body size of C_2 resulted in a weaker exploitative competition strength (see eqn. 3.7). Then, we simulated the stabilizing effect of a trophic whale, a potentially stabilizing additional consumer, by first simulating a food chain under increasing enrichment (carrying-capacity gradient from 1 to 6) and then applied the same gradient to the cascade competition motif, the food chain with an additional consumer that had a body size of 10^8 times those of the basal species. The chosen body-mass ratios match those of the experimental system (Fig. 3.2).

Experimental setup

We conducted an experiment to test the assumptions and predictions of our model. We studied two different food-web motifs: (i) a three-species food chain and (ii) a cascade competition motif including an additional consumer species (Fig. 3.2). The food chain consisted of the springtail *Folsomia candida* (Willem 1902), a small fungivorous species that is well established in laboratory cultures, and as predatory species *Hypoaspis aculeifer* (G. Canestrini, 1884), a small gamasid mite that feeds on springtails. During the experiment, we manipulated soil microbial biomass, which was the basal resource in the system, via the addition of baker yeast *Saccharomyces cerevisiae* (Meyen ex -Hansen, 1883) according to three enrichment levels (0, 30 or 300 mg added per week), and as trophic whales we chose earthworms, here represented by juveniles of the two species *Aporrectodea caliginosa* (Savigny 1826) and *Lumbricus* *terrestris* (Linnaeus 1758). Both species serve as representatives for two different soil dwelling fungivores and two different ecological earthworm groups (endogeic and epigeic to anecic). Endogeic species (*A. caliginosa*) live in upper soil layers whereas anecic species' (*L. terrestris*) burrows can reach down to the mineral soil layer. However, juveniles of *L. terrestris* were shown to be more epigeic (feeding on the soil surface) (Briones, Garnett & Piearce 2005). We cannot exclude competition between the two earthworm species but their different ecology points to more complementary effects. Moreover, choosing two species of earthworms served as an insurance effect for our experiment. Small juveniles (between 50 and 100 mg) of *L. terrestris* are supposably more vulnerable to unfavourable environmental conditions while they can gain high biomass when conditions are optimal. Juveniles of *A. caliginosa* were slightly bigger (150-250 mg) and thus less vulnerable to poor conditions. Both species are well studied under laboratory conditions and can be sustained with low effort (Eisenhauer & Scheu 2008). The experiment was conducted in planar microcosms (20 cm length x 15 cm height x 1 cm width) within a temperature-controlled incubator. Microcosms were filled with 300 g of defaunated soil with a soil water content of ~ 25 %, closed and stored at 20 °C for several days. For defaunation the soil was preliminary frozen at -30 °C for several weeks then dried for two weeks at 60 °C. Subsequently, nutrients released during the defaunation were eluted with demineralized water. At the first day of the experiment, 50 individuals of *Folsomia candida* were put in each microcosm and one individual of each earthworm species was added to half of the microcosms. All springtail individuals had a similar body size (0.04 - 0.06 mg) to ensure synchronized populations in the different microcosms. Earthworms were weighed before the experiment and paired, so that their body masses added up to equal overall earthworm biomass across the experimental replicates (approximately 200 mg fresh weight including gut content). After an initial establishing phase of two weeks, 20 mites were added to the microcosms and the experiment ran for further 63 days. The initial species densities were in the range of empirically estimated densities in forest communities (Ehnes *et al.* 2014). Both motifs (i.e. the food chain and the cascade competition) were established at three nutrient enrichment levels that differed in the amount of yeast added. Level 1 received no fertilization, i.e. only 10 ml of demineralized water per week. Here the only basal resources were the remaining microorganisms in the defaunated soil. Level 2 received 30 mg and level 3 300 mg of yeast per week dissolved in 10 ml of demineralized water. We chose 300 mg per week as it is a resource supply-rate that by far exceeds natural levels of soil microbial biomass (Scharenbroch & Bockheim 2008). Hence, we could demonstrate the effect of massive anthropogenic nutrient input that is often far beyond those limits. In total, the experiment consisted of six different treatments (two motifs x three nutrient enrichment levels) each replicated six times yielding a total of 36 microcosms. The microcosms were kept without light at 20 °C and an air humidity between 60 and 80% to prevent drought. We chose complete dark conditions because we worked with planar microcosms that allowed studying animals in the soil (and measuring their abundances, see below) and wanted to exclude the effect of illumination on deeper soil layers. For fertilizing, watering, and picture taking (in order to measure springtail densities, see below), the microcosms were transferred to a separate climate chamber at 10-15°C for a maximum of 30 minutes. To take the pictures, the microcosms were additionally exposed to an artificial indirect illumination for 2 minutes.

At day 78, the experiment was terminated. Earthworms were collected and weighed, soil samples were taken to measure the microbial biomass via substrate induced respiration (see below) and springtails and mites were extracted by heat (Macfadyen 1953; Kempson, Lloyd & Ghelardi 1963).

Assessment of species abundances and biomasses

Time series of springtail abundances were measured by taking 10 pictures per week and microcosm (5 per planar side). These were afterwards processed via ImageJ (Magelhaes, Ram & Abramoff 2004) to calculate the average springtail density for each microcosm and point in time. We excluded the first three measurements (days 7, 14, and 21) to exclude the initial transient dynamics. Additionally, due to a massive defilement of the microcosms, we were not able to assess springtail abundance at the last time step (day 77). We therefore calculated temporal variation (amplitude) within a treatment as difference between the minimal and the maximal abundance between the days 28 and 70.

Microbial biomass was measured using an automated electrolytic microrespirometer (Scheu 1992) by quantifying the hourly O_2-consumption at 22°C. The substrate-induced respiration that is correlated with the microbial biomass (Beck *et al.* 1997) was calculated from the respiratory response to D-glucose (Anderson & Domsch 1978). The earthworms were weighed (LE225D, d= 0.01 mg, Sartorius AG, D-37075 Göttingen) immediately before and after the experiment (body fresh weight including gut content). We pooled data of the two species and used logarithmic relative biomass ratios $\log_{10}$(biomass at the end / biomass at the beginning) for the statistics. Please see Supplementary Figure S2.1 and Supplementary Table S2.1 for a species specific analysis.

To examine the biomasses of springtails and mites after the experiment, the heat extraction samples were scanned at a resolution of 1200 dpi. We measured the area covered by organisms via ImageJ, which corresponded to mite plus springtail biomasses. The mites on the pictures were counted and the mean body length was measured (1 mm). We then calculated total species biomass using a mass-length regression for gamaside mites ($\log M[\mu g] = 2.064 + 2.857 \log L[mm]$; (Mercer *et al.* 2001)). In the same way, springtail biomass was calculated using a mass-length regression for springtails ($\log M[mg] = 0.662 + 2.439 \log L[mm]$; (Petersen 1975); mean springtail body-length was 0.7 mm) assuming that the rest of the covered area corresponded to springtail biomass.

Statistical analyses

We used ANOVAs in R (R Core Team 2012) to assess the impact of the two independent variables 'enrichment' and 'earthworms' on the dependent variables: biomasses of microbes, springtails and mites, biomass ratios of earthworms, and on the time-series amplitudes. The data were log-transformed prior to the analyses to achieve normal distributions and homogeneity of variances. To test more specifically whether the biomass or amplitude changes between different motifs or different enrichment levels were significant, contrast analyses of the mean of one treatment with other means were employed. The experimental design based on the pre-experimental simulations and hypotheses allowed testing by *a-priori* contrasts.

Results

Modelling

Analysing the bioenergetic model (Fig. 3.1a), we see the effect of an increasing body-mass of C_2 (indicated by its log body mass ratio to the resource on the lower x-axis) on the minima and maxima of the biomass density of the predator species (P). The area at very low log body-mass ratio values (< 5) shows multiple maxima and minima indicating chaotic population dynamics. Increasing the body-mass ratio of C_2 led to limit cycle dynamics (oscillations between one minimum and one maximum, 5 < log body-mass ratio < 15). The difference between the log minima and maxima is increasing within the limited cycle area, indicating accelerating oscillations. The upper x-axis shows the corresponding relative IS (following (McCann *et al.* 1998)**)**. Please note that the upper x-axis is inverse, indicating higher values of relative interaction strengths at lower body-masses of C_2 (see methods section for the conversion between body-mass ratios and relative IS). The dashed line at a log body mass ratio of 8 was taken to produce Fig. 3.1c as it is exactly the body-mass ratio of the animals in our experiment (see Fig. 3.2). Fig. 3.1b shows the effect of an increasing carrying capacity (x-axis) on the minimum and maximum biomass densities in a three-species food-chain. The steep increase in the distance between minima and maxima indicates strongly accelerating population dynamics of resource (brown) and consumer species (green). At a carrying capacity of 4.5 the minima of the basal species fell below the extinction boundary (10^{-30} g/m^2), and as a consequence all species died out. In Fig 3.1c we see the same gradient of carrying capacity but this time affecting the cascade-competition motif consisting of a three-species food-chain (same as in Fig. 3.1b) and an additional consumer (C2) with a log body-mass ratio to the resource of 8 (indicated by the dashed vertical line in Fig 3.1a and consistent with the experimental species C2 in Fig. 3.2). At very low carrying-capacity values, the system was in an equilibrium state, and increasing the carrying-capacity up to a value of 2 did not have any effect (except for a very small increase in biomass density of C2). At higher values, we found a Hopf-bifurcation leading to limit cycle dynamics. There was no state of chaotic oscillations in this model. The point at which minima of the resource species hit the extinction boundary is delayed compared to the food-chain model (at a carrying capacity of 5.8).

Table 3.1 Statistical analyses. *ANOVA table of the effects of enrichment (factorial variable with three levels), earthworms (factorial variable with two levels) and the according interaction term on the biomasses of microorganisms, springtails and mites at the end of the experiment and on the amplitude within the time series of springtail abundance, as well as the effect of enrichment on relative earthworm biomass ratios. The asterisks indicate significant values: ' *** ' = $p \leq 0.001$; ' * ' = $p \leq 0.05$*

		Biomass [log$_{10}$ mg]												**Time series of springtail abundance**		
		Microorganisms			Springtails			Mites			Earthworm (biomass ratios)			Amplitude		
	df	F	p		F	p		F	p		F	p		F	p	
Enrichment	2	5.25	0.011	*	122.9	< 0.001	***	164.4	< 0.001	***	31.1	< 0.001	***	2.16	0.133	
Earthworms	1	1.17	0.288		0.39	0.538		0.07	0.787					18.2	< 0.001	***
Enrichment x Earthworms	2	0.75	0.482		5.10	0.017	*	3.52	0.042	*				4.25	0.024	*
Residuals[1]	30															

[1] Degrees of freedom (df) for residuals for 'Earthworm (biomass ratios)' were 15.

Experiment

ANOVAs (Table 3.1) showed that springtail and mite biomasses and the amplitude of springtail abundance oscillations responded significantly to the interaction between nutrient enrichment and earthworms, indicating that nutrient enrichment had a different effect depending on whether earthworms were present or not. Microbial biomass was not affected by the interaction term, but it responded significantly to nutrient enrichment (ANOVA, Table 3.1). Similarly, the relative earthworm biomass ratios $\log_{10}$(biomass at the end of the experiment / biomass at the beginning) were significantly influenced by nutrient enrichment.

Contrast analyses of springtail and mite biomasses (Fig. 3.3b,c) revealed how nutrient enrichment and earthworm-presence effects interacted: Without earthworms (black boxes), the biomasses of springtails (Fig. 3.3b) and mites (Fig. 3.3c) increased significantly in response to both nutrient enrichment steps, from low (0 mg) to intermediate (30 mg) (springtails: $F_{1,10}= 9.94$, $p= 0.01$; mites: $F_{1,10}= 26.22$, $p< 0.001$) and from intermediate to high nutrient enrichment (300 mg; springtails: $F_{1,10}= 25.81$, $p< 0.001$; mites: $F_{1,10}= 159.00$, $p< 0.001$). With earthworms (grey boxes) only the step from intermediate to high nutrient enrichment resulted in significantly higher biomasses of springtails ($F_{1,10}= 134.50$, $p< 0.001$) and mites ($F_{1,10}= 88.45$, $p< 0.001$) whereas, at the intermediate level, the addition of earthworms reduced springtail and mite biomass significantly (springtails: $F_{1,10}= 4.95$, $p= 0.050$; mites: $F_{1,10}= 6.85$, $p= 0.026$). Earthworm presence thus delayed the effect of nutrient enrichment.

Earthworm biomass ratios (Fig. 3.3d) increased significantly with both nutrient enrichment steps (low to intermediate: $F_{1,10}= 7.37$, $p= 0.02$; intermediate to high: $F_{1,10}= 24.08$, $p< 0.001$). While earthworms lost biomass during the experiment at the low nutrient-enrichment level (negative log-ratio values), they sustained at the intermediate level (log-ratio values around zero), and only under high nutrient enrichment they were able to build up biomass (positive log-ratio values). Please see Supplementary Figure S2.1 and Supplementary Table S2.1 for a species specific analysis. Contrast analyses showed that microbial biomass did not differ significantly between two distinct nutrient-enrichment levels (Fig. 3.3a) and at low nutrient enrichment the presence of earthworms increased microbial biomass ($F_{1,10}= 5.57$, $p= 0.04$).

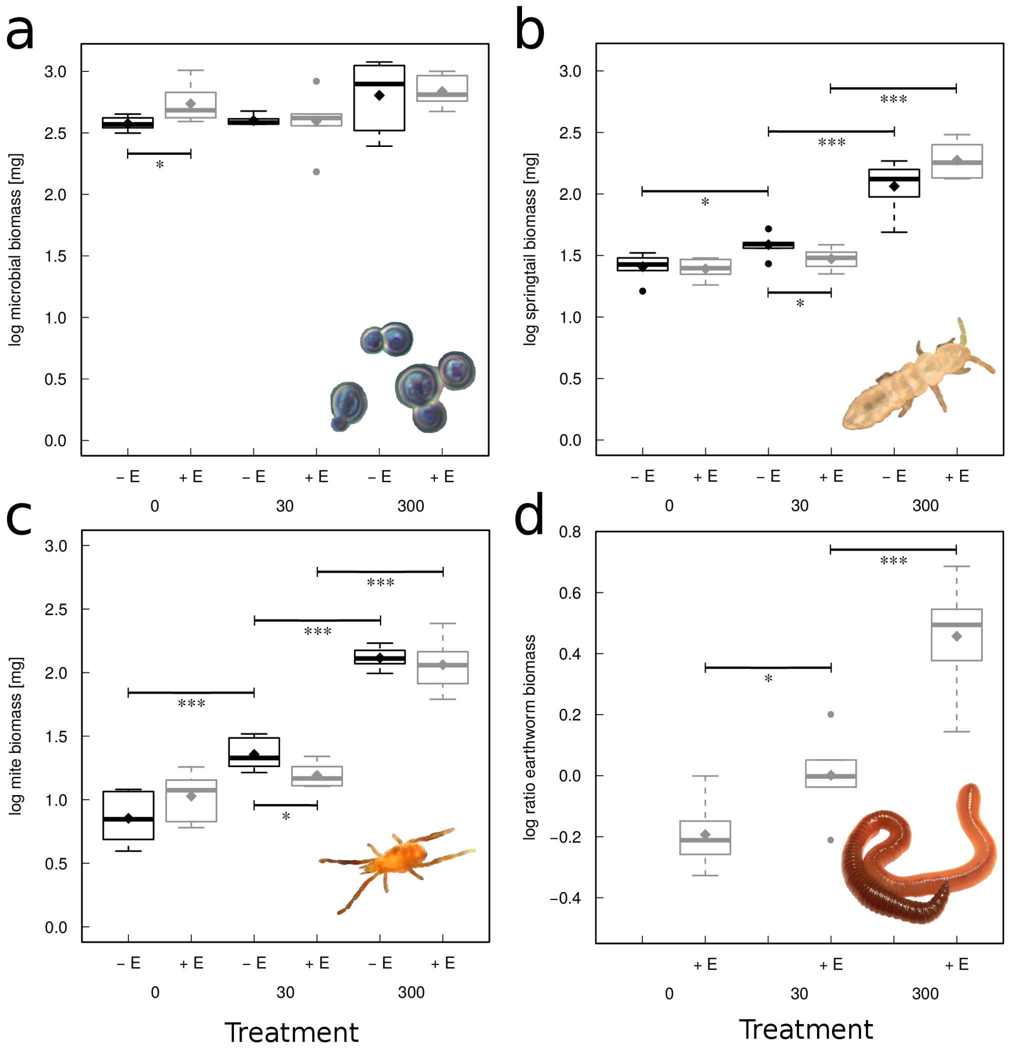

Figure 3.3 Species biomasses. *Biomasses of microbes (**a**), springtails (**b**), mites (**c**) (log transformed data) and relative biomass ratios of earthworms (log[biomass at the end/biomass at the beginning of the experiment]) (**d**) at different enrichment levels (0, 30, 300 mg of yeast added per week) and in the absence (black, -E) or presence (grey, +E) of earthworms. Boxes include 50% of the data from Q25 (or 1st quartile) to Q75 (or 3rd quartile), diamonds indicate mean, bars indicate median (or 2nd Quartile), whiskers are minimal and maximal values of the data excluding outliers (circles). Outliers are exceeding a 95% confidence interval. The significance indexes result from the contrast analyses between the pairs of treatments indicated by the horizontal whiskers, where ' *** ' = $p \leq 0.001$; ' * ' = $p \leq 0.05$. Non-significant p-values are not shown.*

Results of the time-series analyses show that springtail populations underwent one oscillation cycle during the experiment with a peak around day 48 and a minimum towards the end of the experiment (day 57). Mean and peak abundances were lower when earthworms were present (Fig. 3.4a), whereas nutrient enrichment had only a marginal effect. As a measurement of the population stability during the experiment, we used the amplitude of the time series being directly related to the minima/maxima-biomass analyses used in the theoretical framework (Fig. 3.1a).

Enrichment had no significant effect on time-series oscillations when no earthworms were present (Fig. 3.4b), whereas the stabilizing effect of earthworms increased at the high nutrient-enrichment level: the amplitude decreased significantly between intermediate and high enrichment ($F_{1,10}$= 7.95, p= 0.018) and at high enrichment between the treatments with and without earthworms ($F_{1,10}$= 25.59, p< 0.001). Data shown in Figs. 3.3 and 3.4 is also provided online (Schwarzmüller 2014).

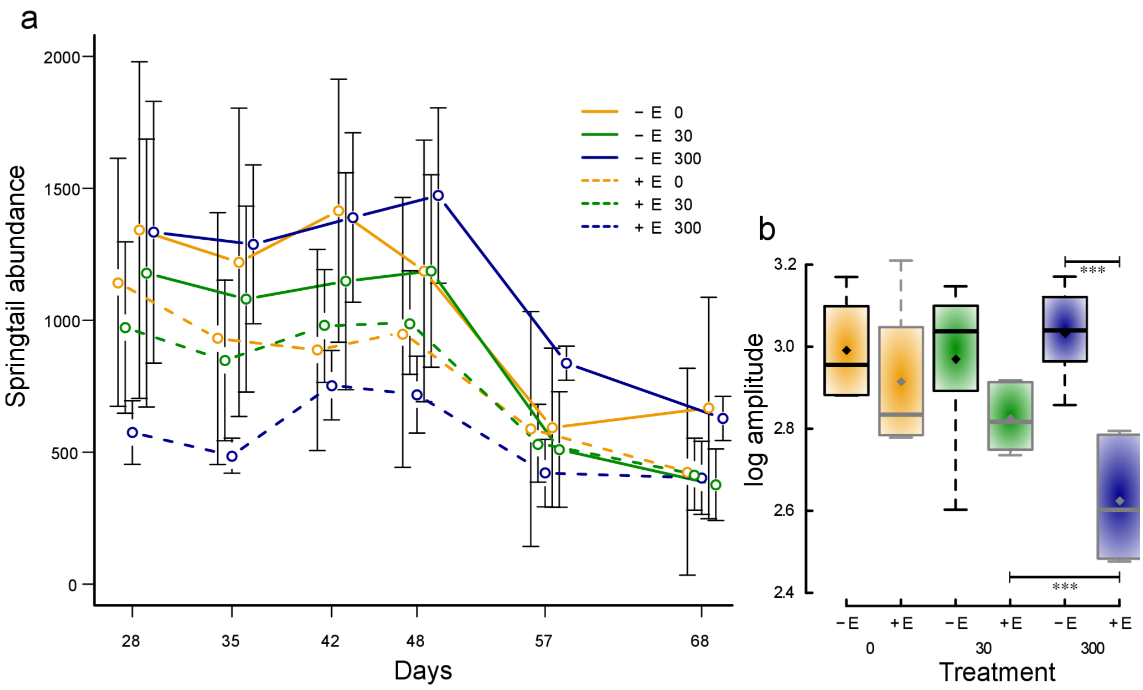

Figure 3.4 Springtail population dynamics. ***(a)*** *Time series of springtail abundance at different enrichment levels (0 [orange], 30 [green], 300 [blue] mg of yeast added per week) and in the absence (solid, -E) or presence (dashed, +E) of earthworms. The dots indicate the mean value within the replicates and the whiskers are the standard deviation. The data points are jittered to improve visualization.*

(b) *Log transformed amplitude values within the time series at different enrichment levels (colours correspond to (a) and in the absence (black, -E) or presence (grey, +E) of earthworms. Boxes include 50% of the data from Q25 (or 1st quartile) to Q75 (or 3rd quartile), diamonds indicate mean, bars indicate median (or 2nd Quartile), whiskers are minimal and maximal values of the data. The significance indexes result from contrast analyses between pairs of treatments indicated by the horizontal whiskers. The coding is: ' *** ' = p ≤ 0.001. Non-significant p-values are not shown.*

Discussion

Stability of both, natural ecosystems and complex theoretical ecosystem models depend on the distribution of interaction strengths between species (de Ruiter, Neutel & Moore 1995; Neutel *et al.* 2007; Heckmann *et al.* 2012). While equally or randomly distributed IS lead to an instability of complex theoretical systems (Gross *et al.* 2009), natural ecosystems often combine high complexity and variability in IS with high stability. This suggests that a more realistic distribution of IS would lead to more reliable predictions (Ings *et al.* 2009). Recent ecosystem models therefore account for species traits such as body mass, which causes a non-random distribution of interaction strengths within food webs. In this study, we synthesize theory on weak trophic interactions with allometric models of IS (Brose *et al.* 2008; Vucic-Pestic *et al.* 2010; Rall *et al.* 2011, 2012). This synthetic theory predicts non-random stabilizing configurations of species, body masses and interactions. Specifically, we predict that large-bodied basal-feeding species, the trophic whales, can buffer food webs against instability that is induced by external stressors such as nutrient enrichment. These predictions found support in a microcosm experiment with earthworms as trophic whales. Together, these results suggest that trophic whales may represent important keystone species that buffer natural ecosystems against externally induced instability, specifically nutrient enrichment.

Estimating interaction-strengths using allometric theory

While the classic weak-interactions concept identified ranges in relative IS (Fig. 3.1a: upper x-axis) preventing unstable oscillations in the cascade-competition motif, the allometric concept allows converting this in ranges in body-mass ratios (Fig. 3.1a: lower axis) yielding dampened population oscillations (Fig. 3.1a, log body-mass ratios of 4.5 to 15) similar to those of a direct manipulation of IS via skewed feeding preferences. In contrast, the per unit biomass consumption rates of the smallest cascade competitors (Fig. 3.1a, left) are too high to prevent unstable oscillations, whereas those of the largest cascade competitors are too small to invade the system and drain energy away from the food chain (Fig. 3.1a, right). The stabilizing effect between these two extremes is achieved by the low per unit biomass respiration, which leads to a massive biomass gain of the additional consumer and thus ensures a constant energy drain away from the food chain. Because of the low per unit biomass consumption rates, the bottom-up forces do not generate additional top-down pressure typically producing the feedback-loop of accelerating oscillations. This allometric concept allows an *a-priori* identification of weak interactions without assuming skewed feeding preferences (McCann *et al.* 1998) or evaluation by pre-experiments (O'Gorman & Emmerson 2009; Rip *et al.* 2010). Moreover, this novel concept allows bridging the gap between theoretical advances and experimental tests by (1) allowing estimation of IS by species body sizes, and (2) providing simple testable hypotheses concerning stability in ecosystems.

Experimental results support the proposed stabilizing effect

Our experimental results show that trophic whales, here represented by earthworms, stabilize enriched food chains and prevent dynamic instability by accumulating biomass. This confirms our biomass-related hypotheses, that enrichment increases species biomasses (H 1a) and that competition with earthworms reduces this effect (H 2a). However, the results also indicate that competition with trophic whales only influences species' biomasses at moderate levels of enrichment. At low enrichment, earthworms had a positive effect on microbial biomass, which is consistent with other empirical data reporting elevated resource availability due to the excretion of nutrient-rich mucus and casts and the stimulation of microbial biomass and activity (Eisenhauer 2010). Negative biomass effects of the earthworms on the biomasses of springtails at intermediate and high resource levels were due to competition for food. Possibly direct negative effects of earthworms on springtails due to feeding of eggs or individuals can be neglected as they occur very rarely (Gutierrez Lopez *et al.* 2006). We are aware, that this experiment is only a snapshot of a more complex ecosystem response to nutrient addition as on a longer time scale earthworms might also show a numeric response to the different resource availabilities. However, we chose this very mechanistic approach to make the earthworm effect invariable over time, thus sustaining a non dynamic and constant energy drain.

Many empirical studies about enrichment effects support the theoretical concept of energy drains, the trophic whales. They show similar patterns of biomass distribution when looking at comparable food-web motifs: enrichment led to a massive biomass gain of an unpredated basal-feeding species that channels energy away from the food web and reduced susceptibility to enrichment of ecosystems containing trophic whales. A recent field study, for example, shows that moose as large herbivores compete with the below-ground system for plant derived resources (Elia *et al.* 2010). Similar to our study, the trophic whales, here represented by moose, reduced biomasses of springtails and mites at medium resource and moose densities. Moreover, consistent with our conceptional expectations, field studies in forest ecosystems demonstrated that earthworms were the only group of soil organisms reacting to fertilization with glucose, whereas the micro-arthropod food web was virtually unaffected (Joergensen & Scheu 1999; Maraun *et al.* 2001). Here, the accumulation of earthworm biomass most likely buffered effects on all other taxa. Similarly, in the Ecuadorian rain-forest, cockroaches presumably represent this trophic position, and they were among the few species responding with biomass gain to enrichment (Sandmann 2007). Certainly, the species of these examples might have some consumers in natural ecosystems. As a general pattern, however, they are not under top-down control by other consumers of the same food web. Hence, they can sustainably drain energy out of the food web. This energy drain away from food-webs has recently been summarized under the concept of 'trophic cul-de-sacs' (Bishop *et al.* 2007). In their paper, they formulated two conditions for a species to serve as a trophic cul-de-sac: 'a species must firstly act as an energy sink and secondly be free of predators' (Bishop *et al.* 2007). Concerning our approach of trophic whales, we would add a third condition: the weak IS as a result of their high body-mass ratios to the resource (Box 3.1). This difference between trophic whales and trophic cul-de-sac has important dynamic consequences. Adding another unpredated consumer irrespective of its body mass does not necessarily stabilize systems (see Fig. 3.1a or McCann *et al.* 1998). Thus, trophic whales combine the concepts of trophic cul-de-sacs and weak interactions to specify a specific class of species that have the potential to buffer natural ecosystems against unstable dynamics induced by nutrient enrichment.

In our study, we applied an experimental design that allowed addressing the predictions of the trophic-whale concept by time-series analyses via a novel visualization technique. The analyses of the time series show that earthworms had a stabilizing effect on the dynamics of springtail populations. Because of the competition for food with earthworms, the growth of springtail populations decreased, and by lowering the peak of the oscillation, earthworms reduced the amplitude within the time series (H 2b). However, we did not find any support for our expectation that enrichment causes stronger oscillations in springtail abundance (H 1b). This was perhaps due to the massive defilement of the highly fertilized microcosms where yeast and springtail faeces reduced the detectability of springtail individuals. Also, it could be noted that the springtail individuals within the highly fertilized microcosms were smaller and not all of them might have been detected via picture analyses. Nevertheless, as shown in comparable studies (O’Gorman & Emmerson 2009) even such short time series can serve as an additional hint on how parameters affect population dynamics.

