



Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt

Lehrstuhl für Terrestrische Ökologie

Plant diversity impacts on arthropod communities and arthropod-mediated processes

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Vollständiger Abdruck der von der Fakultät

Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt
der Technischen Universität München zur Erlangung des akademischen Grades eines

Doktors der Naturwissenschaften (Dr. rer. nat.)

genehmigten Dissertation.

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Prüfer der Dissertation:

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2. Univ.-Prof. Dr. Nico Eisenhauer
Universität Leipzig
3. Dr. Eric Chauvet
Université Paul Sabatier, Toulouse (FRANCE)

Die Dissertation wurde am **31.01.2017** bei der Technischen Universität München eingereicht und durch die Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt am **20.03.2017** angenommen.

To Mr. Gindesberger who taught me to read and write but went away to soon

Acknowledgements

Doing a PhD is not only an adventure into the mists of the unknown guided by the light of Science, it is also a human experience sometimes trampling through the muds of despondency. In the following I would like to thank all the people that helped me in fighting both the mists and the muds over the last 3 years.

My first thanks go to my supervisor Prof. **Wolfgang Weisser** for putting his trust in me and giving just the right dose of freedom and control to safely explore the mists. I was extremely lucky to be supported throughout my work by two amazing Co-supervisors with complementary expertise personifying the benefits of diversity. **Anne Ebeling** was my guardian spirit during data sampling doing tiny but daily miracles in finding solutions to the thousands of issues inherent to field sampling. **Sebastian Meyer** has the rare skill to be able to read through the jumble of badly formed words, sentences and paragraphs that I pompously call manuscript and to see how by re-structuring, re-phrasing, re-doing some analysis the badly formed piece of science can become an actual manuscript. I am deeply grateful to both of them for being available to my diverse questioning and always helping me go forward.

Coming to Jena I was welcomed as a guest in the young and dynamic group of Prof. **Nico Eisenhauer**, who later became my mentor always providing me with encouragement and positive feedbacks on my research. I am deeply grateful to all members of Nico's research group in particular to **Dylan Craven** for insightful discussions on science, to **Mahdav Thakur** for sharing our interests as stats nerds on the last super-cool modeling techniques but also for talking about big ideas and to **Katja Steinauer** for being a cheerful office mate and a great friend.

The Jena experiment gathers together a team of scientists motivated to bring together their expertise to answer the same questions. I would like to thank all members of the research group for creating a scientific cradle where PhDs can grow as scientists. In this regard I would like to especially thank **Cameron Wagg**. As a PhD one is often alone in front of his/her research, not in the Jena experiment where I could share my ups and downs with other fellows during unforgettable summer nights, therefore thank you: **Jordan**

Guiz, Julia Tiede, Jan-Hendrick Düdenhoffer, Sigrid Dassen, Clemens Kleinspehn and Natalie Oram.

Scientists are crazy, they want to sample everything with a high degree of replication with little ideas of the efforts that it implies, lucky for my poor body dedicated people supported me in surmounting field frenzy. I would like to deeply thank the technical assistant at the institute for ecology in Jena for their decisive help in field sampling: **Gerlinde Kratzsch, Silke Schroeckh, Ilka Wolff and Syliva Creutzburg**. Die Gärtner halten das Jena-Experiment zusammen, die waren auch immer bereits zu helfen, vielen danke an: **Silke Hengelhaupt, Ute Köber, Katja Kunze, Heike Scheffler and Steffen Eismann**. Hundreds of anonymous HiWis continuously and through the years weed, sample, process and weigh at the Jena experiment they are the little invisible hands that keeps it all going, thank you.

My gratitude also extends to people at the Institute for Ecology in Jena. Thanks to **Désiré Dotter** for putting some life and joy in the office but also for countless Spielabend, one of the best way to clear your mind after a day in science. Thanks to **Jan Engel** for dropping daily by our office to ask big and small questions and being generally always positive and super motivated. Thanks to **Günther Köhler** for drawing me down from the cozy world of stats down to the messy grounds of nature where field ecologists roam and nothing is normal.

Thank you to all members of the terrestrial ecology group in Freising for creating a nice and friendly environment where an immigrant from Jena could find its place. In particular thanks to **Nadja Simmons** for always sharing with enthusiasm new tools or methods but also for providing me the Latex template for the thesis. To **Maxi Mühlbauer** for being a great office mate, being able to talk one minute about the future of immigration in Europe, the next one about beach volleyball and the next one being busy identifying a wasp that entered the office. To **Mathias Senft** for sharing common excitement about data and R but also for intense Tischtennis sessions. To **Brigitte Grimm** for always finding solutions to my administrative problems despite me being late or sloppy.

I met a super friendly, super-bouncy swing community in Jena, thank you all for the dances and the laughs, in particular thanks to **Toni, Luise (Eichelkraut), Conny and David. Luise (Eichhorn)** quenched some of my outdoor thirst, thanks for sharing tiring but deeply satisfying hiking folly. Despite being mostly away in this strange country which is Germany my friends and family never stopped to support me from this vague place called home. Merci à vous tous pour votre soutien indéfectible, pour toujours être là, la porte grande ouverte lors de mes passages en coup de vent de l'autre côté du Rhin. Merci tout particulièrement à ma famille. Mes **Parents** pour m'avoir ouvert les yeux très tôt au

travers de balade en montagne à la beauté simple et farouche de la nature, alimentant ma fascination pour l'écologie. À **Bruno** (aka Bro'), super et irremplaçable compagnon de jeu tout terrain, des montagnes au poste informatique mais aussi intransigeant et furieux orateur envers la médiocrité humaine généralisée. À mes **Grands-Parents** pour leur douce présence, leur simplicité et leur constance si rare dans un monde où tout va très vite.

Table of contents

| | |
|--|-----------|
| Zusammenfassung | xi |
| Summary | xv |
| 1 Introduction | 1 |
| 1.1 Motivation - Human impacts on the Biosphere | 1 |
| 1.2 Biodiversity Ecosystem Function research - A brief history | 2 |
| 1.3 Early BEF theories | 5 |
| 1.4 BEF theories applied to consumers | 8 |
| 1.5 BEF in multitrophic systems | 10 |
| 1.6 Diversity and stability | 12 |
| 1.7 Arthropods and ecosystem functioning | 13 |
| 1.8 Thesis Outline | 16 |
| 2 Study system and methods | 19 |
| 2.1 The Jena experiment | 19 |
| 2.1.1 The Main Experiment | 19 |
| 2.1.2 The Trait-Based Experiment | 21 |
| 2.1.3 Field management | 22 |
| 2.2 Measurements of vegetation properties | 23 |
| 2.3 Arthropod sampling | 23 |
| 2.4 Arthropod traits | 24 |
| 2.5 Herbivory measurements | 24 |
| 2.6 Predation measurements | 25 |
| 2.7 Data availability | 26 |
| 2.8 Statistical analyses | 28 |
| 2.8.1 Structural equation modelling | 28 |
| 2.8.2 Generalized Linear Mixed-effect Models | 28 |

Table of contents

| | |
|---|-----------|
| 3 Manuscript overview | 31 |
| 4 Main Findings | 41 |
| 5 Discussion | 45 |
| 5.1 Complex shifts in arthropod communities | 46 |
| 5.2 Plant diversity consistently increase herbivory | 48 |
| 5.3 Predation and plant diversity | 50 |
| 5.4 Mechanisms linking plant diversity to herbivory and predation | 51 |
| 5.5 Advance and limitations of BEF experiments | 53 |
| 6 Conclusion | 55 |
| References | 57 |
| Appendix A Curriculum Vitae | 71 |

Zusammenfassung

Der derzeitige Verlust an Biodiversität lässt Bedenken am Weiterbestehen von Ökosystemfunktionen in einer artenarmen Welt aufkommen. Die experimentelle Forschung der letzten 20 Jahre hat ergeben, dass der Einfluss von Biodiversität auf Ökosystemfunktionen mindestens genauso groß ist wie der von globalen Veränderungen. Die meisten dieser Studien haben wenige Ökosystemfunktionen untersucht, wie zum Beispiel Pflanzenproduktivität, während die multitrophischen Auswirkungen des Verlusts an Biodiversität erst vor kurzem in den Fokus gerückt sind. Arthropoden sind ein wichtiger Bestandteil von Graslandökosystemen, da sie Pflanzen mit dem Rest der Nahrungsnetze verbinden. Auch bilden Arthropoden komplexe Interaktionen und trophische Netze. Diese Doktorarbeit untersucht den Einfluss von Pflanzendiversität auf Arthropodengemeinschaften und Ökosystemfunktionen wie Herbivorie und Prädation, die wiederum von Arthropoden reguliert/beeinflusst werden.

Das erste Manuskript befasst sich mit dem Einfluss von Pflanzendiversität auf Arthropodendiversität auf unterschiedlichen Trophienebenen und mit den zugrundeliegenden Mechanismen. Arthropodendichte und -diversität steigt mit der Anzahl an Pflanzenarten, auf verschiedenen trophischen Ebenen. Jedoch unterscheiden sich die dafür verantwortlichen Mechanismen zwischen Herbivoren und Carnivoren. Veränderungen in der Dominanzstruktur entlang des Pflanzendiversitätsgradienten sind ebenfalls abhängig von der trophischen Ebene. Wenn die Dominanz der Herbivoren abnahm, stieg die Dominanz der Carnivoren, was auf verschiedene Grade von Spezialisierung der dominanten Arten der zwei trophischen Ebenen hindeutet.

Das zweite Manuskript beinhaltet eine Zeitreihe von Herbivoriedaten, zusammengestellt aus Daten über 5 Jahre und aus zwei verschiedenen Pflanzendiversitätsgradienten. Herbivorieraten auf Gemeinschaftsebene zeigten eine große Variation im Bereich von 0 bis 31%. Sie waren im Sommer höher als im Frühling. Herbivorieraten stiegen mit der Pflanzendiversität an, unabhängig von Jahr und Diversitätsgradient. Eine wahrscheinliche Erklärung für die Steigerung sind Veränderungen in der Pflanzenqualität oder in den Arthropodengemeinschaften.

Zusammenfassung

Höhere Herbivorieraten entlang eines Pflanzendiversitätsgradienten könnten durch sogenannte “Selection-effects” entstehen, da die Wahrscheinlichkeit, dass in einer diversen Mischung attraktive Pflanzen vorkommen, höher ist, als in einer artenarmen Mischung. Deswegen haben wir im dritten Manuskript den Diversitätseinfluss in seine Komplementaritäts- und Selektionskomponenten aufgeteilt. Die Ergebnisse zeigen, dass der positive Einfluss von Pflanzendiversität auf die Herbivorieraten durch eine Erhöhung der Komplementaritätseffekte verursacht wurde. Das Jahr der Datenerhebung hatte keinen Einfluss auf diesen Zusammenhang, obwohl eine Verminderung in durchschnittlicher Komplementarität über die Jahre hinweg möglicherweise ein Absinken der Herbivorieraten widerspiegelt. Das vierte Manuskript beinhaltet Ergebnisse zu Erhebungen von Prädationsraten mittels drei verschiedener Arten von Beuteködern entlang zweier experimenteller Pflanzendiversitätsgradienten. Es wurde ein positiver und konstanter Einfluss von Pflanzendiversität auf Prädationsraten festgestellt, unabhängig von Jahreszeit und Beuteart. Außerdem zeigten sich ähnliche Effekte in den beiden Pflanzendiversitätsgradienten trotz unterschiedlicher Artenpools, Länge und Altersstruktur.

Das letzte Manuskript stellt die Synthese der Daten zu Arthropodengemeinschaft, Zusammensetzung der Pflanzengemeinschaft und der Ökosystemfunktionen dar, die durch die Arthropoden beeinflusst werden. Mit Strukturgleichungsmodellen wurden die potentiellen Mechanismen, die dem positiven Effekt von Pflanzendiversität auf Herbivorie und Prädationsraten zugrunde liegen, untersucht. Durch die explizite Trennung der Omnivoren von den Herbivoren und Carnivoren zeigten wir, dass Omnivorendiversität einen sehr wichtigen Faktor für die Effekte von Pflanzendiversität auf Herbivorie und Prädationsraten darstellt. Wir fanden heraus, dass Abundanz-gewichtete funktionelle Diversität im Vergleich mit Biomasse, Artenreichtum, Simpsondiversität oder ungewichteter funktioneller Diversität der beste Prädiktor ist. Pflanzenstruktur hat einen starken Effekt auf Herbivorie aber nicht auf Prädation.

Im letzten Manuskript berichtete ich über die überraschende Widerstandsfähigkeit von Ameisengemeinschaften gegenüber einem Jahrhunderthochwasser.

Mit Hilfe eines der ältesten Feldexperimente im Bereich Biodiversität und Ökosystemfunktionen und zusammen mit der Forschergruppe, die sich um diese Plattform herum gebildet hat, hat diese Dissertation unsere Erkenntnisse über die Auswirkungen von Biodiversitätsverlust in einem multitrophischen System erweitert. Diese Dissertation ergab, dass Arthropoden in allen trophischen Ebenen von Veränderungen in der Pflanzendiversität beeinflusst werden. Daraus folgt, dass diverse Ökosystemfunktionen dadurch ebenfalls beeinflusst werden. Das Verständnis dieser Mechanismen, die für die Interaktion zwischen der Diversität von Konsumenten und Produzenten verantwortlich sind,

ermöglicht es uns bessere Managementstrategien in Kulturlandschaften zu entwickeln, um Biodiversität zu schützen und gleichzeitig das gewünschte Niveau an Ökosystemfunktionen zu erreichen.

Summary

Current loss of biodiversity is raising concerns over the functioning of ecosystems in a species-poor world. Two decades of experimental work on biodiversity and ecosystem functions revealed that biodiversity effects on ecosystem functions were at least as large as other global change drivers. Most of these studies focused on few ecosystem functions like plant productivity while multitrophic consequences of biodiversity loss have recently started to gather attention. Arthropods are a key component of grassland systems linking plants to the rest of the food webs but also forming complex interaction and trophic webs. This thesis evaluates the impacts of plant diversity on arthropod communities and on ecosystem functions that are mediated by arthropods, such as herbivory and predation. The first manuscript looked at the effect of plant diversity on arthropod diversity across trophic levels and explored potential mechanisms. Arthropod density and diversity increased with plant richness across trophic levels but the mechanisms responsible for this pattern differed between herbivores and carnivores. Changes in dominance structure across the diversity gradient were also trophic-dependent, while herbivore dominance declined, carnivore dominance increased implying different levels of specialization for the dominant species of the two trophic levels.

In the second manuscript, a time series on herbivory data measured in a standardized way was assembled spanning 5 years of data in two different plant diversity gradients. Community-level herbivory rates showed large variation ranging from 0 to 31% of consumed leaf area and being higher in summer than in spring. Herbivory consistently increased with plant species richness across the years and the two experimental gradients potentially due to changes in plant quality or in arthropod communities.

Increase in herbivory rates along a plant diversity gradient could be driven by so-called selection effects where the presence of attractive plants would be driving the patterns. Therefore, in the third manuscript we partitioned the plant diversity effect on herbivory into a complementarity and a selection component using data collected across 4 years. The results showed that an increase in complementarity along the plant diversity gradient was driving the positive effect of plant diversity on herbivory. This increase was

Summary

not affected by the years even if average complementarity declined over time potentially mirroring the observed temporal decline in herbivory rates.

The fourth manuscript reported results from an assessment of predation rates using three different types of sentinel prey items along two experimental gradients of plant diversity. Consistent and positive effect of plant diversity across seasons and type of baits were found. In addition, similar effects were present in the two plant diversity gradients despite their variations in species pool, gradient length and also gradient age.

