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Context Dependency of Community Dynamics: Predator-Prey Interactions Under Ecological Disturbances

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”To kill an error is as good a service as, and sometimes even better than, the establishing of a new truth or fact.”

—Charles Darwin

Illustration of Darwin’s Fox (Lycalopex fulvipes), endangered.

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Dissertation
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Numerous studies have focused on the drivers of diversity and stability of communities, especially under global change. However, multi-dimensionality of ecosystems due to biotic components (e.g predation, competition and adaptive dynamics) and abiotic factors (e.g. disturbances, resource dynamics and their distinct attributes) cause context-dependent outcomes and challenge the predictions. There are still controversies around complex community dynamics under varying regimes, however, finding mechanistical explanations will illuminate the fate of multispecies assemblages. Using model microbial communities, consisting of bacterial prey and protist predator, combined with simulation modelling and advanced statistics, this thesis investigated the impact of imposed disturbances (i.e. increased dilution rates that simulate density-independent mortality as press or pulse disturbances) *(i)* on transient recovery dynamics of a simple microbial food web, and *(ii)* on bacterial abundance, diversity and community structure in the absence or presence of a protist predator. In addition, this thesis questioned the impacts of species interactions and rapid trait shifts, as a response to predation and competition, on the community dynamics and stability. Our results revealed that the predator suffered more from disturbances over longer time periods. Reduced predation pressure caused a transient phase of prey release during and even after disturbances. Recovery time depended on the strength and duration of disturbances, however, coupling to an alternative resource increased the chance of fast recovery and stabilized the communities. In multi-species prey communities, bacterial abundance, diversity, and community composition were more affected by predation than by the disturbances and resource dynamics. Predator abundance, on the other hand, was strongly affected by the type of disturbance imposed. Importantly, community attributes had differential sensitivities, as reflected by their different response and recovery dynamics. Prey community dynamics varied more temporally and were less stable under predation stress, while prey diversity increased significantly. Predation rapidly induced anti-predation traits, which altered population dynamics of both prey and predator. More importantly, predator and the resistant prey, in turn, elevated the number of direct cause-effect relationships between the community members. Our findings are not limited to the studied system and can be used to understand the dynamic response and recovery potential of many natural predator-prey or hostpathogen systems. They can be used as a base for future studies to illuminate the debates on the future communities.

Contents

Summary

The most indispensable work for ecologists is to develop tools which can predict the fate of communities, especially under global change. In this aspect, a proper understanding of drivers and mechanisms, which shape communities, is of paramount importance. One central problem is that predictions are context-dependent due to the multi-dimensionality of community dynamics. That is, communities are in many cases characterized by high structural complexity and distinct temporal dynamics, and they are in addition governed both by abiotic settings and biotic components. Ecological disturbances, for instance, intervene in coupled oscillating systems such as predator-prey systems, causing long transient phases and differential recovery dynamics. Recovery dynamics strongly depend on particular disturbance attributes such as strength and duration. This is aggravated by the fact that disturbances are usually coupled with other drivers, causing additional complex interactive effects on communities.

Abiotic changes interfere with species dynamics; the community responses to these changes highly depend on the identity of the species and the diversity of species interactions occurring in a system. Moreover, it is difficult to separate the outcome of species interactions from the outcome of adaptive dynamics since species traits may change fast enough, which, in turn, impact their ecological dynamics. A well-known example is that predator driven prey adaptation leads to rapid shifts in communities.

In short, to date, few studies have addressed the problem of predicting community dynamics, which is caused by the interactive effects of abiotic changes, as well as

structure and dynamics of community members. Particularly, relating temporal dynamics of community members and their interactions to the whole community dynamics is still underappreciated. A promising way to resolve the complexities outlined above is to establish a combination of empirical (via highly controlled and replicated laboratory experiments) and theoretical approaches, which would illuminate mechanisms and infer direct cause-effect relationships in natural communities.

This thesis aimed to address the interactive effects of disturbances and resource dynamics on the community response and stability. It particularly elaborated the significance of species interactions, especially trophic interactions and competition, for community response. In addition, it focused on the internal dynamics of multi-species assemblages which are shaped by diverse interactions and adaptive dynamics. It then stressed the importance of inferring causal relationships between community members to fully understand their dynamics.

In particular, this thesis investigated the following aspects: *(i)* The relevance of disturbance attributes (i.e. strength and duration) and of strength of interactions (i.e. connection to alternative resources) for the recovery dynamics of trophically interacting species; *(ii)* the interactive effects of disturbances and resource dynamics on community response and recovery; *(iii)* the role of predation which directly and indirectly top-down controls the communities; *(iv)* the impact of rapid shifts in population dynamics caused by competition and adaptive dynamics, on community stability; *(v)* the possibility to predict community dynamics by revealing direct causal inferences between single components of them.

To this end, microcosms were assembled under highly controlled conditions consisting of bacterial prey with different life history traits and competitive abilities, and a protist predator. This experimental approach allowed us to vary three main parameters, namely predation pressure (i.e. absence or presence of the predator), nutrient concentrations and disturbance regimes. The tested disturbance regimes included a continuous and temperate disturbance (i.e. press) or an instant and severe disturbance (i.e. pulse). These disturbance regimes were established by diluting communities with fresh medium to different degrees, thus causing a density independent mortality. Further, different resource levels were experimentally varied by a gradual or instant resource deprivation.

Species abundances were monitored by several microscopy, cultivation and fingerprinting methods. Time series measurements were taken in order to ascertain stability features of communities such as recovery time, and to understand dynamic properties of species interactions. The microcosm experiments were combined with simulation modelling (e.g. Lotka-Volterra type predator-prey model) and statistical modelling approaches (e.g. linear mixed effect modelling), as well as with advanced statistical methods (e.g. convergent cross mapping) to reveal casual inferences.

The results of these experiments on the one hand confirmed trophic structure as one of the most important drivers of communities. Population abundances were in general sensitive to the type of disturbances applied. This was partly due to the generation times of the species, which impacts their recovery potential between disturbance phases. One of the critical points was, for instance, the population size of the community members, especially that of the top predator and the rare species which had a risk of going extinct.

However, this work furthermore added several key points to the current research. The results highlighted that in a trophically organized community, the impact of disturbances is highly dependent on the trophic level. Usually when a higher trophic level suffers, the lower trophic level profits from the reduced top-down control –similar to the "prey outbreaks" in nature. Interestingly, the extent of this transient phase of uncoupled dynamics could only be controlled by the recovery of the predators, which also depended strongly on the duration and strength of the disturbances. Importantly, the predator's coupling to an alternative resource accelerated the recovery of the predator and increased the stability of the community.

Increased community complexity (i.e. the prey diversity) and the interactions between the biotic (i.e. predator) and abiotic (i.e. disturbances and resource dynamics) drivers yielded diverse community responses due to the interplay between the drivers, as well as the trade-offs between competitive abilities and predation resistance.

This work underlined that prey abundance, diversity, and community composition were more strongly affected by predation than by the disturbance regimes. However, at the same time, the type of disturbance (pulse vs. press) had a stronger impact on the abundance of the predator, which caused an indirect impact on the prey communities. Most importantly, there were notable differences between the sensitivities of different community measures to respond to the disturbances, as reflected by their distinct recovery capacities.

This work also extended the understanding of community dynamics and stability driven by species interactions and adaptive mechanisms. Presence of a predator resulted in distinct community dynamics, as reflected by the single time series of the species and emerging prey phenotypes (as an anti-predation strategy). Highly variable population dynamics that are governed both by fitness differences and equalizing mechanisms (such as grazer pressure on the dominant species and adaptive radiation) reduced the temporal stability of the communities in the presence of the predator. Presence of predator, however, provided an elevated level of diversity and allowed coexistence between prey species. Emergence of the predation-resistant morphotype provided refuge for other prey species and also reduced competition between the prey species. The predator and the resistant morphotypes also established new interactions (causal links) with other species in the community.

In a nutshell, this thesis has contributed to the understanding of predator-prey dynamics, competition, adaptation, and their consequences for community dynamics and stability. In particular, the results have added to the understanding of effects of ecological disturbances and resource dynamics on species interactions within and across trophic levels. Moreover, it has provided a base for moving away from correlation-based statistics, and instead focuses on direct cause-effect relationships between the community components, and furthermore, with their environments. Overall, the key achievements provided by this work can be a valuable foundation for future studies, considering they may be important in establishing intervention tools for conservation biology, biological control, and epidemiology. Finally, the practical and theoretical approaches which were applied in this work might be used to improve the predictions of community dynamics and stability, especially under changing environments.

Zusammenfassung

Das oberste Ziel von Ökologen sollte darin liegen, Werkzeuge zu entwickeln, mit denen man das Schicksal von ökologischen Gemeinschaften gerade vor dem Hintergrund des globalen Wandels voraussagen kann. Insbesondere ist ein tieferes Verständnis der Treiber und Mechanismen, welche Gemeinschaften formen, von ausschlaggebender Bedeutung. Ein wesentliches Problem besteht jedoch darin, dass Voraussagen immer im Kontext der mehrdimensionalen Natur von Ökosystemen stehen. Gemeinschaften sind demnach häufig durch eine hohe, strukturelle Komplexität und ausgeprägte, zeitliche Dynamik gekennzeichnet. Zusätzlich werden sie sowohl von abiotischen Rahmenbedingungen als auch von biotischen Faktoren beeinflusst. Ökologische Störungen greifen beispielsweise in gekoppelte Räuber-Beute-Systeme ein, die sich durch ihre voneinander abhängigen Populationsschwankungen auszeichnen, und verursachen dadurch lange Übergangsphasen und eine veränderte Dynamik ihrer Erholung. Letztere hängt stark von bestimmten Störungsmerkmalen wie Stärke und Dauer ab. Dieser Zusammenhang zwischen Störungseffekten und -merkmalen wird zusätzlich erschwert, dadurch dass Störungen normalerweise an weitere Treibern gekoppelt sind und dadurch zusätzlich komplexe und interaktive Wirkungen auf Gemeinschaften verursachen.

Abiotische Änderungen beeinträchtigen dabei die Dynamik einzelner Arten; die Reaktion der Gemeinschaften auf diese Störungen hängt somit maßgeblich von der Identität der beteiligten Arten und der Vielfalt der Wechselwirkungen dieser Arten innerhalb eines Ökosystems ab. Die klare Auftrennung zwischen dem Effekt der

interspezifischen Wechselwirkungen und der Anpassungsdynamik einzelner Arten ist jedoch schwierig; die Merkmale von Arten können sich schnell verändern, was wiederum deren ökologische Dynamik beeinflusst. Ein bekanntes Beispiel dafür ist die durch Räuber ausgelöste Anpassung von Beuteorganismen, die zu rapiden Veränderungen in Gemeinschaften führen.

Auf Grund der zuvor beschriebenen, komplexen Zusammenhänge haben sich bis dato nur wenige Studien mit der Voraussage der Dynamik ökologischer Gemeinschaften beschäftigt. Insbesondere wird die enge Beziehung der zeitlichen Dynamik einzelner Organismen zur Dynamik der gesamten Gemeinschaft in ihrer Bedeutung noch unterschätzt. Die Kombination aus empirischer und theoretischer Herangehensweise stellt dabei einen vielversprechenden Ansatz zur Auflösung dieser Komplexität dar. Mittels kontrollierter und replizierbarer Laborsysteme können die zugrunde liegenden Mechanismen aufgedeckt und Ursache-Wirkungs-Verhältnisse direkt abgeleitet werden.

Das übergeordnete Ziel dieser Doktorarbeit war es, die wechselseitigen Einflüsse von Störungen und Ressourcendynamik auf ökologische Gemeinschaften zu untersuchen. In erster Line wurde die Bedeutung von Arteninteraktionen, insbesondere von trophischer Interaktion und interspezifischer Konkurrenz, für die Reaktion von Gemeinschaften herausgearbeitet. Ein weiterer Schwerpunkt war die interne Dynamik von Gemeinschaften, die durch vielfältige Interaktionen und adaptive Dynamik ihrer Arten geprägt sind. Zudem wurde die Notwendigkeit hervorgehoben, kausale Beziehungen zwischen den Mitgliedern der Gemeinschaft abzuleiten, um ihre Dynamik vollständig zu verstehen.

Die vorliegende Arbeit untersuchte dabei speziell folgende Aspekte: *(i)* die Relevanz von Störungskennzeichen (d.h. Stärke und Dauer der Störung) und der

Stärke von Wechselwirkungen (z.B. das Vorhandensein alternativer Ressourcen) für die Erholungsdynamik trophisch verbundener Arten; *(ii)* die interaktiven Auswirkungen von Störungen und Ressourcendynamik auf die Reaktion und Erholung der Gemeinschaft; *(iii)* die Rolle von Räuber-Beute-Beziehungen, die die Gemeinschaften direkt und indirekt kontrollieren; *(iv)* die Auswirkungen schneller Veränderungen in Beutepopulationen durch Konkurrenz und Anpassungsdynamik auf die Stabilität der Gemeinschaft; *(v)* die Voraussage der Dynamik von Gemeinschaften anhand direkter Kausalität zwischen einzelnen Mitgliedern dieser Gemeinschaft.

Zu diesem Zweck wurden Mikrokosmen unter kontrollierten Bedingungen erstellt, bestehend aus Beutebakterien mit verschiedenen biologisch-ökologischen Merkmalen und Protisten als mikrobielle Räuber. Dieser experimentelle Ansatz ermöglichte es drei Hauptparameter zu variieren: Fraßdruck (über die Abwesenheit oder das Vorhandensein des Räubers), Nährstoffkonzentration und Störungsregime. Bei den Störungsregimen wurde zwischen einer kontinuierlichen, mäßigen Störung (die sogenannte press disturbance“) und einer unmittelbaren, schweren Störung (die sogenannte ”pulse disturbance”) unterschieden. Diese Störungsregimes wurden durch das Verdünnen der Gemeinschaften mit frischem Medium in unterschiedlichem Verhältnis hergestellt, wodurch eine dichteunabhängige Mortalität ausgelöst wurde. Außerdem wurde die Menge an verfügbaren Ressourcen experimentell durch eine graduelle oder eine abrupte Reduktion variiert.

Die Abundanzen einzelner Arten wurden mit verschiedenen Mikroskopie-, Kultivierungs- und Fingerabdruckmethoden erfasst. Zeitreihenmessungen wurden durchgeführt, um Stabilitätsmerkmale von Gemeinschaften wie z.B. die Erholungsphasen zu ermitteln und um zeitlich dynamische Eigenschaften von Arteninteraktionen zu verstehen. Schließlich wurden diese Experimente mit modellgestützten Simulationen (z.B. Lotka-Volterra Räuber-Beute-Modell), statistischen Modellierungsansätzen (z.B. gemischte lineare Modelle) sowie mit fortgeschrittenen statistischen Methoden (z.B. convergent cross mapping) kombiniert, um kausale Zusammenhänge zu offenbaren.

Die Ergebnisse dieser Experimente bestätigen, dass trophische Strukturen einen der wichtigsten Einflussfaktoren von Gemeinschaften darstellen. Die Abundanz von Populationen war im Allgemeinen empfindlich gegenüber der Art der angewendeten Störung. Dies war teilweise auf die Generationszeiten der Arten zurückzuführen, die das Erholungspotenzial zwischen den Störungsphasen beeinflussen. Einer der kritischen Punkte war zum Beispiel die Populationsgröße der Gemeinschaftsmitglieder, besonders die der Topprädatoren und die der seltenen Arten, welche ein Risiko besaßen, auszusterben.

Darüber hinhaus fügt diese Arbeit dem gegenwärtigen Forschungsstand wichtige Punkte hinzu. Die Ergebnisse betonen, dass in trophisch strukturierten Gemeinschaften, der Einfluss der Störung stark von der trophischen Stufe abhängt. Wenn eine höhere trophische Stufe betroffen ist, profitiert normalerweise die niedrigere trophische Stufe von der verringerten top-down“ Kontrolle, ähnlich dem ”explosionsartigem Anstieg der Beutepopulationen” in der Natur. Interessanterweise kann das Ausmaß dieser vorrübergehenden Phase der entkoppelten Dynamiken nur durch eine Erholung der Prädatoren kontrolliert werden, welche ebenso stark von der Dauer und Stärke der Störung abhängt. Am Wichtigsten ist, dass die Nutzung einer alternativen Ressource durch den Prädatoren seine Erholung beschleunigt und die Stabilität der Gemeinschaft erhöht.

Erhöhte Komplexität der Gemeinschaft (d.h. die Diversität der Beute) und die Interaktionen zwischen biotischen (d.h. Prädatoren) und abiotischen (d.h. Störungen und Ressourcendynamiken) Einflussfaktoren erzielten verschiedene Antworten der

Gemeinschaft auf Grund der Wechselwirkung zwischen den Einflussfaktoren sowie der Trade-offs zwischen kompetitiven Eigenschaften und Resistenz gegen Prädation.

Diese Arbeit unterstreicht, dass die Abundanz, Diversität und Zusammensetzung in der Gemeinschaft der Beute stärker durch die Prädation als durch die Störungscharakteristik beeinflusst waren. Zur selben Zeit hat jedoch die Art der Störung (pulse vs. press) einen starken Einfluss auf die Abundanz der Prädatoren, was wiederum einen indirekten Einfluss auf die Beutegemeinschaft verursacht. Ein Schlüsselaspekt ist jedoch, dass die verschiedenen Messgrößen in Form von unterschiedlich starken Reaktionen auf die Störung nachweisbar waren. Diese Unterschiede spiegeln sich darüber hinaus auch in entsprechenden Erholungskapazitäten wider.

Diese Arbeit hat zudem unser Verständnis über Dynamik und Stabilität ökologischer Gemeinschaften gefördert, die durch die Interaktion von Arten und adaptive Mechanismen angetrieben werden. Die Gegenwart eines Räubers erzeugte klar ausgeprägte Gemeinschaftsdynamiken, wie an den Zeitreihen einzelner Arten und neu entstehenden Beutephänotypen (als Strategie gegen den Prädator) sichtbar wurde. Stark variable Populationsdynamiken, die sowohl von Fitnessunterschieden sowie egalisierenden Mechanismen dominiert werden (wie beispielsweise Fraßdruck und adaptive Radiation), führten zu einer geringeren zeitlichen Stabilität der Gemeinschaften in der Gegenwart eines Räubers. Der Räuber hingegen ermöglichte einen höheren Level an Diversität und ließ Koexistenz zwischen Beutearten zu. Insbesondere die Zuflucht vor dem Räuber, welche durch den fraßresistenten Morphotyp bereitgestellt wurde, und der verringerte Wettbewerb zwischen den Beutearten sind ausschlaggebend. Der Räuber und die resistenten Morphotypen entwickelten zudem neue Interaktionen (kausale Verbindungen) mit anderen Arten in der Gemeinschaft.

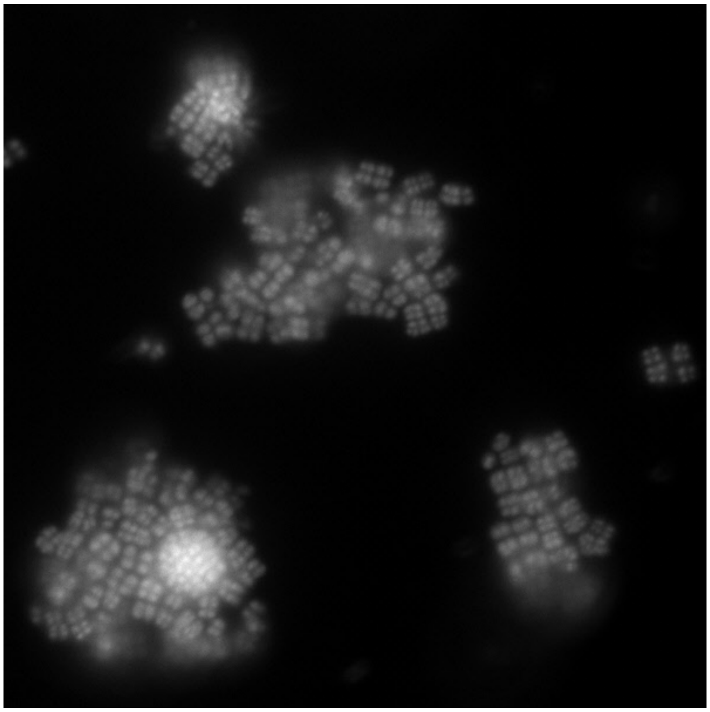
Zusammenfassend hat diese Doktorarbeit dazu beigetragen, unser Verständnis über Räuber-Beute-Beziehungen, Wettbewerb, Adaptation und deren Folgen für die Dynamik und Stabilität von Gemeinschaften zu verbessern. Die Ergebnisse verbessern speziell das Verständnis über die Effekte ökologischer Störungen und Ressourcendynamiken auf die Interaktion von Arten. Ferner konnte mit dieser Arbeit eine Grundlage geschaffen werden, sich von korrelationsbasierten Statistikmethoden zu entfernen und sich stattdessen auf direkte Ursache-Wirkungs-Beziehungen unter den Komponenten der Gemeinschaft sowie ihrer Umwelt zu konzentrieren. Insgesamt können die Schlüsselerrungenschaften dieser Arbeit ein wertvolles Fundament für künftige Studien bieten – gerade im Kontext der Entwicklung und Etablierung neuer Interventionsmethoden für die Naturschutzbiologie, die biologische Kontrolle (von Schädlingen), sowie die Epidemiologie. Zuletzt sind die hier implementierten theoretischen und praktischen Ansätze hilfreich für die Verbesserung der Voraussagen über die Dynamik und Stabilität von Gemeinschaften, besonders unter sich ändernden Umweltbedingungen.

1

Scope and Outline

"...whether it was possible by change of environment, in minute life-forms, whose life-cycle was relatively soon completed, to superinduce changes of an adaptive character, if the observations extended over a sufficiently long period..."

—–William Henry Dallinger,1887



Clumped bacterial cells as a defense against predation

Rapid global change challenges today's ecosystems tremendously. Accordingly, predicting the response of communities to global change is attracting considerable attention. The core problem with this is that the predictions are highly context dependent with respect to the interacting abiotic and biotic factors. For example, different frequencies and intensities of ecological disturbances may induce regime shifts through food chains[1]. Likewise, the adaptation to environmental change might initiate eco-evolutionary feedback mechanisms, which may cause surprising outcomes[2].

Disturbances and the type of species interactions operate on communities in concert[3]. Ecological disturbances may alter, for instance, the top-down and bottom-up control structure, causing cascading changes such as prey outbreaks and even extinction of top trophic levels[4,5]. Still, direct and indirect impacts of disturbances through predation are not well understood and often overlooked. Most studies rely on endpoint measurements (but see[6,7]), however, understanding the response and recovery properties of communities requires time series analysis (i.e. measurements before, during and after the disturbances). In addition to the species interactions, evolutionary dynamics has been identified as the most important biotic component for driving communities[8], however, they have been often separately addressed. It has recently been acknowledged that species traits may change fast enough to affect the ecological dynamics[9–11]. One example is that predation driven adaptation in a prey population may cause rapid shifts in community dynamics[12].

Inferring direct cause-effect relationships might have the potential to resolve these complex community dynamics. Advanced methods to detect causal relationships (e.g. convergent cross mapping[13,14]) have been developed as of late, however, community ecology is only beginning to appreciate these methods which should further be tested to reveal their practicability regarding predictions of community dynamics. Likewise, using a small number of interacting species such as predator-prey or host-pathogen pairs may help to divide complex communities into manageable partitions and offer a platform in which to test hypotheses coupled with mathematical models[15]. Microcosms are the most important candidates to study, both in temporal and spatial scales thanks to the short generation times of the organisms and the highly controllable experimental conditions[16].

The main objective of the thesis was to investigate context dependencies of community response and recovery. To this end, we assembled microcosms under highly controlled conditions consisting of bacterial prey and protist predator species. With this approach, we specifically studied community responses to different disturbance and resource dynamics. We answered the following questions in detail:

(i) *Do transient species dynamics depend on the trophic level and/or types of disturbances (i.e. pulses and presses)? How does the recovery time of the predator change depending on the strength and duration of the disturbances? Do alternative resources increase the chance of fast recovery of the predator?*

(ii) *How do communities respond to the interactions of pulse and press disturbances, as well as resource dynamics? What is the role of predation that interacts with abiotic changes on the prey community response?*

(iii) *How does competition and predation shape community dynamics in concert via combination of competitive abilities and adaptation to predation? Does revealing causal links between species give mechanistic insights into the community dynamics?*

Chapter 2 gives an overview on context dependencies in understanding community dynamics under environmental change. To this end, first, the common forms of ecological disturbances in terms of their durations and frequencies and their impacts on population's transient and long-term dynamics are discussed. Second, focusing especially on the predator-prey interactions, biotic components of context dependency are described by introducing species interactions and evolutionary dynamics, as well as the feedback mechanisms between them. Third, it is touched upon how these drivers and mechanisms shape community assembly, following a general introduction on microbial model systems and potential advanced theoretical methods as tools in ecological theory.

Chapter 3 describes the recovery dynamics of a simple microbial food web consisting of a predator, a prey and a common resource. This system was exposed to two different disturbance regimes: *(i)* a discrete and severe disturbance (pulse), and *(ii)* a long term and mild disturbance (press). The abundances of predator and prey before, during and after the disturbance were monitored. The transient dynamics of both trophic levels under different disturbance strengths and durations, beyond those applied in the experiments, were investigated using an ecological model. Additionally, the consequences of the predator coupling to the alternative resource for the transient recovery dynamics, were investigated. Results showed that transient recovery dynamics depend on the trophic level and the disturbance types. In particular, slowed down recovery of the predator induced a transient phase of prey release which depended on the duration and strength of the disturbances, as well as on the coupling of the predator to an alternative resource.

Chapter 4 focuses on the combined impacts of predation and the disturbance dynamics on the abundances of prey abundance, diversity and community composition. To this end, microcosms of bacterial prey and a protist predators were assembled. Community dynamics were monitored prior to pulse and press disturbances, during and after the disturbances (i.e. the return to experimental pre-disturbance conditions). More specifically, disturbance scenarios were coupled with gradual or instant resource deprivation scenarios. With this work, it was shown that prey abundance, diversity, and community composition were more strongly affected by predation than by disturbances coupled with resource deprivation scenarios. At the same time, the type of disturbance (pulse vs. press) had a stronger impact on the abundance of the predator. However, community measures had differential sensitivities, as reflected by their distinct recovery capacities.

Chapter 5 extends the understanding of community dynamics and stability driven by species interactions and adaptive mechanisms. The dynamics of each single prey species was monitored daily under the absence or presence of a predator. The results highlighted that that presence of a predator resulted in distinct community dynamics, as reflected by the single time series of the species and emerging new prey phenotypes. Highly variable population dynamics reduced the temporal stability when the predator was present, however, the predator provided an elevated level of diversity and coexistence between prey species due to the emergence of predator resistant phenotypes. Additionally, we suggested possibilities to reveal direct causations between the single community components, which might improve the predictions of community dynamics and stability, especially under changing environments.

Chapter 6 summarizes and discusses the main findings considering the strengths and limitations of the microbial model system used.

Chapter 7 presents a short synopsis and an outlook for ultimate combinations of methods potentially allowing a better prediction of the fate of communities under changing environments. Finally, it also gives an overview of fruitful avenues for future research.

2

General Introduction

2.1 Context dependency of community dynamics

While today's ecosystems are faced with a rapid global environmental change, scientists are called upon to predict the response of species assemblages to increasingly variable environments and the resulting consequences for ecosystem functioning. However, ecosystems are complex, non-linear and highly dependent on historical events. In addition, they might adapt under altered conditions and have multiple stable states[17]. Thus, inferences made might be highly context dependent.

Environmental change is a crucial factor in forming community structure, biodiversity patterns, and ecosystem function. Yet, environmental variables fluctuate in time and space, and they often have interactive impacts on ecosystems[18,19]. Temperature, for instance, does not impact the ecosystems in isolation, but in combination with other global change drivers such as nutrient supply[1].

Context dependency might also be caused by species interactions. While environmental change impacts the multispecies assemblages directly by, for instance, changing their physiology, behavior, and life history, indirect effects might be initiated through their resources, predation, competitors and collaborators, as well as altered strength of species interactions[20,21]. Another complexity is that species may evolve under varying environments and even these ecological and evolutionary complexities may interact[11].

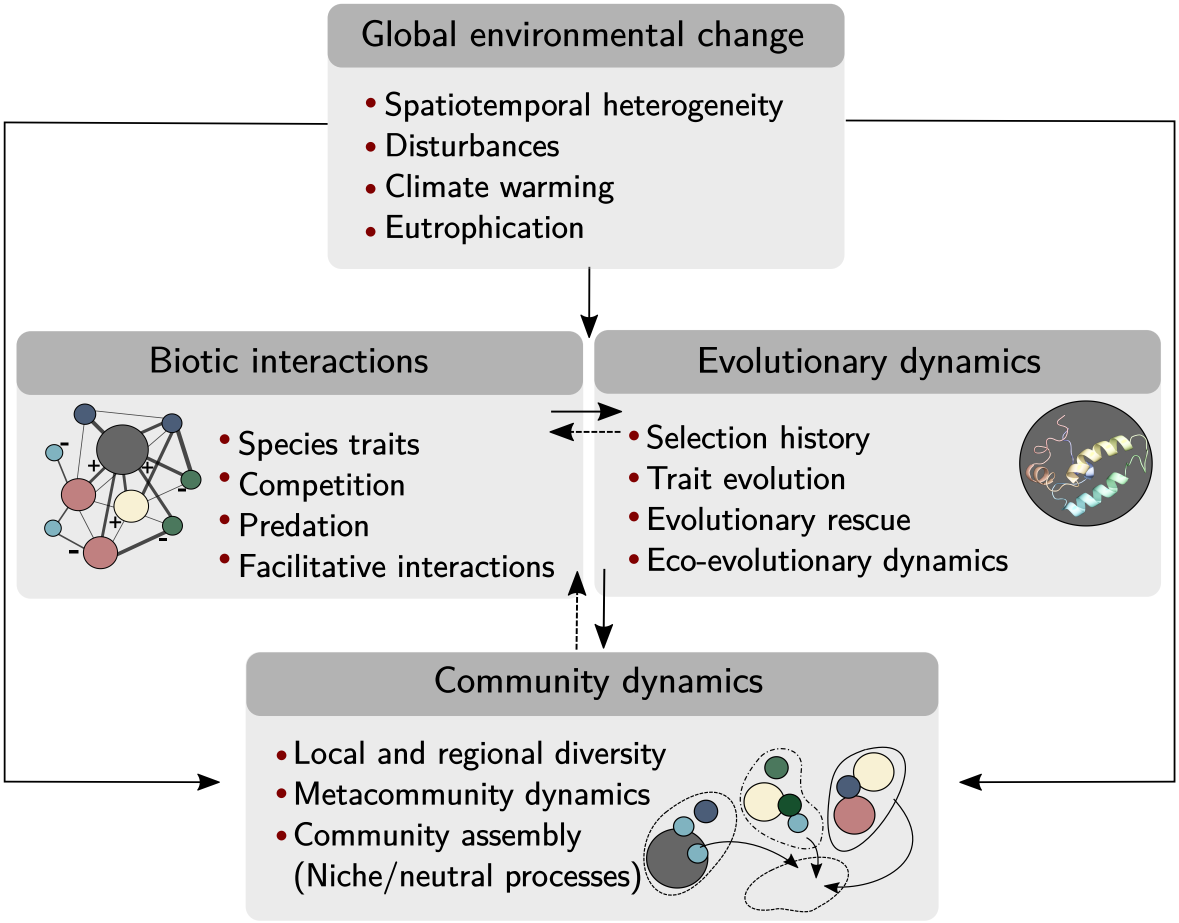


Figure 2.1. Mechanisms/drivers that should be considered in order to predict the impact of global environmental change on the populations/communities. Global change drivers act on communities in concert. They may also affect the community dynamics directly or indirectly via biotic interactions and evolutionary dynamics.

In the following, we will describe the context dependencies of community dynamics. In particular we will address the impact of abiotic changes such as ecological disturbances and the complexity of the communities such as biotic interactions and evolutionary dynamics (see Figure 2.1 for an overview). We will also highlight the importance of microbial model systems as tools in ecology by giving examples of their contribution to the ecological theory. Last but important, we will comment on the necessity of inferring direct cause-effect relationships in order to understand the future of communities.

2.2 Ecological disturbances

Fluctuations occur on all temporal and spatial scales, however they can take the form of discrete **disturbance events** (such as ocean acidification and extreme climate events) that harm the ecosystems[22]. Disturbances are characterized by their intensity, frequency and extent, and are often classified as **short-term and discrete (pulse disturbances)** or **long-term and continuous (press disturbances)** events[23,24] (Figure 2.2). These characteristics largely determine the observed community responses, because they affect species reproduction and survival, as well as interactions between species[25]. For instance, press disturbances may influence the normal variance in community attributes such as relative species abundances, whereas pulse disturbances usually cause dramatic structural and functional community shifts[24]. As a result, communities and their functions may follow different trajectories during and after disturbances. The different trajectories can be described as follows: *(i)* the community structure remains the same **(resistance)**, *(ii)* the community structure changes, but over time returns to its original state **(recovery)**, *(iii)* the community structure changes but function is maintained **(functional redundancy)**, *(iv)* function changes but the community structure does not change **(functional plasticity)** and *(v)* the community structure changes and does neither return nor maintain its function[6,26,27]. Furthermore, disturbances do not only cause mortality, but also alter the niche structure and nutrient fluxes within the affected community. For instance, floods cause resource pulses in aquatic systems[28] or severe drought may cause gradual losses in the water resources[29]. Abiotic conditions affect the intra- and interspecific interactions. For instance, changes in nutrient fluxes may change the competition patterns between the species[30].

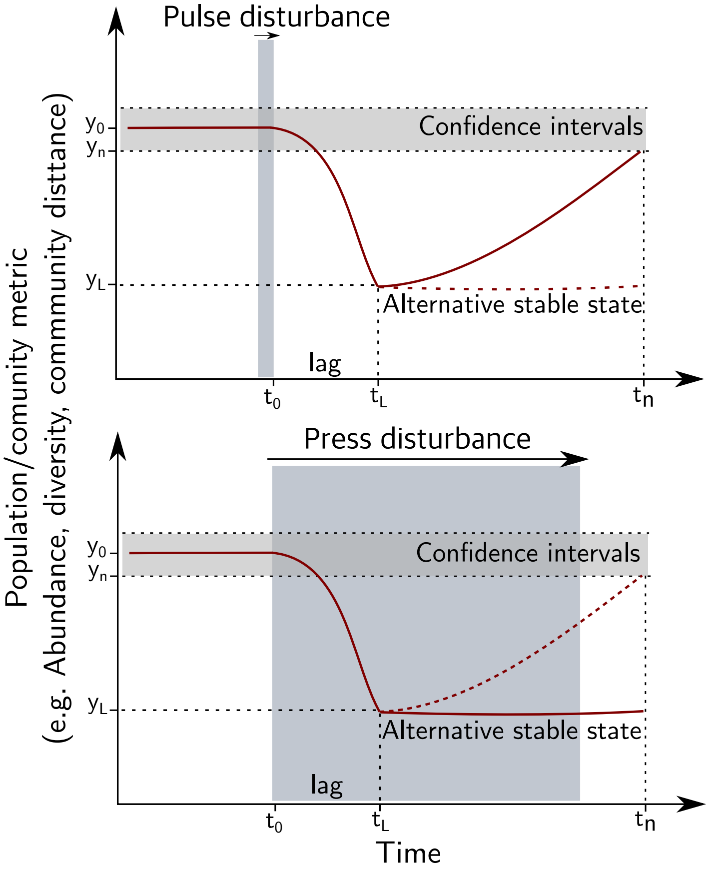


Figure 2.2. Response of a population or community metric to the press and pulse disturbances[24]. y_0 is the pre-disturbance mean value of the parameter of interest. Grey area demonstrates the 95% confidence intervals of the temporal variation. t_0 is where the disturbances which are shown as blue shaded areas begins. Parameter changes $|y_0 - y_L|$ after a time lag $|t_0 - t_L|$ (resistance). Return to y_0 after lag period is described as resilience. The parameter of interest is considered to be recovered if y_n at time point t_n is statistically indistinguishable than the pre-disturbance mean. Alternatively, it may stabilize at a new mean value which is more likely under a press disturbance.