Two recent studies addressed effects of weak interactions on population dynamics. O'Gorman and Emmerson (O’Gorman & Emmerson 2009) found that weak interactors in a diverse marine benthic community, whose strengths were determined in a pre-experiment, reduced variability in both primary and secondary production. Secondly, Rip and colleagues (Rip *et al.* 2010) showed that the interplay between weak and strong interactions, here the coupling of a weak and a strong interaction via a common predator, tends to stabilize experimental food webs, as weak interactions introduce negative covariance to mute strong interactions. Both studies suggest a dampening effect of weak interactions similar to our findings and consistent with theory. The novelty of our approach lies in the *a-priori* prediction of IS by species body-mass ratios. This allometric theory allowed for the first time testing effects of weak interactions in the classic cascade competition module employed by the founding theory (McCann *et al.* 1998) while generalizing the findings across an enrichment gradient as an example of an external stressor.

Caveats

Due to our experimental approach of measuring abundances via picture analyses we were technically not able to obtain time-series of the other food-chain species: mites and microbes. However, we assume that, because of the tight coupling by strong feeding interactions, looking at the intermediate species of the food-chain gives us some information about the overall dynamics along the food-chain.

The choice of species for the experiment also does not allow a clear distinction between the effect of adding a large-bodied trophic whale with weak interactions and the general effect of an additional cul-de-sac consumer irrespective of its body size. However, our exemplary model analyses suggest that adding a consumer (C_2) of the same size as C_1 would not stabilize the system (Fig. 3.1a). Several reasons prevented replication of our experiment with a smaller C_2 species. First, having two similarly sized springtails on yeast as the only resource leads to competitive exclusion of one of them (unpublished results based on lab cultivations). Second, a small C_2 species would most likely also be a prey of the predatory mites as the food-chain top predators, which would hamper their role as cul-de-sac. In other community types, however, disentangling effects of small-bodied cul-de-sac from trophic whales may be possible, which would allow an elegant test of our theory.

Analysing the earthworm data for each species separately (Supplementary Table S2.1 and Supplementary Figure S2.1) reveals that *L. terrestris* was extremely sensitive to the low and intermediate resource conditions. This was possibly due to the low starting weight of the respective individuals (around 50 mg). As the buffering effect of the earthworms was most pronounced at the intermediate resource level, we suppose that *A. caliginosa* was the species driving the pattern, which was also shown by the species-specific analyses presented in Supplementary Figure S2.1. However, *L. terrestris* showed a much higher gain in biomass~~es~~ at the highest resource level, which might point to a species-specific buffering range of trophic whales and should be addressed by subsequent studies.

Finally, our study focussed on a very small sub-part of real ecological systems. Studying the effect of trophic whales in larger networks might quantitatively change the results. However, we think that the stabilizing effect of trophic whales will qualitatively also hold in more complex systems, because the underlying stabilizing effect of weak trophic interactions has also been scaled up from modules to the food-web context (Berlow 1999; Brose *et al.* 2005b).

Conclusion

Our concept of trophic whales as buffering elements within food webs provides a novel mechanistic understanding of how natural ecosystems maintain their stability despite experiencing destabilizing external stressors such as nutrient enrichment. Comparable to buffers in chemical and mechanical systems, trophic whales increase the range in which their systems are stable and generally decrease the vulnerability to external influences. Chemical buffers ensure constant reaction conditions by converting strong into weak, less reactive acids, and mechanical buffers convert kinetic energy which might compromise fragile systems into deformation and, in the end, thermal energy. Similarly, trophic whales take up the 'biological' energy of enhanced resource growth and convert it into their own and – due to low per unit biomass consumption rates and invulnerability to predation - 'less reactive' biomass. Thus, they represent key organisms of many ecosystems with the potential to buffer anthropogenic enrichment of ecosystems. Organisms that fulfil this role in natural ecosystems should be a conservation priority or may serve as promising stabilizing tools in the restoration of enriched ecosystems. Trophic whales such as earthworms, large herbivorous mammals, fungivorous or detritivorous macro-invertebrates or planktivorous birds are common functional components of many ecosystems. Facing the threat of accelerating global change, our results suggest that these common ecosystem components may represent important biotic buffers preventing unstable oscillations in response to external stressors and thus maintaining ecosystem stability and diversity.

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Data Accessibility

Data of this manuscript is available online under http://dx.doi.org/10.6084/m9.figshare.1209443

Chapter 4

Energy fluxes in fragmented ecosystems

Dynamic stability of tri-trophic food chains under nutrient enrichment and habitat isolation

Abstract

Under ongoing global change, natural ecosystems experience a multitude of external stressors that often occur in combination. For example, land-use change affects the isolation and size of remaining habitats as well as their nutrient status. However, we are still lacking integrative ecological theory on how different drivers of global change interact. We studied the combined effects of habitat isolation and nutrient enrichment on the stability of a tri-trophic food-chain. We expanded bioenergetic models to spatially explicit systems of two habitat patches using empirically-derived allometric relationships of animal migration. We found that increasing habitat isolation causes top-predator starvation by weaker per-unit biomass energy influxes. While top predators can easily integrate across isolated habitat patches, the lower biomass densities of their resources that suffer from migrational loss in fragmented landscapes eventually cascades up the food chains. Moreover, we found strong interactions between stressors: the starvation effects of isolation were counteracted by nutrient enrichment that increased energy fluxes along the food chains. In consquence, habitat-isolation has stabilizing effects in eutrophic systems but undermines species diversity in oligotrophic systems. Overall, our mechanistic analyses on how external stressors interactively affect ecosystem energy fluxes provide deeper insights into the future global change of ecological communities.

Introduction

Increasing human land use and the resulting fragmentation and eutrophication of remaining natural habitats are two of the most prominent drivers of global change and cause extinctions of species worldwide (Pimm *et al.* 1995; Sala *et al.* 2000). Specifically, the Millennium Ecosystem Assessment identified the loss of natural habitats and their eutrophication as two of the major reasons for current and future biodiversity loss (Nelson 2005). Additionally, these two drivers are often associated with each other: expanding agricultural and urban areas yield fewer and more isolated habitat remnants, and the intensification of agriculture associated with higher nitrogen deposits increases their nutrient load. Both processes have tremendous effects on species diversity. While the fragmentation of habitats has stronger effects on large and high trophic level species (Hagen *et al.* 2012), nutrient enrichment can lead to overall ecosystem instability and extinction waves (Rosenzweig 1971; Rall *et al.* 2008). However, despite their striking and potentially interactive effects on biodiversity and system stability, these two major factors of global change have rarely been studied in combination (but see Fréville *et al.* 2007). In this study, we employ bioenergetic ecosystem models to address their interactive effects on the dynamic stability of a tri-trophic food chain.

Nutrient enrichment

The way in which excessive supply of basal resources undermines ecosystem stability has widely been studied (Rosenzweig 1971; McCann *et al.* 1998; Rall *et al.* 2008). While the additional energy initially boosts the growth of producer species, it ultimately leads to higher consumer biomass yielding stronger top-down pressure and thus again to a decline in resource biomass. This oscillation between high and low biomass densities propagates through the food web and is regarded as a sign of instability. The higher the amplitudes of these oscillations get, the more likely it is that one of the species goes extinct when reaching one of the biomass minima. More recently, this has been conceptualised as the “principle of energy flux” (Rip & McCann 2011) stating that processes that enhance energy fluxes to the consumer (relative to the consumer loss term) in consumer-resource systems increase the variability of species populations and ultimately reduce system stability.

Habitat fragmentation

Throughout the literature, habitat fragmentation in the context of land-use change is referred to as either habitat loss (fewer and smaller habitat patches) or habitat fragmentation *per se* (breaking apart of habitats leading to more but smaller habitats) (Fahrig 2003). This dichotomy has led to results that are often difficult to interpret. While habitat loss generally has a strong negative effect on biodiversity (Terborgh *et al.* 2001; Solé & Montoya 2006), the effect of habitat fragmentation *per se* is often much weaker and can be both negative or positive (Cooper *et al.* 2012). Both processes, however, only implicitly incorporate another important aspect of land-use change: the isolation of the remaining habitat patches, which has a major impact on immigration rates and, therefore, on their species composition and diversity (Theory of Island Biogeography MacArthur 1967; Gravel *et al.* 2011b). Interestingly, the consequences of these two processes for patch isolation are opposite, 'habitat loss' describes processes that decrease habitat size and increase patch isolation whereas 'habitat fragmentation *per se'* leads to smaller patches but lower isolation (Fahrig 2003). These differences in patch-isolation patterns might be the cause for the sometimes contradictory results. In this study, we therefore focus on the effect of patch isolation (measured as inter-patch distance) in dynamic models of tri-trophic food chains while leaving the size and the number of habitat patches unchanged.

Habitat fragmentation and the resulting uneven distribution of populations across a landscape also challenges ecological theory. Most theoretical studies assume well-mixed populations throughout the whole landscape and parametrise growth and feeding rates on the basis of this assumption. However, heterogeneity of populations can have strong effects on population stability (McCann, Rasmussen & Umbanhowar 2005). The uneven distribution of habitats across a landscape causes an uneven distribution of resources and thus an uneven distribution of species. In a fragmented landscape, we therefore have to distinguish between the remaining habitat patches and the surrounding matrix. While the patches, where the majority of ecological processes such as feeding or growth take place in, can still be treated as “well mixed” habitats, the surrounding matrix is different. Per definition, the matrix is more or less hostile (Kupfer, Malanson & Franklin 2006) and has to be crossed via dispersal or migration if organisms are to reach another patch. Thus, modelling the dynamics of populations in a fragmented landscape becomes a two-level process. The first level focuses on intra-patch dynamics, which is similar to unfragmented systems, and the second level focuses on inter-patch dynamics that cover all aspects of migration between patches. Combining both processes yields the concept of meta-community models (Loreau, Mouquet & Holt 2003; Gravel *et al.* 2010).

Theoretical papers have studied simple (Holt 1977; Koelle & Vandermeer 2005) or more complex model communities (Gravel *et al.* 2011a; Haegeman & Loreau 2014) revealing that their stability is strongly dependent on (1) the dispersal strategy and (2) the loss or extinction rate during dispersal. In this study, we extend this theory by including allometric relationships of dispersal parameters into well established bioenergetic models (Brose *et al.* 2005b; Rall *et al.* 2008) of heterogeneous landscapes with habitat patches.

Combined effect of nutrient enrichment and habitat fragmentation

Nutrient enrichment destabilizes consumer-resource systems by increasing bottom-up energy flows whereas habitat fragmentation is generally associated with decreasing abundances and less trophic levels, due to energy limitation. Relating this to the "principle of energy flux" (Rip & McCann 2011) results in the following hypothesis: as habitat fragmentation reduces the net-energy influx to the predator level, it might compensate for the destabilizing enrichment effect. Interestingly, a similar interaction has already been shown for another driver of global change, environmental warming (Binzer *et al.* 2012; Fussmann *et al.* 2014). Furthermore, the principle of energy flux also gives a statement about the role of predator-prey body-mass ratios. As it assumes allometric scaling of interaction strengths, this implies generally less stable (more variable) systems at lower body-mass ratios. However, current studies suggest an unimodal relation between feeding rates, i.e. interaction strengths, and predator-prey body-mass ratios (Kalinkat *et al.* 2013). This would imply an intermediate region of body-mass ratios where interaction strengths are maximized and systems stability is lower. Finally, this has implications for our initial hypothesis: if fragmentation effects and feeding rates scale with different relationships, the assumption of simply compensatory effects of habitat fragmentation and nutrient enrichment might not hold.

Study interests

In this study, we adapted the principal of energy flux to study spatially explicit habitat patches. To obtain a mechanistic understanding of the processes involved in habitat isolation, we analysed species loss terms (metabolism and migration) and the resulting inter-species energy fluxes. More precisely, we were interested in (1) how increasing inter-patch distance as a measure of patch isolation changes energy fluxes and therefore influences species biomasses and persistence. As our model considers allometric scaling of the parameters (specifically metabolism and feeding, as well as emigration rate and the success of migration) we also investigated (2) how changes in predator-prey body-mass structure influence the resulting patterns in species persistence. Concerning nutrient enrichment, we expected (3) a collapse at very high enrichment levels according to the paradox of enrichment (Rosenzweig 1971; Rall et al. 2008). Finally, we looked at (4) the interaction of enrichment and fragmentation as two of the most prominent anthropogenic drivers of global change and investigated whether they have additive or even compensatory effects on species persistence and systems' variability.

Methods

We are modelling changes in species biomass densities ($B_{i,p}$) over time on patches (p) accounting for intra($\Phi_{i,p}$)- and inter($\Psi_{i,p}$)-patch processes

$$\dot{B}_{i,p}=\Phi_{i,p}+\Psi_{i,p} \quad (4.1).$$

Intra-patch processes include species intrinsic growth and respiration rates as well as feeding interactions between species. Inter-patch dynamics describe the processes that occur between two patches, afterwards referred to as migration. In this study, we look at the dynamics of a three-species food-chain on a two patch system but the general concept can easily be adapted to multi-species and multi-patch systems.

Intra-patch dynamics

Intra-patch dynamics ($\Phi_{i,p}$) for a basal species *i* on patch *p* consist of a logistic growth term ($G_{i,p}$) and the feeding term (f_{ji}) of its predator *j*

$$\Phi_{i,p}=G_{i,p}B_{i,p}\underset{j}{-}f_{ji,p}B_{j,p} \quad (4.2),$$

and are dependent on the biomass densities of both, prey ($B_{i,p}$) and predator ($B_{j,p}$).

The logistic growth term ($G_{i,p}$) follows

$$G_{i,p}=r_i\left(1-\frac{B_{i,p}}{K_{i,p}}\right) \quad (4.3),$$

with r_i [s^{-1}] being the mass dependent maximum growth rate of species *i* and $K_{i,p}$ [gm^{-2}] the carrying capacity for *i* on patch *p*. Both of them are dependent on the body mass of *i* (m_i):

$$r_i=e^{I_r}\cdot m_i^{a_r} \quad (4.4), \text{ and}$$

$$K_i=e^{I_K}\cdot m_i^{a_K} \quad (4.5),$$

with logarithmic intercept values I_r and I_h and the allometric exponents a_r and a_K, respectively. These and all other intercepts are denoted as log-values for readability reasons (see Tab. 1).

The intra-patch dynamics for a predator *j* on patch *p* are the sum of all incoming ($f_{ji,p}$) and outgoing ($f_{kj,p}$) feeding interactions minus the species metabolism x_j [s^{-1}]

$$\Phi_{j,p}=\varepsilon f_{ji,p}B_{j,p}-f_{kj,p}B_{k,p}-x_jB_{j,p} \quad (4.6).$$

The parameter ε is the assimilation efficiency, giving the ratio at which prey biomass is converted into own biomass. This is a constant for distinct feeding types (predators 0.85, herbivores 0.5).

As we consider a tri-trophic food-chain, eqn. 6 characterizes the population processes of the intermediate species, whereas the equation of the top-predator (not shown here) does not contain outgoing feeding interactions. Species' metabolism x_i scales with

$$x_i = e^{I_x} \cdot m_i^{a_x} \qquad (4.7),$$

where I_x is the intercept and a_x the alometric scaling exponent.

Feeding rates follow a generalized Holling type functional response (FR) with predator j feeding on prey i (Kalinkat *et al.* 2013). The number of prey items eaten per-capita predator and time F_{ji} [$\mathrm{Ind_i/s{*}Ind_j}$] scales with

$$F_{ji,p} = \frac{bN_{i,p}^{1+q}}{1+bhN_{i,p}^{1+q}} \qquad (4.8),$$

where $N_{i,p}$ is the density of species i on p [Ind/m²], b is the capture coefficient [m^(2*(1+q))/s*$\mathrm{Ind_j}$], h is handling time [s*$\mathrm{Ind_j/Ind_i}$], and q is the scaling exponent of the functional response. These three scale with both, predator and prey mass in the following way: The handling time is dependent on the body mass of prey (m_i) and predator (m_j)

$$h = e^{I_h} m_i^{a_R} m_j^{a_C} \qquad (4.9),$$

with I_h as the intercept and a_c and a_R as the allometric exponents for consumer and resource mass, respectively. The capture coefficient follows a hump-shaped Rickers-curve

$$b = e^{I_b} m_i^{\beta} \frac{m_j}{m_i} e^{\varepsilon \frac{m_j}{m_i}} \qquad (4.10),$$

with I_b as intercept, β being the allometric exponent for the prey-mass dependency and ε determining the with of the hump. Finally, the scaling exponent of the functional response q scales with

$$q = \frac{q_{max}\left(\frac{m_j}{m_i}\right)^2}{q_0^2 + \left(\frac{m_j}{m_i}\right)^2} \qquad (4.11)$$

where q_{max} is the maximum value for q and q_0 gives the predator-prey body-mass ratio at which $q = q_{max}/2$. We can then rephrase the FR (equ. 8) by multiplying the numerator and the denominator with $1/bh$:

$$F_{ji,p} = \frac{\frac{1}{h} N_{i,p}^{1+q}}{\frac{1}{bh} + N_{i,p}^{1+q}} \qquad (4.12),$$

and substituting with $y = 1/h$ and $N_0^{1+q} = 1/bh$. This leads to

$$F_{ji,p} = \frac{y N_{i,p}^{1+q}}{N_0^{1+q} + N_{i,p}^{1+q}} \qquad (4.13),$$

with y being the maximum feeding rate [Ind$_i$/s*Ind$_j$] and N_0 being the half saturation density of the functional response [Ind$_i$/m²]. By expanding the fraction with prey body mass m_i^{q+1} [g/Ind$_i$] we get

$$F_{ji,p} = \frac{y B_{i,p}^{1+q}}{N_0^{1+q} m_i^{1+q} + B_{i,p}^{1+q}} \qquad (4.14),$$

with $B_{i,p}$ being the biomass-density of species I on p [g/m²]. To convert this into a per-unit biomass flux, we multiply with prey body mass m_i [g/Ind$_i$] and divide by predator mass m_j [g/Ind$_j$].

This yields f_{ij} which is the prey biomass consumed per unit biomass of the predator and per second [g/g*s], the so called per unit biomass energy flux.

$$f_{ji,p} = F_{ji,p} \frac{m_i}{m_j} = \frac{y \frac{m_i}{m_j} B_{i,p}^{1+q}}{B_0^{1+q} + B_{i,p}^{1+q}} \qquad (4.15).$$

Inter-patch dynamics

Inter-patch dynamics describe how a species gets from one patch to the other. A recent review on animal migration patterns (Bonte *et al.* 2012) suggested to consider migration as a process including the steps of emigration, dispersal and establishing as these are processes that can be observed and parametrised in empirical studies. In this study, we concentrated on (1) the emigration trigger and (2) the process of migration itself. Establishing is considered to be always successful.

Thus, the inter-patch dynamics ($\Psi_{i,p}$) are the difference between the immigration into patch p ($I_{i,p}$) an the emigration from patch p ($E_{i,p}$)

$$\Psi_{i,p} = I_{i,p} - E_{i,p} \qquad (4.16).$$

These are coupled via the migrational success of getting from any other patch q to patch p (θ_{qp})

$$I_{i,p} = \sum_q E_{i,qp} \theta_{i,qp} \qquad (4.17).$$

Thus we can describe the inter-patch dynamics by using the two parameters emigration towards ($E_{i,p}$) and migrational success ($\theta_{i,pq}$).

Emigration

The trigger of species migrating from one patch to the other has a tremendous effect on overall system stability (Tromeur, Rudolf & Gross 2013). In our study, we chose a density-dependent emigration rate as the biomass-density of a species in a habitat is directly related to several emigration triggers such as intra-specific competition or food-availability. In this way, the model also accounts for habitat-loss as decreasing habitat size increases the biomass density and therefore the emigration pressure. We parametrised the emigration pressure using empirically derived relationships between population density and species body mass (Peters 1983).

We assume that emigration of a species i from a patch p follows a sigmoidally increasing relationship with its biomass density on p:

$$E_{i_p} = \frac{B_{i,p}^{\gamma}}{\left(B_{M_i} \left(1 - \frac{e_{max_i}}{2}\right)^{-1} \right)^{\gamma} + B_{i,p}^{\gamma}} \cdot e_{max_i} \cdot d \cdot B_{i,p} \qquad (4.18),$$

where B_{ip} is the biomass density of species i on patch p [g/m²], γ is the scaling exponent that gives how strong migration rates react to changes in density, $e_{max,i}$ is maximum fraction of species i that is emigrating per unit time, d is the time scale at which migration is happening [s^{-1}]. $B_{M,i}$ is the body-mass dependent mean biomass density of species i with

$$B_{M_i} = e^{I_M} \cdot m_i^{a_m} \qquad (4.19),$$

where I_M is the intercept that defines the biomass density for a species of 1 g [g/m²], m_i

is the body mass of species *i* and a_m the allometric exponent for the mean biomass densities. Following the values for terrestrial invertebrates from Peters & Wassenberg (1983) we chose a_m as 0.3. I_M was set to 3.63 to have the onset of emigration in the same order of magnitude as the half-saturation density of the functional response. The sigmoidal relationship implies that populations have a low emigration rate at low densities that exhibits a first accelerating and then saturating increase with population density (Fig. 4.1A). Additionally, the allometric parameters chosen cause that small-bodied species have a higher emigration rate than large-bodied species (Fig. 4.1A), because they have higher densities of individuals that disperse across habitats while showing the same biomass density.

Migrational success

The success of dispersal was modelled as a function of the inter-patch distance and the migration ability of the species. Dispersal causes negative effects on species biomasses as it creates an additional loss term. This is due to either travelling costs (i.e. loss of biomass) or even death during migration. However, it has been shown to stabilize meta-ecosystem models under certain conditions (Ruxton 1996; Ruxton, Gonzalez-Andujar & Perry 1997). Following an empirical study, showing that larger species have higher maximum migration distances (Hein, Hou & Gillooly 2012), we modelled the dispersal success as a function of species body masses.

As we model migration as a process that leads to biomass loss, the migrational success (θ_{pq}) of biomass transfer between patches should scale between one and zero and be dependent on the distance travelled and the migration ability of the species. We chose a negative sigmoidal function to describe the decrease in migration success with distance:

$$\theta_{i,pq}=1-\frac{D_{pq}^{\delta}}{\left(\frac{1}{4}D_{max_i}\right)^{\delta}+D_{pq}^{\delta}} \qquad (4.20),$$

where D_{pq} is the distance between the patches *p* and *q*, $D_{max,i}$ is the maximum migration distance of species *i*, and δ is the scaling exponent. A recent study (Hein 2011) showed that the ability of a species to migrate is a function of its body mass and that maximum migration distances scales with body mass following

$$D_{max_i}=e^{I_D}\cdot m_i^{a_D} \qquad (4.21),$$

where I_D is the intercept that defines the maximum migration distance of a species of 1 g, m_i is the body mass of species *i* and a_D the allometric exponent for maximum migration distances. In this study, we chose I_D as 8.08 and a_D as 0.33 (Hein *et al.* 2012). In consequence, the migrational success is high at low distances and quickly decreases with distance, and it generally increases strongly with body mass (Fig. 4.1B).

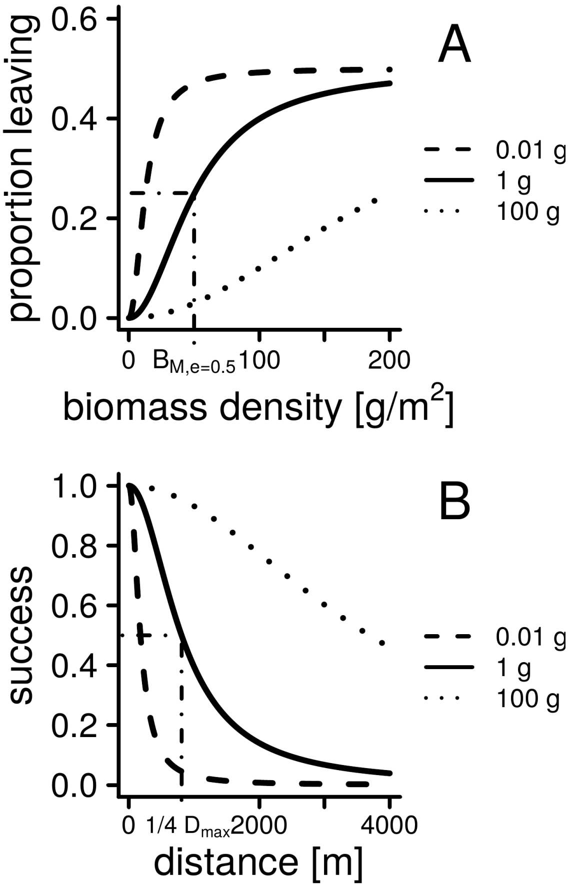

Figure 4.1 Graphical representation of eqn. 18 (A) and eqn. 20 (B)*. A shows the density-dependent emigration for a given e_{max} of 0.5. B shows the distance-dependent success of migration. The different lines indicate the relations for animals of 0.01g (dashed), 1g (solid), and 100g (dotted), respectively.*

Simulation

All simulations were carried out in C++ using the gsl-library (Gough 2009). Body mass of the basal species (m_B) was fixed at 1 mg. Other species body masses were calculated according to predator-prey body-mass ratios ($m_I = m_B * 10^{\text{body-mass ratio}}$, $m_C = m_I * 10^{\text{body-mass ratio}}$) that was systematically varied across simulations. We let the simulation run over an equivalent of 10,000 years. If the biomass density of a species fell below 10^{-12} g/m², the population was considered extinct and the biomass density was set to zero. For all analyses, we only looked at the last tenth of the time series to exclude transient effects, and for the bifurcation diagrams (Fig.4.2 and Supplementary Figures S4.1-4.7) we recorded up to ten minima and maxima values in this time frame.