The fifth manuscript brought together data on arthropod community, plant structure and arthropod-mediated ecosystem functions. Using structural equation modelling we explored the potential mechanisms explaining the positive effect of plant diversity on herbivory and predation through changes in arthropod diversity and plant structural complexity. By explicitly separating omnivores from herbivores and carnivores we could show that omnivore diversity was key in explaining the positive effect of plant diversity on herbivory and predation. We found that abundance-weighted functional diversity was the best predictor of functioning rates compared to biomass, species richness, simpson diversity or unweighted functional diversity. Plant structural complexity had a strong positive effect on herbivory but none on predation.

Finally, the last manuscript reported the surprising resistance of the ant communities to a rare flooding event.

Taking advantage of one of the oldest field site on biodiversity ecosystem function, this thesis expand our knowledge on the multitrophic consequences of biodiversity loss. It revealed that across trophic level arthropods are affected by changes in plant diversity which in turn leads to variations in the rates of functioning of the system. Understanding the mechanisms at play between consumer and producer diversity enable us to design better management strategies in cultural landscapes to conserve biodiversity while providing desirable level of ecosystem functioning.

Chapter 1

Introduction

In amnesiac reverie it is also easy to overlook the services that ecosystems provide humanity. They enrich the soil and create the very air that we breathe. Without these amenities, the remaining tenure of the human race would be nasty and brief. [...] The ethical imperative should therefore be, first of all, prudence. We should judge every scrap of biodiversity as priceless while we learn to use it and come to understand what it means to humanity.

E.O. Wilson, *The diversity of life* (1992)

1.1 Motivation - Human impacts on the Biosphere

Twenty-first century ecologists face a great challenge to provide society a better understanding on how natural *communities* contribute to *ecosystem functions* (Note *italicized* words are concepts defined in the Glossary on page 7). This would allow not only the development of mitigation strategies to reduce human impacts, but also the development of predictive and mechanistic *ecosystem* models to look at biosphere dynamics under different global change scenarios. Historically the study of ecosystems focused on the effect of abiotic parameters, such as temperature or precipitation, on energy and matter flows through systems. However, organisms are breathing, eating, synthesizing chemical compounds, absorbing CO₂ and much more. Therefore, ecosystem functions are not only affected by abiotic parameters but also by organismic communities which inhabit the system [Chapin III et al., 1997]. Thus, the *diversity*, the relative abundance of organisms but also the presence of particular keystone species, such as nitrogen-fixing plants, can all affect ecosystem functioning [Chapin III et al., 2000]. As a result if the community is changing due to anthropogenic pressures such as species invasion, land-use changes,

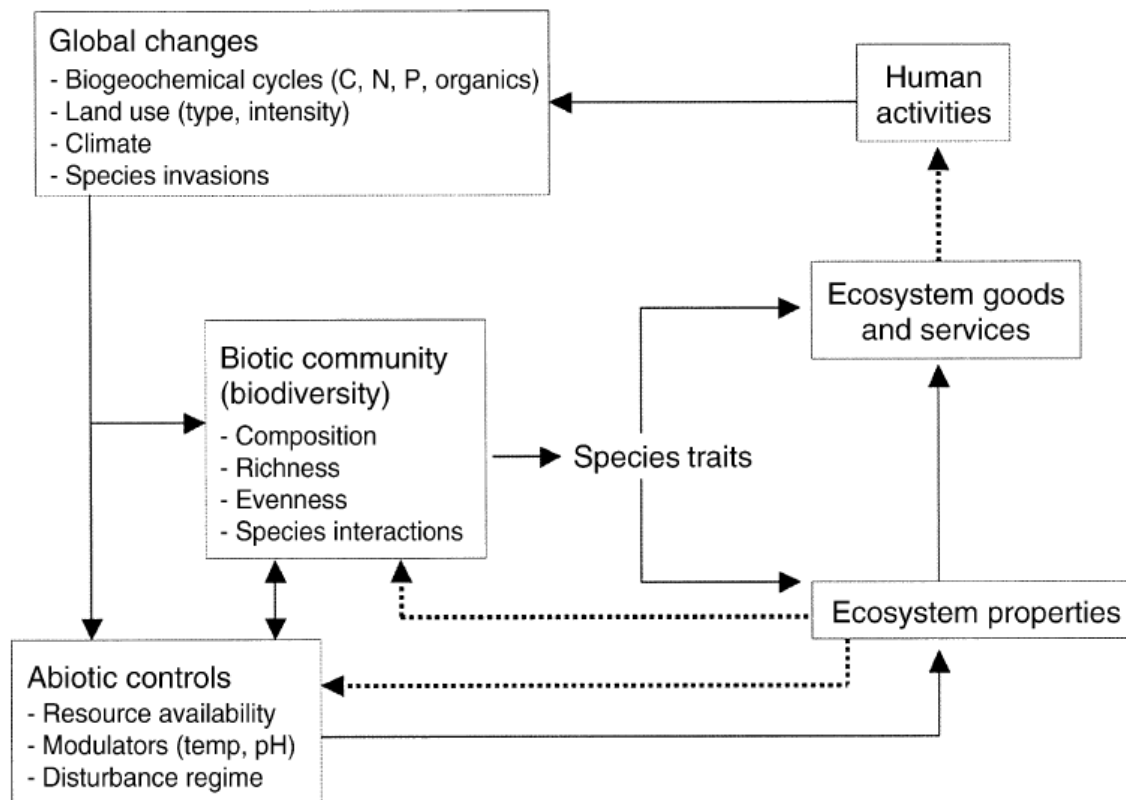


Fig. 1 Relations and feedbacks between human activities, global change drivers and ecosystems. Human activities trigger changes like land-use variations or species invasion which affect both the biotic and abiotic components of the ecosystems. This lead to altered functional traits composition and to changes in ecosystem functioning. Figure from Hooper et al. [2005]

climate changes or exploitation, ecosystem functioning might be affected (Fig. 1). In this context, the broader objective of my thesis is to enhance our understanding of the links between species diversity and ecosystem functions in a grassland system.

1.2 Biodiversity Ecosystem Function research - A brief history

Already Darwin was aware of the links between diversity and ecosystem functions in his book the “Origin of species”, he wrote: “It has been experimentally proved that if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised.” Chp4, pg185, cited in Hector and Hooper [2002]. Darwin referred to an

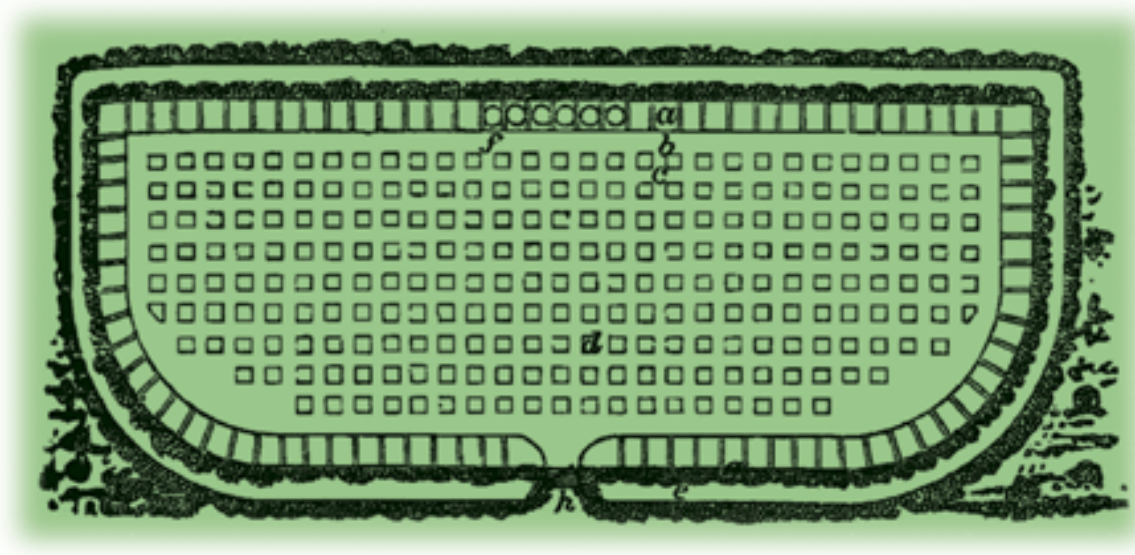


Fig. 2 Experimental design of the first BEF experiment conducted at Woburn Abbey (UK) in 1857 [Hector and Hooper, 2002].

experiment conducted in England in the beginning of the 19th century where different mixtures of grasses and forbs were sown in different types of soil in 242 plots, this was clearly the earliest ecological field experiment and the earliest grassland BEF experiments (Fig. 2).

After this early start little experimental work was done on the links between biodiversity and ecosystem function (BEF) for over a century. In the wake of the Earth Summit in Rio (1992), Schulze and Mooney edited the proceedings of a conference held in Bayreuth on Biodiversity and Ecosystem Function which was published in 1994 [Schulze and Mooney, 1994]. This was the beginning of an explosion of experimental research in laboratory and field settings. Influential papers in this first generation of BEF research are for example: Hector et al. [1999]; Naeem et al. [1994]; Tilman and Downing [1996]. Showing that plant productivity increased with plant diversity across experimental settings and geographical locations. However, controversies quickly arose attacking the interpretation of the experimental results reported in these studies. Huston [1997] and Aarssen [1997] independently raised the concern that biodiversity was not the cause of the observed effects, but rather some hidden treatment. They argued that at higher levels of diversity the probability to include highly performing species was higher. Such an effect was later called sampling effects and a debate arose as to whether such a mechanism was a diversity effect per se or just statistical artifact of the experimental design used (See the discussion in the next section). In addition because of the potential applications

Introduction

of the discoveries in BEF studies for biodiversity conservations, media coverage of the first modern papers [i.e. Naeem et al., 1994; Tilman and Downing, 1996] and the ensuing debate on BEF was relatively strong and passionate [Kaiser, 2000]. Protagonists on both sides of the debate came together to publish a consensus paper that served to summarize the current knowledge and directions for future research [Hooper et al., 2005]. This was quickly followed by two influential meta-analysis which gathered data from hundreds of published BEF studies that showed that increases in *producer* diversity has a positive effect on different ecosystem functions like primary *consumer* abundance and diversity [Balvanera et al., 2006]. In addition, decreasing diversity at different trophic levels lead to decline in biomass at these focal trophic levels through lower resource use [Cardinale et al., 2006]. At the same time critiques emerged concerning the usefulness of BEF studies to motivate biodiversity conservation, one of the implicit goal of BEF studies. Namely, biodiversity is useful to humankind through its effect on ecosystem functions, this is why we should protect it. Srivastava and Vellend [2005] raised three main concerns in this regard: (i) a scaling issue, BEF experiments are in their vast majority on a local-scale when conservation practices operate at the regional scale and there is limited knowledge even today on the links between regional diversity and local ecosystem functioning (but see Smith and Schmitz [2016]). (ii) to allow adequate statistical analysis of BEF experimental data, most BEF studies use random species-loss scenarios whereas under real conditions covariance between *traits* affecting species extinction risks (i.e. large body size) and *functional traits* (i.e. hunting mode) might amplify or weaken the relationships found under random-loss scenarios [De Laender et al., 2016; Duffy et al., 2003]. Several studies compared random and non-random species loss in field experiment and confirmed the differences between the two species loss scenarios [Selmants et al., 2012; Smith and Knapp, 2003]. (iii) drivers of diversity loss (i.e. species invasion, climate change) will affect ecosystem functioning both directly but also indirectly through changes in biodiversity (See Fig. 1). Therefore, it might be that the direct effects of global change drivers on ecosystem functions are much stronger than the indirect effect. Several syntheses revealed since then that biodiversity effect on ecosystem functions are at least as large as other direct drivers like climate warming, nutrient enrichment or herbivory [Hooper et al., 2012; Tilman et al., 2012]. To allow stronger relevance of BEF experimental data, Hillebrand and Matthiessen [2009] and Reiss et al. [2009] independently published pleas towards the BEF field to embrace the complexity inherent in natural ecosystems. They argued for the development of new experiments explicitly tackling functional diversity, multitrophic interactions and multiple ecosystem functions. This call was heard as new experiments manipulating functional diversity at the producer level were created [Ebeling et al., 2014; Tobner et al., 2014], together with

experiments manipulating functional diversity at multiple trophic levels [Lefcheck and Duffy, 2015] and with synthesis on multifunctionality along diversity gradient [Lefcheck et al., 2015]. To wrap up, the field of Biodiversity Ecosystem Function went through several phases from early theoretical and experimental work focusing on the producer level and variation in productivity along experimental species richness gradient up to the recent advance in linking BEF with food web theory in a multitrophic and multifunctional framework [Hines et al., 2015]. In the next sections I will look at the various mechanisms that links biodiversity to ecosystem functions, first at the producer level, then at the consumer levels and finally at multitrophic biodiversity-ecosystem function relations.

1.3 Early BEF theories

The development of the BEF field was a paradigm shifts in ecological studies. Previously diversity was considered as a response variable depending on factors like altitude, productivity or temperature. However ecosystem ecologists brought to community ecology the concept that biotic composition also affect ecosystem functioning [Chapin III et al., 1997], which led to the questioning whether some emergent properties of the biotic communities like species diversity could affect functioning as well [Schulze and Mooney, 1994]. Most of the BEF studies use a loose definition of diversity and usually use it as a synonym of species richness (i.e. Kinzig et al. [2001] but see Glossary). At the producer level there are two main classes of mechanisms that might be responsible for a positive relation between species richness and ecosystem function: sampling effect and complementarity [Tilman and Lehman, 2001]. Sampling effects state that any species is more likely to be present (sampled) in a diverse mixture than in an impoverished one. If a positive co-variance between species dominance and species impact on the focal function is present, and if the community assembly process is random, higher richness leads to higher functioning [Wardle, 1999]. Ecologists do not agree on the relevance of sampling effects for real-world ecosystems. Some argue that to accept sampling effect as a diversity effect in natural systems we need to assume that communities are randomly assembled with respect to the function under study [Wardle, 1999] which is unlikely [Weiher and Keddy, 2001]. While other argue that high diversity ensure that a broad range of trait variation is available in the community before the onset of a selective process which will increase the chance to have dominant species with high impact on the functions in the community [Loreau, 2000]. The second class of mechanisms, complementarity or *niche* differentiation, state that when species differ in: (i) what type of resource they use, (ii) which relative quantities of resources is used, (iii) when they start and stop consuming resources (temporal

Introduction

partitioning) and (iv) where they get their resources from (spatial partitioning). These differences lead locally richer habitats to consume more of the limiting resources [Chase and Leibold, 2003] and therefore lead to greater biomass stocks at the focal trophic level. One major difference between sampling effects and niche differentiation mechanisms is that in the latter several species co-exist, while in the former the dominant species competitively drives all other species in the mixture to extinction. Analysis of long-term experimental data show a shift over time in the main mechanism driving the positive BEF relation. Patterns from earlier years show the signature of sampling effects, while for latter years complementarity effects dominate the BEF relation [Marquard et al., 2009; Tilman et al., 2001]. Pacala and Tillman [2002] argued that this was due to a shift from the importance of exponential growth of the dominant species in the establishment phase of the communities to the slower dynamics of intraspecific competition that leads to niche complementarity in later stages. These results were confirmed by the analysis of two long-term BEF experiments. This analysis revealed that 13 years after the establishment of the diversity gradients the functional redundancy of diverse mixtures declined leading to larger complementarity [Reich et al., 2012]. Recent work have shown that other mechanisms may explain the positive relation between plant species richness and ecosystem function, such as pathogen accumulation in the soil of monocultures [Petermann et al., 2008] or niche differentiation through character displacements in mixtures [Zuppinge-Dingley et al., 2014]. Finally, several theoretical and empirical studies have shown that other diversity metrics could have effects on ecosystem functioning of at least a similar magnitude than species richness [Hillebrand et al., 2008; McGill et al., 2006; Wilsey et al., 2005]. This calls for reporting empirical links between a broader range of diversity metrics and ecosystem functions but also for the development of new theories explicitly dealing with features like dominance and its effect on ecosystem functioning.