2.2.1 Transient dynamics and stability

Most of the explorations in population dynamics have focused on the long-term stable solutions[31]. However, since many natural systems experience disturbances and variable conditions, which can reset coupled oscillating systems (such as predator-prey dynamics), long transient phases may arise. Transient phases play a crucial role to understand the behavior of ecological systems under variable regimes[32] and the patterns of biodiversity[33]. Transient dynamics can be described as the short-term dynamics of a population over time, depending highly on its initial condition[34]. They are useful in characterizing the fluctuating population dynamics after disturbance events, until they reach a stable state asymptotic growth[35].

Transient dynamics are affected by time scales depending on the generation times of the species[36], as well as the characteristics of the disturbances, at which they are exposed[37]. For example, Becks et al. (2005) established a biological system consisting of a bacterivorous ciliate and two bacterial prey species in a chemostat, to observe chaotic population dynamics. Different strengths of the disturbances (simulated as dilution) caused differential dynamics: the system reached a stable state at a higher disturbance rate. On the other hand, intermediate rates caused *chaotic dynamics*[*], and lower rates, had initiated the *limit cycles*[†,39]. Transient dynamics of the populations are also strongly dependent on biotic and abiotic components. For instance, Steiner et al. (2012) analyzed transient dynamics of a zooplankton predator-algal prey model system. They found that the presence of a defending prey besides edible prey, increased predator extinctions at high and low nutrient enrichment levels, but this effect was balanced at high disturbance rates by weakening the invasion of inedible prey[40].

2.2.2 Catastrophic shifts

Transient dynamics are also important for predicting catastrophic shifts in ecosystems. Any ecosystem may exhibit *catastrophic shifts* from one state to another

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[*] Chaotic dynamics are sensitive to the initial conditions, predictable in short-term and become random afterwards.

[†] "A limit cycle is a closed trajectory in phase space having the property that at least one other trajectory spirals into it either as time approaches infinity or as time approaches negative infinity"[38].

even under only small changes of environmental parameters such as climate, nutrient input, toxic chemicals and biotic corruption[41–43]. Thresholds for critical transitions are difficult to predict due to stochasticity; however, estimating the distance to a *threshold (tipping point)* could allow researchers to measure the stability or to realize catastrophes beforehand[44]. Even if a system shows little change before the tipping point, there are warning indicators which occur in non-equilibrium dynamics[45]. In dynamical systems theory, the phenomenon known as the *critical slowing down* refers to these early indicators and it occurs for a range of bifurcations[46]. When the system reaches a bifurcation, as a result of accumulated perturbations, recovery from perturbations becomes slower, therefore the system correlates with its past *(autocorrelation)*, and the size of the fluctuations also increases[45,47,48].

2.3 Species interactions and evolutionary dynamics under environmental change

2.3.1 Species interactions and coexistence

Ecological networks are extremely complex and consist of various inter- and intraspecific interactions. This complexity makes it difficult to assess indirect effects of environmental change, especially in real ecosystems[49]. Thus, scientists are faced with an uncertainty of predicting how and to what degree the individuals within a community will respond to the abiotic changes[1].

Since all single species have their own physiological optimum, given the abiotic alteration and its indirect outcomes, they can be affected differently[15]. Temperature, for instance, can affect the population dynamics indirectly via species interactions, and directly via temperature-dependent parameters such as growth rate, feeding rate, or other metabolic processes; therefore, single-species response in isolation cannot represent its response in a community[50]. An example is that the different reaction norms of coexisting species under environmental change can lead to *mismatches* between species[51]. A model which comprises a ciliate and its bacterial parasite, showed that variable conditions and high temperatures caused declines and higher extinction rates in ciliate populations. In this scenario, the parasite was not only negatively affected from the varying conditions, but also declined its host populations[52]. Another example is that the predators with slow growth rates and large body sizes might be more affected from disturbances. As a result, reduced top-down control may even cause **prey outbreaks**[5]. These responses suggest that the existence of such *trophic asynchrony* in prey-predator or host-parasite systems, and the collapse of one level in the interaction, might cause complex population and range dynamics[53,54].

One of the astonishing aspects of life on Earth is species diversity. Coexistence mechanisms, which maintain species diversity, are of great concern in ecology[55]. As aforementioned, the environmental change intervenes with these mechanisms which makes predictions even more difficult. The concept of niche, for instance, has been commonly used to predict the fate of communities under climate change. Species' fundamental habitat, therefore, is the key assumption in which to determine a species' response to climate change. The fact that species interactions may themselves be affected by climate change and inter-specific interactions is often ignored by climate models[56]. A couple of mathematical models move beyond this, and take into account other types of species interaction on range shifting dynamics (e.g.[57]). Here there is still a need for an empirical/experimental understanding regarding the importance of species interactions under environmental change.

2.4 Eco-evolutionary dynamics

Most of the population models ignore evolutionary changes by assuming that evolutionary dynamics occur over time scales which are too long to influence population dynamics[67]. Theory and observations show that **rapid evolution** may occur in tractable time scales[68,69], it may also prevent population decline and allow the recovery of populations before they go extinct. This so-called **evolutionary rescue** mechanism is an emerging issue in the frame of global change and mitigating its effects[70].

Rapid evolution is known to be forced under challenging environmental conditions including, but not limited to abiotic drivers (e.g. temperature, pH, nutrient availability). Biotic drivers (e.g. predation, facilitation, antagonism) have also significant effects on community dynamics and stability[58,59]. It has often been shown that separating biotic interactions and evolutionary dynamics is difficult[8,60,61]. When environmental change causes natural selection in a population, the resulting trait evolution may modify the environment back, therefore, allowing further change in evolutionary patterns[9]. This kind of cycle indicates **feedback-loops between ecological and evolutionary change**, which in turn influence community dynamics and ecosystem functioning.

Several mechanisms might influence evolutionary dynamics in species mixtures[8]:

(i) Resource restriction may reduce the effective population sizes by competitors, which in turn, lowers the rate of beneficial mutations.

(ii) If the interspecific variation is higher than the intraspecific variation, the new environment acts on the relative abundances leading to the loss of less adapted species.

(iii) There may be a trade-off between the species interactions (e.g. defence mechanisms) and adaptation to the abiotic environment.

(iv) Species may also evolve to depend on other species such as foraging on an end product.

An example of a feedback mechanism has been described by Becks et al. (2012), where it was observed that selection for a *prey defense trait* had fluctuated under cyclic changes of predator abundance in a rotifer-alga microbial model system[62]. Within a prey-predator cycle, the alga evolved to produce *cell clumps* which were too large for the rotifer to digest. This caused the decline of the rotifer population and the increase of the algal population. Since diffusion of nutrients into the cell in clumped populations is restricted, the algae evolved to make small clumps or appear as single cells. This size was favorable for rotifers, and they initiated the cycle again[62]. Feedback loops between ecological and evolutionary dynamics were also predicted to be important in cooperative populations (e.g.[63–65]). Sanchez and Gore (2013), for instance, showed in their yeast model system, that evolution favored cheater individuals which do not cooperate for the good of the community, however, their growth was ultimately limited by the total density of the community. Interestingly, the authors also observed that invasion by cheaters did not cause collapse, but the community became more sensitive to perturbations[66].

2.5 Community assembly mechanisms

The structure of the communities depends on its assembled history, an issue whose importance has been observed almost a century ago (e.g.[71]). However, a new interest on community assembly rules has raised interest into answering this question: *Are communities historically assembled through deterministic (niche/stabilizing), or stochastic (neutral/equalizing) processes[54]?* Contemporary community assembly theory suggests that both deterministic and stochastic mechanisms operate in concert on communities[72]. Importantly, both mechanisms are affected by biotic and abiotic factors[73] (Figure 2.3). Stephen Jay Gould (1989) offered a thought experiment in his book "Wonderful Life: Burgess Shale and the Nature of History": *"I call this experiment replaying life's tape. You press the rewind button and making sure you thoroughly, erase everything that actually happened, go back to any time and place in the past... Then let the tape run again and see if the repetition looks at all like the original"*[74]. Novel mathematical models demonstrate the connection between immigration, demographic stochasticity, and intra-/interspecific interactions (e.g.[75]). Thus, there is now a growing realization that the effect of species interactions on population dynamics may depend on their history (order and timing of immigrations) of community assembly[76], and this relationship is highly shaped by environmental variability and disturbances[77]. Since, one cannot perform Gould's experiment in a real-world application, microbial model systems are a promising path in which to study assembly theories, because they make it possible to reconstruct the history under a set of abiotic environments (e.g.[77,78]).

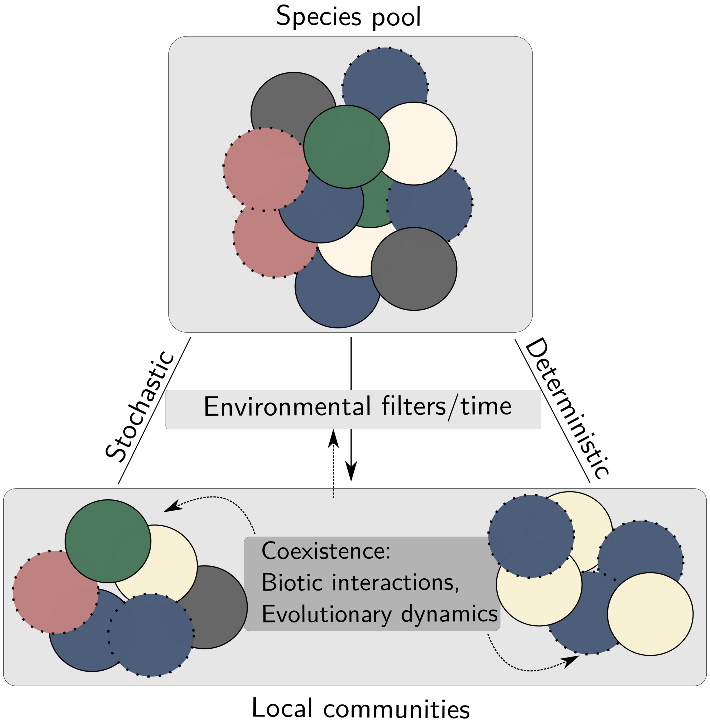

Figure 2.3. Mechanisms/drivers that operate on the community assembly. Environmental filters such as ecological disturbances sort species deterministically out. According to the contemporary theory of community assembly chance events work on the communities along with species sorting. Local communities are shaped by biotic interactions and evolutionary dynamics including eco-evolutionary feedback mechanisms.

2.6 Dealing with complexities

2.6.1 Microbial model systems as a tool in ecology

Understanding the response of species assemblages to variable environments and the resulting consequences for ecosystem functioning is crucial, however, obtaining cause-effect relationships is difficult only by way of observations and long-term experimental manipulations[79]. Therefore, experimental microcosms and mesocosms (including microbial, invertebrate and plant systems) have substantially triggered the testing and developing of ecological and evolutionary theory, and have become useful approaches to understand the potential consequences of global problems such as climate change or loss of biodiversity[79,80]. They make it possible to deconstruct the complexity of a system and to address fundamental questions in simple or even in artificially assembled communities. Thus, they can be considered as bridges between the ecological theory and the real world (Figure 2.4). Like mathematical models, laboratory model systems are intended to obtain information which is impractical or too difficult to gain from the environment[81]. One may think that simplified systems cause the reduction of realism, however, this is not only the problem of model systems, but rather of all scientific experiments[82].

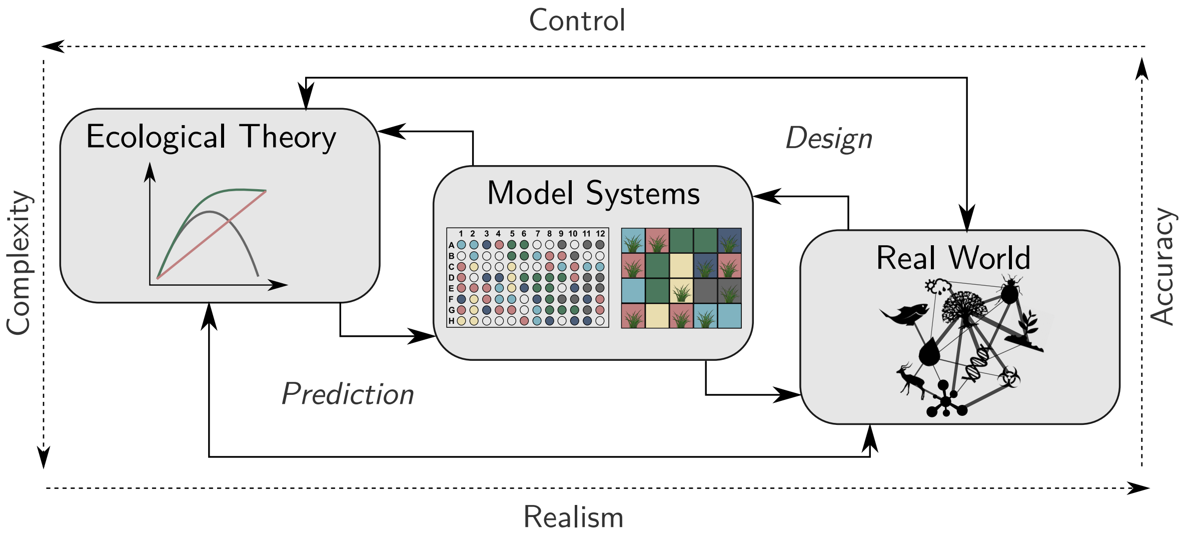

Figure 2.4. Interactions between ecological theory, model systems (lab and field) and real world. Knowledge from both field experiments and microbial model systems can be used to parameterize ecological models when the biological information is not available or impractical to gain from the real world. This information can also be used to design better experiments. Since all systems have their own advantages and disadvantages in terms of controllability, realism, complexity and accuracy, when they are used in concert, better predictions maybe achieved. Modified from[83].

Microorganisms are crucial candidates for testing and unifying ecological theory, as they provide easy to replicate systems with *low running costs*. In addition to their *cost effectiveness*, they are *easy to manipulate* within experimental systems and offer a *high control of abiotic conditions and background environmental noise*. Their small size and short generation times imply the possibility of constructing experiments even with large populations *across spatial and temporal scales*[81,84]. Moreover, tracking *many generations of populations* within a couple of weeks is feasible[84–87]. Since bacteria reproduce asexually, identical populations can be created from a single genotype, which can be stored, allowing for c*omparisons between ancestral and evolved types*[88]. These advantages make microbial model systems an even more suitable system in which to test ecological theories, with respect to the evolution of communities in a set of *varying environmental regimes*, and *feedback between individuals, populations, and the genes*[16,89–91]. Undoubtedly, microbial and higher level organisms have negative analogies which should be considered when extrapolating the experimental results from microbial systems[92–95].

Although the relevance of using microbial model systems to address ecological problems is a matter of ongoing debates (e.g[82,96,97]), they have an old tradition in theoretical ecology. Gause (1934), for instance, developed the *"predator-prey coexistence mechanism"* concept 80 years ago using a protozoan model system[98]. Since then, microorganisms have been used increasingly to address general theories in population/community dynamics under various environmental and biological settings[99–107].

2.6.2 Correlation, causation and the future of predictions

Correlation does often point to real causation, however, in dynamical systems, it is not enough to infer **direct cause-and-effect relationships** between variables due to the following possible reasons: *(i)* correlation between two variables can be **purely coincidence**, *(ii)* correlation can be caused by a **hidden common third variable** that affects both of them, *(iii)* the direction of causation or **bidirectional causation** cannot be inferred directly unless other information exists, *(iv)* Correlations cannot be found or turn to be negative **when more data is available**[13,14,108].

Today correlation does not drive the majority of scientific fields such as econometrics, neuroscience and statistical physics, however, ecology is in its infancy with regards to appreciating statistics as a means to infer direct cause-and-effect relationships[109]. In economical systems, for instance, **Granger causality** has a common use. Granger's concept of causality states that a variable X causes a variable Y, if the prior behaviour of X predicts the future behaviour of Y[110]. However, Granger causality has been developed for stochastic linear systems, which is a distinct difference from the deterministic and non-linear systems in nature. Sugihara et al. tackled this problem from a new perspective, proposing the **Convergent Cross Mapping (CCM)** method[14]. The fundamental idea of the CCM method is that if Y is causally influenced by X, then Y has signatures of X such that the historical record of Y can estimate the state of X. It is based on the **Takens' theorem**[111], which employs time-lagged coordinates of each of two variables to construct shadow manifolds[*] (M_X and M_Y) of their original source manifolds. This shadow manifold is expected to preserve important components of the full causal system. If X causes the dynamics of Y, position of the time points in M_X and M_Y should be closer (Figure 2.5).

Prediction ability is a central problem in ecology[113]. Coupled population dynamics can be explained and predicted by difference and differential equations. This concept was pioneered by Lotka-Volterra and is still the most important communication method in ecology to this day. Simply put, the modelling routine starts with choosing the model structure according to the proposed hypothesis. It follows with parameterizing the equations and analyzing them by comparing with the patterns in nature[114]. This is a cycle that is repeated until the best fit is found, with the risk of having the best parameter combination that is biologically meaningless[115]. Moreover,

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[*] Manifold is a "topological space that locally resembles Euclidean space near each point"[112].

temporally dynamic systems with multiple variables and non-linear relationships between them might be extremely difficult to parameterize predictions from[116]. Trophic networks, for instance, consisting of multiple preys and predators, are systems in which their dynamic consequences are difficult to predict. In addition to that, intraspecific variation in prey communities and their resistance to the predators and competitive abilities, may cause unpredictable dynamic consequences[117–119].

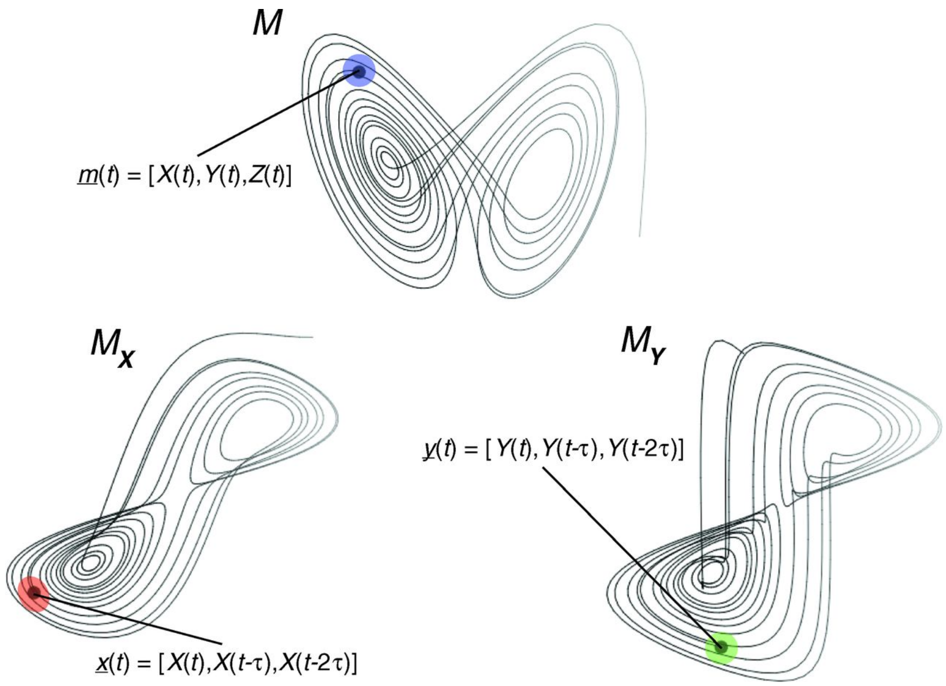

Figure 2.5. Convergent cross mapping (CCM) algorithm[14]. X, Y, Z are variables in a coupled system. M is the original system, M_X and M_Y are the shadow manifolds constructed using lagged-coordinate embeddings of X and Y (lag = τ). Points that are nearby on M_X (red) will correspond temporally to points that are nearby on M_Y (e.g., within the green circle). That is, the points inside the red ellipse and green circle will have corresponding time indices (values for t). This enables us to estimate states across manifolds using Y to estimate the state of X and vice versa using nearest neighbors (3). With longer time series, the shadow manifolds become denser and the neighborhoods (ellipses of nearest neighbors) shrink, allowing more precise cross-map estimates (see[14] for the details).

Modelling practices have already become less equation driven with the increase in computation power. The methodology of individual-based modeling does not specify equations at population level but simulates the individual organisms and their biotic and abiotic interactions[120]. Similarly, cellular automata models are based on local laws at spatial cells[121]. Lastly, empirical dynamic modelling which allows the data to directly determine the model, is very promising for dynamical systems, especially when there is no information available, variables are highly non-linear and the system is too complex to parameterize[122]. In sum, the combination of better-resolved data derived from hypothesis driven controlled experiments with the mentioned sophisticated analytical tools, is the obvious path forward for future research.

2.7 Aims of this study

Although impacts of ecological disturbances on communities, in particular on species diversity and ecosystem functions, have been the main focus in ecology, context dependency caused by interactions between abiotic drivers and biotic components have often been disregarded. Using controlled microbial model systems consisting of bacterial prey and protist predator species (Figure 2.6), we addressed following points:

(i) We investigated the transient dynamics of predator and prey species under press and pulse disturbances. We particularly focused on the recovery time of the predator under different strengths and durations of disturbances and the resource coupling alternative to the prey.

(ii) We studied the changes in prey abundance, diversity and community structure as a response to the interactions of abiotic factors (i.e press and pulse disturbances and resource deprivation) and predation.

(iii) We examined how competition and predation shape community dynamics in concert via combination of competitive abilities and adaptation to predation focusing on the causal links between the species.

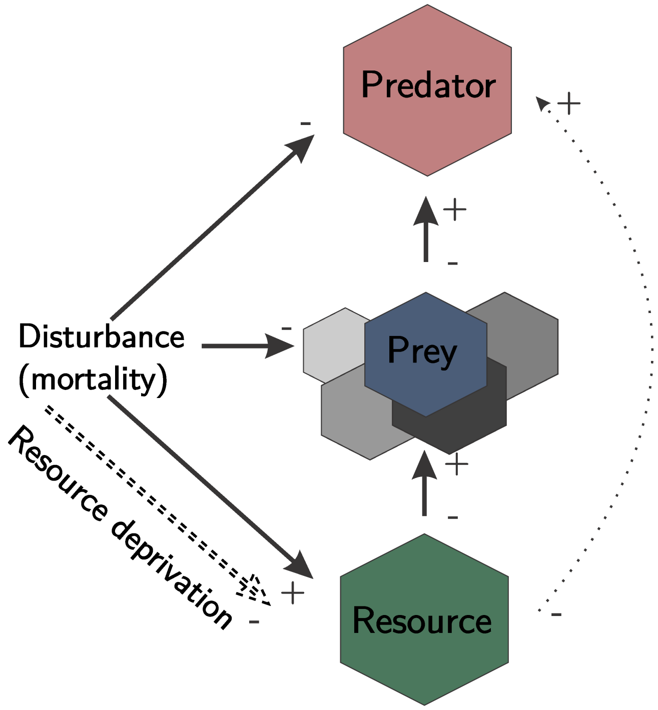

Figure 2.6. Simple illustration of microcosms used in this work.

3

Community Dynamics under Disturbances

3.1 Transient recovery dynamics of a predator-prey system under press and pulse disturbances

Publication:

Karakoç, C., Singer, A., Johst, K., Harms, H. & Chatzinotas, A. Transient recovery dynamics of a predator–prey system under press and pulse disturbances. *BMC Ecology* **17**, 13 (2017).

This work combines experimental and modelling approaches to investigate the transient recovery dynamics of species, which is an interplay between disturbance attributes and food web structure. Results highlighted, for instance, that the divergent population growth of trophic levels where predator suffers, the prey profits. Accordingly, predator recovery depends on the strength and the duration of the disturbances. Importantly, predator's coupling to an alternative resource defines the stability of the community.

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RESEARCH ARTICLE Open Access

Transient recovery dynamics of a predator–prey system under press and pulse disturbances

Canan Karakoç[1], Alexander Singer[2,4], Karin Johst[2], Hauke Harms[1,3] and Antonis Chatzinotas[1,3*]

Abstract

Background: Species recovery after disturbances depends on the strength and duration of disturbance, on the species traits and on the biotic interactions with other species. In order to understand these complex relationships, it is essential to understand mechanistically the transient dynamics of interacting species during and after disturbances. We combined microcosm experiments with simulation modelling and studied the transient recovery dynamics of a simple microbial food web under pulse and press disturbances and under different predator couplings to an alternative resource.

Results: Our results reveal that although the disturbances affected predator and prey populations by the same mortality, predator populations suffered for a longer time. The resulting diminished predation stress caused a temporary phase of high prey population sizes (i.e. prey release) during and even after disturbances. Increasing duration and strength of disturbances significantly slowed down the recovery time of the predator prolonging the phase of prey release. However, the additional coupling of the predator to an alternative resource allowed the predator to recover faster after the disturbances thus shortening the phase of prey release.

Conclusions: Our findings are not limited to the studied system and can be used to understand the dynamic response and recovery potential of many natural predator–prey or host–pathogen systems. They can be applied, for instance, in epidemiological and conservational contexts to regulate prey release or to avoid extinction risk of the top trophic levels under different types of disturbances.

Keywords: Pulse disturbance, Press disturbance, Transient dynamics, Recovery, Trophic interactions, Protist, Bacteria, Predation, Prey release, Food web

Background

Disturbance is one of the key drivers of the dynamics and diversity of communities [1–3] and is defined as a discrete event in time killing or damaging individuals [4]. Disturbances occur in many natural systems with different strengths and durations. They are often classified as pulse disturbances (short-term events) or press disturbances (long-term events) depending on their duration in relation to the generation times of species [5, 6]. These different temporal patterns of disturbances are important for understanding the structural and functional community responses [7]. Press disturbances, for instance, can cause increasing variability in the relative abundances of species, whereas pulse disturbances can cause dramatic structural and functional shifts [8].

Besides the characteristics of the disturbance, the traits of the species and their biotic interactions are important determinants of community responses [9, 10]. However, the indirect impacts of disturbances caused by the biotic interactions are not well understood and are often overlooked. In particular, the trophic status in food webs plays a major role for the species response to disturbances [11–13]. Traits such as large body size, slow growth rate and

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low population size make top predators more vulnerable than other trophic levels. Studies have been shown that a reduced top-down control allowed prey outbreaks with cascading changes in ecosystem structure and function [14–16]. Similarly, in a microcosm study, increasing temperature led to increasing invasion success of a bacterial prey species due to the increased prey release from protozoan predation stress [17].

It is well known that long transient phases of population dynamics may occur in response to disturbances [18] and particularly strong or long-term disturbances may prolong these transient phases [19]. Among the ecological attributes known to affect transient recovery dynamics, the presence and availability of resources are particularly important [8]. It was previously hypothesized that the availability of alternative resources for the predator may increase the persistence of predator–prey systems [20]. Moreover, foraging behavior may be flexible and may change in disturbed environments [21]. Surprisingly, little is known about how the coupling of the predator to an alternative resource affects the recovery dynamics.

In this study, we combined microcosm experiments and modelling to investigate transient recovery dynamics of a simple microbial food web (consisting of predator, prey and a common resource). We exposed this system to disturbances, which we applied as increasing dilution rates. We contrasted two different disturbance regimes (i) a discrete and severe disturbance (pulse), and (ii) a long term and mild disturbance (press). We monitored the abundances of predator and prey before, during and after the disturbance.

In a second step we investigated using an ecological model the transient dynamics of both trophic levels under different disturbance strengths and durations beyond those applied in the experiments. In particular, we studied the consequences of the predator coupling to the alternative resource for the transient recovery dynamics. We found that disturbance strength and duration were decisive for the different transient recovery dynamics of the two trophic levels. In particular, we observed a slowed down recovery of the predator inducing a transient phase of prey release, i.e. temporarily high prey population sizes. Our results also revealed the importance of the predator coupling to an alternative resource which strongly impacted the recovery time of the predator and thus the length of the prey release phase.

Experimental methods and model

Origin and maintenance of stock cultures

The bacterium *E. coli* JM109 harboring a chromosomal green florescent protein (GFP) was used as prey organism. Using this strain allowed us to monitor *E. coli* in the food vacuoles of protists and facilitated controlling for contamination. A single clone grown on a lysogeny broth (LB) agar supplemented with 50 mg/ml kanamycin was used for establishing a pre-culture in liquid LB medium. Incubation was done in 50 ml medium in a 200 ml culture flask for 24 h on a closed rotating shaker at 25 °C. A low salt LB medium (1% tryptone, 0.5% yeast extract, 0.5% NaCl, 50 mg/ml kanamycin) was used for incubation of bacterial pre-cultures. Pre-cultures of the protist *Tetrahymena pyriformis* were established in proteose peptone yeast extract medium (1% proteose peptone, 0.15% yeast extract, 0.01 mM $FeCl_3$) at 25 °C in an incubator without shaking. These pre-cultures were cultivated axenically (i.e. growth on only dissolved nutrients without any bacteria) to avoid transfer of unwanted bacteria to the experimental cultures. *Tetrahymena pyriformis* is able to grow as a bacterivore (i.e. predating on bacterial prey) or as an osmotrophy (via direct uptake of dissolved nutrients). Prior to the experiments, pre-cultures of protists were concentrated by centrifugation (1000*g*, 10 min) and washed with experimental media twice. Both bacteria and protist pre-cultures were enumerated and diluted to the experimental concentrations with the experimental media. Enumeration techniques and all starting concentrations are described below. The *E. coli* JM109 and *Tetrahymena pyriformis* strain that were used in this work have been deposited at the public culture collection of the Department of Environmental Microbiology at the Helmholtz Centre for Environmental Research-UFZ (http://www.ufz.de/index.php?en=37703).

Experimental conditions

We used the above mentioned low-salt (in order to prevent salt damage on protists) LB medium during the experiments as the growth resource for the bacterial prey. The complex carbon source of the LB medium (i.e. yeast extract) served as an alternative resource for the predator. All experimental media were sterilized and filtered through a 0.2-μm pore sized filter. Experiments comprised 20 ml semi-continuous cultures in 50 ml sterile disposable culture flasks. Experimental cultures were always incubated at 25 °C for 24 h without shaking and all other environmental parameters were kept constant.

We found that a daily tenfold dilution prevented the collapse of the populations and resulted in an equilibrium state at which prey and predator coexist. This daily dilution went along with a replenishment of resources (i.e. LB medium) before they were depleted. It also reduced cell debris and excretion products and prevented oxygen depletion during the experiments. The remaining culture after each transfer was used for cell counts.

Experimental design

Three different treatments were applied: undisturbed (control), press disturbance and pulse disturbance. All treatments were replicated three times. All treatments were imposed by diluting the cultures with fresh medium as described below.

Undisturbed control

All replicate microcosms started with equal cell numbers of *E. coli* (3.6 × 10^7 cells ml^{-1}) and *Tetrahymena pyriformis* (4.2 × 10^4 cells ml^{-1}). Each day 2 ml from the cultures were transferred into 18 ml of fresh medium and allowed to re-grow for 24 h following this tenfold dilution.

Press disturbance

After control communities reached the equilibrium dynamics, they were exposed to the press disturbance from day 22 to 32 in separate flasks. Press disturbance was imposed as 40-fold daily dilution (simulating 4 times increased dilution rate compared to the daily constant rate) for a period of 10 days.

Pulse disturbance

Communities that had reached equilibrium dynamics were exposed to the pulse disturbance treatment on day 15. Pulse disturbance was applied as a single 2500-fold dilution (simulating a 250 times increased dilution rate). Initial cell numbers were lower than in the press experiment (i.e. 4 × 10^6 for bacteria and 4 × 10^3 for protists), but started with a similar predator: prey ratio as in the other treatments.

Sampling

A well-mixed 500 µl subsample was fixed with 0.2% Lugol's iodine solution for quantifying protists. Subsamples were diluted if the cells were too many to be counted reliably. Fixed protist cells were counted under an inverted microscope (Olympus CKX41, Olympus America Inc., Melville, NY, USA) with a Sedgewick-Rafter counting chamber (Pyser-SGI Limited, Edenbridge, UK). An additional 15 ml subsample was filtered through a 20 µm mesh filter (CellTrics, Sysmex Partec, Kobe, Japan) to remove protist cells prior to counting bacteria with a Coulter Counter (Multisizer 3, Beckman Coulter, Brea, CA, USA). Cell numbers were recorded every day.

Growth curves

Growth rates of prey and predator were determined by growing the organisms under the same experimental conditions for 24 h (i.e. without dilution). The triplicate cultures contained only prey, predator growing axenically without prey, and prey and predator together. Initial abundances of *E. coli* and *Tetrahymena* sp. were 4 × 10^6 and 2500 cells ml^{-1} respectively. Samples were taken with sterile syringes at 12, 14, 16, 18, 20, 22, 24 h. Protists and bacteria were counted as described above.

Modelling

We modelled the microcosm experiments as a time-discrete version of a Lotka–Volterra type predator–prey model [22]. Particularly, the model considers predator coupling to an alternative resource and the action of disturbances. Justified by experimentally determined growth curves (Additional file 1: Figure S1), we assumed a density limited prey population (P) and an exponentially growing predator (C).

$$P_{t+1} = (1 - d_t)P_t + r_P P_t \left(1 - \frac{P_t}{K_P}\right) - c_P P_t C_t \quad \text{(1a)}$$

$$C_{t+1} = (1 - d_t)C_t + r_C C_t + c_C P_t C_t \quad \text{(1b)}$$

where d_t is the dilution rate (applied once per 24 h), r_P is prey growth rate without predators, K_P is prey carrying capacity, c_P is the prey interaction coefficient describing how much prey is consumed per predator, r_C is the predator growth rate without prey and c_C is the predator interaction coefficient describing the consumption and conversion of prey to changes in C (Table 1). The model was implemented in R (version 3.1.3; [23]).

Note that the parameter r_C is important as it implicitly describes the coupling of the predator to another resource additionally to the prey population. Positive r_C imply coupling to this resource allowing the predator population to grow even in absence of prey. However, the model ignores a potential resource competition among predator and prey. Resource competition is unlikely, due to regularly strong dilution every 24 h. Dilution reduces the potential for resource competition in two ways: it removes predator and prey cells (i.e. reduces the amount of resource consumers) and it additionally renews the resource.