Table 4.1: *Equations, values and according references*

Functions		**Reference**
intrinsic growth rate	$r_i = e^{I_r} \cdot m_i^{a_r}$	
	$\mathbf{I_r}$= -14.53 $\mathbf{a_r}$= -0.25	(Savage *et al.* 2004)
carrying capacity	$K_i = e^{I_K} \cdot m_i^{a_K}$	
	$\mathbf{I_K}$= (0-6) $\mathbf{a_K}$= 0.28	(Meehan 2006a)
capture coefficient	$b = e^{I_b} m_i^{\beta} \frac{m_j}{m_i} e^{\epsilon \frac{m_j}{m_i}}$	
	$\mathbf{I_b}$= -17.90 $\boldsymbol{\beta}$ = 0.0033 $\boldsymbol{\varepsilon}$ = -0.0182	(Kalinkat *et al.* 2013)
handling time	$h = e^{I_h} m_i^{a_R} m_j^{a_C}$	
	$\mathbf{I_h}$= 10.68 $\mathbf{a_R}$= 0.568 $\mathbf{a_C}$= -0.283	(Kalinkat *et al.* 2013)
functional response scaling exponent	$q = q_{max} \left(\frac{m_j}{m_i}\right)^2 \cdot \left(q_0^2 + \left(\frac{m_j}{m_i}\right)^2\right)^{-1}$	
	$\mathbf{q_{max}}$= 3.306 $\mathbf{q_0}$= 1009	(Kalinkat *et al.* 2013)
metabolic rate	$x_i = e^{I_x} \cdot m_i^{a_x}$	
	$\mathbf{I_x}$= -17.01 $\mathbf{a_x}$= -0.31	(Ehnes *et al.* 2011)
mean biomass density	$B_{M_i} = e^{I_M} \cdot m_i^{a_m}$	
	$\mathbf{I_M}$= (3.63)* $\mathbf{a_m}$= 0.3	(Peters 1983)
maximum migration distance	$D_{max_i} = e^{I_D} \cdot m_i^{a_D}$	
	$\mathbf{I_D}$= 8.08 $\mathbf{a_D}$= 0.33	(Hein *et al.* 2012)

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* Intercept of mean biomass density (IM) was set to 3.63 to have the onset of emigration within the same order of magnitude as the half-saturation density of the functional response

Constants			**References**
assimilation efficiency	$\mathbf{e} =$	0.85	(Lang 2012)
emigration scaling exponent	$\boldsymbol{\gamma} =$	2	
maximum migrating fraction	$\mathbf{e}_{\mathbf{max}}=$	0.5	
time scale of fragmentation	$\mathbf{d} =$	1	
migration success scaling exponent	$\boldsymbol{\delta} =$	2	

Results

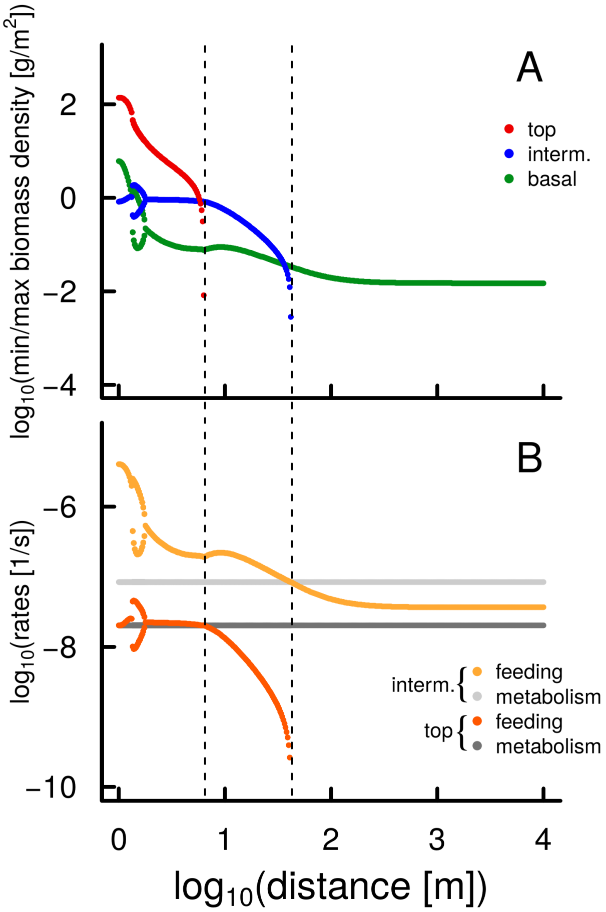

***Figure 4.2 A** Bifurcation diagram showing the effect of inter-patch distance on species biomass densities (minima and maxima shown). red= top species, blue= intermediate species, green= basal species. **B** Corresponding feeding (orange) and metabolic terms (grey) of the intermediate (bright colours) and the top species (dark colours). Dashed lines indicate the extinction-points i.e. the intersection of feeding and metabolic rates. (I_K=4, predator-prey body-mass ratio = 2).*

Increasing the inter-patch distance in a three-species on two-patch system decreased species biomasses and eventually led to extinctions of species (Fig.4.2A). Figure 4.2A shows a bifurcation diagram with increasing inter-patch distance (D_{pq}). At very low distances, the system was in an equilibrium state with the top species showing the highest biomass densities, followed by the basal species, whereas the intermediate species had the lowest biomass densities. Increasing inter-patch distance decreased the biomasses of all three species with top and basal species biomasses showing a much steeper decline than that of the intermediate species. At D_{pq}= 0.81, which corresponds to an inter-patch distance of 6.45 m in our specific example, the top species crossed the extinction boundary (10^{-12} g/m²) and died out (note that the system is parametrized for terrestrial invertebrates). Fig. 4.2B shows that this is exactly the point, where the per-unit biomass energy-flux (dark orange, eqn. 4.15) falls below the species' per-unit biomass metabolic-rate (dark grey, eqn. 4.7). As all other feeding parameters are constant (eqn. 4.15), the reason for the decline in energy flux is a decrease in prey species biomass. Ultimately, this is caused by a decrease in the prey species' migrational success (eqn. 4.20). The top species thus died out, because its prey, the intermediate species, suffered from the increasing migrational loss with increasing distance between the patches. Larger inter-patch distance led to a further decline in biomass densities of the two remaining species. At D_{pq}= 1.62 the intermediate species died out as the per-unit biomass energy-flux (light orange) could not balance the per-unit biomass metabolic-loss (light grey, Fig. 4.2B). This is the same process as for the top species at D_{pq}= 0.81. On top of this general biomass decline, there was a small section with non-equilibrium dynamics. Between $D_{pq} > 0.12$ and $D_{pq} <0.25$ the system was oscillating with relatively small amplitudes. The influence of migration on the different trophic levels becomes even more clear by comparing different migration scenarios (Table 4.2). Scenario 0 is the standard configuration, where the migrational success follows eqn. 20 for all three species (bifurcation diagram in Fig. 4.2). In scenarios 1-3, the success is set to unity (thus eliminating migrational loss) for a single population (top, intermediate, or basal species). In scenarios 4-6, migration success was set to unity for all possible two-species combinations. Finally, scenario 7 is the control, where all species have a migration success value of one (equal to 100%). Additional analyses showed that setting the success to unity in a fully synchronized system, such as this, is equal to switching the migration off (results not shown).

Table 2 Characteristics of the bifurcation diagrams under different migration scenarios*. The values depict the first distance (log values) at which the new dynamic state occurs. "n.c." in the "parameters" section means that the success of the respective species is "not changed" and follows eqn. 20. "NA" means that the respective dynamic state does not occur in the respective scenario.*

scenario				**oscillations**		**extinctions**		
No.	**parameters**							
	success top	success int.	success basal	start	end	top	intermediate	
0	n.c.	n.c.	n.c.	0.13	0.25	0.81	1.63	
1	1	n.c.	n.c.	NA	NA	0.81	1.63	
2	n.c.	1	n.c.	0.13	0.25	1.16	1.63	
3	n.c.	n.c.	1	0.11	0.44	1.53	NA	
4	1	1	n.c.	NA	NA	1.16	1.63	
5	1	n.c.	1	NA	NA	1.53	NA	
6	n.c.	1	1	0.11	0.56	2.91	2.91	*
7	1	1	1	NA	NA	NA	NA	

*In Scenario 6, the basal species died out as well at $D_{p,q}$ = 2.91.

The values in Table 4.2 show how different dynamical states are related to the migrational success of single populations. Interestingly, switching off the loss due to migration by setting the success of a population to unity never had a direct influence on the persistence of this respective population. The influences on systems' variability and species persistence were rather caused by combined top-down and bottom-up forces. Changes in systems' variability with increasing inter-patch distance were entirely related to the success of the top species, as the initial oscillations occurred only when the success of the top species was not fixed to one (Scenarios 0, 2, 3, 6). Changes in persistence patterns, i.e. distance values at which the top or intermediate species died out, where, however, related to the respective lower trophic level. Setting only the success of the intermediate species to one, delayed the extinction of the the top species to larger distance values (Dpq =1.16, Scenario 2). The same value was found when both, intermediate and top-species had no migrational loss (Scenario 4). However, Scenario 4 showed no oscillations (see above). A success of one (100%) for the basal species (Scenario 3) resulted in a longer persistence range of both, the top (until D_{pq} = 1.553) and the intermediate species (no extinction in the simulated distance range). Again, the same pattern was found when the success of the top species was also set to unity but without initial oscillations (Scenario 5).Setting basal and intermediate species' success to one (Scenario 6) led to an extinction of all three species at D_{pq} = 2.92. For a graphical representation of these results please refer to Supplementary Figures S3.1-S3.7.

To relate the findings to the nutrient status and body-mass distribution of the systems, we replicated the simulations over a broad range of predator-prey body-mass ratios and enrichment levels (varying the intercept of the carrying capacity). Fig. 4.3 shows the species persistence over a two-dimensional gradient of patch isolation ($\log_{10}$(distance [m] +1)) and enrichment (I_K) for four values of predator-prey body-mass ratios (A= 0, B= 1, C= 2, and D= 3). We found four main results: (1) when the patches are very close to each other, they behave like single patch systems. In very oligotrophic systems (Fig. 4.3B enrichment (I_K)< 1.63, Fig. 4.3C enrichment (I_K)< 0.63 and Fig. 4.3D enrichment (I_K) < 2.37), increasing enrichment eventually rescued a species from extinction. In Figure 3B this occurs at high isolation levels whereas in Figures 4.3C and D it can be found at very low isolation. Further increasing enrichment then led to unstable systems and the extinction of two or even all three species (only at low isolation; paradox of enrichment), except for systems with high-body mass ratios (Fig. 4.3D). (2) The general trend that patch isolation endangered species persistence was particularly pronounced for oligotrophic systems (i.e. low enrichment: I_K< 4) and consistent across predator-prey body-mass ratios. (3) For eutrophic systems (Figs. 4.3A and B; I_K> 4, Fig. 4.3C I_K > 4.2), we found a hump shaped relationship between patch isolation and number of persisting species. At very low distances, all species died out (Fig 4.3A-C, I_K=8, paradox of enrichment as described above), and slightly increasing the patch isolation first rescued the basal species (Figs. 4.3A and B). An intermediate inter-patch distance even enabled persistence of all three species (Figs. 4.3A-C). Finally (4), at high isolation, the patches again were totally independent from each other but with much higher additional losses. Thus, increasing I_K could only rescue one species in one of the scenarios (Fig 4.3B D_{pq} <2.5) and did not lead to “paradox of enrichment”- extinctions.

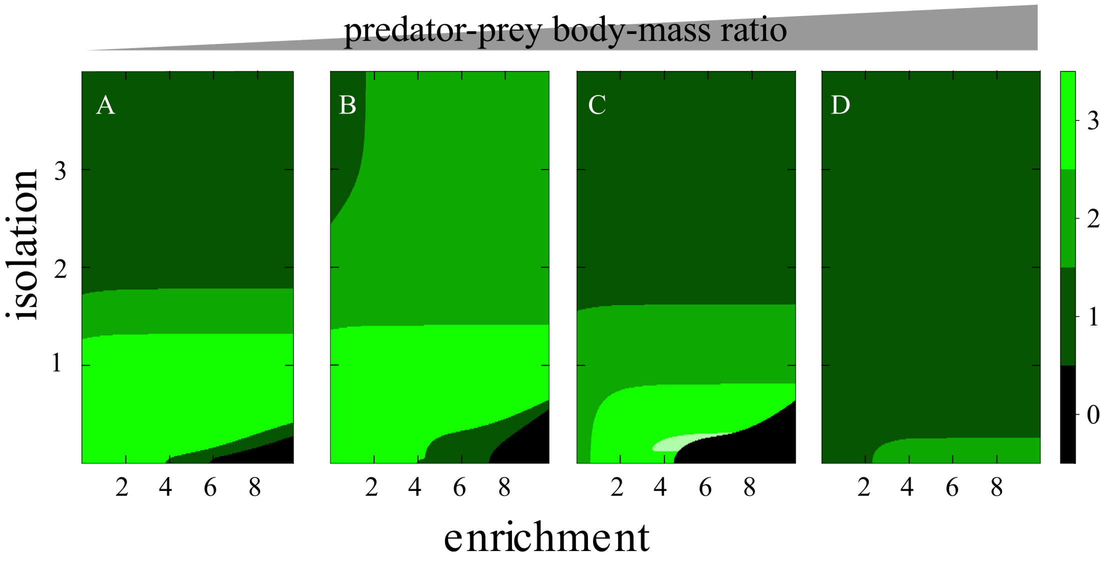

Figure 4.3 Persistence plot for different predator-prey body-mass ratios *(**A**= 0, **B**= 1, **C**= 2, and **D**= 3), showing the interactive effect of enrichment (as I_K on the x-axis) and patch isolation (D_{pq} as log_{10}(distance [m]+1) on the y-axis) on the persistence of species. black= no species survived, darkgreen= only the basal species survived, green= basal and intermediate species survived, light-green= all three species survived. Dashed area in **C** shows oscillating systems.*

Additionally, comparing Figures 4.3A-D we found an effect of increasing predator-prey body-mass ratios on the isolation and enrichment effects. Isolation effects were weaker in systems with intermediate or small body-mass ratios (presented in Fig. 4.3B, body-mass ratio = 1, followed by 3A, ratio= 0, and 3C, ratio=2). When predator-prey body-mass ratios were highest (Fig. 4.3D) there was generally less persistence and also the the effect of increasing isolation was stronger. However, enrichment effects were most pronounced in intermediate or small body-mass ratio systems (Fig. 4.3C followed by 4.3B and 4.3A) and weakest at the highest body-mass ratio values (Fig. 4.3D). Fig 4.3C also shows, that the phenomenon of oscillating systems (dashed area) only occurred across a very narrow parameter space.

Discussion

The multitude of stressors on our world's ecosystems challenges conservation biologists as well as ecological theoreticians. In order to preserve our world's biodiversity, we have to investigate the interplay of several of these stressors and their combined effect on ecosystem stability and diversity. In this study, we expand bioenergetic models (Brose *et al.* 2005b; Rall *et al.* 2008; Heckmann *et al.* 2012; Binzer *et al.* 2012) to multi-patch systems in order to study effects of habitat fragmentation and nutrient enrichment as well as their interactive influence on a tri-trophic food-chain. Patch isolation, as one aspect of habitat fragmentation, was generally shown to have a negative effect on species' biomasses and persistence in empirical systems (Terborgh *et al.* 2001; Solé & Montoya 2006). In our model, increasing the inter-patch distance led to a decrease in species biomass and eventually caused extinctions (see Fig 4.2A). Consistent with empirical studies that reported a stronger effect of habitat fragmentation on high trophic level species (Hagen *et al.* 2012), we found in our model that the top-species died out first. Surprisingly, this happened despite the fact that these species had the highest dispersal success of all species, which contradicted our initial expectations. However, our results suggest that loss due to own dispersal by mortality in the landscape matrix is not the crucial factor. Fig 4.2B shows that at the point of top species extinction (D_{pq}= 0.81), the species potential feeding falls below its metabolic demands, indicating that the extinction due to increased habitat isolation is a bottom-up mediated effect. Migrational loss decreased the biomass density of the intermediate species, which also lowered the per unit biomass flux to the top species and in the end caused its extinction. The same happened with the intermediate-basal species interaction at a higher level of patch isolation (D_{pq}= 1.62). This indicates that the empirically observed pattern of high trophic level species suffering most under habitat fragmentation is caused by a reduction in bottom-up energy fluxes. Food-web theory predicts that energy is lost on its way from the basis of a food chain to the upper trophic levels as the number of loss terms (respiration rates and assimilation inefficiency) increases. Therefore, habitat fragmentation – as a process that adds additional loss terms and weakens energy fluxes – leads to an extinction of energy limited species, which, in our model, were the top predators. The exact relation between, on the one hand, top-down control and systems' variability and, on the other hand, bottom-up energy flows and persistence becomes even more clear when looking at the different migration scenarios depicted in Table 4.2. The oscillations occur in all scenarios where the success of the top species was not fixed at 100%. This suggests that they originated from the intermediate trophic level. A slight reduction in top-down pressure by an onset of migrational loss at the top-predator level apparently was sufficient to induce the oscillations. The end of the oscillations at higher distances, however, seemed to be determined by resource availability. Setting the migrational success of the basal species to unity also enhanced the oscillations in terms of their amplitudes (Supplementary Figures S3.3 and S3.6). The points of extinction of the top and the intermediate species were altered when the basal species did not face migrational loss. While the extinction of the top species was delayed to higher distance values, the intermediate species could persist over the whole simulated distance range. However, setting both, basal and intermediate success to unity (Scenario 6) did result in an extinction of all three species as the basal species suffered from the ever increasing top-down pressure by the intermediate species. In summary, these additional analyses show that the dynamic state of the respective populations is never influenced by their own migrational loss but by those of the trophic levels above or below. Additionally, we found that systems' variability increased when top-down pressure was weakened whereas species persistence was dependent on bottom-up energy supply. The different migration scenarios also make the model more applicable to empirical systems, where usually not all species are migrating. Scenarios 1-6 thus depict the dynamical consequences if only one (1-3) or two (4-6) species are mobile.

The pronounced bottom-up effect on species extinctions does already suggest a strong effect of the systems' nutrient status. Prior studies have already shown that the length of a food chain, or the number of trophic levels in a food web, should be a function of the system's basal energy availability, which can be expressed by the carrying capacity (Post 2002). We found that in our model this was especially true for oligotrophic systems that showed an increase in the number of persistent species with increasing nutrient availability (Fig. 4.3). In eutrophic systems, the paradox of enrichment led to opposite results; higher nutrient supply led to lower persistence (Rosenzweig 1971). The two drivers of global change, therefore, led to two different types of extinctions: (1) habitat fragmentation reduced the energy availability leading to extinction of one species at a time, starting with the highest trophic level and (2) eutrophication led to unstable dynamics of predator-prey pairs and thus extinctions of either two species (if the top-intermediate species interaction was most affected) or even of all three species (if the intermediate-basal species interaction was most affected). One of the key questions of our study was how these two external stressors interact in affecting population persistence. An important concept on how they might interactively influence the dynamics of trophic systems is provided by the so-called “principal of energy flux” (Rip & McCann 2011). Nutrient enrichment increased the consumers net energy influx, whereas habitat fragmentation decreased it. The principle of energy flux thus suggests that they should counteract each other in affecting species persistence. In our experiment we found that, in highly oligotrophic systems, increasing the inter-patch distance led to a decline in the number of surviving species as it additionally reduced net energy fluxes (Fig. 4.3). However, in eutrophic systems that underwent paradox of enrichment dynamics, the additional biomass loss due to migration rescued the system. Similarly, increasing the enrichment in weakly fragmented systems led to paradox of enrichment dynamics, reducing species persistence. In contrast, in higher fragmented landscapes nutrient enrichment potentially increased the number of persisting species. This indicates that paradox of enrichment behaviour is more likely under low isolation, whereas meta-communities with isolated patches might be less prone to enrichment-driven extinctions. Our findings of counteracting effects of habitat fragmentation and enrichment are consistent with a study using a similar model to predict the interaction between enrichment and environmental warming (Binzer *et al.* 2012).

Moreover, our results are in line with other theoretical studies on meta food webs in discrete patches. Prior studies that looked at trophic systems on two patches also found an effect of increasing inter-patch distance (Koelle & Vandermeer 2005) or decreasing patch coupling (Jansen 2001; McCann *et al.* 2005) on stability. Koelle & Vandemeer (2005) studied a tri-trophic food chain on a two-patch system and found that with increasing distance, the patches show asynchronous oscillations that are suggested to be more stable (Loreau & de Mazancourt 2013). However, they also argue that highly isolated systems face extinction risks because of low immigration rates (Hudson & Cattadori 1999). This hump-shaped effect of inter-patch distance on stability is in line with our results and has previously also been shown for predator-prey dynamics on a two-patch system under nutrient enrichment (Jansen 2001). McCann and colleagues (McCann *et al.* 2005) found that this also generally holds for food webs, as low-to-intermediate coupling of local food webs increased system stability by decreasing oscillations. In contrast to these previous studies, we showed that stability of meta-communities is more a result of inter-species energy fluxes. In our model, oscillations arise and are enhanced when the inter-patch distance is low and the nutritional status (the enrichment) is high. Increasing the inter-patch distance or decreasing the enrichment both lead to a decreasing net energy influx to the predator and therefore dampens oscillations (Rip & McCann 2011). However, a further increase of inter-patch distance or decrease in nutrient availability bares the risk of predator starvation.

Our model is built on some limiting assumptions. First, the allometry of feeding interactions considered in our study only holds for predator-prey systems, whereas it does not represent parasite-host or most terrestrial herbivore-plant interactions that are characterized by different consumer-resource body-mass ratios (Brose *et al.* 2006). Second, all rates were parametrized for invertebrates in the body-mass range between micrograms and grams. While this does cover several orders of magnitude, it does not include large migrating animals such as birds or ungulates. Hence, the critical distances reported here should be interpreted concerning small invertebrates, whereas vertebrates operate on different spatial scales. Nevertheless, the generality of the model ensures that qualitatively similar results should be obtained for vertebrates. Third, there is, as always, an issue of data limitation. For example, we did not have data on feeding parameters and dispersal ability of the same species. Hence, we had to assume that general relationships hold across different species. Fourth, we did not consider a time delay with migration and thus assume constant and immediate movement between patches. This is because the use of differential equations requires a time derivative of the modelled processes which is only possible when assuming continuous processes. However, this is in line with previous modelling studies on meta food-webs (Jansen 2001; Koelle & Vandermeer 2005; McCann *et al.* 2005; Gravel *et al.* 2010). Using time delay functions would most likely lead to strong oscillations, even in the parameter space that we considered as stable, which would would reduce the comparability to non-spatial models. Additionally, we assumed that once an animal has crossed the inter-patch distance, the immigration and establishment are always successful. In natural systems, however, this is not necessarily the case. However, the results of our model can still be interpreted in the same way if we consider our success of migration (eqn. 4.20) as a function of an “effective distance” that incorporates success of establishment. Despite these cautionary statements, the model presented here is flexible to include all of these points in future analyses of global change effects on food chains and more complex ecological communities.

In summary, we can stress the importance of energy fluxes in trophic systems and how they are affected by different drivers of environmental change. Especially, we looked at the interactive effect of habitat fragmentation and nutrient enrichment, two of the major drivers of current and future biodiversity loss (Nelson 2005). We did this using a well understood and empirically derived bioenergetic model that has often been shown to match experimental systems (Schneider *et al.* 2012; Kalinkat *et al.* 2013; Fussmann *et al.* 2014) and extended it to multi-patch systems using empirically derived parameters of animal migration. This yielded a flexible modelling framework that can easily be extended to multi-patch systems (Gravel *et al.* 2011a), higher trophic complexity of the communities (Rall *et al.* 2008; Heckmann *et al.* 2012) or other drivers of global change such as environmental warming (Binzer *et al.* 2012). In our study, we identified critically important changes in energy fluxes between populations (Rip & McCann 2011) under increasing patch isolation and related them to empirically observed consequences of habitat fragmentation. Surprisingly, we demonstrated that top-predator extinction under habitat fragmentation is not necessarily caused by loss of habitat area but may also arise from reduced energy fluxes due to migrational losses of the prey species. The analyses presented in Table 4.2 showed that the generality of the findings also holds across different migrational scenarios in possible empirical systems. Additionally, we found surprising interactive effects of patch isolation and enrichment that raise empirically testable questions: First, isolated patches should be less susceptible against enrichment induced oscillations. Second, fragmentation effects might be compensated via an increase in nutrient availability. Together, these results suggest that oligotrophic habitats should be affected more severely by fragmentation than eutrophic habitats. The ecosystem models of our study present one step towards an integrative theory of global change that includes interactive effects of multiple stressors.

Acknowledgements

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Part III
General Discussion

Chapter 5

Synopsis

The current biodiversity crisis (Novacek 2001) is not only a crisis of the world's ecosystems but also a crisis in ecological research. Ecosystems worldwide lose species at an ever accelerating speed (Barnosky *et al.* 2011) and supposedly most species will be extinct long before their role in ecosystems and their contribution to ecosystem functioning will be assessed. In a world where a multitude of external stressors endanger species, as well as ecosystems and their stability and functioning, ecological research has to catch up with the speed of these changes to predict their effects and preserve a diverse and functioning world. Since the study by Sala and colleagues in 2000 (Sala *et al.* 2000), which identified the most important drivers of environmental change, there have been literally tens of thousands of studies on the effects of these drivers (Fig 1.1). Nonetheless, we are still only at the beginning of a conceptual understanding of how environmental change will shape future ecosystems (Brose *et al.* 2012; Lurgi *et al.* 2012b). Especially when it comes to the interactive influence of multiple stressors on the stability of ecological systems, we still lack empirical data, and, more importantly, a common theoretical framework (O'Gorman *et al.* 2012; Lurgi *et al.* 2012b).

In this thesis, I have provided a generalized tool to model the effects of various drivers of environmental change – i.e. an extended version of consumer-resource models (Rosenzweig & MacArthur 1963). Various previous studies have shown that this type of model can be tailored to investigate the effects of specific environmental stressors (Rosenzweig 1971; Vasseur & McCann 2005) and that it can also be used to predict the effects of multiple simultaneous changes in the environment (Binzer *et al.* 2012). I used it to model the effects of three different stressors – warming, nutrient enrichment and habitat fragmentation – on three different food-web motifs comprised of two, three, and four species:

In Chapter 2, I used a temperature-dependent extension of consumer-resource models based on the Arrhenius scaling of biological rates. This has previously been suggested by Vasseur & McCann (2005) who hypothesized a dynamical destabilization of consumer-resource systems with warming. However, I found that increasing temperature stabilized oscillating systems at the risk of predator starvation.

For Chapter 3, I revisited weak-interactions theory. In their 1998 paper, McCann and colleagues found that a three-species food-chain showing oscillations in biomass densities could be stabilized by introducing a weak interaction (McCann *et al.* 1998). Oscillations in a three-species food-chain can be obtained via an increase in carrying capacity (Rosenzweig 1971; Otto *et al.* 2007), which mimics nutrient enrichment. I found that an allometric definition of interaction strengths enabled an *a-priori* identification of “invaders” (additional consumers) that buffered the enrichment effects.

In order to model a fragmented landscape (Chapter 4), I extended the consumer-resource model of a three-species food-chain towards a multi-patch model by introducing additional terms governing inter-patch dynamics. The dispersal between two patches was modelled using an allometric dependence of emigration rates and a distance- and body-mass-dependent migrational success. Increasing inter-patch distance reduced per-unit biomass energy-flux and thus led to extinction of first the top predator and afterwards the intermediate species. Simultaneous nutrient enrichment prevented those extinctions to a certain extent but, at the same time, it led to an increase in system variability.

The principle of energy flux in a changing environment

The research chapters covered a wide variety in environmental stressors as well as in trophic structures. However, I will hereby show that the use of a common theoretical framework, which is the generalized bioenergetic model, offers a deeper insight into the ways in which global-change drivers endanger ecosystem stability and species persistence. Moreover, it allows predictions on the simultaneous effects of multiple stressors by looking at relatively simple characteristics of consumer-resource systems: the energy fluxes.

In their 2011 article, Rip & McCann rephrased consumer-resource theory in terms of the dynamical implication of energy fluxes (Rip & McCann 2011). They found that studies on the dynamic behaviour of theses systems can be consolidated by the so-called “principle of energy flux”. It states that *“any biological trait that increases the energy flux to the consumer, relative to its loss term …* [(net energy flux)]*, tends to make the C-R* [(consumer-resource)] *biomass ratio top heavy (i.e. increases consumer : resource biomass ratio) and less stable (e.g., population dynamics more variable).”*

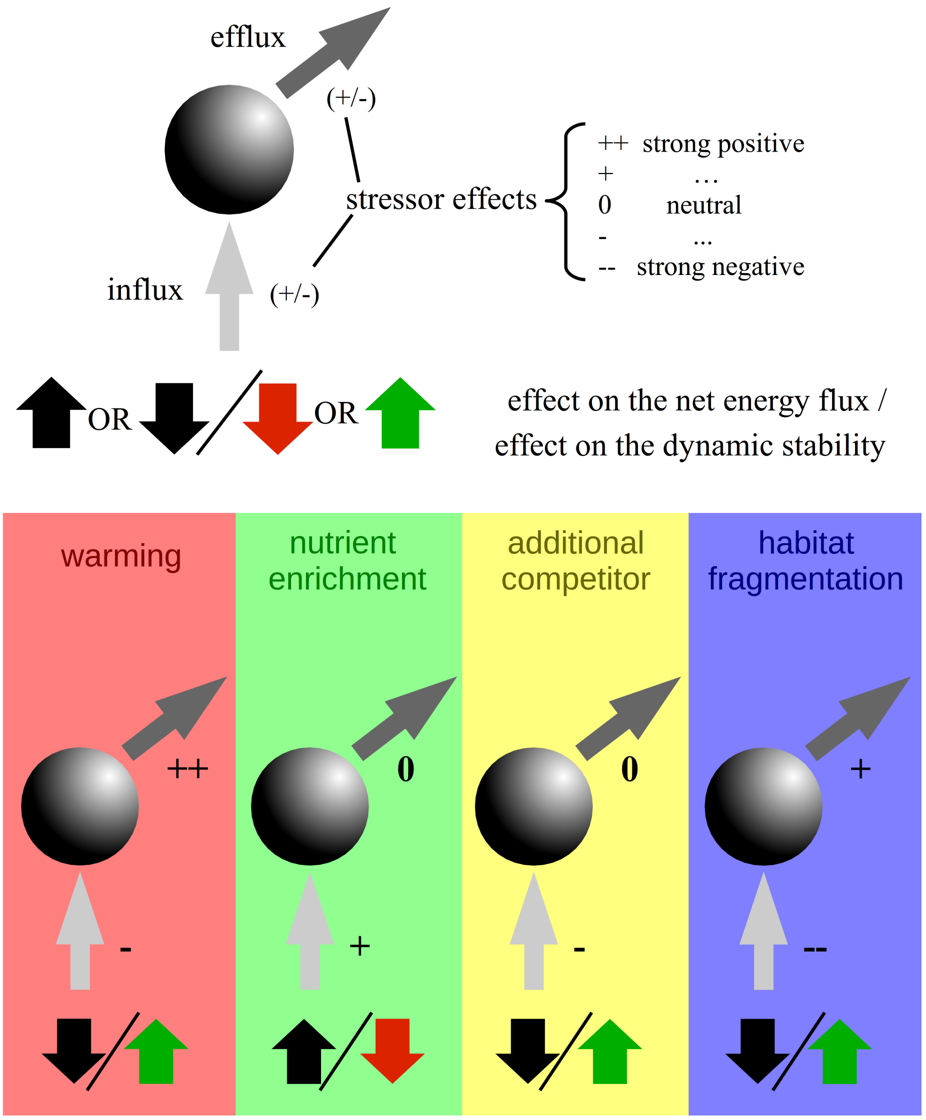


Figure 5.1 *Effects of different drivers of environmental change on biomass influx and efflux on the predator level, the resulting net energy flux and the consequences for dynamic stability.*

*The **upper panel** depicts the general layout:*

- *the predator population is represented by the **black sphere**;*
- *the sum of the influx terms is indicated by the **light grey arrow**,*
- *the **dark grey arrow** depicts the sum over the efflux terms;*
- *and the **symbols (++,+,0,-,--)** alongside these arrows indicate how one of the studied environmental stressors effect the respective fluxes.*
- *The **black arrows below** give the resulting stressor effect on net energy flux (up-arrow = higher net energy flux, down- arrow = lower energy flux)*
- *and the **red and green arrows** depict the consequences on the dynamic stability (green = stabilizing, red = destabilizing).*

*The **lower panels** show the environmental stressors studied in this thesis and their effect on influx, efflux, net flux and dynamic stability. The **background colours** show the respective stressor: red = warming, green = nutrient enrichment, yellow = species invasion and blue = habitat fragmentation.*

As an example, they referred to the “paradox of enrichment” where the “biological trait” of an increased carrying capacity led to enhanced resource growth, which in turn fostered consumer biomass and finally yielded higher top-down pressure (Rosenzweig 1971). Altogether this led to higher mean-biomass densities of consumers but also to high variability and increasing biomass oscillations. In general, the same dynamical consequences can be caused not only by higher resource availability (K↑) but also by more efficient feeding (B_0↓), higher maximum feeding (y↑), or lower predator respiration rates (x↓). Technically, these “changes in biological traits” shift the consumer-resource isoclines in an excitable Rosenzweig-MacArthur equation system (eqn. 1.9) towards unstable equilibrium points (see Fig. 1 in Rip & McCann 2011). In the same vein, contrary changes in biological traits lead to dynamically more stable and less variable systems.

