GEORG-AUGUST-UNIVERSITÄT
GÖTTINGEN

– CENTRE OF BIODIVERSITY AND SUSTAINABLE LAND USE –
SECTION: BIODIVERSITY, ECOLOGY AND NATURE CONSERVATION

Using body mass, metabolism and stoichiometry to assess ecological impacts in a changing environment

Dissertation zur Erlangung des Doktorgrades der
Mathematisch-Naturwissenschaftlichen Fakultäten der
Georg-August-Universität Göttingen

vorgelegt von
Diplom-Biologe

Malte Jochum

aus Wiesbaden

Göttingen, Februar 2016

Referent: Prof. Dr. Ulrich Brose
Korreferent: Prof. Dr. Stefan Scheu
Tag der mündlichen Prüfung: 15. Februar 2016

für Delila und Timea

Contents

Summary

Earth's ecosystems are composed of living organisms and their biotic and abiotic environment. In order to understand the structure and functioning of these ecosystems, ecologists study the interactions of organisms with one another and their environment. The body mass of an organism, its energy demand, and the elemental composition of the body tissue of itself and the resources it depends on are three fundamental aspects of its biology affecting its interactions with other organisms and its environment and, therefore, shaping ecological communities. While a large body of research has established the importance of these drivers, much less is known about how they jointly affect whole-ecosystem processes. This lack of knowledge is partly due to the lack of comprehensive approaches integrating body mass, metabolism and stoichiometry to assess ecosystem structure and functioning in diverse, multitrophic communities.

Body size has fundamental effects on biological rates and ecological interactions and strongly affects living organisms across levels of organisation, from individuals to communities. One major reason for this importance is the effect of body size on an organism's metabolic rate, the rate of energy uptake, transformation and allocation that, in turn, controls important aspects of its biology and defines the organism's energy demand. Ecological stoichiometry is concerned with the balance of chemical substances in ecological interactions and thus puts constraints on consumer-resource interactions. As such, these three drivers play a key role in describing and explaining ecological processes. Over the past centuries, the growing human population has dramatically altered Earth's ecosystems and climate with severe consequences on biodiversity and ecosystem functioning. In this thesis, I provide an important step towards jointly using body mass, metabolism and stoichiometry to assess ecological impacts of changing environmental conditions, as driven by anthropogenic alteration of Earth's ecosystems.

First, in Chapter 2, I review previous research on body size with a focus on insects. Initially, I discuss the historical underrepresentation of insects in body-size research and present recent developments toward a better representation of this important animal group enabled by technological improvements and the availability of high-resolution datasets. I discuss the importance of body size for animal movement and behaviour and highlight their importance for the strength and outcome of trophic interactions. Furthermore, I point to the importance of including both size and non-size effects, such as temperature,

phylogeny, and stoichiometry, in future ecological experiments and theory. Finally, I emphasise the intersection of allometry effects on behaviour and functional-morphology effects on foraging success as promising directions of future research.

In Chapter 3, I present whole-community energy flux as a measure of multitrophic ecosystem functioning and test it by assessing ecological consequences of anthropogenic land use on biodiversity and ecosystem functioning in tropical leaf-litter macro-invertebrate communities in forest, jungle rubber, rubber and oil-palm plantations. Combining metabolic theory and food web theory with previous advances in the energetic view of ecosystem processes, I develop a highly flexible measure that takes into account consumer metabolism, assimilation efficiency, network topology, feeding preferences and loss to higher trophic levels. It can now be used to easily assess and compare ecosystem funtioning across communities in different ecosystem types, carrying out a diverse range of functions that would otherwise be difficult to compare. After establishing consistent declines in species richness, animal density, and biomass from forest to oil-palm macro-invertebrate communities, I find that energy flux also decreases and is able to pick up more fine scale differences between trophic groups than, for example, standing stock biomass can detect. Additionally, I use the novel measure of ecosystem functioning to compare biodiversity ecosystem functioning relationships between land-use systems and find the relationship of species richness and energy flux to be steepest in oil-palm communities. However, different trophic guilds exhibit different patterns here. These results highlight the importance of including trophic complexity into future research on community-level processes and additionally emphasise the ability of the developed ecosystem functioning measure to describe community-level patterns based on only few easily obtainable parameters.

In Chapter 4, I combine the energetic approach developed in the previous chapter with ecological stoichiometry theory to assess multitrophic consumer responses to changing resource quality. Specifically, I test for changes in consumer stoichiometry, biomass, and feeding rates in response to increasing resource carbon:nitrogen ratios. By slightly altering the energy flux calculations, I calculate consumer feeding rates based on metabolic demand and assimilation efficiency in response to varying resource stoichiometry without having to measure feeding rates in the field or laboratory. I find that, instead of altering their body stoichiometry or avoiding low-quality resources, detritivore and predator communities exhibit increased feeding rates when exposed to low-quality resources. Interestingly, detritivore species richness significantly decreases with decreasing resource quality, potentially indicating limited ability of consumer species to perform compensatory feeding due to physiological constraints. Thus, my findings suggest compensatory feeding to be much more common across trophic levels than was previously known. Additionally, the method of calculating consumer feeding rates in response to resource quality is a

highly useful tool for future research on consumer-resource interactions.

Finally, in Chapter 5, I use an information theoretic approach to investigate the effects of basal resource stoichiometry and habitat structure on multitrophic consumer biomass density and diversity. Using this standardised model averaging framework, I am able to directly compare the effects of three habitat structural and seven stoichiometric variables on ten major taxonomic groups and four functional feeding guilds. I find partial support for all specifically tested hypotheses relating certain consumer groups to different stoichiometric and habitat-structural drivers. The tropical macro-invertebrate consumer communities are co-limited by multiple, rather than single, variables with different taxonomic groups controlled by different sets of predictor variables. Interestingly, biomass density and diversity of a given consumer taxon do not always respond homogeneously to a given change in a certain stoichiometric variable, but exhibit a diverse range of response patterns, such as parallel and opposing effects, but also cases where only one of the community characteristics is affected. Consequently, I develop a conceptual framework explaining response patterns found across 80% of the taxonomic consumer groups by assuming a saturating response of biomass, but a hump-shaped response of diversity to increasing availability of a limiting resource. Thus, my findings suggest that tropical consumer communities are co-limited by multiple parameters and highlight the importance of looking at both consumer biomass and diversity when trying to understand community responses to changing environmental conditions. Additionally, I provide a conceptual framework explaining biomass and diversity responses that can now be tested in other ecosystem types.

Taken together, in this thesis, I present novel methods and approaches that jointly use body mass, metabolism and stoichiometry to investigate ecological consequences of changing abiotic and biotic conditions. I develop whole-community energy flux and a method for calculating consumer feeding rates in response to resource stoichiometry and test the ability of these tools to describe ecological processes in complex, real-world communities. Furthermore, I integrate metabolic theory and ecological stoichiometry theory to study consumer-resource interactions across trophic levels. By combining ecological theory with state-of-the-art statistical approaches to develop and test novel methods of assessing ecological processes, this thesis provides a significant advance toward understanding and mitigating ecological impacts of anthropogenic alterations of Earth's ecosystems.

Zusammenfassung

Die Ökosysteme der Erde bestehen aus lebenden Organismen und ihrer belebten und unbelebten Umwelt. Um die Struktur und Funktion dieser Ökosysteme zu verstehen, untersuchen Ökologen die Interaktionen, die solche Organismen untereinander, sowie mit ihrer unbelebten Umwelt eingehen. Die Körpermasse eines Organismus, sein Energiebedarf, sowie die chemische Zusammensetzung seines Körpergewebes und die seiner Ressourcen sind drei fundamentale Bestandteile seiner Biologie. Sie bestimmen die Interaktionen mit anderen Organismen und der unbelebten Umwelt und beeinflussen dadurch ökologische Gemeinschaften. Obwohl die Wichtigkeit dieser drei Aspekte durch viele Forschungsarbeiten herausgebildet wurde, ist ihre gemeinschaftliche Auswirkung auf Prozesse der Ökosystem-Ebene weitgehend unerforscht. Diese Wissenslücke ist zumindest teilweise dadurch verursacht, dass es an umfassenden Ansätzen fehlt, die Körpermasse, Stoffwechsel und Stöchiometrie kombinieren, um Ökosystemstruktur und -funktion in artenreichen Gemeinschaften mit zahlreichen Trophieebenen zu erforschen.

Die Körpermasse eines Organismus hat bedeutende Auswirkungen auf biologische Raten und ökologische Interaktionen und daher, über Organisationsebenen hinweg, auf Individuen und Gemeinschaften. Ein wesentlicher Bestandteil dieser Bedeutung ist der Effekt, den Körpermasse auf die Stoffwechelrate eines Organismus, also die Rate der Energieaufnahme, Transformation und Verteilung, hat. Diese Stoffwechselrate wiederum hat enormen Einfluss auf die Biologie der Lebewesen und bestimmt ihren Energiebedarf. Ökologische Stöchiometrie befasst sich mit der Balance chemischer Substanzen und Elemente in ökologischen Interaktionen und beeinflusst daher die Interaktionen zwischen Ressourcen und Konsumenten. Somit spielen die drei beschriebenen Faktoren eine wichtige Rolle bei der Beschreibung und Erklärung ökologischer Prozesse. In den vergangenen Jahrhunderten hat die stetig wachsende menschliche Population immensen Einfluss auf die Ökosysteme und das Klima der Erde gewonnen. Die hier entstandenen Veränderungen haben nachweislich drastische Auswirkungen auf die weltweite Biodiversität und Ökosystemfunktion. Ziel dieser Doktorarbeit ist es, einen wichtigen Fortschritt zu erzielen, was die Integration von Körpermasse, Stoffwechsel und Stöchiometrie zur Erforschung von ökologischen Auswirkungen veränderter Umweltbedingungen angeht, wie sie durch anthropogenen Einfluss auf weltweite Ökosysteme auftreten.

Zunächst bespreche ich in Kapitel 2 bisherige Forschung zum Thema Körpermasse, mit einem Schwerpunkt auf Insekten. Ich diskutiere die historische Unterrepräsentierung von Insekten in Körpermassen-Forschung und zeige auf, dass diese Organismengruppe in jüngerer Vergangenheit besser repräsentiert ist. Diese Veränderung ist sowohl durch technischen Fortschritt, als auch durch die Verfügbarkeit hochaufgelöster Datensätze ermöglicht worden. Ich diskutiere die Bedeutung von Körpermasse für die Bewegung und das Verhalten von Tieren und unterstreiche die Wichtigkeit dieser Effekte für die Stärke und das Resultat von Fraßinteraktionen. Weiterhin beschreibe ich die Bedeutung der gleichzeitigen Beachtung von Größen-Effekten und solchen, die nicht mit Körpergröße zusammenhängen, wie Temperatur, Phylogenie und Stöchiometrie, für zukünftige Experimente und die Entwicklung ökologischer Theorie. Abschließend hebe ich die Schnittstelle allometrischer Effekte auf Verhalten und der Effekte funktioneller Morphologie auf den Erfolg von Nahrungssuche als wichtiges Objekt zukünftiger Forschung hervor.

In Kapitel 3 beschreibe ich Energiefluss auf Gemeinschaftsebene als ein Maß für trophieebenen-übergreifende Ökosystemfunktion. Ich teste dieses neu entwickelte Maß, indem ich die ökologischen Auswirkungen von Landnutzungsveränderungen auf Biodiversität und Funktion tropischer Laubstreugemeinschaften in Wald, Kautschuk- und Ölpalmenplantagen untersuche. Die Kombination von metabolischer Theorie und Nahrungsnetz-Theorie, sowie vorangegangenen Fortschritten auf dem Gebiet der energetischen Beschreibung von ökologischen Prozessen, ermöglicht die Entwicklung eines vielseitigen und anpassungsfähigen Maßes für Ökosystemfunktion. Dieses Maß berücksichtigt Konsumentenstoffwechsel, Assimilationseffizienz, Netzwerktopologie, Fraßvorlieben und Energieverluste an höhere Trophieebenen. Es ermöglicht den unkomplizierten Vergleich von Ökosystemfunktion zwischen unterschiedlichen Typen von Ökosystemen, die vollkommen verschiedene Funktionen ausführen, deren Vergleich andernfalls schwer zu bewerkstelligen wäre. Nachdem ich den Verlust von Artenreichtum, Abundanz und Biomasse wirbelloser Tiere von Wald zu Ölpalmenplantagen aufgezeigt habe, beschreibe ich, wie auch der Energiefluss in diesen Systemen abnimmt. Mein Energiefluss-Maß ist in der Lage, feinere Veränderungen und Unterschiede zwischen einzelnen trophischen Gruppen zu beschreiben, als dies etwa durch die Beschreibung von Biomassenveränderungen möglich wäre. Darüber hinaus nutze ich das entwickelte Maß zur Beschreibung des vorliegenden Verhältnisses zwischen Biodiversität und Ökosystemfunktion in den verschiedenen Landnutzungssystemen. Der Zusammenhang ist am steilsten in Ölpalmenplantagen, weist jedoch starke Unterschiede zwischen verschiedenen trophischen Gruppen auf. Meine Ergebnisse unterstreichen die Bedeutung der Berücksichtigung trophischer Komplexität in zukünftigen Forschungsvorhaben zur Untersuchung von ökologischen Prozessen auf Gemeinschaftsebene. Darüber hinaus

betonen sie die Eignung des entwickelten Maßes für Ökosystemfunktion, ökologische Prozesse auf Gemeinschaftsebene zu beschreiben, trotz der wenigen Parameter, die zu seiner Berechnung benötigt werden.

In Kapitel 4 kombiniere ich den energetischen Ansatz des vorherigen Kapitels mit ökologischer Stöchiometrie, um Auswirkungen unterschiedlicher Ressourcenqualität auf Konsumenten zu untersuchen. Dazu analysiere ich die Auswirkungen steigenden Kohlenstoff:Stickstoff Verhältnisses der Ressource auf Konsumenten Stöchiometrie, Biomasse und Fraßrate. Ich passe dazu die zuvor entwickelte Energiefluss-Berechnung leicht an und nutze sie, um Fraßraten basierend auf Energiebedarf und Assimilationseffizienz in Abhängigkeit von unterschiedlicher Ressourcenqualität zu berechnen. Sowohl Detritivore, als auch Prädatoren verändern demnach weder die Stöchiometrie ihres Körpergewebes, noch ihre Biomasse, sondern steigern ihre Fraßrate, wenn sie mit niedrigerer Ressourcenqualität konfrontiert werden. Interessanter Weise verringert sich gleichzeitig die Diversität der Detritivoren mit abnehmender Ressourcenqualität. Dieser Effekt weist möglicherweise auf eine begrenzte Fähigkeit hin, die eigene Fraßrate zu steigern, was an physiologischen Einschränkungen der Konsumenten liegen dürfte. Meine Ergebnisse legen kompensatorischen Fraß als generelle Reaktion auf niedrige Ressourcenqualität über Trophieebenen hinweg nahe. Die Methode zur Berechnung von Fraßraten in Abhängigkeit von Ressourcenqualität ist darüber hinaus wertvoll für zukünftige Forschung zu Konsumenten-Ressourcen Interaktionen.

In Kapitel 5 benutze ich einen "information theory"-Ansatz zur Untersuchung des Einflusses von basaler Ressourcen-Stöchiometrie und Habitatstruktur auf die Biomassendichte und Diversität multitrophischer Konsumentengemeinschaften. Dieser Ansatz ermöglicht den direkten Vergleich der Effekte von drei Habitatstruktur-Parametern und sieben Stöchiometrie-Parametern auf die Biomassendichte und Diversität von zehn taxonomischen Konsumentengruppen und vier funktionellen Gruppen. Alle getesteten Hypothesen zum Einfluss verschiedener Parameter auf die Konsumentengruppen finden teilweise Bestätigung. Die untersuchten tropischen Konsumentengemeinschaften sind demnach durch mehrere Parameter anstatt durch einzelne limitierende Faktoren ko-limitiert, wobei verschiedene taxonomische Gruppen durch unterschiedliche Kombinationen von Parametern kontrolliert werden. Interessanter Weise stimmen die Reaktionen von Biomassendichte und Diversität einer Konsumentengruppe auf die Veränderung eines bestimmten Parameters nicht immer überein. Die beiden Aspekte zeigen vielmehr sehr unterschiedliche Reaktionsmuster, wie zum Beispiel parallele und entgegengerichtete Reaktionen, aber auch Fälle, in denen nur einer der Parameter beeinflusst wird, der andere aber nicht. Ich entwickle daher ein Konzept, das Reaktionsmuster erklärt, wie sie in 80% der untersuchten taxonomischen Konsumentengruppen vorkommen. Dieses Konzept erwartet eine sättigende Reaktion von

Biomassendichte, aber eine buckelförmige Reaktion von Diversität auf die zunehmende Verfügbarkeit einer limitierenden Ressource. Meine Ergebnisse zeigen demnach, dass tropische Konsumentengemeinschaften durch mehrere Parameter ko-limitiert sind und unterstreichen die Bedeutung der gleichzeitigen Untersuchung von Biomassendichte und Diversität von Konsumenten, um die Auswirkungen verändeter Umwelteinflüsse auf Gemeinschaftsebene zu verstehen. Darüber hinaus präsentiere ich ein Konzept zur Erklärung von Biomassendichte und Diversität von Konsumentengemeinschaften, dessen Vorhersagen in weiteren Ökosystemtypen getestet werden können.

In der vorliegenden Arbeit präsentiere ich neuartige Methoden und Ansätze zur kombinierten Nutzung von Körpermasse, Stoffwechsel und Stöchiometrie in der Untersuchung von ökologischen Auswirkungen sich verändernder abiotischer und biotischer Bedingungen. Dazu entwickle ich Energiefluss auf Gemeinschaftsebene und eine Methode zur Berechnung von Fraßraten in Abhängigkeit von Ressourcenstöchiometrie und teste die Eignung dieser Hilfsmittel zur Beschreibung von ökologischen Prozessen in komplexen Gemeinschaften. Ich kombiniere metabolische Theorie und ökologische Stöchiometrie, um Konsumenten-Ressourcen Interaktionen trophieebenen-übergreifend zu untersuchen. Durch die Kombination ökologischer Theorie mit modernen statistischen Verfahren zur Entwicklung und Untersuchung neuer Methoden der Erhebung ökologischer Prozesse bietet die vorliegende Arbeit einen deutlichen Fortschritt hin zu Verständnis und Abschwächung ökologischer Auswirkungen anthropogener Veränderungen der globalen Ökosysteme.

Contributions to the research chapters

Chapter 2: Body size and the behavioral ecology of insects: linking individuals to ecological communities

Gregor Kalinkat, Malte Jochum, Ulrich Brose & Anthony I. Dell

All authors conceived and designed the paper; GK wrote the first draft; all authors contributed to the writing; MJ made the figures.

Published in *Current Opinion in Insect Science*, 2015, **9**:24-30, doi:10.1016/j.cois.2015.04.017

Chapter 3: Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning

Andrew D. Barnes*, Malte Jochum*, Steffen Mumme, Noor Farikhah Haneda, Achmad Farajallah, Tri Heru Widarto & Ulrich Brose

ADB, MJ and UB designed the study; ADB, MJ and SM carried out the field and laboratory work; ADB and MJ prepared and analysed the data; all authors interpreted the results and wrote the paper.

* **These authors contributed equally to this work.**

Published in *Nature Communications*, 2014, **5**, 5351, doi:10.1038/ncomms6351

Chapter 4: Decreasing stoichiometric resource quality drives compensatory feeding and consumer species loss across trophic levels

Malte Jochum, Andrew D. Barnes, David Ott, Birgit Lang, Bernhard Klarner, Achmad Farajallah, Stefan Scheu & Ulrich Brose

MJ, ADB and UB designed the study; MJ and ADB carried out the field and laboratory work; MJ and ADB prepared and analysed the data and all authors interpreted the results; MJ wrote a first draft and all authors contributed to the writing.

Chapter 5: How resource stoichiometry and habitat structure drive diversity and biomass density of tropical macro-invertebrate communities

Malte Jochum, Andrew D. Barnes, Patrick Weigelt, David Ott, Katja Rembold, Achmad Farajallah & Ulrich Brose

MJ, ADB and UB designed the study; MJ and ADB carried out the field and laboratory work; MJ and ADB prepared the data; MJ and PW analysed the data and all authors interpreted the results; MJ wrote a first draft and all authors contributed to the writing.

Affiliations of co-authors

Andrew D. Barnes	University of Göttingen J.F. Blumenbach Institute of Zoology and Anthropology, Berliner Str. 28, 37073 Göttingen, Germany
Ulrich Brose	University of Göttingen J.F. Blumenbach Institute of Zoology and Anthropology, Berliner Str. 28, 37073 Göttingen, Germany German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany Friedrich Schiller University Jena Institute of Ecology, Dornburger-Str. 159, 07743 Jena, Germany
Anthony I. Dell	National Great Rivers Research and Education Center (NGRREC) One Confluence Way, East Alton, IL 62024, USA
Achmad Farajallah	Bogor Agricultural University Faculty of Mathematics and Natural Sciences, Darmaga Campus, Bogor 16680, Indonesia
Noor Farikhah Haneda	Bogor Agricultural University Faculty of Forestry, Darmaga Campus, Bogor 16680, Indonesia
Gregor Kalinkat	Eawag Swiss Federal Institute of Aquatic Science and Technology Department of Fish Ecology and Evolution, Seestraße 79, 6047 Kastanienbaum, Switzerland
Bernhard Klarner	University of Göttingen J.F. Blumenbach Institute of Zoology and Anthropology, Berliner Str. 28, 37073 Göttingen, Germany
Birgit Lang	Senckenberg Museum of Natural History Görlitz Am Museum 1, 02826 Görlitz, Germany
Steffen Mumme	has been a member of the J.F. Blumenbach Institute of Zoology and Anthropology, University of Göttingen, but is without affiliation at the moment.
David Ott	University of Göttingen J.F. Blumenbach Institute of Zoology and Anthropology, Berliner Str. 28, 37073 Göttingen, Germany

Affiliations of co-authors

	University of Münster Institute of Landscape Ecology, Heisenbergstr. 2, 48149 Münster, Germany
Katja Rembold	University of Göttingen Biodiversity, Macroecology & Conservation Biogeography Group, Büsgenweg 1, 37077 Göttingen, Germany
Stefan Scheu	University of Göttingen J.F. Blumenbach Institute of Zoology and Anthropology, Berliner Str. 28, 37073 Göttingen, Germany
Patrick Weigelt	University of Göttingen J.F. Blumenbach Institute of Zoology and Anthropology, Berliner Str. 28, 37073 Göttingen, Germany Biodiversity, Macroecology & Conservation Biogeography Group, Büsgenweg 1, 37077 Göttingen, Germany
Tri Heru Widarto	Bogor Agricultural University Faculty of Mathematics and Natural Sciences, Darmaga Campus, Bogor 16680, Indonesia

Part I.

General introduction

Chapter 1.

Introduction

1.1. Aims and scope

Planet Earth is inhabitet by countless organisms shaping its outward appearance and controlling the functioning of important processes, vital to life on Earth and the growing human population. These organisms interact with each other and their non-living environment forming ecosystems (Tansley, 1935), which in sum represent the world's biosphere (Krebs, 2009). Ecology is the study of these organisms and their interactions with their biotic and abiotic environment that affect their distribution and abundance (Krebs, 2009). Ecologists work on different levels of biological organisation including individuals, populations and communities to gain a deeper understanding of nature and how different aspects of organisms and their environment control their growth, reproduction, energy consumption and the flow of matter and energy from one organism to another and through the interaction networks that they build.