The model describes C and P as cells ml^{-1} and is iterated at a time step of 7.5 min, leading to 192 iterations per day. Initial tests showed that the step size was

Table 1 Parameter description and parameter values for the Eqs. (1a and 1b)

Name	Description	Value
d_t	Dilution rate	0.9 $days^{-1}$
r_P	Prey growth rate	0.094 $(7.5\ min)^{-1}$
r_C	Predator growth rate	0.012 $(7.5\ min)^{-1}$
K_P	Prey carrying capacity	4.9 × 10^8 cells ml^{-1}
c_P	Prey interaction coefficient	3.5 × 10^{-6} $cells^{-1}$ ml
c_C	Predator interaction coefficient	1.4 × 10^{-11} $cells^{-1}$ ml

sufficiently small to cover the experimental dynamics measured daily. Model results are displayed in daily time steps corresponding with experimental sampling times. For clarity, we left out the modelling time steps at a finer scale. Therefore, decline due to dilution and regrowth within the 24 h between dilutions are not visible.

To calibrate the model, initially we adjusted parameter values to the measured growth curves (see Additional file 1: Figure S1). Growth rates and prey carrying capacity were calibrated from the respective single species growth curves. Subsequently, interaction parameters were calibrated using the growth experiment with both species. We applied the Nelder–Mead optimization algorithm [24, 25] in R within reasonable wide parameter ranges. We then refined the parameter estimates by calibrating the model additionally to the control treatment. For this purpose, we applied a Latin hypercube approach on a narrow parameter space around the parameter estimates from growth curves. We then selected the parameter set that minimized the fourth power of the sum of relative distances to all cell counts in the control experiment. With the additional calibration to the control experiment we accounted for the possibility of uncontrolled changes in conditions between the separate growth and disturbance experiments.

Evaluation of results

We used the standard metric Nash–Sutcliffe efficiency (E) to quantify the general model efficiency in predicting the experimental data. E ranges between 1.0 (perfect fit) and $-\infty$. An E that is lower than 0 means that the mean value of the experimental data could be a better predictor than the model [26].

To specifically assess the differences between model and data during the first days after the start of the press or the occurrence of the pulse disturbance, we calculated the time of the species response to the disturbance by detectable abundance changes. Specifically, we defined "response time" as the time between the start of the disturbance and the day when species population size left the range of equilibrium sizes (they were calculated for the period from day 7 until disturbance start). Difference between the response times of the model and the data (average of replicates) is stated as "deviation time D_T". Deviations between the recovery times were calculated in the same manner as response time.

For the evaluation of prey release we calculated the covariance between prey and predator population sizes before, during and after disturbance. A negative covariance implies that prey population size strongly increases due to decreasing predator population size thus exhibiting prey release.

Simulation experiments

We applied the calibrated model to simulate situations that would have been difficult to directly control in the experiment. In simulation experiments, we tested the impact of (1) the duration of press disturbance, which we varied between 2 and 12 days, (2) the strength of pulse disturbance (varying between 10 and 10^6 on a 10-logarithmic scale, and (3) the strength of the predator coupling to the resource by varying parameter r_C in the range of 0.007–0.011. In these experiments, we particularly focused on speed of predator recovery, which we calculated in terms of "recovery time". Note that all source codes used in this manuscript are available upon request.

Results

Experimental population dynamics

In the control treatment, an equilibrium state appeared at which prey and predator coexisted (Fig. 1a). Under press disturbance, the prey population started to increase on day 26 reaching a higher equilibrium size than that of the control (Fig. 1b). At the end of the press disturbance, this high equilibrium population size remained for two more days and then turned back to the pre-disturbance size which was reached after full predator recovery on day 33 (at least two replicates were recovered). The predator population declined during press disturbance but started to increase during the disturbance period. After press disturbance ceased, the predator population recovered fully to its pre-disturbance size (Fig. 1b). Increasing negative covariance (*before disturbance cov* $= -0.002$*; during/after disturbance cov* $= -0.292$) indicated a phase of prey release during and after the disturbance (see "Evaluation of results").

Under pulse disturbance, the prey population increased already after one day as a consequence of the reduced predator population size (Fig. 1c). The prey population did not return back to the pre-disturbance level by the end of the experiment. The predator population continued to decline after the pulse but started to recover soon to the pre-disturbance size within 3 days (at least 2 replicates were recovered). Increasing negative covariance (*before disturbance cov* $= -0.003$*; during/after disturbance cov* $= -0.458$) indicated a phase of prey release after the pulse disturbance (see "Evaluation of results").

Modeled population dynamics

As we calibrated our model to the control treatment without disturbance, the fitted model reproduced well the non-disturbed experimental data (Fig. 1a). Also the overall response patterns to the press and pulse disturbances were captured well by the model (Fig. 1b, c). Nevertheless, the modeled population dynamics showed some slight discrepancies to the experimental

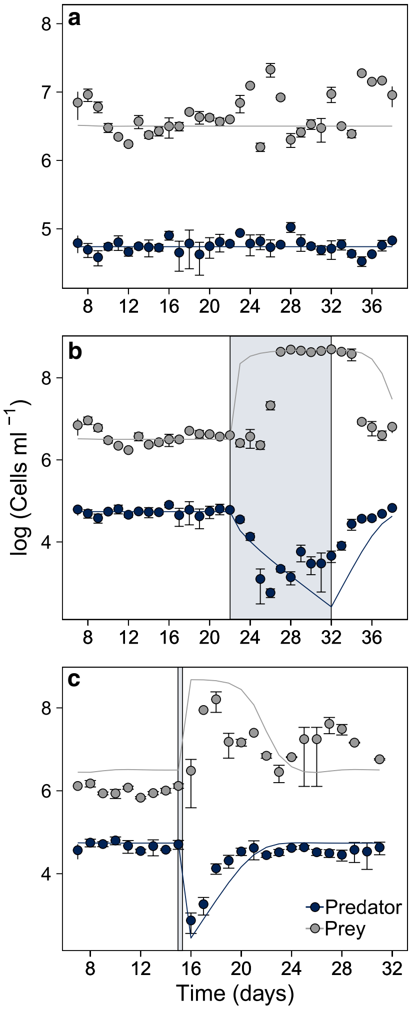

Fig. 1 Transient dynamics of predator and prey without and with disturbances. *Grey* and *dark blue filled circles* correspond to the experimentally determined mean predator and prey population dynamics respectively. *Error bars* represent ± standard deviation. *Solid lines* correspond to the model simulations (only daily time steps are shown). **a** Population dynamics without disturbance; **b** under press disturbance and **c** under pulse disturbance. Control without disturbance is with tenfold daily dilution, press disturbance corresponds to 40-fold dilution between the days 22–32 and pulse disturbance to 2500-fold dilution on the day 15. Disturbance action is shown as *grey shadows*

data. In the control treatment, predator dynamics ($E = -0.01$) were better predicted than the prey dynamics ($E = -0.32$). This is also true for the press disturbance ($E = 0.34$ *and* $E = 0.11$, respectively) and even more pronounced for the pulse disturbance ($E = 0.61$ *and* $E = -0.44$, respectively).

Specifically, some differences between modeled and experimental population dynamics occurred during the first days after the start (press) or the occurrence (pulse) of disturbance. Under press disturbance, the projected prey population showed an earlier response ($D_T = -3$) and late recovery ($D_T > 4.3$), (Fig. 1b). During the press disturbance, the experimental predator population started to increase already within the disturbance duration (around day 28), whereas the modelled population continuously declined, started to increase only after press disturbance ceased at day 32 ($D_T = -1$) and recovered later ($DT = 4.6$), (Fig. 1b).

Under pulse disturbance, the projected prey population size was slightly higher during the pre-disturbance and disturbance period. Experimental prey populations did not recover *until the end of the experiments* (see "Limitations and outlook"; Fig. 1c). Predator recovery to the equilibrium state was longer than in the experiments ($D_T = 4.3$).

Having found qualitatively similar community responses in the experiments and the simulations, we used the model to study more systematically the impact of press disturbance duration on predator (Fig. 2a) and prey (Fig. 2b), as well as pulse disturbance strength on predator (Fig. 2c) and prey (Fig. 2d).

The predator population declined stronger with both increasing press duration or pulse strength and recovered only slowly (Fig. 2a, c). Pulse and press disturbances resulted in a transient phase of decreased predator population sizes. With increasing disturbance impact, recovery times of the predator increased (Fig. 3a, b).

Note that, this was also valid for prey populations. However, it goes unnoticed on the daily sampling basis as the prey population recovered from disturbance within the 24 h sampling interval. Subsequently, it grew to higher population sizes, due to diminished predator stress (Fig. 2b, d). With increasing press duration and pulse strength, the chance increased that the prey population retained a high equilibrium population size for some time during or after the disturbance. Prey population size returned to the lower pre-disturbance equilibrium size only after significant recovery of the predator.

Impact of predator coupling to an alternative resource on predator and prey transient recovery dynamics

Changes in the coupling to the alternative resource r_C impacted predator (Fig. 2e) and prey (Fig. 2f) dynamics considerably under pulse disturbance and in a similar way also under press disturbance (see Additional file 1: Figure S2). As expected, lower values of r_C resulted in lower pre-disturbance equilibrium size of the predator (Fig. 2e) and an accordingly higher prey abundance. From these levels, disturbance reduced predator abundance according to the pulse strength. In contrast, prey grew to carrying

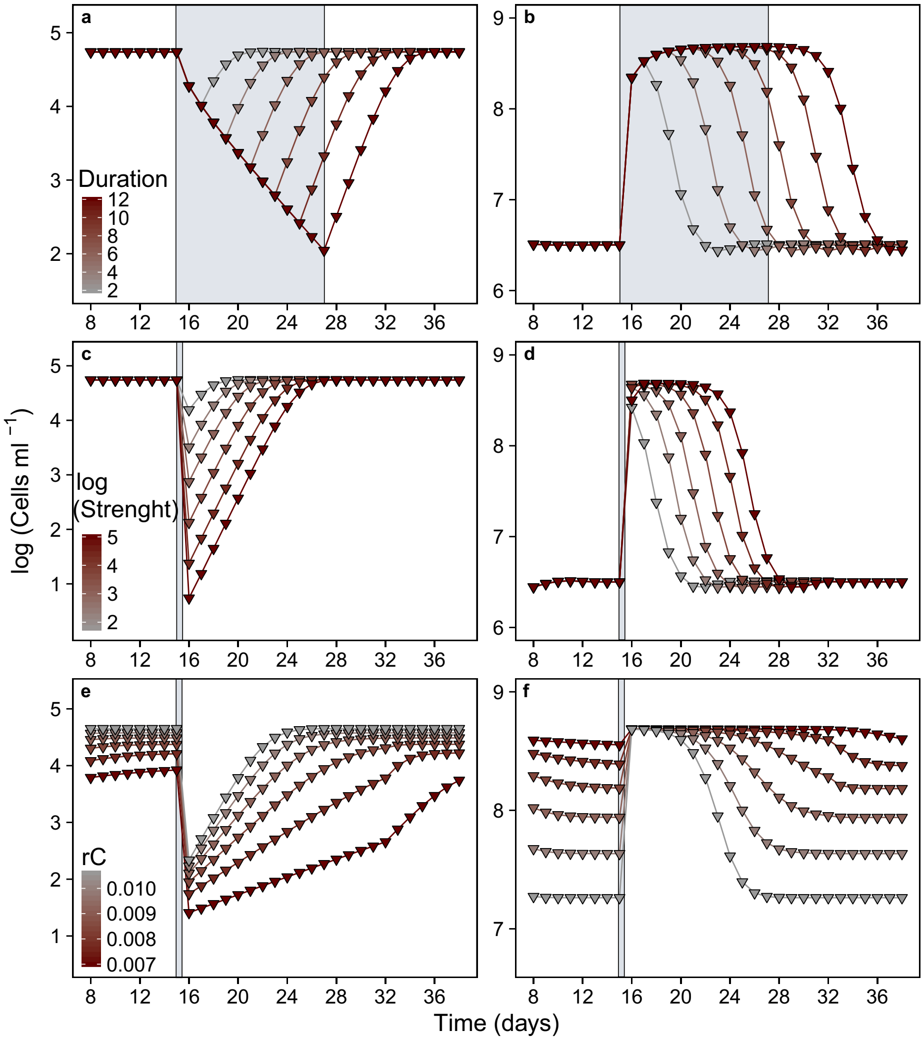

Fig. 2 Impact of disturbance duration, strength and predator coupling to an alternative resource on transient dynamics. **a**, **b** Impact of press disturbance duration (varied from 2 to 12 days) projected by the model simulations for predator (**a**) and prey (**b**). Strength of disturbance was kept constant (40-fold). Disturbance has started on day 15. *Color gradient* shows the shortest (*grey*) to the longest (*dark red*) disturbance duration. **c**, **d** Impact of pulse disturbance strength (varied from 50 to 100,000-fold) projected by the model simulations for predator (**c**) and prey (**d**). *Color gradient* shows the lowest (*grey*) to the highest (*dark red*) disturbance strength. **e**, **f** Impact of predator coupling r_C to an alternative resource besides prey (varied from 0.007 to 0.011) under pulse disturbance (2500-fold dilution) projected by the model simulations for predator (**e**) and prey a (**f**). *Color gradient* shows the lowest (*grey*) to the highest (*dark red*) r_C values. Disturbance action is shown as *grey shadows*

capacity (maximum size that the density dependent prey population can reach) within 24 h, independent of its pre-disturbance abundance (Fig. 2f). Recovery time of the predator extended significantly with decreasing r_C (Fig. 3c). Therefore, the prey population could retain its carrying capacity for a longer time (Fig. 2f).

Discussion

We found strong impacts of the strength and duration of disturbances on the transient dynamics and recovery time of predator and prey, and strong differences among the dynamics of the two species due to their position in the food web. In particular, our results revealed a slowed

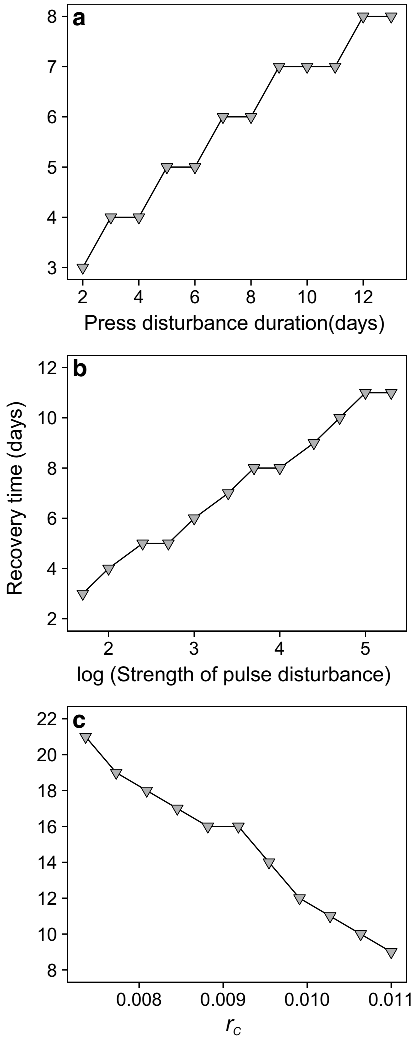

Fig. 3 Recovery time of predator depending on the disturbance duration, strength and resource coupling. We explicitly focused on predator recovery and defined the time a predator population needed to reach the pre-disturbance population size again as "recovery time". Recovery time is calculated as the duration (days) from the end of disturbance to the return to the pre-disturbance population size. **a** The dependence of recovery time of predator on the duration of press disturbance, **b** the strength of pulse disturbance and **c** changing resource coupling r_C resulting from the model simulations

recovery of the predator from the disturbance inducing a temporary phase of prey release. The predator's coupling to an alternative resource was strongly impacting its own recovery time and thus also the length of the prey release phase. These general findings are discussed in the following in more detail.

Transient recovery dynamics of predator and prey may result in prey release

After disturbance ceased, the predator population recovered to pre-disturbance size (Fig. 2a, c). The respective recovery time was strongly related to the disturbance duration and strength (Fig. 3a, b). This finding is highly relevant, because prolonged recovery time, during which population size is low, comes along with increased extinction risk [27]. Extinction of top predators may cause radical changes in ecosystems by altering community structures [28, 29].

We found similar structural changes in our protist-bacteria system. The prey population size considerably increased during and after the disturbances due to missing predation pressure (Fig. 2b, d). This is a clear sign of prey release [16, 30]. Effectively, disturbance had uncoupled the two interacting species, such that the prey population was no longer relevantly affected by its predator. Prey release is common in systems with substantial disturbance on predators, e.g. by hunting [31]. For example, it was previously observed that the prey population release following the hydrological disturbance in a freshwater ecosystem was due to the reduced abundance of large sized predators [16]. A similar pattern has been also observed in an island ecosystem following a hurricane which reduced the abundance of top predators and caused herbivore outbreak [15]. We found that even if disturbance is affecting both species with equal mortality, as in our study, this can initiate prey release. The duration of this prey release depended on both the duration and the strength of the disturbance (Fig. 2b, d). Thus, even if a species is heavily impacted by disturbance (such as the bacterial prey), it might still benefit due to diminished competitor or enemy stress.

Predator coupling to an alternative resource is important for predator recovery and prey release

The use of an alternative resource is a known phenomenon for the studied protist. *Tetrahymena* species are able to grow on dissolved carbon sources and even fail to reduce the density of bacteria offered to them [32]. Foraging may be flexible due to specific predator traits such as absolute time or effort needed for grazing and relative intake rates, which, in turn impact the transient dynamics of the communities [21]. We found that a strong coupling to the alternative resource allowed the predator to reach higher pre-disturbance equilibrium sizes and accelerated the predator's recovery after the disturbances (Fig. 2e). Accordingly, weak couplings are advantageous for the prey (Fig. 2f) and may result in prey release as well. These results support previous findings on the importance of alternative resources for food web stability [33].

Limitations and outlook

Despite its simplicity, our simulation model well reflects the transient dynamics of both predator and prey under pulse and press disturbance. Although this simplicity greatly facilitates a general understanding of the mechanisms, it has also drawbacks coming along with some mismatches between experimental data and model results.

As explained in the results section, the experimental prey population took longer to increase than indicated by the model (Fig. 1b, c) and reached lower values after pulse disturbance (Fig. 1c). Also, the experimental predator population already started to increase, while press disturbance was still impacting the community (Fig. 1b). These responses indicated a weaker impact of disturbance on the predator than expected from the model. We therefore tested the impact of an alternative resource across a range of coupling strengths as this could attenuate the impact of disturbances on the predator. We found that coupling of the predator to an alternative resource did clearly reduce its recovery time (Fig. 3c) but could not reproduce an increase of the predator population already during press disturbance (see Additional file 1: Figure S2). Stronger consumption of an alternative resource could be possible during a phase of increased dilution rates along with very low and high prey abundance. For future work, we suggest to relax the assumption of a constant coupling and to test coupling strengths dependent on prey density.

Another mismatch is that in contrast to model projection, the experimental prey population after pulse disturbance (Fig. 1c) did not completely return to the pre-disturbance equilibrium, but remained slightly elevated. Prey adaptation mechanisms such as cell aggregation and biofilm formation may cause this deviation and might provoke an alternative system state triggered by the disturbance [34–36].

It should also be taken into account that our simple Lotka–Volterra type model ignores possible predator satiation effects (Holling Type II and Type III non-linear functional responses) and assumes a linear functional response (Holling Type I without saturation). This is because the good fit of the L–V model to the experimentally measured predator and prey growth curves (Additional file 1: Figure S1C) indicates that predator's linear functional response describes the empirical data well and therefore density-dependent predation in form of non-linear functional responses is unlikely. However, given the discrepancies, especially during the prey release phase, one should investigate in future the applicability of non-linear functional responses. These investigations can be combined with the above described density dependent couplings to an alternative resource.

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Conclusions

By combining experimental and modelling approaches we found that the interplay of disturbance attributes and food web structure determines the transient recovery dynamics of interacting species. This can lead to diverging population growth with one trophic level suffering and the other one profiting even if disturbance induces the same mortality. Most importantly, coupling of the predator to alternative resources may stabilize the community dynamics. These findings are essential for understanding how through changing disturbance attributes or creation of alternative resources (additional couplings) the transient food web dynamics can be changed to the benefit or harm of a species. These factors should therefore be taken into account in future food web studies. Taking a closer look at the impact of disturbances on species and communities and the resulting transient recovery dynamics might turn out to be pivotal in establishing intervention tools for conservation biology, biological control and epidemiology.

Additional file

Additional file 1: Figure S1. Experimental growth data and the fitted curves of prey alone, predator alone and prey–predator interaction. **Figure S2.** Impact of predator coupling r_C to an alternative resource besides prey under press disturbance.

Authors' contributions

CK, KJ, AS and AC designed research; CK made the lab experiments, AS performed the simulations; AC and HH supervised the lab experiments; KJ supervised the theoretical part; CK, AS, KJ, HH and AC interpreted the results and wrote the paper. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The datasets supporting the conclusions of this article are available in the Dryad Digital Repository [37], http://dx.doi.org/10.5061/dryad.1gq66.

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4

Interactions of Community Drivers

4.1 Interactions between predation and disturbances shape prey communities

Publication:

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This work combines experiments and statistical modelling approaches used to investigate the interplay between predation and multiple abiotic conditions, which determined the response of the prey community in terms of in abundance, diversity, structure, and their recovery. Results turned out to be very context dependent due to the interactions between abiotic and biotic components. Also, the measured responses reflected differential recovery potentials. This work, therefore, indicated the necessity of analyzing multiple response measures with a time resolution and the interactions of community drivers to allow for us to fully understand the behavior of communities under disturbances.

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Interactions between predation and disturbances shape prey communities

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Ecological disturbances are important drivers of biodiversity patterns. Many biodiversity studies rely on endpoint measurements instead of following the dynamics that lead to those outcomes and testing ecological drivers individually, often considering only a single trophic level. Manipulating multiple factors (biotic and abiotic) in controlled settings and measuring multiple descriptors of multi-trophic communities could enlighten our understanding of the context dependency of ecological disturbances. Using model microbial communities, we experimentally tested the effects of imposed disturbances (i.e. increased dilution simulating density-independent mortality as press or pulse disturbances coupled with resource deprivation) on bacterial abundance, diversity and community structure in the absence or presence of a protist predator. We monitored the communities immediately before and after imposing the disturbance and four days after resuming the pre-disturbance dilution regime to infer resistance and recovery properties. The results highlight that bacterial abundance, diversity and community composition were more affected by predation than by disturbance type, resource loss or the interaction of these factors. Predator abundance was strongly affected by the type of disturbance imposed, causing temporary relief of predation pressure. Importantly, prey community composition differed significantly at different phases, emphasizing that endpoint measurements are insufficient for understanding the recovery of communities.

Ecological disturbances affect interspecific interactions and, consequently, community dynamics[1,2]. Trophic interactions also play a crucial role in community dynamics as predators shape prey communities by affecting the strength of species interactions[3–13]. However, there is a lack of studies on the combined effects of disturbances and predators on prey communities[14]. Such studies would not only help to explain the response of complex multitrophic communities[15] to anthropogenic disturbances, they are also indispensable for understanding synergistic and compensatory effects on the communities, which may cause ecological surprises and even irreversible outcomes[16].

Disturbances are characterized by their intensity, frequency and extent, and are often classified as short-term and discrete (pulse disturbances) or long-term and continuous (press disturbances) events[17,18]. These disturbance characteristics largely determine the observed community responses, because they affect species reproduction and survival, as well as interactions between species[19]. For instance, press disturbances can influence community attributes such as relative species abundances beyond normal background variation, whereas pulse disturbances usually cause dramatic structural and functional community shifts[17]. As a result, communities and their functions may follow different trajectories during the disturbance and after the disturbance ends: *(i)* the community structure remains the same (resistance), *(ii)* the community structure changes, but over time returns to its original state (recovery), *(iii)* the community structure is changed but function is maintained (functional redundancy), *(iv)* function changes but the community structure does not change (functional plasticity) and *(v)* the community structure changes and neither returns nor maintains its function[20–22]. However, most of the studies do not quantify and compare the community composition between the pre-disturbance phase, the phase following the onset of the disturbance, and the phase after the disturbance (but see[10,21,23,24]).

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When causing mortality, disturbances may alter niche structure and nutrient fluxes. For instance, fire results in biomass sequestration in soil and strong rainfall can transfer terrestrial nutrients to aquatic systems[25]. Such resource deprivations may occur in different disturbance scenarios. Prolonged severe drought may cause, for example, a gradual loss of water resources and progressive changes in the physiological status of plants[26].

Partial deprivation of resources may also change the competition patterns between species, giving an advantage to species with high resource affinity[27].

Predation and disturbances may interact in complex ways in their effects on prey communities[28]. Predation as a biotic pressure in concert with abiotic disturbances may change prey abundances, diversity and community composition[29]. Many predators are characterized by selective feeding/predation modes and predation success is controlled by traits of their potential prey, such as its size[30,31]. The predators' physiological states, sizes and growth rates can be affected by abiotic disturbances; predators with slow growth rates and large body sizes are usually most affected by disturbances. As a result, reduced top-down control due to disturbances may even cause prey outbreaks[32].

In this study, we addressed the combined impact of predation and disturbances on species abundances, diversity and community composition. To this end, we assembled communities of bacterial prey and a protist predator in controlled laboratory settings and monitored the community dynamics prior to disturbances, during disturbances and four days after disturbances (i.e. the return to experimental pre-disturbance conditions). More specifically, we coupled increased community dilution simulating mortality with gradual or instant resource deprivation. Measurements taken at different phases of the experiment allowed us to examine the resistance and recovery properties of the communities. Since the disturbances that we imposed remove equal fractions of prey and predator individuals, we expected that a reduced predator density (resulting in larger clearance zones for nourishment) might favor the prey due to reduced contact frequency[33–36]. This, in turn, would result in higher prey abundances. Thus, the magnitude of change in prey populations, their resistance or recovery upon disturbance might be mediated by the predator.

Methods

Experimental methods. *Organisms.* *Agrobacterium rhizogenes* (α-Proteobacteria), *Kocuria rhizophila* (Actinobacteria), *Sphingobium sp.* (α-Proteobacteria) and *Williamsia sp.* (Actinobacteria) were used as prey. These prey species are common free-living microorganisms in aquatic and soil ecosystems and vary in their population growth (Supplementary Material A) covering the breadth of population growths representative of natural communities[6,11,37]. Prior to the experiments, they were grown in pure cultures in Brunner-CR2 medium[6] overnight at 25 °C in a shaking incubator. Abundance of prey individuals during the experiment was estimated with a particle counter (Multisizer™ 3, Coulter Counter, Beckman Coulter, USA). Precultures of the ciliate predator *Tetrahymena pyriformis* (with an average length and width of 20 × 50 µm) were maintained in proteose peptone yeast extract medium[38] at 25 °C in an incubator without shaking. They were cultivated axenically (growth only on dissolved nutrients without bacteria) before the experiments to avoid transfer of unwanted bacteria to the experimental cultures. Prior to the experiment they were concentrated by centrifugation (10 minutes, 1,000 g) and washed with experimental medium. Controls without microorganisms, samples plated at each sampling point, and the previously known fingerprinting pattern of each species were used to screen for possible contamination. All strains are available on request from the public Culture Collection of the Department of Environmental Microbiology at the Helmholtz Centre for Environmental Research – UFZ (http://www.ufz.de/index.php?en=13354).

Experimental design. Static microcosms consisted of 20 mL of Brunner-CR2 medium in 50-mL cell culture flasks which were incubated at 25 °C in the dark. Prey cultures were diluted in the experimental medium evenly; total prey number was adjusted to 1.8×10^7 cells mL^{-1}, predator number was 4.2×10^4 cells mL^{-1}. This computes to approximately 400 prey per predator[6,10,11,37]. We performed daily 10-fold dilutions by transferring 10% of the community into a fresh medium thus eliminating the complications caused by dead cell debris, low oxygen levels and influences of high culture density. This replacement is necessary to prevent population collapse[39]. Cultures were shaken well before each transfer and sampling.

Thirty microcosms were started with the same inoculum and incubated for 14 days, corresponding to approximately 30–60 generations (Supplementary Material F) for the prey and the predator species used. We employed two trophic regimes (predator absent and present), two disturbance types (press and pulse), and two kinds of resource deprivation (absent and present). Resource deprivation was discrete in pulse disturbance experiments and gradual in the press disturbance experiment (Fig. 1). Each treatment was replicated three times and randomly placed in the incubator. We ran controls (without any disturbance) for 14 days as daily serial transfers involving 10-fold dilution throughout the experiment. The pre-disturbance regime consisted of four days of daily serial transfers involving 10-fold dilution to reach the equilibrium dynamics. Simulated press disturbance was then imposed as a 20-fold community dilution of the fresh medium every 12 hours over five days, whereas pulse disturbance was imposed as two 1,000-fold community dilutions within five days (on day 5 and 9; Fig. 1). Note that this simulated mortality is by definition different from mortality caused by disease, stress, intoxication, or predation, which leaves at least part of the dead biomass in the system.

In addition, we simulated resource deprivation by diluting the pre-disturbance medium that serves as a resource for the prey with autoclaved distilled water (Fig. 1). In press disturbance experiments, we diluted the resource gradually by 2.5% at each of the 20 disturbance transfers. In pulse disturbance experiments, we reduced the resource by 25% at each of the two disturbance transfers. These treatments finally resulted in a deprivation of 50% of the initial resources and remained at this resource level during the post-disturbance stage. Disturbances were followed by a period during which pre-disturbance dilution regimes (daily 10-fold dilution) were applied.

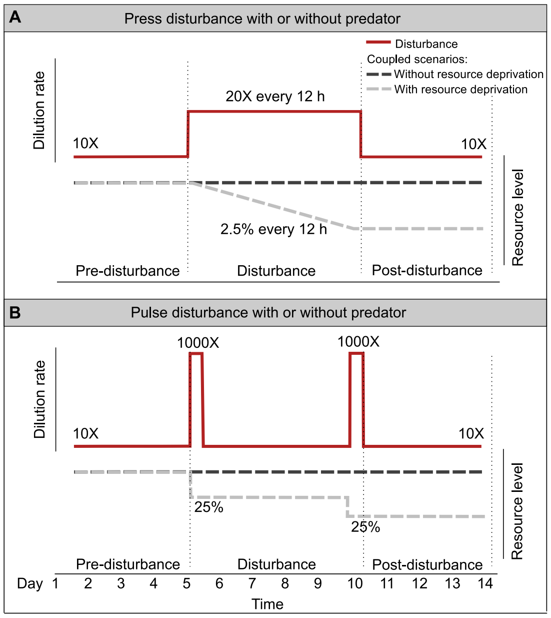

Figure 1. Experimental design. (**A**) Press disturbance with or without the predator. (**B**) Pulse disturbance with or without the predator. Dilution factors indicate the strength of simulated mortality and resource levels indicate the degree of resource deprivation: For press disturbance 2.5% reduction steps with 20-fold community dilution at each step, and, for pulse disturbance, 25% reduction steps with 1,000-fold community dilution at each step was applied. Vertical dashed lines delimit the three phases and indicate the times of sampling.

Samples were taken prior to the disturbance (day 5), at the end of the disturbance (day 10) and four days after the disturbance (day 14).

Community composition estimation. Bacterial community composition was estimated by 16 S rRNA-gene based terminal restriction fragment length polymorphism (T-RFLP) analysis. Applying the restriction enzyme MspI made it possible to distinguish the specific T-RF of each bacterial prey species. Data were normalized to eliminate differences in total signal intensity between the different samples. We used only the four species-specific T-RFs and their relative abundances for the analyses. The T-RF of one species (*Williamsia sp.*) was absent due to competitive exclusion, and was thus removed from the analysis (see Supplementary Material B for a detailed description).

Species abundance estimation. Cell numbers of *Tetrahymena pyriformis* were estimated by counting cells fixed with 0.2% Lugol's iodine solution under an inverted microscope (Olympus CKX-41) with the help of a counting chamber (Sedgewick Rafter Cell, Pyser-SGI Limited, UK). A subsample of the microbial community was fixed with 4% paraformaldehyde solution and total abundance of bacteria was estimated using a particle counter as mentioned above.

Data analysis. All statistical analyses and visualizations were performed in R version 3.4.0[40]. We used *alpha* level 0.05 unless stated differently. All source codes used in this manuscript are available upon request. Our four dependent variables were total prey and predator abundance, prey diversity (measured using the Shannon-Weiner index) and community composition. We calculated the magnitude of change in total prey abundance relative to control treatments (averaged over replicates) without predation and disturbance and the magnitude of change in predator abundance relative to control treatments without disturbance: $A_{relative} = \ln(A_{treatment})/\ln(\overline{A}_{control})$. By doing so, we accounted for any directional change with time in control treatments. We assessed the impact of predation, disturbance and their interaction on prey abundances, and of disturbance on predator abundance with linear mixed effect models using the function mixed() in the afex package[41]. Main effects of predation, disturbance type, resource deprivation and phase were included in the analysis. Additionally, two-way interactions between all main effects were included. We did not include higher-order interactions to avoid overfitting. The phase was treated as a fixed factor, because we were specifically interested in the differences of response variables at the different phases. The model included a microcosm as a random intercept effect structure to account for variation among cultures due to factors other than those included as explanatory in the model. The significance of effects was tested using two-tailed Type III F- on the global model using a parametric bootstrap with 10,000 simulations. Model residuals were visually assessed for homogeneity and normality. The effects on predator

Total prey abundance			
Effects	**df**	**χ^2**	**p**
Predation	**1,71**	**134.35**	**<0.001**
Disturbance	**1,71**	**20.97**	**<0.001**
Resource	**1,71**	**19.43**	**<0.001**
Phase	**2,71**	**215.11**	**<0.001**
Predation x disturbance	1,71	0.56	ns.
Predation x resource	**1,71**	**10.52**	**0.004**
Disturbance x resource	1,71	0.61	ns.
Predation x phase	**2,71**	**239.05**	**<0.001**
Resource x phase	**2,71**	**33.69**	**<0.001**
Disturbance x phase	**2,71**	**18.55**	**<0.001**
Total predator abundance			
Disturbance	**1,35**	**19.17**	**0.002**
Resource	1,35	3.21	ns.
Phase	**2,35**	**173.71**	**<0.001**
Disturbance x resource	1,35	1.67	ns.
Disturbance x phase	**2,35**	**48.21**	**<0.001**
Resource x phase	**2,35**	**31.49**	**<0.001**

Table 1. Fixed effects in linear mixed-effects models of prey and predator abundance response to predation and disturbance. Df is degrees of freedom, χ^2 and p values were derived from the parametric bootstrap. Significant effects are highlighted in bold.

Effects	**df**	**χ^2**	**P**
Predation	**1,71**	**17.66**	**0.002**
Disturbance	1,71	3.86	ns.
Resource	1,71	3.41	ns.
Phase	**2,71**	**49.23**	**<0.001**
Predation x disturbance	1,71	0.35	ns.
Predation x resource	**1,71**	**16.34**	**<0.001**
Disturbance x resource	1,71	1.65	ns.
Predation x phase	**2,71**	**14.98**	**0.004**
Disturbance x phase	2,71	0.89	ns.
Resource x phase	2,71	1.20	ns.