The environmental stressors studied in Chapters 2-4 were all reported to affect species through changes in these biological traits. In the following, I will present environmental-change effects on the reported traits, I will then show the resulting changes in energy fluxes and finally I will categorize the environmental stressors according to their effects on system stability (Fig. 5.1).

For nutrient enrichment (Chapter 3) I found results consistent with current literature (Rosenzweig 1971; McCann *et al.* 1998; Rip & McCann 2011). By enhancing resource growth, enrichment increased the influx while leaving the efflux unchanged. The resulting increase in net flux resulted in a less stable system (Fig. 3.1 B). Addition of a consumer that acts as an energy drain (“trophic whale” in Chapter 3), in turn, led to a decrease in net flux as it reduced resource availability (Fig. 3.3). As a consequence, oscillations were minimized (Figs. 3.1 and 3.4). Chapter 3 also provides an example of how different drivers of environmental change can interact (see below).

Some of the drivers affect multiple traits simultaneously. The resulting consequence on net energy flux and system stability therefore depends on the exact relationship between stabilizing and destabilizing effects. Warming (Chapter 2), for example, had a positive effect on maximum feeding rates and predator's respiration rates. However, it also decreased the carrying capacity and the half-saturation density (Fig 2.1). In Chapter 2, I showed that the dynamical outcome of a consumer-resource model under environmental warming depended on which of the biological traits was affected more strongly. The strength of warming effects is given by the activation energies of the different rates. In Figure 2.3, I identified the different combinations of activation energies that led to the different dynamical outcomes. In cases where the reduction in resource availability (negative activation energy of the carrying capacity; E_K) was stronger than the increase in hunting efficiencies (negative activation energy of half-saturation density; E_{B0}), net energy flux was diminished and the system was stabilized (Fig. 2.3, the two panels on the right). The opposite case of a stronger influx due to warming and thus less stable systems was suggested by Vasseur & McCann (2005). However, I only found this for a minority of possible combinations of activation energies (8.9%, Fig. 2.3) when the increase in hunting efficiencies was stronger than the decrease in maximum prey densities.

Finally, habitat fragmentation (Chapter 4) led to additional biomass loss on all trophic levels and thus increased predator efflux and decreased the influx. This resulted in a weaker net flux and a more stable system. More precisely, fragmentation effects on the mortality were stronger for smaller animals at lower trophic levels (Fig. 4.1). Consequently, the decrease in energy influx was stronger than the increase in efflux (Fig. 5.1). Thus, reducing fragmentation effects on predator mortality could not rescue it from extinction. However, reducing the mortality of its prey led to a higher influx and thus postponed the extinctions towards higher levels of fragmentation (Tab. 4.2).

The results of Chapters 2 and 4, however, identify a conceptual problem of the principle of energy flux: A higher dynamic stability does not necessarily equal a higher persistence. While habitat fragmentation and warming both stabilized oscillating systems at low intensities, an ongoing increase of these stressors led to extinction of the top predator due to energy limitation. In Chapter 2 this occurred when metabolism increased more strongly with warming than maximum feeding (Fig. 2.3). A slight reduction in net energy flux might therefore stabilize consumer-resource systems both dynamically and in terms of species numbers. A strong decline, however, will lead to extinction of the top-predator and might even trigger secondary extinction events (Riede 2012). Throughout the literature, warmer and more fragmented systems are associated with simpler food webs comprising less species and showing lower maximum trophic levels due to this energy limitation (Petchey *et al.* 1999; Brooks *et al.* 2002).

Interactive influence of environmental stressors

Categorizing environmental stressors according to their influence on influx and efflux on the predator level enables predictions of the interactive influence of multiple stressors on dynamic stability. As nutrient enrichment fostered net energy flux, it might be counteracted by applying other stressors that reduce the energy flux. For warming this has been shown in both theoretical and empirical studies (Binzer *et al.* 2012; Shurin *et al.* 2012). In Chapter 4, I showed this effect for habitat fragmentation and in Chapter 3 for the addition of a weak competitor. However, Chapter 3 illustrates a limitation for this compensating effect in more complex trophic systems. The assumptions on how the dynamic stability changes are only valid if the focal level is the dominating oscillator in the system. In Chapter 3 this is true if the additional competitor is large i.e. the interaction strength is weak. If the interaction between the new competitor and the resource is strong, the energy flux to the predator is still weakened but in this case the system is dominated by the new oscillator (Fig. 3.1 and McCann *et al.* 1998).

An alternative way of looking at the presented interactions, is that an increase in nutrient availability might rescue top predators in systems that face energy limitation due to warming, habitat fragmentation or species invasions. However, no matter which of these two perspectives is chosen, the parameter space in which such a compensation occurs is limited.

In addition to these examples of antagonistic stressor effects, the principle of energy flux also allows the identification of stressors that act additively. Warming and habitat fragmentation, for example, are two stressors that often occur simultaneously and that might actually cause each other (see Chapter 1.5). As both processes weaken energy influx, their simultaneous occurrence will enhance the trend towards simpler food webs with less trophic levels (Petchey *et al.* 1999; Brooks *et al.* 2002). This effect might even be more pronounced if warming alters animal behaviour towards more frequent dispersal and thus strengthens the effect of fragmentation (Eklöf *et al.* 2012).

Consequently, possible three-way interactions between nutrient enrichment, warming and habitat fragmentation might be predicted in the same way. To compensate for the additive negative effect of fragmentation and warming, the necessary level of nutrient enrichment should be considerably higher. Phrasing it from the other perspective: simultaneous occurrence of fragmentation and warming might compensate for higher levels of nutrient enrichment.

One aspect that has not been included in this synopsis so far is the effect of body-size structure on net energy flux. Rip & McCann argued that a low predator-prey body-mass ratio should lead to a higher influx and therefore to less stable systems (Rip & McCann 2011). On the other hand, systems that have a high predator-prey body-mass ratio were reported to suffer from energy limitation (Otto *et al.* 2007). This is based on the assumption of constant allometric scaling of feeding rates. However, recent empirical studies suggest hump-shaped relationships of interaction strengths with body-masses, e.g. via functional responses, and thus an intermediate predator-prey body-mass ratio where interaction strength is maximized (Kalinkat *et al.* 2013). Figure 4.3 illustrates this as it shows that at intermediate body-mass ratios (Fig. 4.3 b and c) the effect of nutrient enrichment is strongest and that of fragmentation is weak. On the other hand, at very high body-mass ratios (Figure 4.3d) energy flux is already too weak for enrichment to cause oscillations.

The link to the “real” world – ecological experiments

So far, I have shown that bioenergetic models can be tailored towards specific needs and that understanding them can give deep insights into the “How?” and “Why?” of species extinctions under global change. Although these models are constructed in a very general way they can also predict the outcome of specific ecological experiments. In Chapter 2, the predictions of reduced biomass oscillations owing to environmental warming matched the results of microcosm experiments in a bacteria-ciliate interaction. The corresponding time-series analyses also showed the predicted predator extinction due to starvation at very high temperatures. Rosenzweig's prediction (Rosenzweig 1971) that increasing the nutrient availability should lead to stronger predator-prey oscillations was validated in a similar microbial system by Fussmann and colleagues (Fussmann *et al.* 2000). This also matches the findings of Chapter 3 where fertilization increased predator-prey biomass-ratios and thus made the system “top heavy” (see above under “principle of energy flux”). An additional consumer delayed this effect to higher levels of fertilization (see Fig. 3.3) and decreased variability in prey abundances (Fig. 3.4). Chapter 4 does not contain an empirical part that tests the model predictions. However, reduction in variability of consumer-resource systems owing to fragmentation has recently been shown in a separate study (Cooper *et al.* 2012). The authors of this study also found predator extinction due to a reduction of energy influx at high levels of fragmentation.

How to proceed?

A common framework like consumer-resource theory – that is general but at the same time flexible enough towards specific extensions – can enhance the informative value of model analyses and predict the outcome of possible experiments. Similarly, other data-driven theories like allometric theory (Peters 1983), temperature-scaling theory (Gilbert *et al.* 2014) or ecological stoichiometry (Sterner & Elser 2002), as well as their combinations (Ott *et al.* 2014) can act as a backbone of ecological research. To stay in this metaphor, the flesh added to the bones will be the acquisition of good and meaningful empirical data as, for example, obtained by respiration measurements (Ehnes *et al.* 2011) or functional response experiments (Rall *et al.* 2012; Kalinkat *et al.* 2013). Ecologically sound models will use this body of theory and data to come up with predictions on higher levels of ecological organisation that can finally be tested in ecological experiments, both in the field and in the lab.

This four-fold process of an established theoretical framework, theory-driven data-acquisition, ecological modelling and ecological experiments, that was presented throughout this thesis, will facilitate future findings.

Future studies might, in this vein, tackle some of the limitations of the models that I have presented in the research chapters. A possible extension to Chapter 2, for example, could cover the reported reductions in species body masses with temperature (Brose *et al.* 2012). Nutrient enrichment, as in Chapters 3 and 4, could be extended towards a stoichiometric perspective, which would actually involve directly measurable environmental parameters and not an arbitrary concept of maximum carrying capacity. Finally, for the model in Chapter 4, the integration of synergistic (more than just additive) effects of environmental stressors would also be of interest, such as of warming and fragmentation as reported by Eklöf *et al.* (2012).

Ecosystem models, like the ones that I have presented throughout this thesis, are stepping stones between ecological theory and small-scale empirical data on the one hand and ecological experiments and forecasts at the ecosystem scale on the other hand. Models that depict trophic interactions are of special interest as they govern the energetic backbone of ecosystems. Flexible modelling tools that can be tailored towards specific questions without losing their general applicability are of special importance as they themselves can become “data-driven theory”. Finally, experiments that are based on the hypotheses of such models can help to validate the underlying assumptions, or to show their restrictions. A general view on multiple models, as presented in this synopsis, provides in-depth understanding and deeper insights into environmental stressor effects on ecosystems.

Part IV

Appendix

Supplementary Information on the research chapters

Ecological stability in response to warming

– Supplementary information –

[†]Florian Schwarzmüller, [†]Katarina E. Fussmann, Ulrich Brose, Alexandre Jousset & Björn C. Rall

† These authors contributed equally to this work.

Supplementary Methods

Simulations

We used a bioenergetic predator-prey model, where the biomass-densities of a prey *R* and its predator *C* follow

$$B'_R = r_R B_R \left(1 - \frac{B_R}{K}\right) - \frac{y_{CR} B_R}{B_{0_{CR}} + B_R} B_C$$

(S1.2) and

$$B'_C = \varepsilon \frac{y_{CR} B_R}{B_{0_{CR}} + B_R} B_C - x_C B_C$$

(S1.3),

where B'_R and B'_R are the changes in biomass density of prey and predator [g/m²], respectively. r_R is the population growth rate of *R* [s^{-1}], *K* is the carrying capacity [g/m²], y_{CR} is maximum consumption rate of *C* on *R* [s^{-1}], B_0 is the half-saturation density [g/m²], ε is the dimensionless assimilation efficiency (0.85 for carnivores), and is x_c the metabolic rate of the predator [s^{-1}]. In this kind of biomass model, the metabolic rate of the predator population is parameterized as biomass loss due to respiration, whereas metabolic and death rates of the resource are included in the maximum growth rate. Resource mortality is assumed to be caused only by predation as described by the functional-response term.

Following metabolic theory, we accounted for body-size and temperature dependencies of the rates:

$$r_R = r_0 e^{E_r \frac{T - T_0}{kTT_0}}$$

(S1.4),

$$K = K_0 e^{E_K \frac{T - T_0}{kTT_0}}$$

(S1.5),

$$y_{CR} = y_0 e^{E_y \frac{T - T_0}{kTT_0}}$$

(S1.6),

$$B_{0_{CR}} = B_{0_0} e^{E_{B_0} \frac{T - T_0}{kTT_0}}$$

(S1.7), and

$$x_C = x_0 e^{E_x \frac{T - T_0}{kTT_0}}$$

(S1.8).

r_0, K_0, y_0, B_{00} and x_0 are mass dependent normalization constants calculated for the intercept temperature (T_0) of 293.15 K and a species with a body mass of 100 mg feeding on a 1 mg prey.

Within the extended writing of the Arrhenius equation, determining the temperature dependency of the rates, T defines the current temperature [K] and k is the Boltzmann constant [$8.617*10^{-5}$ eV K^{-1}]. E_r, E_K, E_y, E_{B0} and E_x are activation energies [eV] determining the exponent of the temperature dependencies (see Supplementary Table S1.1).

Supplementary Table S1.1 shows the empirically derived parameter values used in the model. Means and standard deviations of activation energies of K, y, B_0 and were taken from our database (Supplementary Table S1.4), those of r were taken from Savage et al. (2004). Mass-dependent normalisation constants were calculated using various empirical studies: K from Meehan (2006), r from Savage et al. (2004), y and B_0 from Rall et al. (2012), and x from Ehnes et al. (2011).

Laboratory methods

Functional response

Functional responses were measured in 96 well plates containing bacterial suspensions in OS 1:10 without a carbon source to avoid bacterial growth. Bacteria were inserted after a serial scheme diluting the concentration for twelve times in a 1:2 ratio. After adding ciliates to a final concentration of 100 cells/µl, the experiment was started in a M200 plate reader (Tecan, Männedorf, Switzerland). The total volume of one sample was 100 µl. Six treatments of each dilution step received ciliate solution yielding a final concentration of 100 predators/µl. Two treatments of each dilution step were used as control treatments without predators receiving the same amount of OS 1:10. Functional response experiments were replicated at 15, 20, 25 and 30 °C. Optical density (OD600) and green fluorescence (excitation, 485 nm; emission, 520 nm; gain, 80) were recorded every five minutes over a time span of 8 hours. With the help of a calibration series where OD-values and green fluorescence signals were compared to cell counts these measurements were converted to cell concentrations. Time span utilized for statistical analysis was two hours after start, ending eight hours later, to exclude transient dynamics in the beginning of the experiment. Plates were shaken every two minutes ensure homogeneous suspensions.

Statistics

Functional response analyses

Statistical analyses of the microcosm functional response experiments were conducted with **R** (R Development Core Team 2010). We used the Roger's random equation to analyse the functional response data, due to decreasing cell counts during the time of the experiment (Royama 1971; Rogers 1972):

$$N_e = N_0\left(1 - e^{aN(hN_e - P\tau)}\right) \qquad \text{(S1.9).}$$

In this equation, N_e represents consumed prey, N_0 initial prey density, P the predator density. h handling time, a attack rate, while τ is the overall time of the experiment. This recursive equation was solved by using the additional packages NLME (non-linear mixed effects) (Pinheiro *et al.* 2011) and EMDBOOK (Bolker 2012):

$$N_e = N_0 - W\frac{\left(ahN_0 e^{-a(P\tau - hN_0)}\right)}{ah} \qquad \text{(S1.10).}$$

In this equation W stands for the Lambert W function (Bolker 2008). Attack rates a and handling times h follow a deduced form of the Arrhenius equation (Vasseur & McCann 2005):

$$h = h_0 e^{\frac{E_h(T - T_0)}{kTT_0}} \qquad \text{(S1.11),}$$

$$a = a_0 e^{\frac{E_a(T - T_0)}{kTT_0}} \qquad \text{(S1.12),}$$

where h_0 and a_0 are normalization constants at the intercept temperature, T_0 (293.15 K). T is the temperature (in K), k is the Boltzmann constant (8.62x10−5 eV −1) and E_h and E_a are activation energies in eV.

Supplemental Results

Simulations

In the main document, we used overall mean values of activation energies for the physiological rates to give an first impression of their dynamical consequences (Chapter 2, Fig. 2.2). As there are four different possible dynamical outcomes depending on the combination of activation energies (increasing or decreasing oscillations with warming, both either with persisting or extinct predators, see Chapter 2, Fig. 2.3), we replicated the simulations with the mean values corresponding to each of the cases (Supplementary Figures S1.1 - 4).

Please note that the time series shown in this supplement focus on the long-term dynamics, whereas those in the main text were reduced to initial dynamics to allow comparisons with experimental data. In the supplementary figures S1.1-4, the system-state at the end of the time series is therefore directly related to the one shown in the corresponding bifurcation diagram.

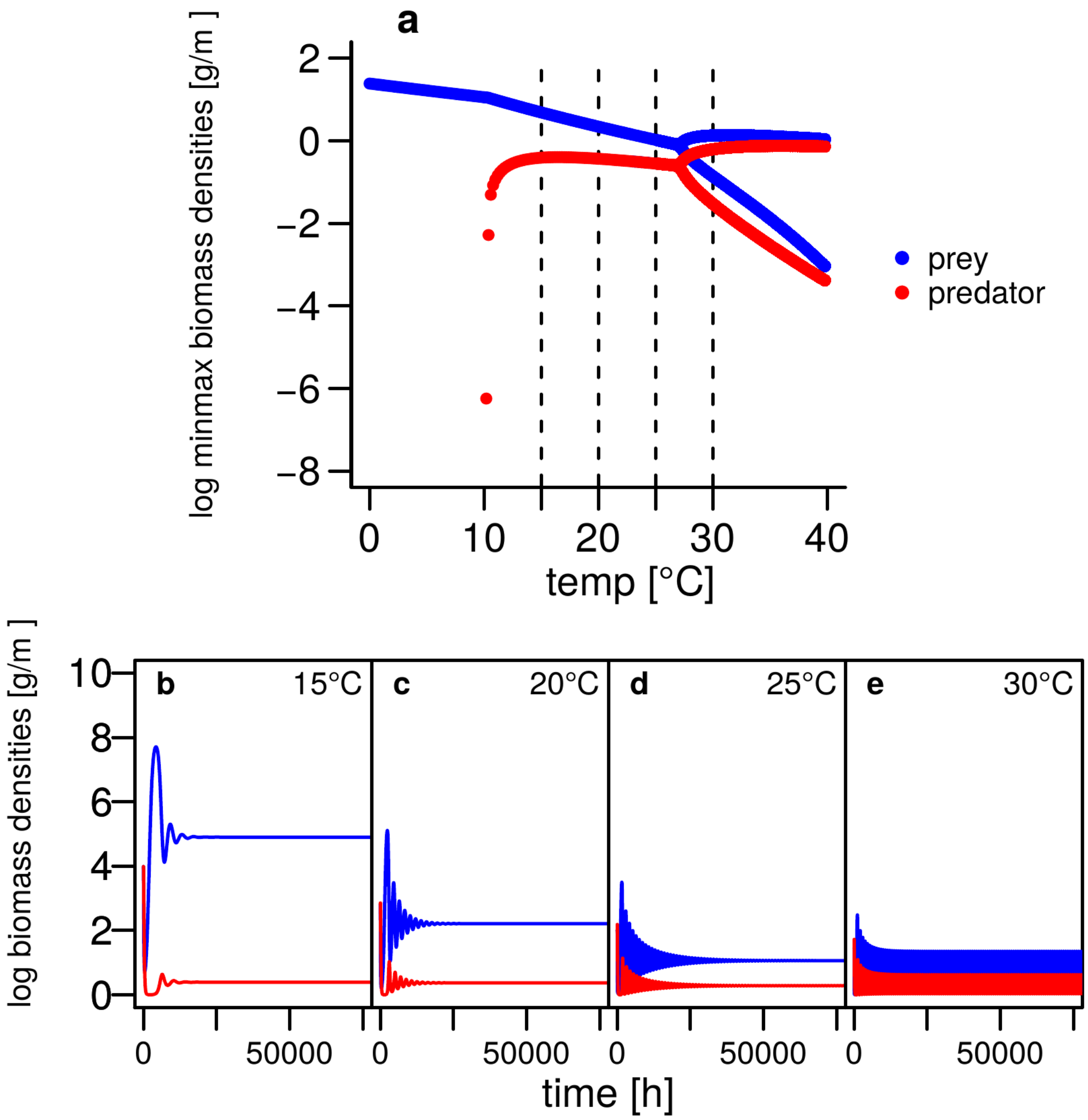
Supplementary Figures S1.1 and S1.2 show the warming response as it was predicted by former studies (Vasseur & McCann 2005). In these scenarios, foraging efficiency reacts more strongly to warming than the maximum prey density (compare Fig. 2.3 in Chapter 2). Therefore, warming increases top-down pressure and the system is destabilized (i.e., the amplitudes of the oscillations decrease). The occurring oscillations are comparable to others that originate from increased system-energy flow relative to the consumer loss term as described under the principle of energy flux or the paradox of enrichment (Rosenzweig 1971; Rip & McCann 2011).

Supplementary Figure S1.3 shows that there are scenarios with an equilibrium state over the whole temperature range, whereas Supplementary Figure S1.4 shows the most frequent case of warming stabilizing population dynamics at the risk of predator extinction at high temperatures.

Functional Responses Measurements

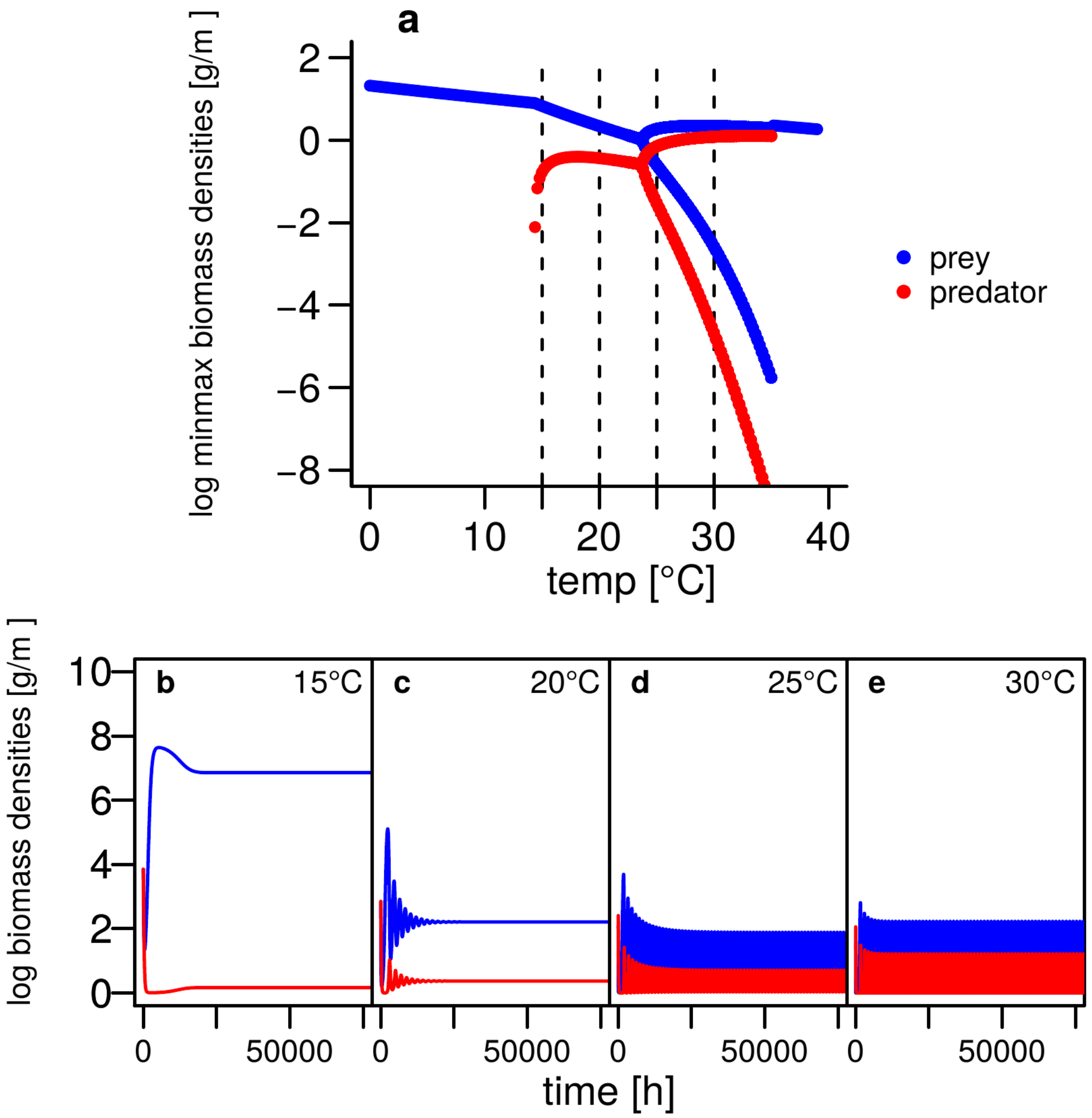
Per capita feeding rates increased slightly with warming (Supplementary Figure S1.6). More precisely, attack rates showed no significant increase, whereas handling times decreased significantly with a rather shallow slope (Supplementary Table S1.2).