It has long been acknowledged, that the body size of an individual organism governs not only its own physiology, growth or locomotion, but also its interactions with the abiotic and biotic environment, such as, for example, the consumption of resources (Peters, 1983). One major aspect of an organism's biology that is driven by its body size - and temperature - is its metabolic rate, which is the rate of energy and material uptake, transformation and expenditure (Brown *et al.*, 2004). Through metabolism, body size therefore has major implications for many trophic - that is feeding-related - and non-trophic interactions with other organisms, with effects on higher levels of organisation such as populations, communities and ecosystems (Schramski *et al.*, 2015). Aside from these size-based considerations, organisms - and their environment - are made of matter formed by molecules that, in turn, consist of atoms of many different chemical elements. These elements are not randomly assembled to form living organisms, but rather form distinct building blocks of tissues and organs and therefore occur in more or less strict proportions (Redfield, 1958; Sterner & Elser, 2002). Organisms differ in their relative elemental composition (i.e., stoichiometry) depending on their trophic position

within the community, the habitat they live in or the biome they inhabit (Elser *et al.*, 2000a; McGroddy *et al.*, 2004). Ecological stoichiometry studies the "balance of multiple chemical substances in ecological interactions and processes" (Sterner & Elser, 2002). It therefore provides a useful tool to investigate ecological consequences of organism elemental composition such as the impact of changing resource stoichiometry on consumer populations. Because of their broad implications for organisms and their interactions, body mass, metabolism and stoichiometry are useful in assessing and predicting ecological processes and, consequently, the ecological impact of changes in environmental conditions that affect these fundamental biological variables. For thousands of years, the growing human population has strongly altered ecosystems, starting with early impacts of human hunting and agriculture (Steffen *et al.*, 2011). However, the beginning of the industrial revolution in the 18th century has launched an epoch of anthropogenic domination of our planet (Zalasiewicz *et al.*, 2011). In the mean time, human activity has clearly altered Earth's climate, biogeochemical cycles, the water cycle and biodiversity (Vitousek *et al.*, 1997a; Steffen *et al.*, 2011), with subsequent impacts on the functioning of ecosystems worldwide (Hooper *et al.*, 2005; Cardinale *et al.*, 2012).

In this thesis, I aim to provide an important advance in knowledge on how changes in organism body mass, metabolism and stoichiometry can interactively be used to assess ecological consequences of changing biotic and abiotic conditions for consumer communities and ecosystem functioning. Specifically, first, I review existing research on body size, with special attention to body-size impacts on movement and behaviour that, in turn, strongly affect ecological interactions. I point out that, historically, insects are underrepresented in body-size research. Furthermore, I highlight the advantages and limitations of using body size as a predictor for ecological processes and where further non-size related aspects need to be included to develop more powerful ecological theory **(Chapter 2)**. Second, I use a large data set on tropical macro-invertebrates and their leaf-litter resources to develop and test novel approaches to ecosystem functioning and ecological stoichiometry research. I develop a measure of whole-community energy flux to assess multitrophic ecosystem functioning and apply this measure to the tropical leaf-litter invertebrate data set to assess consequences of anthropogenic land use on biodiversity and ecosystem functioning **(Chapter 3)**. Subsequently, I assess consumer responses to changing resource quality across trophic levels, using carbon:nitrogen (C/N) ratios to determine stoichiometric quality of resource and consumer body tissue. I calculate consumer feeding rates in response to varying resource quality from their metabolic demand and assimilation efficiency without having to measure their feeding in the field **(Chapter 4)**. Finally, I extend existing approaches that combined metabolic theory and ecological stoichiometry to assess consumer-community responses to changing resource stoichiometry. Using a model averaging framework, I assess resource-stoichiometry effects

on consumer biomass and diversity and compare my results to those from former research on temperate communities that did not include diversity effects **(Chapter 5)**. Combining different ecological theories and developing novel approaches to answer urgent ecological questions, my thesis represents a major step towards understanding and quantifying ecological responses to fundamental changes in important biotic and abiotic factors, as driven by the overwhelming anthropogenic alteration of our planet.

1.2. Body size and metabolism

Throughout the literature, different terminology is used to describe the effects of body size. Specifically, the terms body size and body mass are sometimes used synonymously. Throughout this thesis, when describing general patterns, I will use the term body size. However, when referring to specific use of body mass as the dry or wet weight of organisms (an important component of body size), as used in Chapters 3, 4 and 5, I will use the term body mass. Body size is one of the most fundamental traits of every living organism, mainly because of the constraints that the laws of physics impose on it (Schmidt-Nielsen, 1984). With increasing body length of an organism, its surface area and volume are altered with different exponents (2 and 3, respectively), changing the ratios of body length, surface area and volume to one another. Most biological processes are directly related to one of these ratios. While respiration or excretion for example, take place across surfaces (area), the amount of energy or material to be transferred across this surface depends on the volume of the organism. Larger organisms therefore need to more efficiently transfer energy and material across their surfaces (Begon, 2006). The fact that large animals need more energy than small ones has long been acknowledged (Kleiber, 1932), and early work has clearly related body size to energy and material demand because of the surface-area-to-volume ratio (Rubner, 1883). In ecology, much attention has been paid to the metabolic rate of an organism; that is, the rate of energy and material uptake, transformation and expenditure (West *et al.*, 1997, 1999; Brown *et al.*, 2004). However, even in early studies, the exponent of the relationship between body size and energy demand (i.e., metabolic rate) was debated. While intraspecific variation was explained by a 2/3 exponent, derived from surface-to-volume ratios (Rubner, 1883), interspecific variation in metabolic rates was found to scale with body mass with an exponent of 3/4 (Kleiber, 1947). While larger animals therefore have a higher energy demand than small animals, their mass-specific metabolic rate is smaller (Brown *et al.*, 2004; White, 2010), meaning that they use energy more efficiently. A theoretical foundation for the three-quarter-scaling was proposed decades later by West *et al.* (1997, 1999) who explained this exponent by the fractal geometry of hierarchical branching networks within organisms (Savage *et al.*, 2008). Ever since the manifestation of these ideas in the Metabolic Theory of Ecology (MTE)

(Brown *et al.*, 2004), they have been and still remain to be debated (Hirst *et al.*, 2014; Glazier, 2015). Specifically, the universality of the 3/4 exponent is frequently doubted (White, 2010). However, there are also approaches that expand metabolic theory to increase accuracy in the prediction of metabolic rates based on body mass. For example, Ehnes *et al.* (2011) have demonstrated that adding phylogenetic information improves the calculation of metabolic rates in invertebrates.

Irrespective of the debate on the exact exponent of metabolic scaling relationships, body size clearly affects fundamental aspects of an organism's biology, such as individual growth, the ingestion and excretion of material and reproduction (Peters, 1983). Such relationships of organism properties to body size are called allometric relationships (Gould, 1966). By incorporating the number of organisms and their size structure, these scaling relationships with body size can be used to assess ecosystem-wide processes, such as biomass production (Peters, 1983; Brown *et al.*, 2004). Interestingly, animal abundance is also related to body size, with small organisms being more abundant than large ones. This general statement seems to hold across levels of scale with, for example, more small than large individuals within a population, or small bodied species showing higher densities (Damuth, 1981; White *et al.*, 2007; Ehnes *et al.*, 2014). Consequently, metabolic theory predicts population density to follow a -3/4 power law with population-averaged body mass, which further translates into a positive quarter-power scaling of population biomass with body mass (Brown *et al.*, 2004).

Aside from its effect on population density and biomass, body size also affects trophic relationships. Predators are usually larger than their prey and there is a positive relationship between prey size and predator size (Warren & Lawton, 1987; Cohen *et al.*, 1993). However, there are differences in naturally occurring predator-prey body size ratios between ecosystems and consumer types (Brose *et al.*, 2006). Moreover, body size has important implications for food-web structure, as it affects species' degree distributions (i.e., the number of links) such as vulnerability (number of predators), generality (number of prey) and linkedness (total number of trophic links) (Digel *et al.*, 2011). Across ecosystem types, predator body mass furthermore increases with trophic level (Riede *et al.*, 2011). However, body mass does not only affect who eats whom, but also determines the strength of this trophic interaction. Thus, larger predators attack more prey and process them faster, with both relationships (body mass with attack rate and handling time) exhibiting an optimum at intermediate predator-prey body mass ratios (Rall *et al.*, 2012). Additionally, changes in the size structure of one species can have cascading consequences for food webs (Jochum *et al.*, 2012). As we will see, such allometric relationships have far-reaching consequences on food webs and ecosystem functioning and are susceptible to anthropogenic alteration of natural ecosystems.

Although body size has strong impacts across ecological scales, there are important

effects independent of body size that drive individual-based biological rates (Brown *et al.*, 2004), as well as ecological interactions and community structure (Petchey *et al.*, 2008; Boukal, 2014). One of the most obvious size-independent effects is temperature which controls individual biological rates (Brown *et al.*, 2004; Dell *et al.*, 2011) as well as ecological interactions (Rall *et al.*, 2012; Dell *et al.*, 2014b) with subsequent effects on ecological stability (Fussmann *et al.*, 2014; Binzer *et al.*, 2015). Additionally, phylogeny can help explaining body-size unrelated variation in metabolic rates and food-web structure (Ehnes *et al.*, 2011; Naisbit *et al.*, 2012). Furthermore, the structure of ecological networks in general is most accurately predicted when incoporating a few size-independent traits, such as matching traits for consumers and resources (Eklöf *et al.*, 2013). Thus, although body size and metabolism drive many important biological rates and control ecological processes through species interactions, incorporating additional environmental parameters and traits will improve the power of ecological models and theory. When studying ecological consequences to changing biotic and abiotic conditions, it is therefore imperative to consider body size as a biological parameter of striking importance for ecological processes and additionally take into account variation in non-size drivers of ecological processes.

Historically, many of the described patterns driven by body size have been exclusively studied in vertebrates and mammals (Peters, 1983), with invertebrates only more recently receiving the attention they deserve considering their importance for ecosystem processes (Seastedt & Crossley, 1984; Yang & Gratton, 2014) due to their high diversity and sheer biomass (Wilson, 1987). Thus, incorporating invertebrates into further research on body-size effects seems important.

1.3. Interactions and ecological networks

The notion that different forms of life interact with each other is probably as old as mankind. Over the past centuries, ecologists have studied interactions between individuals, species and functional groups, stimulated by early research on the linkages between different actors in natural communities, such as the description of Darwin's "entangled bank" (Darwin, 1859). Organisms can have facilitative or detrimental effects on each other and ecology focuses on such interactions, with competition, predation, parasitism and mutualism being perhaps the most prominent examples (Begon, 2006; Krebs, 2009). Most of the patterns described below hold for interactions between individuals, species or functional groups. However, for simplicity, I will mainly refer to interactions on the species level. When looking at nature's complexity, it is apparent that an interaction between two focal species not only affects theses interactors, but also indirectly impacts other related species within the community (Wootton, 1994; Begon,

2006). Such insight has led to early approaches of assembling these single interactions into interaction chains or cycles (Elton, 1927) that enabled predictions on how a change at one point of the community propagates through the system and leads to further changes in other compartments. The early concept of relatively simple food chains and cycles was later extended to so called food webs - networks of trophic interactions (links) between species (nodes) sharing a certain habitat - that became more and more highly resolved (Dunne, 2006). Such food webs have been and continue to be intensively studied both empirically and theoretically. Historically, most research on interaction chains and networks has concentrated on feeding interactions (trophic interactions) (Pimm, 1982; Dunne, 2006), although considerable effort has also been made in the fields of mutualistic and host-parasitoid networks (Ings *et al.*, 2009). Furthermore, over the last decades, some progress has been made with incorporating non-feeding interactions into ecological networks of feeding interactions (Ings *et al.*, 2009; Olff *et al.*, 2009; Kéfi *et al.*, 2012).

When studying ecological consequences of biotic and abiotic alterations, it is important to take ecological network structure into account. In the above section, we have already seen that body size can affect ecological interactions and thus network structure. Other examples for parameters driving ecological interactions are morphological or chemical defenses (Petchey *et al.*, 2008), traits that determine spatio-temporal overlap between interacting species and their foraging behaviour or vulnerability (Boukal, 2014) as well as resource stoichiometry (Fagan & Denno, 2004; Shurin *et al.*, 2006). A recent study on dimensionality of consumer search space has furthermore found striking differences in the relationship of consumer body mass and consumption rate depending on the type of consumer search space, with consumption rates being much higher for consumers that search for resources in 3D (volume) in comparison to 2D (surface) (Pawar *et al.*, 2012).

One reason why trophic interaction networks have been extensively studied is that they provide an excellent example of how structure determines function in natural ecosystems (Pimm, 1982). Specifically, food-web research covers a wide range of topics from fundamental structural properties to the implications of these properties for food-web dynamics and stability in response to perturbations (Dunne, 2006). Initially, food webs have been treated as binary networks showing either presence or absence of species (nodes) and interactions (links) (Ings *et al.*, 2009). However, over the last decades, important advances have been made towards quantifying both nodes and links within such networks (Bersier *et al.*, 2002; Woodward *et al.*, 2005; Banašek-Richter *et al.*, 2009) using density or body mass information (Brose *et al.*, 2006) and different measurements of interaction strength (Wootton & Emmerson, 2005). To relate structure and function in ecological networks, it is important to consider the strength of interactions, as these interactions control ecosystem processes (Wootton & Emmerson, 2005).

Trophic interactions have proven to be of high importance for ecological processes as

they represent the flux of matter and energy through these networks and therefore enable us to assess functional processes of ecosystems. Quantifying the strength of such trophic interactions (Berlow *et al.*, 2004) should be key to studying ecological processes and thus approaches to simplify the assessment of consumption rates and the flux of matter and energy in field and laboratory studies should facilitate future ecological research.

1.4. Flux of matter and energy

Trophic interactions represent matter and energy flux from one interactor to another and thus trophic networks build the energetic backbone of ecosystems (Lindeman, 1942; Pimm, 1982). Both matter and energy flux are fundamental aspects of biological systems as they describe how communities of living organisms are linked to their abiotic environment (Begon, 2006). However, there are fundamental differences between these two aspects. Organisms need chemical elements and compounds to build their body tissues and they need energy to perform work. While chemical substances are taken up at the lowest level of the community, transferred through the system, released and then possibly taken up again, each joule of energy can only be used once (Begon, 2006). Hence, although matter and energy flux are tightly interwoven, they represent two different facets of ecological processes. Consequently, when trying to describe such processes, it will be useful to investigate both the flux of matter and energy through the given ecological network.

In energetic networks, nodes typically represent trophic groups as pools of biomass or nutrients rather than taxonomic species (Ings *et al.*, 2009). In his famous article on trophic dynamics in ecological systems, Lindeman (1942) described ecosystems as a hierarchical set of trophic levels that each take up and transform energy from the level below and transfer it to the next higher level. The efficiency of this transfer is a key concept of this energetic view (Andersen *et al.*, 2009). As such, life on Earth is predominantly driven by solar energy that is taken up by autotrophic producers using photosynthesis to transform the energy into organic material, a process referred to as primary production. This biomass pool is then exploited by the first consumer level and so on up the trophic food chain, with decreasing productivity of trophic levels (Lindeman, 1942). Productivity decreases because not all energy produced at the lower level is consumed by higher levels, not all material consumed is assimilated through consumer gut walls and not all energy assimilated is used to produce biomass available for higher levels to feed on (Begon, 2006). The amount of available energy at a given trophic level thus depends on transfer efficiencies such as consumption efficiency, assimilation efficiency and production efficiency. Consumption efficiency is the proportion of the productivity at a given trophic level that is consumed (eaten) by the next higher level. What is not taken up by the higher level dies uneaten and is processed by the decomposer system. Assimilation efficiency

describes what fraction of the consumed energy is transferred across the gut walls, in contrast to the energy that is excreted and again utilised by the decomposer system. Of this assimilated energy, production efficiency describes the part that is used to produce new biomass, while the rest is lost as heat during respiration. The product of these three efficiencies is the trophic transfer efficiency between two trophic levels (Begon, 2006). Due to these restrictions to energy transfer, productivity decreases with trophic level which often leads to a pyramidal structure of energy availability and thus biomass at the trophic levels of a community (Elton, 1927). All energy taken up by the decomposer system is then in turn transferred up the trophic ladder until it is released as respiratory heat. Depending on the ecosystem type, the amount of energy channeled through the decomposer system can vary considerably. In forests, the vast majority of net primary production is channeled as detritus (Cebrian, 1999) making forest decomposer systems very important for global energy and matter transfer.

Because the flux of energy is such a fundamental process within natural ecosystems, its quantification is of high importance and consequently several approaches to quantify energy flux within communities have been suggested over the last decades (de Ruiter *et al.*, 1993; Bersier *et al.*, 2002; Ulanowicz, 2004; Reuman & Cohen, 2005). An underlying theme of these studies is that, in order to study ecosystems, ecologists should focus on processes instead of objects and therefore measure fluxes rather than stocks (Ulanowicz, 2004). In order to achieve this goal, ecological network analysis (ENA) offers different tools to quantitatively assess energy and material flow in networks using simulation modeling (Wulff *et al.*, 1989). This approach first relies on qualitative information such as the taxa / compartments present in the focal system and the network structure indicating who eats whom in the community. Second, investigators need to quantify as many stocks and transfer rates, as well as physiological requirements of the nodes within the given community as possible (Ulanowicz & Scharler, 2008). Thus, at least a few characteristic flows (e.g., primary productivity) need to be measured in the field or alternatively inferred from literature resources. Finally, the strength of all other transfer rates is analytically computed using input / output analysis tools on the basis of expected balance between energy going in and out of each node (Ulanowicz, 2004; Ulanowicz & Scharler, 2008). Another approach to quantify relative flux through trophic links employed data on population consumption, production, mean body mass and numerical abundance from an intensively studied food web to test different models for their prediction strength (Reuman & Cohen, 2005). Thereafter, relative flux was best predicted by the product of prey production and consumer consumption, both predicted from allometric relationships. Another promising approach to quantifying feeding rates and thus energy flux between trophic interactors is that described by de Ruiter *et al.* (1993) and subsequently employed by several other studies (Moore *et al.*, 1993; de Ruiter

et al., 1994, 1995; Neutel *et al.*, 2002). Aiming to study nutrient cycling in soil food webs, de Ruiter *et al.* (1993) extended a former framework of Hunt *et al.* (1987) and calculated feeding rates taking into account biomass pools, death and predation rates as well as assimilation and production efficiency. Additionally, they went beyond simple network topology by accounting for feeding preferences of consumers feeding on several prey types and the relative abundance of the prey populations. Their calculation of feeding rates represents a highly sophisticated method to assess multitrophic energy flux. While these approaches represent highly advanced frameworks for calculating energy flux within ecological networks, they are mainly based on population-level data for stocks and process rates such as biomass, production or consumption. Using such higher-level data can result in over- or underestimating the real patterns, because, for example, the energy demand of a population with a given biomass critically depends on the body-mass structure within the population. This body-size structure affects population energy demand because of the non-linear scaling of metabolic rate with body mass. While it is important to be able to generalize some measures, it might be ideal to gather individual-level data on at least some stocks or process rates. To achieve more realistic values of energy flux, it therefore seems promising to combine and integrate system-level theory with population-level and individual-level data (Schramski *et al.*, 2015).

While the energy taken up through photosynthesis can only be used once and is finally lost from the ecosystem as respiratory heat, energy transfer is closely related to the transfer of chemical elements and thus matter in ecosystems (Begon, 2006). Globally, chemical elements are stored in and cycled through the atmosphere, lithosphere, hydrosphere and biosphere. While in the first three spheres they exist in inorganic form, the biosphere stores and transfers chemical elements in organic compounds that comprise the body of living, dead and decaying organisms (Begon, 2006). Nutrient elements are taken up by plants as inorganic molecules or ions from the atmosphere or dissolved in water, then used to build organic compounds forming biomass that can be transferred up the food chains and finally released again. They can thus be endlessly cycled through food chains and their abiotic environment (Begon, 2006).

Aiming to study ecological processes in response to altered biotic and abiotic conditions, a combined investigation of energy and matter flux seems fruitful. This perspective allows for simultaneous incorporation of body mass and metabolic demand, ecological interaction networks and the availability of chemical elements across trophic levels. Ecological stoichiometry theory provides a framework to study the importance of such chemical elements for the interactions between organisms and their biotic and abiotic environment (Elser *et al.*, 2000a; Sterner & Elser, 2002).

1.5. Ecological stoichiometry

Within the biosphere, chemical elements are bound in the bodies of organisms dead and alive. These bodies are built from about 25 biologically relevant chemical elements (Frausto da Silva & Williams, 2001; Kaspari, 2012) in relatively strict proportions (Redfield, 1958; Sterner & Elser, 2002; McGroddy *et al.*, 2004). Thus, living organisms must largely maintain homeostasis, which means they need to restrict the variation of their elemental content in response to changes in their environment and resources (Sterner & Elser, 2002). Consequently, gradients in elemental availability affect consumer communities (Hessen, 1992; Orians & Milewski, 2007). By studying the balance and dynamics of key elements, ecologists have gained understanding of a broad range of topics, such as consumer and prey population dynamics, interactions, food-web dynamics, production and nutrient cycling (Elser *et al.*, 2000a; Cross *et al.*, 2005). While traditional research on elemental ratios has focused on carbon (C), nitrogen (N) and phosphorus (P) and the ratios between these elements (Redfield, 1958), more recent research includes a wider range of elements and specific hypotheses and theories have been developed in order to explain and predict consumer responses to changes in the availability of certain elements (Kaspari & Yanoviak, 2009; Kaspari, 2012; Sperfeld *et al.*, 2012; Ott *et al.*, 2014a). In chemistry, the term stoichiometry refers to the conservation of mass and energy and the law of definite proportions in chemical reactions (Sterner & Elser, 2002). Consequently, ecological stoichiometry describes the balance of chemical elements or substances in ecological interactions (Sterner & Elser, 2002). Drawing on earlier concepts by Lotka (1925) and Reiners (1986), Sterner & Elser (2002) condensed the principles of ecological stoichiometry theory in their 2002 book. This field of ecological research has the ability to integrate across levels of organisation including genes, cells, organs, individual organisms, populations and ecosystems (Elser *et al.*, 1996, 2000b).

In order to meet their energetic demand and build up biomass while keeping relatively strict homestasis, consumers depend on both the quantity and quality of their resources (Urabe & Sterner, 1996; Sterner, 1997; Frost *et al.*, 2005b; Persson *et al.*, 2010; Ott *et al.*, 2012). However, the stoichiometry of resources and their consumers can differ markedly (Elser *et al.*, 2000a; Martinson *et al.*, 2008; Fanin *et al.*, 2013), a phenomenon referred to as stoichiometric mismatch (Frost *et al.*, 2005a; Hillebrand *et al.*, 2009). Depending on the trophic position of the consumer and its feeding type, this mismatch can be more or less pronounced, with consumers at higher trophic levels usually less constrained by their resources than consumers at lower levels, especially those feeding on autotrophs or detritus (Elser *et al.*, 2000a; Fagan *et al.*, 2002; McGroddy *et al.*, 2004). In addition to this mismatch, herbivores and detritivores face large variation in the nutritional value of autotrophic resources and their leftovers (Sterner & Elser, 2002; Persson *et al.*, 2010;

Hillebrand *et al.*, 2014). Moreover, there are differences in the stoichiometric limitation between ecosystem types (Elser *et al.*, 2000a, 2007). Limitation of autotroph production can have cascading consequences on higher trophic levels (Malzahn *et al.*, 2007; Boersma *et al.*, 2008). However, such impact of resource stoichiometry on consumers is mediated by physiological processes such as acquisition, incorporation and release of elements, with differences in the pathways of these processes between different kinds of consumer organisms (Anderson *et al.*, 2005; Frost *et al.*, 2005b).

Over the last decades, considerable advances have been made in the study of resource-stoichiometric impacts on consumer communities. Specifically, consumer population density has been related to resource quality in grassland and forest ecosystems (Mulder *et al.*, 2005; Kaspari & Yanoviak, 2009). Moreover, there is a growing body of research on integrating allometric scaling with resource elemental stoichiometry (Allen & Gillooly, 2009; Hillebrand *et al.*, 2009; Mulder & Elser, 2009; Mulder *et al.*, 2011; Ott *et al.*, 2014b). Specifically, Ott *et al.* (2014b) recently extended earlier approaches combining the metabolic theory of ecology (West *et al.*, 1997; Brown *et al.*, 2004) and ecological stoichiometry theory (Elser *et al.*, 2000a; Sterner & Elser, 2002) to explain population biomass densities of temperate forest litter invertebrates. They found population biomasses to be largely driven by interactions of stoichiometric ratios of the basal litter resource and population-averaged body mass. In a further study, they detailed their analysis for several phylogenetic subsets of their data and tested specific hypotheses on the constraints that the varying availability of certain elements imposes on different consumer taxa (Ott *et al.*, 2014a). These results suggest that consumers in natural systems might often be co-limited by several limiting nutrients rather than being constrained by a single limiting element as would be expected from Liebig's law of the minimum (Von Liebig, 1840). This result confirms similar findings from other studies that suggest consumer growth and ecological processes to be co-limited by several stoichiometric variables (Kaspari *et al.*, 2008; Kaspari, 2012; Sperfeld *et al.*, 2012). Besides the impacts on consumer density and biomass, consumer diversity is expected to also respond to changes in resource supply ratios (Cardinale *et al.*, 2009; Hillebrand & Lehmpfuhl, 2011). At an imbalanced resource supply, where balance is defined as closeness to the consumer needs (Klausmeier *et al.*, 2004), fewer resources have the ability to limit consumer performance, leading to reduced species coexistence (Cardinale *et al.*, 2009). Consequently, a study on Panamanian forest floor communities found stoichiometric variables to control arthropod diversity (Sayer *et al.*, 2010). However, it seems that comprehensive studies testing hypotheses on the impact of resource stoichiometry on consumer diversity under field conditions are scarce.