Table 2. Fixed effects in a linear mixed-effects model of prey diversity *(H)* response to predation and disturbance. Df is degrees of freedom, χ^2 and p values were derived from the parametric bootstrap. Significant effects are highlighted in bold.

abundance were assessed analogously by using disturbance type, resource deprivation and their interactions as fixed effects and individual microcosms as random effects.

Prey diversity was calculated with the Shannon-Weiner index (*H*)[42]. We calculated the magnitude of prey diversity change relative to the control (averaged over replicates) treatment as: $H_{relative} = H_{treatment}/\overline{H}_{control}$ and used linear mixed effect models as described above. The results of the mixed-model analyses are presented as analysis of variance (ANOVA) tables (Tables 1–3). Pairwise differences between each treatment (predation, disturbance and resource deprivation) and at each time point were assessed with t-tests using the Satterthwaite approximations for denominator degrees of freedom using the lsmeans[43] and multcompView packages[44]. Bonferroni-Holm corrections were used to take into account multiple comparisons. Model predictions were visualized with the sjPlot package[45]. Deviation coding approach was used, which compares the individual treatment means with the grand mean. We checked if inferences changed due to the averaging of the control replicates by pairing each of the treatment replicates with one of the randomly sampled control replicates and by subsequently calculating the respective relative abundance. The abundances of some species were so low that they resulted in relative abundances ($A_{relative}$) that were too low. Similarly, we had some samples where only the most dominant species was detected by the fingerprinting method; this may have been caused by the reduced detection limit due to the resolution power of the method and the sample size. Since such extreme values may influence the model fit we examined Cook's distances to assess the level of influence of extreme data points using the influence.ME package[46]. Influential extreme data points were removed. To assess how removal of extreme data points affected the inferences we also run analyses on the complete data set.

We tested the impact of main effects and their interactions on the community composition using the relative prey species abundances with a redundancy analysis (RDA) using the rda() function in the vegan package[47]. Since

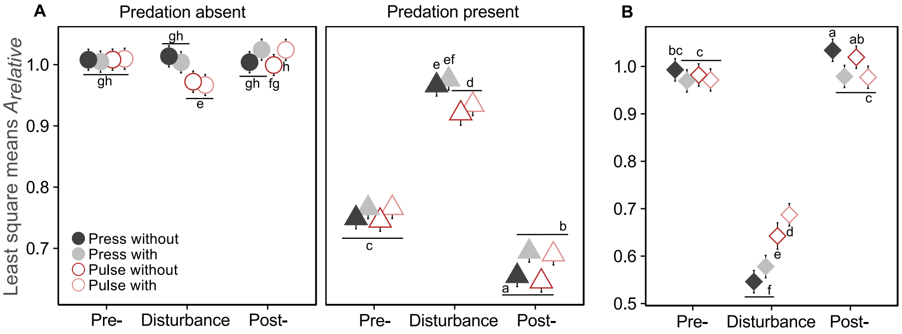

Figure 2. Magnitude of change in prey abundance relative to the control under the absence and presence of the predator and disturbance treatments (**A**), magnitude of change of predator abundance relative to the control under disturbance treatments (**B**). Colors code for the disturbance treatments; "press" and "pulse" are the disturbance types, "with" indicates that the disturbance is coupled with a resource deprivation and "without" is without resource deprivation. Points represent least square means for each treatment and the error bars are the confidence intervals. Bonferroni-Holm corrected multiple comparisons are shown as letters. Groups sharing the same letter are not statistically different.

the control communities did not differ significantly between the phases ($F_{2,9} = F = 0.849$, $p = 0.451$), we eliminated them from the analysis in order to test the effect of resource deprivation. We tested whether adding a given variable in presence of others would increase the amount of variation significantly by checking variance inflation factors (all variance inflation factors <10).

The data were assigned to subsets according to the three phases to assess how the communities were affected by the treatments between the different time frames. Accordingly, we compared the change in community structure from the pre-disturbance to the disturbance phase, from the disturbance to post-disturbance phase, and from the pre-disturbance to the post-disturbance phase. We performed PERMANOVA to test the significance of the change in community structure by using a full randomization test (9999 permutations) to calculate the F-statistics. Since sampling times are far enough apart compared to the generation times of the organisms, we assumed that temporal autocorrelation between repeated measurements is negligible. Our analysis further indicated the lack of time dependency in the data (Supplementary information G). Finally, we partitioned the percentage of variation explained by predation, disturbance treatments and their two-way interactions using RDA. We measured the variation in the levels of dispersion across treatments using the betadisper() function in the vegan package.

Data availability. The datasets generated and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Results

Effect of predation and abiotic disturbances on total species abundances.

We found significant effects of predation, disturbance type, resource deprivation and disturbance phase on the abundances of prey species (Table 1, Fig. 2A). Additionally, several interactions among the main effects were significant (Table 1).

Prey abundance was unaffected by resource deprivation when the predator was absent; however, in the presence of a predator prey abundance was higher under resource deprivation than with unchanged resources (Fig. 2A, Supplementary Fig. S1). In microcosms without a predator, prey abundance remained stable throughout all phases. In presence of a predator, on the other hand, prey abundance was lower in the pre-disturbance phase and increased during disturbance to an abundance similar to that observed without predation. In the post-disturbance phase, prey abundance dropped below pre-disturbance levels (Fig. 2A, Supplementary Fig. S1).

Predator abundance was affected by disturbance type, disturbance phase and several interactions between the main factors (Table 1). Predator abundances did not differ between press and pulse disturbance in the pre- and post-disturbance phases. However, during the disturbance phase the predator abundance was higher in pulse disturbance treatments than in the press disturbance ones (Fig. 2B, Supplementary Fig. S2). The impact of resource deprivation was only visible during the post-disturbance phase, that is, predator abundance was higher in the absence of resource deprivation.

Effect of predation and abiotic disturbances on prey diversity.

We found that predation and disturbance phase significantly affected prey diversity. We additionally found significant interaction between predation and resource deprivation treatment (Table 2). Thus, there was no difference in prey diversity when disturbance was coupled with resource deprivation in microcosms without a predator. However, in the presence of a predator resource deprivation had a negative effect on prey diversity (Fig. 3, Supplementary Fig. S3). The effect of predation on prey diversity changed over time: predation pressure reduced prey diversity in the pre-disturbance phase compared to the treatment without a predator. This effect was even more pronounced in the disturbance phase and diminished in the post-disturbance phase (Fig. 3, Supplementary Fig. S3). Nevertheless, prey diversity was

Effect	df	*Pre- vs. Disturbance*		*Disturbance vs. Post-*		*Pre- vs. Post-*	
		F	p	F	p	F	p
Predation	1,48	**72.506**	**<0.001**	**24.613**	**<0.001**	**24.613**	**<0.001**
Disturbance	1,48	1.875	ns.	0.038	ns.	0.038	ns.
Resource	1,48	**4.403**	**0.022**	*2.511*	*0.084*	*2.511*	*0.088*
Phase	1,48	**18.943**	**<0.001**	**3.272**	**0.043**	3.278	**0.042**
Predation × disturbance	1,48	1.079	ns.	0.051	ns.	0.051	ns.
Predation × resource	1,48	*2.895*	*0.071*	*5.009*	*0.006*	**5.009s**	**0.006**
Disturbance × resource	1,48	*2.647*	*0.087*	0.482	ns.	0.482	ns.
Predation × phase	1,48	**17.132**	**<0.001**	**9.262**	**<0.001**	**9.262**	**<0.001**
Disturbance × phase	1,48	2.098	ns.	0.038	ns.	0.038	ns.
Resource × phase	1,48	0.217	ns.	1.045	ns.	1.045	ns.

Table 3. Results of redundancy analysis. Df is degrees of freedom, F-statistics and p-values were derived from permutation tests. Significant effects are highlighted in bold and marginally significant effects ($p < 0.1$) in italics.

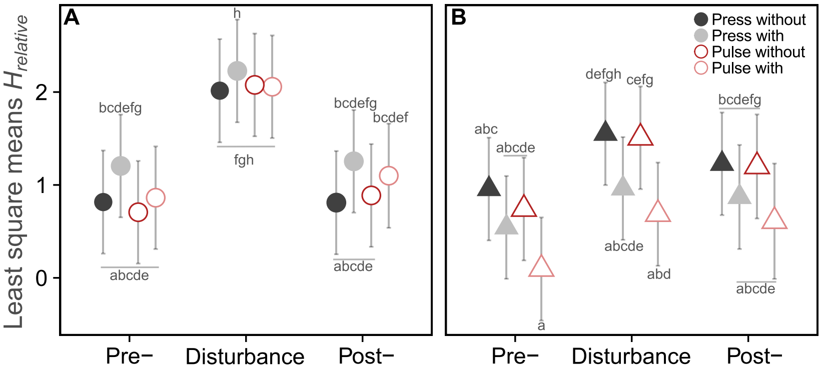

Figure 3. Magnitude of change in prey diversity *(H)* relative to the control under different disturbance treatments in the absence (**A**) or presence (**B**) of a predator. Colors code for the disturbance treatments, "press" and "pulse" are the disturbance types, "with" indicates that the disturbance is coupled with a resource deprivation and "without" is without resource deprivation. Points represent least square means for each treatment and the error bars are the 95% confidence intervals. Bonferroni-Holm corrected multiple comparisons are shown as letters. Groups sharing the same letter are not detectably different.

slightly higher during the post-disturbance phase than during the pre-disturbance phase, both in the absence and in the presence of predation.

Differences in the individual means of each treatment from the mean over all treatments for all the linear mixed effect models are shown in Supplementary Figs S4–6 The results were qualitatively the same when we randomly coupled a control replicate with the treatment replicate for calculating the relative abundances/prey diversity and used the full dataset in analyses (no removal of extreme data points), see Supplementary Table S2–4

Effect of predation and abiotic disturbances on overall prey community composition. Prey community composition differed significantly between the different phases. Additionally, predator presence significantly affected prey community composition, and differently so in different phases (Table 3, Fig. 4, Supplementary Figs S7–8).

There was greater variability in the composition of communities exposed to the predator than those not exposed to a predator, as indicated by the large data spread of the respective replicate microcosms during pre- and post-disturbance ($F_{1/24} = 8.657$, $p = 0.002$; post-disturbance $F_{1/24} = 11.262$, $p = 0.001$ respectively). Resource deprivation was only significant in the pre-disturbance/disturbance comparison, while interaction between predation and resource deprivation gained importance in the disturbance/post-disturbance comparison (Table 3). Other marginal effects are shown in Table 3. In each comparison, the highest variation in community composition was explained by the effect of predation (Supplementary Fig. S9).

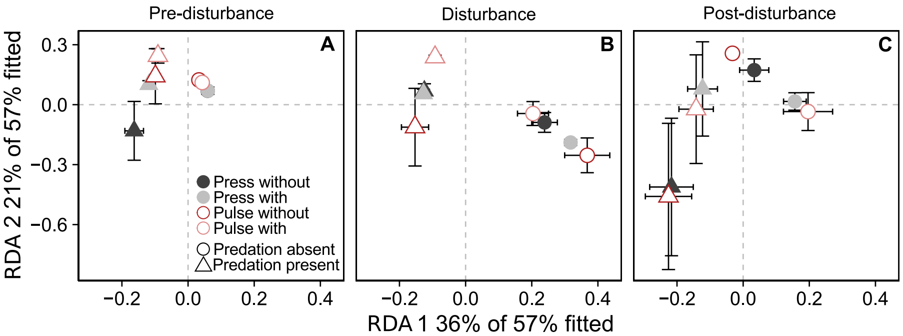

Figure 4. The first two axes of the RDA analysis. Circles represent the treatments without and triangles with predation. "Press" and "Pulse" are the disturbance types, "with" indicates that the disturbance is coupled with a resource deprivation and "without" is without resource deprivation. Error bars for vertical and horizontal axes display the ± standard error. Both axes are significant (RDA1: $F_{1,72} = 57.415$, $p = < 0.001$; RDA2: $F_{1,72} = 33.202$, $p = < 0.001$).

Discussion

Understanding combined effects of multiple disturbances on microbial communities is essential in the face of ongoing global change and multiple disturbances acting simultaneously. Here we showed that prey abundance, diversity and community composition were more strongly affected by predation than by disturbances (resource deprivation and dilution). At the same time, the type of disturbance (pulse vs. press) had a strong impact on the abundance of the predator. Our experimental system is simplified and the results are not meant to be extended to complex microbial communities. Due to the low number of species involved, our inferences cannot be extrapolated to real-world ecosystems. The results obtained from this study do, however, provide a good basis for further studies.

In our experimental system the top-down control affected the prey abundances and community composition much more strongly than the bottom-up effects (Figs 2 and 4, Tables 1 and 3). Indeed, as hypothesized, the delayed recovery of the predator in the disturbance phase and thus a reduced top-down control resulted in prey abundances similar to treatments without predation pressure (Fig. 2, Table 1, Supplementary Fig. S1). These findings are in line with other studies showing that systems experiencing continuous or discrete disturbances imposed on predators (e.g. by hunting or anthropogenic removal) often show prey release[32,48]. For instance, hydrological disturbances in wetlands resulted in smaller predator size, which in turn led to excessive growth of prey[32]. Furthermore, in a microcosm study predators were found to reduce prey abundance by almost 50%, although disturbances diminished this effect significantly[49].

Even though the effects of predation on prey abundances and community were the most pronounced, they were moderated by the bottom-up effects, underlining the importance of both abiotic and biotic factors for community dynamics[50]. Thus, the bottom-up effect in the form of a resource deprivation resulted in slightly higher prey abundance in the post-disturbance phase (Fig. 2A, Table 1, Supplementary Fig. S1). Such higher prey abundances under resource deprivation contradict the hypothesized positive effect of resource availability on the recovery of communities[27]. However, the observed effect is minor (compared to the effect of the predation) and may potentially be explained by the strong interspecific competition triggered by reduced resource availability. Such interspecific competition has indeed resulted in an increased relative abundance of the most competitive species *A. rhizogenes* (Supplementary information B and Table S1, Supplementary Fig. S7).

It is important to note that our results must be interpreted bearing in mind the caveats associated with our not fully factorial experimental design. For instance, different resource deprivation treatments were coupled with the two disturbance types, respectively. Although this design has limitations for understanding how resource deprivation and disturbance interact, the rationale behind it was to mimic plausible natural conditions, such as continuous resource removal due to periodic drought[51] or rapid removal of biomass after flood events[52].

Predator abundance decreased more strongly under press than under pulse disturbance. Each press disturbance event was applied every 12 h, which is closer to the generation time of the prey (ca. 2–4 generations per day) than the intervals between the two pulse disturbance events (5 d); press disturbance therefore has a higher potential to push populations to extinction or to an alternative state (e.g. equilibrium at lower population sizes)[53]. This effect, however, was only visible in the disturbance phase possibly indicating a high recovery potential of the predator independent of the disturbance type. Further, resource deprivation affected predator abundance positively during disturbance and negatively thereafter (Fig. 2B, Table 2, Supplementary Fig. S2). Such reduced predator abundance partly explains the higher prey abundance under those treatments. In short, mean prey and predator abundances tended to recover; still, in presence of a predator the abundance of prey was lower at the end of the experiment than in the pre-disturbance phase. This might be a transient behavior[54] due to the short duration of the experiment.

In our experiment both predator and prey species were affected by disturbances at the same rate, however, the low population size of the predator was enough to initiate a prey release. A reduced abundance of individuals at the top trophic level is highly relevant, since a prolonged recovery time caused by an increased disturbance duration and strength, and diminished availability of alternative resources[10] during which population size is low, poses an increased extinction risk[55]. Extinction of top predators may cause radical changes in ecosystems by altering community structure[8,33,56]. Specific prey groups may also increase in abundance and reduce the evenness of the community[57], and even cause invasions[58].

Note that *Tetrahymena* species are able to grow on dissolved carbon sources[59] and foraging on bacteria may be flexible due to specific predator traits such as absolute time or effort needed for grazing and relative intake rates[60]. We ignored the consumption rate of the prey resources by the predator, because our previously conducted experiments showed it to be negligible (unpublished data). However, we do not exclude the possibility that the ability of the predator to feed on prey resources could have resulted in competition for the resources, which might have affected the response of the predator[10].

Disturbance may affect diversity by enhancing coexistence and evenness in communities[61]. In our experiments, in contrast, prey diversity was lower in the presence of the predator. Interaction of predation with resource deprivation also correlated with a reduced diversity, which might result from the higher relative abundance of dominant species in the community (Fig. 3, Table 2, Supplementary Fig. S7). Both predation and resource deprivation acted as 'environmental filters' according to the niche principle (*sensu*[62]) by filtering out the species that cannot sustain a certain level of predation or resource limitation, thus resulting in the replacement of those species by the resistant and competitive ones; accordingly, the community structure became more simplified.

Previous studies found that ecosystem functions are usually affected by disturbances depending on their intensities and frequencies[53,63]. For instance, recovery potential after a pulse disturbance (e.g. flood) might be high, whereas recovery after a press disturbance (e.g. drought) may take considerable time[18]. Yet, the disturbance type had a small or no consistent influence on the prey communities in our study. We found that predation explained most of the variation in the community composition (Fig. 4, Table 3, Supplementary Fig. S9). It is possible that the difference between press and pulse disturbances in our experiments was not strong enough to cause a change in the community structure.

Our study demonstrates importance of following the prey community over time, because both prey abundance and community composition changed during and after disturbance[64]. Moreover, the effect of disturbance types and resource deprivation on the prey community was phase-dependent (Figs 2–4). However, our work can only offer a limited understanding of the temporal community dynamics because we sampled the community composition only once after the disturbance, at a time point that may have been too early to infer full recovery. Indeed, most of the literature suggests that microbial communities recover to their original state quickly[20]. However, at first sight, our communities may seem to be still in a transient state[65] due to the short duration of the experiments, that is, given more time, they might turn to the original state. Yet, under predation pressure communities have ultimately changed (i.e., we observed species replacement) and a return to a pre-disturbance composition did not seem possible within the time-frame of the experiment (Supplementary Fig. S7). Similarly to a previous study[49], in control communities (with predation, without disturbance) dominant species were replaced by a resistant one. This resulted in a clear distinction between communities with and without disturbances under predation (Supplementary Fig. S7–8), indicating a possible trade-off between competitive ability and resistance to predation[66,67]. Note that such community change may be a result of our experimental setup. In particular, we removed 90% of the populations during each transfer, thus, the risk of stochastic extinction might be elevated. Additionally, our experimental system was closed and did not allow immigration into the microcosms, which is known to maintain local biodiversity[68–70]. Several studies have also shown that rapid prey adaptation within generations is possible[71,72] and environmental fluctuations may intervene in adaptation processes[73].

To sum up, we found that the interplay between predation and disturbance determined the response of the bacterial community in terms of diversity and structure. We demonstrated that it is essential to consider multiple response measures from species abundances to community structure, because they differ in their sensitivity to disturbances, as reflected by different recovery dynamics. Future studies should include measurements of community composition at several time points (e.g. see ref.[24]) throughout the disturbance exposure to understand community stability properties and mechanisms underlying them. We found that even for such a relatively simple two-trophic level community the responses to multiple abiotic and biotic disturbances were complex and in several cases disturbances interacted in their effects on bacterial community. However, predation was the main driver of prey abundance and community composition, indicating that a significant portion of the variation in prey community response is due to the top-down control, which deserves further attention in future disturbance ecology research.

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Author Contributions

C.K. and A.C. designed research; C.K. conducted the lab experiments and analyzed the data, A.C. supervised the lab experiments; V.R. supervised the statistical analysis; C.K. and V.R. interpreted the results; C.K., V.R., H.H. and A.C. wrote the paper.

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5

Species Interactions and Evolutionary Dynamics Shaping Communities

5.1 Summary

Numerous studies have focused on the drivers of species diversity and stability of communities. Species interactions and emergent adaptive dynamics are found to interact and cause very dynamic context-dependent outcomes. One way to resolve this complexity is to investigate the single component dynamics and to deduce direct cause-and-effect relationships in controlled settings. Apart from that, there is increasing interest in model-free predictions of causal inferences in complex systems. Bridging these two separate concepts might be useful to gain insights into complex community dynamics. To this end, we assembled microcosms composed of competing bacterial species in the absence or presence of a protist predator, and performed time series observations. We hypothesized that the deterministic impact of a predator on prey communities might cause differential community dynamics and stability. More specifically, we analyzed individual time series of the species with multi-spatial convergent cross mapping to reveal causal networks between the predator, the edible prey, and prey potentially adapting to predation. We found that prey community dynamics varied more, and were less stable under predation stress, while prey

diversity increased significantly. Predation rapidly induced anti-predation traits, which altered population dynamics of both prey and predator. More importantly, predator and the resistant prey, in turn, boosted the number of direct cause-effect relationships between the community members. Our results stress the potential of implementing advanced methods to fully understand dynamic communities driven by species interactions and rapid adaptive trait changes.

5.2 Introduction

Understanding the mechanisms that influence community dynamics and stability is one of the most crucial challenges in ecology[123,124]. While the most appreciated mechanism is species diversity[125], species interactions and evolutionary dynamics have recently been identified as some of the crucial biotic components driving communities[62,126–130]. However, due to the complexity of species interactions, mechanisms of community dynamics remain highly context dependent. Systems with multiple resources and consumers, for instance, may have complex dynamic outcomes.

5.2.1 Predator-Prey Dynamics and Community Stability

There is a body of literature proving that predation pressure on competing species plays an important role in species dynamics (e.g.[131–133]). Although research is populated with such studies on competition, predation and the trade-off between them, most of the studies still rely on long-term, non-dynamic responses[134]. Ecological systems, however, are dynamic[114]; they adapt and shift with species interactions, which in turn affect the communities. Species may even adapt in relatively short periods, affecting their ecological dynamics, therefore, ignoring species interactions and evolutionary dynamics may further cause false interpretations of community dynamics[135]. More specifically, predator-prey dynamics are not only influenced by population dynamics, but also from the life history and morphological traits[136]. It is now highly recognized that these traits may change fast enough that they, in turn, affect the ecological dynamics[9,10]. Both phenotypic plasticity* and rapid contemporary evolution* affect the fitness of individuals and their populations[137–139] driving predator-prey dynamics[10,119] and community structures[140]. Importantly, these emergent effects of predators on prey cannot be predicted based on the pairwise interactions[141]. Productivity, stability and diversity of predator–prey communities may change due to the evolutionary interplay of the defense traits[12,117,119,142–144]. Studies show that the presence of weak trophic interactions and prey defense may stabilize community dynamics[145–147], on the other hand, predator resistant species may strongly destabilize communities by changing the amplitude and phase of predator-prey cycles[117,119,148], therefore increasing population variability and enhance extinctions[40,149], as well as frequency-dependent selection of prey phenotypes[119,142,150].

5.2.2 Causal inferences

The long-standing question that is puzzling ecologists is how to gain mechanistic understanding and predict the fate of communities in such dynamical systems. Classical approaches such as Lotka-Volterra models are restricted in their ability to predict community dynamics due to the complexity of species interactions (e.g. indirect interactions) and evolutionary dynamics. Further, inferring direct cause-effect relationships between species and their environments is ambitious, and may lead to incorrect assumptions when relying on classical statistical approaches based on correlations. Fortunately, inferring causal relationships in dynamical systems does not depend on the correlations. Recently, Sugihara et al. (2012) introduced **convergent cross mapping (CCM)** to determine statistical causality in dynamical systems[14]. In brief, CCM implies that causal dynamics can be reconstructed using an individual time series, which is conceptualized as the shadow

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*A single genotype produces different phenotypes in different environments.

*Genetic change which is rapid enough to visibly impact an ecological change.

manifolds (representing coherent trajectories) of the true causal system. If the shadow manifolds can be used to predict points from each other's time series, we can infer that these variables are causally related, as well as the direction of the causation (see Methods section). Detecting causality in natural systems have been increasingly appreciated and developed[13,151–153], and has a great potential to understand mechanisms shaping communities.

5.3 Aim of the study

We assumed that using controlled experiments with statistical advances might guide further studies to resolve context dependencies in community dynamics and stability, due to emergent species dynamics, since they might allow to infer direct cause-and-effect relationships between species, their traits, adaptive responses, and their dynamic consequences. To this end, we assembled laboratory microbial communities consisting of competing bacterial prey species under absence or presence of a protist predator species. We then performed time series measurements of the population dynamics of each species to ask how predation and competition contributed to community dynamics through phenotypic change and investigated *(i)* the difference between prey community dynamics with and without predator stress, *(ii)* consequences of predation on the induced prey adaptation, prey diversity and community stability and *(iii)* possibility to infer causal relationships between competing species, predator and potentially resistant species.

5.4 Methods

5.4.1 Organisms

Agrobacterium rhizogenes (**A**, α-Proteobacteria, white colonies), *Kocuria rhizophila* (**K**, Actinobacteria, yellow colonies), *Sphingobium sp.* (**S**, α-Proteobacteria, gold colonies) and *Williamsia sp.* (**W**, Actinobacteria, pink colonies) were used as prey. These prey species are common free-living microorganisms in aquatic and soil ecosystems and vary in their population growth and competitive abilities (competitive abilities are A>K>S>W; see[154]) covering the breadth of population growths representative of natural communities[107,154,155]. Their different colony colors allow a clear distinction and thus quantification on agar plates[107]. Prior to the experiments, they were grown in pure cultures in Brunner-CR2 medium[107] overnight at 25°C in a shaking incubator. Pre-cultures of the ciliate predator *Tetrahymena pyriformis* (with an average length and width of 20x50 μm) were maintained in proteose peptone yeast extract medium[156] at 25°C in an incubator without shaking. They were cultivated axenically (growth only on dissolved nutrients without bacteria) before the experiments to avoid transfer of unwanted bacteria to the experimental cultures. Prior to the experiment they were concentrated by centrifugation (10 minutes, 1000 x g) and washed with experimental medium. Controls without microorganisms, samples plated at each sampling point, and the known colony colors of each species were used to screen for possible contamination. Morphotypes of A (**Am**; small white colonies) and K (**Km**; yellow rough colonies) were also quantified on agar plates thanks to their distinct colony color and shapes. All strains are available on request from the public Culture Collection of the Department of Environmental Microbiology at the Helmholtz Centre for Environmental Research – UFZ (http://www.ufz.de/index.php?en=13354). A phylogenetic tree of the used species and the morphotypes based on 16S gene was provided in the Supplementary Figure S5.

5.4.2 Microcosm experiments and estimation of species abundances

Triplicate microcosms were started with the full even mixture of prey species either with or without predator. Static microcosms consisted of 20 mL of Brunner-CR2 medium in 50-mL cell culture flasks which were incubated at 25°C in the dark. Prey cultures were diluted in the experimental medium evenly; total prey number was adjusted to $1.8x10^7$ cells mL^{-1}, predator number was $4.2x10^4$ cells mL^{-1}. This computes to approximately 400 prey per predator[107,154]. We performed daily 10-fold dilutions by transferring 10% of the community into a fresh medium thus eliminating the complications caused by dead cell debris, low oxygen levels and influences of high culture density. This replacement is necessary to prevent population collapse[157]. Cultures were shaken well before each transfer. The microcosms were incubated for 34 days, corresponding to approximately 60-120 generations for the prey and the predator species[154]. The remaining culture after each transfer was used to estimate the species abundances during the experimental period from 3 days to 34 days after the start of the experiment. All bacterial species were quantified by plating on Brunner CR-2 medium. All visible, differently colored colonies were recorded after 2 days of incubation at 25°C using different dilutions from 10^3 to 10^8. Cell numbers of *Tetrahymena pyriformis* were estimated by counting cells fixed with 0.2% Lugol's iodine solution under an inverted microscope (Olympus CKX-41) with the help of a counting chamber (Sedgewick Rafter Cell, Pyser-SGI Limited, UK).

5.4.3 Statistical analysis

Time series of each species in each microcosm were shown as rank clocks using codyn package for R[158]. Prey diversity in each microcosm was calculated with the Shannon-Wiener index, H[159]. Three community stability measures (i.e. variance ratio, synchrony and stability) were also calculated using codyn package: Variance ratio was calculated as the community variance divided by the sum of individual population variances (Equations 5.1a, 5.1b; see[158,160]).

$$VR = \frac{Var(C)}{\sum_i^N Var(x_i)} \tag{5.1a}$$

$$Var(C) = \sum_{i=1}^{N} +2 \left(\sum_{i=1}^{N-1} \sum_{j=i+1}^{N} Cov(x_i, x_j) \right) \tag{5.1b}$$

where $Var(C)$ is the variance of community x_i and x_j are the individual population variances[158,160]. Values greater than one indicate the positive, while values smaller than one indicate the negative species covariance.

Synchrony was calculated as the variance of aggregated species abundances divided by the summed variance of individual species (0 is perfect asynchrony, 1 is perfect synchrony; equations 5.2a, 5.2b; see[158,161]).

$$Syncrony = \frac{\sigma(x_T)^2}{\left(\sum_i \sigma_{x_i}\right)^2} \tag{5.2a}$$

$$x_T(t) = \sum_{i=1}^{N} X_i(t) \tag{5.2b}$$

Lastly, stability stands for temporal mean divided by the temporal variation[158,162].

Casual links between the species were determined using CCM. The basic principle of CCM is as following: Consider time series of hypothetical variables X and Y. CCM relies on Takens' Theorem[111], which employs time-lagged coordinates of each of two variables (consider X and Y) to construct shadow manifolds (M_x and M_y) of their original source manifolds. This shadow manifold represents a coherent trajectory and is expected to preserve important components of the full causal system. If X causes the dynamics of Y, position of the time points in M_y and (M_x should be close.

Algorithmic and visual descriptions of this CCM are available in the supplement of[14].

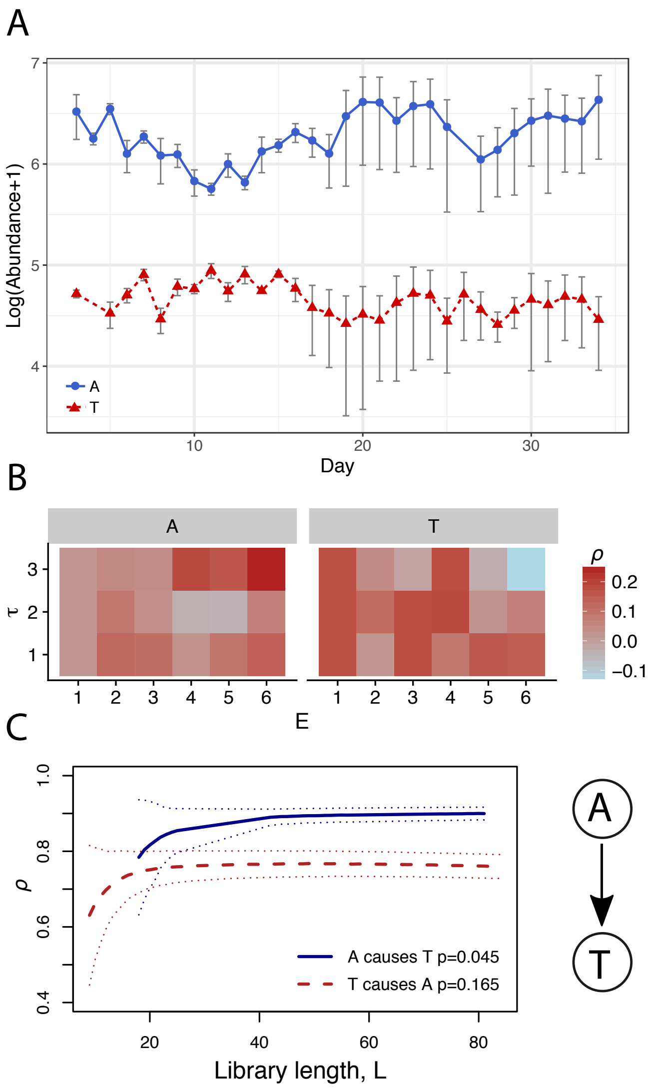


Figure 5.1. Determination of causal networks. **A:** An example for time series information of two species from the replicated microcosms. **B:** Best combination of E which is the number of time steps that are used for predictions, and τ which is the length of time steps used (time delay of the causal effect), to retain retained the maximum Pearson correlation coefficient, ρ which is the predictive forecasting power. **C:** Convergent cross mapping to obtain Pearson correlation coefficient which defines the causation (uni-/bidirectional) between two species, and significance test showing the significance of causal links.

Although CCM may perform well on short time series ($\sim$ 30 observations), especially when the causal interactions are week, long time series should be run to make up for potential observation errors[14]. Clark and his colleagues (2015) recently presented a multispatial CCM approach[13] and the respective R package multispatialCCM[163] to compensate for brevity in time series if there is a sufficient number of replications (Figure 5.1). Multi-spatial CCM is based on dewdrop regression[164], which combines information from time series from similar dynamical systems with bootstrapping[13]. This step is called simplex projection (which tests the ability of a process to predict its own dynamic) and has been applied to one variable at once previously[14]. Simplex projection depends on the number of time steps that are used for predictions (embedding dimension, **E**) which are estimated by leave-one-out cross-validation. The best E is retained to maximize the Pearson correlation coefficient, ρ which is the predictive forecasting power[151]. Another tuning parameter is τ which is the length of time steps used (time delay of the causal effect) and highly depended on the data (maximum 3 for this data set). We chose the best combination of E and τ at which ρ is maximum (see[165]; Supplementary Figure S3a-d). In order to prevent overfitting, maximum E was fixed to 6. We then checked the data for nonlinear signals that are not dominated by noise; we determined if the predictive ability declines with increasing time (see[13]; Supplementary Figure S4a-d). We did not remove the data whose dynamics might be stochastic, since those series resulted in no or very weak causal interactions. Using CCM_boot() and CCM_significance_test() functions, we monitored the bi-directional causal relationships and their significances between all of the possible combinations of species with or without predator (Supplementary Figure S4a-d). Count data is log(x+1) transformed previous to the analysis. One species (W) could not be quantified due to the rare abundance or competitive exclusion, and thus was removed from the analysis. All statistical analysis were performed in R, version 3.4.2[166].