Supplementary Figures



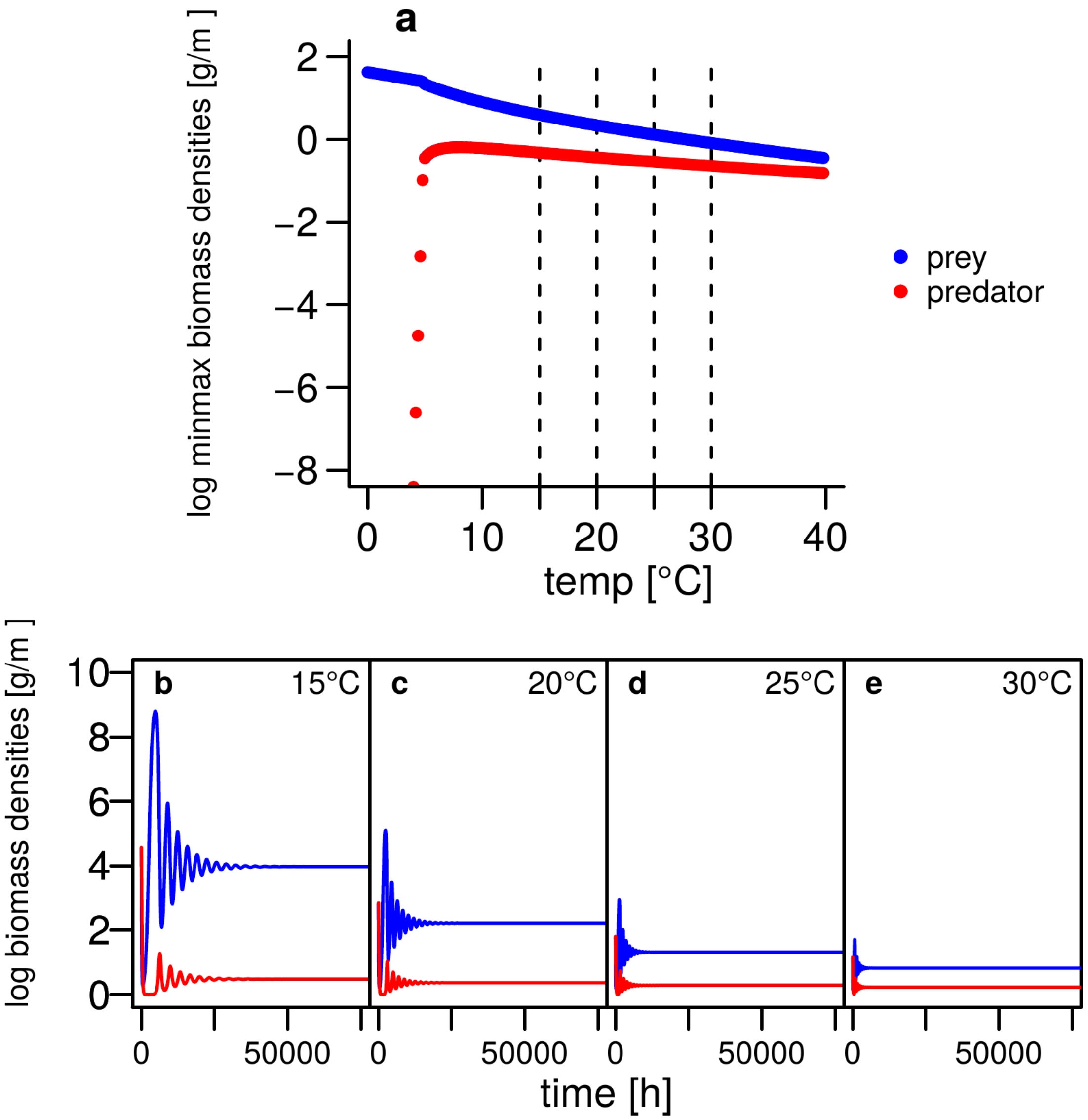
Supplementary Figure S1.1 | Destabilizing without extinction. *E_k = -0.508, E_r = 0.840, E_x = 0.428, E_mi = 0.708, E_B0 = -0.678.*

***a** Bifurcation diagram showing the minimum and maximum values of logarithmic biomass densities within a time-series in dependence of temperature. Dashed lines indicate the temperatures of which **b-e** show the corresponding time-series. Blue: prey densities; red: predator densities.*



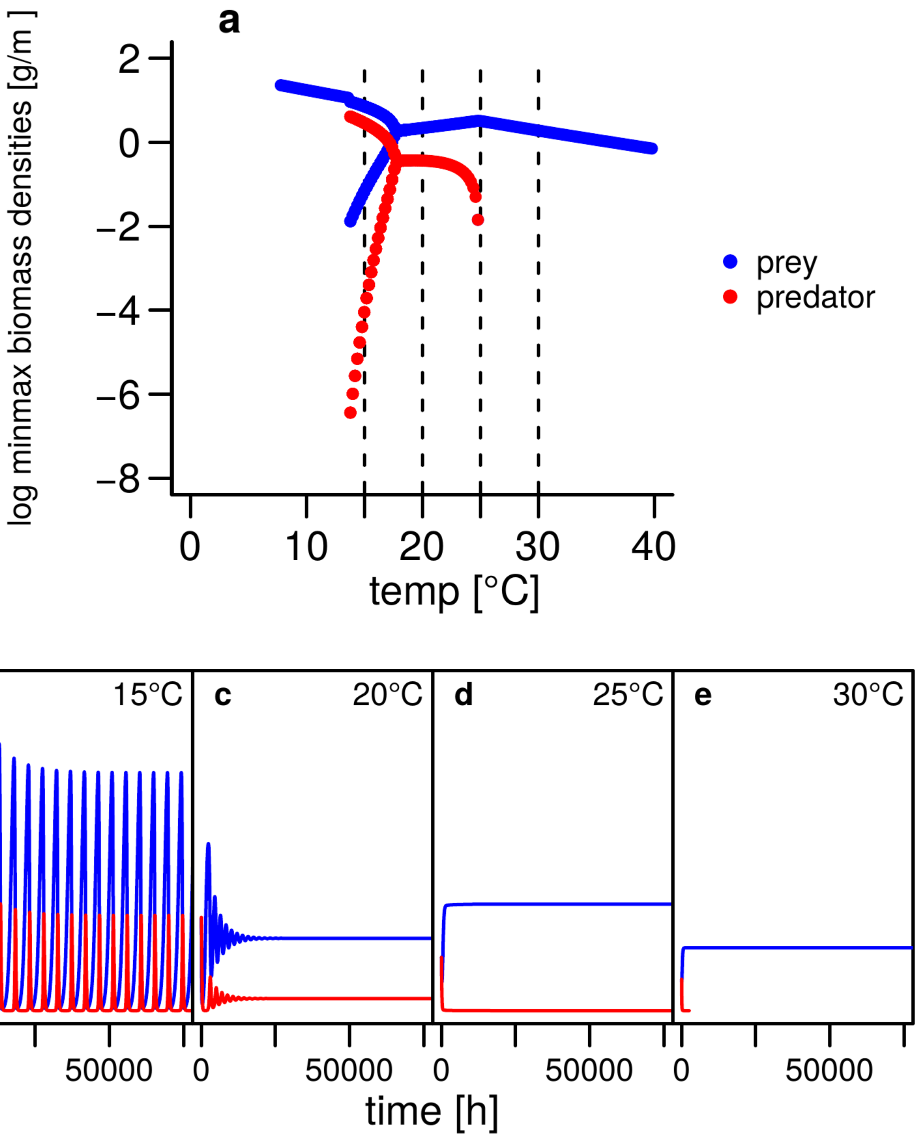
Supplementary Figure S1.2 | Destabilizing with extinction. *E_k = -0.459, E_r = 0.840, E_x = 0.512, E_mi = 0.973, E_B0 = -0.817.*

a *Bifurcation diagram showing the minimum and maximum values of logarithmic biomass densities within a time-series in dependence of temperature. Dashed lines indicate the temperatures of which* ***b-e*** *show the corresponding time-series. Blue: prey densities; red: predator densities.*



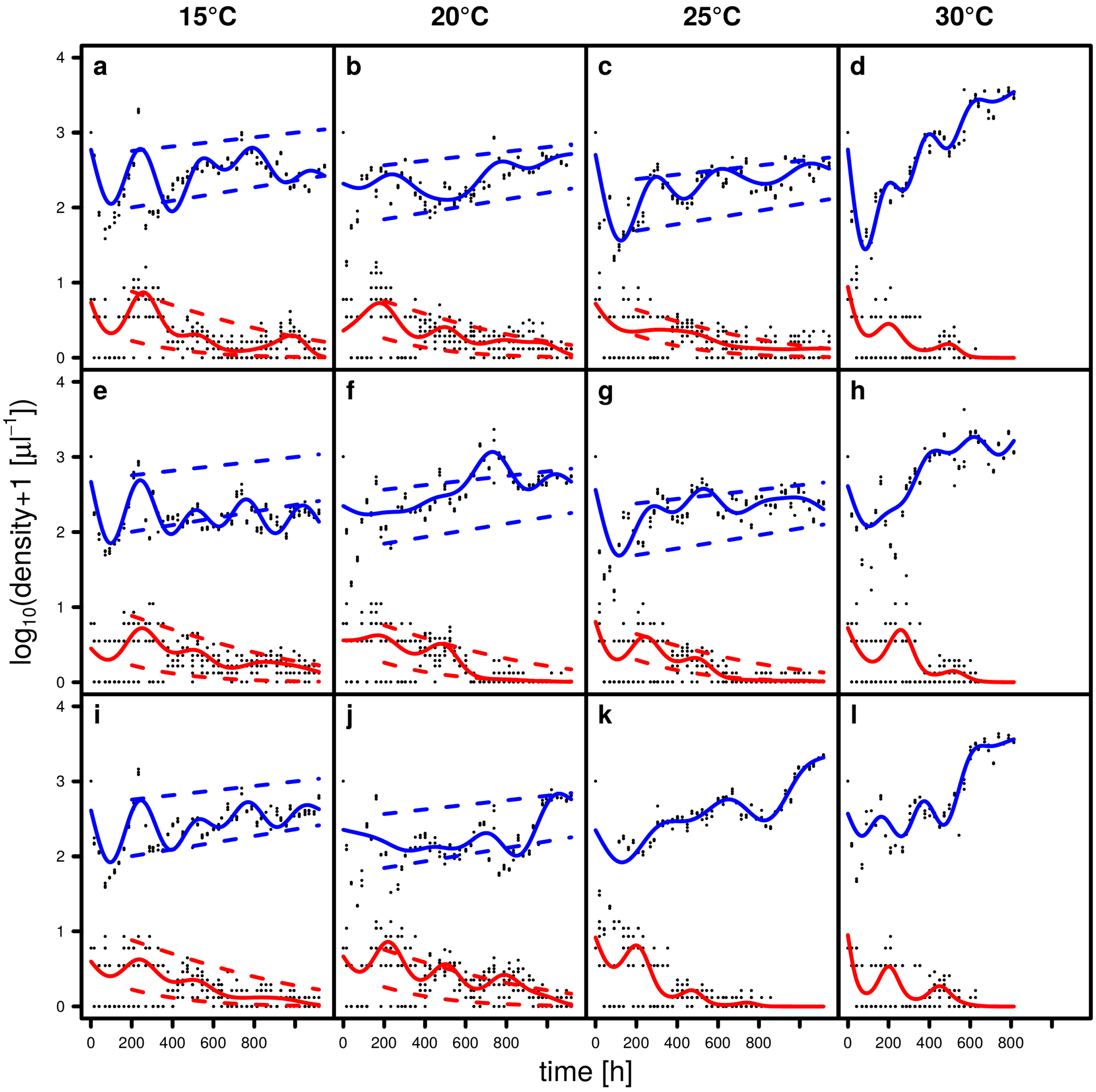
Supplementary Figure S1.3* | *Stabilizing without extinction. *E_k = -0.701, E_r = 0.840, E_x = 0.482, E_mi = 0.818, E_B0 = -0.270.*

a *Bifurcation diagram showing the minimum and maximum values of logarithmic biomass densities within a time-series in dependence of temperature. Dashed lines indicate the temperatures of which b-e show the corresponding time-series. Blue: prey densities; red: predator densities.*

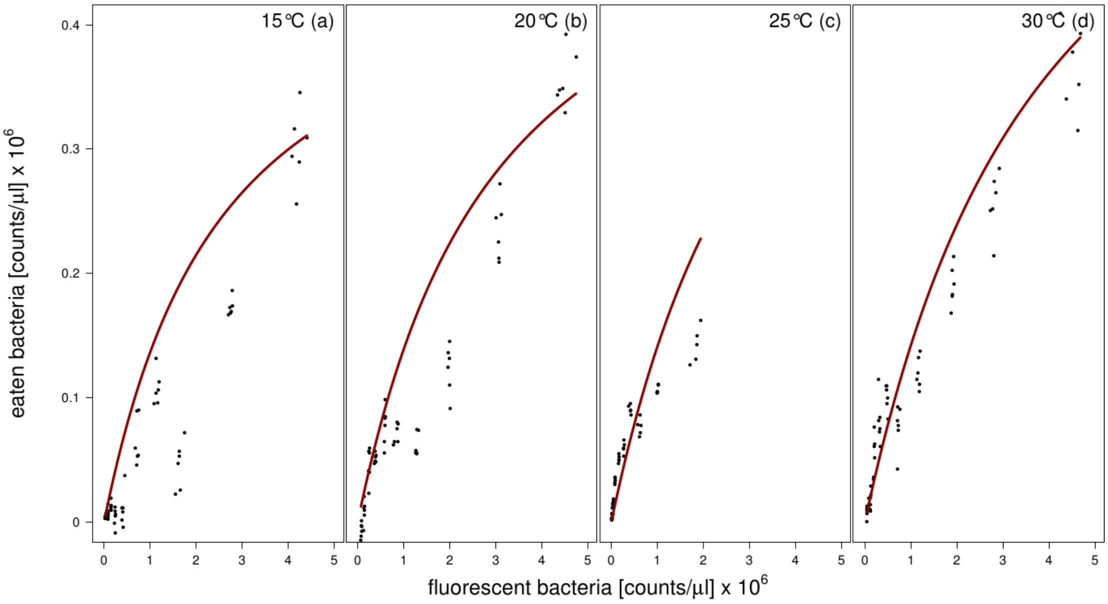


Supplementary Figure S1.4 | Stabilizing with extinction. *E_k = -0.823, E_r = 0.840, E_x = 0.696, E_mi = 0.338, E_B0 = 0.001.*

a *Bifurcation diagram showing the minimum and maximum values of logarithmic biomass densities within a time-series in dependence of temperature. Dashed lines indicate the temperatures of which* ***b-e*** *show the corresponding time-series. Blue: prey densities; red: predator densities.*



***Supplementary Figure S1.5 | Time Series of Tetrahymena pyriformis and Pseudomonas fluorescens CHA19-GFP** Replicates of the time series at **a, e, i** 15, **b, f, j** 20, **c, g, k** 25 and **d, h, l** 30°C fitted with a gam-model with Poisson distribution. Red lines show abundances of the predator T. pyriformis over time while blue lines show prey densities. Dotted lines in the according colours show quantile regressions.*



Supplementary Figure S1.6 | Functional response results for after 60 minutes.
Graphs show the feeding rates in dependence of bacterial density (x-axis) at, a, 15°C, b, 20°C, c, 25°C and d, 30°C.

Supplementary Tables

Supplementary Table S1.1: Model parameters.

	normalisation constant	*E [mean]*	SD_{Ea}
K	5.623	-0.772	0.357
r_R	$8.715*10^{-7}$	0.84	0.4
y_{CR}	$8.408*10^{-6}$	0.467	0.443
B_{0CR}	3.664	-0.114	0.639
x_C	$2.689*10^{-6}$	0.639	0.286

Supplementary Table S1.2: Activation Energies as estimated by functional response fitting.

parameters	estimate	s.e.	p
a_0	$6x10^{-7}$	$6x10^{-2}$	<0.001
E_a	-0.03	0.036	0.38
h_0	0.61	0.026	<0.001
E_h	-0.19	0.051	<0.001

Supplementary Table S1.3: Statistical estimates for the analyses of the temperature dependence of amplitude strength. Effects are given for the ln-transformed normalized amplitude values, the Arrhenius temperature (activation energy: E_{linear}), the squared Arrhenius temperature (activation energy: $E_{squared}$), the amplitude sequence number (slope: $a_{sequence}$), as well as the allowed interactions.

	estimate	*Std. Error*	*DF*	*t-value*	*p-value*
intercept	-1.07	0.54	64	-1.98	0.0517
E_{linear}	3.99	1.42	5	2.82	<0.05
$E_{squared}$	5.39	1.68	5	3.20	<0.05
$a_{sequence}$	0.03	0.17	64	0.19	0.8477
$E_{linear} : a_{sequence}$	-1.21	0.42	64	-2.92	<0.01
$E_{squared} : a_{sequence}$	-1.39	0.51	64	-2.75	<0.01

Supplementary Table S1.4: Statistical outputs of each single regression analyses.

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temperature levels	temperature range	R²	reference
maximum resource density	Arthropoda	NA	Aedes albopictus	-1.38	0.36	0.009	8	3	4	0.71	(Alto & Juliano 2001)
maximum resource density	Bacteria	NA	Aerobacter aerogenes	-0.71	0.18	0.012	7	7	35	0.75	(Greene & Jezeski 1954)
maximum resource density	Bacteria	NA	Enterococcus faecium	-0.90	0.34	0.029	10	10	44	0.47	(Zanoni *et al.* 1993)
maximum resource density	Bacteria	NA	Lactobacillus plantarum	-0.67	0.15	0.001	16	9	18.5	0.59	(Zwietering *et al.* 1991)
maximum resource density	Bacteria	NA	Pseudomomas1	-0.68	0.51	0.253	6	6	30	0.31	(Greene & Jezeski 1954)
maximum resource density	Bacteria	NA	Pseudomonas2	-0.29	0.25	0.304	6	6	30	0.26	(Greene & Jezeski 1954)
foraging efficiency	Arthropoda	Acartia hudsonica	Thalassiosira constricta	0.52	0.20	0.120	4	4	12	0.77	(Durbin & Durbin; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Amblyseius californicus	Tetranychus urticae	0.39	0.16	0.253	3	3	10	0.85	(Gotoh, Nozawa & Yamaguchi 2004; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Amblyseius longispinosus	Aponychus corpuzae	0.07	0.09	0.477	5	5	20	0.18	(Zhang *et al.* 1998; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Amblyseius longispinosus	Schizotetranychus nanjingensis	0.01	0.24	0.977	6	6	25	0.00	(Zhang *et al.* 1999; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Anisopteromalus calandrae	Rhyzopertha dominica	-0.47	0.47	0.424	4	4	15	0.33	(Menon, Flinn & Dover 2002; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Anisopteromalus calandrae	Sitophilus zeamais	0.23	0.07	0.174	3	3	10	0.93	(Smith 1994; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Aphidius colemani	Aphis gossypii	0.04	0.13	0.788	5	5	20	0.03	(Zamani *et al.* 2006; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Aphidius matricariae	Aphis gossypii	0.05	0.16	0.753	5	5	20	0.04	(Zamani *et al.* 2006; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Calathus fuscipes	Alphitobius diaperinus	0.45	0.36	0.286	6	6	25	0.27	(Vucic-Pestic *et al.* 2011; Rall *et al.* 2012)

foraging efficiency	Arthropoda	Calathus fuscipes	Drosophila hydei	0.02	0.06	0.799	6	6	25	0.02	(Vucic-Pestic *et al.* 2011; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Celithemis fasciata	Chironomus tentans	0.00	0.05	0.982	3	3	10	0.00	(Gresens, Cothran & Thorp 1982; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Cephalonomia waterstoni	Cryptolestes ferrugineus	-0.19	0.08	0.253	3	3	10	0.85	(Flinn 1991; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Chaoborus americanus	Daphnia pulex	-0.33	0.41	0.569	3	3	10	0.39	(Spitze 1985; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Chaoborus americanus	Daphnia pulex	-0.30	0.46	0.629	3	3	10	0.30	(Spitze 1985; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.12	0.17	0.557	5	5	20	0.13	(Xia, Rabbinge & Van Der Werf 2003; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.20	0.16	0.295	5	5	20	0.35	(Xia *et al.* 2003; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.30	0.07	0.020	5	5	20	0.87	(Xia *et al.* 2003; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.27	0.10	0.073	5	5	20	0.71	(Xia *et al.* 2003; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.40	0.21	0.156	5	5	20	0.54	(Xia *et al.* 2003; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.66	0.13	0.016	5	5	20	0.89	(Xia *et al.* 2003; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.38	0.04	0.002	5	5	20	0.97	(Xia *et al.* 2003; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.30	0.05	0.009	5	5	20	0.93	(Xia *et al.* 2003; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.59	0.06	0.002	5	5	20	0.97	(Xia *et al.* 2003; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.35	0.05	0.005	5	5	20	0.95	(Xia *et al.* 2003; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.54	0.09	0.008	5	5	20	0.93	(Xia *et al.* 2003; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.70	0.08	0.003	5	5	20	0.96	(Xia *et al.* 2003; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.55	0.10	0.010	5	5	20	0.92	(Xia *et al.* 2003; Rall *et al.* 2012)

foraging efficiency	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.54	0.08	0.006	5	5	20	0.94	(Xia *et al.* 2003; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.68	0.08	0.004	5	5	20	0.96	(Xia *et al.* 2003; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Coenosia attenuata	Drosophila melanogaster	-0.52	0.21	0.246	3	3	12	0.86	(Gilioli, Baumgartner & Vacante 2005; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Coleomegilla maculata	Leptinotarsa decemlineata	-1.97	0.71	0.220	3	3	6	0.89	(Munyaneza & Obrycki 1997; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Coleomegilla maculata	Myzus persicae	-1.22	0.24	0.007	6	6	18.9	0.86	(Sentis, Hemptinne & Brodeur 2012; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Cycloneda sanguinea	Aphis gossypii	0.19	0.85	0.858	3	3	10	0.05	(Isikber; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Encarsia formosa	Bemisia tabaci	0.50	0.31	0.352	3	3	12	0.72	(Enkegaard 1994; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Harpalus rufipes	Alphitobius diaperinus	0.43	0.29	0.216	6	6	25	0.35	(Vucic-Pestic *et al.* 2011; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Harpalus rufipes	Drosophila hydei	-0.21	0.31	0.533	6	6	25	0.10	(Vucic-Pestic *et al.* 2011; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Ischnura elegans	Daphnia magna	0.20	0.18	0.327	6	6	22.5	0.24	(Thompson 1978; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Neoseiulus californicus	Tetranychus urticae	0.36	0.09	0.061	4	4	15	0.88	(Ahn, Kim & Lee 2010; Rall *et al.* 2012)
foraging efficiency	Fish	Perca fluviatilis	Chaoborus obscuripes	-0.38	0.18	0.171	4	4	9	0.69	(Persson 1986; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Piona exigua	Ceriodaphnia dubia	0.00	0.00	0.377	4	4	12	0.39	(Butler & Burns 1993; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Piona exigua	Ceriodaphnia dubia	0.00	0.00	0.119	4	4	12	0.78	(Butler & Burns 1993; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Piona exigua	Daphnia carinata	0.00	0.02	0.900	3	3	7	0.02	(Butler & Burns 1993; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Podisus maculiventris	Spodoptera exigua	-0.06	0.09	0.627	3	3	9	0.31	(Mohaghegh, De Clercq & Tirry 2001; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Podisus nigrispinus	Spodoptera exigua	0.43	0.77	0.676	3	3	9	0.24	(Mohaghegh *et al.* 2001; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Pterostichus melanarius	Alphitobius diaperinus	0.69	0.35	0.121	6	6	25	0.49	(Vucic-Pestic *et al.* 2011; Rall *et al.* 2012)

foraging efficiency	Arthropoda	Pterostichus melanarius	Drosophila hydei	-0.18	0.12	0.212	6	6	25	0.36	(Vucic-Pestic *et al.* 2011; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Ranatra dispar	Anisops deanei	-0.63	0.13	0.134	3	3	10	0.96	(Bailey 1989; Rall *et al.* 2012)
foraging efficiency	Fish	Rutilus rutilus	Chaoborus obscuripes	-0.62	0.52	0.356	4	4	9	0.42	(Persson 1986; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Scolothrips takahashii	Tetranychus urticae	0.22	0.17	0.417	3	3	10	0.63	(Gotoh *et al.* 2004; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Scolothrips takahashii	Tetranychus viennensis	1.06	0.01	0.003	3	3	10	1.00	(Ding-Xu, Juan & Zuo-Rui 2007; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Scolothrips takahashii	Tetranychus viennensis	-0.09	0.05	0.215	4	4	15	0.62	(Ding-Xu *et al.* 2007; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Scymnus levaillanti	Aphis gossypii	0.85	0.62	0.402	3	3	10	0.65	(Isikber; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Stethorus japonicus	Tetranychus urticae	0.98	0.18	0.114	3	3	12	0.97	(Gotoh *et al.* 2004; Rall *et al.* 2012)
foraging efficiency	Arthropoda	Telenomus reynoldsi	Geocoris punctipes	-0.86	0.31	0.067	5	5	15	0.73	(Cave & Gaylor 1989; Rall *et al.* 2012)
foraging efficiency	unicells	Tetrahymena pyriformis	Pseudomonas flurescens	0.16				4	15	2.00	this study
foraging efficiency	Arthropoda	Theocolax elegans	Rhyzopertha dominica	0.35	0.84	0.717	4	4	12.5	0.08	(Flinn & Hagstrum 2002; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Acartia hudsonica	Thalassiosira constricta	0.52	0.20	0.120	4	4	12	0.77	(Durbin & Durbin; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Amblyseius californicus	Tetranychus urticae	0.41	0.07	0.112	3	3	10	0.97	(Gotoh *et al.* 2004; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Amblyseius longispinosus	Aponychus corpuzae	0.23	0.08	0.062	5	5	20	0.74	(Zhang *et al.* 1998; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Amblyseius longispinosus	Schizotetranychus nanjingensis	0.44	0.14	0.032	6	6	25	0.72	(Zhang *et al.* 1999; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Anisopteromalus calandrae	Rhyzopertha dominica	1.14	0.43	0.115	4	4	15	0.78	(Menon *et al.* 2002; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Anisopteromalus calandrae	Sitophilus zeamais	1.00	0.33	0.094	4	4	15	0.82	(Smith 1994; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Aphidius colemani	Aphis gossypii	0.32	0.10	0.055	5	5	20	0.76	(Zamani *et al.* 2006; Rall *et al.* 2012)

maximum feeding rate	Arthropoda	Aphidius matricariae	Aphis gossypii	0.15	0.13	0.324	5	5	20	0.32	(Zamani *et al.* 2006; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Calathus fuscipes	Alphitobius diaperinus	0.27	0.04	0.020	4	4	15	0.96	(Vucic-Pestic *et al.* 2011; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Calathus fuscipes	Drosophila hydei	0.20	0.12	0.160	6	6	25	0.43	(Vucic-Pestic *et al.* 2011; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Celithemis fasciata	Chironomus tentans	0.29	0.04	0.023	4	4	15	0.96	(Gresens *et al.* 1982; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Cephalonomia waterstoni	Cryptolestes ferrugineus	-0.19	0.08	0.253	3	3	10	0.85	(Flinn 1991; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Chaoborus americanus	Daphnia pulex	0.57	0.32	0.327	3	3	10	0.76	(Spitze 1985; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Chaoborus americanus	Daphnia pulex	0.20	0.56	0.783	3	3	10	0.11	(Spitze 1985; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Coccinella septempunctata	Aphis gossypii	0.39	0.16	0.092	5	5	20	0.67	(Xia *et al.* 2003; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Coccinella septempunctata	Aphis gossypii	0.37	0.13	0.067	5	5	20	0.72	(Xia *et al.* 2003; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Coccinella septempunctata	Aphis gossypii	0.23	0.06	0.035	5	5	20	0.82	(Xia *et al.* 2003; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Coccinella septempunctata	Aphis gossypii	0.25	0.13	0.137	5	5	20	0.58	(Xia *et al.* 2003; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Coccinella septempunctata	Aphis gossypii	0.21	0.14	0.235	5	5	20	0.42	(Xia *et al.* 2003; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Coccinella septempunctata	Aphis gossypii	0.15	0.08	0.141	5	5	20	0.57	(Xia *et al.* 2003; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Coccinella septempunctata	Aphis gossypii	0.10	0.06	0.210	5	5	20	0.46	(Xia *et al.* 2003; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Coccinella septempunctata	Aphis gossypii	0.19	0.07	0.074	5	5	20	0.71	(Xia *et al.* 2003; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Coccinella septempunctata	Aphis gossypii	0.31	0.09	0.171	3	3	10	0.93	(Xia *et al.* 2003; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.09	0.03	0.067	4	4	15	0.87	(Xia *et al.* 2003; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.04	0.05	0.499	5	5	20	0.16	(Xia *et al.* 2003; Rall *et al.* 2012)