Taken together, ecological stoichiometry offers fundamental ecological theory as well as specific approaches to studying ecological interactions. Over the past decades, much

research has focussed on consumer-resource interactions between single species pairs and on lower trophic-level processes such as herbivory. In order to gain a more thorough understanding of matter and energy flux and ecosystem processes, it seems important to take into account interactions across the food chain, especially between higher trophic levels. Furthermore, when trying to assess ecological change in response to altered biotic and abiotic conditions, it seems essential to integrate over trophic levels and at the same time take into account individual-level data.

1.6. Anthropogenic alteration of planet Earth

The growing human population has impacted our planet for thousands of years (Steffen *et al.*, 2011). However, the anthropogenic alteration of Earth's ecosystems is accelerating (Vitousek *et al.*, 1997a) and has led scientists to proclaim a new epoch of geological time, the anthropocene, where many important processes on Earth are dominated by human activity (Crutzen, 2002; Zalasiewicz *et al.*, 2011). Humans have thereafter significantly altered Earth's climate, important biogeochemical cycles and the water cycle, largely transformed the land surface, and significantly altered biodiversity throughout the planet (Vitousek *et al.*, 1997a; Steffen *et al.*, 2011; IPCC, 2014).

Anthropogenically driven climate change is one of the major drivers of human domination of Earth's ecosystems (Vitousek *et al.*, 1997a). Together with other anthropogenic drivers, enhanced emission of greenhouse gases, mainly CO_2, has caused global mean temperatures to rise extraordinarily over the past centuries with severe consequences for global sea levels, precipitation and extreme weather events (IPCC, 2014). Climate change clearly impacts ecological communities by causing range shifts and phenological shifts and affecting species abundance patterns (Parmesan & Yohe, 2003), which in turn have severe consequences for ecological interactions. If, for example, two species respond differently to changing environmental conditions, their potential to interact is limited (Parmesan, 2006). Moreover, through rising temperatures and altered water and nutrient supply, climate change affects the size structure of ecological populations and communities, increasing relative abundance of small compared to large organisms and shrinking average body size (Daufresne *et al.*, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011). As we have seen, body size is of striking importance for an organism's individual performance and its interactions with the abiotic and biotic environment. However, not only individuals are affected, but warming has the potential to alter ecosystem functioning via community size structure (Dossena *et al.*, 2012). One key aspect of such ecosystem responses is likely to be the increase of biological rates such as metabolic rates with increasing temperature (Brown *et al.*, 2004). This increase in metabolic demand is further indirectly driven by warming though the facilitation of small

organisms, which also leads to higher mass-specific metabolic rate (Brown *et al.*, 2004). Together, increased metabolic demand might therefore be one key aspect of ecosystem consequences of global warming (Schramski *et al.*, 2015).

Aside from the dramatic effects of anthropogenically induced global warming on ecosystems, human activity has also significantly altered global biogeochemical cycles and the water cycle (Vitousek *et al.*, 1997a; Steffen *et al.*, 2011). Alteration of the carbon cycle has not only led to temperature increases, but also directly affects properties of living organisms, for example by enhancing plant growth and altering the tissue chemistry of autotrophs with potential consequences on resource quality for herbivores (Vitousek *et al.*, 1997a). Another biogeochemical cycle significantly affected by human activity is the nitrogen cycle (Vitousek *et al.*, 1997b). Nitrogen naturally occurs in great quantities in the atmosphere as N_2. To make it available for the biosphere, it naturally requires fixation by living organisms. Consequently, the amount of nitrogen fixation affects ecosystem properties such as productivity and species composition (Vitousek *et al.*, 1997a). By more than doubling the global nitrogen fixation, humans therefore impose a powerful alteration on natural ecosystems (Vitousek *et al.*, 1997b). In addition to the carbon and nitrogen cycles, the phosphorus cycle has been severely altered, mainly due to fertilizer application (Smith *et al.*, 1999). Increased input and availability of these and other nutrients into natural ecosystems (i.e., eutrophication) leads to altered ecosystem structure and function (Smith *et al.*, 1999). Interestingly, carbon, nitrogen and phosphorus are not only three examples for elements with dramatically altered global cycling, but also, as we have seen, extremely important for natural biological processes.

Human land use undoubtedly has dramatically altered ecosystems at a global scale, with increasing impacts from early hunting and agriculture to modern high-intensity use of natural resources (Steffen *et al.*, 2011). However, the growing human population increasingly depends on a functioning biosphere (Foley *et al.*, 2005). Land-use decisions therefore have to increasingly balance the needs of the human population and the conservation of the ecosystem functions it depends on (DeFries *et al.*, 2004). Among the multiple aspects of human land use, the expansion of agricultural areas and the following intensification are widely accepted to have important consequences across the globe (DeFries *et al.*, 2004; Foley *et al.*, 2005). Large-scale conversion to agriculturally used systems causes habitat loss and fragmentation, which, although going hand in hand, can have contrasting effects on ecosystem properties such as biodiversity (Fahrig, 2003; Tscharntke *et al.*, 2012). While habitat loss is generally found to decrease biodiversity, fragmentation has much weaker and sometimes even positive effects on biodiversity (Fahrig, 2003). The subsequent agricultural intensification is characterised by extensive application of fertilizers and pesticides (Matson *et al.*, 1997; Tilman *et al.*, 2002). Tropical forests are among the most severely affected systems (Gibbs *et al.*, 2010; Lewis *et al.*,

2015), which is especially worrying given the high biodiversity value of these ecosystems (Myers *et al.*, 2000).

The above examples show that human activities affect ecosystems and their functioning through a variety of pathways. These pathways include as intermediate steps, but are not restricted to, land-use change and biodiversity loss, effects on body size and metabolism, changing nutrient availability and effects mediated by anthropogenically driven climate change and global warming. Anthropogenic activity thus impacts major drivers of ecological processes and functioning across levels of organisation. Among other aspects, human activities alter the body-size structure of communities, organism metabolic demand by altering surface temperature and the availability of chemical elements in ecosystems worldwide. When trying to assess ecological consequences in a changing environment, it therefore seems important to take into account these important aspects of ecological functioning and anthropogenic alteration.

1.7. Ecosystem functioning and the effect of biodiversity

It has been predicted that the conversion and degradation of habitats through human land use are among the most important drivers of terrestrial biodiversity change (Sala *et al.*, 2000). This has recently been shown to be true for a wide range of ecological assemblages (Newbold *et al.*, 2015) with already reported and predicted further impacts on ecosystem functioning and human wellbeing (Cardinale *et al.*, 2006; Díaz *et al.*, 2006; Cardinale *et al.*, 2012). There is a vast body of research on biodiversity-ecosystem functioning (Loreau *et al.*, 2001; Hooper *et al.*, 2005; Cardinale *et al.*, 2012; Tilman *et al.*, 2014) with theories on the causes for this relationship ranging from positive diversity effects on productivity or stability to its negative effect on the invasibility of ecosystems (Tilman *et al.*, 2014). Cardinale *et al.* (2012) defined biodiversity as "the variety of life" often measured as richness of life forms, while ecosystem functions are defined as "ecological processes that control the fluxes of energy, nutrients and matter through an environment". The relationship between these two is generally described to be positive and often found to be saturating, which leads to accelerating loss of function with a loss in richness (Cardinale *et al.*, 2012). Additionally, if diversity is lost across several trophic levels, functioning decreases more drastically than if only within-trophic level diversity is lost (Cardinale *et al.*, 2012). While historically many studies focussed on single ecosystem functions, there is now a trend towards assessing ecosystem multifunctionality (Reiss *et al.*, 2009; Maestre *et al.*, 2012; Byrnes *et al.*, 2014; Tilman *et al.*, 2014). In this vein, it has been suggested that studies focussing on single processes potentially underestimate the biodiversity needed for the simultaneous maintenance of multiple processes (Hector & Bagchi, 2007).

Different stocks and process rates are used as proxies for ecosystem functioning (Hooper *et al.*, 2005). While many studies on multitrophic diversity loss used biomass as a proxy for functioning (Duffy *et al.*, 2007), other studies suggested process rates such as the flux of energy or material as adequate measures (Hooper *et al.*, 2005; Srivastava & Vellend, 2005). Given the importance of trophic complexity (Duffy *et al.*, 2007) for the functioning of ecosystems it seems important to integrate across trophic levels and take the whole food-web structure into account when trying to establish measures as proxies for ecosystem functioning or even multifunctionality (Reiss *et al.*, 2009). As such, calculating energy and matter flux through ecological networks, as described in section 1.4, is a promising way of capturing ecosystem functioning across trophic levels. At the same time, it is a useful approach to assess ecosystem multifunctionality as the flux of energy between different compartments can be attributed to such different functions like decomposition, herbivory or predation.

1.8. Study system — Why study macro-invertebrates in tropical leaf litter?

Tropical ecosystems are among the most important biodiversity hotspots worldwide with high numbers of endemic species being more and more penned up in smaller areas by habitat loss and fragmentation (Myers *et al.*, 2000). This process is largely driven by anthropogenic alteration of tropical rainforests (Lewis *et al.*, 2015) caused by the growing human population and the increasing demand for food and biofuel production (Laurance *et al.*, 2014). Deforestation and subsequent agricultural intensification are severe threats to these biodiversity hotspots (Matson *et al.*, 1997; Gibbs *et al.*, 2010) with Southeast Asia being among the most severely affected areas worldwide (Achard *et al.*, 2002; Lewis *et al.*, 2015). Deforestation and conversion to agriculturally used systems has caused concerning levels of biodiversity loss in Southeast Asia, especially over the past century (Sodhi *et al.*, 2004; Wilcove *et al.*, 2013). Land-use conversion to plantation agriculture, such as oil palm, plays a crucial role for deforestation and intensification in the area and dramatically impacts biodiversity levels (Fitzherbert *et al.*, 2008; Koh & Wilcove, 2008; Wilcove & Koh, 2010). Such biodiversity loss is known to negatively impact ecosystems and their functioning (Hooper *et al.*, 2005; Cardinale *et al.*, 2012; Hooper *et al.*, 2012; Newbold *et al.*, 2015). Additionally, conversion to such agriculturally used systems goes hand in hand with a critical alteration of vegetation structure, above- and below-ground biomass, as well as net primary productivity (Kotowska *et al.*, 2015). These changes will most likely affect the basal resource stoichiometry, making these systems an ideal case to study resource quality effects on consumers. Furthermore, forest conversion alters

animal community structure and the relative abundance of different functional groups (Ewers *et al.*, 2015). Together with expected changes in community size structure, these changes make the altered tropical forest areas an optimal system for studying differences in metabolic demand and energy flux. Thus, altered tropical forest systems are a key area for studying ecological responses to changing environmental conditions and anthropogenic alterations of natural ecosystems.

Tropical rainforests are inhabited by around six million invertebrate species with a single hectare containing thousands of species (Hamilton *et al.*, 2010, 2011). These "little things that run the world" (Wilson, 1987) are responsible for carrying out a diverse range of ecosystem processes (Seastedt & Crossley, 1984; Yang & Gratton, 2014). In tropical rainforests, invertebrates dominate ecosystem processes, such as, for example, predation (Novotny *et al.*, 1999), herbivory (Coley & Barone, 1996), pollination (Bawa, 1990; Ollerton *et al.*, 2011) and decomposition (Handa *et al.*, 2014). Decomposition of dead organic material is strongly driven by plant and decomposer diversity, with large-bodied decomposer organisms being of critical importance for litter decomposition in terrestrial ecosystems (Handa *et al.*, 2014). Because of their ubiquity (Hamilton *et al.*, 2010, 2011), variability of functional types and large body mass range (Mumme *et al.*, 2015), their importance for key ecosystem processes (Handa *et al.*, 2014) and anthropogenic pressures threatening their natural environment (Lewis *et al.*, 2015), macro-invertebrate communities in tropical leaf litter are an ideal study system to assess ecosystem processes across functional groups and trophic levels.

The research chapters of this thesis predominantly focus on litter macro-invertebrate communities of tropical lowland rainforests in Sumatra, Indonesia. Within the framework of the large-scale collaborative research project EFForTS ("Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems (Sumatra, Indonesia)"), I quantitatively sampled macro-invertebrate communities across two landscapes and 32 study sites in lowland rainforest, jungle rubber, rubber and oil-palm plantations to assess the structure and functioning of these diverse invertebrate communities and their response to anthropogenic land-use change and the resulting alteration of their biotic and abiotic environment.

1.9. Research objectives and chapter outline

In the research chapters of this thesis, I address how changes in body mass, metabolism and resource stoichiometry jointly affect complex ecological communities by altering consumer-resource interactions and the flux of energy through these networks. In order to gain this understanding, first, I review previous research on body size with a focus on insect movement and behavior to highlight what body size can teach us about the functioning of

ecological communities (**Chapter 2**). Second, I investigate the impact of anthropogenic land use on diverse tropical litter macro-invertebrate communities and develop a measure of multitrophic energy flux as a proxy for ecosystem functioning (**Chapter 3**). Third, I zoom in on consumer-resource interactions by studying consumer responses to changing resource quality as described by elemental stoichiometry (**Chapter 4**). Finally, I scale up this stoichiometric view to investigate the consequences of varying basal resource stoichiometry on macro-invertebrate consumer diversity and biomass density and develop a conceptual framework explaining diverse response patterns of these two community characteristics (**Chapter 5**).

The first step towards incorporating body size in novel approaches and ecological theory is to review existing body-size research. Consequently, in **Chapter 2**, I present previous research on body size and point out that much of our mechanistic understanding of body-size effects in ecology is originally based on vertebrates and mammals. I discuss how, more recently and due to technical improvements and the availability of high-resolution data sets, body-size research has shifted towards including invertebrates and especially insects. I pay special attention to body-size effects on movement and behaviour with their effects on animal foraging and thus trophic interactions. By drawing on recent advances in the field, I argue that ecological theory will further profit from incorporating size and important non-size aspects such as phylogenetic relatedness, mobility, environmental temperature or ecological stoichiometry to gain a deeper understanding of ecological processes and explain variation in ecological processes formerly solely explained by body size. Finally, I highlight some promising areas of future research.

In **Chapter 3**, I assess consequences of tropical land-use change on the biodiversity and functioning of litter macro-invertebrate communities from land-use systems of differing intensity. Specifically, I develop a highly adaptable measure of multitrophic ecosystem functioning enabling comparison of ecosystem functioning across ecosystems. By using the animal data set obtained from quantitative sampling of litter communities from lowland rainforest, jungle rubber, rubber and oil-palm plantations, I first investigate differences in species richness, density and biomass density across trophic groups. Furthermore, using a recently compiled data base on invertebrate metabolic rates, I calculate the energy demand of the invertebrate communities based on individual metabolic rates and compare that among the trophic groups and land-use systems. Subsequently, combining metabolic theory and food web theory, I develop a novel measure of energy flux between trophic compartments of ecological networks that can be analytically calculated for any sampled ecological community. Finally, I use this proxy for multitrophic ecosystem functioning to compare the relationship between species richness and ecosystem functioning across the focal land-use systems.

In **Chapter 4**, I build on the obtained knowledge from the first two research chapters

by combining ecological stoichiometry theory with body mass and metabolism-dependent calculations of consumer feeding in response to varying resource quality. Specifically, I test three distinct hypotheses of how consumers of different trophic levels, namely predators and detritivores, will respond to varying resource quality measured as C:N ratio of their respective resources. I hypothesize that, in response to decreasing stoichiometric quality, consumers will either (H1) exhibit stoichiometric flexibility in their own body tissue (i.e., shift their body stoichiometry), (H2) avoid habitats comprising low-quality resources (i.e., decrease in biomass) or (H3) alter their consumption rates (i.e., compensate for low resource quality by up-regulated feeding). To test these hypotheses, I modify the calculation for between-compartment energy flux to yield consumer feeding rates in response to varying resource stoichiometry, based on metabolic demand and assimilation efficiency. This method can be used to calculate feeding rates from a few easily obtainable parameters, instead of having to actively measure feeding rates in the field. Finally, I discuss consequences for consumer diversity and possible mechanisms that mediate such consequences in response to varying resource quality.

In **Chapter 5**, I widen the stoichiometric perspective by assessing consumer-community responses to changes in habitat structure and basal resource stoichiometry as indicated by seven chemical elements. Building on recent advances combining ecological stoichiometry and metabolic theory in temperate litter communities, the objective of this chapter is to (a) investigate joint effects of population-averaged body mass and stoichiometric and habitat-structural parameters on population biomass density in tropical systems and (b) to test for effects of these predictor variables on consumer diversity. I specifically make use of a standardised model averaging approach to test for consumer diversity and biomass density responses. Drawing on former research on ecological stoichiometry, I test a set of specific hypotheses relating consumer community characteristics to changes in habitat structural and stoichiometric variables, such as the structural elements hypothesis predicting certain consumer taxa to respond to changes in the availability of chemical elements specifically important for their biology. I detail the analysis for ten major taxonomic consumer groups and four functional feeding guilds and compare my results to those from temperate forest litter systems. Finally, I discuss diverse response patterns of consumer diversity and biomass density and develop a conceptual framework that successfully explains patterns found in the vast majority of the studied tropical invertebrate consumer groups. The predictions of this framework can now be tested in other ecosystems to assess contrasts between different ecosystem types or changes in the response patterns triggered by environmental change.

Part II.

Research chapters

Chapter 2.

Body size and the behavioral ecology of insects: linking individuals to ecological communities

Gregor Kalinkat, Malte Jochum, Ulrich Brose & Anthony I. Dell

Abstract

The role of body size as a key feature determining the biology and ecology of individual animals, and thus the structure and dynamics of populations, communities, and ecosystems, has long been acknowledged. Body size provides a functional link between individual-level processes such as physiology and behavior, with higher-level ecological processes such as the strength and outcome of trophic interactions, which regulate the flow of energy and nutrients within and across ecosystems. Early ecological work on size in animals focused on vertebrates, and especially mammals. More recent focus on invertebrates, and insects in particular, that spans levels of organization from individual physiology to communities, has greatly expanded and improved our understanding of the role of body size in ecology. Progress has come from theoretical advances, from the production of new, high-resolution empirical data sets, and from enhanced computation and analytical techniques. Recent findings suggest that many of the allometric concepts and principles developed over the last century also apply to insects. But these recent studies also emphasize that while body size plays a crucial role in insect ecology, it is not the entire story, and a fuller understanding must come from an approach that integrates both size and non-size effects. In this review we discuss the core principles of a size-based (allometric) approach in insect ecology, together with the potential of such an approach to connect biological processes and mechanisms across levels of organization from individuals to ecosystems. We identify knowledge gaps, particularly related to size constraints on insect movement and behavior, which can impact the strength and outcome of species interactions (and especially trophic interactions) and thus link individual organisms to communities and ecosystems. Addressing these gaps should facilitate a fuller understanding of insect ecology, with important basic and applied benefits.

2.1. Introduction

"In scaling, as in so many other areas of biology, we know far more about homeotherms than about poikilotherms or unicells. Since most organisms are not homeotherms, a great deal of work is required before our knowledge would be proportional to animal abundance." Peters (1983)

The body size of any organism strongly constrains many aspects of its physiology and ecology (Peters, 1983; Kleiber, 1947; Damuth, 1981; Calder, 1983; Brown *et al.*, 2004). In insects, size influences their metabolic rate (Ehnes *et al.*, 2011; Harrison *et al.*, 2014), their individual growth rate (Angilletta *et al.*, 1996) and stoichiometric properties (Ott *et al.*, 2014b), how fast they move (Dudley & Srygley, 1994; McPeek *et al.*, 1996; Yang, 2000), how often they encounter prey (Gergs & Ratte, 2009; Pawar *et al.*, 2012) and how many prey they consume (Kalinkat *et al.*, 2013), and a huge suite of other traits central to their daily lives (Peters, 1983; Brown *et al.*, 2004; Chown & Gaston, 2010). Because size is so important for individuals, patterns in the size distributions of groups of insects have crucial influences on the structure and function of higher levels of biological organization, such as populations, communities, and ecosystems (e.g. by affecting decomposition, primary productivity and carbon cycling; Rudolf & Rasmussen (2013); Schramski *et al.* (2015)). Body size is also easy to measure directly, or at least estimate, while at the same time can be used as a proxy for many other physiological and ecological traits (Jacob *et al.*, 2011). Thus, a size-based understanding of insect ecology should be both attainable and useful, with significant basic and applied benefits.

To date, studies of body size in ecology have focused primarily on vertebrates (Peters, 1983; Kleiber, 1947; Damuth, 1981; Calder, 1983) and vascular plants (West *et al.*, 1999; Muller-Landau *et al.*, 2006), although more recent work that focuses on insects (and, more generally, on invertebrates) addresses this imbalance (e.g. Ehnes *et al.* (2011); Chown & Gaston (2010); Chown *et al.* (2007); DeLong (2011); Gouws *et al.* (2011); Riede *et al.* (2011)). The high taxonomic, ecological and functional diversity of insects, and the fact they span roughly nine orders of magnitude in mass (Figure 2.1) and are common in many of Earth's ecosystems (especially on land and in freshwater), make them an excellent study group to investigate size-related patterns and processes in ecology. To separate our paper from two excellent recent reviews (Chown & Gaston, 2010; Boukal, 2014) we pay particular attention to how size influences insect movement and behavior, which impacts how insects forage and thus has significant implications for the strength and outcome of species interactions, and especially trophic interactions (Gergs & Ratte, 2009; Pawar *et al.*, 2012; McGill & Mittelbach, 2006; Dell *et al.*, 2014b). At the same time, quantifying behavior and movement in accurate and precise ways is becoming

easier due to the development of novel automated methods (Dell *et al.*, 2014a). A more mechanistic understanding of species interactions should enable linkage of the ecology of individuals to higher levels of ecological organization (Boukal, 2014). This research area, at the intersection between behavioral (i.e. movement ecology; Holyoak *et al.* (2008)) and community (e.g. food web ecology; Boukal (2014); Brose (2010)) ecology, is characterized by significant advances in recent years on both empirical and theoretical fronts that is resulting in a deeper understanding of the role of body size in insect ecology. For example, the integration of allometric scaling with visual acuity and environmental drivers has furthered our understanding of the mechanisms that influence prey encounter and consumption rate (Gergs & Ratte, 2009; Pawar *et al.*, 2012; McGill & Mittelbach, 2006). The historical focus of size-based research on vertebrates and plants means that throughout our review we draw strongly from literature that is not insect focused, which is justified given the apparent universality of many allometric principles across domains of life (Peters, 1983; Calder, 1983; Brown *et al.*, 2004; Chown & Gaston, 2010; Boukal, 2014).