Box 1: Glossary of important terms

Biodiversity: variations of life forms at different organizational levels (genes, species, ecosystems), in this thesis the word biodiversity will be used to refer to its broader sense.

Taxonomic diversity: variations of life forms at the species level based on the relative abundance of individual species, in this thesis the use of the word diversity will refer to taxonomic diversity.

Functional diversity: variations of life forms at the species level measuring differences in functional traits across species.

Trait: “A well-defined, measurable property of organisms, usually measured at the individual level and used comparatively across species” [McGill et al., 2006].

Functional trait: A trait directly affecting species contributions to ecosystem functions.

Producer: Photoautotrophs organisms, organisms that use the light as their energy source to turn inorganic carbon into organic compounds. Typically a plant.

Consumer: Chemoheterotrophs organisms, organisms that use chemical energy from organic compounds to fuel their metabolism. Typically an animal.

Ecosystem function: Stocks and fluxes of matter within and between ecosystem compartments (Plants, Primary consumers, Secondary consumers ...).

Ecosystem: Spatially-defined dynamic complex between communities and their environment interacting as a functional unit.

Community: “an assemblage of populations of plants, animals, bacteria and fungi that live in an environment and interact with one another, forming together a distinctive living system” [Whittaker, 1975].

Niche: “the joint description of the environmental conditions that allow a species to satisfy its minimum requirements [...] along with the set of per capita effects of that species on these environmental conditions” [Chase and Leibold, 2003].

Herbivory: The process of animal species eating living plant tissues.

Predation: The process of animal species actively hunting, killing and eating animal prey.

Disturbance: Abrupt change in the abiotic conditions, beyond their normal range, in a system [Schowalter, 2012].

1.4 BEF theories applied to consumers

The early theories and experimental work done on biodiversity and ecosystem function focused on the producer level. However, in real systems producers are not isolated from their consumers and consumer communities strongly affect ecosystem functioning. Both in terms of standing stocks at different trophic levels but also in terms of increasing the fluxes between ecosystem compartments [Chapin III et al., 2011].

Response of consumer biomass to variation in consumer diversity may be qualitatively different to what is observed at the producer level due to the potential overexploitation of preys leading to the collapse of prey populations [Ives et al., 2005]. In addition, consumer-consumer antagonistic interactions like intraguild predation [Polis et al., 1989] can also affect the links between consumer diversity and biomass. Ives et al. [2005] developed a series of theoretical models incorporating various mechanisms to the ones already present in the BEF literature (sampling and complementarity effects) with the added complexity of consumer population dynamics to predict relations between consumer diversity and consumer biomass. Their models revealed several interesting facts: when consumers are moderate generalists the relationship between consumer diversity and consumer density turn from linear to hump-shaped. Increasing consumer diversity from low to medium levels increase the amount of resource available to the consumer communities. But, when going from medium to high consumer diversity, prey species may become overexploited and driven to extinction. This in turn, reduce the amount of available resources which reduce consumer densities. More interesting, by including intraguild predation in the models, the relationship between consumer diversity and consumer density turn from hump-shaped to monotonically and linearly increasing and this irrespective of the strength of the intraguild predation. So it seems that intraguild predation may serve to stabilize consumer food webs by preventing the extinction of prey species. A result that is in agreement with several lines of empirical and theoretical research [Konno, 2016; Stouffer et al., 2007]. Cardinale et al. [2006] compiled data from 111 studies across trophic levels and found that consumer (herbivores, predators and decomposers) standing stocks were higher in species mixtures than the average standing stocks when each consumer species were alone.

Consumer diversity may not only affect the stocks of biomass present at different trophic levels, consumer diversity may also exert a control on the fluxes of matter throughout the system. Potentially all ecosystem functions mediated by consumers, such as pollination or decomposition may be responding to shifts in consumer diversity. In this thesis I focus on two consumer-mediated fluxes: *herbivory* - the transfer of matter from

1.4 BEF theories applied to consumers

the producer to the consumer level; and *predation* - the transfer of matter from animal preys to higher trophic levels (See definitions in Box).

Herbivore species are competing between themselves for the access to their resources. The presence of widespread interspecific competition between herbivore species leads to resource partitioning and specialization [Denno et al., 1995]. However despite resource partitioning and spatio-temporal segregation herbivore species might still indirectly affect one another when herbivores share the same plant host, for example through trait-mediated indirect interactions [Ohgushi et al., 2012]. Plants subject to herbivory might show short-term decrease in plant nutritional quality [Denno and Roderick, 1992] and increase the concentration in their defense and toxic compounds resulting in lower fitness for herbivore individuals feeding on them [Van Dam et al., 2005]. There are also some examples where different herbivore species feeding on the same host plant may facilitate each other's. For example the presence of aphids on a plant create a nutrient sink and other aphid species profit from the increased quality of the phloem circulating close to this nutrient sink [Forrest, 1971]. The emergent community-level effect of herbivore diversity on resource depletion (i.e. herbivory) was found to be positive in a meta-analysis looking at 70 studies in both terrestrial and aquatic systems [Cardinale et al., 2006].

Predator diversity may also affect the predation rates, depending on the relative importance of various mechanisms the emergent effect of predator diversity on community-level predation rates may change direction and magnitude [Roubinet, 2016]. These mechanisms include complementarity and synergetic effects [Snyder et al., 2006], sampling effects [Straub and Snyder, 2006], antagonistic interactions [Finke and Denno, 2005] or intraguild predation [Snyder and Wise, 2001]. The links between predator diversity and predation rates have important implications in the context of biological control with potentially high economic impacts [Letourneau et al., 2015]. However, several meta-analysis reported mixed results concerning the relations between predator diversity and predation rates [Cardinale et al., 2006; Griffin et al., 2013; Katano et al., 2015; Letourneau et al., 2009] asking whether the effects of predator diversity are general across ecosystem types [Tylianakis and Romo, 2010]. Schmitz [2007] argue that depending on the natural history of the predators, predation pressure may show different types of relation with predator diversity. For instance, predators with similar hunting mode and habitat domain will tend to interfere with one another and even maybe predate on one another [Polis et al., 1989], in these conditions increasing predator richness lead to risk-reduction effect on their preys. Therefore the effects of predator diversity on top-down control of prey populations will ultimately depend on the trait distribution and complementarity between the predator species [Schmitz, 2007].

1.5 BEF in multitrophic systems

Variations in diversity at one trophic level might affect the diversity and functioning of other trophic levels through a vast array of potential mechanisms. In the following section I will focus only on bottom-up diversity effects i.e. the impacts emerging from diversity variations at the producer levels on consumer diversity and consumer-mediated functions. This by no means imply that top-down and cascading effects are less important or widespread [Schmitz et al., 2000; Srivastava and Vellend, 2005].

Plant diversity have bottom-up effects on the consumer communities across trophic levels [Scherber et al., 2010]. There are various hypotheses explaining this relation. Consumers have specific niches determined both by abiotic conditions such as temperature and humidity as well as community composition [Chase and Leibold, 2003]. Higher diversity of producers increases the number of resource types available to primary consumers and lead to a broader array of structural and microclimatic conditions [Schmitz, 2008b]. Together these effects increase the number of niches available to different consumer species irrespective of their trophic levels, this is the resource heterogeneity or niche hypothesis. Consumers not depending on plants for their food sources (i.e. predators) might be affected by variations in plant diversity both directly through structural and microclimatic changes but also indirectly through changes in the community and diversity of their preys.

Plants are at the basis of most terrestrial food webs, higher standing stocks at the plant levels means that there is, potentially, more energy available for higher trophic levels. These increase in biomass across trophic levels would then lead to higher densities of consumers which would increase diversity through sampling effects and species accumulation curves or through higher degree of local persistence due to larger population sizes [Wright, 1983]. Together these mechanisms makes the productivity or more individual hypothesis [Srivastava and Lawton, 1998]. Both the niche and productivity hypotheses predict positive relation between plant and consumer diversity.

A meta-analysis of 27 studies published between 1954 and 2004 revealed that the diversity of primary consumers was increasing with plant diversity [Balvanera et al., 2006]. Scherber et al. [2010] reported that positive bottom-up effects of plant richness on consumer richness were widespread throughout both the aboveground and belowground food webs. Analysis in a long-term grassland diversity experiment revealed that both herbivores and carnivores arthropod species richness were increasing with plant richness, but that the mechanisms driving these relations were trophic-dependent with herbivores showing results supporting the niche hypothesis and carnivores supporting the productivity hy-

pothesis [Haddad et al., 2009]. Moreover, variation in different aspects of plant diversity could also lead to similar patterns between plant and arthropod diversity but due to different mechanisms [Dinnage et al., 2012]. For instance, Cook-Patton et al. [2011] showed that the positive effect of plant genetic diversity on arthropod richness were due to productivity while plant species richness effect were explained through resource specialization and were in line with the niche hypothesis.

Prey diversity can affect the efficiency of resource-use by their consumers, in other words prey diversity can affect the strength of top-down control [Duffy et al., 2007]. Four main hypotheses have been developed: (i) Dilution hypothesis: as diversity increases the relative abundance of the host of specialized consumers decreases lowering consumer efficiency in resource consumption [Root, 1973], (ii) Variance in edibility hypothesis: diverse prey communities are more likely to contain unpalatable prey species that, due to their escape from consumption, may out compete other palatable species [Duffy, 2002], (iii) Enemies hypothesis: diverse mixtures attract more predators which may control herbivores populations and lower their impacts on plant communities [Root, 1973], (iv) Balanced diet hypothesis: more diverse resource pools increase the range of nutritional inputs leading to larger consumer biomass and higher top-down control [DeMott et al., 1998]. The first three hypothesis predict a negative relation between prey diversity and consumption rates on the preys, while the last one predict the opposite pattern.

Several meta-analysis looked at the effect of prey diversity on top-down control, Hillebrand and Cardinale [2004] gathered studies on marine periphyton and found that the impact of grazers declined with increasing periphyton diversity. They attributed this pattern to either a variation in edibility or to a faster recovery of diverse prey assemblages. Balvanera et al. [2006] combined 103 studies on biodiversity and ecosystem function mainly from grassland systems and found that higher plant richness decreased plant damages. Jactel and Brockerhoff [2007] collected information from 119 tree-diversity studies and also reported a decline in herbivory with tree diversity, they conclude that their results could arise from dilution effects. Edwards et al. [2010] assembled data from 59 benthic experiments looking at the effect of consumer removal along a gradient of prey richness, they found reduced top-down control with increasing prey diversity concluding that variation in resistance to consumer was the likely mechanism.

Plant diversity can also indirectly affect predation rates through various mechanisms [Letourneau et al., 2009]. First of all, as plant diversity increases plant biomass [Hooper et al., 2005] the amount of energy available to all higher trophic levels increase leading

Introduction

to larger consumer standing stocks and to increased consumption rates [Oksanen et al., 1981]. Second, as described in a previous section, plant diversity also increases predator diversity and higher predator diversity can have a variety of effects on predation rates depending on specific predator community trait distribution [Preisser et al., 2007; Tylianakis and Romo, 2010]. Third, plant diversity may shift predator voracity either through sampling effect since predator species have varying feeding rates [Douglass et al., 2008] or through compensatory feeding to track changes in prey nutritional quality along diversity gradients [Abbas et al., 2014]. Fourth, plant diversity increases consumer diversity across trophic levels [Haddad et al., 2009] and all hypotheses reviewed in the previous paragraph (i.e. dilution hypothesis ...) may also be at play between carnivores and their preys. Finally, local structural complexity increases with plant diversity [Randlkofer et al., 2010] and this might lead to diverse effects on predation. Successfully locating and handling prey may be more difficult and time-consuming in complex local habitats [Diehl, 1988] reducing predation rates. On the other hand, complex habitats reduce intraguild predation by providing hiding places to predators and this may positively affect predation on the lower trophic levels [Finke and Denno, 2006]. In summary the emergent effect of plant diversity on community-level predation is hard to predict due to the great number of potential mechanisms that are predicted to have effects in different directions and with potentially different magnitude [Roubinet, 2016].

Multitrophic interactions can have strong effects on ecosystem functions measured at different trophic levels. The multitude of potential direct and indirect interactions between the different trophic levels make it difficult to predict the direction of the effect of species loss on multitrophic functioning [Thebault and Loreau, 2003]. In this context, BEF experiments provide valuable insights into the mechanisms driving multitrophic interactions.

1.6 Diversity and stability

Beyond affecting stocks and rates of ecosystem processes at any point of time, diversity can also affect the temporal stability of these processes. From the first theoretical papers on diversity-stability relations [McNaughton, 1977] up to recent empirical evidence [Isbell et al., 2015], this topic have been intensely studied and reviewed [Ives and Hughes, 2002]. In a recent theoretical study Loreau and Mazancourt [2013] showed that three main mechanisms were explaining the effects of diversity on ecosystem stability: (i) asynchrony of species response to environmental variations, (ii) differences in species response to

1.7 Arthropods and ecosystem functioning

perturbations (see Wright et al. [2016] for empirical evidence) and (iii) reduction in competition which is stabilizing through functional complementarity.

Disturbances, such as drought, fertilization or floods, are particularly interesting to study the diversity-stability relationships especially since disturbances are expected to increase in frequency and severity due to global change [Field, 2012]. This theme is central in biodiversity-ecosystem function research, Tilman and Downing reporting increase in drought resistance with plant richness in an early influential paper [Tilman and Downing, 1996].

More generally, consumer communities response to disturbance depend on many factors including the type of disturbance, the severity of the disturbance or the local disturbance history [Schowalter, 2012]. Negative impacts of disturbance on these communities may also be mitigated by some habitat property such as the plant diversity [Proulx et al., 2010]. In the case of natural flooding events recent studies have shown that high-diversity plots had higher soil porosity due to complex rooting systems compared to low-diversity plots which led to improved plant performance after a flood in high vs low diversity plots [Wright et al., 2016]. As a result arthropod communities, especially species spending part of their life-cycle in the soil, may be less affected by flooding events in habitats having high local plant diversity.

1.7 Arthropods and ecosystem functioning

The sheer number of arthropod species is staggering, there are presently 1.21 million described arthropod species from a total of 1.64 million across all taxa. We may compare this number to the sobering 70 000 vertebrate or 335 000 vascular plant species currently described (Roskov et al. [2016], Fig. 3). As Haldane puts it: “The Creator would appear as endowed with a passion for stars, on the one hand, and for beetles on the other, for the simple reason that there are nearly 300,000 species of beetle known, and perhaps more, as compared with somewhat less than 9,000 species of birds and a little over 10,000 species of mammals.” [Haldane, 1949]. Arthropods are everywhere being adapted to life in all habitats from marine to freshwater and terrestrial systems. Due to this high diversity and the widespread presence of arthropods in every system it is logical to assume that arthropods are essential for ecosystem functioning [Weisser and Siemann, 2004]. The focus of this thesis is on arthropod contribution to two ecosystem functions: herbivory and predation.