5.5 Results

5.5.1 Community dynamics

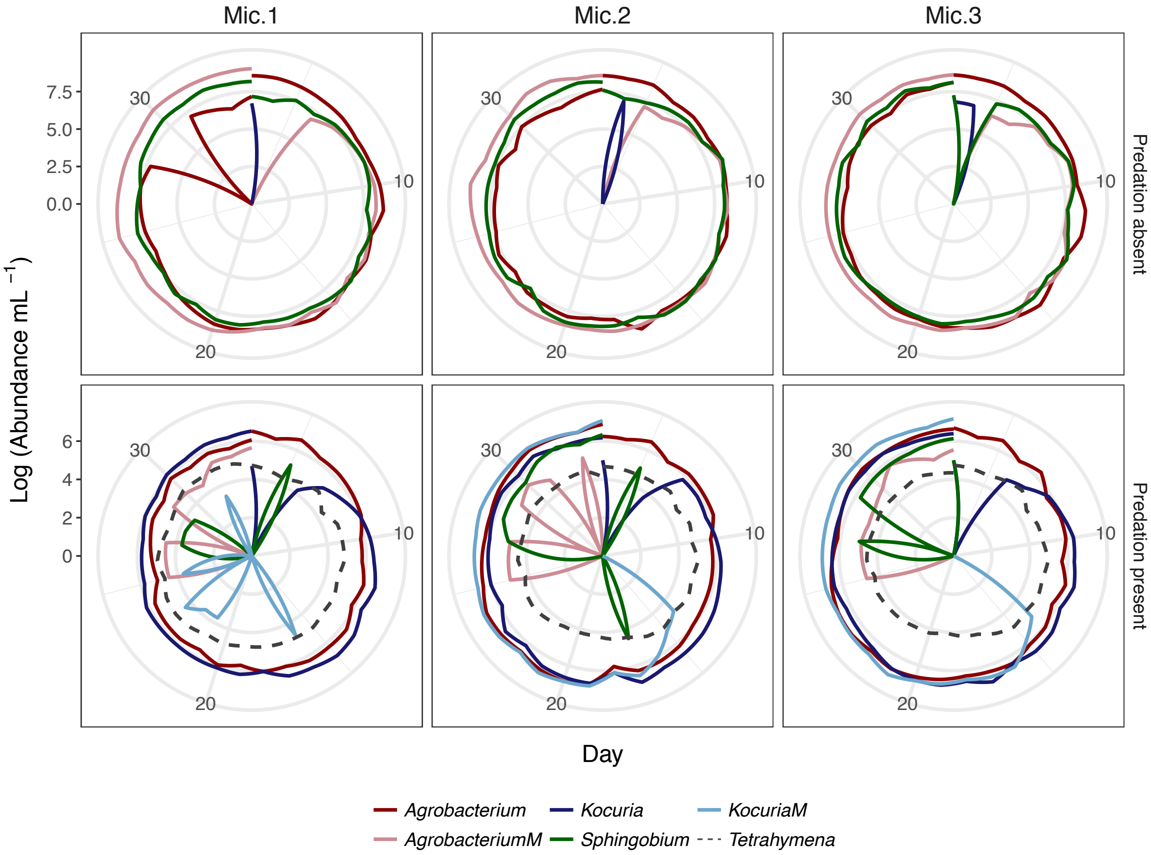


Figure 5.2. Rank clock plots of prey and predator abundances in the replicated microcosm with and without the ciliate predator. Shown are the three prey species (*Agrobacterium sp.*, *Kocuria sp.* and *Sphingobium sp.*) and the two new morphotypes appearing during the experiments (*Agrobacterium sp.*M, *Kocuria sp.*M). Vertical black bars indicate the starting "12 o'clock" position on the rank clock.

Predation affected the temporal dynamics of prey species (Figure 5.2) and significantly reduced the total prey abundance (approximately from 10^8 to 10^6 per mL, Supplementary Figure S1). In microcosms without the predator, a new *Agrobacterium sp.* morphotype (Am) which forms a biofilm on the liquid-air interface (Supplementary Figure S2a) appeared on day five. *Kocuria sp.* (K) was outcompeted, or reduced to under the detection limit (when it is not possible to estimate the abundance due to the overgrowth of the dominant species, approximately 10^5 c.f.u./mL). Species rank abundance was A>Sphingobium sp. (S)>Am until day 9. Between day 9 and day 19 species abundances were similar, however, changed thereafter to Am>S>A, and remained constant until the end of the experiments.

Communities with the predator, on the contrary, were more variable. K increased in abundance and stayed relatively stable, and was also dominant between day 10 and day 17. Further, a new *Kocuria sp.* morphotype (Km) which makes large cell clumps (potentially as an anti-predator strategy; Supplementary Figure S2b), dominated two of the microcosms after day 21 following its appearance on day 14. This came along with a reduced predator abundance and also the re-appearance of S and Am after day 25. We could not quantify *Williamsia sp.* (W) by plating on agar, however, DNA fingerprinting showed that on the first days after the start of the experiment W was present in microcosms with the ciliate predator (data not shown).

5.5.2 Dynamics of prey diversity and community stability

In the absence of predation, the prey community was most even between the days 9-19 until Am dominated the community (Figure 5.2). Decreased abundance of A and S caused a decrease in species diversity. In comparison, gradual changes were visible when the predator was present. The first peak in diversity was on day 5, when K reached the abundance level of A (Figure 5.3a). This diversity level slightly reduced with the domination of K until the Km increased. However, abundance dynamics of prey and the respective diversity varied between the replicate microcosms which included predators, i.e. Km became dominant only in two microcosms (Figure 5.2). After a period of maximum evenness from day 18 to day 22, diversity increased with the re-appearance of S and Am on day 25 (Figure 5.2 and 5.3a).

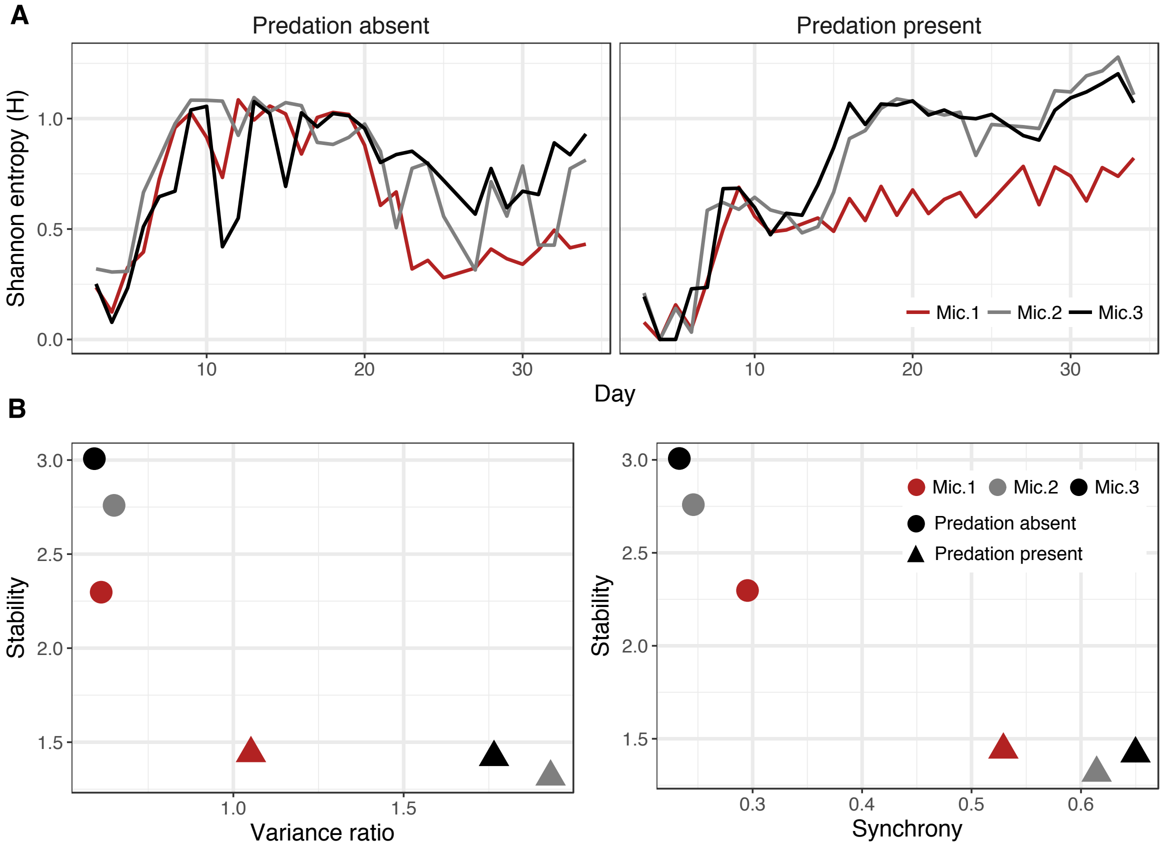


Figure 5.3. (A) Dynamics of prey diversity without (left panel) and with (right panel) predator calculated as Shannon-Wiener index. (B) Community stability in relation to the variance ratio (left panel) and the synchrony (right panel) of microcosms with (triangles) and without (circles) predator. Colors are coding the different microcosms.

Both variance ratio and synchrony were significantly different between microcosms with or without predator (Figure 5.3b). Microcosms without predator had the lowest variance ratio and synchrony (t = -3.569, df = 4, p = 0.023; t = -8.377, df = 4, p = 0.001), whereas the stability was higher (t = 6.125, df= 4, p = 0.004). Although the variance ratio was lower in the microcosm without the dominant (potentially predation resistant) morphotype, stability did not differ from the ones with the respective morphotype.

5.5.3 Causal links between the species dynamics

Predation, in the long term, not only allowed the establishment of a more diverse community (Figure 5.3a) but resulted also in a significantly higher number of causal links within the communities (Figure 5.4). We detected 10 significant and 5 marginally significant causal links when the predator was present (Figure 5.4, Supplementary Figure S4a-c). The potentially predation-resistant morphotype Km and A had the highest amount of causal links (from highest to lowest: A>Km>K/Am>T>S). Interestingly, the morphotypes Km and Am, even though they appeared later in the experiment (day 14 and day 25, respectively), drove the dynamics of the other three species. Moreover, the only species dynamics that forced by the predator was that of the potentially resistant morphotype Km. The only detectable causation in the microcosms were between A and S (S causes A). This might be caused by their relatively linear behavior time series when the predator was absent (Supplementary Figure 4d).

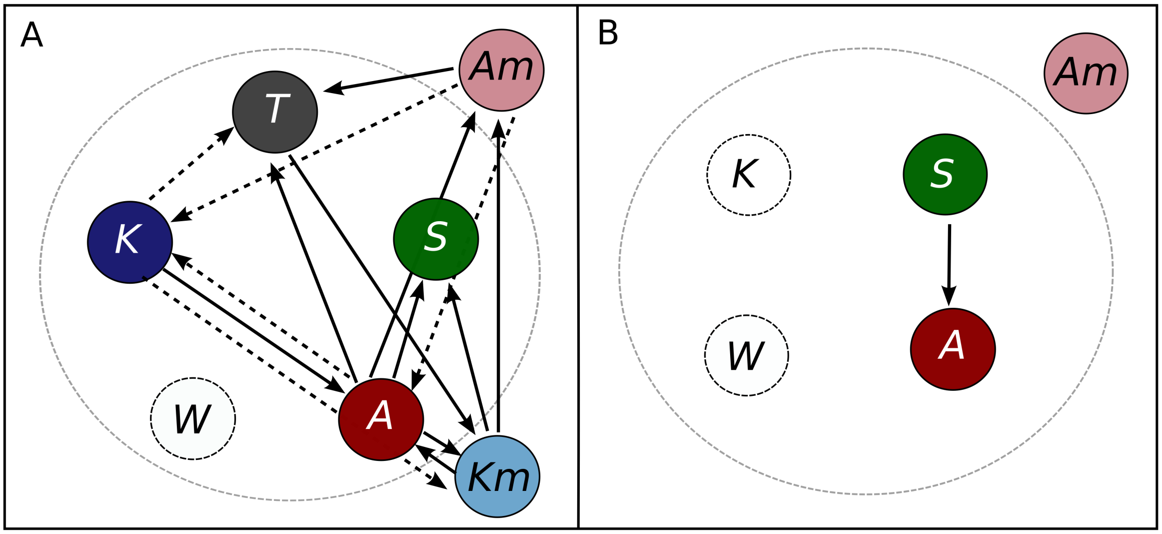


Figure 5.4. Causal links in microcosms with (A) and without (B) predator derived from multispatial CCM. Prey and predator species are shown as circles and their initials. ”m” indicates the new morphotypes of prey species appearing during the experiment. Solid lines ($p < 0.05$) and dashed lines ($p < 0.1$) show the significant causations. Arrowheads indicate the direction of the causation. Unfilled circles show the species extinct or below detection limit.

5.6 Discussion

Investigating communities in relation to the environmental settings is important to serve to the debate on the impact of species dynamics and community stability[158]. However, evolutionary dynamics are often neglected when interpreting community data. Hiltunnen et. al. (2014) showed that it is difficult to observe ecological outcomes in a consumer-resource system (i.e. virus-bacteria) longer than one or two oscillations, due to fast adaptive evolution[135]. It is now highly recognized that trait values may change fast enough, and in turn could affect the ecological dynamics[9,10] and drive communities[130,167]. Accordingly, communities may be stabilized or destabilized based on their eco-evolutionary dynamics[136,148,168].

Despite increasing experiments and subsequently the acknowledgment that species interactions and evolutionary dynamics affect community dynamics and temporal stability, there is still lack of mechanistic insight into the single components' dynamics of communities. In this work, we have brought novel concepts, which go beyond traditional experiments and analysis, together and tried to demonstrate how species interactions (i.e. competition and predation) and evolutionary dynamics drive communities. The outcomes of this simplified experimental system are not meant to be extended to complex microbial communities; this study does, however, conceptually provide a basis for further studies. We also suggested possibilities to reveal direct causations between the single community components.

In our experiments, the main differences between the two setups (i.e. communities with and without predator) were total prey abundance and differential species dynamics. Further, two different morphotypes came into play, which affected community dynamics. Morphotype Am which was able to form a biofilm at the air-liquid interface was common in the microcosms without a predator (Figure 5.2, Supplementary Figure 2a). Note that this kind of niche divergence is well known for static cultures[169]. However, we have not seen this morphotype in the microcosms with the predator except where its abundance was reduced below a certain level (Figure 5.2). High predator pressure, on the other hand, initiated predominance of a potentially resistant clumped morphotype (Figure 5.2, Supplementary Figure 2a). In the following, we explain possible reasons of these patterns.

Predation has usually a negative effect on per capita growth rate of prey species, thereby reducing competition between prey and supporting coexistence[93]. Similarly, in our experiment, total prey abundance was approximately 100 times lower when the predator was present (Supplementary Figure 1). However, we did not see higher coexistence and prey diversity at the beginning of the experiments (Figure 5.2). Instead, one species (K) became more advantageous in the presence of the predator and competitively excluded when the predator was absent, the opposite was true for another species (S). Indeed, higher diversity and coexistence was initiated by the appearance of a potentially predation resistant prey (Km). CCM results have also shown that the number of causal links might be increased by the appearance of emerging morphotypes. Predation is often associated with the evolution of prey defense mechanisms[141,142,170]. Larger cell sizes[150] or colony formation[40,119,171,172], for instance, may offer refuge from the predator. However, phenotypic change depends on several factors such as the cost of the phenotype, interactions with the other species' phenotypes and the population density[127]. Our work supports the general idea that clump formation occurs only in presence of a predator and that it may be a disadvantage in the absence of a predator since it comes along with a reduction of the competitive ability[117,147]. Nevertheless, it was shown that prey might suffer from immediate fitness costs of anti-predation strategy, such behavior may be beneficial in time under ongoing predation stress[173,174]. In contrast, the biofilm forming morphotype Am dominated only in microcosms without predator. The circulation of the medium induced by the ciliate movement as well as the potential trade-off between the cost of biofilm formation and keeping the population size stable under may explain this pattern[175,176].

Note that it has been shown that adaptation may appear in a cyclical way that the prey genotypes vary between defended and undefended[10]. This may then lead to cyclical changes in population dynamics within a few generations[62,117,119]. Such cycles are not visible in our time series data, however, CCM results showed a bidirectional causation between the CCM of *"undefended"* A and *"defended"* Km. Prey defense can cause a negative feedback in a predator by decreasing the consumption of prey; cost incurred for defense on the other hand causes a decrease in prey fitness[177,178]. It was also shown that fast adaptation in response to selection promoted temporal species coexistence[179]. Eventually, this repetitive cycle may contribute to the system's stability (as reviewed in[180]). In our experiment, we found a causal interplay between K, its resistant morphotype Km, and predator T (e.g. K causes T, T causes Km). This causal interplay is not sufficient to infer a cyclic population behavior, however, it still suggests that the longer time series and high number of species might reveal these kinds of cyclic behavior.

Nevertheless, our work supports that the community was significantly driven by the predator through the dominance of the predation-resistant prey[40,181]. Changes in the dominance patterns (K>A) and appearance of the resistant morphotype (Km) initiated the rare species increase in abundance. This might have two reasons: *i)* reduced predator abundance, *ii)* refugee provided by the superior competitors. Fridley et. al (2007) suggested, for instance, that refuges for competitively inferior species were provided by dominant species, preventing their competitive exclusion[182]. Therefore, one of the reasons which increases the higher prey coexistence under predation is that a high predator pressure on the most dominant species might increase the survival rates of the rare ones[107,183]. Interestingly, CCM also proved that the dynamics of rare Am and S was driven by the resistant Km.

It is often acknowledged that the genetic character displacement due to intraspecific competition may contribute to the community stability[184]. Stabilizing mechanisms are known as mechanisms that favor rare species and tend to prevent extinctions, however, this is only possible when fitness differences are not too great[180]. There is often a trade-off between stress tolerance and competitive ability of species. We have seen a strong negative covariance of prey species when the predator was absent. This is because an increase in abundance of morphotype Am went along with the decrease of the other species abundances. Since total abundance did not change drastically, greater negative covariance/higher asynchrony was associated with increased stability. On the contrary, prey species incubated with the predator showed positive covariance, especially when a resistant morphotype was abundant, while total abundance and diversity significantly differed reducing temporal stability. In microcosms with a higher predator and a lower resistant morphotype abundance, the species were close to behaving independently (variance ratio is close to 1, Figure 5.3B), however, temporal stability of these microcosms were not different than in the latter ones. These results also show the context dependencies of stability measures caused by species interactions and evolutionary dynamics. To mention, stability might fluctuate through time, although it is often assumed as being constant[134]. Intrinsic variability (for instance, due to trait distribution of species[185], and change in trait frequencies[167] of non-linear systems causes erroneous interpretation of stability calculated as for instance, as coefficient of variation of species abundances[145]).

There are several caveats of this study which need to be considered when interpreting the results. *Tetrahymena sp.* is able to grow on dissolved carbon sources[186]. We ignored the consumption of prey resources by the predator, however, the caveats associated with this ability, might have affected the response of the predator. The observed community dynamics may be partly a result of our experimental setup. In particular, we removed 90% of the populations during each transfer, thereby reducing the strong predation and competition effects and elevating the risk of stochastic extinctions. Additionally, the spatially isolated microcosms do not allow immigration, which is one of the most important factors driving communities[187–190]. The high dilution rate of the system has probably also contributed to a reduction of the competition effect and the predation pressure. This might have challenged the prediction ability of CCM. Some of the time series (for instance preys when there is no predator present) indicated the possible stochastic behavior (e.g. Pearson correlation coefficient did not reduce with the prediction step), therefore, causal inference was not existing or not detectable. The multi-spatial CMM approach was also not adequate for detecting causalities in time series which were short, as those for the emerging morphotypes. This problem might be resolved either by increasing the number of replicates or the length of the measurements[13]. Another problem is the strong synchrony, especially caused by delayed predator-prey interactions, which might prevent the detection of bidirectional causation. Future work might consider the extended application of a recently developed CCM that considers time-delayed interactions[153]. What we neglected in our study is that the predators may also evolve as a response to prey defense depending on the growth rates of the predator on different prey types, leading cycles of predator-prey coevolution[10]. CMM revealed that the predator's dynamics is driven by prey species, indicating possible coevolution is possible when more data are available.

Trophic networks consisting of multiple preys and predators are systems whose dynamic consequences are difficult to predict. In addition to that, intraspecific variation in prey communities in their resistance to their predators and competitive abilities may cause unpredictable dynamic consequences[10,117–119,191]. They especially become difficult to analyze with correlation-based methods or with Lotka-Volterra type models. For instance, complex dynamics with many nonlinearly interacting variables (e.g. marine systems) are sensitive to parameterization and can hardly be expected to be predictive[192]. Therefore, empirical dynamic modelling approaches will have an important role in future ecological research. It is especially useful when results from experiments are not easily interpretable regarding the species response under varying environments[13].

5.7 Synopsis

Understanding the dynamic consequences of complex communities remains a challenge in ecology, which is an exciting avenue to explore. The basis for understanding the key components of ecosystems and the consequences of rapid environmental change, is only possible with the appreciation of the temporal variability of the food webs[193]. It is also clear that univariate measures of diversity and stability might not completely give insight into the complex interactions within a community. The majority of literature reflects that the impacts of predation and defense mechanisms affect species diversity and community stability. However, outcomes are also found to be highly context dependent and difficult to generalize. For instance, outcomes might be dependent on the degree of prey phenotypic variation and the strength of trade-offs among phenotypes in anti-predator strategies and competitive ability[10,117,150]. A majority of experiments, including ours, have used simplified model systems with a minimal number of interacting species. How outcomes translate to natural communities still remains largely unresolved, however, such studies are still the key for an ultimate realization of community dynamics. Last but important, we stress out the necessity of inferring direct cause-and-effect relationships between community components. Combined with multi-species microcosms experiments and observation driven high-dimensional models (e.g.[33]), application of CCM to investigate causal links between biotic and abiotic components (e.g.[194]) which might improve the predictions of community dynamics and stability, especially under changing environments.

6

General Discussion

Current ecological research is challenged by the impacts of global environmental change. As a result, there is a rapid growth in literature that focuses on the effects of global change drivers on multispecies systems. Concerns have been raised, which question the context dependencies of the outcomes and thus the reliable predictions of future communities. Therefore, the next decade is likely to witness a considerable rise in studies concentrating on the search for mechanistic explanations regarding community dynamics in emerging ecosystems.

To date, few studies have addressed the problem of multi-dimensionality in communities and their environments caused by complex interactions of community members and abiotic factors[195]. In other words, there is still a considerable amount of controversy surrounding temporal dynamics of species and their interactions. What is even more, despite the increasing interest and the availability of advanced methods, inferring direct cause-effect relationships between community members, as well as the dynamics of biotic (e.g. adaptation, extinction) or abiotic (e.g. disturbances, resource dynamics) conditions has not been established in community ecology[109]. Ideally, empirically and computationally less demanding and mechanistic studies are needed to understand behaviors of communities.

The present thesis has dealt with the question how to solve the problem of complexity in community ecology research. It has focused on the internal dynamics of multispecies assemblages which are driven by species interactions, more specifically by predator-prey interactions, as well as on adaptive strategies of prey species. It has especially searched for ways to explain species diversity and stability of communities in a more mechanistic manner by using controlled microbial microcosms, modelling approaches and advanced statistical methods. Moreover, this thesis has also focused on ecological disturbances, in the form of density independent community mortality, and their impact on the community dynamics. Last, yet important, it has addressed resource dynamics, in the form of deprivation, and its interplay with disturbances as well as species interactions.

As a result, this thesis has contributed to the understanding of predator-prey dynamics and their consequences for community dynamics and stability. In particular, the results have added to the understanding of effects of ecological disturbances and resource dynamics on species interactions. Furthermore, it has provided an example for going beyond correlation-based statistics and inferring direct cause-effect relationships between the community components and further with their environments.

Given that our findings are based on simplified systems consisting of a limited number of species, the results should consequently be treated with considerable caution (Box 6.1). The outcomes of this thesis cannot be directly extrapolated to the communities in nature; nevertheless, they provide a sound base to understand the internal and external mechanisms affecting community dynamics both for microbial systems and communities of higher organisms. Above all, this work represents an initial step toward further studies to understand community dynamics inferring cause and effect relationships more directly. Thus, besides providing a conclusion of the outcomes, this chapter will also point to the possible empirical and theoretical approaches for improving our predictions concerning the fate of communities under emerging ecosystems.

Box 6.1: Simplicity vs. complexity. Traditional vs. high throughput

- The first criticism would be the number of species and factors: *Why choosing 2-5 species, but not hundreds of them?* The critical aim of this study was to pioneer and/or answer some of the major questions in community ecology research caused by the context dependencies, while approaching it in a mechanistic time/cost efficient way. This is, to some extent, the aim of every study using model systems. As it is evident from its name, model systems do not aim to mimic nature, but rather model, notably not different than in mathematical models. We are aware of the limitations of the system we used, however, we see the outcomes of our study as the predecessor for future studies on elevated scales.

- One can also question why traditional culture-based methods were applied, although they are increasingly replaced by high-throughput methods. Without a doubt, these methods are valuable in that they reveal real diversity and community composition; for instance, in natural habitats. Still, revealing mechanisms of community dynamics under changing environments more directly needs controlled settings. High-throughput methods should, therefore, be considered as complementary in order to explain species interactions in their natural environments.

6.1 Communities under disturbances: Predator–prey dynamics

Disturbance is one of the key drivers of the dynamics and diversity of communities[196–198] and is defined as a discrete event in time, killing or damaging individuals[199]. Disturbance is a matter of scale and context; it occurs with different frequencies, magnitudes, extents and periodicities[24,27]. There are two disturbance types we distinguished according to their durations, and the generation times of the species exposed: *pulse (discrete/short-term)* and *press disturbances (continuous/long term)*[24]. On logical grounds, different temporal patterns (sequences, frequencies and strengths) of disturbances are important for understanding the structural and functional community responses[25]. Press disturbances, for instance, can cause increasing variability in the relative abundances of species, whereas pulse disturbances can cause dramatic structural and functional shifts[200]. Note that mortality was used to simulate disturbances in this work. That is often criticized as not representing the natural disturbances. The rationale behind this preference was stated in the Box 6.2.

Predation, likewise, is one of the most important interaction types driving communities[201]. Predators not only impact the survival of prey species, but also affect intra-/interspecific competition between prey species and their anti-predation strategies over ecological and evolutionary timescales. To that end, we especially addressed how disturbances and other environmental settings (i.e. resource deprivation) intervene in these dynamics (Figure 6.1)

Considering multiple prey species that possess different life history traits and competitive abilities, we found that the response of the bacterial community in terms of abundance, diversity and community structure, is determined by the interplay between predation and disturbances **(Chapter 4)**. This thesis, therefore, provides an additional support for the importance of top-down control as indicated by the significant portion of the variation in prey community response. Another key aspect to remember is that ultimate replacements between predation sensitive and resistant prey species, indicated a possible trade-off between competitive ability and resistance to predation[3,16] **(Chapter 4)**.

Broadly speaking, these results highlight the *"prey release"* mechanisms **(Chapters 3 and 4)**, which is in line with the responses of predator-prey systems experiencing continuous or discrete anthropogenic disturbances in nature[5,202]. Above all it suggests that top-down control deserves further attention also in disturbance ecology research.

Box 6.2: Rationale behind disturbances simulated as removing part of the communities.

In the first place, it is crucial to mention the underlying reason for using mortality to simulate disturbances in this work. One can argue that killing or removing parts of communities does not represent natural disturbances. This is a strong argument considering disturbances such as extreme weather events or chemical load, which directly affect physiology of the organisms. The reason for using mortality as an approximation of disturbance events is drawn from the definition of the disturbances used in this thesis. In ecological literature, disturbance, perturbation, and stress are often used as synonyms mistakenly. **Perturbation** can be described as *"departure from a normal state"* according to Picket and White (1985). Although it is a broad definition, it is useful to differentiate this term from stress and disturbance. For this thesis we adapted the views of Wotoon (1998) on disturbance and stress[203]. According to this view, the main difference between **stress** and **disturbance** is the limit of their effect on the species. In other words, while a disturbance event can cause severe mortality, stress may change the performance of the species without causing a drastic change in the mortality of species. These are broad definitions which we considered useful as a solid base for the disturbances we applied. We used *dilution of populations in fresh media* to test mortality, which is a method commonly used in testing such disturbance effects in microcosms[80,204–206]. Note that, in natural systems, mortality might leave cell debris and in turn dissolved nutrients behind, which in our system, is not the case.

Another point this thesis puts forward is the distinct community dynamics caused by the disturbance frequency and strength **(Chapters 3 and 4)**. Population abundances were in general sensitive to the type of disturbances applied supporting previous findings (e.g.[1,207]). This is partly due to the generation times of the species. That is, in order to recover populations need a certain distance between the disturbance events. Another critical point is the population size of the community members, especially that of the top predator and the rare species, which have a risk of going extinct. The extinction of top predators is highly relevant in nature, as it may subsequently cause drastic changes in the prey community structure or even result into higher invasion probability[208], altering whole ecosystems functions[209–211]. Although top-down control was central in our experiments, bottom-up control in a form of resource deprivation resulted, for instance, in elevated prey abundances. At first sight, this contradicts with the general view that the resource availability may increase the recovery ability (e.g.[30]), however, in our case inter- and interspecific competition between the prey species caused such an increase **(Chapter 4)**.

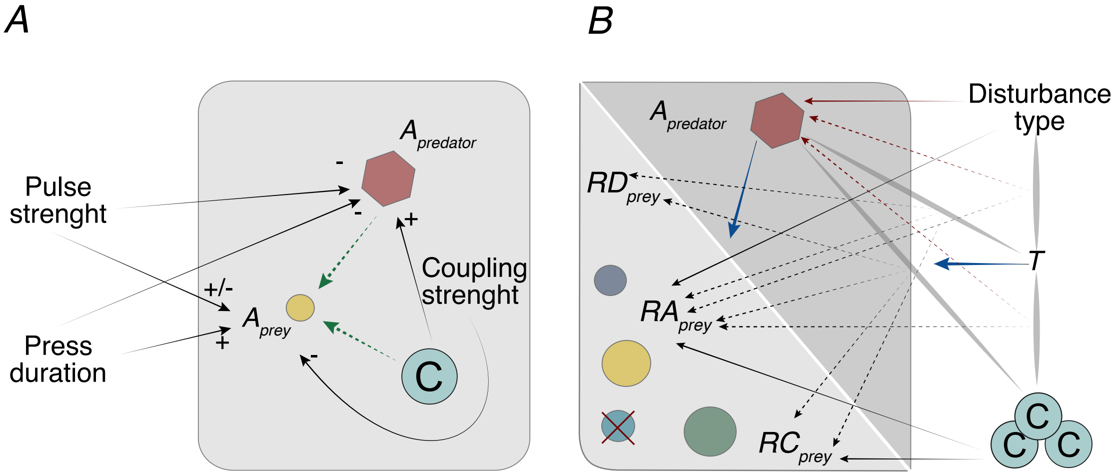


Figure 6.1. A graphical summary of the outcomes of this thesis. **I)** Impact of disturbance strengths and durations, as well as the coupling of predator to an alternative resource on the recovery of communities. Green dashed lines are the direct consumptive impacts, solid lines are the mechanisms which were revealed in this study. Disturbance strength and duration had a negative impact on the predator abundance. Although prey profited from the disturbances, stronger pulses caused critically reduced abundances. Predator coupling increases the community stability by supporting its recovery. **II)** Significant interactive effects of predation and abiotic changes -different types of disturbances and coupled resource dynamics (C)- on the prey community attributes (i.e abundance, RA_{prey}; diversity, RC_{prey}; and community composition, RC_{prey} relative to the communities without predation). Blue solid lines stand for the predator impact on all prey community attributes and the impact of disturbance phase (T) on the whole system. Impacts of factors on the predator abundance are shown as red, on the prey communities as black. Solid lines are the direct impacts of factors, grey shaded lines are the interactions between the factors and dashed lines are the impacts of interactions on the community attributes.

Transient dynamics of the species strongly depended on the strength and duration of the disturbances, and the trophic position of species **(Chapter 3)**. These disturbances usually caused divergent population growth (i.e. increased prey and decreased predator) by effectively uncoupling prey and predator species, as reflected by the reduced covariance. Prey release, as expected, depended on predator recovery which was slowed down with increasing duration and strength of the disturbances. However, the impact of disturbances depended on the other biotic and abiotic settings. Alternative resource coupling for instance, stabilized the community dynamics preventing the possible extinction[212].

Our findings indicated that it is essential to consider multiple response measures since they have different sensitivities to disturbances as reflected by the distinct recovery dynamics of species abundances or community structure[6]. Moreover, community measures were in general, different, at each time point sampled (i.e. pre-, during, and post-disturbance periods); therefore, understanding recovery dynamics fully requires also time series measurements. End-point measurements are not informative enough to fully comprehend stability properties of communities within the disturbances[7,85]. In addition, findings supported that more attention should be paid on the transient states of communities as they may provide relevant information regarding the assembly history and the potential community structure at a future time point[32,40].

6.2 Temporal species dynamics and community assembly

In **Chapter 5**, we turned back to the roots of internal dynamics of the communities and questioned how temporal dynamics of species impact coexistence, diversity, and stability (Figure 6.2). As we have mentioned before, systems with multiple resources and consumers have complex dynamic outcomes. This is due to the interplay between predation and competition, as well as adaptive mechanisms, which occur within ecologically relevant time periods[9,10]. Changes in species traits affect the fitness of individuals, populations, and accordingly, the community structures[137–140]. These complex interactions and dynamic outcomes, at the end, are difficult to resolve and predict, using for instance Lotka-Volterra type models or correlation-based statistical methods. To tackle this problem, we obtained time series information for each of the species in the prey communities, with or without a predator under controlled settings. We then tested for causal links between each pair of species (using the convergent cross mapping approach; see[13,14] and **Chapter 5** for more information) to understand direct cause-effect relationships between competing species, predation and phenotypic change.

One particularly striking aspect of the time series analyses was that two emerging distinct phenotypes altered the community dynamics in different ways. One phenotype was able to form biofilms on the air/liquid interface of the static cultures without predation, indicating niche divergence to reduce competition (similar to[169]). This divergence was rare when the predator was present, suggesting a certain cost which caused a disadvantage for the populations to keep the population size stable. In contrast, high predation pressure initiated the predominance of a resistant morphotype (similar to[119,171], which would probably reduce the competitive ability of a prey when the predator is absent[117,147]. Predation in general reduces prey growth per capita and prey competition, thus elevating coexistence[213]. Slightly different than that, we found a gradual increase in prey diversity which was also due to the emerging morphotypes. Moreover, causality tests highlighted the increased number of causal links when a predator was present. This is apparently not only due to the predator but also to the emerging morphotypes, which established new interactions with other species in the community. Interestingly, we also found bidirectional causations between the species (that is to say, species drive the population dynamics of each other). The bidirectional causations between resistant and sensitive prey indicate a possible balance between fitness differences and equalizing mechanisms, which is believed to be cyclic in time[10,179].