maximum feeding rate	Arthropoda	Coccinella septempunctata	Aphis gossypii	0.13	0.06	0.291	3	3	10	0.81	(Xia *et al.* 2003; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.04	0.03	0.257	5	5	20	0.39	(Xia *et al.* 2003; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Coccinella septempunctata	Aphis gossypii	-0.07	0.01	0.029	4	4	15	0.94	(Xia *et al.* 2003; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Coccinella septempunctata	Aphis gossypii	0.05	0.02	0.062	5	5	20	0.74	(Xia *et al.* 2003; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Coenosia attenuata	Drosophila melanogaster	0.82	0.30	0.109	4	4	18	0.79	(Gilioli *et al.* 2005; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Coleomegilla maculata	Leptinotarsa decemlineata	0.41	0.48	0.484	4	4	8	0.27	(Munyaneza & Obrycki 1997; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Coleomegilla maculata	Myzus persicae	0.68	0.10	0.003	6	6	18.9	0.92	(Sentis *et al. 2012*; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Cycloneda sanguinea	Aphis gossypii	0.91	0.33	0.221	3	3	10	0.88	(Isikber; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Encarsia formosa	Bemisia tabaci	1.43	0.35	0.152	3	3	12	0.94	(Enkegaard 1994; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Harpalus rufipes	Alphitobius diaperinus	0.33	0.06	0.007	6	6	25	0.87	(Vucic-Pestic *et al.* 2011; b)
maximum feeding rate	Arthropoda	Harpalus rufipes	Drosophila hydei	0.38	0.14	0.057	6	6	25	0.64	(Vucic-Pestic *et al.* 2011; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Ischnura elegans	Daphnia magna	0.71	0.22	0.032	6	6	22.5	0.72	(Thompson 1978; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Neoseiulus californicus	Tetranychus urticae	0.38	0.04	0.012	4	4	15	0.98	(Ahn *et al.* 2010; Rall *et al.* 2012)
maximum feeding rate	Fish	Perca fluviatilis	Chaoborus obscuripes	0.36	0.14	0.120	4	4	9	0.77	(Persson 1986; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Piona exigua	Ceriodaphnia dubia	0.63	0.17	0.063	4	4	12	0.88	(Butler & Burns 1993; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Piona exigua	Ceriodaphnia dubia	0.53	0.07	0.016	4	4	12	0.97	(Butler & Burns 1993; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Piona exigua	Daphnia carinata	1.21	0.40	0.095	4	4	12	0.82	(Butler & Burns 1993; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Podisus maculiventris	Spodoptera exigua	0.24	0.01	0.017	3	3	9	1.00	(Mohaghegh *et al.* 2001; Rall *et al.* 2012)

maximum feeding rate	Arthropoda	Podisus nigrispinus	Spodoptera exigua	0.75	0.44	0.338	3	3	9	0.74	(Mohaghegh *et al.* 2001; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Pterostichus melanarius	Alphitobius diaperinus	0.30	0.08	0.017	6	6	25	0.80	(Vucic-Pestic *et al.* 2011; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Pterostichus melanarius	Drosophila hydei	0.14	0.04	0.028	6	6	25	0.74	(Vucic-Pestic *et al.* 2011; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Ranatra dispar	Anisops deanei	0.56	0.33	0.230	4	4	15	0.59	(Bailey 1989; Rall *et al.* 2012)
maximum feeding rate	Fish	Rutilus rutilus	Chaoborus obscuripes	0.70	0.21	0.080	4	4	9	0.85	(Persson 1986; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Scolothrips takahashii	Tetranychus urticae	0.65	0.00	0.002	3	3	10	1.00	(Gotoh *et al.* 2004; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Scolothrips takahashii	Tetranychus viennensis	0.52	0.08	0.025	4	4	15	0.95	(Ding-Xu *et al.* 2007; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Scolothrips takahashii	Tetranychus viennensis	0.46	0.09	0.041	4	4	15	0.92	(Ding-Xu *et al.* 2007; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Scymnus levaillanti	Aphis gossypii	1.84	0.25	0.084	3	3	10	0.98	(Isikber; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Stethorus japonicus	Tetranychus urticae	0.94	0.17	0.117	3	3	12	0.97	(Gotoh *et al.* 2004; Rall *et al.* 2012)
maximum feeding rate	Arthropoda	Telenomus reynoldsi	Geocoris punctipes	0.26	0.03	0.003	5	5	15	0.97	(Cave & Gaylor 1989; Rall *et al.* 2012)
maximum feeding rate	unicells	Tetrahymena pyriformis	Pseudomonas flurescens	0.19				4	15	2.00	this study
maximum feeding rate	Arthropoda	Theocolax elegans	Rhyzopertha dominica	2.11	0.45	0.042	4	4	12.5	0.92	(Flinn & Hagstrum 2002; Rall *et al.* 2012)
metabolism	Arthropoda	Abax paralellepipedus	NA	0.63	0.06	0.000	49	5	20	0.74	(Ehnes *et al.* 2011)
metabolism	Reptiles	Acabthodactylus boskianus	NA	0.59	0.21	0.050	7	7	30	0.79	(Andrews & Pough 1985; Al-Sadoon 1986; White *et al.* 2006)
metabolism	Reptiles	Acanthodactylus erythrurus	NA	0.51	NA	NA	4	4	15	1.00	(Andrews & Pough 1985; White *et al.* 2006)
metabolism	Reptiles	Acanthodactylus opheodurus	NA	0.65	NA	NA	3	3	15	0.98	(Al-Sadoon & Spellerberg 1985a; White *et al.* 2006)
metabolism	Reptiles	Acanthodactylus pardalis	NA	0.35	NA	NA	4	4	15	0.90	(Andrews & Pough 1985; White *et al.* 2006)

metabolism	Reptiles	Acanthodactylus schmidti	NA	0.60	NA	NA	3	3	15	1.00	(Al-Sadoon & Spellerberg 1985a; White *et al.* 2006)
metabolism	Reptiles	Acanthodactylus schreiberi	NA	0.34	NA	NA	4	4	15	0.97	(Andrews & Pough 1985; White *et al.* 2006)
metabolism	Reptiles	Acanthodactylus scutellatus	NA	0.61	NA	NA	4	4	15	0.95	(Andrews & Pough 1985; White *et al.* 2006)
metabolism	Reptiles	Acanthophis praelongus	NA	0.50	NA	NA	4	4	9	0.81	(Bedford & Christian 1998; White *et al.* 2006)
metabolism	Arthropoda	Achipteria coleoptrata	NA	0.85	NA	NA	4	4	15	0.94	(Luxton 1975; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Achipteria holomonensis	NA	1.02	NA	NA	3	3	10	0.99	(Stamou 1986; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Achipteria oudemansi	NA	0.48	NA	NA	6	6	22	0.85	(Stamou *et al.* 1995; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Reptiles	Acrantophis dumerili	NA	0.74	NA	NA	3	3	14	1.00	(Chappell & Ellis 1987; White *et al.* 2006)
metabolism	Amphibians	Acris crepitans	NA	0.76	0.12	0.000	10	3	20	0.87	(Gatten Jr., Miller & Full 1992; White *et al.* 2006)
metabolism	Arthropoda	Adoristes ovatus	NA	0.78	NA	NA	4	4	15	1.00	(Luxton 1975; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Alaskozetes antarcticus	NA	0.70	0.08	0.000	27	3	10	0.94	(Block 1977; Young 1979; Caruso *et al.* 2010; Ehnes *et al.* 2011)
metabolism	Reptiles	Aligator mississippiensis	NA	0.79	NA	NA	6	6	25	0.99	(Lewis & Gatten Jr. 1985; White *et al.* 2006)
metabolism	Annelida	Allolobophora caliginosa	NA	0.49	0.10	0.129	4	4	13	0.99	(Byzova 1965; Phillipson & Bolton 1976; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Alopecosa juv.	NA	0.34	0.34	0.348	12	3	7	0.13	(Ehnes *et al.* 2011)
metabolism	Arthropoda	Alopecosa spec	NA	0.84	0.11	0.000	39	5	14	0.64	(Ehnes *et al.* 2011)
metabolism	Reptiles	Amblyrhynchus cristatus	NA	0.93	0.03	0.020	4	4	15	1.00	(Bartholomew & Lasiewski 1965; Bennett, Dawson & Bartholomew 1975; White *et al.* 2006)
metabolism	Amphibians	Ambystoma maculatum	NA	0.50	0.11	0.002	12	6	25	0.85	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Ambystoma tigrinum	NA	0.49	0.18	0.017	14	6	20	0.55	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Fish	Ameiurus nebulosus	NA	0.62	0.02	0.000	6	3	20	1.00	(Bokma 2004; White *et al.* 2006)
metabolism	Reptiles	Amphibolurus barbatus	NA	0.54	NA	NA	3	3	17	0.99	(Bartholomew & Tucker 1963; Andrews & Pough 1985; White *et al.* 2006)
metabolism	Amphibians	Amphiuma means	NA	0.80	0.11	0.000	14	9	25	0.86	(Gatten Jr. *et al.* 1992; White *et al.* 2006)

metabolism	Amphibians	Aneides hardii	NA	0.37	NA	NA	5	5	20	0.92	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Fish	Anguilla japonica	NA	0.83	NA	NA	29	16	17	0.92	(Bokma 2004; White *et al.* 2006)
metabolism	Reptiles	Anguis fragilis	NA	0.37	NA	NA	3	3	15	1.00	(Al-Sadoon & Spellerberg 1985a; Andrews & Pough 1985; White *et al.* 2006)
metabolism	Reptiles	Anniella pulchra	NA	0.41	0.08	0.035	5	5	24	0.95	(Kamel & Gatten 1983; Fusari 1984; Andrews & Pough 1985; White *et al.* 2006)
metabolism	Reptiles	Antaresia childreni	NA	0.90	0.05	0.038	4	4	9	1.00	(Bedford & Christian 1998; White *et al.* 2006)
metabolism	Reptiles	Antaresia stimsoni	NA	0.19	0.20	0.521	4	4	9	0.78	(Bedford & Christian 1998; White *et al.* 2006)
metabolism	Annelida	Aporectodea caliginosa	NA	0.54	0.05	0.000	53	8	25	0.74	(Ehnes *et al.* 2011)
metabolism	Annelida	Aporectodea rosea	NA	0.64	0.19	0.007	14	3	10	0.68	(Ehnes *et al.* 2011)
metabolism	Arthropoda	Armadillidium vulgare	NA	0.69	0.08	0.000	49	12	25	0.68	(Edney 1964; Reichle 1968; Saito 1969; Al-Dabbagh 1976; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Reptiles	Aspidites melanocephalus	NA	0.87	NA	NA	4	4	9	1.00	(Bedford & Christian 1998; White *et al.* 2006)
metabolism	Amphibians	Batrachoseps attenuatus	NA	0.52	0.06	0.001	7	4	20	0.97	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Arthropoda	Belba corynopus	NA	0.65	NA	NA	4	4	15	1.00	(Luxton 1975; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Bembidion	NA	0.71	0.07	0.000	42	6	20	0.82	(Ehnes *et al.* 2011)
metabolism	Reptiles	Blanus cinereus	NA	0.49	NA	NA	3	3	15	0.89	(Al-Sadoon & Spellerberg 1985a; White *et al.* 2006)
metabolism	Reptiles	Boa constrictor	NA	0.89	NA	NA	3	3	14	1.00	(Andrews & Pough 1985; Chappell & Ellis 1987; White *et al.* 2006)
metabolism	Amphibians	Bolitoglossa occidentalis	NA	0.71	0.24	0.098	5	3	20	0.81	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Bolitoglossa subpalmata	NA	0.73	NA	NA	4	4	15	0.98	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Boulengerula taitanus	NA	0.52	NA	NA	3	3	15	1.00	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Bufo americanus	NA	0.39	0.18	0.076	10	6	20	0.92	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Bufo boreas	NA	0.31	0.20	0.139	16	7	25	0.38	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Bufo bufo	NA	0.47	0.11	0.004	9	5	19	0.77	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Bufo cognatus	NA	0.46	0.14	0.042	6	6	25	0.80	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Bufo marinus	NA	0.55	0.16	0.007	12	7	20	0.80	(Gatten Jr. *et al.* 1992; White *et al.* 2006)

metabolism	Amphibians	Bufo terrestris	NA	0.69	0.15	0.010	7	5	25	0.97	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Bufo woodhousii	NA	0.33	0.27	0.300	6	5	15	0.62	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Reptiles	Bunopus tuberculatus	NA	0.40	NA	NA	3	3	15	0.99	(Al-Sadoon & Abdo 1989; White *et al.* 2006)
metabolism	Arthropoda	Calathus fuscipes	NA	0.55	0.06	0.000	81	6	25	0.50	(Ehnes *et al.* 2011)
metabolism	Arthropoda	Calathus melanocephalus	NA	0.54	0.06	0.000	53	6	25	0.62	(Ehnes *et al.* 2011)
metabolism	Reptiles	Candoia carinatus	NA	0.80	NA	NA	3	3	14	1.00	(Chappell & Ellis 1987; White *et al.* 2006)
metabolism	Arthropoda	Carabodes coriaceus	NA	0.87	NA	NA	3	3	10	0.99	(Berthet 1964; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Carabodes marginatus	NA	0.66	NA	NA	3	3	10	0.95	(Berthet 1964; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Carabus auratus	NA	0.85	0.10	0.000	41	5	14	0.67	(Ehnes *et al.* 2011)
metabolism	Fish	Catostomus commersonii	NA	0.72	0.13	0.002	8	3	10	0.89	(Bokma 2004; White *et al.* 2006)
metabolism	Arthropoda	Ceratozetes gracilis	NA	0.86	0.16	0.014	6	4	15	0.90	(Wood & Lawton 1973; Luxton 1975; Mitchell 1979b; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Ceratozetes kananaskis	NA	0.72	NA	NA	4	4	15	0.97	(Mitchell 1979b; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Fish	Chaenocephalus aceratus	NA	-0.13	NA	NA	17	4	6	0.06	(Bokma 2004; White *et al.* 2006)
metabolism	Reptiles	Chalcides ocellatus	NA	0.46	NA	NA	8	8	30	0.98	(Al-Sadoon & Spellerberg 1985b, 1987; Andrews & Pough 1985; White *et al.* 2006)
metabolism	Arthropoda	Chamobates cuspidatus	NA	1.21	NA	NA	3	3	10	1.00	(Berthet 1964; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Reptiles	Chelydra serpentina	NA	0.88	NA	NA	3	3	20	1.00	(Gatten Jr 1978; White *et al.* 2006)
metabolism	Fish	Cirrhinus cirrhosus	NA	0.84	0.21	0.002	14	3	10.5	0.98	(Bokma 2004; White *et al.* 2006)
metabolism	Reptiles	Cnemidophorus tigris	NA	0.67	NA	NA	3	3	17	1.00	(Andrews & Pough 1985; White *et al.* 2006)
metabolism	Reptiles	Corallus caninus	NA	0.77	NA	NA	3	3	14	0.99	(Chappell & Ellis 1987; White *et al.* 2006)
metabolism	Reptiles	Corallus enhydris	NA	0.68	NA	NA	3	3	14	1.00	(Chappell & Ellis 1987; White *et al.* 2006)
metabolism	Amphibians	Crinia parinsignifera	NA	0.54	0.03	0.000	7	7	30	0.99	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Crinia signifera	NA	0.57	0.05	0.000	10	7	30	0.96	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Reptiles	Crotaphytus collaris	NA	0.58	NA	NA	3	3	17	1.00	(Andrews & Pough 1985; White *et al.* 2006)
metabolism	Amphibians	Cryptobranchus alleganiensis	NA	0.61	NA	NA	3	3	20	1.00	(Gatten Jr. *et al.* 1992; White *et al.* 2006)

metabolism	Arthropoda	Cryptopygus antarcticus	NA	0.39	0.18	0.030	46	6	20	0.45	(Block & Tilbrook 1975, 1978; Procter & Bliss 1977; Block 1979; Caruso *et al.* 2010; Ehnes *et al.* 2011)
metabolism	Fish	Cyprinus carpio carpio	NA	0.37	0.10	0.001	24	7	25	0.93	(Bokma 2004; White *et al.* 2006)
metabolism	Arthropoda	Damaeus clavipes	NA	0.68	0.10	0.020	5	4	15	0.96	(Wood & Lawton 1973; Luxton 1975; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Fish	Dasyatis sabina	NA	0.27	0.63	0.678	10	8	2.7	0.84	(Bokma 2004; White *et al.* 2006)
metabolism	Annelida	Dendrobaena veneta	NA	0.41	0.06	0.000	35	8	21.3	0.63	(Ehnes *et al.* 2011)
metabolism	Amphibians	Desmognathus fuscus	NA	0.36	0.16	0.047	14	7	15	0.77	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Desmognathus ochrophaes	NA	0.59	0.10	0.000	19	7	16	0.82	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Desmognathus quadramaculatus	NA	0.41	0.12	0.005	15	5	20	0.65	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Arthropoda	Dicyrtomina minuta	NA	0.93	0.13	0.086	4	4	9	0.98	(Zinkler 1966; Petersen 1981; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Reptiles	Diplometopon zarudnyi	NA	0.40	NA	NA	6	6	25	0.93	(Al-Sadoon 1986; White *et al.* 2006)
metabolism	Reptiles	Dipsosaurus dorsalis	NA	0.63	NA	NA	7	7	25	0.96	(Bennett & Dawson 1972; Andrews & Pough 1985; White *et al.* 2006)
metabolism	Annelida	Eisenia foetida	NA	0.52	0.05	0.000	46	18	31	0.87	(Knoz 1957; Byzova 1965; Mitchell 1979a; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Annelida	Eiseniella tetraedra	NA	0.47	0.14	0.018	8	8	18	0.71	(Knoz 1957; Byzova 1965; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Amphibians	Ensatina eschscholtzi	NA	0.49	NA	NA	3	3	11	1.00	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Reptiles	Epicrates cenchria	NA	0.73	NA	NA	3	3	14	0.99	(Chappell & Ellis 1987; White *et al.* 2006)
metabolism	Arthropoda	Ereynetes macquariensis	NA	0.23	0.09	0.234	4	3	10	0.95	(Goddard 1977a; Caruso *et al.* 2010; Ehnes *et al.* 2011)
metabolism	Reptiles	Eryx colubrinus	NA	0.74	NA	NA	3	3	14	1.00	(Chappell & Ellis 1987; White *et al.* 2006)
metabolism	Reptiles	Eumeces obsoletus	NA	0.89	NA	NA	3	3	17	1.00	(Andrews & Pough 1985; White *et al.* 2006)
metabolism	Amphibians	Eurycea bislineata	NA	0.61	0.15	0.015	7	6	19	0.81	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Eurycea multiplicata	NA	0.48	0.33	0.199	9	5	20	0.56	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Arthropoda	Euzetes globulus	NA	0.93	0.08	0.000	7	6	25	0.97	(Berthet 1964; Zinkler 1966; Wood & Lawton 1973; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Fish	Exodon paradoxus	NA	0.85	NA	NA	3	3	10	1.00	(Bokma 2004; White *et al.* 2006)

metabolism	Arthropoda	Folsomia manolachei	NA	1.77	NA	NA	3	3	9	1.00	(Petersen 1981; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Folsomia quadrioculata	NA	0.76	NA	NA	6	3	9	0.95	(Petersen 1981; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Fish	Gadus morhua	NA	0.41	0.12	0.002	51	5	10	0.96	(Bokma 2004; White *et al.* 2006)
metabolism	Arthropoda	Gamasellus racovitzai	NA	0.48	0.09	0.000	18	3	10	0.94	(Goddard 1977b; Caruso *et al.* 2010; Ehnes *et al.* 2011)
metabolism	Fish	Gambusia affinis	NA	0.39	NA	NA	3	3	10	1.00	(Bokma 2004; White *et al.* 2006)
metabolism	Arthropoda	Geolycosa domifex	NA	1.22	NA	NA	3	3	7	0.91	(Anderson 1970; Moulder & Reichle 1972; Humphreys 1977; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Geophilidae	NA	0.81	0.06	0.000	135	20	25	0.66	(Ehnes *et al.* 2011)
metabolism	Arthropoda	Glomeris	NA	0.74	0.06	0.000	53	10	25	0.73	(Ehnes *et al.* 2011)
metabolism	Annelida	Glossoscolex paulistus	NA	0.21	0.03	0.020	5	5	20	0.98	(Abe & Buck 1985; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Amphibians	Gyrinophilus danielsi	NA	0.71	NA	NA	3	3	23	1.00	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Gyrinophilus porphyrictus	NA	0.77	0.32	0.141	5	4	20	0.82	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Arthropoda	Harpalus	NA	0.72	0.09	0.000	38	6	17	0.66	(Ehnes *et al.* 2011)
metabolism	Reptiles	Helicops modestus	NA	0.35	NA	NA	3	3	10	0.94	(Andrews & Pough 1985; White *et al.* 2006)
metabolism	Reptiles	Hemidactylus frenatus	NA	0.99	0.18	0.113	4	4	10	0.98	(Andrews & Pough 1985; White *et al.* 2006)
metabolism	Arthropoda	Hemileius initialis	NA	0.69	NA	NA	4	4	15	1.00	(Luxton 1975; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Hogna lenta	NA	0.73	0.11	0.096	4	3	20	0.98	(Anderson 1970, 1996; Ford 1977a; Greenstone & Bennett 1980; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Amphibians	Hyla chrysoscelis	NA	0.75	0.01	0.010	4	3	20	1.00	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Hyla cinerea	NA	0.35	0.14	0.063	7	7	20	0.82	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Hyla gratiosa	NA	0.35	0.01	0.027	4	4	24	1.00	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Hyla versicolor	NA	0.28	0.20	0.295	5	5	20	0.50	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Arthropoda	Hypochthonius rufulus	NA	0.93	NA	NA	4	4	15	0.99	(Berthet 1964; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Reptiles	Iguana iguana	NA	0.60	NA	NA	3	3	17	0.99	(Andrews & Pough 1985; White *et al.* 2006)

metabolism	Arthropoda	Isopoda	NA	0.25	0.07	0.003	21	4	25	0.84	(Ehnes *et al.* 2011)
metabolism	Arthropoda	Isotomiella minor	NA	0.56	NA	NA	3	3	9	0.95	(Petersen 1981; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Julidae	NA	0.66	0.04	0.000	127	17	25	0.72	(Ehnes *et al.* 2011)
metabolism	Reptiles	Klauberina riversiana	NA	0.84	NA	NA	3	3	10	1.00	(Mautz 1979; Andrews & Pough 1985; White *et al.* 2006)
metabolism	Reptiles	Lacerta agilis	NA	0.52	NA	NA	3	3	15	1.00	(Al-Sadoon & Spellerberg 1985a; White *et al.* 2006)
metabolism	Reptiles	Lacerta vivipara	NA	0.62	0.04	0.000	14	7	30	0.96	(Al-Sadoon & Spellerberg 1985b; Andrews & Pough 1985; Patterson & Davies 1989; White *et al.* 2006)
metabolism	Fish	Lampetra fluviatilis	NA	0.92	0.07	0.000	46	9	11.6	0.98	(Bokma 2004; White *et al.* 2006)
metabolism	Fish	Lampetra planeri	NA	0.94	NA	NA	17	7	10.3	0.39	(Bokma 2004; White *et al.* 2006)
metabolism	Reptiles	Lampropeltis miliaris	NA	0.64	NA	NA	3	3	10	0.99	(Andrews & Pough 1985; White *et al.* 2006)
metabolism	Arthropoda	Lepidocyrtus	NA	0.69	NA	NA	3	3	9	0.87	(Petersen 1981; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Reptiles	Lepidophyma gaigeae	NA	0.75	NA	NA	4	4	15	0.96	(Mautz 1979; Andrews & Pough 1985; White *et al.* 2006)
metabolism	Reptiles	Lepidophyma smithi	NA	0.63	NA	NA	3	3	10	0.99	(Mautz 1979; Andrews & Pough 1985; White *et al.* 2006)
metabolism	Arthropoda	Liacarus coracinus	NA	0.90	NA	NA	3	3	10	0.96	(Berthet 1964; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Reptiles	Liasis fuscus	NA	0.88	NA	NA	4	4	9	0.93	(Bedford & Christian 1998; White *et al.* 2006)
metabolism	Reptiles	Liasis olivaceus	NA	0.67	0.23	0.207	4	4	9	0.93	(Bedford & Christian 1998; White *et al.* 2006)
metabolism	Reptiles	Lichanura trivirgata	NA	0.78	NA	NA	3	3	14	0.99	(Chappell & Ellis 1987; White *et al.* 2006)
metabolism	Fish	Limanda limanda	NA	0.71	NA	NA	3	3	10	1.00	(Bokma 2004; White *et al.* 2006)
metabolism	Arthropoda	Lithobius forficatus	NA	0.78	0.04	0.000	252	17	26	0.74	(Ehnes *et al.* 2011)
metabolism	Arthropoda	Loricera pilicornis	NA	0.67	0.04	0.000	49	6	25	0.84	(Ehnes *et al.* 2011)
metabolism	Annelida	Lumbricus castaneus	NA	0.13	0.09	0.235	7	7	15	0.91	(Gromadska 1962; Byzova 1965; Meehan 2006b; Ehnes *et al.* 2011)

metabolism	Annelida	Lumbricus terrestris	NA	0.35	0.04	0.000	74	11	21.3	0.95	(Byzova 1965; Fitzpatrick *et al.* 1987; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Lycosa godeffroyi	NA	0.41	NA	NA	8	6	36	0.74	(Anderson 1996; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Lycosidae	NA	0.37	NA	NA	3	3	10	1.00	(Reichle 1968; Hadley, Ahearn & Howarth 1981; Anderson & Prestwich 1982; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Annelida	Megascolex mauritii	NA	0.40	0.02	0.000	79	5	20	0.91	(Saroja 1959; Ehnes *et al.* 2011)
metabolism	Fish	Micropterus salmoides	NA	0.45	0.09	0.007	7	4	15	0.99	(Bokma 2004; White *et al.* 2006)
metabolism	Fish	Microstomus kitt	NA	0.36	NA	NA	3	3	10	1.00	(Bokma 2004; White *et al.* 2006)
metabolism	Reptiles	Morelia spilota	NA	0.81	NA	NA	3	3	14	1.00	(Chappell & Ellis 1987; White *et al.* 2006)
metabolism	Reptiles	Morelia spilota spilota	NA	0.56	NA	NA	4	4	9	0.86	(Bedford & Christian 1998; White *et al.* 2006)
metabolism	Reptiles	Morelia spilota variegata	NA	-0.36	0.07	0.125	4	4	9	1.00	(Bedford & Christian 1998; White *et al.* 2006)
metabolism	Fish	Mugil cephalus	NA	0.66	0.07	0.000	18	9	14	0.88	(Bokma 2004; White *et al.* 2006)
metabolism	Arthropoda	Nanhermannia elegantula	NA	0.97	NA	NA	3	3	10	0.97	(Berthet 1964; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Nanorchestes antarcticus	NA	0.73	0.82	0.390	15	3	10	0.58	(Block 1976; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Reptiles	Natrix maura	NA	0.71	NA	NA	6	6	30	1.00	(Hailey & Davies 1986; White *et al.* 2006)
metabolism	Reptiles	Natrix natrix helretica	NA	0.91	NA	NA	7	7	30	0.98	(Hailey & Davies 1986; White *et al.* 2006)
metabolism	Reptiles	Natrix natrix persa	NA	0.74	NA	NA	7	7	30	0.99	(Hailey & Davies 1986; White *et al.* 2006)
metabolism	Arthropoda	Nebria brevicollis	NA	0.26	0.06	0.000	67	6	25	0.39	(Ehnes *et al.* 2011)
metabolism	Amphibians	Necturus maculosus	NA	0.65	0.14	0.004	9	6	20	0.80	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Arthropoda	Nemobius silvestris	NA	0.62	0.52	0.255	13	8	3	0.89	(Krüger 1958; Ehnes *et al.* 2011)
metabolism	Arthropoda	Nothrus silvestris	NA	0.98	0.17	0.000	15	4	15	0.86	(Berthet 1964; Webb 1969; Thomas 1979; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Notiophilus	NA	0.94	0.19	0.000	24	5	14	0.56	(Ehnes *et al.* 2011)
metabolism	Amphibians	Notophthalmus viridescens	NA	0.14	0.16	0.395	9	5	20	0.22	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Occidozyga martensii	NA	0.38	NA	NA	5	5	20	0.92	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Arthropoda	Ocypus ophtalmicus	NA	0.85	0.06	0.000	32	5	20	0.89	(Ehnes *et al.* 2011)
metabolism	Fish	Oncorhynchus mykiss	NA	0.49	0.05	0.000	81	16	21	0.91	(Bokma 2004; White *et al.* 2006)