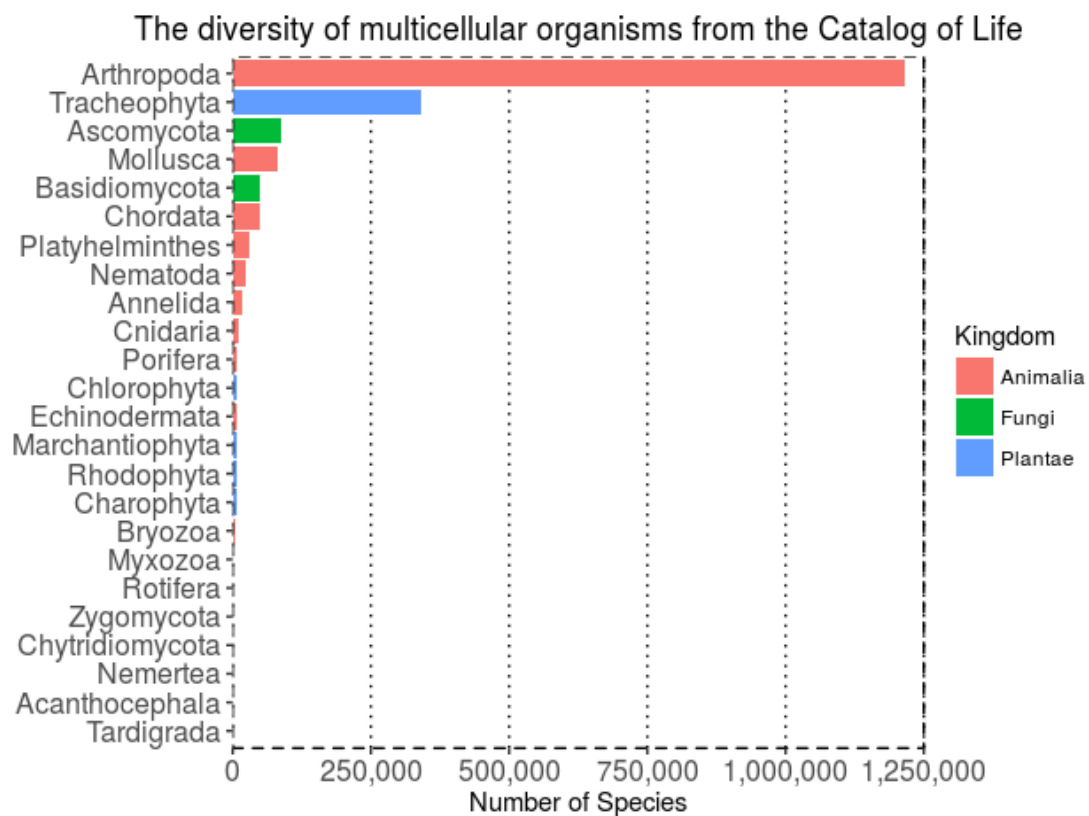


Fig. 3 Estimated species richness for multicellular taxa retrieved from the Catalog of Life version June 2016 [Roskov et al., 2016]

1.7 Arthropods and ecosystem functioning

Many arthropods are phytophagous, approximately half of the insect species are feeding on plants [Strong et al., 1984] making the first link between producers and higher trophic levels and starting the energy transfer in many food webs. Arthropod herbivory have wide ranging effects on the plant communities. Herbivores can control plant species richness and community composition both directly through intensive grazing and indirectly through plant-plant competitive interactions [Crawley et al., 1983]. For example, by selectively feeding on the dominant plant species, herbivores can release subordinate plant species from the fierce competition of the dominant plant species and increase local plant diversity [Schmitz, 2008b]. Herbivores can also affect the process of community succession both by changing plant relative abundance but also through their effects on nutrients cycling [Collins, 1961]. Herbivores are subtracting nutrients from plant tissues using these nutrients for their own growth or excreting them to maintain stoichiometric balance. Nutrients turnover time is much faster in consumers than in plants [Chapin III et al., 2011] therefore herbivores enable nutrients recycling that would otherwise stay immobilized in living plant tissues. In addition, herbivores can cause nutrients leaching from damaged plant tissues increasing nutrient concentration in canopy throughfall [Nitschke et al., 2014].

Numerous arthropod species are carnivorous and potentially influence many different ecosystem properties. Carnivorous arthropods may maintain prey population sizes under control preventing pest outbreaks [Letourneau et al., 2009]. This concept is behind biological control actions which try to control crop pest species by using natural enemies [Roubinet, 2016]. Biological control is an important ecosystem service in agricultural landscapes and large research efforts are undertaken to understand how biological control can be optimized [Landis et al., 2000]. Predation may also affect the outcome of interspecific competition between prey species affecting prey community structure [Schmitz and Suttle, 2001] similar to the effect of herbivores on plant communities. However, depending on the aspects of competition under study but also on the specificity of the predation, predation might promote, reduce or have no impact on interspecific competition between preys [Chase et al., 2002]. Arthropod predators may also have effects on the plant community by impacting the foraging behavior of herbivores. Schmitz and colleagues conducted a set of very convincing studies in an old-field grassland system. They explored the interactions between predatory spider traits, grasshopper feeding strategies and plant communities. One of their most striking result is that depending on the hunting mode of the spider species, the grasshopper switch their feeding from *Solidago* forbs to grasses impacting plant community composition [Schmitz, 2008a]. In addition, some of their recent work showed that changes in chemical composition in grasshopper carcasses triggered by the

Introduction

stressful presence of spiders in the environments lead to lower decomposition rates of adjacent plant litter [Hawlena et al., 2012].

1.8 Thesis Outline

The aim of this thesis is to understand how plant diversity affects arthropod communities and arthropod-mediated functions in a grassland system (See Fig. 4).

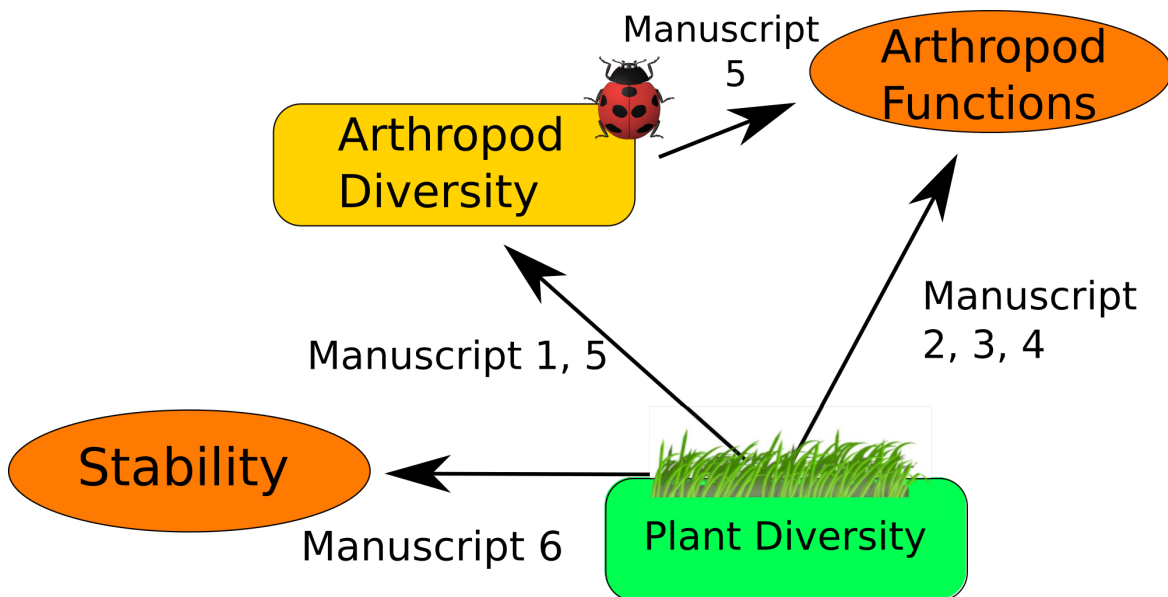


Fig. 4 Schematic representation of the overall aim of this thesis and the specific aspects explored in the different manuscripts.

Unraveling the mechanistic relationships between these different components will have implications both for fundamental as well as applied science. As developed in the preceding paragraphs many hypotheses exist on the multitrophic importance of diversity for explaining multiple ecosystem functions, this work will provide a step forward by presenting patterns in accordance or in disagreement with these various hypothesis. Moreover, results from this work might also provide rough guidance for managing grassland systems. Below are the questions that will be answered in this thesis:

Q1: How does plant diversity affect herbivores and carnivores arthropod diversity?

In manuscript 1, I explore the direct and indirect links between plant diversity and different aspects of arthropod diversity at two trophic levels. I used arthropod community data collected on an experimental field site 8 years after the onset of the experiment

to compute various diversity metrics reflecting different aspects of diversity. In a first step bivariate models were built between plant diversity and arthropod diversity. In a second step structural equation models were built to disentangle plant diversity, plant productivity and plant identity effect on arthropod diversity.

Q2: What is the effect of plant diversity on invertebrate herbivory? The second manuscript is a synthesis of invertebrate herbivory estimation measured across two plant diversity gradient across five years. This extensive dataset allowed us to investigate the consistency of plant diversity effect on invertebrate herbivory across seasons, years and experimental gradients. Strikingly consistent positive effects of plant diversity on herbivory rates were found. In a second step, in manuscript 3, I partitioned the diversity effect on herbivory adapting the classical complementarity/ selection approach to the herbivory data. This allowed us to better understand the mechanisms at play behind the effects discussed in manuscript 2.

Q3: What is the effect of plant diversity on invertebrate predation? In manuscript 4, I present the results from intensive sampling of invertebrate predation rates under field conditions. Taking advantage of recently published work on rapid ecosystem function assessment (REFA, Meyer 2015) a set of different sentinel preys were exposed and removal rates were estimated. This is the first study to actually measure predation rates in a biodiversity experiment and our results showed a strong response of predation to plant diversity.

Q4: Can we explain plant diversity effect on arthropod-mediated functions (herbivory and predation) through multitrophic shifts in arthropods biomass and diversity? Manuscript 5 combines arthropod community data with arthropod-mediated processes to test specific hypothesis linking plant diversity to herbivory and predation. With the help of structural equation models this study investigated the causal pathways between plant diversity, arthropod communities and arthropod-mediated processes.

Q5: Does plant diversity mitigate ant survival to a major flooding event? In Manuscript 6, I report the findings of unexpected high ant survival after a 200-year flood event that occurred on the field site in early summer 2013. I compared data from earlier samplings to post-flood samplings to investigate the potential mechanisms affecting ants survival.

The final part of this thesis contain a discussion of the important findings in light with the current literature.

Chapter 2

Study system and methods

2.1 The Jena experiment

The Jena experiment was created in 2002 in the floodplain of the river Saale in the town of Jena, Germany (50° 55' N, 11° 35' E, 130 m.a.s.l). This area was originally a grassland that has been converted into an arable field in the early 60ies and was highly fertilized for 40 years to grow vegetables and wheat. The yearly average air temperature in Jena is 9.9°C and the averaged cumulated annual precipitation is 610mm [Hoffmann et al., 2014]. The soil of the field site is an Eutric Fluvisol originating from up to 2 meter thick loamy fluvial sediments being almost free of stones. The texture of the top soil vary from loam near the river to silt loam as the distance to the river increases [Fischer et al., 2015]. The Jena Experiment field site contains several diversity gradients [Ebeling et al., 2014; Roscher et al., 2004]. I describe below the two gradients used in this thesis. In addition, the field arrangement is presented in Fig. 5.

2.1.1 The Main Experiment

In the Main experiment a pool of 60 grassland plant species belonging to Molinio-Arrhenatheretea meadows [Ellenberg and Leuschner, 1996] was formed. Species selection was based on central European flora as well as on expert knowledge [Roscher et al., 2004]. Four plant functional groups were created based on 17 plant traits collected from the literature, these traits included morphological traits (growth form, vegetative height . . .), phenological traits (foliage seasonality, start of flowering . . .) and one physiological trait the ability to fix nitrogen (See Table 1 in Roscher et al. [2004]). A PCA was run on the resulting trait matrix and it revealed that plant species may be separated into 4 functional groups: Grasses, Small Herbs, Tall Herbs and Legumes. Each plot was sown in 2002 with a specific set

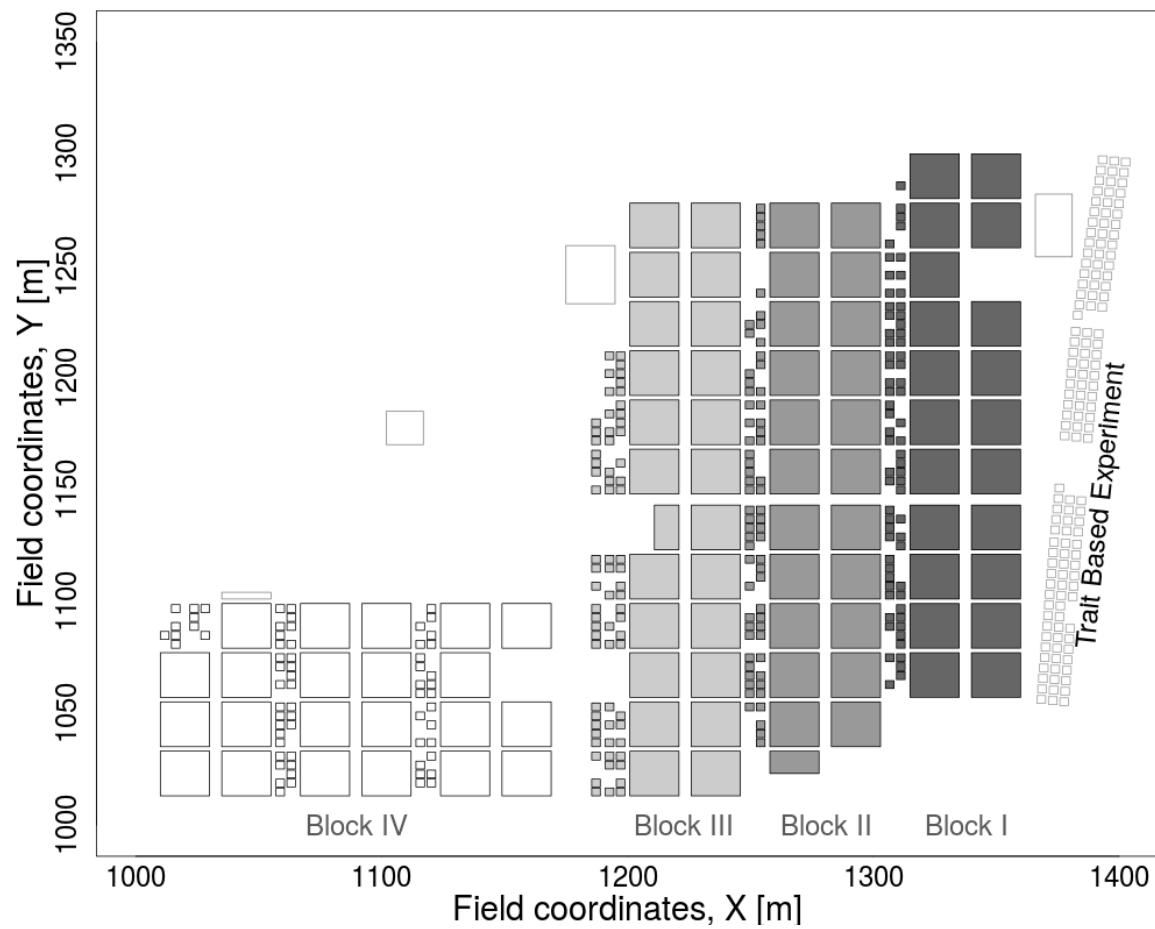


Fig. 5 Overview of the spatial arrangement of the Jena Experiment field site. The rectangles represent the different plots. The large rectangles linked to Block I-IV form together the main experiment, the smaller rectangles form other diversity gradients not included in this thesis.

of plant species from the species pool to form a gradient in species richness but also in functional diversity. Functional diversity is the number of plant functional groups sown in the plots, it was set to be as orthogonal as possible to plant species richness to allow the separation of richness effects from functional diversity effects. The species richness gradient ranges from 1 (ie monoculture) to 60-species mixture on a logarithmic scale (Species richness levels: 1, 2, 4, 8, 16, 60 species). Each species richness level was replicated 16 times except for the 16 level which has 14 replicates and the 60 level which has 4 replicates. As a result the main experiment has a total of 82 plots, However, two monocultures were abandoned in 2009 as no target plant species were present in them. To account for variation in soil texture four blocks with equal number of plots were established parallel to the river to remove any confounding soil effects on experimental results. The plots of the main experiment had originally an area of 20 x 20 meter, which was reduced in 2009 to an area of 6 x 7 meter.