2.2. Key recent developments in the field of allometry

Recent years have seen significant moves forward on a number of research fronts, but undoubtedly some of the most important advancements have come in the development of a predictive theoretical framework about size effects in ecology, which is mechanistically based on well-understood biological and physical mechanisms. Perhaps most impactful has been the Metabolic Theory of Ecology (MTE), which suggests that the power-law relationship between body size and metabolic rate that persists across taxa and ecosystems arises because of the ubiquitous fractal structure of transportation networks within organisms (Brown *et al.*, 2004; West *et al.*, 1997). MTE aims to predict the structure and function of higher levels of biological organization (e.g. populations, communities, ecosystems) from the level of an individual organism, with a particular focus on metabolic rate (Brown *et al.*, 2004; Schramski *et al.*, 2015). In MTE, individual body size and body temperature are considered key drivers of many ecological processes, via their direct effects on metabolic rate (Brown *et al.* (2004); Ehnes *et al.* (2011); also see Figure 2.2 a), with subsequent effects on trophic (Dell *et al.*, 2014b, 2011; Rall *et al.*, 2012) and other types of species interactions and thus communities and ecosystems (Brown *et al.*, 2004; Schramski *et al.*, 2015). Thought to also be related to the allometry of metabolic rates, size-abundance scaling models characterize the commonly observed pattern of most ecological communities comprising many small and few large organisms (Damuth (1981); White *et al.* (2007); Ehnes *et al.* (2014); see Figure 2.2 b). This community-wide pattern has important implications for trophic interactions, as individual consumers are more likely to

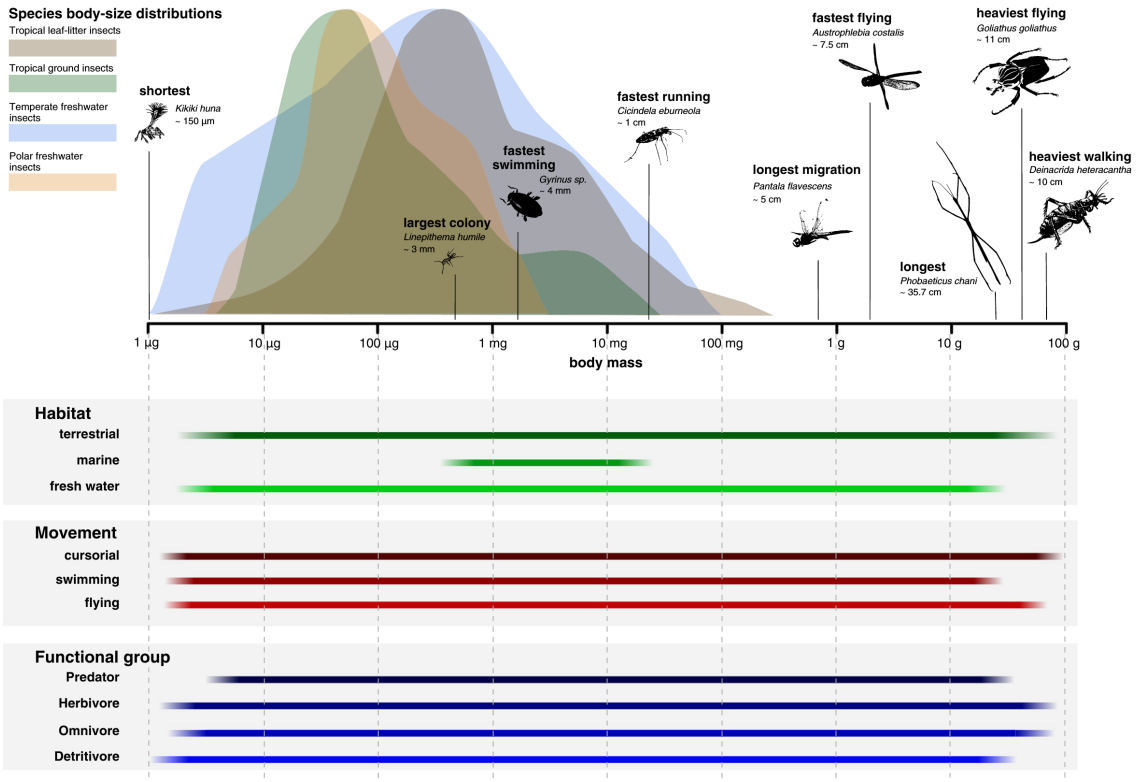

Figure 2.1 – Schematic overview of the ecology of insects in relation to their body mass. Upper panel: Examples for outstanding insect species representing the spread of the group in regard to body size, number of species, habitat, movement and ecological function. Also shown are four example species body-size distributions (transparent colored areas), detailing the number of species of different average body sizes within each community. Each of the four distributions are normalized to equal height on the y-axis: tropical leaf-litter insects (brown, n = 548; Barnes *et al.* (2014)), tropical ground insects (green, n = 228; Dell *et al.* (2015)), temperate freshwater insects (blue, n = 25; Hudson *et al.* (2013)), polar freshwater insects (orange, n = 16; O'Gorman *et al.* (2012)). Lower panel: Estimated spread of body mass for insects within different habitats, movement types and functional groups.

encounter the more abundant smaller resources they often feed on (Brose *et al.*, 2006), a pattern which appears crucial for the stability of invertebrate predator–prey interactions and food webs (Kalinkat *et al.*, 2013, 2011). The validity and generality of the simple yet powerful MTE remains hotly debated (Hirst *et al.*, 2014; Glazier, 2015), and indeed recent analyses of insect data suggest that alternative models might outperform MTE in explaining certain empirical patterns (Harrison *et al.* (2014); Chown *et al.* (2007); but see Riveros & Enquist (2011)). One of these alternative models is the cost of locomotion rooted in biomechanical principles (Harrison *et al.*, 2014; Kram & Taylor, 1990), which stresses the importance of locomotion for insect metabolism, physiology and ecology (see below).

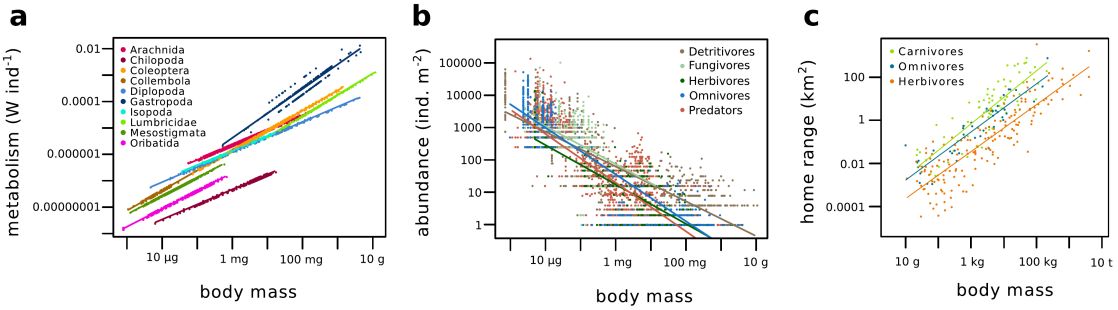

Figure 2.2 – Relationship between body mass and the example traits: metabolic rate (a), abundance (b) and home range (c). Different phylogenetic groups (a) and functional groups (b and c) show variation in their scaling with body mass. Figures reproduced from Ehnes *et al.* (2014) (a and b) and Kelt & Van Vuren (2001) & Jetz *et al.* (2004) (c). Data for (a) and (b) are for 870 species of litter and soil invertebrates from a large-scale biodiversity study in Germany, data for (c) are from 279 mammal species.

Owing to technological limitations in the past (e.g. size of devices for bio-logging; Kissling *et al.* (2014)), available empirical studies of allometric scaling in movement ecology (e.g. migration) were almost exclusively restricted to vertebrates (Kelt & Van Vuren (2001); Jetz *et al.* (2004); Hein *et al.* (2012); also see Figure 2.2 c). By contrast, there are numerous studies on the size scaling of insect movement from laboratory-based comparative physiology and morphology (e.g. Full *et al.* (1990); Vogel (2008)), while more recent studies address insect-specific patterns across larger spatial and temporal scales (e.g. allometric effects on dispersal in butterflies; Stevens *et al.* (2012)). Moreover, it appears that for insect movement, and its implications for higher-level ecological processes, the allometry of morphology (and not just total body size) is especially important (e.g. wing size-body size relationships; Sacchi & Hardersen (2012)). To date, our understanding of the energetic implications of these relationships are also unclear. Although small animals require more energy to travel a given distance relative to their body mass (Pontzer, 2007), more recent work suggests that maximum migration distance should be similar when considered in relation to body length, which does not scale linearly

with total mass (Hein *et al.*, 2012). Additionally, the diverse modes of insect movement (e.g. flying, swimming, running; Figure 2.1) provide a unique opportunity to explore additional size-related constraints on dispersal, with potentially crucial implications for meta-community structure (De Bie *et al.*, 2012). Most prior studies concentrate on larger scale movement, such as dispersal and migration, while research addressing the scaling of more local traits related to individual behavior and foraging, which, although important for species interactions, is largely absent for insects (Dial *et al.*, 2008). Thus, while research on the allometry of insect movement and foraging behavior is occurring (e.g. Kissling *et al.* (2014)), more is required to obtain a clearer picture of the mechanistic basis of a phenomenon already well recognized: body size is key in shaping the strength and outcome of species interactions, and especially trophic interactions.

2.3. Body size and trophic interactions

The role of body size has long featured prominently in studies of trophic interactions (Riede *et al.*, 2011; Brose *et al.*, 2006; Warren & Lawton, 1987; Schneider *et al.*, 2012), and integration of energetic considerations into the picture has allowed ecologists to better understand the pivotal role of size for consumer–resource dynamics, and food webs more generally (Yodzis & Innes, 1992; Otto *et al.*, 2007; Petchey *et al.*, 2008; Berlow *et al.*, 2009). For instance, in a recent study on forest soil invertebrates, Ehnes *et al.* (2014) showed that accounting for the efficiency of energy transfer between trophic levels could explain deviations from the basic assumptions of MTE and mass-abundance rules more generally. Likewise, Ott *et al.* (2014b) recently showed that allometry interacts with the stoichiometry of the basal resource to determine the distribution of biomasses across the food web populations. From this and other related work it is becoming clearer that explaining the outcome and strength of trophic interactions requires information in addition to body size, which may or may not relate to body size in simple ways.

One area that is receiving a lot of current attention is the foraging behavior of consumers, which many authors now see as crucial to trophic interactions (Pawar *et al.*, 2012; Dell *et al.*, 2014b; Brose, 2010; Petchey *et al.*, 2008; Pawar *et al.*, 2014). For example, the hump-shaped relationship observed between attack rates and body size for a wide range of animals, including terrestrial (e.g. Kalinkat *et al.* (2013)) and aquatic insects (e.g. Gergs & Ratte (2009)), may be partly explained by foraging behavior. In their analysis of functional responses and size selectivity of notonectid predators and their daphnid prey, Gergs & Ratte (2009) used video tracking experiments to disassemble the attack rates of classical functional responses into encounter rates and success rates. They found that while encounter rates increased with body size following a quadratic relationship, success rates were characterized by a hump-shaped relationship (Gergs & Ratte, 2009). Encounter

rates are assumed to be driven by the consumer's detection ability (related to their foraging behavior) following allometric relationships (Kiltie, 2000), which have successfully been used to build an allometric vision and motion model of optimal foraging (Pawar *et al.*, 2012; McGill & Mittelbach, 2006). Interestingly, a meta-analysis of vertebrate studies suggests these detection probabilities are driven by temporal perception which, in turn, is related to body size, with smaller animals showing a higher temporal resolution of the sensory system (Healy *et al.*, 2013). Rigorous tests of the allometric relationships of detection probabilities and the relation to temporal perception and foraging decision in insects remain elusive. The hump-shaped relationship in attack rates (Kalinkat *et al.*, 2013; Brose, 2010) or in capture success (Gergs & Ratte, 2009) might also be driven by the asymmetry between higher maneuverability in small prey and maximum foraging speed in large predators, as has been explored in fish (Domenici, 2001). Again, we are not aware of comparable research on insects. A detailed analysis of these relationships should also concentrate on burst speed and acceleration potential, which are presumably important for trophic interactions (Vogel, 2008; Dickinson *et al.*, 2000).

In the context of trophic interactions, functional morphology and the intertwined consumer foraging mode have been proposed as one of the main concepts that explains why a trophic interaction occurs between any given predator–prey pair. This implies a match between the 'tools' available for a predator to capture and overcome a particular prey, and the 'tools' available for a prey to evade capture from that particular predator (Boukal, 2014; Ferry-Graham *et al.*, 2002; Eklöf *et al.*, 2013; Klecka & Boukal, 2013). Integrating these traits into an allometric framework appears to us a useful advancement of current food web models, where a considerable portion of the variation in predator–prey interactions remains unexplained by more simple size-based approaches (examples include Rall *et al.* (2011) for terrestrial predators; Klecka & Boukal (2013) for aquatic predators). Prior attempts to connect functional morphology and allometric scaling for movement relationships have focused on dispersal (Barnes *et al.*, 2015) and migration (Sacchi & Hardersen, 2012), but similar research on trophic interactions is required. For instance, flying performance in dragonflies not only depends on total body size but also wing morphology (i.e. the morpho-allometric relationship between body size and wing size; Sacchi & Hardersen (2012)), with important influences on sexual selection and optimization of different flying tasks (Sacchi & Hardersen, 2012). Similarly, functional morphology is key to understanding non-body size related differences in locomotion performance in terrestrial (Pontzer, 2007) and aquatic (Xu *et al.*, 2012) insects: where on land the effective length of body appendages responsible for movement accounts for most of the variation (Pontzer, 2007), the relationship for aquatic movement seems to be more complicated (Xu *et al.*, 2012). Hence, given their diverse modes of living and their large range of body size (Figure 2.1), investigating these relationships in insects would seem

useful for further understanding bio-mechanical constraints on foraging behavior (Boukal, 2014). Given each of these considerations, it now seems feasible to extend current scaling frameworks to integrate allometric scaling relationships across levels of organization, from the physiology and morphology of individuals to trophic interactions and ultimately to the energetics of entire communities and ecosystems (Eklöf *et al.*, 2013; Klecka & Boukal, 2013).

2.4. Future directions

Globally, insects are an important functional component of terrestrial and freshwater systems, often with strong economic and cultural importance for humans (Yang & Gratton, 2014). By integrating body-size related information such as physiological constraints (as characterized by the MTE — Brown *et al.* (2004); Schramski *et al.* (2015) — or competing approaches — Harrison *et al.* (2014); Chown *et al.* (2007)), together with body-size relationships for consumer-resource pairs (Brose *et al.*, 2006) and entire food webs (Riede *et al.*, 2011; Digel *et al.*, 2011), ecologists now have a better understanding of ecosystem stability and functioning. Thus, patterns in insect body size distributions, together with intra-specific and inter-specific allometric relationships, are important for a wide range of basic and applied questions. For instance, allometric effects can explain how predator loss in soil-litter systems affects crucial ecosystem functions such as litter decomposition and nutrient cycling (Schneider *et al.*, 2012). Moreover, intraspecific size distributions apparently have far-reaching consequences at the community level (Rudolf & Rasmussen, 2013; Jochum *et al.*, 2012), but most often these data are not available. Therefore, there is a need for continued development of highly-resolved empirical datasets, such as population body size distributions for multiple interacting species (Gouws *et al.* (2011); Dell *et al.* (2015)) or body-mass variation across various levels of insect phylogeny Chown & Gaston (2010). Insect-specific analyses of subsets of existing data bases for species interactions (e.g. Dell *et al.* (2011); Rall *et al.* (2012)) are a logical next step. Future research on individual-level interactions of insects from a diverse range of ecosystems might then shed light on important ecosystem mechanisms, providing a deeper understanding of how crucial ecological functions are organized and maintained. One particularly useful approach appears to be novel automated methods (Dell *et al.*, 2014a), which should help elucidate the mechanistic link between individual-level, morphologically and physiologically constrained behavior and higher levels of ecological and biological organization.

A generalized version of allometric theory needs to be developed that is able to account for apparent non-size related variation, by incorporating additional behavioral and functional morphological traits. The first steps toward this goal have already been made in

quantitative studies of food webs and other ecological networks: for instance, Naisbit *et al.* (2012) used a 'two-dimensional' approach where phylogenetic relatedness could explain food-web structure better than body size alone. In addition, Eklöf *et al.* (2013) showed that the structure of different types of ecological networks are best explained by models that incorporate approximately three to four additional traits (e.g. habitat type, mobility, phenology, phylogenetic information; Eklöf *et al.* (2013)) together with body size. Here again, functional morphology was explicitly highlighted (e.g. fruit size and bill gape for frugivorous birds; Eklöf *et al.* (2013)). Additional traits and relationships that should be incorporated into an extended framework of ecological allometry in insects include environmental temperature (e.g. Brown *et al.* (2004); Dell *et al.* (2014b, 2011); Rall *et al.* (2012)), the degree of hunger of predators (Simpson & Raubenheimer, 2000) and their experience with handling particular prey (Raine & Chittka, 2008), the stoichiometry of food resources (Shurin *et al.*, 2006), and even the individual 'personality' of predators (Kalinkat, 2014; Modlmeier *et al.*, 2015). Thus, a full and mechanistic understanding of insect ecology will only be achieved by approaches that integrate both size and (apparent) non-size effects (Boukal, 2014). We particularly encourage approaches addressing the link between allometric constraints on behavior with functional morphology and foraging relationships to gain a better understanding of the processes that shape the typical hump-shaped relationship between predator–prey size ratios and capture success (Gergs & Ratte, 2009; Kalinkat *et al.*, 2013; Brose, 2010). Although this topic has been investigated with vertebrates (e.g. Kiltie (2000); Healy *et al.* (2013); Domenici (2001)), a similar integration of such relationships is required for insects and other invertebrates.

Future research at the intersection between insect behavioral and community ecology should therefore embrace, and ultimately integrate, these approaches to establish a new framework that links distinct layers of biological and ecological organization.

Acknowledgments

G.K. was supported through the Leibniz Competition (SAW-2013-IGB-2) and by a postdoctoral fellowship from the German Academic Exchange Service (DAAD). M.J. was funded by the Deutsche Forschungsgemeinschaft (DFG) SFB990/1. Funding bodies had no involvement in the planning or writing of this manuscript, nor in the decision to submit it for publication. We thank Walter Jetz for sharing the original data used in Figure 2.2 c. We would also like to thank Jacintha Ellers and Cécile Le Lann for the invitation to contribute to this issue and two anonymous reviewers for their insightful comments on an earlier version of the manuscript.

Chapter 3.

Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning

Andrew D. Barnes*, Malte Jochum*, Steffen Mumme, Noor Farikhah Haneda, Achmad Farajallah, Tri Heru Widarto & Ulrich Brose

*** These authors contributed equally to this work.**

Abstract

Our knowledge about land-use impacts on biodiversity and ecosystem functioning is mostly limited to single trophic levels, leaving us uncertain about whole community biodiversity-ecosystem functioning relationships. We analyse consequences of the globally important land-use transformation from tropical forests to oil-palm plantations. Species diversity, density, and biomass of invertebrate communities suffer at least 45% decreases from rainforest to oil palm. Combining metabolic and food-web theory, we calculate annual energy fluxes to model impacts of land-use intensification on multitrophic ecosystem functioning. We demonstrate a 51% reduction in energy fluxes from forest to oil-palm communities. Species loss clearly explains variation in energy fluxes, but this relationship depends on land-use systems and functional feeding guilds, whereby predators are the most heavily affected. Biodiversity decline from forest to oil palm is thus accompanied by even stronger reductions in functionality, threatening to severely limit the functional resilience of communities to cope with future global changes.

3.1. Introduction

The transformation from natural ecosystems to agricultural land use and its continued intensification has led to extensive losses in biodiversity and ecosystem services (Gibbs *et al.*, 2010) resulting in the degradation of human well-being (Díaz *et al.*, 2006). The transformation of lowland tropical rainforest to oil-palm (*Elaeis guineensis* Jacq.) plantations has gained more recent attention as an especially severe threat to tropical biodiversity (Gilbert, 2012; Koh & Wilcove, 2007). In the last 25 years the total plantation area of oil palm has tripled, with current global estimates of over 15 million hectares (Gilbert, 2012), making this crop one of the world's most rapidly expanding forms of agriculture (Fitzherbert *et al.*, 2008). It is now clear that the expansion of oil-palm agriculture is one of the greatest causes of deforestation (Wilcove *et al.*, 2013; Koh *et al.*, 2011) and this threat appears to be increasing without respite as Indonesia, one of the world's leaders in oil palm, makes plans to double production by 2020 (Koh & Ghazoul, 2010). The rapid expansion of such large-scale land-use transformation raises questions about the impending implications for biodiversity and ecosystem functioning in the tropics.

Despite a broad consensus that biodiversity is positively correlated with ecosystem functioning in controlled experiments (Cardinale *et al.*, 2006; Hooper *et al.*, 2005), there are few real-world examples of such biodiversity-ecosystem functioning relationships (Foster *et al.*, 2011; Otto *et al.*, 2008). In fact, until now there have been no studies that explore the relationship between biodiversity and ecosystem functioning in ecosystems undergoing agricultural land-use transformation to oil palm. Thus, our knowledge of this globally important land-use conversion is strongly limited. Furthermore, over the past decade there have been important advances towards multitrophic approaches in research investigating biodiversity-ecosystem functioning relationships (Cardinale *et al.*, 2006; Duffy, 2002; Petchey *et al.*, 2004; Schneider *et al.*, 2012; Schneider & Brose, 2013). Despite these advances, however, we are still substantially limited by the lack of clear approaches to quantify single measures of ecosystem functioning that can be compared among any combination of trophic levels. This has resulted in our inability to directly look at whole-community relationships between entire species assemblages and the respective functional processes carried out in these communities.

Here, we use the total energy flux between functional feeding guilds as a measure of multitrophic ecosystem functioning, as many studies have suggested process rates, such as energy fluxes, to be important proxies for ecosystem functioning (Hooper *et al.*, 2005; Duffy, 2002; Srivastava & Vellend, 2005). Depending on the resource pool that the energy flux comes from, these fluxes can be directly related to ecosystem services such as decomposition (de Ruiter *et al.*, 1994; Handa *et al.*, 2014), plant biomass production

(Enquist *et al.*, 2007; Tilman *et al.*, 2006), or biocontrol through predation (Cardinale *et al.*, 2003). These energy flux calculations are based on metabolic scaling theory (Brown *et al.*, 2004) and principles of food web energy dynamics (de Ruiter *et al.*, 1994). Using individual metabolic rates that are dependent on body mass, environmental temperature, and phylogenetic grouping (de Ruiter *et al.*, 1994; Ehnes *et al.*, 2011), combined with resource-specific assimilation efficiencies (de Ruiter *et al.*, 1993) and energy loss to predation (de Ruiter *et al.*, 1994), we present this energy flux calculation as a unified measure of multitrophic ecosystem functioning (Figure 3.1). Studies that incorporate diversity across trophic levels to test the relationship between biodiversity and ecosystem functioning have predominantly used only biomass as the measure of ecosystem function (Duffy *et al.*, 2007). However, the metabolic activity and thus the energy processing rates of these biomass pools can vary substantially. Integrating over body mass, phylogeny and temperature with their constraints on metabolic rates, and additionally taking into account assimilation efficiencies and loss to predation, our measure of whole-community energy flux inherently incorporates not only biomass, but also other important ecosystem attributes enabling the quantification of emergent functional properties of ecosystems that would otherwise remain undetected. As such, our measure of energy flux provides a comprehensive and robust measure of multitrophic ecosystem functioning that can be utilized for modelling biodiversity-ecosystem functioning relationships for any assemblage of taxonomic groups, whilst incorporating multiple ecological functions.

In the tropical lowland rainforests of Sumatra, Indonesia, which have been undergoing vast land-use transformation to oil palm (Koh *et al.*, 2011), we quantify the impacts of this transformation ranging from tropical secondary rainforest, jungle rubber, and intensively managed rubber, to oil palm. We utilize data gathered from 32 sites on Sumatra, Indonesia, comprising 2415 populations of 871 species. Firstly, we investigate the biodiversity value of jungle rubber, conventional rubber, and secondary forest compared to oil-palm agriculture by comparing observed species richness, density and biomass of litter-associated macro-invertebrate communities across these systems. Secondly, as a multitrophic measure of the rate of ecosystem processes carried out by these communities, we calculate total solid fresh-mass energy flux in a system by incorporating community metabolism (Ehnes *et al.*, 2014), resource-specific assimilation efficiencies and biomass loss to predation (de Ruiter *et al.*, 1994) into whole-community energy flux equations (Figure 3.1). This provides a quantitative measure of multitrophic ecosystem functioning, defined here as the total flux of energy from any resource pool to consumer trophic levels. Additionally, this measure can be attributed to specific functional feeding guilds within communities to look for patterns in ecosystem functioning at different trophic levels. Using the energy-mass flow conversion (Peters, 1983), we express energy flux as kilograms per hectare, per year, and explore the relationship between total species diversity and energy

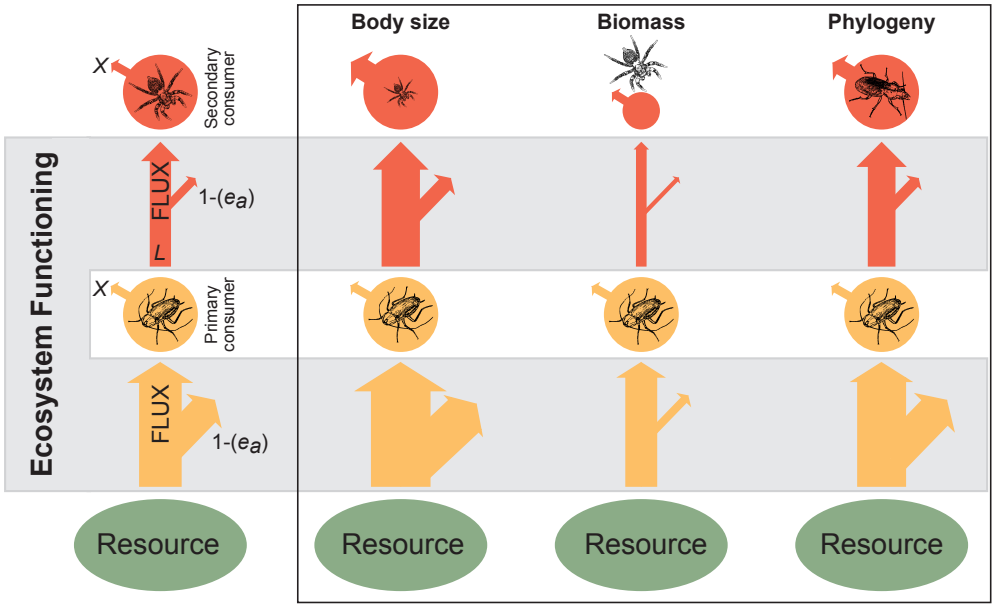

Figure 3.1 – Energy fluxes along a conceptual food chain as a measure of multitrophic ecosystem functioning. Energy flux between two nodes is calculated as $F = \frac{1}{e_a} \cdot (X + L)$, where F is the total energy flux into the network node of a feeding guild (vertical red and yellow arrows), ea is the diet-specific assimilation efficiency (denoted by diagonal arrows arising from the flux arrows), X is the per-unit-mass metabolic demand of the feeding guild (which is non-linearly dependent on body sizes, temperature, and phylogeny), and L is the loss to predation from the node (for the yellow node, this is equal to the flux to the red secondary consumer node). Here, we demonstrate three examples where changes in mean body size (size of black animal icons), biomass (diameter of red and yellow circles), or phylogeny (black animal icons) on any trophic level (here, demonstrated by the secondary consumer guild) can result in non-proportionally altered total energy flux (sum of all arrow widths in the food chain).

flux, distinguishing among four transformation systems to test for land-use dependent biodiversity-ecosystem functioning relationships. Our results demonstrate strong losses in species diversity which in turn predict reductions in whole-community energy fluxes. However, these reductions are strongest in oil-palm systems, suggesting that land-use conversion from forest to oil palm causes disproportionally strong losses in multi-trophic ecosystem functioning.