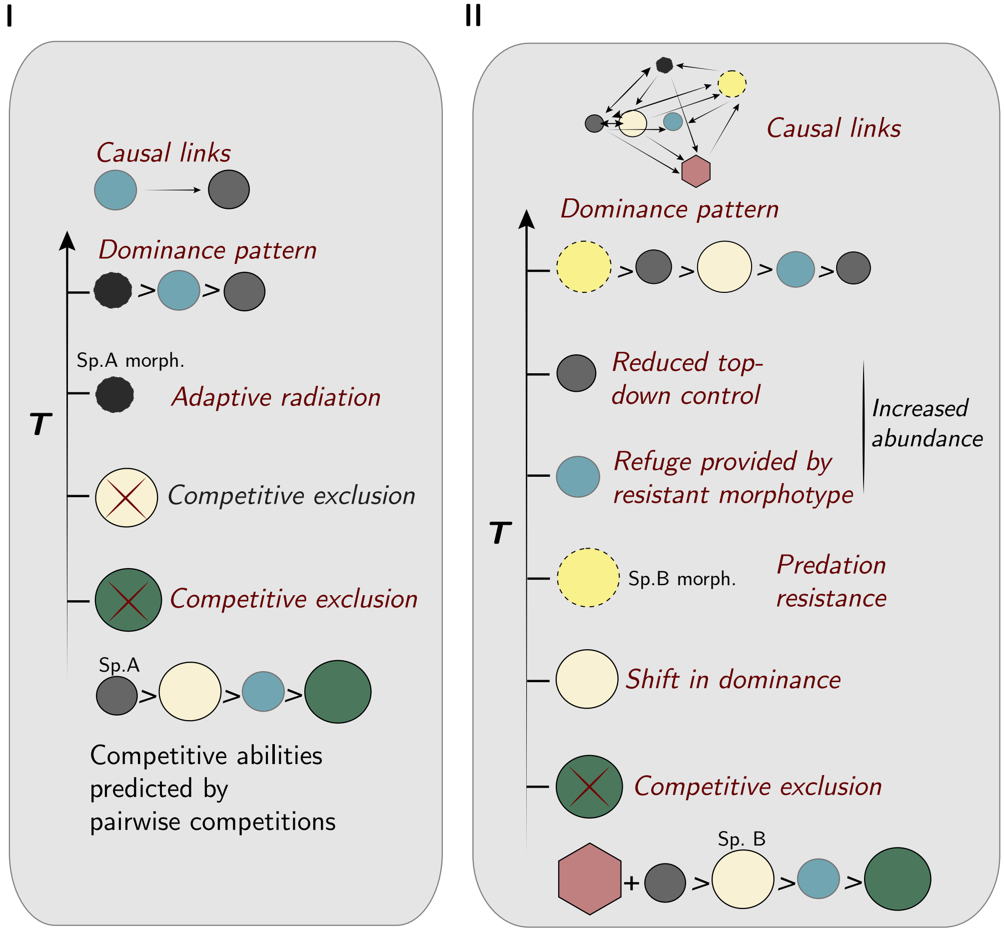


Figure 6.2. Simplified illustration of the temporal dynamics of communities, which were deduced in this work. Assembled species with a known hierarchy at the beginning of the experiments are shown at the bottom. Time line *(T)* shows the important dynamic shifts in the communities and the suggested mechanisms. Hierarchy (i.e. dominance pattern) at the end of the experiments are shown at the top of the figure. Causal relationships and their directions are also illustrated as arrows according to the causal analysis. I) Prey communities in the absence of predator species. species A morph. is the morphotype of species A, which formed biofilm at the liquid-gas phase. II) Prey communities in the presence of the predator species. species B morph. is the morphotype of species B, which forms large clumps as a response to predation presence. Predation provides high temporal variation and reduced stability, at the same time, it provides elevated species diversity and increased causations between species.

Previous studies showed that predators might increase the diversity of prey species: for instance, by controlling the dominant species abundance, it allows for rare species to grow (e.g.[107]). On the other hand, our work showed that the superior competitor and resistant prey drive the community dynamics, contributing to the coexistence and diversity in the microcosms with predator. First, high predation stress on the superior competitor led the appearance of resistant phenotype. Second, invasion of this phenotype reduced the predator abundance in time, increasing the survival rate of the rare species increased due to and providing refugee due to the large cell clumps.

Regarding temporal stability, we have seen a strong negative covariance (i.e. abundance of one species increases while other one decreases) of prey species when the predator was absent. Since the total abundance did not change drastically, greater negative covariance/higher asynchrony was associated with increased stability. On the contrary, prey species showed positive covariance (opposite to negative covariance), especially when a resistant morphotype was abundant. Total abundance and diversity significantly differed, therefore reducing temporal stability. At first sight, it seems predation destabilizes the communities. However, this is due to the definition of stability, namely temporal mean divided by the temporal standard deviation[162]. Moreover, communities might be experiencing a transient state, and when more time is given, they may stabilize, or cyclic behavior of species (e.g. equalizing and stabilizing events) may become more visible. Several caveats of our study are summarized in Box 6.3.

Box 6.3: Notes on caveats of our systems

- ✎ The regular transfer of our populations into fresh medium was chosen to prevent population collapse and density dependent mechanisms. However, by doing so we potentially increased the risk of **stochastic extinctions** due to the removal of **90%** of the population during each transfer. Our closed systems did not allow **immigration**, which is believed to be is one of the most important mechanisms for maintaining diversity, immigration may have thus resulted in changed community structures. Accordingly, this restriction might have led to potentially wrong assumptions of the local diversity[72,103,214].

- ✎ Another possible source of error, which is to some extent the problem of many ecological studies, is the duration of experiments, and the possibility that they have been in a **transient state** through the end of the experiments. We tried to compensate this possibility by time series measurements, however, due care must be paid when interpreting the results due to extremely non-linear and dynamic nature of the communities.

- ✎ A minor source of uncertainty might be predator behavior and adaptation that we, to some extent, neglected. It is, for instance, known that *Tetrahymena sp.* is able to grow on dissolved carbon sources[186]. We ignored the consumption of prey resources by predator (except in **Chapter 3** which describes this behavior as a model parameter), however, we should bear in mind, that the caveats associated with this ability, might have affected the response of prey and predator. Nevertheless, competition between predator and prey for the prey resources can be neglected in our set-up due to the daily refreshment of the resources.

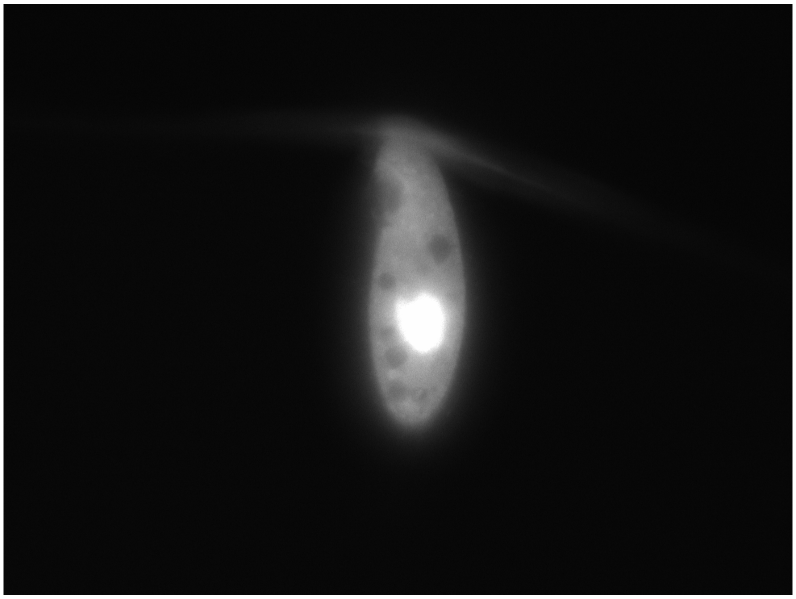
- ✎ Another downside is that we also ignored a potential adaptation of the predators to prey defense. Depending on the growth rates of predators on different prey types this may lead to cycles of predator-prey **coevolution**[10,135]. It has been shown that predator coevolution feeds back on population sizes and alters the direction of eco-evolutionary dynamics[135]. Nevertheless, our observations on the prey adaptation is only the first step, and has to be analyzed explicitly, for instance, on the genomic level.

7

Synthesis and Outlook

"The alchemists in their search for gold discovered many other things of greater value."

—–H. D. Thoreau: Walden



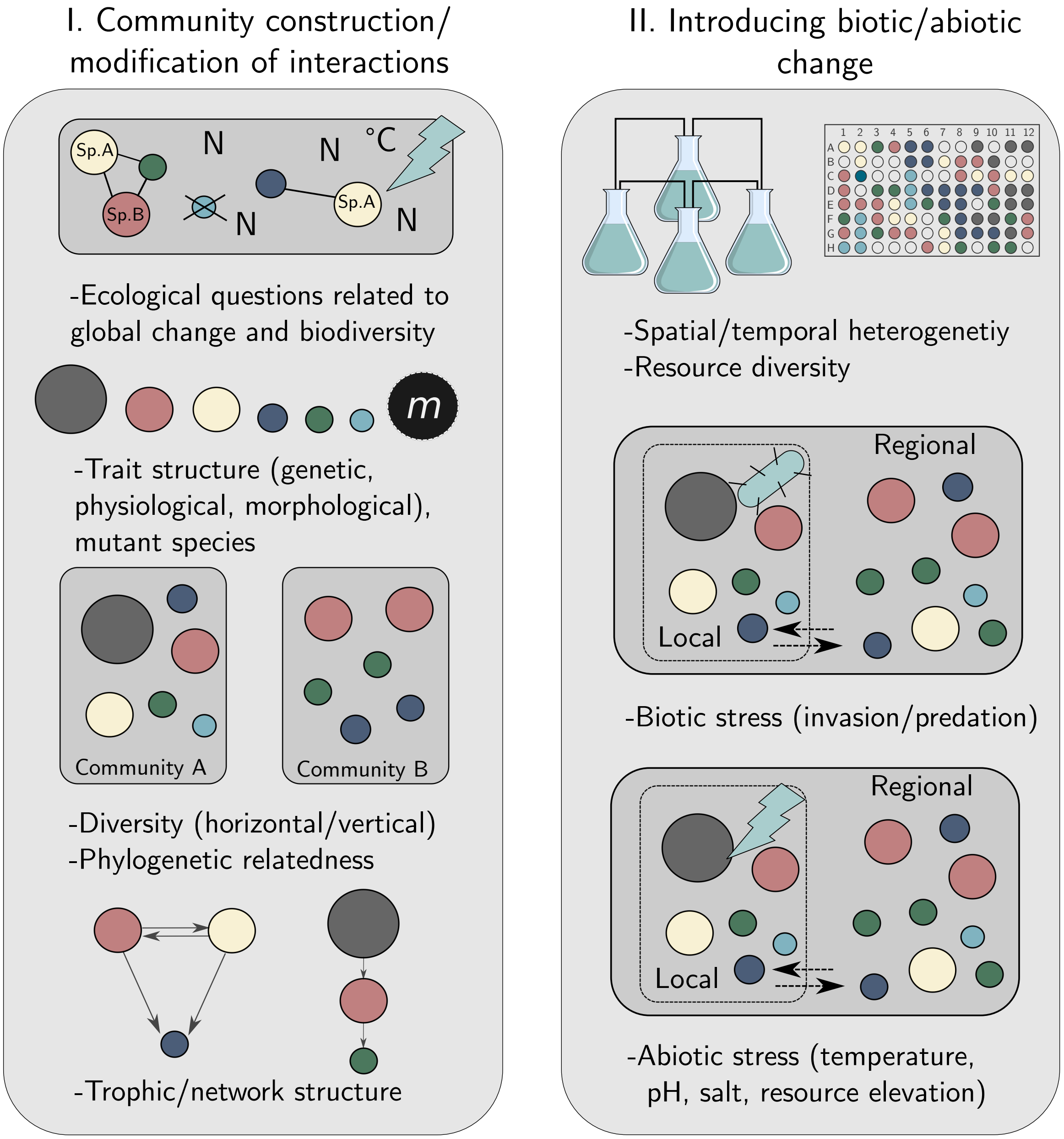
Tetrahymena sp.

In this thesis we found that the dynamics of species are dependent on the strength and duration of the disturbances, and the position of species on the trophic level.

Disturbances effectively uncoupled prey and predator species and initiated “prey release” in which prey abundance had exceeded its equilibrium, which depends on the predator recovery. Recovery, likewise, depended on the duration and strength of disturbances. In effect, the connectivity to an alternative resource (i.e. rate of using the dissolved resources) was also crucial for recovery.

Considering multiple prey species possess different life history traits and competitive abilities, the outcomes were complex and depended on the interplay between predation, disturbance and resource dynamics. Varying sensitivities of the different community measures, as reflected by their contrasting recovery times, added on to this complexity and context dependency. We demonstrated bi-directional causation between phenotypic change, and community dynamics depending on the predator presence. We also showed the direct cause-effect relationships between competing prey species, predator and anti-predation strategies, while revealing higher causal links between the prey species under predator stress.

This thesis encouraged us to demonstrate the ultimate use of microbial model systems, advanced measurement techniques, as well as advanced statistics and modelling approaches in future studies (Figure 7.1). We also briefly touched the important topics that future research should contemplate, including complex, especially non-hierarchical, species interactions, searching for causal links between global change, genes, organisms and their functions, as well as impacts of local processes on the larger scales (i.e. metacommunities). Considering these potential aspects, we propose in the next paragraphs further research should be undertaken in the following areas using microbial model systems. Figure 7.1. summarizes the highly controlled bottom-up approaches that should be considered.



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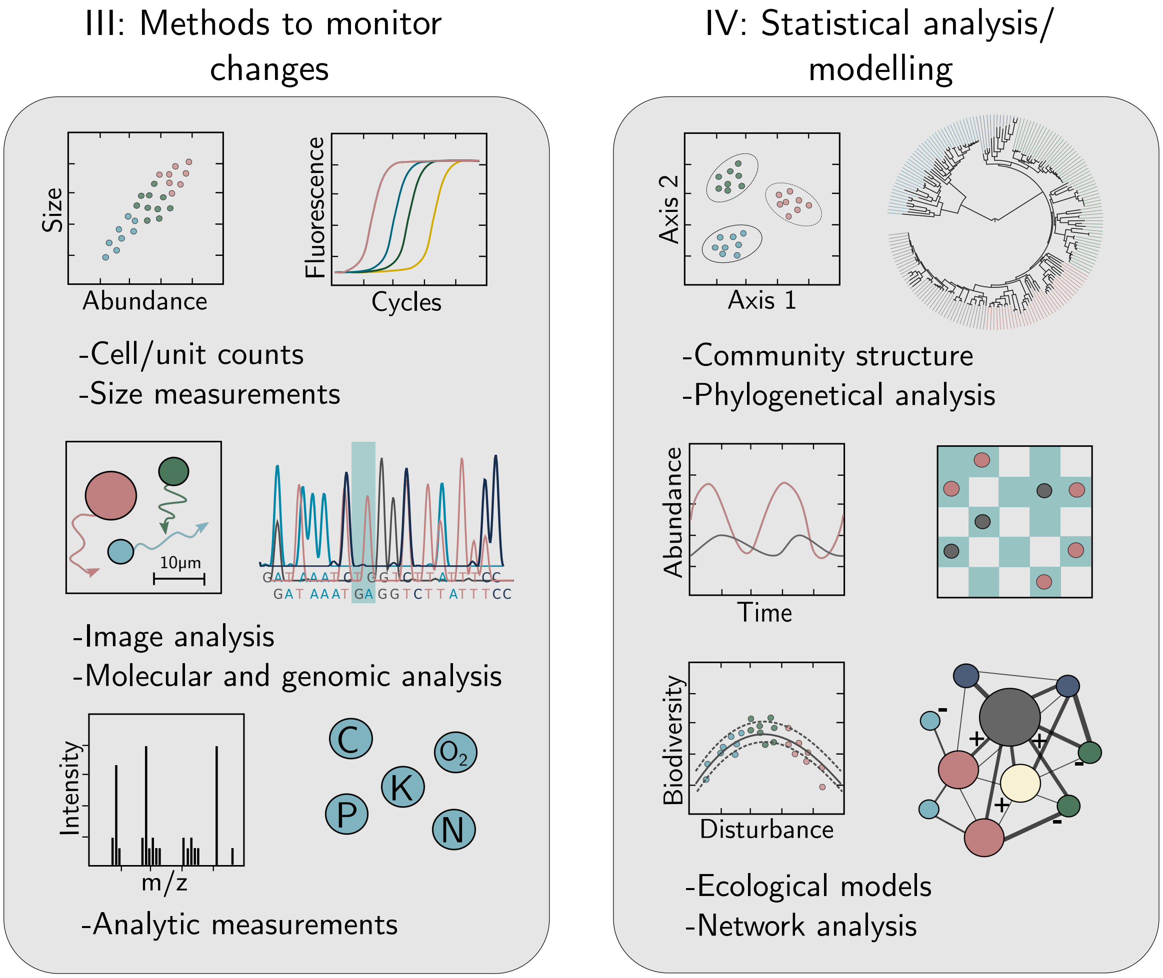

Figure 7.1. Bottom-up approach to create highly controlled microbial model systems. I) First, communities can be set up with respect to a particular hypothesis: It is potentially possible to assemble according to their genetic, physiological and morphological traits (including mutants). Horizontal and vertical diversity, evenness and phylogenetic history of species can be modified. For instance, a specific trophic structure (e.g intraguild predation) can be studied. II) Second, a specific environmental spatio-temporal heterogeneity can be introduced using laboratory tools (e.g. using connected culture flasks to create metacommunities, different structural and chemical elements to create niches and spatial structures). It is possible to modify biotic (e.g. invasion) and abiotic (e.g. temperature) stress/disturbances. III) There are several tools/techniques are available to, for instance, define size and abundances, behavioral and genetic features, chemical compositions and activities of individuals, populations and communities IV) Lastly, findings can be combined with, for instance, modelling or advanced statistics to define the change in community structure, species traits and interactions in time and space.

7.1 Increasing complexity of species interactions

At first, multispecies studies are necessary to understand ecological and evolutionary responses of species interactions, within changing environments[8]. We suggest that microbial model systems provide cost-efficient ways of studying fast predictions and testable hypotheses which may be relevant for the management of future communities and ecosystems.

Predator-prey interactions and competition have a central place in ecology (they were also the central focus in this thesis), however, there are many type of species interactions in nature, not all of them necessarily hierarchical. Potential eco-evolutionary dynamics may critically affect communities with **cooperative social behaviors**, since the survival of species depend on the cooperation between them[66]. **Rock-paper-scissors interactions** (such as communities with allelopathic plants, toxic sessile invertebrates, and antibiotic producing microbes) might show complex outcomes under varying environments. Members involved in this kind of interactions may even evolve under stressful environments to protect the other individuals in the community, which would ultimately increase the survival rates of the populations[215]. It has been previously shown that these kinds of interactions can be established in the lab, for instance, using mutant species[216,217].

7.2 Going further from causal links

We previously mentioned that combined with multi-species microcosms experiments, observation driven high-dimensional models (e.g.[33]) and application of CCM to investigate causal links between biotic and abiotic components (e.g.[194]), might serve as a sturdy base for future theories on population and community dynamics (Box 7.1). In this way, it might even be possible to find links between phylogeny, species traits, community dynamics and environmental change (similar to[218]). Today's technology and advances in methods such as transcriptomics[219], fluorescence techniques, Raman spectroscopy[220], flow cytometry[221] and stable isotope probing[222], will open the "black box" of communities (similar to the concept suggested for BEF research[223]) and allow for a biological understanding of direct cause and effect relationships between individuals and their environments. The effect of these ecological interactions and relationships on relevant **functions and processes** under global change should be investigated, such as degradation/purification (including buffer capacities), plant growth promotion, delivering other microbial functions etc. They might even reveal indirect impacts of environmental stressors such as temperature variability on the **metabolic rate of the organisms**, as well as their demographic consequences. They could also shift species-based to i**ndividual-based community ecology**, which would allow for more predictive ecological theory[224]. Better predictions, in turn, may even serve the development of **early warning systems of critical transitions** that result in community collapse (e.g. series of extinctions after disturbances)[41,42,44,45,225].

7.3 Metacommunities

Metacommunities are defined as regions made up of small-scale communities which are connected by dispersal, and potentially contain different set of biotic and abiotic features[226]. Communities are driven by both local and regional processes, which are the ultimate keys to understanding the behavior of metacommunities. However, manipulating disturbances and dispersals is difficult in larger scales. There are a couple of examples that use microbial microcosms to test such as effect of dispersal and timing on species diversity[103], dispersal rate and local adaptation[227,228], and the importance of dispersals and disturbances[187]. Livingston and his colleagues, for example, used multi-trophic protist microcosm landscapes to understand the impact of predators on the prey species sorting and spatial distribution[229]. They revealed the necessity to include predators as a separate explanatory factor in spatial analysis, since their strong effects otherwise may mistakenly be attributed to the stochastic defects such as dispersal limitation[229]. After all, studies combining multidimensional local processes, from species interactions and evolution, to disturbances and resource dynamics, in metacommunites, are needed to serve unified ecological theory.

Box 7.1: On the importance of direct cause-effect relationships

Difference and differential equations (e.g. Lotka-Volterra type models) are key methods in ecology for communicating clearly and forming theories; however, the predictive ability of models has always been a matter of criticism[113], due to the highly *non-linear behavior* of nature. For instance, complex dynamics with many nonlinearly interacting variables (e.g. marine systems) are sensitive to parameterization and can hardly be expected to be predictive[192]. Mathematical models search for the best *parameter combination series*, causing the perfect fit in the time series, but with the risk of not being meaningful and mechanistically uninformative, in a biological sense[115]. As Ye et al. (2015) has pointed out, science may be moving into a new era, in which equations will not play a major role in explaining dynamic systems[153]. This may in part, due to the ever-increasing computation power technology has provided for us. It is now possible to apply *individual-based modeling* where individual organisms and their environment are directly simulated[120].

Correlations can be also extracted from available data; however, it was shown that these correlations have not occurred when more data are analyzed[230]. *Correlation based methods* (e.g. cross-correlation and principal component analysis) only determine interactions when the variables act independently and the effects are separable[116]. Moreover, correlations between variables might be found due to *chance*, or can be caused by a common *co-variable*, however they are not necessarily causally related[108]. Introduction of causality rules in such a system might distinguish if dynamics of species are directly related or forced by another species/environmental variable.

Trophic networks consisting of multiple preys and predators have dynamic consequences that are difficult to predict. In addition to that, *intra- and interspecific variation* in prey communities may cause unpredictable dynamic consequences due to their *resistance* to their predators and *competitive abilities*[10,117–119,191,231]. For example, when prey evolves quickly as response to predator population dynamics, a statistical inference about the interaction strength is not reliable anymore[10]. Thus, *empirical dynamic modelling* approaches will have an important role in future ecological and evolutionary research.

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8

Appendix

8.1 Declaration of the authorship

I herewith declare that:

- I have written this thesis autonomously incorporating my own ideas and judgments; I have made use of no other resources than stated and direct or indirect quotations from other work have been marked accordingly; full reference of their source has been provided in the proper way.
- All persons are listed that provided me with support for the selection and evaluation of the material for my thesis; nature and scope of my own contribution and the share of the co-authors is listed in "Author contributions of published articles" (8.2).
- No other persons have provided support and thereby contributed to the thesis; in particular, no PhD consultants were used, and no third party has received direct or indirect financial benefits in goods and services for work that stands in relation to the work presented in the thesis.
- No other persons have provided support and thereby contributed to the thesis; in particular, no PhD consultants were used, and no third party has received

direct or indirect financial benefits in goods and services for work that stands in relation to the work presented in the thesis.

- No other persons have provided support and thereby contributed to the thesis; in particular, no PhD consultants were used, and no third party has received direct or indirect financial benefits in goods and services for work that stands in relation to the work presented in the thesis.
- This thesis has not been submitted in an equal or similar form for examination for the degree of doctorate or any other degree at another academic institution, and has not been published.
- No further unsuccessful doctoral examination process has taken place.

Place/Ort	Date/Datum	Signature/Unterschrift

8.2 Author contributions of published articles

Author (the first and the senior) contributions for the two articles enclosed in this work and the statement of executive authorship of unpublished chapter are listed on the following pages:

Publication 1: Page 128

Publication 2: Page 129

Thesis Chapter: Page 130

Author contribution statement, Canan Karakoç

Context Dependency of Community Dynamics: Predator-Prey Interactions Under Ecological Disturbances

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Author contribution statement:

Title	**Transient recovery dynamics of a predator–prey system under press and pulse disturbances**
Journal	*BMC Ecology*
Authors	Canan Karakoç, Alexander Singer, Karin Johst, Hauke Harms, Antonis Chatzinotas

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Canan Karakoç	- Design of research - Lab experiments - Statistical analysis - Data interpretation - Manuscript writing	Signature Canan Karakoc
Alexander singer	- Design of research - Simulation experiments - Data interpretation - Manuscript writing	
Karin Johst	- Design of research - Supervision of the theoretical part - Data interpretation - Manuscript writing	
Hauke Harms	- Design of research - Data interpretation - Manuscript writing	
Antonis Chatzinotas	- Design of research - Supervision of the lab experiments - Data interpretation - Manuscript writing	Signature

Author contribution statement, Canan Karakoç

Context Dependency of Community Dynamics: Predator-Prey Interactions Under Ecological Disturbances

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Author contribution statement:

Title	**Interactions between predation and disturbances shape prey communities**
Journal	*Scientific Reports*
Authors	Canan Karakoç, Viktoriia Radchuk, Hauke Harms, Antonis Chatzinotas

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Canan Karakoç	- Study concept - Design of experiments - Lab experiments - Data analysis - Interpreting results - Manuscript writing	Signature
Viktoriia Radchuk	- Supervision of statistical analysis - Interpreting results - Manuscript writing	
Hauke Harms	- Manuscript writing	
Antonis Chatzinotas	- Study concept - Design of lab experiments - Supervision of lab experiments - Manuscript writing	Signature

Statement of Executive Authorship, Canan Karakoç

Context Dependency of Community Dynamics: Predator-Prey Interactions Under Ecological Disturbances

Title	**Species Interactions and Evolutionary Dynamics Shaping Communities (Chapter 5)**
Journal	*Thesis Chapter*
Author	Canan Karakoç

Hereby, I declare that I am the executive author of the above thesis chapter.

Canan Karakoç

Canan Karakoç

8.3 List of publications and conference contributions

Publications

1. **Karakoç, C.**, Singer, A., Johst, K., Harms, H. & Chatzinotas, A. Transient recovery dynamics of a predator–prey system under press and pulse disturbances. *BMC Ecology* **17**, 13 (2017). ****Chapter 3***
2. **Karakoç, C.**, Radchuk V., Harms, H. & Chatzinotas, A. Interactions between predation and disturbances shape prey communities. *Scientific Reports* **8**, 2968 (2018). ****Chapter 4***

Additional Publications

1. Ozbayram E.G., Akyol Ç., Ince B., **Karakoç C.**, Ince O. Rumen bacteria at work: Bioaugmentation strategies to enhance biogas production from cow manure. *Journal of Applied Microbiology*, **124**, 491–502 (2018).
2. Sendek A.,* **Karakoç C.***, Wagg C., Domínguez-Begines J., Martucci de Couto G., Van der Heijden M.G.A., Naz A.A., Lochner A., Chatzinotas A., Klotz S., Gómez-Aparicio L., Eisenhauer N. Drought modulates interactions between arbuscular mycorrhizal fungal diversity and barley genotype diversity, *under review.* **These authors contributed equally to this work.*
3. **Karakoç, C.**, Chatzinotas, A. Species interactions and rapid phenotypic changes drive temporal dynamics of predator-prey systems, *in prep.*
4. Kuppardt A., **Karakoç C.**, Chatzinotas A. Impact of stoichiometric gradients on dynamics of a microbial freshwater community in microcosm experiments, *under review.*

Presentations

1. Several talks and posters at the Helmholtz Center for Environmental Research - UFZ, Departments of Environmental Microbiology and Ecological Modelling; HIGRADE Graduate School; German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Germany. *Since 2013.*
2. **Talk: Karakoç C.**, Patterns and processes under environmental fluctuations: Experiments with microbial model systems. University of Thessaly, Department of Biochemistry and Biotechnology, Larissa, Greece. *11/2014 & 02/2016*.
3. **Talk: Karakoç C.**, Lin, Y. & Chatzinotas, Understanding community assembly mechanisms through integrative approaches, **EEF-SiTE - Ecology at the Interface**, Rome, Italy. *09/2015*
4. **Poster: Karakoç C.**, Singer, A., Johst, K., Harms, H., Chatzinotas, A. Transient dynamics of trophically interacting species after disturbance. **HETEROCLIM: The response of organisms to climate change in heterogeneous environments**, Loches, France. *06/2014*
5. **Talk: Karakoç C.**, Understanding the role of species interactions under environmental change: Microbial model systems as tools in ecological theory. **YoMo Workshop - Ecological modeling across disciplines**, Hann. Münden, Germany. *05/2014*.

8.4 Acknowledgments

No doubt, last few years have been the toughest time of my life, and I would have not survived without the support of my supervisors, colleagues, friends and family, in a number of ways.

First and foremost, I owe my deepest gratitude to Antonis Chatzinotas for initializing my project and providing me the freedom to develop it. Without his guidance, optimism, enthusiasm, encouragement and tremendous patience, this thesis would hardly have been completed.

I am deeply grateful to Hauke Harms for warmly accepting me to his department, supervising this work, and for giving critical, constructive and insightful feedbacks. I owe many thanks to William Stanley Harpole for accepting to examine this thesis.

My heartfelt appreciation goes to Karin Johst, Alexander Singer and Viktoria Radchuck for the most fruitful collaboration. Publications would not have materialized without them. I also would like to show my greatest appreciation to Yue Lin for his insightful ideas and suggestions, which made this thesis more interesting.

I owe lots of thanks to my working group, Microbial Interactions Ecology, all the past and current members, for their continuous support. But, I have to mention Bärbel, René, Peter, Anke and Muhammad for the guidance, precious discussions and side projects that were direct and indirect intellectual contribution to this work. I also thank to Verena, Anett, Andreas, Johathan and Nicole for their great help and patience in the lab.

I want to thank all UMB at the UFZ, which was part of my life for the past years. All the talks, seminars, discussions; administrative and technical help contributed a piece in this thesis. Many thanks also to Christin, Tom, Anja, Inga, Nawras and many other colleagues at the department for the discussions and suggestions.

I also want to thank Nico Eisenhauer and his team, especially Agnieszka and Alfred, who enabled a great side project at the iDiv, which was an indirect but a precious intellectual contribution to my work.

I owe thanks to Markus for his unconditional support first, and expertise in programming, which helped me to sort out practical problems, second. Special thanks to Nicholas for encouragement to finalize my thesis and helping me to write clear and lively texts. I am grateful to all of my friends for being cheer leaders and helping me to overcome my occasional desperations.

Finally, I thank my family who have supported me longest.

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8.5 Supplementary material for Chapter 3

Additional file 1

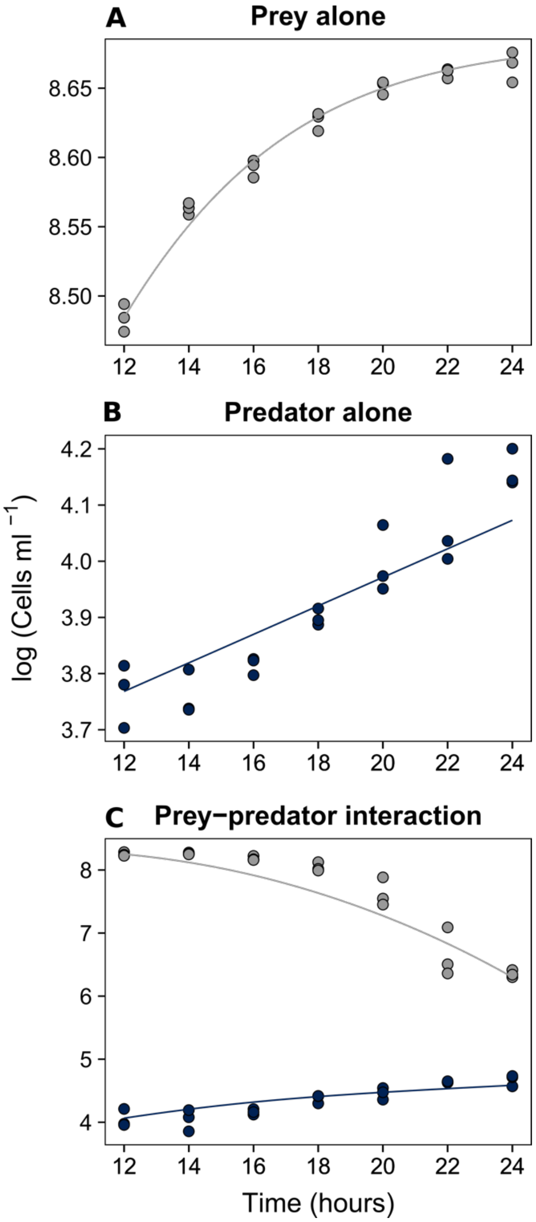

Figure S1: Experimental growth data (circles) and the fitted curves (solid line) of prey alone (A), predator alone (B) and prey-predator interaction (C) as described in the methods section of the main text.

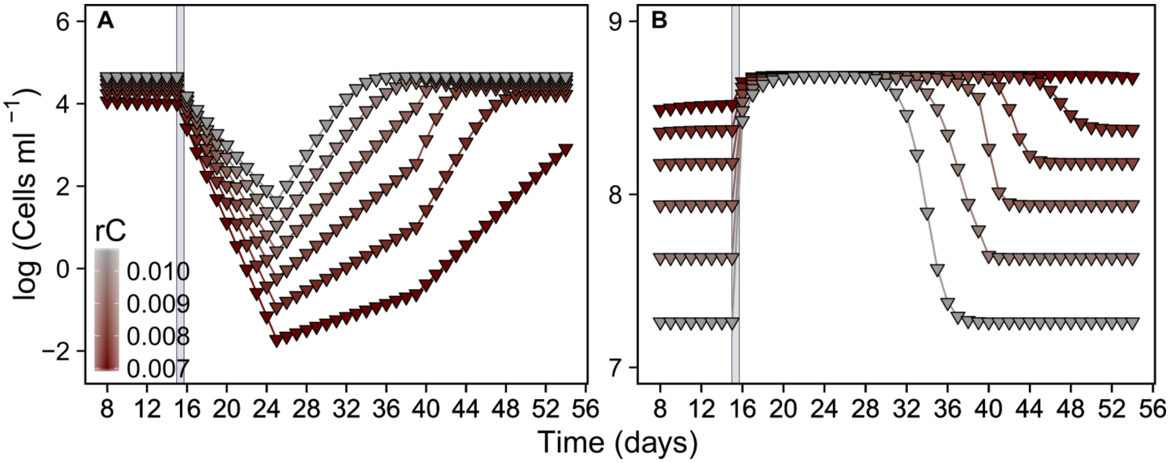

Figure S2: Impact of predator coupling "r_C" to an alternative resource besides prey (varied from 0.007 to 0.011) under press disturbance (40-fold dilution) projected by the model simulations for predator (A) and prey (B). Color gradient shows lowest (grey) to highest (dark red) r_C values. Disturbance action is shown as grey shadows.

8.6 Supplementary material for Chapter 4

Supplementary Information 1

A. Extended description of the prey relative abundance determination methods

Bacterial DNA was extracted using the NucleoSpin® Tissue Kit (Macherey-Nagel, Düren, Germany) and 16S rRNA genes were amplified by PCR using the FAM-labelled bacterial forward primer 27f (5-AGA GTT TGA TCM TGG CTC AG-3) and the reverse universal primer 1492r (5-CGG TTA CCT TGT TAC GAC TT-3). Each 25-mL reaction consisted of 12,5 µl master mix (Bioline, London, UK), 5pmol of each primer and 10ng of sample DNA. Thermocycling was carried out with an initial denaturation step at 95°C (5 min), 35 cycles of denaturation at 95°C (45 sec), annealing at 56°C (45 sec) and primer extension at 72°C (1 min) and extension step at 72°C (10 min). Fluorescently labeled PCR products were purified with SureClean (Bioline, London, UK) and approximately 20 ng of them were digested with2U restriction enzyme MspI (New England Biolabs GmbH, Frankfurt/Main, Germany) at 37°C for 16 hours. Terminal-restriction fragments (T-RFs) were separated and detected in a capillary sequencer (ABI Prism® 3130, Applied Biosystems, Foster City, CA, USA) with an internal size standard (GeneScan 500 ROX, Applied Biosystems). T-RFLP electropherograms were analyzed using GeneMarker® (Soft Genetics, State College, PA, USA).