2.1.2 The Trait-Based Experiment

The Trait-Based Experiment was created to further investigate functional diversity effects on ecosystem function but also to track the effect of diversity on individual species along a diversity gradient, which was not possible in the main experiment due to the large species pool. Six plant traits related to resource acquisition in space and time were measured in species monocultures in the main experiment in 2003 and 2004 (Table 1 in Ebeling et al. [2014]). A PCA was run on this trait matrix, this PCA revealed the position of the species along the functional axis. The first two axes explained together 66% of the variation in trait values and were used to establish the gradient of functional diversity. The first axis separated species based on their spatial resource use (ie rooting depth, canopy height . . .) while the second axis separated species based on their temporal resource use (growth start, flowering start). Based on these results three pools containing 8 plant species each were formed (Fig. 6). Pool 1 contain species along the first axis situated at intermediate position on the second axis, pool 2 contain species along the second axis situated at intermediate position on the first axis and finally pool 3 contain species situated at both extreme of the two axis. Each pool was then divided into 4 sectors with two plant species in each of them. Functional diversity (FD_{Jena}) at the plot level is then defined as the distance between the sectors represented in the plot varying between 1 and 4. For example a plot containing the following plant species from the Pool 1: *Festuca rubra* and *Phleum pratense*, has a species richness of 2 and a FD_{Jena} of 2 as the two species come from neighbouring sectors. Another example, a plot containing the following species from Pool 2: *Holcus lanatus*, *Geranium pratense* and *Dactylis glomerata*, has a species richness is 3 and FD_{Jena} is also

Study system and methods

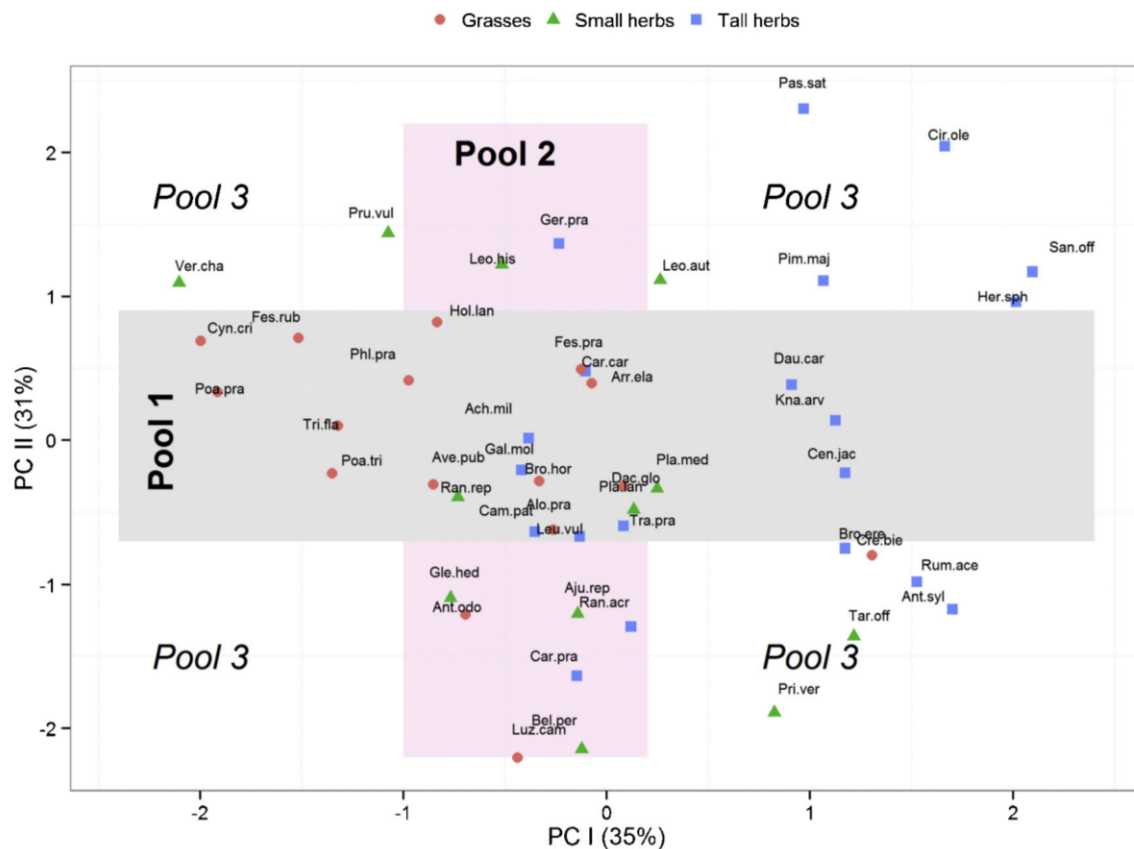


Fig. 6 First two PCA axis based on 6 plant traits for the plant species pool of the Jena Experiment (excluding legumes). Pool 1 is based on the first axis, Pool 2 on the second axis and Pool 3 is the extreme of the two axis. Figure from [Ebeling et al., 2014]

3. In the TBE sown plant species richness gradient took the following values 1, 2, 3, 4 and 8 which were replicated respectively 8, 16, 12, 9 and 1 times per Pool. In total the TBE consists of 138 plots (46 per Pool) with an area of 3.5 x 3.5 meter. The plots were sown with their respective seed mixture in autumn 2010, but due to a flood event in January 2011, plots were sown again in spring and autumn 2011 to ensure proper community establishment.

2.1.3 Field management

The plots are managed following the common practice for unfertilized meadows in the region, they are mown twice a year, around May and August. To maintain the target plant communities the plots are manually weeded three times per year in April, July and September.

2.2 Measurements of vegetation properties

The measurements of standard vegetation parameters were done twice a year at peak biomass towards the end of spring (usually end of May) and in late summer (usually in August).

Plant biomass was collected at two random locations within the plots using 20 x 50 cm metallic frames. Plants growing higher than 3cm above the ground were cut and identified to species-level. All sown species (i.e. plant species belonging to the mixture sown in the specific plot) were dried at 70°C for 72 hours and weighted to the nearest 0.1 g. The values were averaged per plot between the two replicates and multiplied by ten to extrapolate to g per m².

Plant cover was estimated in subplots of 3 x 3 m. Sown species cover were estimated as community values in percent using a decimal scale [Londo, 1976]: 1: ≤ 1%, 2: ≤ 5%, 10: 6-15%, 20: 16-25%, 30: 26-35%, 40: 36-45%, 50: 46-55%, 60: 56-65%, 70: 66-75%, 80: 76-85%, 90: 86-100%; community cover data were directly estimated as percentage (cover < 1% is coded as 0.5).

Leaf area index (LAI) was measured using the LAI-2000 Plant Canopy Analyzer (LI-COR, Lincoln, USA). On a per plot base we conducted ten measurements along a transect of 5m. Replicates per plot were averaged for our analyses.

2.3 Arthropod sampling

Arthropods were sampled on the experimental field site using two methods: (i) pitfall traps to capture the ground-living fauna and (ii) suction sampling for arthropods evolving in the vegetation. Pitfall traps were made of plastic cups of 4.5 cm in diameter buried in the ground so that the lid of the traps was at the level of the ground. The traps were filled with a solution of formaldehyde (3%) and had a small roof above them to prevent rain to enter the traps. In the main experiment there were two traps per plot and in the TBE one trap per plot. Traps were left open for two weeks and after that emptied. The collected individuals were subsequently stored into ethanol (70%). The pitfall traps were emptied ten times over the vegetation period between April and September. The second method, suction sampling, consisted in covering the vegetation with a 0.75 cubic meter biocenometer (metallic frame covered on five sides with gauze) and using a modified vac-

Study system and methods

cum cleaner (Kärcher A2500, Kärcher GmbH, Winnenden, Germany) to collect all flying and resting arthropod individuals. The collected individuals were then stored into ethanol (70%). Suction sampling was done between 2 and 3 times over the vegetation period and each plot had 2 replicates. Adult individuals belonging to the following taxa were then identified to the species level by taxonomists: Coleoptera, Orthoptera, Hemiptera (Heteroptera, Auchenorrhyncha and Sternorrhyncha), Araneae, Isopoda and Myriapoda. For each species we only kept records from individuals sampled using the appropriate methods, for example carabid individuals were discarded from the suction samplings or cicads were only identified if sampled with suction sampling.

Ant sampling was conducted in 2006 and in 2013 using baited traps. One sugar-rich and one protein-rich trap were set per plot. The traps consisted of petri dishes of 20cm diameter with approximately 10g of bait material. Thirty minute after setting the traps in the plots the number of ant worker present in the petri dishes was assessed.

2.4 Arthropod traits

Two trait databases were used, the first one was assembled on data from the Jena Experiment by Ebeling et al (unpubl. manuscript) the second one was published by Gossner et al. [2015]. We primarily used data from the first database and completed species missing from this database by data from the second one. Traits used were: Trophic guild (herbivores, omnivores and carnivores), Feeding mode (chewer, sucker or extra intestinal digestion), vertical stratum (ground, vegetation, soil, tree or indifferent) and body size (in mm). Using the order-specific allometric equations published by Barnes et al. [2014] body size was turned into fresh mass (in mg) to compute consumer biomass.

2.5 Herbivory measurements

Aboveground invertebrate herbivory was estimated twice per year between 2010 and 2015 in the main experiment and between 2012 and 2015 in the TBE. Herbivory measurements were synchronized with the plant biomass sampling in late spring and summer before the mowing of the field site. For each sown plant species in each plot, thirty leaves were randomly selected from the plant materials. Dead, decaying or leaves damaged by the sampling were discarded, only for some species growing close to the ground like *Plantago media* did we also use damaged leaves to estimate herbivory rates. For each randomly selected leaves the total area showing herbivory damages was visually estimated helped

by circular templates of diameter ranging from 1mm² to 500mm². Four different types of herbivory damages are usually found on the observed leaves: chewing, leaf-mining, sucking and rasping damages [Loranger et al., 2014] but all damage types were pooled together. After estimating the area damaged by invertebrate herbivores we passed the leaves through a leaf area meter (LI-COR 3100C, LI-COR Lincoln USA) which estimated the remaining leaf area. Because chewing damages are not measured by the leaf-area meter we calculated a correction factor (*CF*) which is the proportion of total herbivory coming from chewing damages based on data collected in 2010 by Loranger et al. [2014]. The herbivory rates h_{ik} of species i in plot k was then computed as follow:

$$h_{ik} = \frac{D_{ik}}{(A_{ik} + CF_i * D_{ik})} \quad (2.1)$$

Where D_{ik} is the summed leaf area damaged by invertebrate herbivory and A_{ik} is the remaining leaf area. Then we derived community-level herbivory rates using a weighted-average:

$$h_k = \sum_{i=1}^s \frac{h_{ik} * B_{ik}}{B_k} \quad (2.2)$$

Where s is the number of plant species in plot k and B is the leaf biomass. Since plant biomass is weighted including all plant parts (stems, flowers . . .), we used trait data collected in the monoculture by Heisse et al. [2007] of all species both in late spring and summer to compute the species and season-specific leaf biomass ratio, or in other words the proportion of plant biomass that is made up by leaves.

2.6 Predation measurements

Aboveground predation was measured in both the main and trait-based experiment in May and August 2014 each time 2 weeks before the biomass harvest. In each month the sampling took place on 7 days. Per day and per plot a total of 10 baits were exposed with a minimum distance of 50cm between two adjacent baits. The baits were exposed either on the ground or in the vegetation at approximately half of the selected shoot height. The baits were exposed in specific positions within the plots, these positions stayed fixed throughout the measurements and were marked with colorful cocktail sticks (See Fig. 7). The types of baits exposed at each position changed randomly during the measurements. The baits were set in the morning between 9 and 12am on all the plots, and we assessed removal or attack rates on the baits after approximately 24 hours of exposure. Three different types of baits were used following the Rapid Ecosystem Function Approach

Study system and methods

(REFA, Meyer et al. [2015]): pea aphids, mealworm and plasticine dummies. Pea aphids (*Acyrtosiphon pisum*, HARRIS 1776) colonies were raised and cultivated on broad beans (*Vicia faba*, LINNAEUS) in a climate chamber at 20°C and 50% air humidity. Each morning during the sampling campaign 4th instar or adult individuals with a size of at least 1mm were glued to white labels using water-proof glue (Patex 100% Kleber). After 24 hours of exposure, the removal or not of the aphids was recorded. Ten aphid baits per plot and per season were exposed, resulting in a total of 4400 baits. Mealworm (larvae of the beetle *Tenebrio molitor*, LINNAEUS, 1758) were bought from a pet store and stored at 7°C for a maximum of two weeks to prevent the larvae for developing into adults. Mealworms were pinned to the ground or to a plant shoots using insect needles (0.35 x 38 mm, Bioform, Nürnberg, Germany). As for the aphids removal rates of mealworm baits were assessed after 24 hours of exposure. 40 mealworm baits per plot and per season were exposed, resulting in a total of 17600 exposed baits. Green plasticine (Staedtler Noris Club, Nürnberg, Germany) was used to form dummies: plain cylinder of 0.6 x 2 cm in size to vaguely resemble lepidopteran larvae [Meyer et al., 2015]. Dummies were pinned either on the ground or in the vegetation using insect needles (0.35 x 38 mm). After exposure dummies were checked for predation marks using a stereo microscope with a 5 times magnification. Predation marks were classified into broad categories of predators based on the large collection of photographs from Low et al. [2014] and our own photographs taken on the field site. We used five categories of marks: rasping marks (gastropods), mandibular marks (chewing insects), teeth marks (rodent), beak marks (bird) and stylet (predatory bugs) or ovipositor marks (e.g. by parasitic hymenoptera). In total, we exposed 8800 dummy baits.

2.7 Data availability

All data collected and used in the framework of this thesis are available in the Jena-Experiment database <http://www.the-jena-experiment.de/Data.html>. Individual datasets associated to specific publication have also been published in PANGAEA <https://www.pangaea.de/about/>.

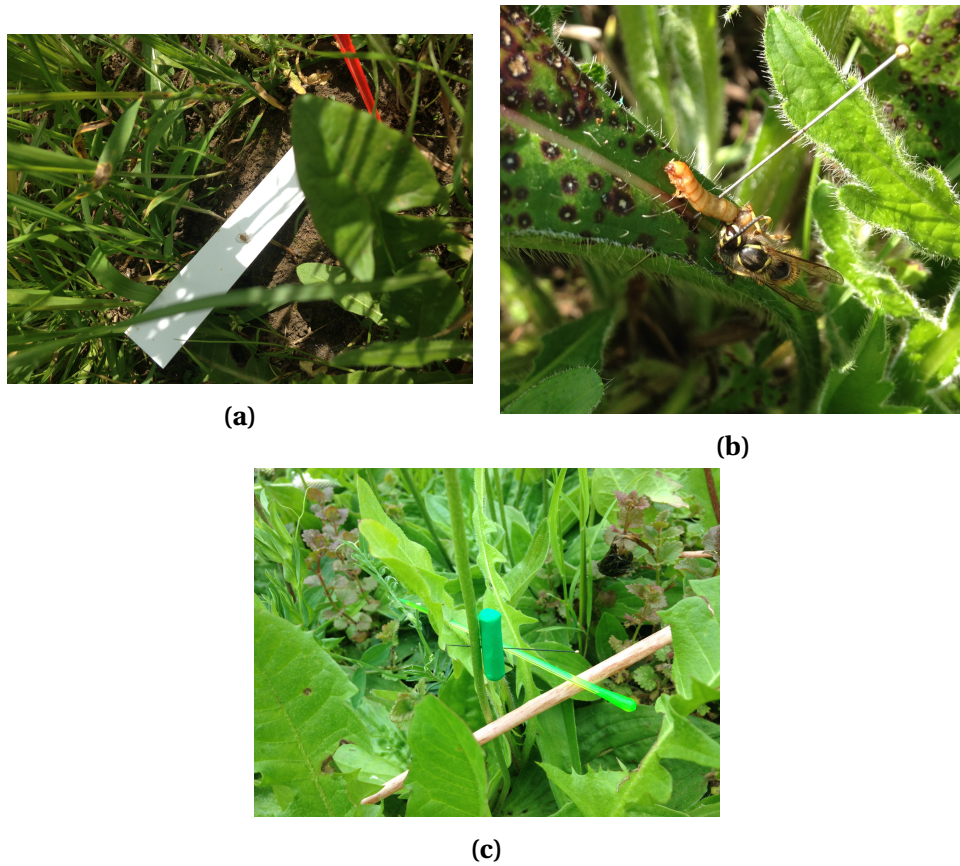


Fig. 7 Pictures of the different baits used in this study, (a) single aphid clued to a white plastic lable and exposed on the ground, (b) mealworm pinned to the vegetation and being attacked by a wasp, (c) dummy made from plasticine and pinned to the vegetation.