metabolism	Fish	Oncorhynchus nerka	NA	0.52	0.12	0.002	12	6	20	0.97	(Bokma 2004; White *et al.* 2006)
metabolism	Arthropoda	Oniscus asellus	NA	0.71	0.06	0.000	68	16	25	0.79	(Phillipson & Watson 1965; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Fish	Ophiodon elongatus	NA	0.74	0.63	0.269	14	9	3.2	0.93	(Bokma 2004; White *et al.* 2006)
metabolism	Arthropoda	Oppia nova	NA	0.92	NA	NA	3	3	10	0.87	(Berthet 1964; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Oppia subpectinata	NA	0.90	NA	NA	3	3	10	1.00	(Berthet 1964; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Oribatella quadricornuta	NA	1.16	NA	NA	3	3	10	1.00	(Berthet 1964; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Fish	Orthodon microlepidotus	NA	0.56	0.09	0.002	8	7	20	0.88	(Bokma 2004; White *et al.* 2006)
metabolism	Arthropoda	Parachipteria willmanni	NA	1.10	0.27	0.007	9	3	10	0.87	(Berthet 1964; Wood & Lawton 1973; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Pardosa amenatata	NA	0.93	NA	NA	10	9	12	0.96	(Scholander *et al.* 1953; Anderson 1970; Moeur & Eriksen 1972; Humphreys 1977; McQueen 1980; Greenstone & Bennett 1980; Kotiaho 1998; Kotiaho *et al.* 1998; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Pardosa astrigera	NA	0.68	0.27	0.088	6	3	10	0.69	(Ford 1977a; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Pardosa lugubris	NA	0.70	0.07	0.000	50	7	21.9	0.68	(Ford 1977b; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Pardosa palustris	NA	0.79	0.14	0.000	26	5	14	0.59	(Ehnes *et al.* 2011)
metabolism	Arthropoda	Parisotoma notabilis	NA	0.52	NA	NA	3	3	9	0.97	(Petersen 1981; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Fish	Petromyzon marinus	NA	0.75	0.12	0.100	4	4	15	1.00	(Bokma 2004; White *et al.* 2006)
metabolism	Arthropoda	Phidippus regius	NA	0.63	NA	NA	3	3	20	0.99	(Miyashita 1973; Myrcha & Stejgwillo-Laudanska 1973; Humphreys 1977; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Philonthus	NA	0.98	0.10	0.000	11	4	14	0.93	(Ehnes *et al.* 2011)
metabolism	Reptiles	Phrynosoma m'calli	NA	0.63	NA	NA	3	3	17	1.00	(Andrews & Pough 1985; White *et al.* 2006)
metabolism	Amphibians	Phyllomedusa sauvagei	NA	0.66	NA	NA	6	6	28	1.00	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Reptiles	Physignathus lesueurii	NA	0.67	NA	NA	3	3	17	1.00	(Andrews & Pough 1985; White *et al.* 2006)

metabolism	Arthropoda	Pilogalumna allifera	NA	0.55	NA	NA	6	6	22	0.91	(Stamou *et al.* 1995; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Pirata latitans	NA	0.80	0.10	0.000	32	6	14	0.71	(Nakamura 1972; Schmitz 2004; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Pisaura mirabilis	NA	0.73	0.10	0.000	35	5	14	0.70	(Ehnes *et al.* 2011)
metabolism	Reptiles	Pitupophis catenifer affinis	NA	0.54	NA	NA	4	4	30	0.89	(Greenwald 1971; White *et al.* 2006)
metabolism	Fish	Platichthys flesus	NA	0.60	0.48	0.305	6	4	10	0.59	(Bokma 2004; White *et al.* 2006)
metabolism	Fish	Platichthys stellatus	NA	0.72	0.13	0.000	22	15	11	0.71	(Bokma 2004; White *et al.* 2006)
metabolism	Arthropoda	Platynothrus peltifer	NA	0.79	0.19	0.008	8	5	25	0.79	(Berthet 1964; Thomas 1979; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Platynus dorsalis	NA	0.78	0.05	0.000	98	10	25	0.72	(Ehnes *et al.* 2011)
metabolism	Amphibians	Plethodon cinereus	NA	0.42	0.05	0.000	14	10	20	0.91	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Plethodon dorsalis	NA	-0.04	0.00	0.019	4	4	15	1.00	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Plethodon glutinosus	NA	0.57	0.21	0.038	9	6	20	0.62	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Plethodon jordani	NA	0.70	0.05	0.000	9	7	20	0.98	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Plethodon neomexicanus	NA	0.17	NA	NA	5	5	20	0.89	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Fish	Pleuronectes platessa	NA	0.45	0.08	0.000	26	4	15	0.81	(Bokma 2004; White *et al.* 2006)
metabolism	Reptiles	Podarcis hispanica	NA	0.81	0.05	0.000	10	7	30	0.98	(Al-Sadoon & Spellerberg 1985a; Patterson & Davies 1989; White *et al.* 2006)
metabolism	Reptiles	Podarcis muralis	NA	0.52	NA	NA	3	3	15	0.84	(Al-Sadoon & Spellerberg 1985a; White *et al.* 2006)
metabolism	Arthropoda	Poecilus versicolor	NA	0.72	0.05	0.000	47	5	25	0.82	(Ehnes *et al.* 2011)
metabolism	Arthropoda	Pogonognathellus flavescens	NA	1.07	NA	NA	3	3	9	1.00	(Zinkler 1966; Petersen 1981; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Polydesmida	NA	0.33	0.19	0.101	24	3	9	0.54	(Ehnes *et al.* 2011)
metabolism	Arthropoda	Porcellio laevis	NA	0.78	0.20	0.004	11	7	25	0.67	(Edney 1964; Lardies, Catalán & Bozinovic 2004; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Porcellio scaber	NA	0.85	0.10	0.000	59	13	24.6	0.59	(Wieser 1965; Saito 1969; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Porcellionides pruinosus	NA	0.45	0.09	0.003	8	6	20	0.93	(Reichle 1968; Cloudsley-Thompson 1969; Al-Dabbagh & Marina 1986; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Protaphorura armata	NA	0.63	0.05	0.000	7	6	15	0.99	(Zinkler 1966; Petersen 1981; Meehan 2006b; Ehnes *et al.* 2011)

metabolism	Arthropoda	Protaphorura meridiata	NA	0.22	NA	NA	5	5	20	0.89	(Argyropoulou & Stamou 1993; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Reptiles	Psammodromus algirus	NA	0.74	NA	NA	3	3	15	1.00	(Al-Sadoon & Spellerberg 1985a; White *et al.* 2006)
metabolism	Amphibians	Pseudacris triseriata	NA	0.51	0.28	0.104	10	6	20	0.43	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Reptiles	Pseudemys scripta	NA	0.81	NA	NA	4	4	30	1.00	(Gatten Jr. 1974; White *et al.* 2006)
metabolism	Amphibians	Pseudoeurycea gadovii	NA	0.66	NA	NA	3	3	20	1.00	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Pseudoeurycea goebeli	NA	0.78	NA	NA	3	3	20	1.00	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Reptiles	Pseudonaja nuchalis	NA	0.61	NA	NA	4	4	9	0.95	(Bedford & Christian 1998; White *et al.* 2006)
metabolism	Arthropoda	Pseudophonus rufipes	NA	0.63	0.05	0.000	96	10	25	0.65	(Ehnes *et al.* 2011)
metabolism	Fish	Pseudopleuronectes americanus	NA	1.22	0.15	0.000	56	7	19	0.72	(Bokma 2004; White *et al.* 2006)
metabolism	Amphibians	Pseudotriton ruber	NA	0.78	0.02	0.015	4	3	20	1.00	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Arthropoda	Pterostichus melanarius	NA	0.70	0.06	0.000	84	7	25	0.62	(Ehnes *et al.* 2011)
metabolism	Arthropoda	Pterostichus niger	NA	0.66	0.07	0.000	36	5	20	0.80	(Ehnes *et al.* 2011)
metabolism	Arthropoda	Pterostichus oblongopunctatus	NA	0.66	0.07	0.000	70	10	25	0.62	(Ehnes *et al.* 2011)
metabolism	Reptiles	Python curtis	NA	0.73	NA	NA	3	3	14	1.00	(Chappell & Ellis 1987; White *et al.* 2006)
metabolism	Reptiles	Python molurus	NA	0.80	NA	NA	3	3	14	1.00	(Andrews & Pough 1985; Chappell & Ellis 1987; White *et al.* 2006)
metabolism	Reptiles	Python regius	NA	0.77	NA	NA	3	3	14	1.00	(Chappell & Ellis 1987; White *et al.* 2006)
metabolism	Reptiles	Python reticulatus	NA	0.74	NA	NA	3	3	14	1.00	(Chappell & Ellis 1987; White *et al.* 2006)
metabolism	Reptiles	Python sebae	NA	0.70	NA	NA	3	3	14	1.00	(Chappell & Ellis 1987; White *et al.* 2006)
metabolism	Arthropoda	Rabidosa rabida	NA	0.65	NA	NA	3	3	10	1.00	(Moulder & Reichle 1972; Ford 1977a; Schmitz 2004; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Amphibians	Rana arvalis	NA	0.83	NA	NA	6	6	25	1.00	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Rana cancrivora	NA	0.70	0.06	0.008	5	4	15	0.98	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Rana catesbeiana	NA	0.54	0.13	0.001	19	9	25	0.78	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Rana clamitans	NA	0.58	0.12	0.040	5	5	20	0.93	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Rana erythraea	NA	1.10	NA	NA	5	5	20	0.93	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Rana esculenta	NA	0.57	0.22	0.019	17	10	19	0.63	(Gatten Jr. *et al.* 1992; White *et al.* 2006)

metabolism	Amphibians	Rana pipiens	NA	0.63	0.06	0.000	30	12	25	0.81	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Rana sylvatica	NA	0.23	0.06	0.015	7	5	20	0.91	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Rana temporaria	NA	0.51	0.21	0.028	20	17	25.3	0.27	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Rana virgatipes	NA	0.71	NA	NA	3	3	20	1.00	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Arthropoda	Rhysotritia ardua	NA	1.08	NA	NA	3	3	10	0.99	(Berthet 1964; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Fish	Salmo salar	NA	0.59	NA	NA	3	3	12	1.00	(Bokma 2004; White *et al.* 2006)
metabolism	Arthropoda	Salticus scenicus	NA	0.61	0.10	0.000	31	6	14	0.57	(Itô 1964; Myrcha & Stejgwillo-Laudanska 1973; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Fish	Salvelinus fontinalis	NA	0.51	0.05	0.000	64	4	15	0.98	(Bokma 2004; White *et al.* 2006)
metabolism	Fish	Salvelinus namaycush	NA	0.72	0.09	0.000	33	16	13	0.84	(Bokma 2004; White *et al.* 2006)
metabolism	Reptiles	Sauromalus hispidus	NA	0.71	NA	NA	9	7	25	0.99	(Bennett 1972; Andrews & Pough 1985; White *et al.* 2006)
metabolism	Reptiles	Sceloporus graciosus	NA	0.91	NA	NA	3	3	12	1.00	(Andrews & Pough 1985; White *et al.* 2006)
metabolism	Reptiles	Sceloporus occidentalis	NA	0.87	NA	NA	7	7	25	0.37	(Dawson & Bartholomew 1956; Francis & Brooks 1970; Bennett & Gleeson 1979; Gleeson 1979; Tsuji 1988; White *et al.* 2006)
metabolism	Reptiles	Sceloporus olivaceus	NA	1.58	NA	NA	3	3	10	1.00	(Andrews & Pough 1985; White *et al.* 2006)
metabolism	Reptiles	Sceloporus undulatus	NA	1.16	NA	NA	4	4	15	0.95	(Andrews & Pough 1985; White *et al.* 2006)
metabolism	Reptiles	Sceloporus variabilis	NA	0.71	NA	NA	3	3	25	1.00	(Tsuji 1988)
metabolism	Arthropoda	Scheloribates cf. latipes	NA	0.49	NA	NA	6	6	22	0.83	(Stamou *et al.* 1995; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Reptiles	Scinus mitranus	NA	0.55	NA	NA	6	6	25	0.96	(Al-Sadoon 1986)
metabolism	Fish	Scyliorhinus canicula	NA	0.49	0.08	0.000	22	4	10	0.83	(Bokma 2004; White *et al.* 2006)
metabolism	Fish	Scyliorhinus stellaris	NA	-1.89	1.30	0.220	7	5	3	0.80	(Bokma 2004; White *et al.* 2006)
metabolism	Fish	Sebastes diploproa	NA	0.36	NA	NA	9	3	10	0.74	(Bokma 2004; White *et al.* 2006)
metabolism	Amphibians	Siren lacertina	NA	0.57	0.25	0.066	9	5	20	0.72	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Arthropoda	Sminthurinus	NA	0.61	NA	NA	3	3	9	0.92	(Petersen 1981; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Sminthurus viridis	NA	0.52	NA	NA	4	4	25	1.00	(Zinkler 1966; Meehan 2006b; Ehnes *et al.* 2011)

metabolism	Reptiles	Spalerosophis cliffordi	NA	0.66	0.06	0.000	9	8	26.8	0.95	(Dmi’el & Borut 1972; Andrews & Pough 1985; White *et al.* 2006)
metabolism	Fish	Squalus acanthias	NA	1.33	0.27	0.000	20	4	4	0.93	(Bokma 2004; White *et al.* 2006)
metabolism	Arthropoda	Steganacarus magnus	NA	0.69	0.08	0.000	24	8	25	0.86	(Berthet 1964; Webb & Elmes 1972; Wood & Lawton 1973; Luxton 1975; Webb 1975; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Steganacarus spinosus	NA	0.42	NA	NA	4	4	15	0.94	(Luxton 1975; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Stereotydeus villosus	NA	0.70	0.18	0.009	9	3	10	0.87	(Goddard 1977a; Caruso *et al.* 2010; Ehnes *et al.* 2011)
metabolism	Arthropoda	Supraphorura furcifera	NA	0.71	NA	NA	3	3	9	0.95	(Petersen 1981; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Reptiles	Tarentola mauritanica	NA	0.51	NA	NA	3	3	15	1.00	(Al-Sadoon & Spellerberg 1985a; White *et al.* 2006)
metabolism	Amphibians	Taricha granulosa	NA	0.54	0.09	0.000	13	5	20	0.86	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Amphibians	Taricha torosa	NA	0.61	0.15	0.001	16	5	15	0.73	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Arthropoda	Tectocepheus velatus	NA	0.97	NA	NA	3	3	10	1.00	(Berthet 1964; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Arthropoda	Tenuiphantes zimmernanni	NA	0.55	NA	NA	11	9	12	0.98	(Anderson 1970, 1996; Hagstrum 1970; Moulder & Reichle 1972; Humphreys 1977; McQueen 1980; Anderson & Prestwich 1982; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Reptiles	Terrapene ornata ornata	NA	1.12	NA	NA	4	4	30	0.95	(Gatten Jr. 1974; White *et al.* 2006)
metabolism	unicells	Tetrahymena pyriformis	NA	0.96	NA	NA	NA	3	11.5	2.00	(Laybourn & Finlay 1976)
metabolism	unicells	Tetrahymena pyriformis	NA	0.32	NA	NA	NA	3	11.5	2.00	(Laybourn & Finlay 1976)
metabolism	Arthropoda	Tetrodontophora bielanensis	NA	0.64	0.01	0.011	4	3	15	1.00	(Zinkler 1966; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Reptiles	Thamnophis sirtalis parietalis	NA	0.58	NA	NA	6	6	25	0.92	(Aleksiuk 1971; White *et al.* 2006)
metabolism	Reptiles	Thamnophis sirtalis sirtalis	NA	0.60	NA	NA	5	5	20	0.99	(Aleksiuk 1971; White *et al.* 2006)
metabolism	Amphibians	Thorius sp.	NA	0.58	NA	NA	3	3	20	1.00	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Fish	Thymallus arcticus arcticus	NA	0.43	NA	NA	4	4	8	0.87	(Bokma 2004; White *et al.* 2006)
metabolism	Arthropoda	Trachelipus rathkii	NA	0.77	0.17	0.001	13	3	10	0.68	(Ehnes *et al.* 2011)
metabolism	Reptiles	Trachydosaurus rugosus	NA	0.72	NA	NA	3	3	17	0.98	(Andrews & Pough 1985; White *et al.* 2006)

metabolism	Arthropoda	Trichoniscus pusillus	NA	0.62	NA	NA	3	3	10	1.00	(Meyer & Phillipson 1983; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Amphibians	Triturus vulgaris	NA	0.24	NA	NA	3	3	19	0.69	(Gatten Jr. *et al.* 1992; White *et al.* 2006)
metabolism	Arthropoda	Trochosa	NA	0.65	0.05	0.000	53	6	18.5	0.89	(Ehnes *et al.* 2011)
metabolism	Arthropoda	Tydeus tilbrooki	NA	0.43	0.14	0.086	5	3	10	0.96	(Goddard 1977a; Caruso *et al.* 2010; Ehnes *et al.* 2011)
metabolism	Reptiles	Uromastyx microlepis	NA	0.84	0.08	0.008	5	5	20	0.98	(Zari 1991; White *et al.* 2006)
metabolism	Reptiles	Uta mearnsi	NA	0.88	NA	NA	3	3	17	0.96	(Andrews & Pough 1985; White *et al.* 2006)
metabolism	Reptiles	Uta stansburiana	NA	0.72	NA	NA	4	4	20	0.95	(Dawson & Bartholomew 1956; Andrews & Pough 1985; White *et al.* 2006)
metabolism	Reptiles	Varanus exanthematicus	NA	1.00	NA	NA	3	3	10	0.97	(Wood *et al.* 1978; White *et al.* 2006)
metabolism	Reptiles	Varanus gouldi	NA	0.72	NA	NA	3	3	17	0.97	(Andrews & Pough 1985; White *et al.* 2006)
metabolism	Reptiles	Varanus gouldii	NA	0.72	0.07	0.000	11	9	25	0.96	(Bennett 1972; Thompson & Withers 1992; Christian & Conley 1994; White *et al.* 2006)
metabolism	Reptiles	Varanus panoptes	NA	0.82	0.08	0.010	5	5	19.5	0.98	(Thompson & Withers 1992; Christian & Conley 1994)
metabolism	Reptiles	Xantusia henshawi	NA	0.56	NA	NA	3	3	10	1.00	(Mautz 1979; Andrews & Pough 1985; White *et al.* 2006)
metabolism	Arthropoda	Xenillus tegeocranus	NA	0.77	NA	NA	4	4	15	1.00	(Luxton 1975; Meehan 2006b; Ehnes *et al.* 2011)
metabolism	Amphibians	Xenopus laevis	NA	0.39	0.14	0.019	15	7	10	0.59	(Gatten Jr. *et al.* 1992; White *et al.* 2006)

'Trophic Whales' as Biotic Buffers
Weak Interactions Stabilize Ecosystems against Nutrient Enrichment.

- Supplementary Information -

Florian Schwarzmüller, Nico Eisenhauer, Ulrich Brose

Model description

The population dynamics follow a consumer-resource model (Yodzis and Innes 1992) that was updated with new allometric coefficients (Ernest *et al.* 2003; Brown *et al.* 2004) and extended to multi-species systems (Brose, Berlow & Martinez 2005; Brose, Williams & Martinez 2006; Heckmann *et al.* 2012), where

$$\dot{B}_R = r_R G_R B_R - x_I y_I B_I F_{IR}/e_{IR} - x_W y_W B_W F_{WR}/e_{WR} \qquad \text{(S2.1a)},$$

$$\dot{B}_I = -x_I B_I + x_I y_I B_I F_{IR} - x_T y_T B_T F_{TI}/e_{TI} \qquad \text{(S2.1b)},$$

$$\dot{B}_T = -x_T B_T + x_T y_T B_T F_{TI} \qquad \text{(S2.1c), and}$$

$$\dot{B}_W = -x_W B_W + x_W y_W B_W F_{WR} \qquad \text{(S2.1d)}$$

describe changes in relative biomass densities of the resource (*R*, Eq. S2.1a), intermediate (*I*, S2.1b) and top species (*T*, S2.1c) and the trophic whale (*W*, S2.1d). In these equations, B_i is the biomass density of population *i*, r_R is *R*'s mass-specific maximum growth rate, G_R is *R*'s logistic growth rate (Eq. 4), y_i is the maximum consumption rate of the consumers relative to their metabolic rate x_i, e_{ji} is *j*'s assimilation efficiency when consuming population *i*.

The functional response, F_{ij}, describes the realized fraction of i's maximum rate of per capita consumption achieved when consuming species *j*:

$$F_{ij} = \frac{B_j^h}{B_{0,i} + B_j^h} \qquad \text{(S2.2)}$$

where *h* is the Hill-exponent which regulates the shape of the curve of the functional response (*h*=1, Holling type II (Real 1977)), and $B_{0,i}$ is the half-saturation density of the functional response i.e. the prey density where half of the maximum feeding rate is reached.

Biological rates *r*, *x* and *y* (growth, metabolism and maximum consumption) scale with body mass, *M*: $r, x, y \propto M^{-0.25}$. *r*, *x*, *y* were normalized to the growth rate of resource species (thus, $r_R = 1$), and *y* was normalized to *x*. The maximum consumption rate was constant ($y = 8$); *x* increased with the body-mass ratio to the resource species:

$$x_i = a\left(\frac{M_i}{M_R}\right)^{-0.25} \qquad \text{(S2.3)}$$

where *a* is an organism-group specific constant.

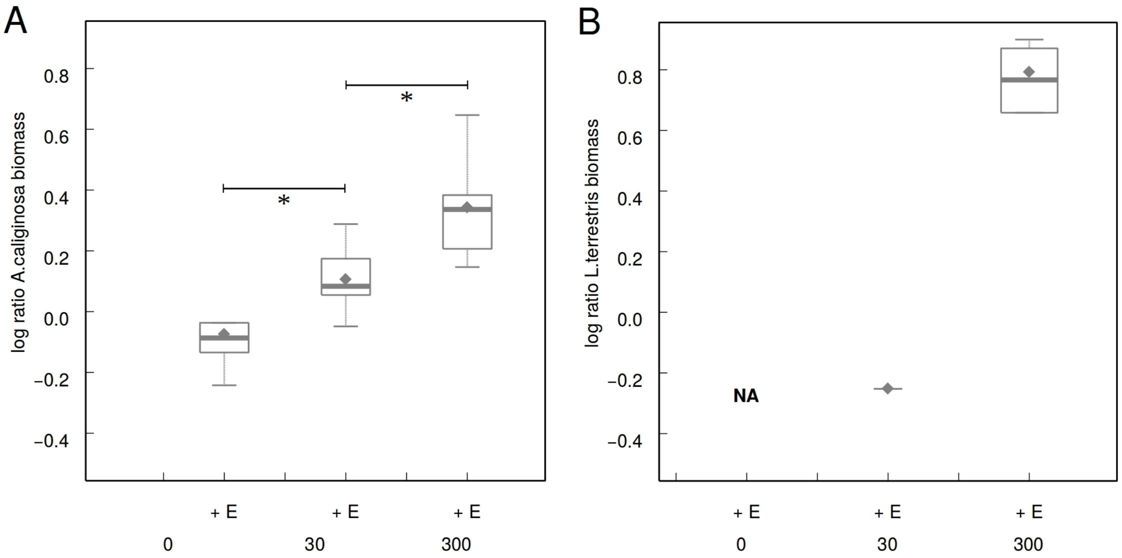
The growth of the resource species G_R follows a logistic growth

$$G_R = (1 - \frac{B_R}{K}) \tag{S2.4}$$

where B_R is the biomass density and K is the carrying capacity of the system. We used the following constant model parameters: e_{ij}=0.85, $B^0{}_I = B^0{}_T$= 0.5, $B^0{}_W$= 2 and a= 0.314 for invertebrate consumers.

Supplementary Table S2.1: Earthworm biomasses at the beginning and at the end of the experiment

Microcosm number	**Amount of yeast added**	**Biomasses at the beginning [mg]**			**Biomasses at the end [mg]**			Log ratio of biomass at the end divided by biomass at the beginning
		Aporrectodea caliginosa	*Lumbricus terrestris*	Combined	*Aporrectodea caliginosa*	*Lumbricus terrestris*	Combined	
1	0	160.2	61.7	221.9	221.3	0	221.3	-0.0012
2	0	200.2	59.0	259.2	184.0	0	184.0	-0.1488
3	0	155.0	72.7	227.7	125.7	0	125.7	-0.2580
4	0	250.6	54.3	304.9	143.5	0	143.5	-0.3273
5	0	185.3	49.6	234.9	153.4	0	153.4	-0.1851
6	0	204.3	55.5	259.8	150.0	0	150.0	-0.2385
7	30	164.1	72.0	236.1	146.8	0	146.8	-0.2064
8	30	146.9	89.4	236.3	168.4	50.0	218.4	-0.0342
9	30	146.1	30.7	176.8	283.6	0	283.6	0.2052
10	30	177.1	35.1	212.2	227.0	0	227.0	0.0293
11	30	197.5	46.8	244.3	224.1	0	224.1	-0.0375
12	30	155.1	50.8	205.9	231.7	0	231.7	0.0513
13	300	153.9	88.6	242.5	682.3	495.0	1177.3	0.6862
14	300	172.9	50.4	233.3	383.9	400.0	783.9	0.5454
15	300	182.6	70.0	252.6	387.0	427.8	814.8	0.5086
16	300	206.8	32.2	239.0	333.0	0	333.0	0.1440
17	300	215.3	41.9	255.2	301.8	311.1	612.9	0.3771
18	300	176.3	69.0	245.3	426.4	314.2	740.6	0.4799

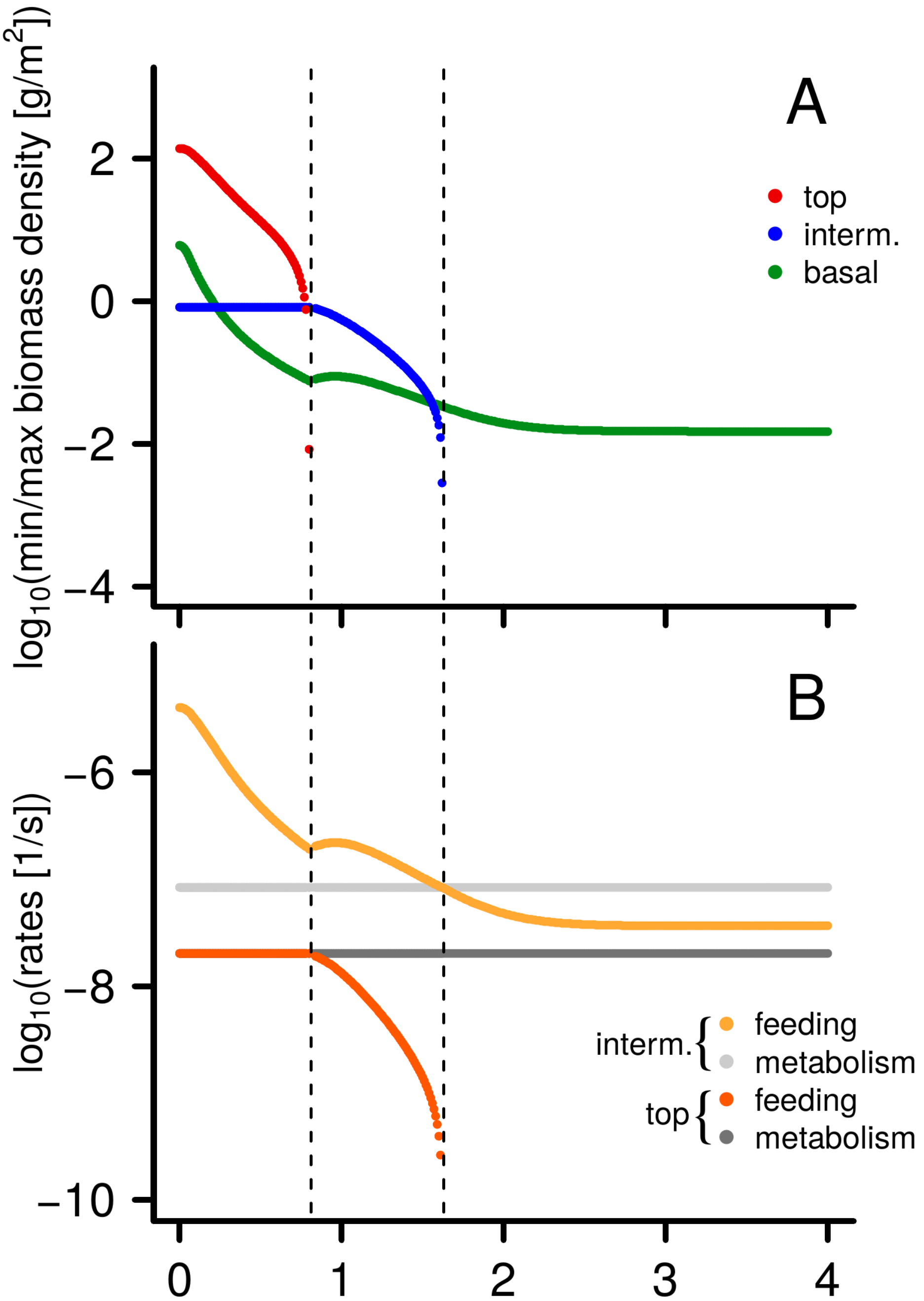


Supplementary Figure S2.1: *relative biomass ratios of **A** A. caliginosa and **B** L. terrestris, respectively. Shown is the log ratio of biomasses at the end of the experiment divided by the biomass at the beginning of the experiment at different enrichment levels (0, 30, 300 mg of yeast added per week). Boxes include 50% of the data from Q25 (or 1st quartile) to Q75 (or 3rd quartile), diamonds indicate means, bars indicate medians (or 2nd Quartile), whiskers are minimal and maximal values of the data excluding outliers. Outliers are exceeding a 95% confidence interval. The significance indexes result from the contrast analyses between the pairs of treatments indicated by the horizontal whiskers, where ' * ' = p ≤ 0.05. Non-significant p-values are not shown.*