B. Competitive ability of prey species used

To determine the competitive ability, we cultivated the prey organisms for 24 h alone and in all possible pairwise combinations, starting with the same cell number. We plated a subsample and counted the colony forming units (c.f.u.) of each organism using their distinguishable colors after 2 days[1]. All monocultures and combinations were replicated four times.

We estimated competitive ability of species following the approach of Fox (2002) and Haddad et al. (2008). We first calculated the response of species i, and the effect of i on j when they grew together using the following index[2]:

$$CR_{ijk} = {(K_i - N_{ijk})}/{K_i} \tag{1}$$

where K_i is the abundance of species i in the single species trial, averaged over the four replicates, and N_{ijk} is the abundance of species i when grown together with competitor j in replicate k.

We then calculated the competitive ability considering sum of all the responses and effects of a species[3]:

$$CA_j = \frac{1}{n}\left(\sum_i CR_{ij} - \sum_i CR_{ji}\right) \tag{2}$$

where the first summation is the effect of a focal species on each other species, the second summation is the response of a focal species, and n is the number of species. Negative CA indicates poor competitive ability, whereas positive C indicates good competitive ability. Zero CA indicates that the effects of a focal species on each other species are cancelled out by the responses of the focal species to other species, resulting in a neutral net competitive ability of the species.

Table S1. Competitive ability of the species. Mean competitive ability and confidence intervals were determined by bootstrapping procedure.

Species	**Ability**	**Percentiles**
Agrobacterium sp.	0,487	(0,426; 0,530)
Koccuria sp.	0,292	(0,271; 0,330)
Sphingobium sp.	0,041	(0,006; 0,087)
Williamsia sp.	-0,820	(-0,851; -0,789)

C. Predictions of linear mixed effect models

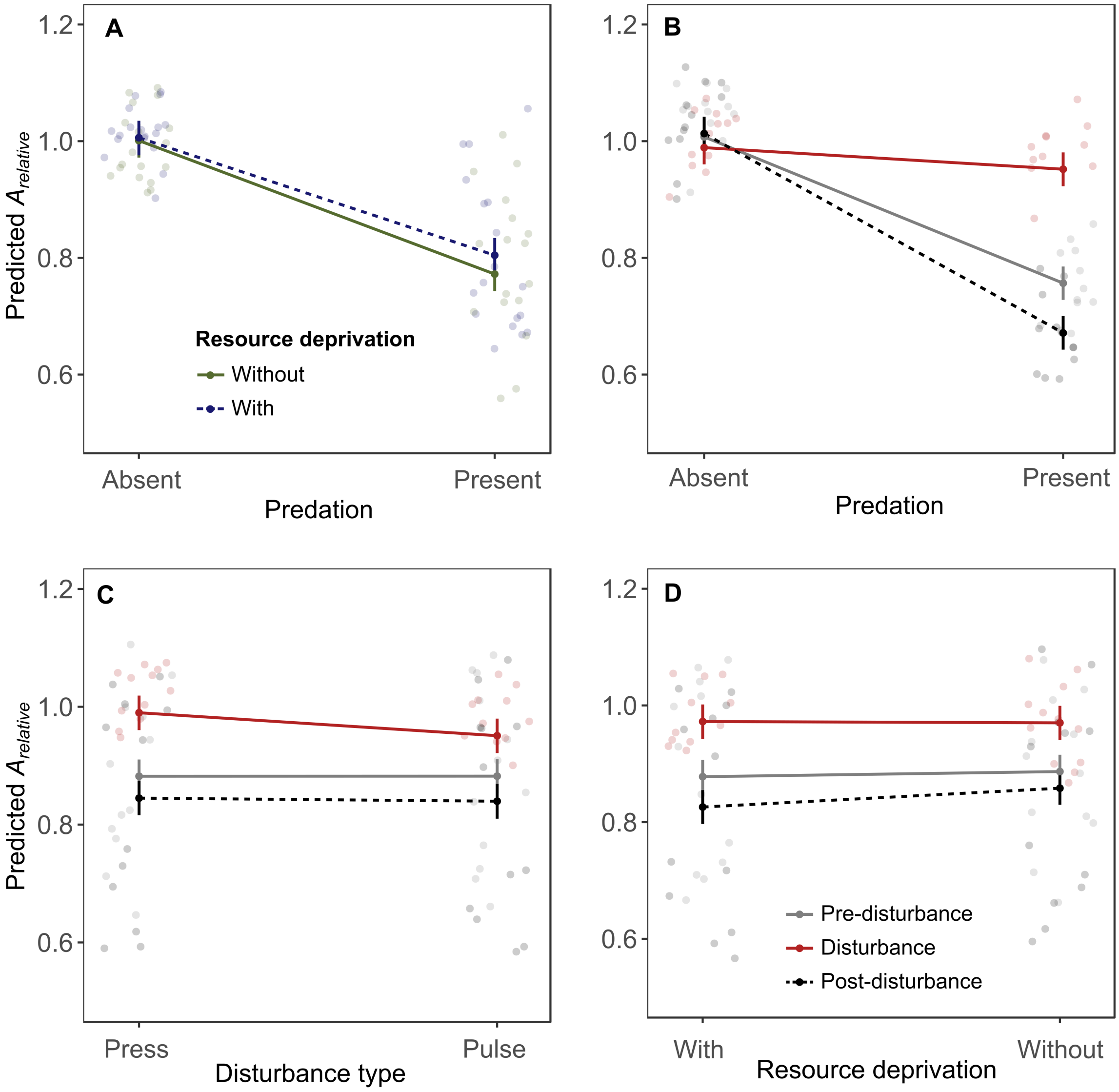

Figure S1. Significant two-way interactions in the model predicting relative prey abundance. Shaded points are all the predictions, solid points are the means and vertical lines are the confidence intervals.

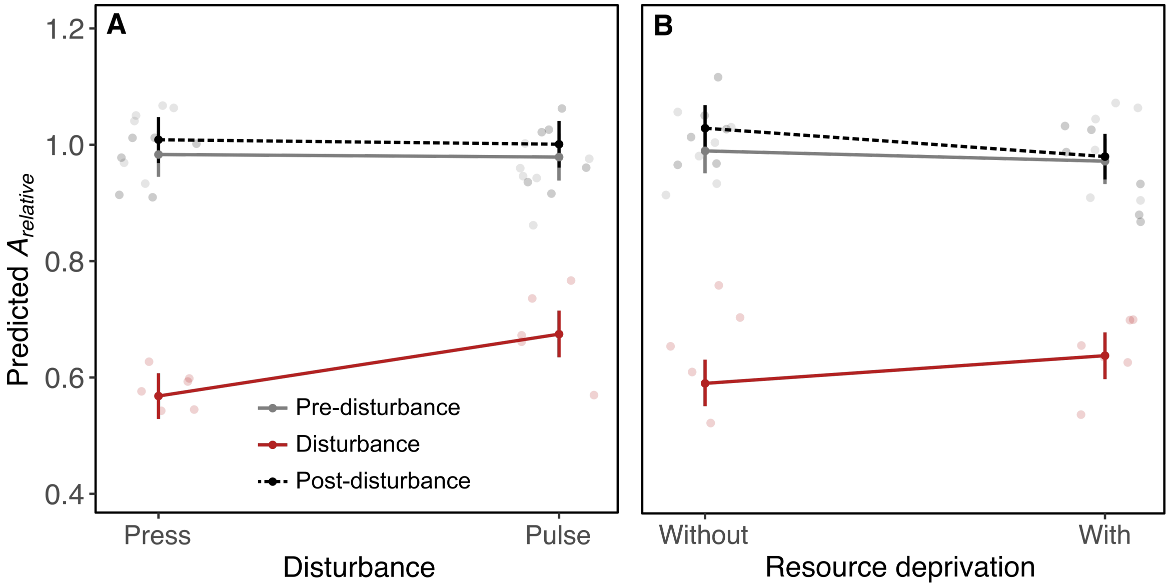

Figure S2. Significant two-way interactions in the model predicting relative predator abundance. Shaded points are all the predictions, solid points are the mean and vertical lines are the confidence intervals.

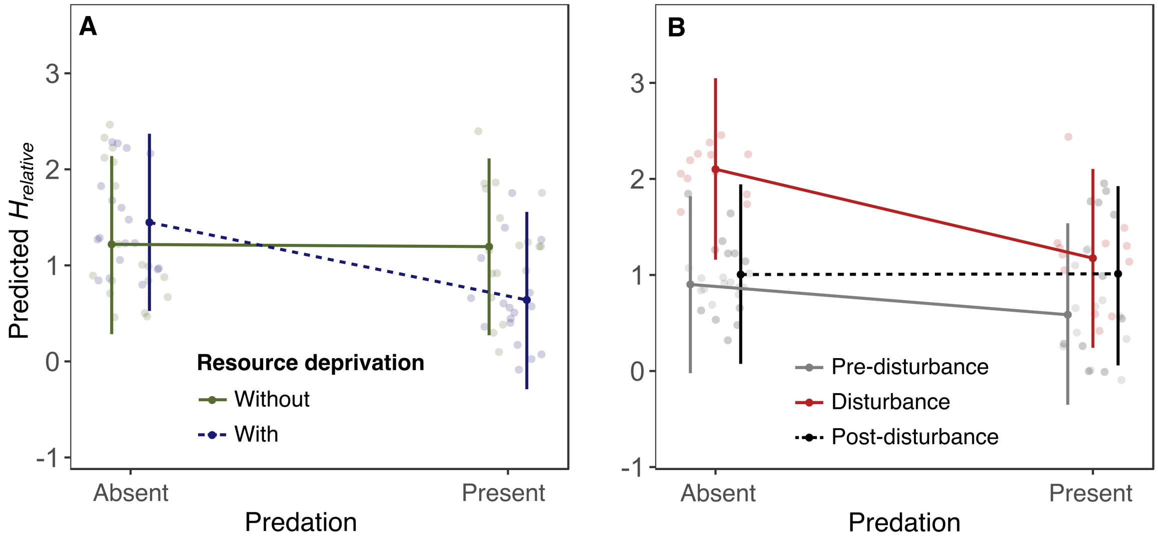

Figure S3. Significant two-way interactions in the model predicting relative prey diversity. Shaded points are all the predictions, solid points are the mean and vertical lines are the confidence intervals.

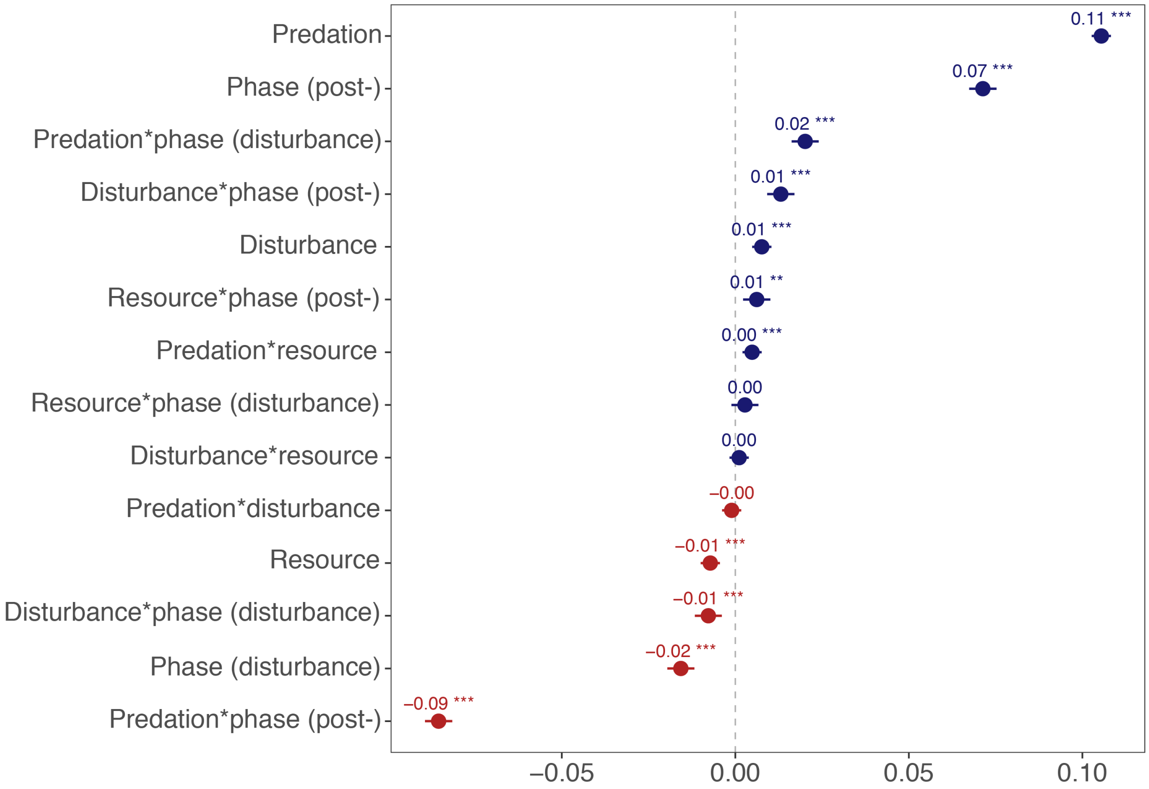

Figure S4. Regression coefficients from linear mixed effect model of effect of experimental treatments on relative prey abundance. Baseline is the mean of all factors. Shown factor levels are predation (present), disturbance type (pulse) and resource deprivation (present). Disturbance phases were stated in brackets. Points represent the mean and lines are the 95% confidence intervals. Positive and negative effects are shown as blue and red respectively (Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1).

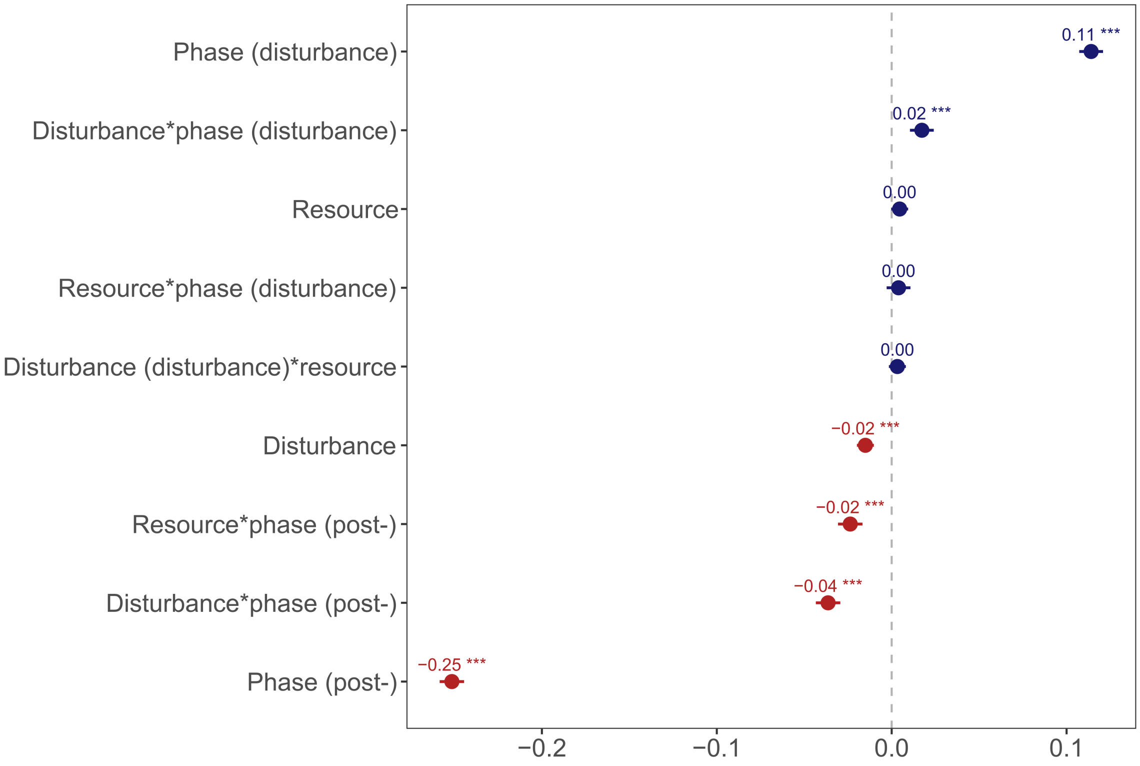

Figure S5. Regression coefficients from linear mixed effect model of effect of experimental treatments on relative predator abundance. Baseline is the mean of all factors. Shown factor levels are predation (present), disturbance type (pulse) and resource deprivation (present). Disturbance phases were stated in brackets. Points represent the mean and lines are the 95% confidence intervals. Positive and negative effects are shown as blue and red respectively (Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1).

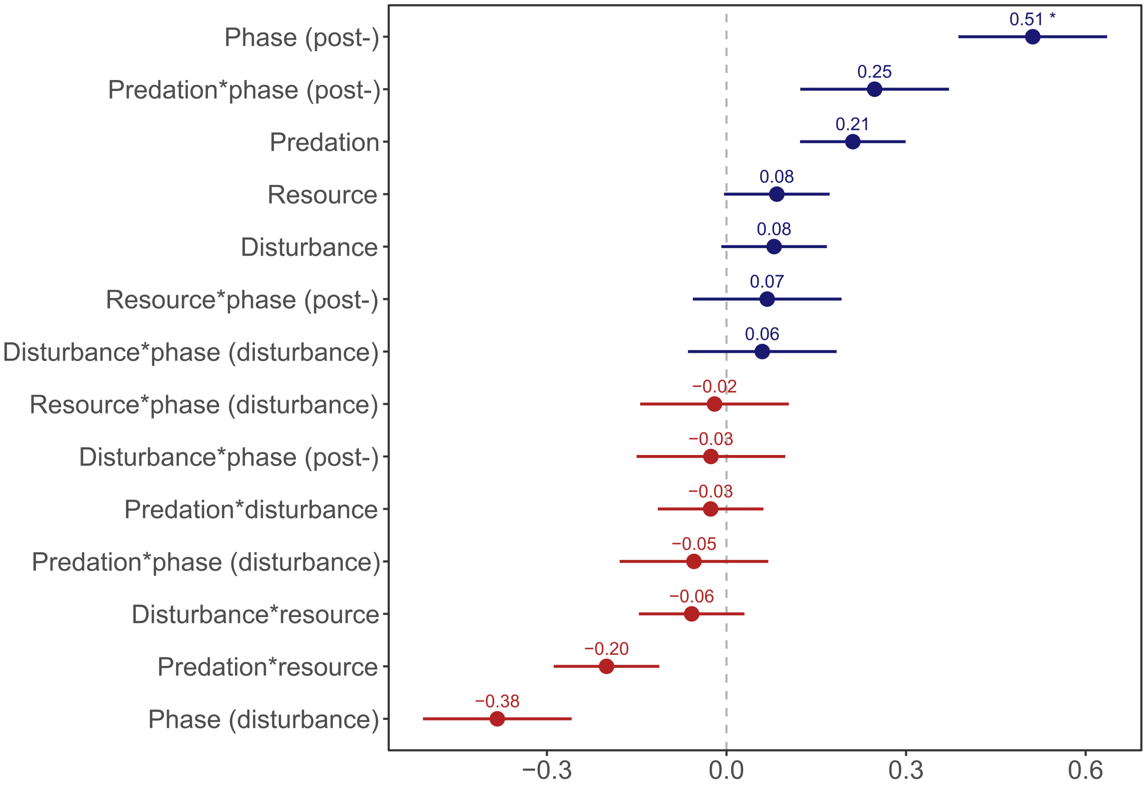

Figure S6. Regression coefficients from linear mixed effect model of effect of experimental treatments on relative prey diversity. Baseline is the mean of all factors. Shown factor levels are predation (present), disturbance type (pulse) and resource deprivation (present). Disturbance phases were stated in brackets. Points represent the mean and lines are the 95% confidence intervals. Positive and negative effects are shows as blue and red respectively (Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1).

D. Relative abundances and community structure of prey species in different treatments

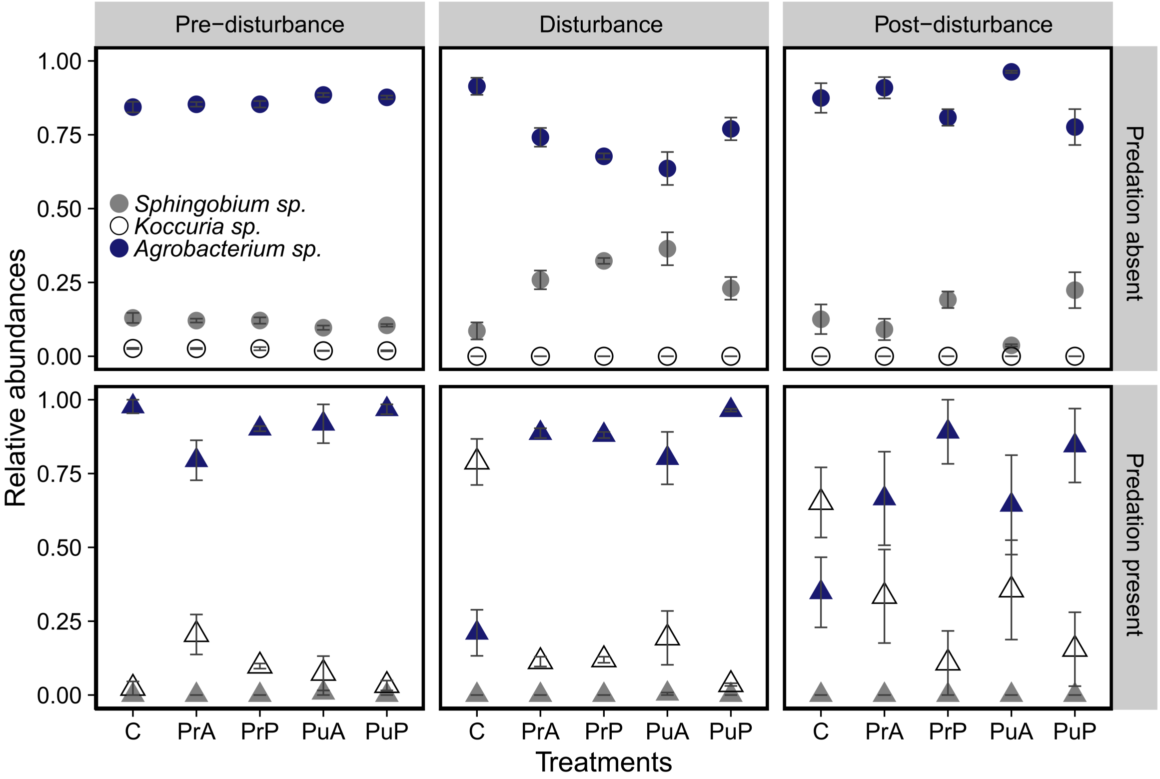

Figure S7: Relative abundances of the prey species determined by T-RFLP profile as explained in the main text. C: Control, Pr: Press disturbance, Pu: Pulse disturbance, A: Without resource deprivation, P: With resource deprivation.

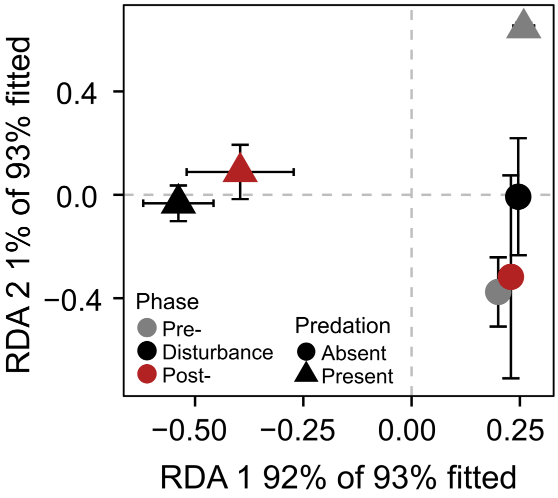

Figure S8. Communities without disturbance and resource deprivation treatments. The first two axes of the RDA analysis. Circles represent the control treatments without and triangles with predation. Colors code for the disturbance phases. Error bars display the ± standard error for vertical and horizontal axes.

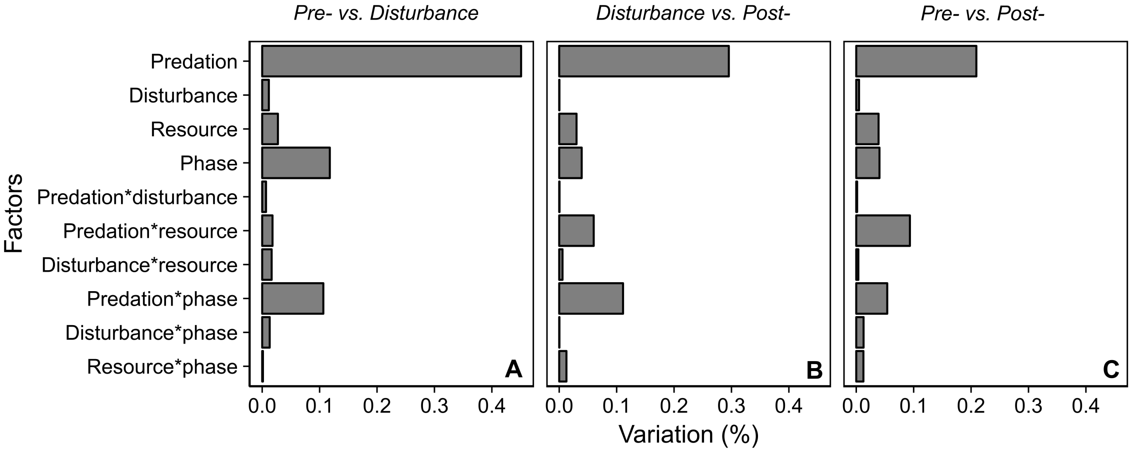

Figure S9. Variation in community composition explained by the main factors and their two-way interactions for the pre- vs. disturbance **(A)**, disturbance vs. post- **(B)** and pre- vs. post-disturbance phase **(C)**. Total variation explained for different phase comparisons is 67%, 56% and 47%.

A. Sensitivity of results to data removal and averaging of the control replicates

Table S2. Fixed effects in linear mixed-effects models of prey and predator abundance response to predation and disturbance on the full data set. Df is degrees of freedom, χ^2 and p values were derived from parametric bootstrap. Significant effects are highlighted in bold.

Total prey abundance			
Effects	**df**	χ^2	**p**
Predation	**1,72**	**134.35**	**<0.001**
Disturbance	**1,72**	**20.97**	**<0.001**
Resource	**1,72**	**19.43**	**<0.001**
Phase	**2,72**	**215.11**	**<0.001**
Predation x disturbance	1,72	0.56	ns.
Predation x resource	**1,72**	**10.52**	**0.006**
Disturbance x resource	1,72	0.61	ns.
Predation x phase	**2,72**	**239.05**	**<0.001**
Resource x phase	**2,72**	**33.69**	**<0.001**
Disturbance x phase	**2,72**	**18.55**	**0.006**
Total predator abundance			
Disturbance	**1,36**	**14.33**	**0.002**
Resource	1,36	3.96	ns.
Phase	**2,36**	**155.20**	**<0.001**
Disturbance x resource	1,36	0.02	ns.
Disturbance x phase	**2,36**	**41.18**	**<0.001**
Resource x phase	**2,36**	**14.55**	**0.006**

Table S3: Fixed effects in linear mixed-effects model of prey diversity *(H)* response to predation and disturbance on the full data set. Df is degrees of freedom, χ^2 and p values were derived from the parametric bootstrap. Significant effects are highlighted in bold.

Effects	**df**	χ^2	**P**
Predation	**1,72**	**14.14**	**0.01**
Disturbance	1,72	1.70	ns.
Resource	1,72	1.96	ns.
Phase	**2,72**	**44.81**	**<0.001**
Predation x disturbance	1,72	0.03	ns.
Predation x resource	**1,72**	**12.93**	**<0.001**
Disturbance x resource	1,72	0.73	ns.
Predation x phase	**2,72**	**16.60**	**0.001**
Disturbance x phase	2,72	1.63	ns.
Resource x phase	2,72	2.13	ns.

Table S4. Effects of the main factors and interactions on the abundances/diversity relative to the averaged and randomly sampled control replicate for each treatment. Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05.

Prey abundance relative to the control treatment		
Effect	***Randomly Sampled***	***Averaged***
Predation	***	***
Disturbance	***	***
Resource	***	***
Phase	***	***
PredationXdisturbance	ns.	ns.
PredationXresource	**	**
DisturbanceXresource	ns.	ns.
PredationXphase	***	***
DisturbanceXphase	***	***
ResourceXphase	**	***
Predator abundance relative to the control treatment		
Effect	***Randomly Sampled***	***Averaged***
Disturbance	***	**
Resource	ns.	ns.
Phase	***	***
DisturbanceXresource	ns.	ns.
DisturbanceXphase	***	***
ResourceXphase	***	***
Prey diversity relative to the control treatment		
Effect	***Randomly Sampled***	***Averaged***
Predation	*	**
Disturbance	ns.	ns.
Resource	ns.	ns.
Phase	***	***
Predation*disturbance	ns.	ns.
Predation*resource	***	***
Disturbance*resource	ns.	ns.
Predation*phase	**	**
Disturbance*phase	ns.	ns.
Resource*phase	ns.	ns.

B. Estimation of generation times of species

In order to have an idea about the life history of the used bacterial species, we monitored the growth curves of pure cultures (n=8) in 24-well plates at the experimental temperature and in the experimental medium. Optical density was measured at 600nm every 30min. We then fitted a logistic growth model using nls function in R. The used species had approximately 2-4 generations per day (Figure S10, Table S5).

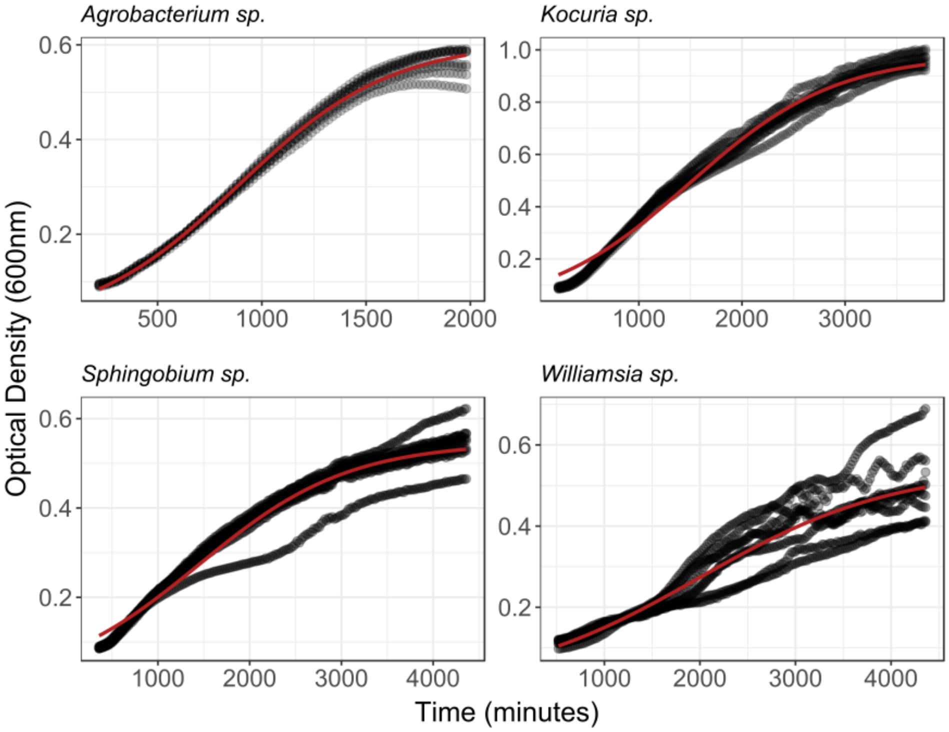

Figure S10. Growth curves of prey species (n=8) and logistic growth fit.

Table S5. Growth rates and carrying capacities of prey species.

Species	**r(d^{-1})**	**K (OD)**
Agrobacterium sp.	3.927	0.608
Koccuria sp.	2.035	0.981
Sphingobium sp.	1.765	0.546
Williamsia sp.	1.404	0.544

The predator grows also with approximately 2-4 generations per day, which is comparable with the prey growth rate (Figure S11).

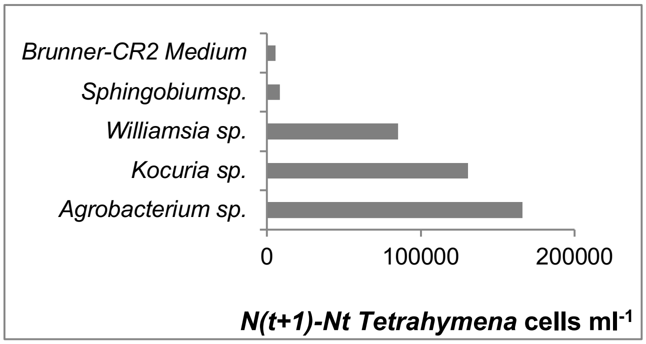

Figure S11. Growth of *Tetrahymena sp.* with and without prey bacteria.

A. Testing for possible time dependency

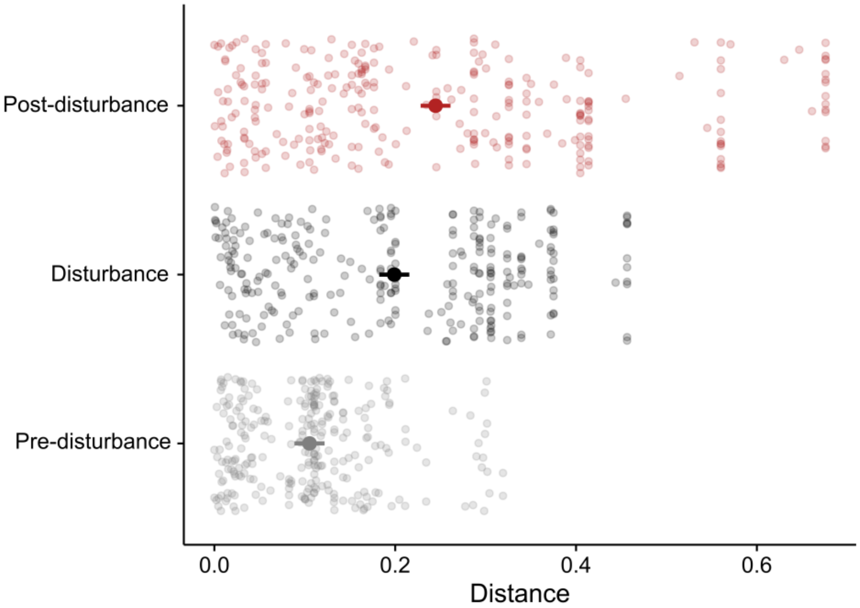

Figure S12: Pairwise Euclidean distances between samples at each phase. Solid points and lines indicate for each phase the estimates from least square means with their confidence intervals.