2.8 Statistical analyses

2.8.1 Structural equation modelling

Structural equation modelling is a set of techniques that allow the specification of multivariate models with potentially complex interaction and indirect effects between variables [Grace et al., 2010]. A structural equation model (SEM) is formed of two components: the structural model which is a set of equations that are forming the potential causal links between variables and the measurement model which relate latent variables to their measured indicators. These are the two major benefits of using SEMs: the possibility to model complex and indirect relations between variables and the ability to explicitly model theoretical constructs. SEM provide information on the relationship between the modelled variables with path coefficients which are related to regression coefficient. Since SEMs allow indirect effects one is able using the path coefficients to get information on the direct, indirect and total effect of one variable on the other. SEM use the hypothesized model together with the observed variance-covariance matrix to estimate the path coefficient, several methods are available to estimate the coefficients. In this thesis I used Maximum Likelihood estimation which is similar to regression models. In the case of non-normal data, Maximum Likelihood estimation with robust standard errors and adjusted test statistics were used. Once the path coefficients have been estimated the model provide a predicted variance-covariance matrix. Various index of model fitness exist measuring different aspects of model fitness. The observed and predicted variance-covariance functions are compared and a discrepancy function is computed which is tested for significance using a chi-square test. A model is judged acceptable if the p-value for the chi-square test is higher than 0.05. Another class of model fitness indices compare the hypothesized model to a null model and compute the difference between the chi-square values of the null and hypothesized model, in this thesis I will use the Tucker Lewis index which is independent of sample size, a model is deemed acceptable when the TLI value is higher than 0.9. In the manuscript 5 I will compare models based on different hypotheses using the Bayesian information criterion which penalize against complex models.

2.8.2 Generalized Linear Mixed-effect Models

In manuscripts 2 to 4 Generalized Linear Mixed effect Models (GLMMs) were used [Bolker et al., 2009]. These models have two types of effects: fixed effects, similar to the effects in GLMs and random effects which represent some groupings in the data. GLMMs only

estimate one parameter per random effect: the standard deviation between the different groups. For example if we measured the reactivity of 20 people at different time of day we would have two fixed effect: the average response time (the intercept) and the effect of the time of the day on the reactivity (the slope). In this model up to two random effects could be estimated: one taking into account variation in mean response time between persons (some people might have played a lot of video games and be very responsive) and one taking into account variation between persons in the effect of the time of the day (some people might be more affected than others by the daily passing of time). The great advantage of GLMM is that it takes into account non-independence between the data points without having to estimate one parameter per grouping level. Going back to the example of response time, in a classical GLM one would have to estimate two parameters per person (one for the intercept and one for the slope) making it a total of 40 parameters to estimate and interpret. In such situation the interest do not lie in knowing if individual A has faster response rates than individual B, the interest is mostly in how variable are the effects between the individuals but more pragmatically in controlling for non-independence in the data to allow correct inference. GLMMs provide similar output to GLMs including regression coefficient estimates and standard errors. However, estimating the denominator degrees of freedom to compute F values is tricky in GLMMs as the effective size of the dataset (number of data point - number of estimated parameters) is difficult to compute. A random effect with a number of levels K could be estimated with 1 to $K - 1$ parameters [Bolker et al., 2009]. In the paper I therefore use sequential Likelihood Ratio Test (LRT) to test for the effect of individual fixed effect parameters. LRT compare the log-likelihood between two nested models and test the significance of the difference between the models using a chi-square test. The approach I used was to sequentially drop all fixed-effect terms in the models and compute at each step a LRT. The sequence of dropping was based on the explanatory power of the variables starting with the most complex interaction having the lowest explanatory power up to main effects with high explanatory power.

Chapter 3

Manuscript overview

This thesis contains six manuscripts, for which the publication status, a brief summary and the contributions of the authors are given.

Manuscript 1: Experimental Manipulation of Grassland Plant Diversity Induces Complex Shifts in Aboveground Arthropod Diversity

Lionel R. Hertzog, Sebastian T. Meyer, Wolfgang W. Weisser and Anne Ebeling

Published 2016 in PLoS One 11(2):e0148768. doi:10.1371/journal.pone.0148768.

Changes in producer diversity cause multiple changes in consumer communities through various mechanisms. However, past analyses investigating the relationship between plant diversity and arthropod consumers focused only on few aspects of arthropod diversity, e.g. species richness and abundance. Yet, shifts in understudied facets of arthropod diversity like relative abundances or species dominance may have strong effects on arthropod-mediated ecosystem functions. Here we analyze the relationship between plant species richness and arthropod diversity using four complementary diversity indices, namely: abundance, species richness, evenness (equitability of the abundance distribution) and dominance (relative abundance of the dominant species). Along an experimental gradient of plant species richness (1, 2, 4, 8, 16 and 60 plant species), we sampled herbivorous and carnivorous arthropods using pitfall traps and suction sampling during a whole vegetation period. We tested whether plant species richness affects consumer diversity directly (i), or indirectly through increased productivity (ii). Further, we tested the impact of plant community composition on arthropod diversity by testing for the effects of plant functional groups (iii). Abundance and species richness of both herbivores and carnivores increased with increasing plant species richness, but the underlying mechanisms differed between the two trophic groups. While higher species richness in herbivores was caused by an increase in resource diversity, carnivore richness was driven by plant productivity. Evenness of herbivore communities did not change along the gradient in plant species richness, whereas evenness of carnivores declined. The abundance of dominant herbivore species showed no response to changes in plant species richness, but the dominant carnivores were more abundant in species-rich plant communities. The functional composition of plant communities had small impacts on herbivore communities, whereas carnivore communities were affected by forbs of small stature, grasses and legumes. Contrasting patterns in the abundance of dominant species imply different levels of resource specialization for dominant herbivores (narrow food spectrum) and carnivores (broad food spectrum). That in turn could heavily affect ecosystem functions mediated by herbivorous and carnivorous arthropods, such as herbivory or biological pest control.

All authors conceived and developed the idea for the manuscript. WWW and AE designed the experiment. AE collected the data. LRH and STM analyzed the data. LRH wrote the first draft. All authors commented on subsequent versions of the manuscript.

Manuscript 2: Consistent increase of herbivory along two experimental plant diversity gradients over multiple years

Sebastian T. Meyer, Lukas Scheithe, Lionel R. Hertzog, Anne Ebeling, Cameron Wagg, Christiane Roscher and Wolfgang W. Weisser

Rejected by Ecology, In revision.

Global species loss has motivated research on the functional importance of biodiversity documenting that plant species richness affects many plant-related ecosystem functions. In contrast, there is little knowledge on the effects of plant species richness on functions related to higher trophic levels, such as the consumption of biomass by animals, i.e. herbivory. Previous studies have shown positive, neutral, or negative effects of plant species richness on arthropod herbivory. In the framework of a grassland biodiversity experiment (the Jena Experiment), we investigated herbivory (the proportion of leaf area damaged and the amount of leaf biomass consumed by herbivores) along two experimental gradients of plant species richness ranging from 1 to 60 species (Main Experiment) and from 1 to 8 species (Trait-Based Experiment) for five and three years, respectively. Additionally, plant functional diversity, based on traits related to plant performance, was manipulated as the number of functional groups in a community (Main Experiment) or a gradient of functional trait dissimilarity (Trait-Based Experiment). Herbivory at the level of plant communities ranged from 0 to 31% (0 and 33.8 g/m²) in the Main Experiment and 0 to 8% (0 and 13.7 g/m²) in the Trait-Based Experiment, and was on average higher in summer than in spring. For both experimental gradients and all years investigated, we found a consistent increase in leaf area damage and consumed biomass with increasing plant species richness. As mechanistic explanations for effects of plant species richness, we propose changes in plant quality and herbivore communities. The presence of specific plant functional groups significantly affected herbivory, but we found little evidence for effects of plant functional diversity. The general positive relationship between plant species richness and herbivory might be a mechanism contributing to effects of plant species richness on other ecosystem functions like productivity and nutrient mineralization. Furthermore, effects of plant species richness are not restricted to herbivores but might cascade up the food-web affecting higher trophic levels.

STM conceived and developed the idea of the manuscript. STM and WWW designed the experiment. STM, LRH, LS, CW and CR collected the data. LS and LRH formatted the data.

STM, LS and LRH analyzed the data. STM wrote the first draft. All authors commented on subsequent versions of the manuscript.

Manuscript 3: Complementarity effect explain increasing invertebrate herbivory along a diversity gradient

Lionel R. Hertzog, Anne Ebeling, Wolfgang W. Weisser and Sebastian T.Meyer

In preparation.

Different mechanisms may be at play to explain the relationships between biodiversity and ecosystem function. Diversity effects can be partitioned into a complementarity and a selection effect. However this method was so far applied mostly to plant biomass but not to other ecosystem functions like herbivory. In this study we partitioned the plant diversity effect on herbivory rates across 4 years of data into complementarity and selection effects using the null hypothesis that herbivory rates at the plant species level are independent to the diversity in the mixtures. The results show that an increase in complementarity along the plant diversity gradient is driving the positive net diversity effect on herbivory rates. This relationship was consistent across the years even if the average strength of complementarity effect declined with time. We found no evidence for selection effect driving the relationship between plant diversity and herbivory. Our results show that all plant species in diverse mixture experience, on average, higher consumption rates by herbivores which is driving the positive relation between plant diversity and herbivory. These results are consistent with the diet mixing hypothesis implying plasticity in herbivores feeding strategies.

LRH, STM and WWW conceived and developed the idea. STM and WWW designed the experiment. STM and LRH collected the data. LRH and STM analyzed the data. LRH wrote the first draft. All authors commented on subsequent versions of the manuscript.

Manuscript 4: Higher plant diversity increase predation by invertebrates

Lionel R. Hertzog, Anne Ebeling, Wolfgang W. Weisser and Sebastian T. Meyer

In review by Oecologia.

Global declines in biodiversity have raised concerns over the implications of diversity loss for the functioning of ecosystems. Plant diversity loss has impacts throughout food webs affecting both consumer communities and ecosystem functions mediated by consumers. Effects of plant diversity loss on invertebrate predators have been documented, yet little is known how these translate into variations in predation. We measured predation rates along two plant diversity gradients in grassland experiments manipulating species richness and functional diversity. Measurements were conducted at two different heights (ground and vegetation) and in two different season (spring and summer), using three different types of baits. Our results show that predation rates generally increase with plant species richness, but effects are seasonally variable and are much more pronounced on the ground than in the vegetation. Plant functional diversity did not consistently affect predation rates in our experiments. Our findings show that plant diversity affects the consumer-mediated ecosystem function predation. Potential mechanistic explanations include higher complementarity between predator species or reduced intraguild predation with increasing structural complexity at higher plant diversity. These results underline the importance of high local plant diversity for natural pest control.

All authors conceived and developed the idea for the manuscript. LRH, STM and AE designed the experiment. LRH and AE collected the data. LRH and STM analyzed the data. LRH wrote the first draft. All authors commented on subsequent versions of the manuscript.

Manuscript 5: Omnivore diversity is driving positive plant diversity effect on herbivory and predation

Lionel R. Hertzog, Anne Ebeling, Wolfgang W. Weisser and Sebastian T. Meyer

In preparation.

Plant diversity loss impacts consumer communities and also consumer-mediated ecosystem functions such as herbivory or predation. Previous studies have shown that plant diversity causes positive bottom-up effects on consumers across trophic levels. However few studies have explored the mechanisms linking plant diversity to consumer-mediated ecosystem functions through consumer communities. Using data from an experimental field site we explored direct and indirect plant diversity effects on herbivory and predation through shifts in arthropod biomass and diversity but also through changes in plant structural complexity. We found that consumer biomass was not causing the positive effect of plant diversity on herbivory and predation. Rather consumer simpson diversity and abundance-weighted functional diversity explained part of the plant diversity effect on herbivory and predation. Interestingly herbivores and carnivores diversity had negative effects on rates of functioning while omnivores diversity always had positive effects. In addition plant structural complexity had positive effects on herbivory but not on predation. Our study revealed the importance of consumer dominance structure and functional diversity across trophic levels for explaining plant diversity effect on herbivory and predation.

All authors conceived and developed the idea. WWW, AE and STM designed the experiment. LRH, AE and STM collected the data. LRH and STM analyzed the data. LRH wrote the first draft. All authors commented on subsequent versions of the manuscript.

Manuscript 6: High Survival of *Lasius niger* during Summer Flooding in a European Grassland

Lionel R. Hertzog, Anne Ebeling, Sebastian T. Meyer, Nico Eisenhauer, Christine Fischer, Anke Hildebrandt, Cameron Wagg and Wolfgang W. Weisser

Published 2016 in PLoS One 11(11):e0152777. doi:10.1371/journal.pone.0152777.

Climate change is projected to increase the frequency of extreme events, such as flooding and droughts, which are anticipated to have negative effects on the biodiversity of primary producers and consequently the associated consumer communities. Here we assessed the effects of an extreme early summer flooding event in 2013 on ant colonies along an experimental gradient of plant species richness in a temperate grassland. We tested the effects of flood duration, plant species richness, plant cover, soil temperature, and soil porosity on ant occurrence and abundance. We found that the ant community was dominated by *Lasius niger*, whose presence and abundance after the flood was not significantly affected by any of the tested variables, including plant species richness. We found the same level of occupation by *L. niger* at the field site after the flood (surveyed in 2013) as before the flood (surveyed in 2006). Thus, there were no negative effects of the flood on the presence of *L. niger* in the plots. We can exclude recolonisation as a possible explanation of ant presence in the field site due to the short time period between the end of the flood and survey as well as to the absence of a spatial pattern in the occupancy data. Thus, the omnipresence of this dominant ant species 1 month after the flood indicates that the colonies were able to survive a 3-week summer flood. The observed ant species proved to be flood resistant despite experiencing such extreme climatic events very rarely.

LRH and WWW conceived and developed the idea for the manuscript. LRH and WWW designed the experiment. LRH, AE, CF, AH and CW collected the data. LRH and STM analyzed the data. LRH wrote the first draft. All authors commented on subsequent versions of the manuscript.

Chapter 4

Main Findings

Plant diversity has widespread consequences for the functioning of higher trophic levels. Before entering into the general discussion of this thesis, I will briefly outline below the central results from the manuscripts included in this thesis.

The first manuscript investigated the response of arthropod diversity across trophic levels to changes in plant diversity and composition. Loss of plant diversity affected both the herbivorous and the carnivorous arthropods. The community data showed that halving plant species richness lead to a decrease of 19% in herbivore density and to a decrease of 4% in carnivore density. Notably the presence of small-statured forbs, such as plantain species, increased carnivore density by 21%. Arthropod species richness also responded to changes in plant species richness; halving plant richness led to a decline of 2.4 herbivores and 0.9 carnivores species. I found evidence that different mechanisms generated the general pattern of decreasing density and diversity across trophic groups. While herbivores were strongly and directly impacted by plant species richness providing support for niche-based hypothesis, carnivores were indirectly affected by plant productivity as predicted by the productivity hypothesis. Arthropod dominance structure was also affected by plant richness but the direction of this effect was trophic-dependent. Herbivore dominance declined by 18 percentage points along the diversity gradient but carnivore dominance increased by 7 percentage points. These results suggest different specialization of dominant species. Dominant herbivore species were specialists and their decline in relative abundance across the plant species richness gradient was likely due to the concomitant decline in density of their preferred host species. On the other hand, dominant carnivore species were generalists that generally profited from the increase in resource availability along the plant species richness gradient (Manuscript 1).