3.2. Results

Transformation to oil palm leads to biodiversity loss

Using generalized linear mixed effects models, we show that transformation of tropical rainforest to oil-palm plantations leads to severe losses in species richness (45% decline), animal density (48% decline) and biomass (52% decline) (Figure 3.2 a-c and Table 7.1), supporting previous studies suggesting that land-use transformation to oil palm poses

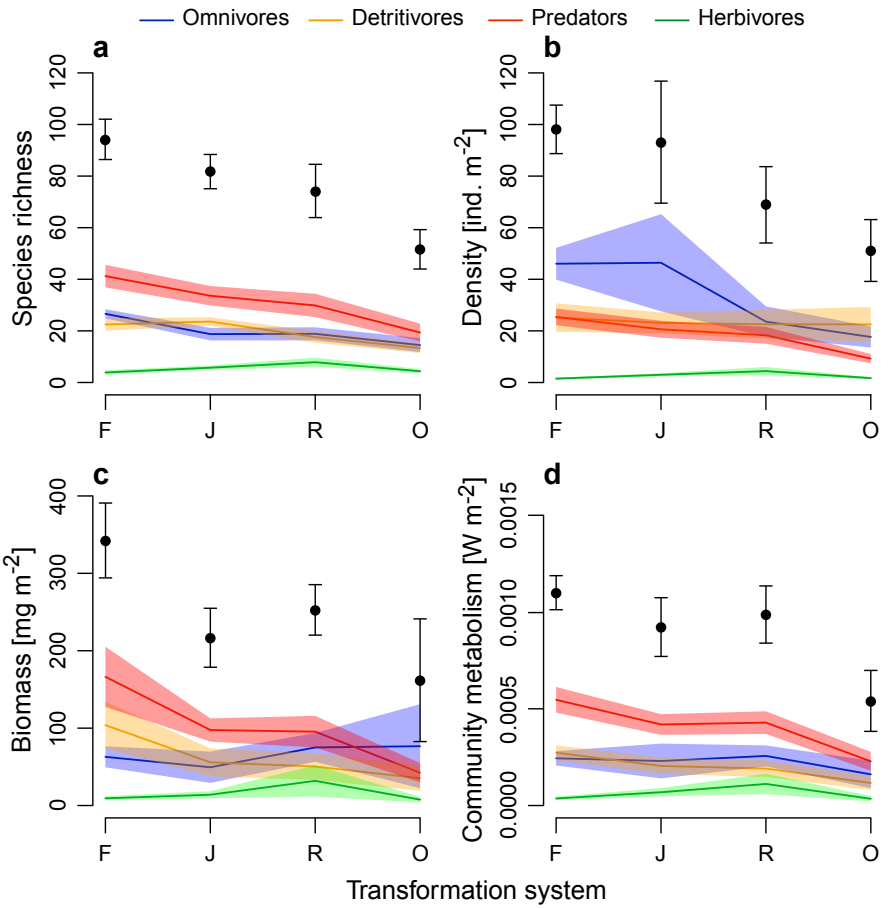

Figure 3.2 – Effects of land-use transformation on macro-invertebrate communities. Mean ($\pm$ SE, $n = 32$) species richness (a), density (b), biomass (c), and community metabolism (d) of the total community (black points) and of each functional feeding guild (coloured lines) for the four land-use transformation systems: forest (F), jungle rubber (J), rubber (R) and oil palm (O).

one of the greatest threats to global biodiversity (Gilbert, 2012). Beyond mere diversity effects, land-use transformation altered animal densities and biomass, threatening to not only drive species extinctions but also to eliminate vital ecological functions. The effects of land-use transformation on species richness and animal densities were additionally dependent on functional feeding guilds, with predators decreasing in species richness and density most rapidly (Figure 3.2 a-c and Table 7.1) as could be expected for higher trophic level feeding guilds (Purvis *et al.*, 2000). Such alteration of higher trophic levels is likely to have severe indirect functional impacts on other functional guilds within the trophic network (Jochum *et al.*, 2012).

Community metabolism

Summing up individual metabolic rates, we demonstrate that transformation of forest to

oil palm yields a 51% decrease in community metabolism, with jungle rubber and rubber only 16% and 10% below forest levels of community metabolism, respectively. However, all systems yielded significantly higher community metabolism than oil palm (Figure 3.2 d and Table 7.1). As such, we show that ecosystem energy processing is critically reduced in oil-palm plantations. Interestingly, biomass responses to land-use transformation among feeding guilds were not clearly comparable to responses in community metabolism (Figure 2 c,d). This suggests that systematic changes in species composition, body-mass distributions (Figure 7.1) and biomass exhibited a complex interaction in determining the functional consequences of land-use transformation.

Whole-community energy fluxes and ecosystem functioning

Aiming to visualize the complex interplay between community biomass dynamics and energy flux, we constructed energy networks for the four transformation systems (Figure 3.3) based on total energy fluxes as a promising way to quantify multitrophic ecosystem functioning (Figure 3.1). In addition to the general decreases in biomass (node sizes in Figure 3.3) and energy processing rates (arrow widths in Figure 3.3), we also found a systematic shift from predator to omnivore dominance when comparing forest and oil-palm systems. Specifically, we found predator biomass in oil palm yielded only 25% of their biomass in forest (0.424 and 1.664 $kg\ ha^{-1}$, respectively), while the predator-driven energy flux was reduced to 46% of the energy flux driven by predators in forest (30.697 and 66.816 $kg\ ha^{-1}\ yr^{-1}$, respectively). In contrast, omnivore biomass in oil palm was 22% higher than in the forest (0.767 compared to 0.629 $kg\ ha^{-1}$), while omnivore-driven energy flux in the oil palm was 47% lower than in forest communities (32.531 compared to 61.900 $kg\ ha^{-1}\ yr^{-1}$) (Table 7.2), suggesting a considerable mismatch of biomass and energy flux, partly dependent on the trophic group in question. In our analyses, this disparity finds its explanation in varying body-mass distributions (Figure 7.1) and assimilation efficiencies that strongly modify how biomass translates into total resource assimilation rates (Figure 3.1). These results suggest that biomass, alone, may be an unsuitable proxy for general ecosystem functioning in animal communities.

Multitrophic biodiversity-ecosystem function relationships

Until now, most studies investigating biodiversity-ecosystem function relationships have focused on single trophic levels (Balvanera *et al.*, 2006; Ives *et al.*, 2004). We present a new approach to easily quantify multitrophic ecosystem functioning, requiring only information on body mass, phylogeny, temperature, and assimilation efficiencies to overcome previous limitations in biodiversity-ecosystem functioning research. Utilizing this approach, we also investigated the relationship between species richness and ecosystem functioning, identifying a clear linear positive effect of diversity on total energy flux (Figure 3.4 a and

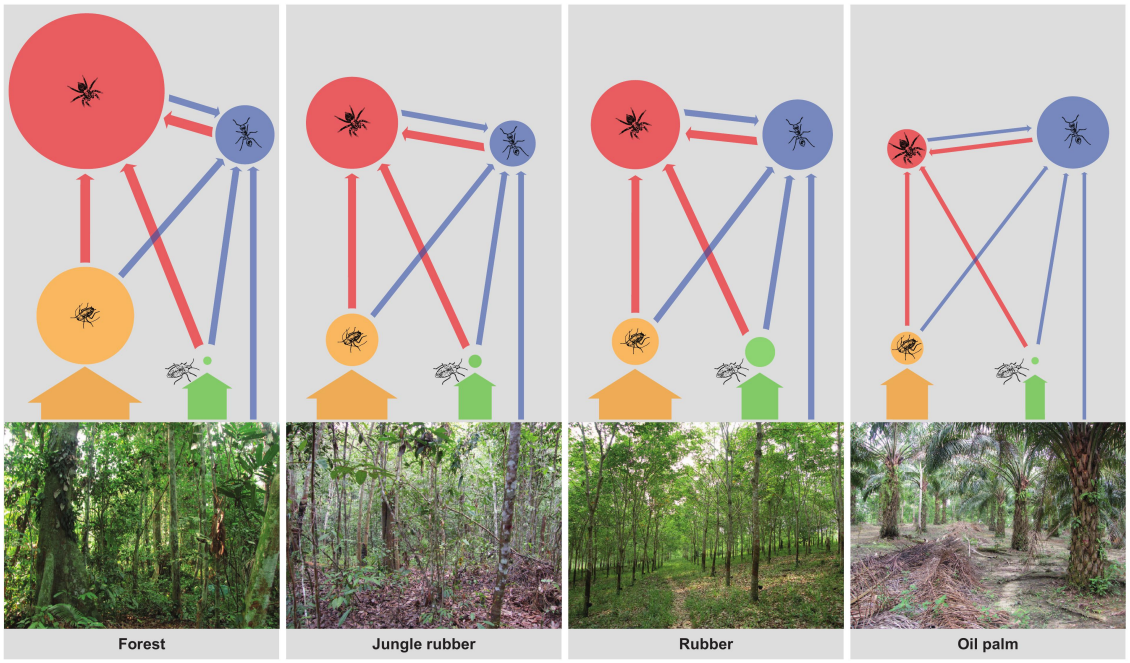

Figure 3.3 – Effects of land-use transformation on community energy networks. Energy networks displaying the relative annual energy flux (coloured arrow width weighted by calculated energy flux [$kg\ ha^{-1}\ yr^{-1}$]) and biomass (coloured node diameter weighted by total biomass) among the functional feeding guilds: predators (red), omnivores (blue), detritivores (yellow), and herbivores (green). Each panel represents an energy network for one of the four land-use transformation systems.

Table 7.3). The relationship between diversity and energy flux was dependent on land-use transformation system, whereby oil palm and jungle rubber showed the strongest decrease in energy flux per unit loss in species richness (Figure 3.4 a and Table 7.3). Our results suggest that each loss of species in oil palm and jungle rubber therefore would be followed by proportionately higher losses in energy flux, compared with equal species losses in forest and rubber. We found the same pattern as in the overall trend for the predator group, which showed transformation system-dependent relationships between species richness and energy flux (Figure 3.4 b). However, for omnivores, detritivores and herbivores there was a linear effect of diversity on energy flux driven by these groups, but this effect was independent of transformation system (Figure 3.4 b and Table 7.3). This implies that studies focusing on single trophic levels, or even specific species, may fail to detect the alteration of ecosystem processes resulting from land-use transformation. These results call for a wider application of multitrophic approaches that not only measure one ecosystem property, such as total productivity or decomposition, but that also aim to assess whole-community ecosystem processes such as total energy flux.

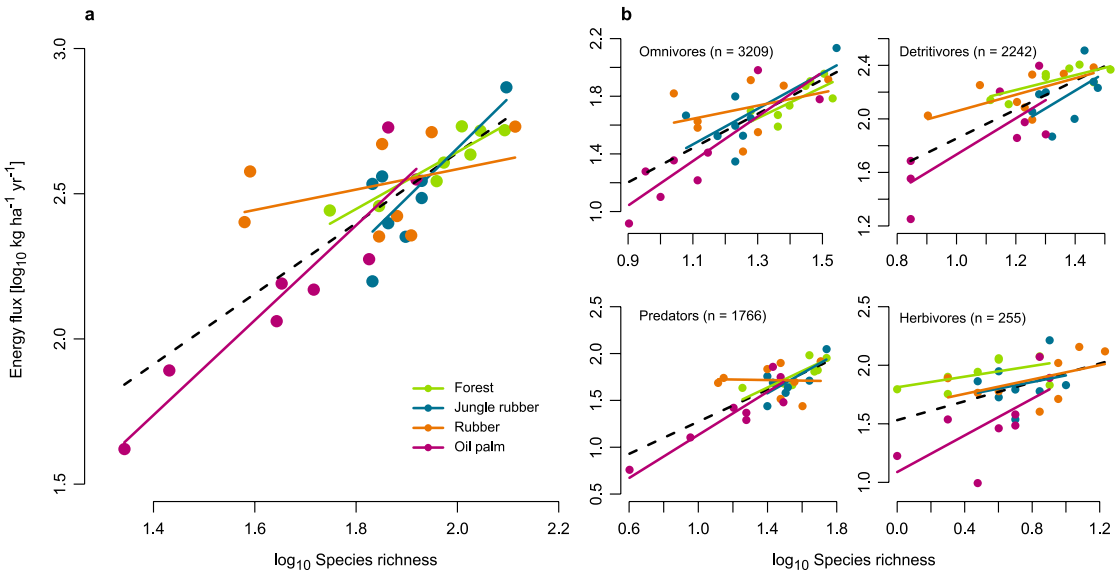

Figure 3.4 – Relationship between species richness and community energy fluxes. Linear mixed effects models for (a) entire communities and (b) separated into functional feeding guilds. Black dashed lines denote overall model fits and coloured lines indicate different land-use transformation systems.

3.3. Discussion

Our study reflects previous findings that the transformation of forest systems to oil palm has severe impacts not only on single animal populations, but also on communities as a whole. In particular, species richness and animal biomass are most significantly affected. Furthermore, jungle rubber and rubber appear to represent intermediate steps in land-use intensification. Their higher levels of biodiversity and ecosystem functioning indicate that they potentially provide higher ecological value than oil palm. As such, these rubber land-use systems could present economically viable, lower intensity land-use alternatives.

By taking a multitrophic ecosystem functioning approach we demonstrate that, at the community level, species loss leads to a direct linear decrease in ecosystem functioning. This means that any species loss will be followed by a proportionate loss in function, and this relationship becomes proportionately stronger in more intensive transformation systems such as oil-palm plantations. Thus, every one of the few species in high-intensity land-use systems is functionally more important than species in low-intensity systems where functional redundancy is likely to be higher (Laliberté *et al.*, 2010). Without explicit consideration of multiple trophic levels, such emergent properties are likely to be overlooked. Our study demonstrates the crucial implications of tropical land-use intensification for biodiversity and ecosystem functioning across multiple trophic levels, suggesting that these globally important impacts will likely resonate beyond previously explored trophic boundaries.

3.4. Methods

Study site and sampling design

Sampling took place in the Jambi province of Sumatra, Indonesia, a region known as a hotspot for biodiversity, but that has also already undergone extensive deforestation (Wilcove *et al.*, 2013; Sodhi *et al.*, 2004). In the second half of the last century, Sumatra's forests have experienced vast transformation to rubber and oil palm monocultures (Wilcove & Koh, 2010; Laumonier *et al.*, 2010). This large-scale land-use conversion has left Sumatra with a very limited area of natural forest mainly restricted to national parks and even here, where logging has been reduced, it has not come to a complete halt (Gaveau *et al.*, 2007). This severe and extensive land-use transformation, that has progressed already further than in most other tropical landscapes, makes Sumatra a unique and ideal example system for studying the impacts of land-use conversion on biodiversity and ecosystem functioning.

We sampled secondary rainforest, jungle rubber, rubber and oil-palm systems, replicated eight times across two landscapes ($n = 32$) (Figure 7.2). Sites were selected by first looking for landscapes in the Jambi province that still contained secondary rainforest. Secondly, we identified all lowland areas with little or no slope and then randomly selected two landscapes with 16 sites each. Among all of the 32 sampling sites, we maintained a minimum distance of 120 m to insure independence of the epigaeic invertebrate communities sampled. The secondary-forest regions lie within two protected areas, Bukit Duabelas National Park and Harapan Rainforest, and represent the least impacted land-use system. Jungle rubber—forest stands with a high percentage of rubber trees that are still regularly harvested—represents a low-impact agroforestry system (Gouyon *et al.*, 1993). Rubber and oil-palm plantations serve as locally common (Laumonier *et al.*, 2010) high-impact monocultures. The 32 sites were carefully selected so that they were all of a similar age and from equal elevations close to sea-level. All agricultural systems (jungle rubber, rubber, oil palm) were treated and harvested by their owners with intensities typical for the respective transformation system.

Animal sampling and calculation of response variables

Animal sampling took place between early October and early November 2012. All organisms were collected based on Permit No. 51/KKH-5/TRP/2014 issued by the Indonesian Institute of Sciences (LIPI) and the Ministry of Forestry (PHKA). In all 32 of the 50 x 50-m sites, we sampled once in each of three 5 x 5-m subplots by sieving the leaf litter from 1 m^2 through a coarse sieve of 2 cm width mesh. 7472 macro-invertebrates

were hand-collected from the sieving samples and stored in 65% ethanol. Specimens were identified to morphospecies and assigned to one of four feeding guilds: omnivores, detritivores, predators and herbivores, based on morphology and literature.

As biodiversity studies always suffer from under-sampling and correlation of sample size with species richness, we compared observed species richness to both extrapolated and rarefied species richness, calculated in the 'vegan' package in R (R Core Team, 2014), to assess the accuracy of our species sampling effort. To extrapolate sampled species richness, we used the non-parametric 2nd order jacknife estimator (Brose *et al.*, 2003) to calculate extrapolated species richness from the three 1 m^2 subsamples at each of the 32 sites, revealing an estimated mean sampling coverage of 56% (s.d. of $\pm$ 2.393%) making the 2nd order jacknife estimator the most accurate extrapolation method (Brose *et al.*, 2003). Additionally, we calculated sample-based rarefaction, whereby rarefaction curves were calculated for each of the 32 sampled sites and then cut off at the sample size of the smallest sample (40 individuals). Because of the very high attrition of data during the rarefaction procedure (a total of 6192 out of 7472 individuals, or 83%, were removed), the rarefied species richness yielded very little resemblance to observed species richness when comparing across transformation systems, resulting in almost no pattern of rarefied richness among transformation systems (Figure 7.3). The jacknife2 extrapolated species richness, however, was extremely closely correlated with observed species richness (Pearson's $\rho = 0.993$) patterns among transformation systems (Figure 7.3), suggesting that our observed species richness did in fact accurately capture realistic patterns in total species diversity across the land-use transformation systems.

For each of the 7472 animals collected, we measured individual body length to an accuracy of 0.1 mm using stage micrometers. We then converted all measured individual body lengths to fresh body mass using length-mass regressions and, where necessary, dry mass-fresh mass relationships from the literature (Table 7.4), yielding an estimated fresh mass in mg for every collected individual. Where family-specific relationships were not available or animal body lengths in our collection fell outside of the size ranges of published regressions, we then used regressions from higher-order taxonomic groupings. For heavily damaged individuals that could not be measured for body length, we assigned these individuals a fresh body mass from the median body mass of all animals from the same species or order where only one individual of that species was collected. We then calculated community biomass (mg fresh mass m^{-2}) for each of the 32 communities by summing together all individual body masses calculated from length-mass regressions as derived from the individually measured body lengths.

We calculated individual metabolic rates for all 7472 animals using body masses, temperature, and phylogeny (Ehnes *et al.*, 2011) (Table 7.5). Temperature was measured over a period of at least 2.5 months at 30 cm depth below the soil surface in each site

and averaged for each transformation system in each of the two landscapes. From this, community metabolism was calculated by summing together all individual metabolic rates within each of the 32 sites, providing the total metabolic demand for each of the 32 communities. Using diet-specific assimilation efficiencies (de Ruiter *et al.*, 1993), energy loss to predation and community metabolism, we analytically calculated energy fluxes for each of these communities (de Ruiter *et al.*, 1994) using the formula

$$F = \frac{1}{e_a} \cdot (X + L), \tag{3.1}$$

where F is the total energy flux into the network node of a feeding guild, e_a is the diet-specific assimilation efficiency, X is the metabolic demand of the feeding guild, and L is the loss to predation that the feeding guild is subjected to (Figure 3.1 and Supplementary Methods 7.1). In order to calculate the fluxes between the functional feeding guilds, we constructed a general network of feeding relationships (link structure in Figure 3.3) that represents a null model for an energy network structure where no active preferences are assumed. We assumed that, of our four functional feeding guilds, energy fluxes to predators were split up equally into the three animal guilds below them. Energy fluxes to detritivores and herbivores were assumed to come from only detritus and plant material, respectively. Omnivores were assumed to receive energy in equal 25% proportions from the other three functional feeding groups (predators, detritivores and herbivores, making 75%) and the remaining 25% from both plant and detritus material combined (Supplementary Methods 7.1).

To assess how these assumptions of feeding preferences might affect the calculations of total energy fluxes, we reconstructed the energy networks so that omnivores were assumed to only consume plant and detritus material (50% derived from each) but with no energy derived from animal material. We then recalculated total energy fluxes and found an overall decrease of up to 54%, which appeared to be highly consistent among the different land-use transformation systems. This consistency between models was especially evident after calculating the loss of energy flux in the three agriculturally used systems compared with the forest system, demonstrating a maximum of only 3% disparity between the two models (Figure 7.4). This sensitivity analysis indicated that our presented method is highly robust in calculating differences in energy fluxes among different systems. Accordingly, the null model was accepted as the simplest model with the least diet preferences assumed. However, we still suggest that studies adopting this method of energy flux calculation should assign feeding preferences with caution, or employ other techniques such as stable isotope analysis to estimate feeding preferences.

Statistical analyses

Using mixed effects models (GLMM's), we tested the effects of 'transformation system' and its interaction with functional feeding guild on community responses, with 'landscape' as a random effect. 'Density', 'biomass', and 'community metabolism' were log_{10}-transformed to meet assumptions of normality and 'species richness' (overdispersed poisson-distributed data) was modelled on a negative binomial distribution. We additionally explored biodiversity-ecosystem functioning relationships by first testing for linearity of relationships using untransformed data. Once linearity was established, we then tested for the effects of log_{10}-transformed 'species richness' and its interaction with 'transformation system' on 'energy flux' for overall data and repeated again for data from separate feeding guilds. Additionally, because we suspected that our analyses could be affected by spatial autocorrelation, we calculated Moran's I values for each model's residuals and tested for spatial autocorrelation using the Moran's I standard deviate (Dormann *et al.*, 2007) in the 'spdep' package in R 3.0.2 (R Core Team, 2014). Results from these tests provided no support for the spatial autocorrelation of variation in any of the response variables tested (all Moran's I test results yielded $P > 0.4$).

For all GLMM's, we applied a backwards stepwise selection procedure to obtain the model of best fit, based on the Akaike Information Criterion (AIC). In this procedure, we constructed full models that contained all possible predictors and their interactions ('transformation system' and 'feeding guild' for general community response models; 'species richness' and 'transformation system' for biodiversity-ecosystem functioning models), and compared these full models and the model of the backward selection procedure to a null, intercept-only model. The model that yielded the lowest AIC score, with a minimum Δ AIC of 2 units, was selected as the model of best fit. All analyses were conducted with the 'nlme' and 'lme4' packages in R 3.0.2 (R Core Team, 2014).

Acknowledgments

We thank Megawati, Rizky Nazarreta, Keisha Disa Putirama, Rosario Reza Valentino Lasse for assistance in the field and laboratory. Roswitha Ehnes provided additional metabolic rate regression parameters and Christian Guill assisted in solving energy-flux equations. Ana Meijide, Alexander Knohl, Oleg Panferov and team provided climate data. We also thank the village leaders, local site owners, PT REKI, and Bukit Duabelas National Park for granting us access to their properties. This study was financed by the Deutsche Forschungsgemeinschaft (DFG) in the framework of the collaborative German-Indonesian research project CRC990.