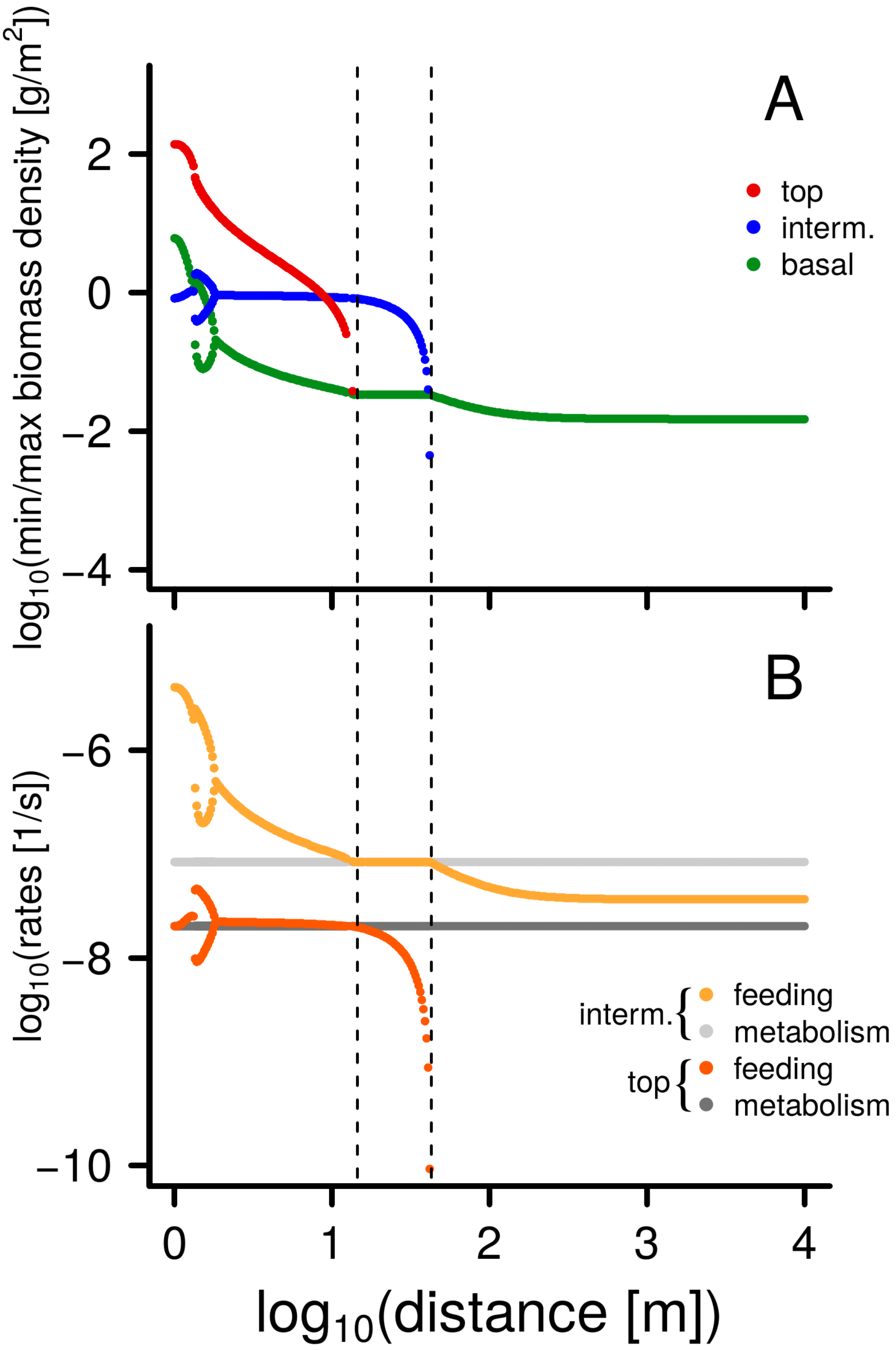
Energy fluxes in fragmented ecosystems
Dynamic stability of tri-trophic food chains under nutrient enrichment and habitat isolation

– Supplementary information –

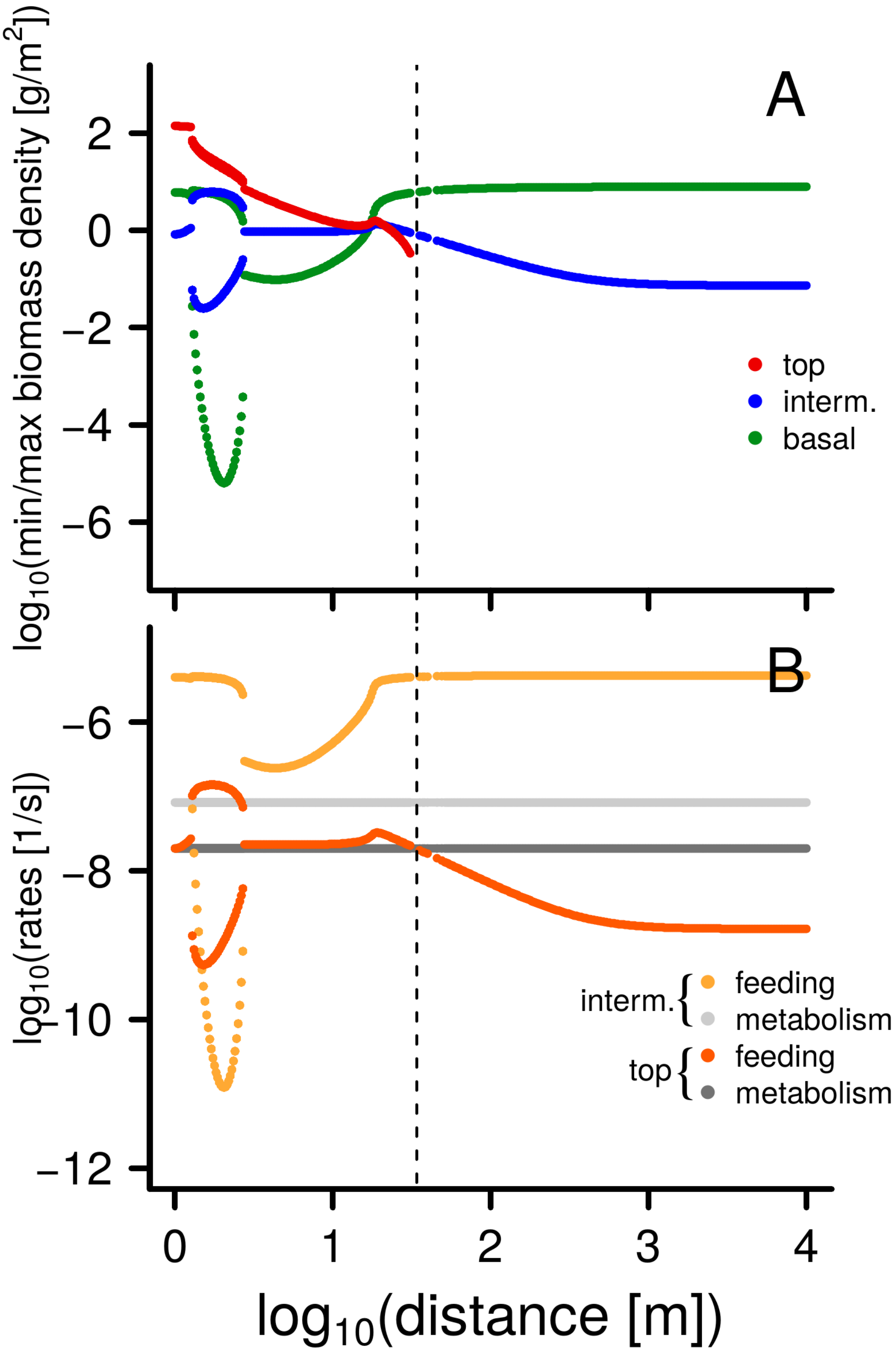
Florian Schwarzmüller & Ulrich Brose



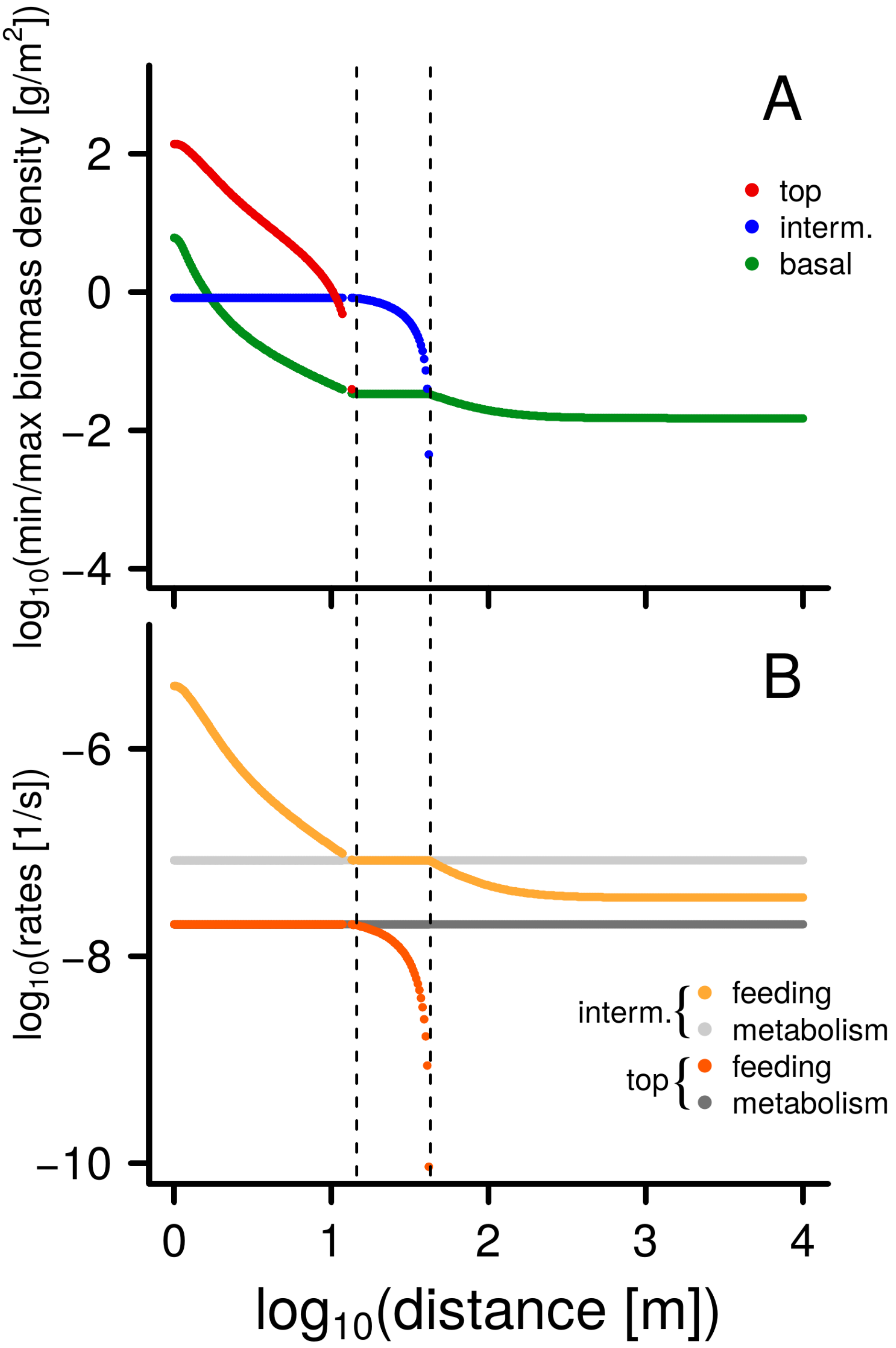
Supplementary Figure S3.1: Scenario 1. Success of top species = 1.
***A** Bifurcation diagram showing the effect of inter-patch distance on species biomass densities (minima and maxima shown). red= top species, blue= intermediate species, green= basal species. **B** Corresponding feeding (orange) and metabolic terms (grey) of the intermediate (bright colours) and the top species (dark colours). Dashed lines indicate the extinction-points i.e. the intersection of feeding and metabolic rates. (I_K=4, predator-prey body-mass ratio = 2).*



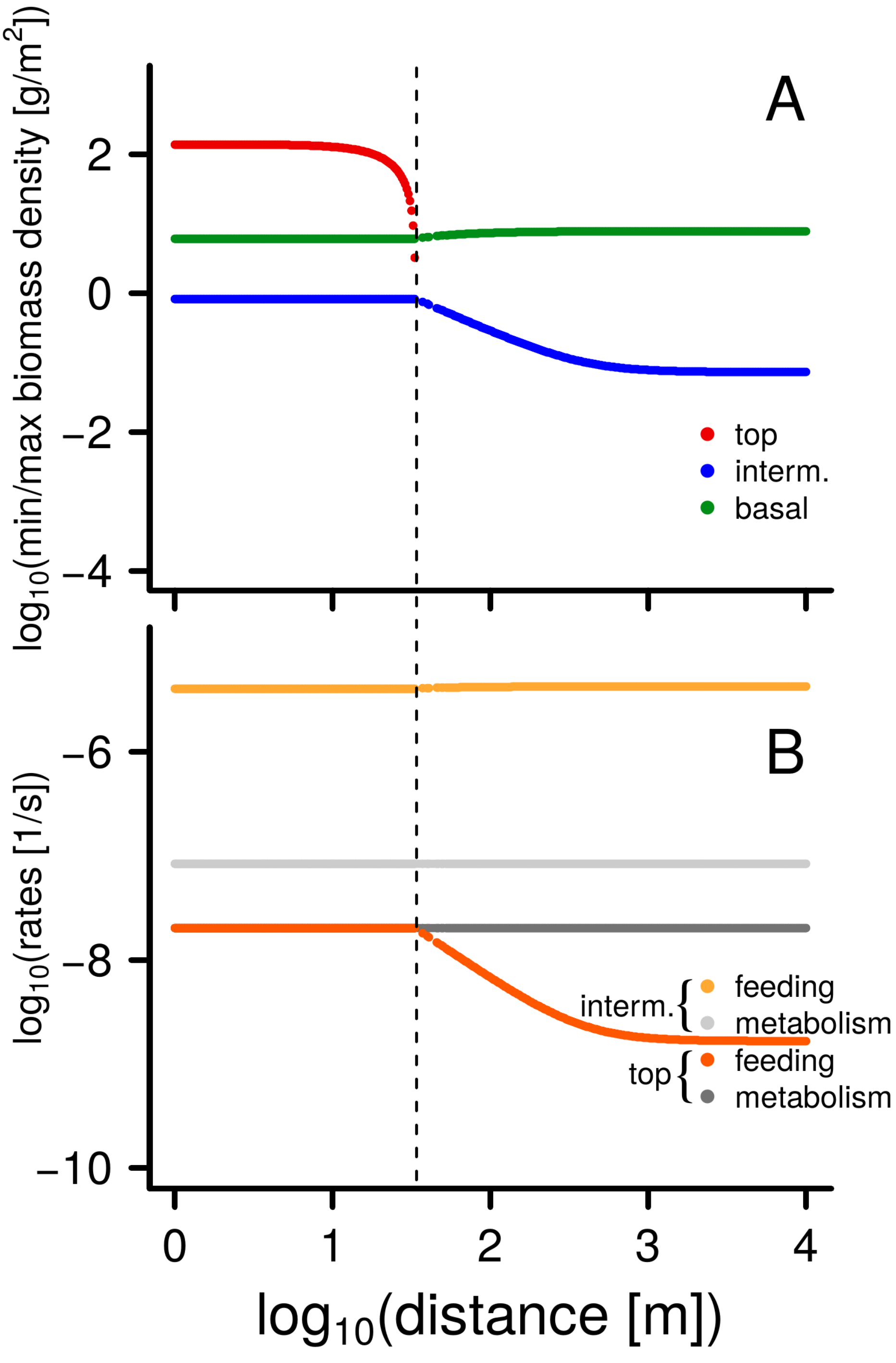
Supplementary Figure S3.2: Scenario 2. Success of intermediate species =1. ***A*** *Bifurcation diagram showing the effect of inter-patch distance on species biomass densities (minima and maxima shown). red= top species, blue= intermediate species, green= basal species.* ***B*** *Corresponding feeding (orange) and metabolic terms (grey) of the intermediate (bright colours) and the top species (dark colours). Dashed lines indicate the extinction-points i.e. the intersection of feeding and metabolic rates. (I_K=4, predator-prey body-mass ratio = 2).*



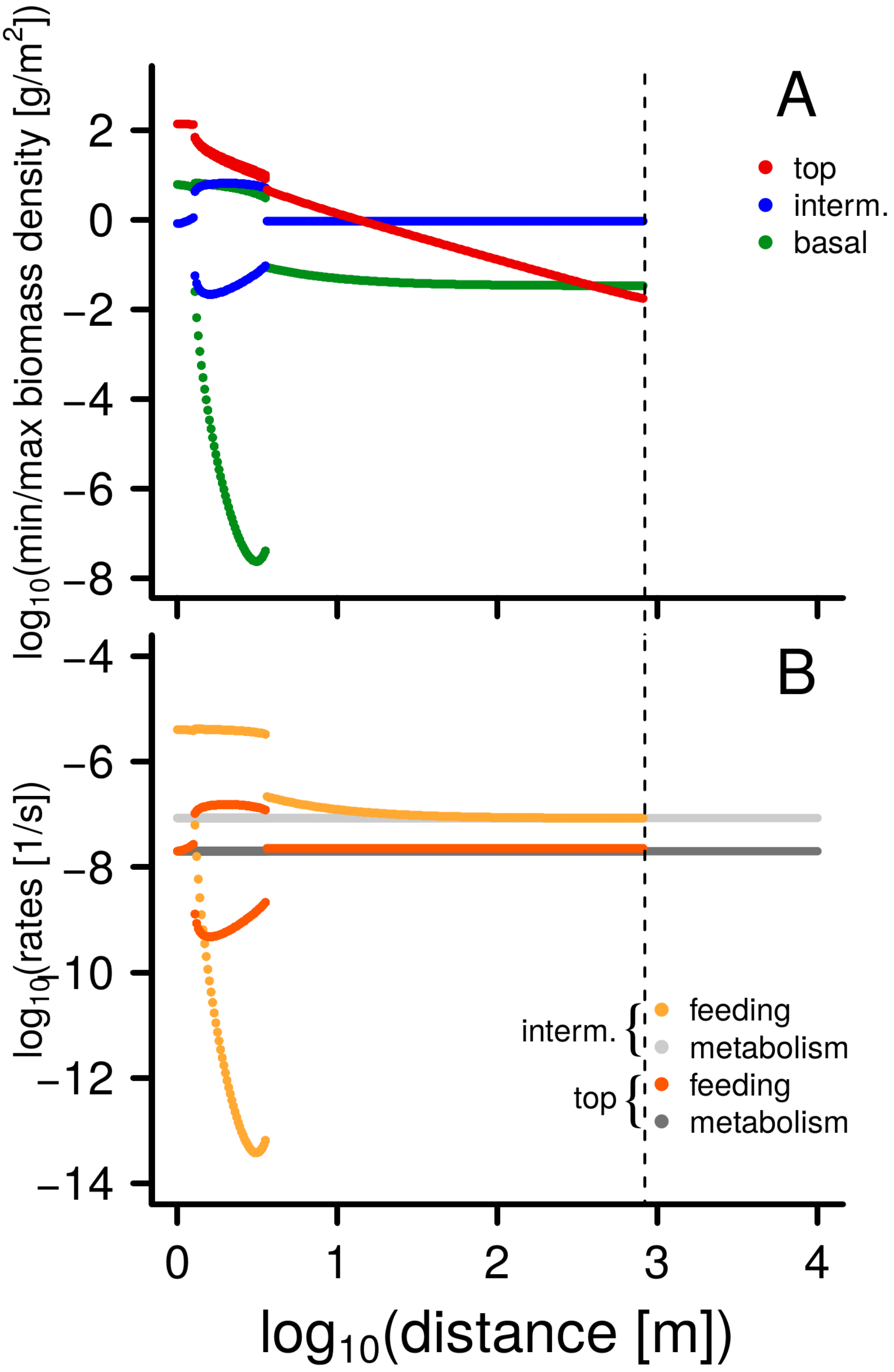
Supplementary Figure S3.3: Scenario 1. Success of basal species = 1.
***A** Bifurcation diagram showing the effect of inter-patch distance on species biomass densities (minima and maxima shown). red= top species, blue= intermediate species, green= basal species. **B** Corresponding feeding (orange) and metabolic terms (grey) of the intermediate (bright colours) and the top species (dark colours). The dashed lines indicates the extinction-point i.e. the intersection of feeding and metabolic rates. (I_K=4, predator-prey body-mass ratio = 2).*



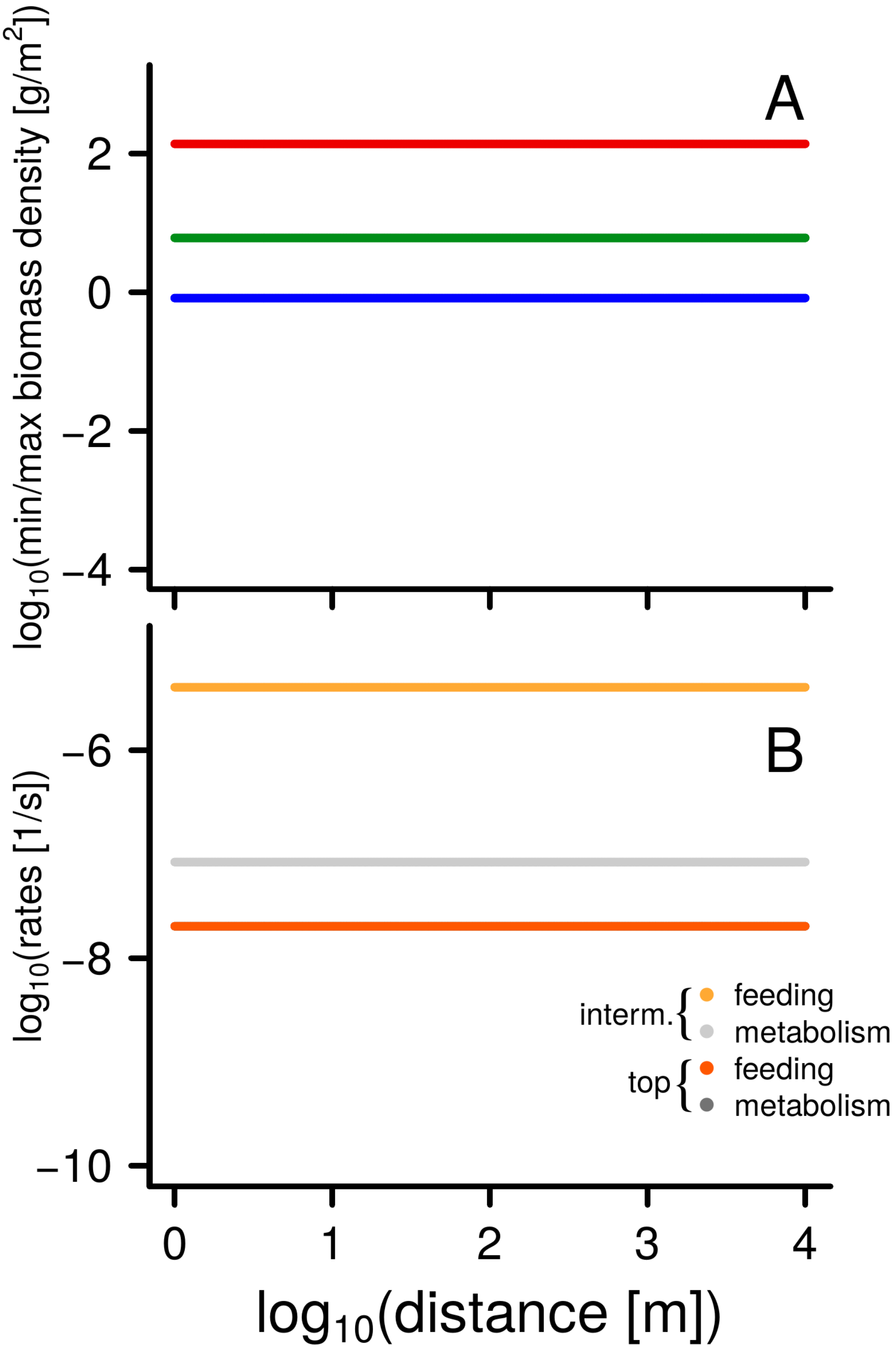
Supplementary Figure S3.4: Scenario 4. Success of top and intermediate species = 1. A *Bifurcation diagram showing the effect of inter-patch distance on species biomass densities (minima and maxima shown). red= top species, blue= intermediate species, green= basal species.* ***B*** *Corresponding feeding (orange) and metabolic terms (grey) of the intermediate (bright colours) and the top species (dark colours). Dashed lines indicate the extinction-points i.e. the intersection of feeding and metabolic rates. (I_K=4, predator-prey body-mass ratio = 2).*



Supplementary Figure S3.5: Scenario 5. Success of top and basal species = 1. ***A*** *Bifurcation diagram showing the effect of inter-patch distance on species biomass densities (minima and maxima shown). red= top species, blue= intermediate species, green= basal species.* ***B*** *Corresponding feeding (orange) and metabolic terms (grey) of the intermediate (bright colours) and the top species (dark colours). The dashed line indicates the extinction-point i.e. the intersection of feeding and metabolic rates. (I_K=4, predator-prey body-mass ratio = 2).*



Supplementary Figure S3.6: Scenario 6. Success of intermediate and basal species = 1. A *Bifurcation diagram showing the effect of inter-patch distance on species biomass densities (minima and maxima shown). red= top species, blue= intermediate species, green= basal species.* ***B*** *Corresponding feeding (orange) and metabolic terms (grey) of the intermediate (bright colours) and the top species (dark colours). Dashed line indicate the extinction-point. (I_K=4, predator-prey body-mass ratio = 2).*



Supplementary Figure S3.7: Scenario 7. Success of all species = 1.
A *Bifurcation diagram showing the effect of inter-patch distance on species biomass densities (minima and maxima shown). red= top species, blue= intermediate species, green= basal species.* ***B*** *Corresponding feeding (orange) and metabolic terms (grey) of the intermediate (bright colours) and the top species (dark colours). (*I_K*=4, predator-prey body-mass ratio = 2).*

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Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertation selbstständig angefertigt und die benutzten Quellen und Hilfsmittel vollständig angegeben habe. Weiterhin erkläre ich, bisher noch keinen Promotionsversuch unternommen zu haben und dass die Dissertation weder in ähnlicher noch in gleicher Form einer anderen Prüfungsbehörde vorgelegt wurde.

Göttingen, den 03.03.2015

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Conference Contributions

Schwarzmüller, F.: Trophic interactions in a spatial network: arrangement of habitat patches and its influence on local and global community dynamics, Oral presentation at the BES and SFE Joint Annual Meeting, December 9-12 2014, Lille, France

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