Main Findings

In the second manuscript, I looked at the effects of plant diversity on invertebrate herbivory across 5 years of data and two experimental diversity gradients. The results showed consistent and positive effects of plant species richness on herbivory rates. Herbivory rates increased on average from 0.82% in monocultures up to 1.82% in 60-species mixtures. In addition, the effect of plant species richness on herbivory rates was stronger in summer than in spring. The effect of plant species richness was independent from the year of sampling but herbivory rates showed an average decline with time from 1.50% in 2010 to 0.50% in 2014. Legumes and small-statured forbs increased herbivory rates by a third while grasses reduced herbivory rates (Manuscript 2).

The pattern of increasing herbivory rates with plant richness may be driven by different mechanisms, for example the increased likelihood of finding attractive plants in diverse mixture could be driving the patterns. In the third manuscript I adapted the diversity partitioning approach to herbivory, expressed in terms of consumed plant biomass, and separated selection from complementarity effects. Complementarity effects increased significantly across the plant species richness gradient, from 0.05 g/m² in communities with two species to 0.37 g/m² in communities with 8 species. This increase was the main driver of the positive relation between plant species richness and herbivory rates. The average complementarity effect on plant herbivory decreased by 90% over time, mirroring the decline in herbivory rates reported in Manuscript 2.

The fourth manuscript used sentinel preys to assess predation rates across two gradients of plant diversity. The results revealed positive plant richness effects on predation rates across two experimental gradients and two seasons (spring and summer). Along the plant diversity gradient predation rates rose for all bait types and across seasons, the observed increase ranged from 20 percentage points for dummy baits up to 48 percentage points for pea aphid baits when comparing monocultures to 60-species mixtures. One exception was the decline in predation rates for mealworm baits in spring, further experimental manipulations revealed that this decline was due to bird predation.

In the fifth manuscript I explored the mechanisms explaining the positive effect of plant richness on herbivory and predation. To this end, I analyzed shifts in arthropod communities in three trophic guilds (herbivores, omnivores and carnivores) and plant architecture, which were then related to herbivory and predation rates. I found that the effects of plant species richness on herbivory or predation rates were not mediated through consumer biomass. In other words, positive plant richness effects on herbivory

and predation cannot be explained by increased consumer biomass in high-diversity mixture. Omnivores are rarely explicitly considered in multitrophic analyses which may, according to my results, lead to biased conclusions. Indeed, structural equation models revealed that omnivores strongly determined changes in herbivory and predation across the plant species richness gradient. Omnivore simpson diversity and abundance-weighted functional diversity explained 50% and 33% of the positive effect of plant species richness on herbivory and predation. Plant structure also explained a significant portion of the positive effect of plant diversity on herbivory rates. Predation rates on the other hand, was not affected by plant structure (Manuscript 5).

In the last manuscript I showed that ants in the Jena Experiment field site were particularly resistant to a major flooding event. The occupancy of the field site was as high one month after the flood as it was in a pre-flood survey. None of the collected predictor variables such as plant diversity, soil porosity, plant cover or flood intensity could explain the patterns of ant occupancy. The resistance of such common species to disturbance may provide higher stability in ecosystem functioning despite increasing anthropogenic pressures on ecosystems (Manuscript 6).

Chapter 5

Discussion

Our science, so grandiose compared to our weak means, so miserable in front of the limitless limbo of the unknown, what does she know of the absolute truth? Nothing. The world is interesting to us only through the ideas that we form about it. The idea gone everything become sterile, chaos, nothingness. A ragbag of facts is not science; it is a cold catalog. It needs to be thaw, to be invigorated by the fire of the soul; it needs the intervention of the idea and the enlightenment of the reason; it needs to be interpreted.

J.-H. Fabre, *La vie des insectes* (1910)

Historically, ecosystem ecology focused on the impacts of abiotic factors on ecosystem functions. More recently, interests have shifted towards looking at biotic impacts on ecosystem functions. Two seminal reviews of experimental work [Hooper et al., 2012; Tilman et al., 2012] revealed that species loss could have impacts on plant productivity of similar magnitude as other global change drivers like CO_2 enrichment, nutrient addition or climate warming. This shows that independent of other global change drivers, biodiversity loss can have major impacts on ecosystem functions. Yet, we currently have little knowledge on global biodiversity trends [McGill et al., 2015] with the exception of particularly charismatic taxa, such as birds, mammals or butterflies. Even if new sampling efforts are under way promoted by various frameworks like the Group on Earth Observation - Biodiversity Observation Network (<http://geobon.org/>). Or the counterpart of the IPCC for biodiversity: the Intergovernmental Platform for Biodiversity and Ecosystem Services (ipbes.net). Besides recording biodiversity trends 21st century ecologists also need to understand the mechanisms linking biodiversity to ecosystem functions in complex systems to help the development of assessments and scenarios [Brose and Hillebrand, 2016]. My dissertation expand the existing knowledge on the multitrophic impacts of plant diversity

loss.

5.1 Complex shifts in arthropod communities

That every species in the biotic communities is closely linked to all other species is a common feature of ecological networks [Montoya and Solé, 2002]. Consequently, species loss will propagate through the food chains, indirectly affecting non-adjacent trophic levels [Thebault and Loreau, 2003]. In this section I discuss the consequences of plant diversity loss for arthropod communities across trophic levels. Focusing first on the response of arthropod species richness and in a second step discussing our results on shifts in the dominance structure.

The results from Manuscript 1 revealed that apparently similar diversity patterns across trophic levels were in fact driven by different mechanisms. While herbivore richness was directly driven by plant richness, carnivore richness was driven by the productivity of the system.

The response of herbivore richness supports the niche-based hypothesis which can be traced back to Lotka's theoretical work showing that a stable system resistant to invasion could only support as many consumer species as there are different resource axes [Chase and Leibold, 2003]. In other words, adding new plant species create niche space for new herbivore species to invade the system. Several observational and experimental studies have found support for the control of consumer diversity through niche-based processes. In another long-term grassland biodiversity experiment at Cedar Creek in Minnesota, herbivorous insects increased in richness along plant diversity gradient even after controlling for density and plant productivity effects [Haddad et al., 2009, 2001]. Similar patterns were observed in managed meadows across Switzerland for bee species [Albrecht et al., 2007]. In a study of land-use effects on herbivorous arthropod diversity, Simons et al. [2014] showed that land-use effect on herbivore diversity were mediated by plant richness rather than plant biomass. Together these results show that if supporting high richness of herbivorous arthropods is a management or a conservation target, practitioners should strive to maintain high plant diversity within the habitat. Recent works have shown how agri-environmental schemes can increase diversity of herbivorous arthropods [Badenhausser et al., 2015; Caro et al., 2016; Lebeau et al., 2015].

In contrast, I found that carnivore diversity was not directly driven by plant diversity but rather by plant biomass. Communities with higher levels of plant biomass had higher

5.1 Complex shifts in arthropod communities

number of carnivore species. This finding coincides with the exploitative ecosystem hypothesis of [Oksanen et al., 1981] which predicts that carnivores can maintain themselves only beyond certain threshold of plant biomass. Therefore, new plant species positively impact carnivores richness by providing more basal resource to trophic webs, which may then support higher number of carnivorous species. Using 23 published food webs Ward et al. [2015] showed that predator biomass increased along a productivity gradient through detritus-based channels and have stronger top-down control on grazing channels. To support carnivore diversity managers should therefore strive to increase plant biomass but also to provide alternative resources to carnivores a strategy already emphasized by Landis et al. [2000] or Jonsson et al. [2008].

The use of one unique diversity index, species richness, has been criticized for revealing a limited number of mechanisms while failing to capture the dynamic of other aspects of community composition and structure [Wilsey et al., 2005]. For instance, changes in dominance structure may have stronger impacts on ecosystem functioning than species loss [Hillebrand and Matthiessen, 2009]. For this reason, I also explored patterns in consumer evenness and dominance in response to plant diversity in Manuscript 1.

The results for herbivores show that plant richness had both direct and indirect effects on herbivores' dominance structure. Plant richness directly reduces dominance and increase evenness of herbivorous insect communities. At the same time, greater productivity led to lower herbivore evenness and greater dominance by a few species. These results imply that as additional resources become available to herbivore communities, few dominant species are able to capture these resources to a greater extent than subordinate species. In other words, increasing ecosystem productivity while keeping plant richness constant may lead to greater herbivore dominance. Depending on the functional traits of these dominant species, this increase in herbivore dominance may have multiple potential effects on ecosystem function [Hillebrand and Matthiessen, 2009]. However, this effect may be counterbalanced by increasing plant species richness. Based on these findings, one may make some recommendations for management practices in agricultural systems. For example, if maintaining the evenness of herbivore communities is one management goal, gains in productivity should be offset by similar gains in plant richness.

For carnivores, I found the opposite pattern, i.e. that plant richness increased dominance. However, the presence of small-statured forbs had larger effects on carnivores' dominance and evenness than the effect of plant species richness. Plots with small-statured forbs had lowered evenness and higher dominance of carnivores than plots without them. Small-statured forbs also led to higher abundance of carnivores. Therefore, small-statured forbs

Discussion

appear to increase the abundance of a few dominant arthropod species resulting in lower evenness. Previous work have already emphasized the importance of particular plant functional groups on consumer diversity [Siemann, 1998]. While Rzanny et al. [2013] showed the importance of legumes in structuring arthropod communities. Conservation strategies should therefore track the specific effects of particular plant functional group on the desired outcomes as such plant composition effects are likely to be context-dependent [Joern and Laws, 2013].

The results from Manuscript 1 set the stage for examining variation in arthropod-mediated ecosystem functions. In the next sections I will discuss the observed changes in herbivory and predation rates along a plant species richness gradient and will then relate changes in arthropod communities with shifts in ecosystem functions.

5.2 Plant diversity consistently increase herbivory

Herbivory profoundly affect ecosystems, shifting plant communities, mediating bottom-up and top-down control of consumer communities but also fastening nutrient cycling [Schmitz, 2008b]. Herbivores consume only a fraction of the available plant materials, typically around 10% in various systems [Crawley et al., 1983]. This observation led to a considerable body of theoretical work which tried to explain why all these potentially available resources were left untouched [Hairston Jr and Hairston Sr, 1993; Oksanen et al., 1981]. One such explanation was that, depending on the number of trophic levels, the outcome of multitrophic interactions might lead to a barren or a green world [Chapin III et al., 2011]. In the previous section, I reported concomitant increase in herbivorous and carnivorous diversity along a plant richness gradient potentially increasing trophic complexity [Schneider et al., 2016]. Depending on the relative strength of bottom-up and top-down forces these increase could lead to different patterns of herbivory [Leroux and Loreau, 2015]. In this section I discuss the links between plant diversity and herbivory rates and explore the potential mechanisms driving these links.

Results from Manuscript 2 revealed consistent positive effects of plant richness on herbivory rates. A number of previous meta-analysis reported the opposite effect, namely overall negative effect of plant diversity on community-level herbivory rates in experimental systems [Balvanera et al., 2006; Edwards et al., 2010; Hillebrand and Cardinale, 2004; Jactel and Brockerhoff, 2007]. Theoretical expectations of relation between community-level herbivory and plant diversity are diverse [Duffy et al., 2007]. Our results can be

5.2 Plant diversity consistently increase herbivory

explained by dietary mixing. A diverse diet provides to generalist herbivores higher fitness [Unsicker et al., 2008], leading to higher population size and potentially larger impacts on standing plant biomass [Duffy et al., 2007]. Current work on the invertebrate community in the Jena experiment shows an increase in the proportion of oligophagous herbivore species at the expense of monophagous species along the plant species richness gradient (Ebeling et al, in revision). Oligophagous species which likely increase their feeding rates in response to a greater diversity of resources.

The increase in herbivory with plant richness might also be driven by attractive plant species i.e. species with high herbivory rates, which would be more likely to be present in more diverse mixture. This was tested in Manuscript 3 where I showed that complementarity rather than sampling effects explained the increase in community-level herbivory along the plant species richness gradient. These results coincide well with the dietary mixing hypothesis as higher complementarity means higher consumption rates across all plant species. However, these results do not coincide with results from previous studies that have found that the presence of a particular plant functional group drove herbivory rather than plant richness [Joshi et al., 2004; Scherber et al., 2006]. One must note, however, that the experimental plant species richness gradient used in Manuscript 3 did not include any legumes, while the cited studies did. Legumes usually have very important impacts on ecosystem functioning in unfertilized meadows.

Variation in plant traits might also explain the observed pattern of increasing herbivory with plant diversity. Previous studies in the Jena experiment have found that models based on plant traits developed in monocultures did not scale up to the polycultures [Loranger et al., 2012, 2013]. These models showed important non-additive effects that increased with plant diversity. Therefore, plant traits alone cannot explain herbivory rates, rather a combination of species-level (e.g. leaf nitrogen concentration) and community-level factors (e.g. plant richness) provide the best explanation for variations in herbivory rates [Loranger et al., 2013]. Finally, my results show long-term decline in herbivory rates. This decline did not affect the positive effect of plant richness on herbivory which stayed present across the years (Manuscript 2). Potential reasons for this decline include progressive changes in plant quality during the conversion of the experimental site from arable land to an unfertilized meadow. Nitrogen availability to plants quickly dropped after the first year of the experiment [Oelmann et al., 2011a] while phosphorus slowly declined over time [Oelmann et al., 2011b].

Mechanistic models used in combination to empirical data may provide further insights into the drivers of multitrophic dynamics. Recently Konno [2016] published a

Discussion

mechanistic food-web model and parametrized it based on empirical data. The model mostly predicts a stable green world for terrestrial systems, i.e. a limited amount of herbivory. In addition, as long as carnivores are mostly generalists the dynamic is not affected by species richness while the opposite is true for systems where carnivores are specialists (i.e. parasitoids). Further work could try to parametrized such mechanistic model with data from the Jena experiment and investigate both the predictive power of the model but also the drivers governing food web dynamics across a diversity gradient.

5.3 Predation and plant diversity

Predators have large influence on ecosystems [Schmitz, 2008a] and current trophic downgrading have unanticipated impacts on ecosystem functioning [Estes et al., 2011]. In a previous section I showed how plant diversity was affecting carnivore diversity and dominance structure. Based on these results, predation rates and top-down control may, in turn, be affected by plant diversity. In the following section I discuss the relation between plant diversity and predation rates and the issue inherent with estimating predation rates in field conditions.

There are many potential links between plant diversity and predation rates that are all acting at the same time and the data presented in my thesis only represent the emergent effect [Letourneau et al., 2009]. However, based on the empirical patterns showed in Manuscript 4, certain mechanisms need to be explored in greater detail, as they predict a positive relationship between plant diversity and predation. These possible mechanisms include: (i) resource-based mechanisms, where plant diversity increases plant productivity and predator biomass (see Manuscript 1) and leads to higher consumption rates of the predator communities; (ii) diversity-based mechanisms, where complementarity and synergies dominate predator-predator interactions and lead to a positive relationship between predator richness and predation; (iii) structural-based mechanisms, higher structural complexity reduces intraguild predation and leads to increased top-down control on lower trophic levels.

The reported increase in predation with plant richness could potentially affect interspecific competition between prey species [Chase et al., 2002; Chesson and Kuang, 2008] leading to shifts in prey community. Increased predation may also affect prey foraging behavior, preys avoiding risky locations [Preisser et al., 2007; Schmitz, 2008a]. Recent evidence showed that predators can also affect decomposition rates of plant litter by increasing stress levels in their preys [Hawlena et al., 2012] which would in turn affect

5.4 Mechanisms linking plant diversity to herbivory and predation

nutrient cycling.