Chapter 4.

Decreasing stoichiometric resource quality drives compensatory feeding and consumer species loss across trophic levels

Malte Jochum, Andrew D. Barnes, David Ott, Birgit Lang, Bernhard Klarner, Achmad Farajallah, Stefan Scheu & Ulrich Brose

Abstract

Living organisms are constrained by both resource quantity and quality. Ecological stoichiometry offers important insights into how the elemental composition of resources, such as their nitrogen concentration, affects their consumers. If resource quality decreases, consumers can respond by shifting their body stoichiometry, avoiding low-quality resources, or through up-regulation of feeding rates to maintain the supply of required elements while excreting the excess carbon (i.e., compensatory feeding). We analysed multitrophic consumer body stoichiometry, biomass, feeding and species richness along a resource-quality gradient in the litter of tropical forest systems. We did not detect shifts in consumer body stoichiometry or decreases in consumer biomass in response to declining resource quality. However, we found increased feeding in response to low-quality resources across trophic levels. Furthermore, we found reduced detritivore species richness in response to resource quality depletion. Our study reveals how resource quality controls consumer feeding rates across multiple trophic levels.

4.1. Introduction

All living organisms are subject to the persistent struggle of finding and exploiting the resources that they depend on. Traditionally, ecological research has concentrated on the available resource quantity in terms of biomass or abundance. Over the last decades, however, the concept of ecological stoichiometry (Elser *et al.*, 2000a) has shifted our focus to resource and consumer elemental composition. In this context, we study how animals — from individuals to communities — respond to changing resource quality and how such changes alter diversity at multiple trophic levels.

The biomass of living organisms consists of a number of different chemical elements occuring in more or less strict proportions (Redfield, 1958; Sterner & Elser, 2002; McGroddy *et al.*, 2004). In ecological stoichiometry, special attention has been paid to carbon (C), nitrogen (N) and phosphorus (P) as central elements of animal development, activity and growth (Fanin *et al.*, 2013), with a focus on carbon-to-element-ratios and their impacts on individuals, populations and communities (Sterner & Elser, 2002; Hillebrand *et al.*, 2014; Ott *et al.*, 2014b). To fulfil their energetic demand and build up biomass, consumers depend on both resource quantity and quality (i.e., resource elemental stoichiometry) (Urabe & Sterner, 1996; Sterner, 1997; Frost *et al.*, 2005b; Persson *et al.*, 2010; Ott *et al.*, 2012). However, depending on the trophic positioning of consumers and their resources, there can be a considerable gap between the stoichiometry of their resources and consumer body tissue (Elser *et al.*, 2000a), also referred to as stoichiometric mismatch (Hillebrand *et al.*, 2009). Compared to the imbalance between consumers at higher trophic levels and their heterotrophic prey (Fagan *et al.*, 2002), this mismatch is more pronounced between primary consumers and their autotrophic resources, and even more so for detritivores than herbivores (Elser *et al.*, 2000a; McGroddy *et al.*, 2004). Moreover, heterotroph body stoichiometry is less flexible than that of their autotrophic resources (Sterner & Elser, 2002; Frost *et al.*, 2005b; Hillebrand *et al.*, 2014) (but see Persson *et al.* (2010); McFeeters & Frost (2011)). Therefore, heterotrophs — especially those feeding on autotrophic resources — need strategies to deal with decreasing resource nutritional quality. Generally, the options are limited for individuals facing changing resource quality. Specifically, we propose that these options comprise three main possibilities: consumers (H1) vary in their degree of homeostasis and are capable of shifting their mean body stoichiometry (Persson *et al.*, 2010) to account for low-quality resources, (H2) avoid habitats with low-quality resources (Sterner & Elser, 2002; Hillebrand *et al.*, 2009) or (H3) alter their consumption rates (i.e., exhibit compensatory feeding) (Cruz-Rivera & Hay, 2000; Hillebrand *et al.*, 2009; Ott *et al.*, 2012) (Figure 4.1, columns H1, H2 and H3).

Some species have evolved higher carbon-to-nutrient ratios in their body tissue than

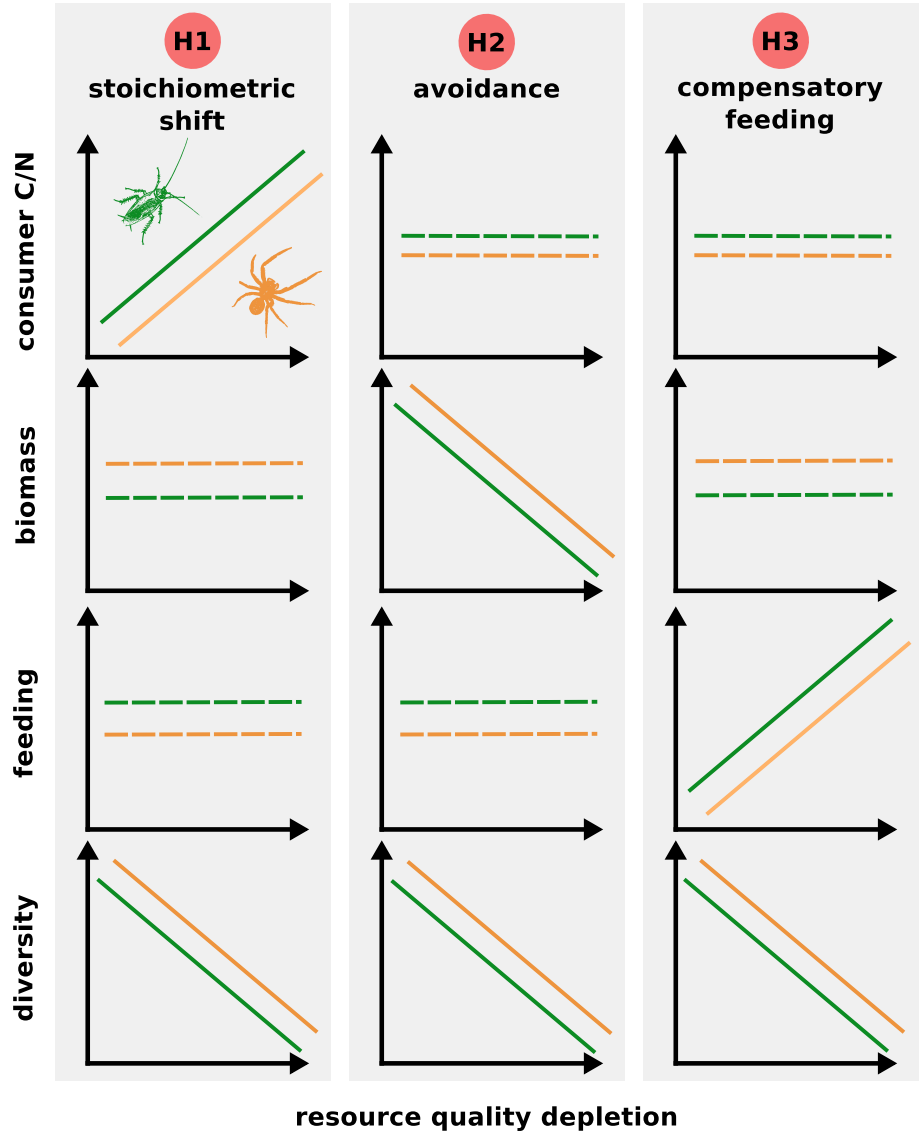

Figure 4.1 – Hypotheses of animal responses to resource quality depletion: In response to resource quality depletion, heterotrophic consumers may (H1, left column) shift their own body stoichiometry, (H2, middle column) show an avoidance reaction, or (H3, right column) exhibit compensatory feeding. In consequence, animal body stoichiometry, biomass, per-unit-biomass feeding and diversity are expected to show specific patterns as indicated for detritivores (green) and predators (orange) in the three columns. Solid diagonal lines show expected responses to resource quality depletion and their direction; dashed horizontal lines show expected null-responses for the three hypotheses.

others (Fagan *et al.*, 2002), and some organisms can regulate their body stoichiometry to a certain degree (Persson *et al.*, 2010; McFeeters & Frost, 2011). Shifted relative abundance towards organisms capable of shifting their body stoichiometry in response to low-quality resources, would enable consumer feeding rates and community biomass to remain constant (Figure 4.1, H1). Furthermore, stoichiometric constraints could alter consumer diversity by inducing specialisation and stable coexistence (Andersen *et al.*, 2004; Moe *et al.*, 2005). However, due to strong stoichiometric constraints for heterotrophs (Sterner & Elser, 2002; Hillebrand *et al.*, 2014), only few species are likely to have evolved very high carbon-to-nutrient ratios or sizeable stoichiometric phenotypic plasticity (Persson *et al.*, 2010). Therefore, we would expect decreased consumer diversity in response to low-quality food (Figure 4.1, H1).

Low nutrient availability or resource quality can also cause reduced feeding and invoke an avoidance response by the consumer community (Frost & Elser, 2002; Hillebrand *et al.*, 2009; Ott *et al.*, 2012). If not all consumers present can deal with high carbon-to-element ratios, less individuals would be able to persist in the given locale, leading to decreased consumer biomass and diversity (Figure 4.1, H2). This would occur as a result of the consumer community shifting towards individuals that can deal with low-quality resources. As such, the number of persisting species would be reduced, subsequently also reducing total community biomass (Borer *et al.*, 2012). However, the remaining consumer community could maintain the same consumption rates because of their adaptations to low-quality resources.

Some species can significantly increase their consumption rate when exposed to a low-quality diet; a mechanism referred to as compensatory feeding (Cruz-Rivera & Hay, 2000). They increase uptake of rare elements and, at the same time, release excess elements through a variety of mechanisms (Frost *et al.*, 2005b). If consumers exhibit this behaviour (Cruz-Rivera & Hay, 2000; Ott *et al.*, 2012), the consumer feeding rate increases substantially with degrading resource quality (Figure 4.1, H3), resulting in a reduced trophic efficiency (Hillebrand *et al.*, 2009). Hence, consumer biomass and stoichiometry could be maintained, while consumer diversity would be reduced because it is likely that only certain species can exhibit compensatory feeding (Cruz-Rivera & Hay, 2000; Ott *et al.*, 2012), a mechanism also depending on the ability to process excess elements resulting from increased ingestion (Anderson *et al.*, 2005). If consumers could fulfil their energetic demands through compensatory feeding, consumer stoichiometry and biomass would not respond to resource quality depletion, but consumer feeding per unit biomass would increase and diversity would decrease (Figure 4.1, H3).

Empirical evidence for population- or even multitrophic community-level consequences of resource quality depletion is scarce because most studies on stoichiometric imbalances between consumers and their resources have focused on the individual level (Moe *et al.*,

2005) (but see Fagan & Denno (2004)). Moreover, research on terrestrial systems, and especially detritus-based systems, is scarce (Sterner & Elser, 2002), although their resource C : N ratios tend to deviate strongly from those of their heterotrophic consumers (Elser *et al.*, 2000a). In this study, we tested the three alternative predictions of community-level consequences of varying resource quality along a terrestrial leaf litter quality gradient in tropical decomposer systems (Figure 4.1, H1-H3). We combined measurements of nitrogen and carbon concentrations of local leaf litter and the consumer community with consumer biomass, feeding and species richness, as a measure of diversity, of multitrophic invertebrate communities (Chapter 3). For the first time, we demonstrate that, when taking the whole community into account, altered resource stoichiometry causes consistent responses across trophic groups from detritivores to predators.

4.2. Methods

Study site and sampling design

In the tropical lowland of the Jambi province, Sumatra, Indonesia, sampling took place in secondary rainforest, jungle rubber, rubber and oil-palm systems, replicated eight times each across two landscapes ($n = 32$) (Chapter 3). The four land-use systems differ strongly in tree biomass and productivity (Kotowska *et al.*, 2015) and are dominated by very different vegetation, suggesting that their leaf litter, as the basal resource of the decomposer communities, provides a strong gradient of resource quality.

Animal and leaf-litter sampling

Animal and leaf-litter sampling was conducted between early October and early November 2012, as described in Chapter 3. On three 5 x 5 m-subplots of every 50 x 50 m-site, we sieved the leaf litter layer from one square meter. All animals visible to the naked eye were collected and stored in ethanol. We sampled 7,472 macro-invertebrates from the leaf litter of the 32 sites and identified them to morphospecies (see Table 8.1 and 8.2 for sampled taxa and further information on the identification process). Furthermore, we measured individual body length, and assigned all animals to one of four trophic guilds: predators, omnivores, detritivores or herbivores, based on morphology and literature (see Table 8.1 and 8.2). Individual body masses were calculated using literature-based length-mass regressions (Chapter 3). We treated leaf litter as the main resource for detritivores, keeping in mind that certain detritivores will exploit dead animal material or other alternative food sources. To assess local quality of the leaf-litter resources, we sampled leaves of the dominant leaf types per site (see Table 8.3) from the subplots where animals were sampled. Additionally, to control for effects of habitat structure and detritivore resource quantity we measured dry litter mass ($g\ cm^{-2}$) on each of these subplots of the

32 sites. On an area of 16 x 16 *cm*, the litter layer was removed and weighed after drying and removal of inorganic matter and coarse woody debris.

Stoichiometric analyses of animal and leaf-litter samples

While phosphorus (P) concentration differs markedly between autotrophic and heterotrophic organisms (Fanin *et al.*, 2013), it does not show considerable changes between insect consumers of different trophic levels (Woods *et al.*, 2004; Martinson *et al.*, 2008). In order to assess multitrophic responses to changing resource stoichiometry, we therefore concentrated on C : N ratios, since nitrogen concentration differs both between autotrophs and heterotrophs (Fanin *et al.*, 2013) and between consumers of different trophic levels (Fagan *et al.*, 2002). Especially for the leaf litter, other resource quality traits than C : N, such as lignin or cellulose content, have been shown to affect decomposition rates (Anderson *et al.*, 2004; Hättenschwiler & Jørgensen, 2010). However, to a certain degree, C : N accounts for such structural carbon compounds (Ott *et al.*, 2014a). To describe resource quality across autotrophic and heterotrophic resources, we therefore chose C : N ratios, keeping in mind that there are additional factors that affect resource quality for consumers.

Aiming to assess macro-invertebrate body stoichiometry, we chose the largest and smallest and at least one intermediately sized animal from each of the four trophic guilds per site (see Table 8.4) and measured the nitrogen (N) and carbon (C) concentration as mass percentage of their dry body tissue using an elemental analyser / mass spectrometer set-up (Langel & Dyckmans, 2014). From these data, we calculated the average C : N ratio of the four feeding guilds per site.

Similar to the stoichiometric analysis of the animals, carbon and nitrogen concentration as mass percentage of dried leaf material was individually measured for each leaf type and subsequently the C : N ratio calculated. Stoichiometric ratios for leaf types were weighted according to their relative importance in the local litter (Kotowska *et al.*, 2015) (see Table 8.5). For the leaf litter, we additionally analysed phosphorus concentration in order to test our hypotheses using C : P ratios. However, we did not have sufficient animal material to analyse phosphorus concentration of the animal tissue and therefore only tested a subset of the hypotheses (those on biomass, feeding rate and diversity of detritivores) with these data (see Figure 8.1).

Calculation of community response variables

From the animal data set, we calculated species richness as a measure of predator and detritivore diversity as the number of species present on the three sampled square meters per site. We used individual body mass (M) and the local soil temperature (T, in Kelvin, see Table 8.6) together with phylogeny-specific parameters from a recent study (Ehnes

et al., 2011) to calculate metabolic rates (I) for each individual animal as

$$ln\, I = ln\, i_{0PG} + a_{PG}\, ln\, M - E_{PG}\left(\frac{1}{kT}\right), \tag{4.1}$$

where i_{0PG}, a_{PG} and E_{PG} are the phylogenetic-group specific intercept, allometric exponent and activation energy and k is Boltzmann's constant. Subsequently, we calculated community biomass (mg fresh mass m^{-2}) and metabolism ($W\ m^{-2}$) for each trophic guild (predators, omnivores, detritivores and herbivores) independently, summing up the body masses and metabolic rates of the individual animals from one square meter (Chapter 3).

Feeding rates of detritivore and predator communities were calculated using their guild metabolism, X, and assimilation efficiency, e_a. Assimilation efficiency defines the percentage of food uptake that is used for respiration and growth instead of being lost through excretion. This percentage has been shown to increase with the nitrogen concentration of the food resource for different consumer taxa (Pandian & Marian, 1985, 1986). To obtain more accurate quantitative relationships for our arthropod consumers, we complemented literature data on insects (Pandian & Marian, 1986) with further arthropod assimilation efficiency data and food nitrogen data based on a broad literature survey (see Table 8.7). We performed a model selection procedure (see Supplementary methods 8.1) to obtain the best fits for the data, resulting in an exponential relationship for decomposers and a Michaelis-Menten model for predators (see Figure 8.2). Using the obtained regressions, we calculated site-specific assimilation efficiencies for detritivores and predators in response to the local nitrogen concentration of their resources (see Figure 8.3).

Subsequently, we calculated per-unit-biomass consumer feeding, F_C, of detritivores and predators independently as

$$F_C = \frac{X}{e_a \cdot B_C}, \tag{4.2}$$

where X is the metabolism, e_a is the assimilation efficiency and B_C is the biomass of the consumer guild, each of these parameters being site-specific. This calculation of consumer feeding does not involve energetic losses to higher trophic levels (Chapter 3) but specifically aims to assess the per-unit-biomass feeding rate that the consumers would need to fulfil their energetic demands. For the predators, we accounted for the effect of other prey resources by weighting the nitrogen concentrations of locally present prey guilds (omnivores, detritivores and herbivores) by their relative abundance amongst potential prey organisms per site (see Table 8.8) to calculate the assimilation efficiency. Finally, we weighted the resulting predator feeding by the relative abundance of detritivores to only

present patterns generated from their feeding on the focal prey guild.

Statistical analyses

Using R Version 3.2.2 (R Core Team, 2015), we used linear mixed effects models (nlme package) to test our hypotheses. First, we tested for an effect of litter C : N on detritivore C : N, as well as detritivore C : N on predator C : N. Then we tested for effects of litter and detritivore C : N on detritivore and predator biomass, feeding, and species richness, respectively. In order to test for these effects, we applied a model selection procedure (see Supplementary methods 8.2), additionally controlling for possible effects of habitat structure (litter mass) and resource availability (litter mass for detritivores and detritivore biomass for predators). We used data from a large-scale research project originally designed to investigate land-use effects across four different land-use systems within two different landscapes on Sumatra, Indonesia. Therefore, in order to account for the hierarchical structure of the study design and possible differences between landscapes and land-use systems, but focus on the effects of resource quality across these different land-use systems and landscapes, we nested land-use system within landscape as random effects in each model. Possible differences between the landscapes and land-use systems are therefore accounted for by the random effect structure of the models. The assumptions of normality were checked for each model and, where necessary, variables were log_{10}-transformed.

4.3. Results

We analysed carbon and nitrogen concentrations of 250 animals from 185 species of predators (136 individuals, 106 species), and detritivores (114 individuals, 79 species), as well as 169 leaf-litter specimens (see Table 8.3 and 8.4 for numbers of stoichiometrically analysed leaf and animal specimens per site). Animal C : N ratios ranged from 3.17 to 15.15 with an average of 4.58 (4.24 for predators, 4.98 for detritivores), while litter C : N ratios ranged from 18.05 to 70.29 with an average of 39.29. Hence, the average leaf litter C : N ratio was 7.9 times as high as the body C : N ratio of the detritivore consumers, whereas the average detritivore C : N was only 1.2 times as high as predator C : N ratios. At the same time, the average nitrogen concentration of the leaf litter was 1.28% with a range from 0.60% to 2.70%, while the average detritivore nitrogen concentration was 9.32% with a range from 2.16% to 18.00%. Hence, while C : N ratios were more variable in the leaf litter, nitrogen concentration was much more variable in the animal body tissue. Detritivore biomass and predator species richness increased with litter mass, whereas detritivore and predator feeding decreased (Table 4.1). Detritivore biomass did not have any significant effects. Overall, the results suggest that the depletion of resource quality

(increasing C : N ratio) affects both of the consumer guilds' feeding rates and detritivore diversity, but not their stoichiometry and biomass.

Table 4.1 – Summary table for the best selected (see Methods and Supplementary methods 8.2) linear mixed effects models testing the results of litter C : N (litterCN) and litter mass (LM) on detritivore (Det) C : N (CN), biomass (B), feeding (F) and species richness (S), as well as detritivore C : N (DetCN), litter mass and detritivore biomass (DetB) on predator (Pre) C : N, biomass, feeding and species richness. Land-use system nested within the landscape was used as a random factor for all models to account for the study design. Bolded p-values indicate significant resource C : N effects plotted in Figure 4.2 and italicised p-values indicate significant responses to litter mass.

Response and model formula	**Model parameter**	**Estimate**	**Std Error**	**t-value**	**p-value**
detritivore C:N	intercept	5.299	0.210	25.289	0.000
DetCN ~ LM	LM	-3.968	1.986	-1.998	0.058
predator C:N	intercept	0.732	0.082	8.932	0.000
log_{10}(PreCN) ~ log_{10}(DetCN)	log_{10}(DetCN)	-0.158	0.118	-1.337	0.194
detritivore biomass	intercept	2.951	1.550	1.903	0.070
log_{10}(DetB) ~ log_{10}(litterCN) + LM	log_{10}(litterCN)	-1.229	1.012	-1.215	0.237
	LM	5.786	1.619	3.574	*0.002*
predator biomass	intercept	2.890	0.827	3.495	0.002
log_{10}(PreB) ~ log_{10}(DetCN) + LM	log_{10}(DetCN)	-1.831	1.139	-1.607	0.122
	LM	2.629	1.356	1.940	0.065
detritivore feeding	intercept	-6.783	0.700	-9.688	0.000
log_{10}(DetF) ~ log_{10}(litterCN) + LM	log_{10}(litterCN)	1.413	0.457	3.093	**0.005**
	LM	-1.845	0.731	-2.525	*0.019*
predator feeding	intercept	-2.921e-06	3.129e-06	-0.934	0.361
PreF ~ log_{10}(DetCN) + LM	log_{10}(DetCN)	9.269e-06	4.291e-06	2.160	**0.042**
	LM	-1.125e-05	4.205e-06	-2.675	*0.014*
detritivore species richness	intercept	81.332	18.669	4.357	0.000
DetS ~ log_{10}(litterCN)	log_{10}(litterCN)	-39.406	11.762	-3.350	**0.003**
predator species richness	intercept	51.708	24.766	2.088	0.049
PreS ~ log_{10}(DetCN) + log_{10}(DetB) + LM	log_{10}(DetCN)	-57.960	33.436	-1.733	0.098
	DetB	6.702	3.635	1.844	0.079
	LM	100.607	38.174	2.635	*0.016*

All three hypotheses expected decreasing consumer diversity with increasing resource C : N. Accordingly, detritivore species richness decreased with increasing litter C : N ($p = 0.003$, Table 4.1, Figure 4.2 g). However, there was no significant change in predator species richness following increased detritivore C : N (Table 4.1, Figure 4.2 h). The linear mixed effects models predicted a loss of 56% for detritivore species richness along their respective resource quality gradient in these tropical forest litter communities. Resource quality, therefore, affected consumer diversity only at the lower trophic level. However, to decide which of our hypotheses is supported by our data, the responses of consumer C : N, biomass and feeding need to be taken into account.