In order to evaluate whether our assumption of absence of temporal autocorrelation holds we tested whether relative distances among samples are maintained from one phase to the other (Figure S12, Table S6). For this, we calculated the pairwise Euclidean distances among all samples at each phase using vegdist() function in the vegan package for R[4]. We then tested whether the pairwise differences differ among phases (i.e. time points) by fitting a linear mixed effect model using lmer() function (lme4[5] R package). Identity of each pair was used as random effect and disturbance phase as fixed effect. To test whether the pairwise differences on average (as estimated from the mixed effect model) changed from one phase to the other we applied t-tests using lsmeans with Bonferroni-Holm correction[6].

Table S6: Multiple comparisons of pairwise Euclidean distances between each phase.

Contrast	***df***	***t-ratio***	***p***
Pre-disturbance – Disturbance	552	-9.032	<0.001
Pre-disturbance – Post - disturbance	522	-13.441	<0.001
Disturbance – Post-disturbance	522	-4.408	<0.001

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1. Saleem, M., Fetzer, I., Dormann, C. F., Harms, H. & Chatzinotas, A. Predator richness increases the effect of prey diversity on prey yield. *Nat. Commun.* **3,** 1305 (2012).
2. Fox, J. W. Testing a simple rule for dominance in resource competition. *Am. Nat.* **159,** 305–319 (2002).
3. Haddad, N. M. *et al.* Species' traits predict the effects of disturbance and productivity on diversity. *Ecol. Lett.* **11,** 348–356 (2008).
4. Oksanen, J. *et al. vegan: Community Ecology Package.* (2016).
5. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* **67,** (2015).
6. Lenth, R. *lsmeans: Least-Squares Means.* (2017).

8.7 Supplementary material for Chapter 5

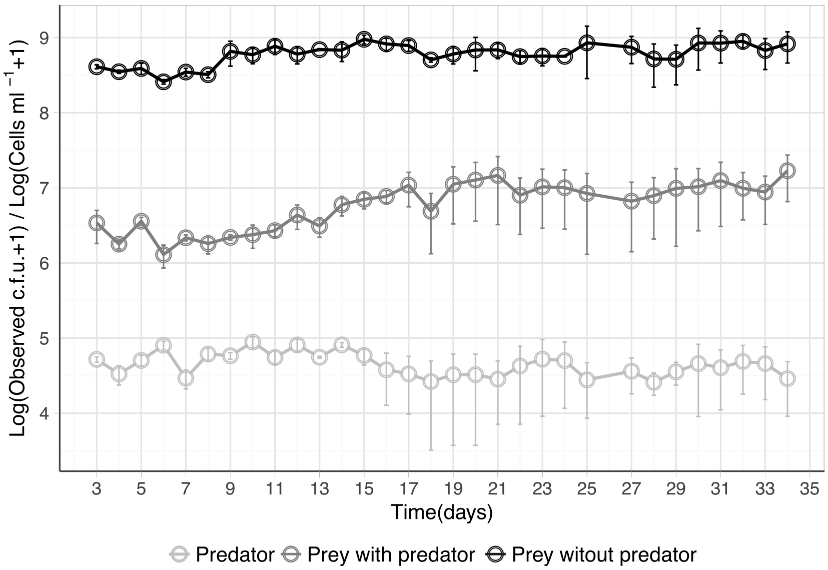

Figure S1. Total abundance of prey species with and without the predator. Predator abundance was estimated as the cells per mL and prey abundance as the total colony forming units per mL. Points are the mean estimated abundances, error bars are the ± SD.

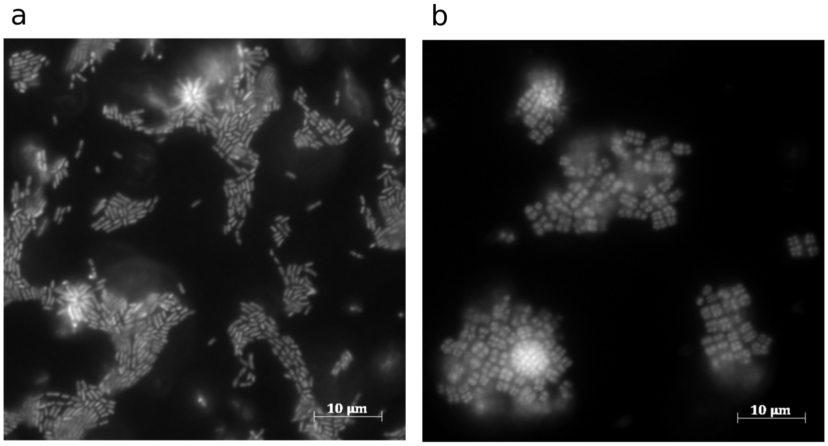

Figure S2. Microscope pictures of the biofilm forming Am (a, *Agrobacterium sp.* morphotype) and the large clump forming Km (b, *Kocuria sp.* morphotype). Samples fixed, filtered and dyed as in[*]

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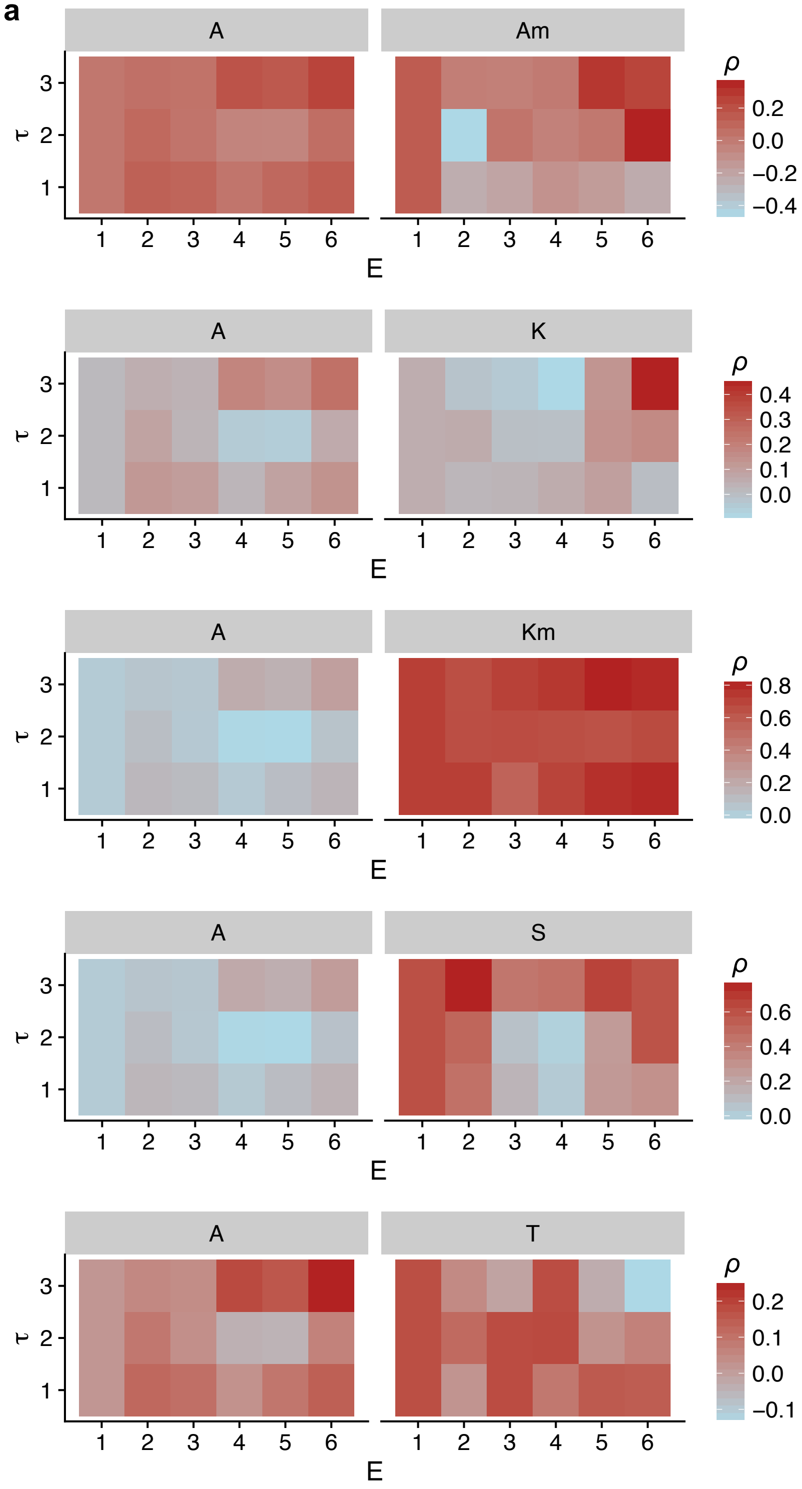
[*] Johnke, J., Boenigk, J., Harms, H. & Chatzinotas, A. Killing the killer: predation between protists and predatory bacteria. *FEMS Microbiol Lett* **364** (2017).



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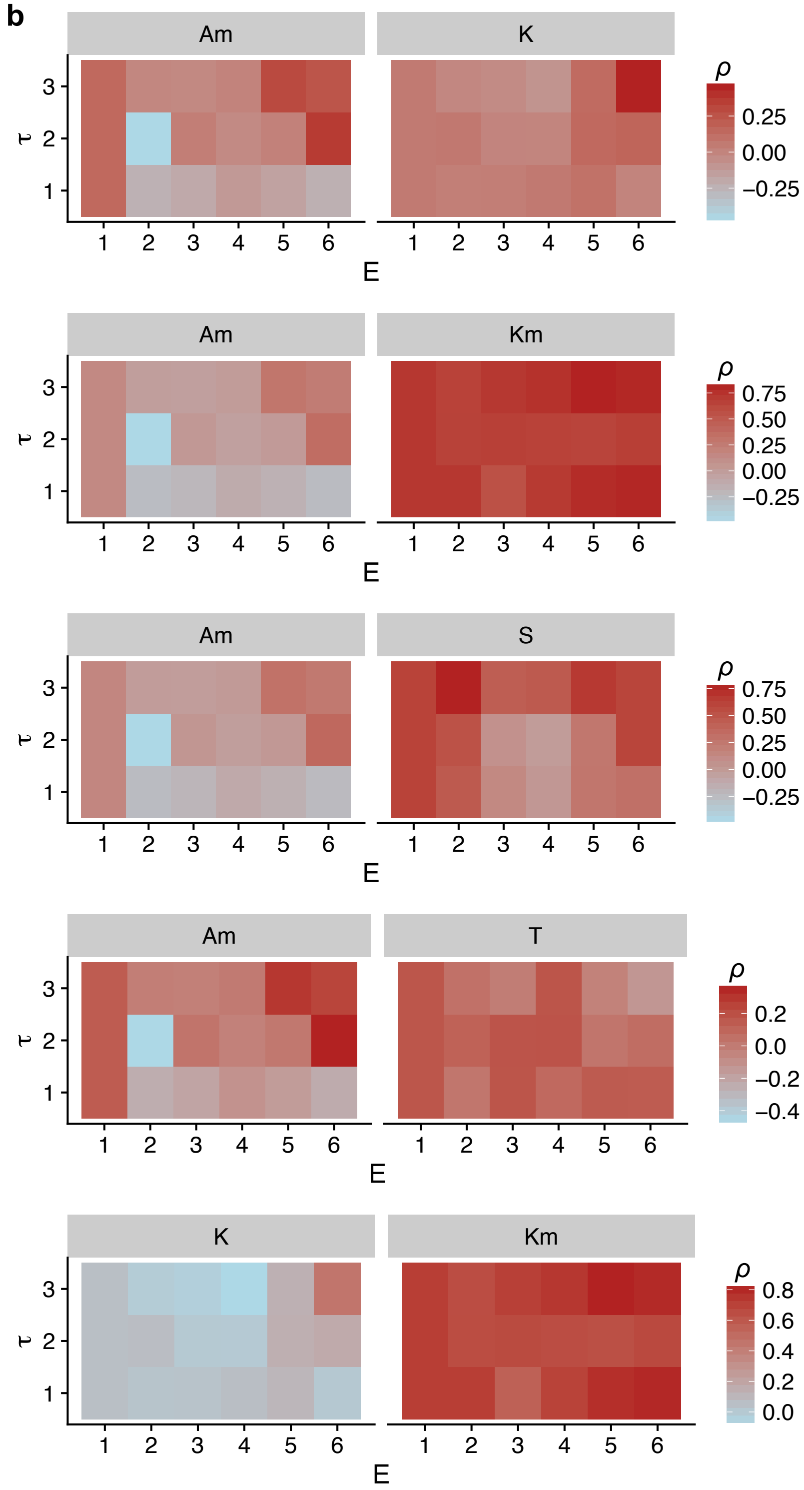

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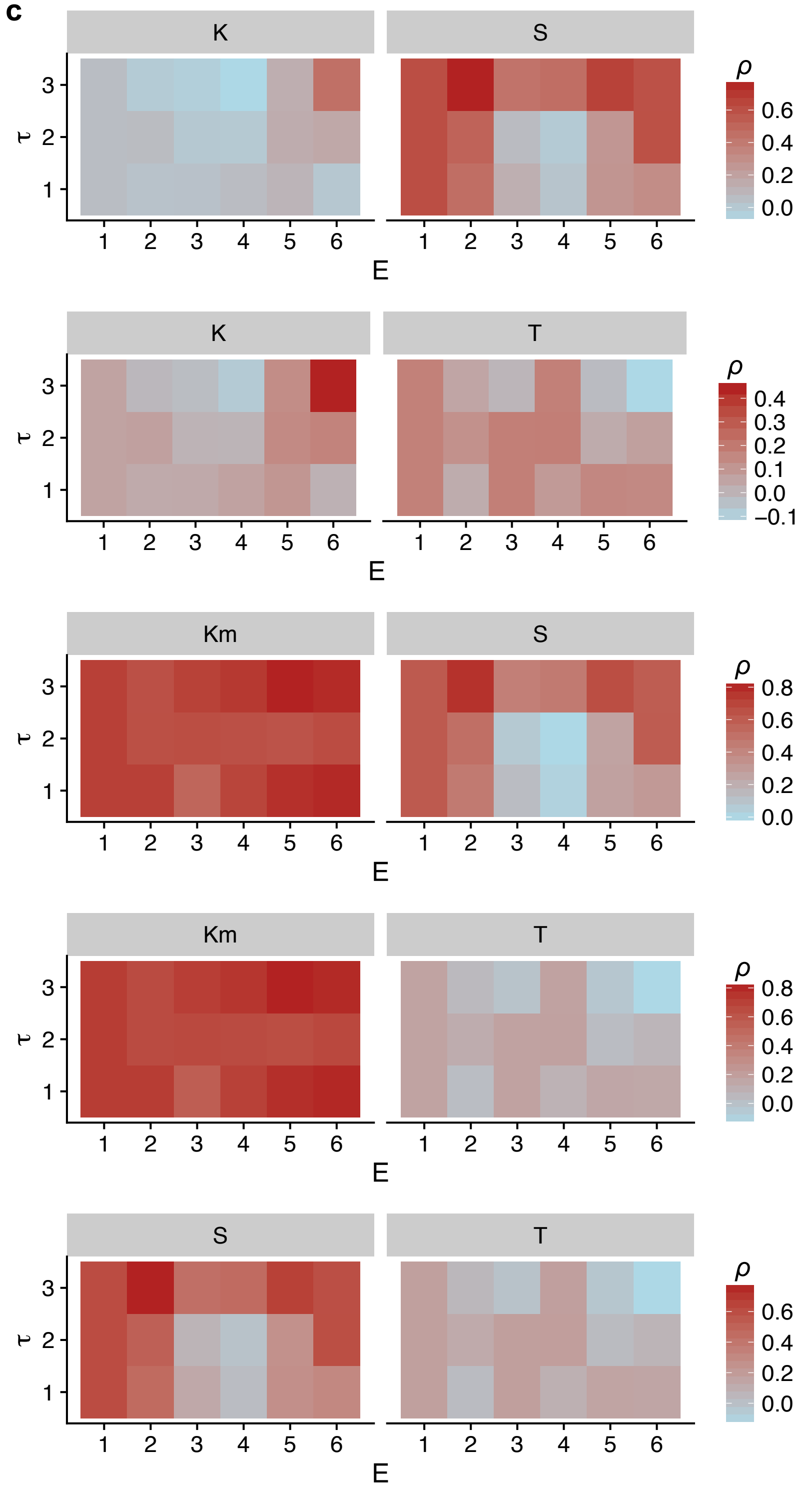

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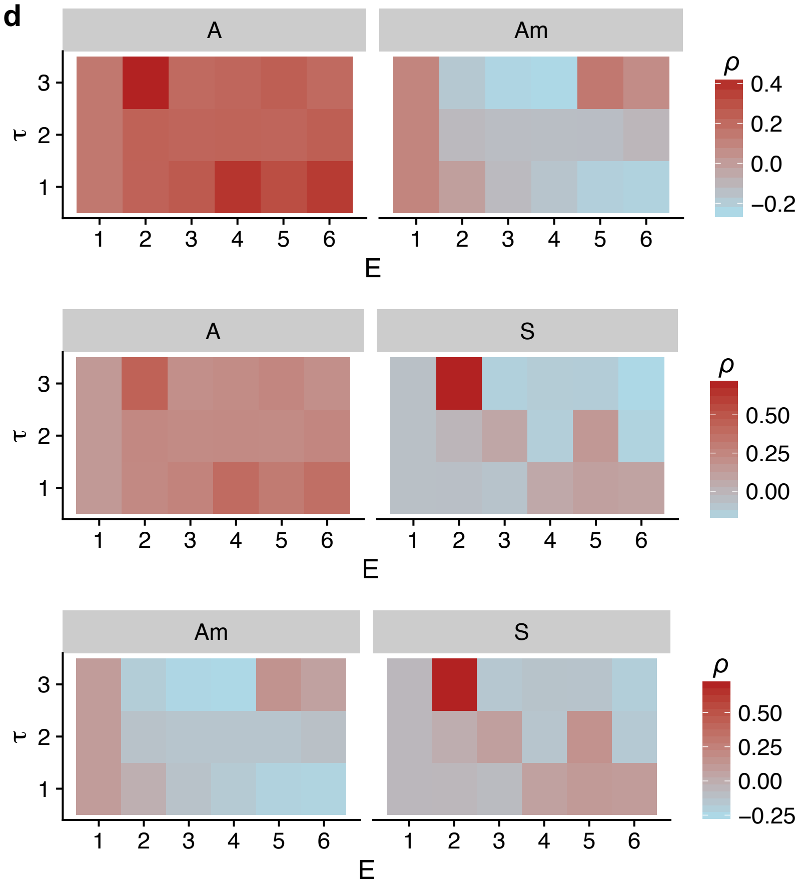
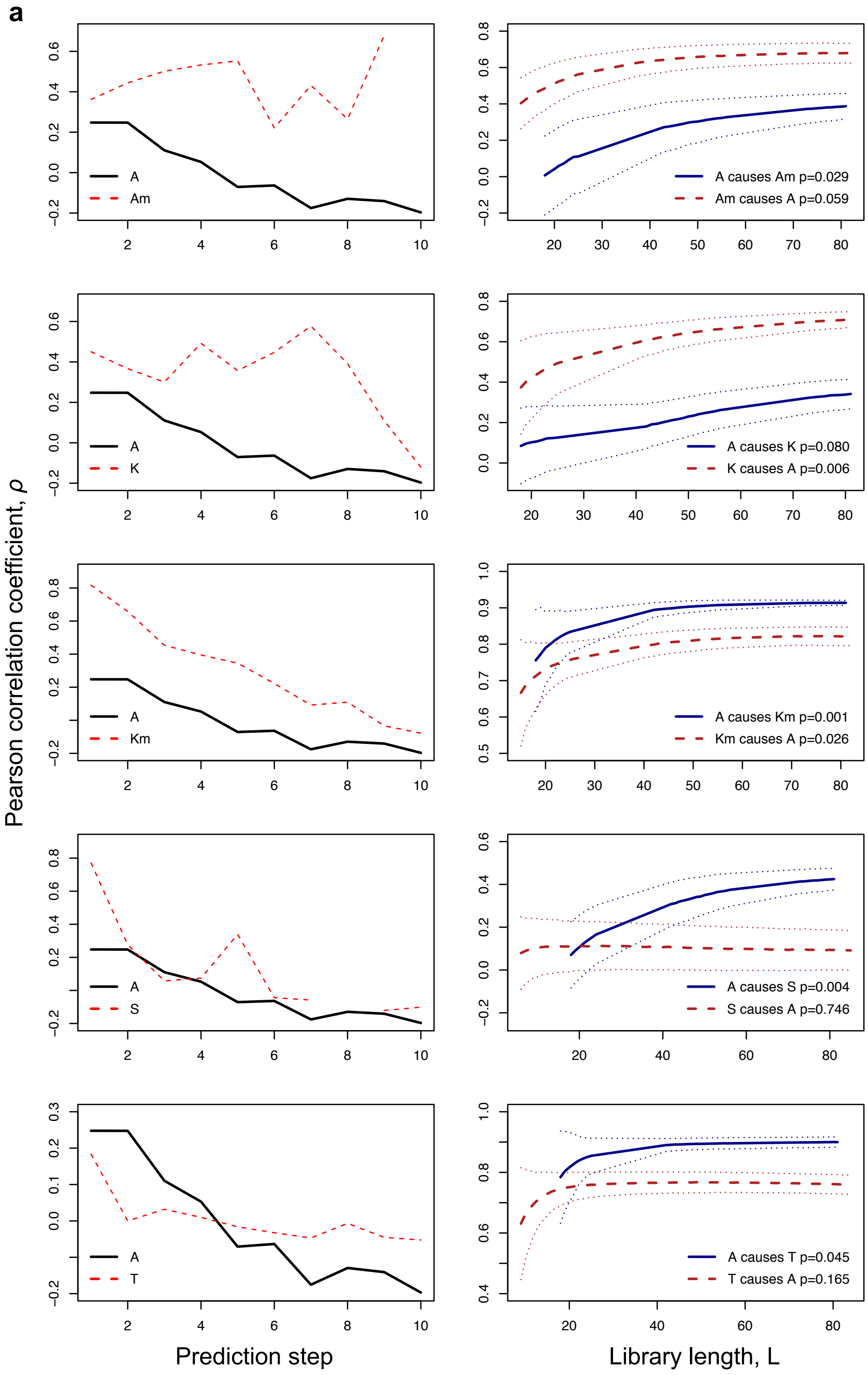


Figure S3. Pearson correlation coefficient (ρ) for each species combination as a function of length of the time steps used time delay of the causal effect (τ) and embedding dimension (E) for microcosms without predator (a,b,c) and microcosms without predator (d). Best combination of τ and E, which increased ρ was used in CCM analysis.



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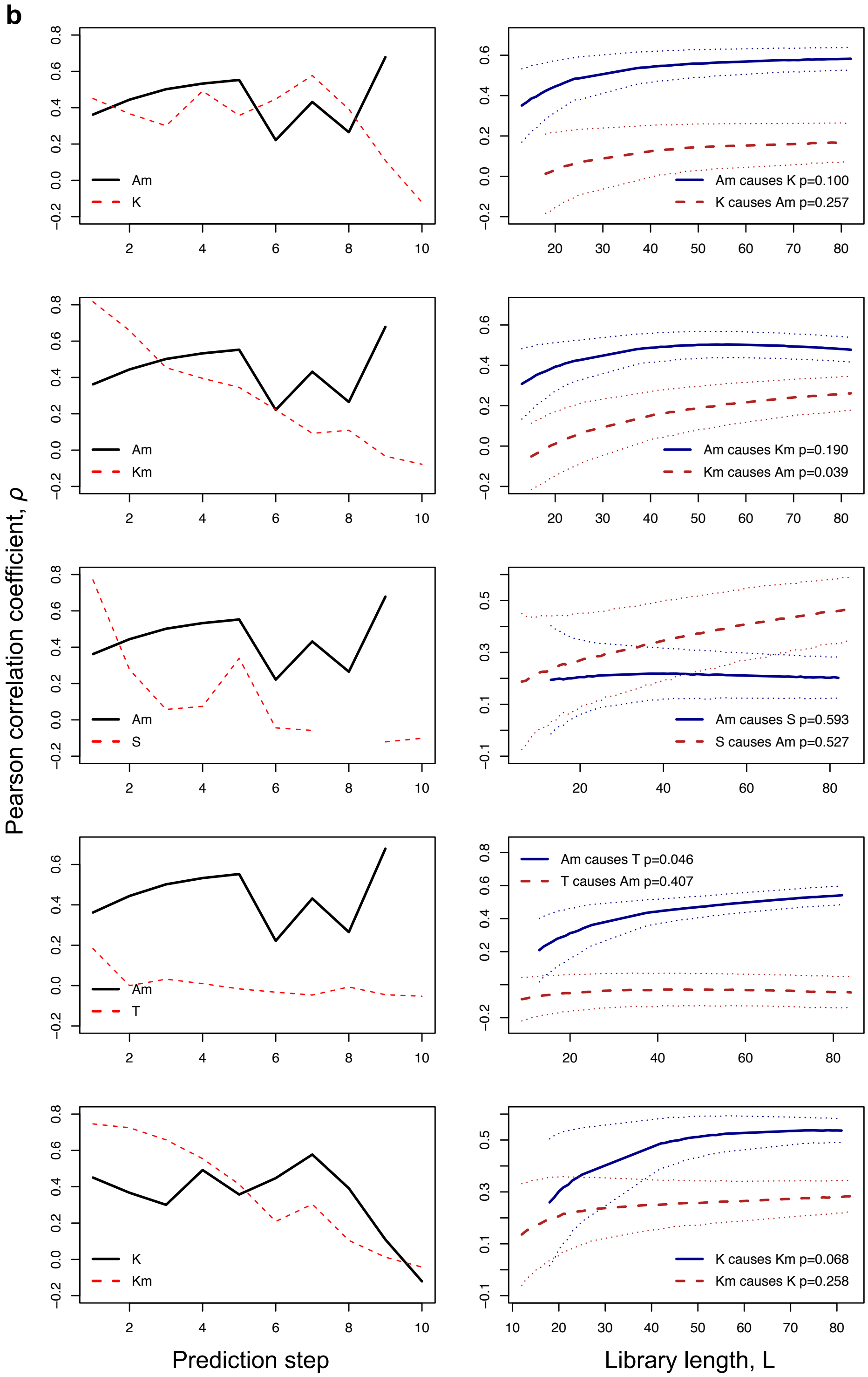

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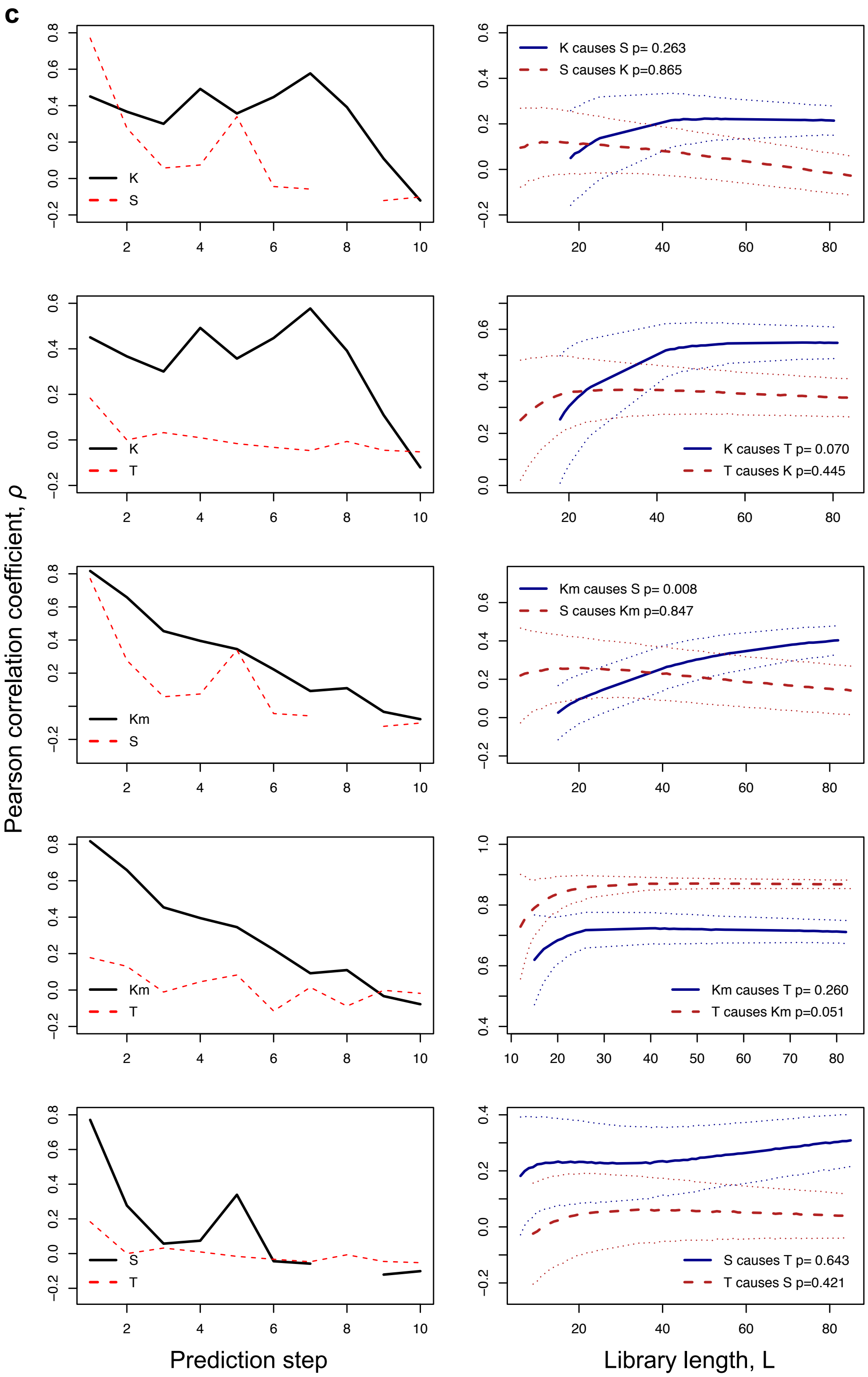

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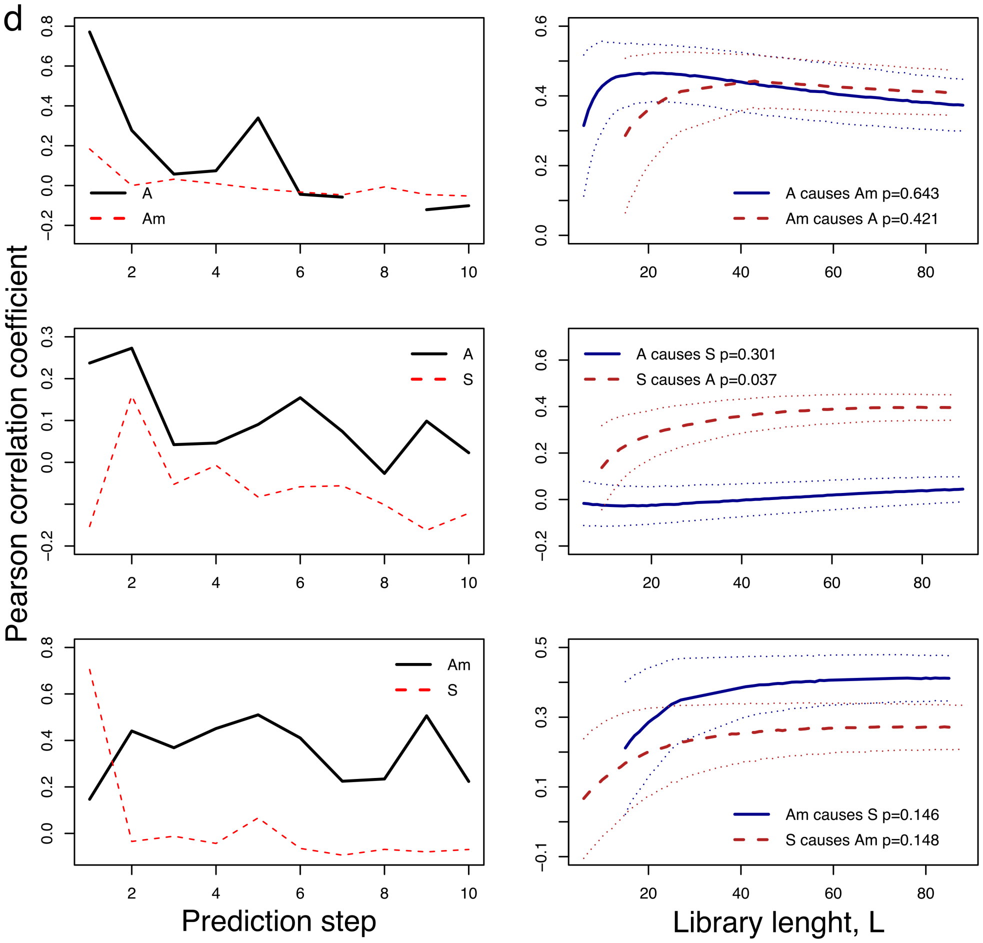

Figure S4. Left panel shows the Pearson correlation coefficient (ρ) as a function of prediction step, ρ should ideally reduce with increasing prediction step (see Methods of the main text). Right panel shows the multispatial CCM. a,b,c are for microcosms with and d for microcosms without predation. Solid and dashed lines show mean and ± SD from bootstrapped iterations. Causal forcing is indicated when the Pearson correlation coefficient is significantly greater than zero for large library length, L (number of historical observations times the number of replicates) and that increases significantly with increasing L. Legends show the direction of the causes and their significances.

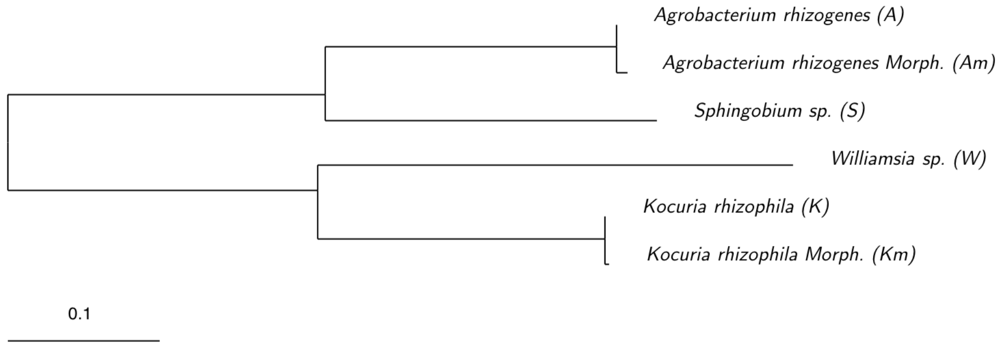

Figure S5. Phylogenetic tree of the set of four species used in this study and the two morphotypes. The tree is based on the full 16S gene and the branch lengths indicate the number of substitutions per base pair.