In agro-ecosystems drivers of predation have been intensely scrutinized as a way to enhance natural control of pest populations. Several reviews and meta-analysis have looked specifically at the effect of crop diversity on pest abundance, natural enemy abundance, crop damages and crop yields [Andow, 1991; Letourneau et al., 2009]. Letourneau et al. [2011] provided evidence that intercropping strategies increase natural enemy abundance, reduce pest damages and increase crop yield. Such effects also scale up to the landscape level where generalist predators have been found to be positively affected by landscape complexity [Chaplin-Kramer et al., 2011]. My results provide further support for the positive effect of local plant diversity on predation rates.

However, assessing predation rates using sentinel preys come with certain caveats [Lövei and Ferrante, 2016]. Sentinel preys are immobile, predators using movement cues will be ignored. In addition, plasticine dummies do not provide any chemical or behavioral cues to potential predators. Nevertheless, such method have been used with success in many studies [Meyer et al., 2015] but it is still unknown how potential predators perceive and process such artificial prey items [Lövei and Ferrante, 2016]. Despite these limitations a recent review showed that sentinel preys provide relevant estimation of relative predation rates across environmental gradients [Lövei and Ferrante, 2016]. Further work should strive to combine sentinel prey data with other more labor-intensive but more precise methods like camera-trapping [Pietz and Granfors, 2000] or gut-content analysis [Tiede et al., 2016].

5.4 Mechanisms linking plant diversity to herbivory and predation

Previous sections reported increasing rates of energy transfer across trophic levels along a plant diversity gradient. In the following section I will discuss the two main results from the analysis in Manuscript 5 which combined consumer community shifts with measured rates of herbivory and predation across the plant diversity gradient. Namely, (i) consumer biomass did not mediate plant diversity effects on herbivory and predation rates. This did not support the hypothesis that higher plant diversity increases consumer biomass which then leads to higher herbivory and predation rates. (ii) Omnivore diversity had strong positive effects on both herbivory and predation.

Discussion

Consumer density or consumer biomass are often used as a proxy for herbivory and predation rates. Studies investigating the effect of management practices often draw conclusions on potential shifts in ecosystem functioning from consumer biomass data. For example 70% of the response analyzed in Chaplin-Kramer et al. [2011] meta-analysis of landscape effect on pest control measured consumer abundance rather than predation pressure or crop yield. My analysis reveals that changes on herbivory and predation driven by producer diversity are not detectable when only quantifying consumer biomass. At a minimum, applied studies should measure at least one index of consumer taxonomic diversity when exploring management consequences and trying to link their results to ecosystem functioning.

Biomass is the most commonly used currency in theoretical models of multitrophic dynamics [Loreau, 2010] based on the assumption that energetic and matter constraints are the main links between BEF [Barnes et al., 2014]. As a result, tracking metabolic activities and nutrient relative availability enable understanding of BEF relationships in dynamic systems [Brose and Hillebrand, 2016]. My results, based on data collected in controlled conditions, show that dominance structure and functional diversity of the consumers are the main links between BEF. The two lines of evidence could be combined by investigating how varying metabolic and matter demands affect species relative abundance and dominance structure [Vellend, 2016]. While at the same time explicitly considering consumer traits and life-history [Miller et al., 2014]. Future research should aim to confirm the main drivers of bottom-up diversity effects on consumer-mediated functions in dynamic systems [Brose and Hillebrand, 2016].

My analysis also revealed the large impact of omnivores on functioning rates, despite having lower biomass and diversity than herbivores or carnivores. This result implies that taking into account flexibility in consumer strategies is needed to understand the multitrophic consequences of diversity loss. Earlier classification of consumers into few numbers of trophic groups may lead to biased conclusions [Hunter, 2009]. In this context combining food-web theory and BEF is a promising avenue of future research [Hines et al., 2015]. Current advances in allometric theory also provide the opportunity to quantify feeding rates as probability distribution embracing the variable aspect of feeding links [Schneider et al., 2016].

There is currently much interest to broaden the scope of BEF experiments. By considering multiple trophic levels [Brose and Hillebrand, 2016], by relaxing the static aspect of most of the classic experiments [Brose and Hillebrand, 2016] but also by considering the impact of different environmental drivers and their interaction [De Laender et al.,

2016]. In this context, my results show the importance of consumer relative abundance and functional diversity in mediating bottom-up diversity effects. Future studies should therefore record and analyze such data.

5.5 Advance and limitations of BEF experiments

In the last part of this thesis I would like to discuss the type of knowledge gained from BEF experiments. Funding and publication become more and more competitive requiring ecologists to justify their research in terms of societal benefits. As a result it is capital to reflect on what can say biodiversity experiment and their limitations.

Since its beginning BEF research aim at answering questions of societal importance, for example in the preface of the Biodiversity and Ecosystem function book, Schulze and Mooney ask: “How are the many services that ecosystems provide to humanity altered by modifications of ecosystem composition? [...] What is the role of individual species in ecosystem function”. Therefore, the BEF field is often loosely interpreted as providing arguments for species conservation, because a diverse system provides higher functioning it is in our best interest, as a society, to preserve biodiversity [Duffy, 2009; Naeem, 2009]. Such arguments were heavily criticized in the late 90s and the early 2000s as results and evidences were not consistent [Wardle et al., 1997] and issues with experimental design and results interpretation were raised [Huston, 1997; Wardle, 1999].

Beyond these technical issues Srivastava and Vellend [2005] attacked two of the key assumptions of BEF research as providing a case for species conservation, they argued that (i) biodiversity is not declining at the scale at which biodiversity experiments are conducted and (ii) increase in ecosystem functions is not unambiguously wanted to conserve natural systems, for instance increased productivity in lakes is not a desirable outcome. The first argument recently re-emerged and is currently heavily debated with studies reporting no changes in local species richness [Dornelas et al., 2014; Supp and Ernest, 2014; Vellend et al., 2013] and critiques being raised [Gonzalez et al., 2016; Wright et al., 2014] and answered [Vellend et al., 2016]. While the second argument is usually sidestepped and no explicit mentions of desired level of functioning in natural systems is being made. Recent studies have developed the concept of multifunctionality bundling together many functions and analyzing how biodiversity affect levels of multifunctionality [Lefcheck et al., 2015] interestingly in such studies some functions are inversed to represent that lower values are judged to be better.

Maybe the best way to finish this short critic of BEF contribution to species conservation

Discussion

is to cite the Foreword of Paul Ehrlich in the Schulze and Mooney book: “Biodiversity and Ecosystem Function: Need We Know More? [...] from the viewpoints of science, clearly (the answer) is yes; from the viewpoints of taking actions to preserve biodiversity, the answer is equally clearly no”.

If BEF experiments do not provide justification to preserve diversity, what do these experiments tell us? Two papers came out recently by Wardle [2016] and Eisenhauer et al. [2016] that discuss the merits and limits of B-EF experiments. The first paper mainly attacked the design of BEF experiments where species composition in the plots is randomly drawn from the species pool (i.e. Roscher et al. [2004]). Species-poor communities are random subsets of species-rich mixture, making the diversity gradient in BEF experiments reflect an artificial version of natural diversity gradients, which show non-random pattern of species turnover [Leps, 2004]. Different correlations between species likelihood of extinction and their functional importance can lead to a broad range of biodiversity ecosystem function relationships [De Laender et al., 2016; Larsen et al., 2005]. Classical BEF experiments by assuming no correlation between extinction proneness and species functional importance (random extinction scenario) are only exploring one of the hypothetical relations BEF relations. Albeit one that is unlikely to happen in natural system hampering comparison of the impacts of different global change drivers on ecosystem function [Hooper et al., 2012; Tilman et al., 2012]. Eisenhauer et al. [2016] responded by arguing that new global experimental networks are on the rise to address the links between global change drivers, biodiversity and ecosystem functions [Hautier et al., 2014]. In addition, no experiment could ever dream to portray with fidelity what may happen in natural system yet experiments are an essential tool in a scientist’s toolbox to test new emerging theories [Brose and Hillebrand, 2016; Lawton, 1995].

I would argue that this is what happened in the BEF field where policy makers in Rio de Janeiro, Brazil asked the scientific communities for evidence on the link between biodiversity and ecosystem function leading to a joint development of theories and experiment that showed that biodiversity does impact ecosystem functions [Hooper et al., 2005]. Now the next challenge for scientists include but are not limited to: understanding how this relationship is affected by global change drivers [Craven et al., 2016; De Laender et al., 2016; Grace et al., 2016; Hautier et al., 2014], how biodiversity at different spatial scales affects local functioning [McGill et al., 2015], how diversity loss across trophic levels affect functioning [Estes et al., 2011; Hines et al., 2015], and explicitly acknowledging what level of functioning is desirable for specific systems connecting biodiversity research to social and political sciences [Adams et al., 2004].

Chapter 6

Conclusion

'I wish it need not have happened in my time', said Frodo.

'So do I', said Gandalf, 'and so do all who live to see such times. But that is not for them to decide. All we have to decide is what to do with the time that is given us.'

J.R.R. Tolkien, *The Fellowship of the Ring* (1954)

Global loss of biodiversity should be a major concern to human society not only for ethical, cultural or economic reasons but also because species loss impact the movement of energy, nutrients and matter through the ecosystems. Arthropods occupy an important place in grassland ecosystems, being both highly diverse and performing key ecosystem functions. In this thesis, I have shown that despite showing consistent patterns of increasing densities and diversity across a plant diversity gradient, different mechanisms affected herbivorous and carnivorous arthropods. I showed that both herbivory and predation rates increased with plant diversity, a pattern that was consistent over time for herbivory rates and across sampling methods for predation rates. In the last manuscript, I found that the increase in herbivory and predation rates was best explained by arthropod dominance structure and functional diversity. But also that omnivores were driving most of the positive effect of plant diversity on herbivory and predation rates. These results will inform future work in theoretical and applied contexts.

In theoretical literature about diversity-ecosystem function, links for consumers are mostly based on biomass and species richness, while in this work these two metrics had minimal effects on observed herbivory and predation rates. This calls for developing theory explicitly based on shifts in dominance structure and arthropod traits. While efforts are underway, there is little theoretical or experimental efforts to develop hypotheses and

Conclusion

predictions of dominance shifts impacts on ecosystem functioning. In addition, by revealing the importance of omnivores over herbivores or carnivores in mediating bottom-up diversity effects, I argue that future work should explore the consequences of consumer plasticity in feeding behavior. This could be achieved through building food web models using stochastic individual-based approaches guided by metabolic and stoichiometric constraints on consumers.

Some tentative recommendations for future applied studies, especially in agricultural systems, can also be derived from this thesis. I found that consumer biomass and species richness were poor predictors of herbivory and predation rates. Future monitoring or empirical works linking consumer communities and their variations to ecosystem functioning should use at least one diversity metrics based on dominance and/or functional diversity. It appears to be erroneous to expect higher functioning rates with increasing consumer biomass or species richness. This conclusion deserves further scrutiny in natural systems or along environmental gradients. Biological control programs should also further explore the potential of omnivores. They are able to maintain stable populations even when potential herbivorous pest species are at low densities. Thus, continuous control of pests population by omnivorous insects may prevent future outbreaks. Omnivores may be more complex to manage, as they may also damage commercial crops. However, our analysis revealed that predation rates increased faster than herbivory rates. Therefore, additional damages to crops would likely be offset by extra top-down control. Finally, in managed systems where high levels of functioning are desirable, increasing local plant species richness will likely increase the rate of energy transfer to higher trophic levels and, thus, facilitate faster nutrient turnover reducing the needs for fertilization.

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Appendix A

Curriculum Vitae



Lionel Hertzog

Curriculum Vitae

Ausbildung

- 2013– Promotion an der Technische Universität München (TUM)
Titel *Impacts of Plant Diversity Changes on Arthropod Communities and Arthropod-mediated Processes*
Betreuer Prof. W. Weisser (TUM), Dr. A. Ebeling (FSU Jena) und Dr S. Meyer (TUM)
- 2011–2013 Master of Science an der Universität Bonn im Master Organismische und Evolutionäre Biologie, Note: 1.3 (ECTS: A)
MSc Thesis *Predictive Distribution Models under Global Change: Using Field Sampling to Validate Methodological Choices*
Betreuer Pierre Jay-Robert und PD Klaus Riede
- 2010–2011 Erasmusjahr an Leeds University (UK)
- 2008–2011 Bachelorstudium an Université de Strasbourg (FR) in Biologie, Note: 14/20 (ECTS: B)
- 2008 Baccalauréat scientifique an Lycée Louis Armand, Mulhouse (FR), Note: 16/20 (ECTS: A)

Arbeitserfahrungen

- 2013– wissenschaftlicher Mitarbeiter an der Technische Universität München
- 2013 Praktikum im Centre National de la Recherche Scientifique (CNRS) in Montpellier (FR)
- 2012 Praktikum am Max-Planck Institut für Ornithologie, Radolfzell (DE)
- 2008–2009 Betreuung verschiedene Jugendfreizeiten in Frankreich

Veröffentlichungen

Hertzog LR, Ebeling A, Weisser WW and Meyer ST (In review), Higher plant diversity increase invertebrate predation rates.

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1/3

Ebeling A, ..., **Hertzog LR** et al (In review), Plant diversity induces shifts in functional composition across trophic levels.

Meyer ST, ..., **Hertzog LR** et al (2016), Biodiversity effects strengthen over time as ecosystem functioning declines at low and increases at high biodiversity, *Ecosphere* **7**(12):e01619.

Hertzog LR, Ebeling A, Meyer ST, Eisenhauer N, Fischer C, Hildebrandt A, Wagg C and Weisser WW (2016), High Survival of *Lasius niger* during Summer Flooding in a European Grassland, *PlosOne*, **11**(11):e0152777.

Hertzog LR, Ebeling A, Meyer ST and Weisser WW (2016), Experimental manipulation of grassland plant diversity induces complex shifts in aboveground arthropod diversity, *PlosOne*, **11**(2):e0148768.

Hertzog LR, Jay-Robert P and Besnard A. (2014), Field validation shows bias corrected pseudo-absence selection is the best method for predictive species distribution modelling, *Diversity and Distributions*, **20**, 1403-1413

Baldacchino F, Puech L, Manon S, **Hertzog LR**, and Jay-Robert P (2014). Biting behaviour of Tabanidae on cattle in mountainous summer pastures, Pyrenees, France, and effects of weather variables. *Bulletin of entomological research*, **104**(04), 471-479.

Präsentationen

- 2016 Präsentation auf der GFÖ Jahrestagung in Marburg, Titel: Linking community shifts to function in multitrophic system: influence of plant diversity on grasslands arthropods
- 2015 Präsentation auf der European Ecological Foundation Konferenz in Rom (IT), Titel: Increase in predation rates along an experimental plant diversity gradient
- 2014 Poster auf der BES/SFE Konferenz in Lille (FR), Titel: Arthropod community shifts along a plant diversity gradient
- 2014 Präsentation bei der Thüringischen entomologischen Gesellschaft, Titel: Arthropodengemeinschaften in einer sich verändernden Welt: Einblicke in das Jena-Experiment - 12 Jahre Wiesen-Forschung
- 2014 Präsentation auf der GFÖ Jahrestagung in Hildesheim, Titel: Arthropod community shifts along a plant diversity gradient

Lehrerfahrungen

- 2014, 2015 Blockpraktikum in Graslandökologie
- 2014 Workshop in "Generalized Linear Mixed-effect Models" für Ökologen

EDV- Kenntnisse

- Grundlagen Perl, C++
- Fort. Python, OpenOffice, Linux, Microsoft Office, QGIS, ArcGIS
- Experte R, \LaTeX

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2/3

Sprachen

Französisch Muttersprache

English Fließend (schreiben, sprechen, lesen)

Deutsch Fließend (sprechen, lesen), Mittelstufe (schreiben)

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3/3