The stoichiometric-shift hypothesis (H1) expected consumer C : N to increase and consumer diversity to decrease with increasing resource C : N, while consumer biomass and feeding remain constant. However, neither detritivores, nor predators significantly altered their body C : N in response to increasing resource C : N (Table 4.1 and Figure 4.2 a,b). Given the lack of significant consumer stoichiometric shifts, our data did not

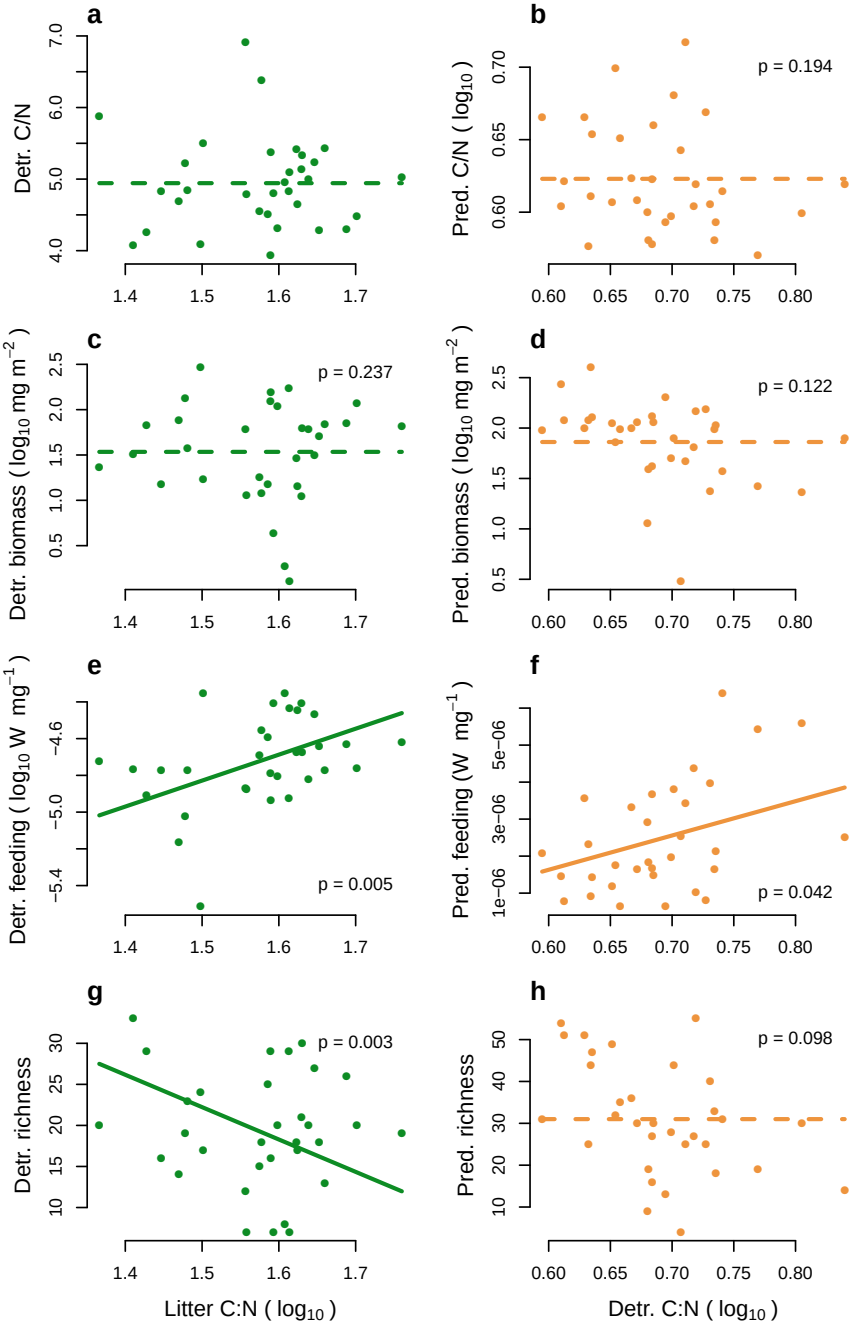

Figure 4.2 – **Consumer responses to resource quality depletion.** Linear mixed effects models for (left column, green lines and points) detritivore C : N (a), biomass (c), feeding (e) and species richness (g) in response to increasing litter C : N as well as (right column, orange lines and points) predator C : N (b), biomass (d), feeding (f) and species richness (h) in response to increasing detritivore C : N for each site ($n = 32$). Relationships shown and p-values presented are for just resource C : N (see Table 4.1) from the best selected models (see Methods and Supplementary methods 8.2). Regression fits for (e) and (f) show the effect of C : N on feeding while holding litter mass ($g\ cm^{-2}$) constant at its mean. Feeding is per-unit-biomass feeding of the respective feeding guild per site. Solid and dashed lines show significant and insignificant relationships, respectively. Where indicated, data were log_{10}-transformed to meet the assumptions of normality.

support the stoichiometric-shift hypothesis.

The avoidance hypothesis (H2) assumed a decrease in consumer biomass and diversity with increasing resource C : N, while consumer C : N and feeding were not expected to change. However, we found that consumer biomass was not altered significantly (Table 4.1, Figure 4.2 c,d) by resource quality depletion. Without significant changes in detritivore or predator biomass, our data also did not support the avoidance hypothesis.

Finally, the compensatory-feeding hypothesis (H3), expected consumer feeding to increase and consumer diversity to decrease with increasing resource C : N. In fact, per-unit-biomass consumer feeding increased significantly with increasing resource C : N ($p = 0.005$ for detritivores and $p = 0.042$ for predators, Table 4.1 and Figure 4.2 e,f). The linear mixed effects models predicted an increase of 254% for the detritivore feeding and 87% for the predator feeding along their respective resource-quality gradients. Overall, given the significant increase in consumer feeding, along with the decrease in detritivore species richness in response to resource quality depletion, our analyses provide support for the compensatory-feeding hypothesis (H3) across trophic levels.

4.4. Discussion

Our investigation of multitrophic consumer responses to resource quality depletion shows that compensatory feeding is not restricted to basal consumer groups, such as herbivores or detritivores, but rather represents a general pattern across trophic levels. Furthermore, a decline in resource quality leads to marked losses in consumer diversity at lower trophic levels, which could be a result of the restricted ability of many consumer species to exhibit compensatory feeding. Our analyses suggest that consumer communities respond to resource quality depletion by increasing their feeding rates, rather than altering their body stoichiometry or avoiding the low-quality resources. Even though autotrophic and heterotrophic resources differ strongly in the constraints that they impose on consumers, we found this pattern to hold across trophic levels. Hence, of the three hypotheses that we tested, our data only supported the compensatory feeding hypothesis (H3).

Resource-driven stoichiometric shift

We did not find significant changes in consumer body C : N ratios with decreasing resource C : N. These findings suggest that neither detritivores, nor predators altered their body stoichiometry in response to resource quality depletion. Although some heterotrophs can exhibit a somewhat variable body stoichiometry (Persson *et al.*, 2010; McFeeters & Frost, 2011) depending on environmental conditions which affect their physiological pathways (Frost *et al.*, 2005b), our results are in line with former studies showing that, overall, heterotrophic body stoichiometry is much less flexible than that of autotrophs

(Sterner & Elser, 2002; Persson *et al.*, 2010; Hillebrand *et al.*, 2014). Within a species, variability of body stoichiometry might overall be relatively low (but see Persson *et al.* (2010); McFeeters & Frost (2011)), but whether heterotrophs or autotrophs show more variability depends on the way this variability is defined (e.g., nitrogen concentration or C : N ratio). Our data show that variation in heterotrophic nitrogen concentration is higher than variation in leaf litter nitrogen concentration. Despite this substantial variability in animal body nitrogen concentration, we did not find evidence that varying resource stoichiometry drives consumer body stoichiometry. As a result, there were large absolute mismatches between consumers and resources, in particular between detritivores and the leaf litter. Hence, without evidence for consumers significantly altering their body stoichiometry in response to changing resource quality, the stoichiometric-shift hypothesis (H1) was not supported by our data.

Avoidance of low-quality resources

Under the avoidance hypothesis (H2), we expected consumer biomass to decrease with resource quality depletion, but detritivore and predator biomass were not significantly altered. If heterotrophs remain stoichiometric homeostasis or maintain their feeding rates in response to decreasing resource quality, the energy reaching the consumer level must be reduced and, consequently, consumer biomass would decline. Generally, experimental nitrogen or CNP enrichment increases invertebrate biomass or abundance in soil (Maraun *et al.*, 2001) and grassland ecosystems (Haddad *et al.*, 2000). Here, however we are looking at more subtle changes in resource stoichiometry rather than experimental fertilisation of the ecosystem, which confounds changes in resource quantity (primary production) and quality (resource stoichiometry).

Although tests of the avoidance hypothesis are rare, other studies have also shown that resource stoichiometry does not necessarily affect consumer biomass or abundance. In this vein, a recent paper investigating plant effects on decomposer and herbivore communities in grasslands found no effect of plant C : N ratios on decomposer abundance (Ebeling *et al.*, 2014). Nitrogen concentration in plants has also been reported to yield no discernible effects on arthropod communities in a shortgrass prairie (Kirchner, 1977), while other studies found strong arthropod responses to fertiliser input (Haddad *et al.*, 2000; Maraun *et al.*, 2001). Our data on detritivore and predator communities in tropical leaf-litter systems did not show significant consumer biomass responses to increasing resource C : N ratios. Therefore, in these systems, another mechanism seems to enable maintainance of consumer biomass and stoichiometric homeostasis while resource quality changes.

Recent work on temperate forests has shown resource stoichiometry to affect biomass densities of litter macro-invertebrates (Ott *et al.*, 2014b). Specifically, higher nitrogen and phosphorus availability (low C : N and C : P ratios) in the local leaf litter resulted

in increased population biomass densities. Interestingly, the positive effect of nitrogen availability on consumer biomass was especially pronounced for large-bodied species. When comparing the body sizes from our tropical data set with those of Ott *et al.* (2014b), on average, the temperate animals have much larger body masses (18.40 ± 0.63 *mg* fresh weight, mean ± SE) than the tropical animals (3.16 ± 0.33 *mg* fresh weight, mean ± SE). Furthermore, the tropical litter C : N ratios (38.32 ± 1.35, mean ± SE) were higher than the temperate ratios (28.67 ± 0.50, mean ± SE). Thus, the missing biomass response to changing resource C : N ratio in our tropical data set might be caused by small body masses and comparably high resource C : N ratios. Further comparisons of such tropical and temperate data sets will help to reveal the underlying mechanisms of resource quality depletion and structural differences between the tropical and temperate arthropod consumer community responses. However, here we did not find significant resource-quality effects on consumer biomass so that the avoidance hypothesis (H2) was not supported by our data.

Compensatory feeding to account for stoichiometric resource depletion

Both detritivore and predator per-unit-biomass feeding increased substantially with increasing C : N ratios of their resources (254% and 87% increase, respectively). This is in line with prior reports of compensatory feeding in detritivores confronted with poor resources (Ott *et al.*, 2012) and herbivores facing increasing stoichiometric mismatch with their resources (Hillebrand *et al.*, 2009). Our study thus extends these findings to the multitrophic community level of ecosystems. Therefore, the condition supporting the compensatory-feeding hypothesis (H3) was met by our data.

Because assimilation efficiency increases exponentially with resource nitrogen concentration for detritivores (see Figure 8.2), an increase in litter C : N—indicating decreasing nitrogen concentration, and thus decreased assimilation efficiency—could only lead to higher per-unit-biomass feeding rates, given that biomass and metabolism are not altered simultaneously. Although leaf litter nitrogen concentration did not show high variability (0.60 - 2.70%), the exponential increase of assimilation efficiencies at such low resource nitrogen levels resulted in increased feeding rates. This exponential increase indicates the strong limitation of assimilation efficiency that detritivores suffer from at low nitrogen concentrations in their litter resources. Notably, predators showed the opposite pattern; a weak increase in assimilation efficiency with increasing resource nitrogen concentration (see Figure 8.2), but a large variability in the latter (2.16 - 18.00%). Ultimately, the combination of resource nitrogen concentration variation and the different scaling relationships between resource nitrogen and assimilation efficiency for detritivores and predators resulted in significantly increased per-unit-biomass feeding with decreasing resource quality across trophic levels.

While compensatory feeding has been shown before (Hillebrand *et al.*, 2009; Ott *et al.*, 2012), we expand this knowledge to community responses to resource quality depletion as we present data from multiple trophic levels. Our analyses show that compensatory feeding is likely a general response to resource quality depletion across trophic levels and consumer feeding types.

How resource quality affects species diversity

All three hypotheses expected consumer diversity to decrease with decreasing resource quality. However, the mechanisms behind this diversity loss likely are tightly coupled with the other community responses to resource quality depletion. Our data suggest that the mechanism driving consumer diversity in response to resource quality depletion in tropical litter communities might be found in the consumers' compensatory feeding response. Across trophic levels, increased feeding rates to compensate for reduced resource nitrogen were the only detected response of litter dwelling arthropods in our communities. Reduced resource quality likely imposes trait-dependent ecological filtering, selecting for species that are able to perform compensatory feeding. In order to compensate for lower food quality through increased ingestion, dealing with excess nutrients is important. A variety of pre- and postabsorptive processes to deal with excess elements has been found in different consumer taxa, with generalist species showing higher plasticity in their physiological pathways than specialists (Anderson *et al.*, 2005; Frost *et al.*, 2005b). Ultimately, this could result in locally reduced species richness due to the inability of many specialist heterotrophic species to up-regulate their feeding rates being incapable to adequately process excess elements. Reduced consumer diversity in response to imbalanced nutrient supply has recently been related to the reduced number of potentially limiting resources, leading to less coexistence (Gross & Cardinale, 2007; Cardinale *et al.*, 2009; Hillebrand & Lehmpfuhl, 2011). In this vein, our findings suggest that, at least for detritivores, diversity in tropical litter communities is tightly coupled to resource C : N imbalance, while other studies found phosphorus to be the main limiting element in such systems (Sayer *et al.*, 2010). Our data suggest that nitrogen seems to be important in driving consumer feeding and diversity in response to shifting resource stoichiometry. Interestingly, phosphorus also increased detritivore feeding but did not affect species richness of detritivores (see Figure 8.1). Fully including phosphorus would potentially add to the variation explained by the models. However, our results show that nitrogen is sufficient to explain the links between resource quality, consumer feeding, and diversity.

Future directions

The feeding rate calculations in our study were partially based on the scaling of assimilation efficiencies with resource nitrogen concentration. However, rather than only

using resource element concentration, focusing on the stoichiometric mismatch between consumer and resource body tissue and its consequences for consumption and energy fluxes within ecosystems is a promising next step. Furthermore, although we focus on resource C : N ratios, terrestrial arthropod communities may also be limited in their biomass density and feeding capacity by resource sodium and calcium concentrations, which are important for maintaining membrane gradients (Kaspari *et al.*, 2009, 2014) and building calcareous exoskeletons (e.g., isopods) (Kaspari & Yanoviak, 2009), respectively. Additionally, the phosphorus concentration of the litter may stimulate microbial biomass production with potential positive bottom-up effects on arthropod biomass (Elser *et al.*, 1996; Kaspari *et al.*, 2008). In this vein, two recent field studies showed that arthropod biomass densities may be driven by nitrogen and sulphur concentrations in the litter of American tropical forest stands (Kaspari & Yanoviak, 2009) or nitrogen, phosphorus and sodium in European forests (Ott *et al.*, 2014a). While the consistent importance of nitrogen supports the choice of this element for our study, future studies could thus employ our approach to address the interactive role of nitrogen, phosphorus and sodium in driving arthropod community responses to changing resource conditions (Fagan & Denno, 2004).

While soil food webs have a complex structure integrating up to six trophic levels (Scheu & Falca, 2000; Digel *et al.*, 2014), we have simplified our community approach to the broad trophic groups of detritivores and predators. However, with better resolved trophic structure of these communities, investigating how relative amounts of nitrogen, phosphorus, sodium and calcium change along the food chain (Martinson *et al.*, 2008) and differently alter consumer responses to resource depletion across trophic levels seems promising. Furthermore, investigating the effects of changes in other elements on consumer diversity and feeding rates across trophic levels will be a future challenge to unravel new patterns in community structure. Additionally, our data present consumer-community responses to changing resource quality at a single point in time. Testing our hypotheses repeatedly over time to detect possible differences in the consumer communities' response could therefore lead to further insights on the nature of the resource-quality effect.

Conclusions

Our data highlight how reduced resource quality triggers increased consumption of consumers across trophic levels. Detritivore species richness decreases with resource quality depletion, possibly because the ability to exhibit compensatory feeding is not ubiquitous, thus allowing only species and individuals with this ability to persist under reduced resource quality. Small changes in resource stoichiometry can therefore have far reaching consequences for their consumers, which need to increase their time and energy

expenditure for feeding, thereby decreasing time and energy available for other activities such as reproduction. In addition to providing insights into fundamental processes that structure communities and ecosystems, our study also triggers further questions on how global agricultural expansion and intensification as well as climate change might affect ecosystems by altering elemental availability for consumer organisms throughout trophic networks in these systems. Our results present a promising step towards research on ecosystem-wide ecological stoichiometry effects by taking into account the underlying mechanisms that drive consumer-resource interactions at different trophic levels.

Acknowledgments

We thank Megawati, Rizky Nazarreta, Keisha Disa Putirama, Rosario Reza Valentino Lasse for assistance in the field and laboratory. Diana Lakeland prepared the animals for C : N analysis. Roswitha Ehnes provided additional metabolic rate regression parameters and Martyna Kotowska provided additional data on relative litter fall. Ana Meijide, Alexander Knohl, Oleg Panferov and team provided climate data. This study was financed by the Deutsche Forschungsgemeinschaft (DFG) in the framework of the collaborative German-Indonesian research project CRC990. We also thank the village leaders, local plot owners, PT REKI, and Bukit Duabelas National Park for granting us access to and use of their properties. U.B. gratefully acknowledges the support of the German Centre for integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig funded by the German Research Foundation (FZT 118). This study was conducted using organisms collected based on Permit No. 2695/IPH.1/KS.02/XI/2012 recommended by the Indonesian Institute of Sciences (LIPI) and issued by the Ministry of Forestry (PHKA).

Chapter 5.

How resource stoichiometry and habitat structure drive diversity and biomass density of tropical macro-invertebrate communities

Malte Jochum, Andrew D. Barnes, Patrick Weigelt, David Ott, Katja Rembold, Achmad Farajallah & Ulrich Brose

Abstract

The high diversity of soil communities is crucial for the process of decomposition in terrestrial ecosystems such as tropical forests. However, the leaf litter that these communities consume is of particularly poor quality as indicated by elemental stoichiometry. Recently, the biomass density of temperate litter consumer communities has been shown to be jointly driven by stoichiometric and allometric variables. This study expands previous research to the tropics and additionally investigates the effects of stoichiometric and habitat structural predictors on consumer diversity across ten major taxonomic groups. We tested a set of hypotheses predicting responses of consumer diversity, abundance or biomass to variation in resource stoichiometry and habitat structure. We found support for all tested hypotheses, supporting the idea of a non-Liebig world in tropical forest systems, whereby consumers are controlled by multiple rather than single limiting factors. Using a standardized model averaging approach, the joint assessment of consumer biomass density and diversity responses enabled us to identify differences and similarities in the magnitude and direction of such responses to resource stoichiometric and habitat structural variation. While consumer diversity was largely driven by litter mass, consumer biomass densities were dominated by interactions of body mass with stoichiometric variables. The observed patterns provide interesting insights to the consumer dependence on resource quantity and quality in tropical litter communities. We discuss contrasts in consumer diversity and biomass density responses to stoichiometric and habitat structural variation and offer a conceptual framework explaining variable response patterns in the two community variables.

5.1. Introduction

Invertebrates are not only extraordinarily diverse (Wilson, 1987), they are also of critical importance for ecosystem functioning (Seastedt & Crossley, 1984; Yang & Gratton, 2014). One example for such an ecosystem function is decomposition of dead organic material in terrestrial and aquatic ecosystems (Gessner *et al.*, 2010; Handa *et al.*, 2014). In terrestrial ecosystems, ninety percent of the primarily produced biomass is returned to the organic matter pool of the soil ecosystem (Cebrian, 1999; Coleman, 2013) for highly diverse and trophically complex consumer communities to thrive on (Hättenschwiler *et al.*, 2005; Nielsen *et al.*, 2011; Digel *et al.*, 2014). These consumers critically depend on the quantity and quality of their resources and the habitat conditions they are exposed to (Cruz-Rivera & Hay, 2000; Cardinale *et al.*, 2009; Klarner *et al.*, 2014; Ott *et al.*, 2014a; Lang *et al.*, 2013). Ecological stoichiometry allows for investigating impacts of resource elemental quality on consumers (Elser *et al.*, 2000a; Sterner & Elser, 2002). For heterotroph communities that rely on terrestrial plant leaf litter, stoichiometric resource quality (hereafter resource stoichiometry) is particularly poor (Elser *et al.*, 2000a; Ott *et al.*, 2014a,b), especially in tropical ecosystems (McGroddy *et al.*, 2004).

Together, ecological stoichiometry (Elser *et al.*, 2000a) and metabolic theory (Brown *et al.*, 2004) comprehensively explain consumer population biomass and abundance patterns (Allen & Gillooly, 2009; Mulder & Elser, 2009; Mulder *et al.*, 2011; Ott *et al.*, 2014b). In temperate forest litter communities, for example, population biomass density of arthropod consumers has been shown to be driven by allometric (i.e., effects of population-averaged body mass) and stoichiometric (i.e., carbon-to-element ratios of resources) variables (Ott *et al.*, 2014b), with differences between taxonomic groups (Ott *et al.*, 2014a). Interestingly, resource stoichiometry does not only affect consumer biomass densities. Consumer diversity can also be affected by resource stoichiometry, as has been conceptually argued by Cardinale *et al.* (2009) and found in a field study on arthropod communities in a tropical forest (Sayer *et al.*, 2010). Consumer diversity decreases with imbalance of resource availability, where balance is defined as the similarity between consumer elemental requirements and the availability of these resources (Klausmeier *et al.*, 2004). This decrease in diversity might be mediated by a lower number of resources potentially constraining consumers in an imbalanced state, leading to a reduced potential for species to coexist (Hillebrand & Lehmpfuhl, 2011). Instead of following Liebig's law of the minimum (Von Liebig, 1840), which states that organisms are constrained by a single limiting element, consumer growth (Sperfeld *et al.*, 2012) and ecological processes such as decomposition (Kaspari *et al.*, 2008) seem to be co-limited by multiple stoichiometric variables (Kaspari, 2012).

In recent years, several hypotheses have been developed to explain and predict consumer

responses to changing resource stoichiometry. Here, we specifically consider the growth rate hypothesis (Sterner & Elser, 2002; Elser *et al.*, 2000b), the secondary productivity hypothesis (Kaspari & Yanoviak, 2009), the structural elements hypothesis (Kaspari & Yanoviak, 2009) and the sodium shortage hypothesis (Kaspari *et al.*, 2009). The growth rate hypothesis (Sterner & Elser, 2002; Elser *et al.*, 2000b) and the secondary productivity hypothesis (Kaspari & Yanoviak, 2009) predict increasing microbial biomass and consequently increasing abundance of microbi-detritivores in response to increased phosphorus (P) availability. Furthermore, population biomass density and diversity of meso- and macro-fauna may be affected by P (Sayer *et al.*, 2010; Ott *et al.*, 2014a). The structural elements hypothesis (Kaspari & Yanoviak, 2009) stresses the influence of certain elements that are of particular importance for a consumer taxon because of their prominent role in molecules that are basally required for certain morphological traits of the taxon. Two such examples are the importance of calcium (Ca) for woodlice and millipedes for producing their calcareous exoskeletons, or nitrogen (N) for arachnids for producing silk (Kaspari & Yanoviak, 2009), as recently demonstrated for temperate forests (Ott *et al.*, 2014a). The sodium (Na) shortage hypothesis (Kaspari *et al.*, 2009) predicts decomposer and herbivore abundance to increase in response to elevated Na availability; a mechanism driven by the shortage of Na in plant tissue relative to consumer body tissue, because plants use potassium (K), while animals use Na to maintain their membrane gradients. Termites, for example, have been shown to strongly increase in abundance following Na fertilisation (Kaspari *et al.*, 2009, 2014), with cascading positive effects on predatory ants (Kaspari *et al.*, 2009). In temperate forests, Ott *et al.* (2014a) found Na availability in the litter to affect the biomass densities of springtails, earthworms, snails, mites and woodlice. In addition to the above-mentioned hypotheses, the diversity of tropical soil arthropods has also been shown to increase with litter Na and Ca concentration as well as with dry mass of the Oe (fermentation) horizon (Sayer *et al.*, 2010). Moreover, sulphur (S) in tropical litter was found to have a positive effect on the abundance of millipedes, oribatid mites and springtails (Kaspari & Yanoviak, 2009), while it affected very few consumer groups in temperate forest litter systems (Ott *et al.*, 2014a). In Chapter 4, we showed that increasing leaf litter N concentration drove higher detritivore diversity. In this study, we investigate the effects of resource stoichiometry on the diversity and biomass density of different taxonomic groups and functional feeding guilds.

In addition to these stoichiometric hypotheses, habitat structural parameters have been suggested to control diversity, abundance and biomass of litter arthropods. For example, the ecosystem size hypothesis (Post *et al.*, 2000; Post, 2002; Brose & Martinez, 2004; Kaspari & Yanoviak, 2009) predicts higher diversity, longer food chains (i.e., more trophic levels) and more complex food webs in ecosystems that comprise larger habitat space. While litter depth, as a measure of habitat size for litter-dwelling arthropods, has been

shown to increase predatory arthropod abundance in tropical forests (Kaspari & Yanoviak, 2009), other studies from tropical (Sayer *et al.*, 2010) and temperate forest soil systems (Ott *et al.*, 2014a) did not find any such effect. Consumer diversity is also predicted to increase with habitat heterogeneity (Tews *et al.*, 2004). Litter diversity has been used as a surrogate for micro-habitats in temperate litter communities, where it was found to have effects on woodlice but not on predatory consumers (Ott *et al.*, 2014a). In addition to habitat size and heterogeneity, soil acidity has also been shown to affect the abundance of bacteria, fungi and microarthropods in soil ecosystems (Mulder *et al.*, 2004) and even body mass-biomass relationships of grassland invertebrates (Mulder & Elser, 2009). At lower taxonomic levels, pH additionally affected the diversity of arthropods (Mulder *et al.*, 2004). While most of these hypotheses stress the importance of stoichiometric and habitat structural parameters for consumer biomass density or abundance, it remains to be investigated whether the same restrictions apply to consumer diversity.

The objective of this study was twofold: a) to complement analyses of Ott *et al.* (2014a) and Ott *et al.* (2014b), who found that allometric and stoichiometric variables jointly drive consumer biomass densities in temperate forest systems, by testing the above described hypotheses in tropical litter communities; and b) to test for effects on consumer diversity and compare these effects to those on biomass density. In order to achieve these goals, we applied a model averaging approach (Burnham & Anderson, 2002; Grueber *et al.*, 2011) to simultaneously account for the effects of multiple limiting parameters that are hypothesised to constrain consumer community structure and ecosystem functioning (Sperfeld *et al.*, 2012; Ott *et al.*, 2014a), especially in tropical ecosystems (Kaspari *et al.*, 2008). We used a data set of 7,472 macro-invertebrate individuals of 871 species and 2,414 populations across 32 sites in tropical lowland rainforest and plantation systems on Sumatra, Indonesia. By simultaneously investigating macro-invertebrate diversity and biomass density in tropical leaf litter communities varying in their resource stoichiometry and habitat structure, our study presents a major contribution to existing research and opens up important questions on the nature of the diversity and biomass responses and the mechanisms behind these effects.

5.2. Methods

Study site and sampling

Animal and leaf-litter material was sampled in the tropical lowland of the Jambi province, Sumatra, Indonesia, between October and November 2012. Across two landscapes (near Bukit Duabelas National Park and Harapan Rainforest), eight 50 x 50 m sites were established in each of four land-use systems, lowland rainforest, jungle rubber, rubber and oil-palm plantations (n=32) (Chapter 3). Animal communities and leaf-litter material

were sampled on each of three 5 x 5 m subplots per site, as described in Chapter 3 and 4. To quantitatively sample the animal communities from the leaf-litter layer, on each subplot, we sieved all leaf litter from one square meter through a 2 cm width mesh, hand-collected all 7,472 animals visible to the naked eye and stored them in 65% ethanol for further processing.

To measure local leaf-litter stoichiometry, the dominant leaf types on each site were sampled for stoichiometric analysis (see Table 8.3). Furthermore, to quantify local plant species richness, at each site, all trees with a diameter equal to or larger than 10 cm at breast height as well as all vascular plants on five 5 x 5 m subplots were identified. To assess local habitat structure and resource quantity, we used dry litter mass ($g\ cm^{-2}$) measured on each subplot by removing the litter layer on an area of 16 x 16 cm, after which all coarse woody debris and inorganic matter was removed and the litter sample was dried and weighed. We used soil pH analysed on the same sites in a 1:4 soil-to-water ratio by Allen *et al.* (2015) as an additional structural habitat parameter.

Stoichiometric analysis of leaf-litter samples

For each of the 169 leaf types, total carbon (C) and nitrogen (N) concentration was analysed by an automated CHNSO analyser from an amount of 5 mg dry material. Furthermore, phosphorus (P), potassium (K), sulfur (S), calcium (Ca), magnesium (Mg) and sodium (Na) concentrations of the same dried material were measured after HNO_3 digestion by ICP-OES analysis (Perkin Elmer Optima 5300 DV). We calculated carbon-to-element ratios (C : X) for all analysed elements based on mg per g dry weight of the analysed material. Subsequently, we weighted these C : X ratios of single leaf types according to relative importance in local leaf litter (see Table 8.5).

Calculation of consumer community responses

We measured the body length of all 7,472 animals and calculated individual body mass using length-mass regressions from the literature (see Table 7.4 for further information on length-mass regressions). All individuals were then identified to morphospecies and assigned to the feeding types predator, omnivore, detritivore or herbivore, based on morphology and literature (see Tables 8.1 and 8.2 for further information on sampled taxa and feeding type). To assess effects on consumer diversity, we calculated species richness as the number of morphospecies present in the sampled three square meters at each of the 32 sites. For further analysis, all animals from one morphospecies at a given site were grouped as a population. Subsequently, we calculated population-averaged body mass and population biomass for each of these 2,414 populations from 871 species. Finally, for a more detailed analysis of the consumer community responses to changing habitat structure and resource stoichiometry, we split our dataset into the

four functional feeding guilds (detritivores, predators, omnivores and herbivores) and additionally selected ten taxonomic groups: ants (Formicidae), cockroaches (Blattodea), centipedes (Chilopoda), beetles (Coleoptera), millipedes (Diplopoda), woodlice (Isopoda), termites (Isoptera), harvestmen (Opiliones), crickets (Orthoptera, of which 95% of the individuals were Gryllidae) and spiders (Araneae) (see Table 8.1 for further information on species and individual numbers and body sizes of the groups and Table 9.1 for population numbers for each animal group).

Statistical analyses

To assess the effect of habitat structure and resource stoichiometry on macro-invertebrate diversity and biomass density, we employed a model averaging approach following Burnham & Anderson (2002) and Grueber *et al.* (2011) using the "MuMIn" package (Barton, 2015) in R Version 3.2.2 (R Core Team, 2015). We first established a full model including all possible predictor variables. We used linear mixed effects models with the "nlme" package in R (Pinheiro *et al.*, 2014), with land-use system nested within landscape as random effects to account for the nested study design and to account for random variability among land-use systems while focusing on stoichiometry and habitat structure predictor effects. Before setting up the models, we tested for collinearity among all predictor variables using Pearson correlation coefficients, but did not find any correlation coefficients larger than 0.75 (see Table 9.2) and thus included all predictors in the analysis (Zuur *et al.*, 2007). To meet the assumptions of normality, we furthermore log_{10}-transformed all predictor variables (except pH), as well as species richness, biomass and population-averaged body mass. The full model for testing diversity effects across the 32 sites included the three structural predictors (litter mass, plant species richness and pH) as well as the seven C:X ratios for N, P, K, Ca, Mg, Na and S. Henceforth, when describing effects of a certain element, we refer to the effect of their C:X ratios. In the models testing for biomass responses of all consumer populations across the 32 sites, we allowed for interactions of each predictor with population-averaged body mass (subsequently denoted as M*X, indicating an interaction of body mass with C:X ratio) of the respective group as a co-variable. In a second step, we computed all models for all possible predictor-variable combinations and ranked them by AICc (Akaike's Information Criterion). We then chose a set of best models, defined by a maximum ΔAICc of 4 compared to the model with the lowest AICc (see Table 9.1 and 9.3 for further information). In a third step, this set of best candidate models was then used to perform model averaging using maximum likelihood and the zero method ("full average"), which is recommended when trying to establish which predictor has the strongest effect on the response variable (Grueber *et al.*, 2011; Nakagawa & Freckleton, 2011). For comparison of effect sizes among models, we calculated range-standardized model coefficients for each of the predictors (Grace, 2006). Raw

coefficients β_{xy} were standardized to $\beta std_{xy} = \beta_{xy} \cdot (x_{max} - x_{min})/(y_{max} - y_{min})$, where max and min values are the largest and smallest occurring variable value, respectively. The standardized coefficients thus yield dimensionless coefficients showing the proportional change in y across the range of x, while simultaneously controlling for all other predictors in the model. This procedure was repeated for every subset of the data (overall data set, four functional feeding guilds, ten taxonomic groups), yielding one averaged model for species richness and one model for the body mass-biomass relationship for each consumer group. Finally, to obtain a goodness-of-fit measure, we calculated pseudo-r^2 values for each averaged model as the r^2-value of a linear model of the observed values against the values predicted by the averaged model.

5.3. Results

The ten habitat structural and stoichiometric predictor variables showed a diverse range of effects on species richness and biomass density of the ten taxonomic consumer groups. While litter mass and phosphorus had the strongest effects on species richness across consumer groups (Figure 5.1 and 5.2), consumer biomass was best predicted by the interactions of body mass with nitrogen, potassium and sulphur (Figure 5.3), followed by the three structural predictors litter mass, plant species richness and pH. Note that the large summed absolute standardized estimates (upper bar graph in Figure 5.3) for nitrogen and potassium are driven by single strong effects on termites (positive) and millipedes (negative), respectively.

Species richness

When investigating the effects of habitat structure and resource stoichiometry on consumer species richness, we found that litter mass and P had the strongest effects on overall species richness (Figure 5.1 and 5.2). Both litter mass (Figure 5.1 a) and phosphorus concentration (Figure 5.1 b) had positive effects on overall species richness (note that a negative effect of the C:P ratio in Figure 5.1 translates into a positive effect of P concentration in Figure 5.2). When comparing the relative strength of the ten predictor variables on the ten taxonomic groups, litter mass had the largest sum of absolute standardized estimates (3.44, Figure 5.2, upper bar graph), followed by P (1.32), Ca (0.98), K (0.94), plant species richness (0.90), S (0.83), N (0.77), Na (0.67), Mg (0.57) and pH (0.21). While litter mass and potassium had only positive effects on species richness across taxonomic groups, all other predictors imposed positive and negative effects on different taxonomic groups. Of all models on species richness, the models for woodlice and crickets had the highest proportion of variance explained according to the pseudo-r^2 values (0.76 and 0.74, respectively), while termite richness was the most poorly explained

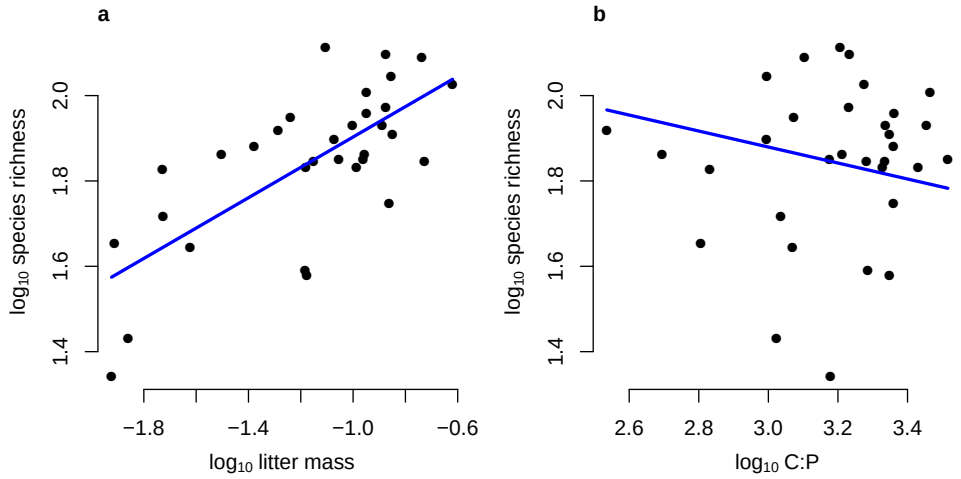

Figure 5.1 – Effects of litter mass and phosphorus availability on overall macro-invertebrate species richness of tropical litter communities. Response of overall species richness to the two parameters that had the strongest effect sizes from the model averaging procedure: a) litter mass and b) phosphorus concentration (note that a higher C:P ratio expresses a lower P concentration). Shown are results from linear mixed effects models including just litter mass and C:P, respectively. For each of the 32 sites, dry litter mass was originally measured in $g\ cm^{-2}$, C:P represents the ratio of carbon and phosphorus content measured in $mg\ g^{-1}$ dry litter mass and species richness is the number of morphospecies present in the three sampled square meters per site.

response variable (0.24), with the average pseudo-r^2 value of the taxonomic group species richness models being 0.56.

When exploring the specific effects of the ten predictor variables on consumer group species richness, we found that litter mass clearly dominated the models by affecting all consumer groups. While species richness of ants, cockroaches, beetles, crickets and spiders increased strongly with litter mass, centipedes, millipedes, woodlice, termites and harvestmen were rather weakly affected. The strongest effect of plant species richness was an increase in harvestmen species richness. Soil pH had a mixture of weak positive and negative effects, for example increasing ant and beetle richness, but decreasing cockroach and harvestmen richness. Among the stoichiometric parameters, nitrogen imposed mostly positive effects on species richness, which summed up to a rather strong increase of detritivore species richness with basal resource N concentration. Phosphorus had a negative effect on species richness of cockroaches, beetles and millipedes, but a positive effect on ant, woodlice, harvestmen and spider species richness. This led to rather strong effects on the different functional feeding guilds, whereby detritivores were slightly negatively affected but all other guilds and the overall invertebrate community were positively affected. Potassium was the only stoichiometric variable with exclusively positive effects on animal species richness. Interestingly, calcium had a strong negative effect on woodlice species richness, while not affecting species richness of any of the

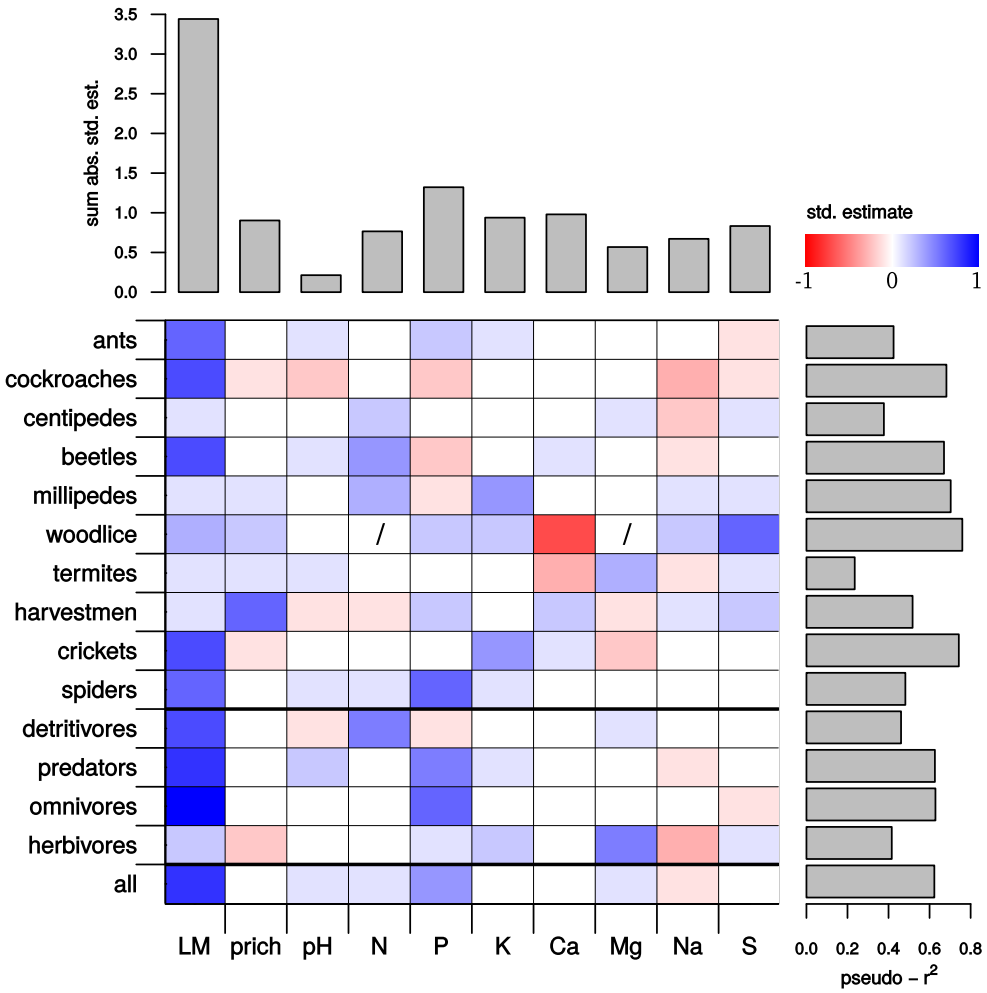

Figure 5.2 – **Model averaging results for macro-invertebrate species richness of tropical litter communities.** Range-standardized estimates for the effects of structural and stoichiometric basal resource traits on species richness of ten major taxonomic groups, the four functional feeding guilds and the overall data set. The estimates are averaged over a set of best candidate models (ΔAICc ≤ 4). Coloured rectangles in the grid show positive (blue) and negative (red) standardized estimates, with stronger colour depicting stronger effects. White rectangles depict absolute estimates of below 0.01 and "/" signs depict predictors that did not remain in any of the best candidate models. The upper bar graph shows summed absolute standardized estimates for each predictor for the ten taxonomic groups. The right bar graph shows a pseudo-r^2 value as a goodness-of-fit measure. Abbreviations: LM (litter mass) and prich (plant species richness). For simplicity, a negative effect of C:X is shown as a positive effect of the element X here.

functional feeding guilds. Magnesium and sodium both had a mixture of positive and negative effects on different animal groups, most strongly affecting herbivore species richness. Sulphur, finally, had mostly positive effects, with the increase in woodlice species richness being the strongest effect. Finally, looking at the overall data set, the species richness model exhibited positive effects of litter mass, pH, N, P and Mg, while Na was the only element negatively affecting overall species richness.

Body mass-biomass relationship

When testing the effects of habitat structural and stoichiometric variables on consumer biomass density, we found that the biomass models were generally dominated by interactions between body mass and the structural and stoichiometric predictors, rather than by direct effects of these variables (Figure 5.3). The only taxonomic-group-specific model having intermediately strong direct effects on biomass was the model on termite biomass density, while also exhibiting strong interactions with body mass. Some interactions of body mass with the structural and stoichiometric variables were especially important. In particular, body mass interacted very strongly with nitrogen and potassium in their effects on termites (strong positive interaction of M*N), and millipedes (strong negative interaction of M*K). Sulphur and body mass also interactively affected several taxonomic groups, highlighting the importance of this element for the body mass-biomass relationship of consumer communities. The summed absolute estimates of body mass with the three structural predictors were also dominated by single strong effects. The separate taxonomic-group-specific biomass models had a high proportion of variance explained (mean pseudo-r^2 of 0.82), with the cricket biomass model having the best (0.93) and the termite biomass model having the weakest fit (0.51).

When testing the specific effects of the habitat structural and stoichiometric variables on the biomass densities of our consumer groups, we found that, in contrast to its dominance in the species richness models, litter mass had many weak positive direct effects, and only one stronger interaction with body mass (on termite biomass). Plant species richness had a weak direct positive effect on harvestmen biomass and a slightly stronger positive interaction with woodlice body mass. As in the species richness models, pH did not have any strong effects. When testing the effects of the stoichiometric variables, we found that nitrogen had both a positive direct and an interactive effect with body mass on termite biomass. It furthermore exhibited a positive interaction with body mass on ant biomass. Compared to the species richness models, phosphorus had only minor importance in the biomass models, with just the beetle model exhibiting a moderately positive interaction of P with body mass. Potassium also exhibited the above-mentioned very strong negative interaction with body mass in millipede biomass. Calcium had a direct positive effect on woodlice biomass and a stronger direct negative effect on termite biomass. As in

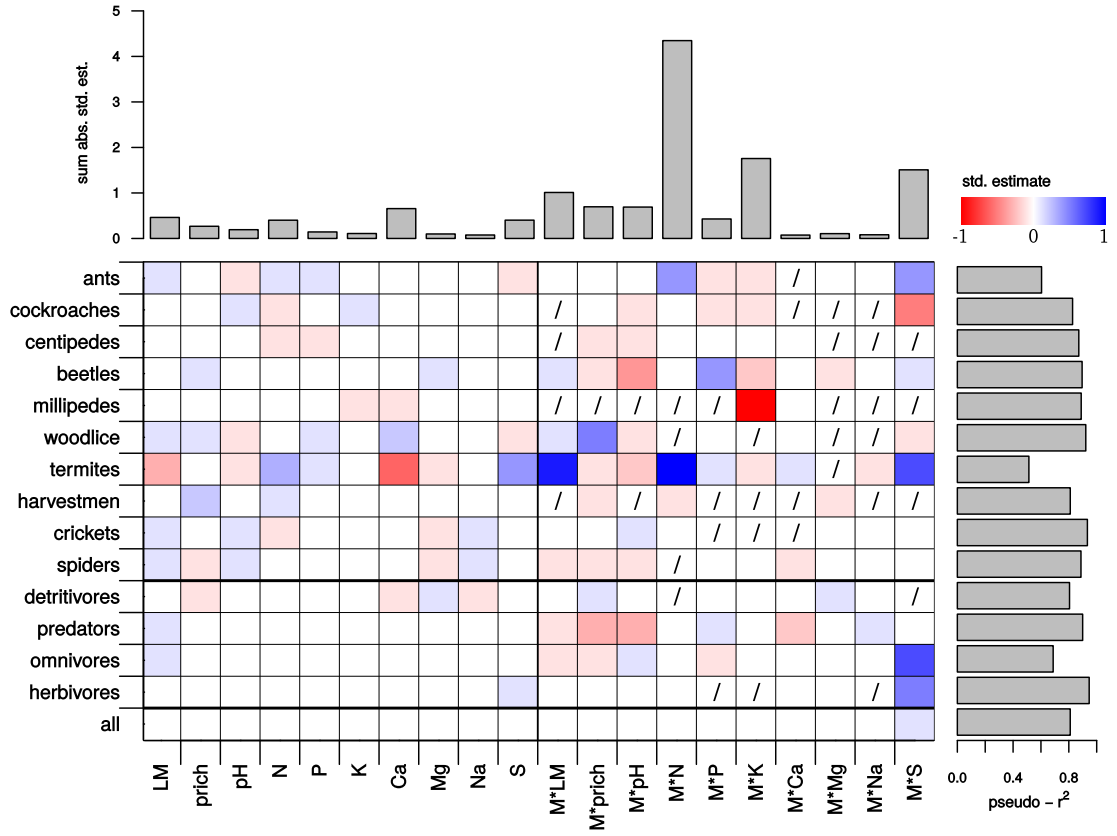

Figure 5.3 – Model averaging results for the body mass-biomass relationship of tropical litter macro-invertebrates. Range-standardized estimates for the effects of population-averaged body mass (M), as well as structural and stoichiometric basal resource traits and the M*trait interactions on population biomass of ten major taxonomic groups, the four functional feeding guilds and the overall data set. The estimates are averaged over a set of best candidate models (ΔAICc $\leq$ 4). Coloured rectangles in the grid show positive (blue) and negative (red) standardized estimates, with stronger colour depicting stronger effects. White rectangles depict absolute estimates of below 0.01 and "/" signs depict predictors that did not remain in any of the best candidate models. The upper bar graph shows summed absolute standardized estimates for each predictor for the ten taxonomic groups. The right bar graph shows a pseudo – r^2 value as a goodness-of-fit measure. Abbreviations: LM (litter mass) and prich (plant species richness). For simplicity, a negative effect of C:X is shown as a positive effect of the element X here and similarly, a negative interaction of C:X with M is shown as a positive M*X interaction. The absolute standardized estimates of M*K on millipede biomass (1.56) and of M*N on termite biomass (3.93) are the only values above 1 and therefore set to the darkest red and blue for simplicity.

the species richness models, magnesium and sodium had only very weak effects in the biomass models. Sulphur, finally, exhibited several strong interactions with body mass in the biomass models that led to the omnivore and herbivore models exhibiting a strong positive interaction of sulphur and body mass. Interestingly, the biomass model of the complete animal data set had a strongly reduced number of important effects with only the M*S interaction exhibiting a weak positive impact on overall biomass, which might be driven by the positive interactions of the ant and termite groups that present a remarkable proportion of the overall populations in the data set (see Table 9.1).

Contrasting species richness and biomass density responses

When comparing the species richness and biomass models, it is important to keep in mind that the two model sets deal with a different number of observations (32 site-averages for the species richness models and a much larger number of populations on these sites for the biomass models, see Table 9.1) and predictor variables (only direct effects of predictor variables in the species richness models, but interactions with body mass in the biomass models). This means that, although we cannot make concrete generalisations about the importance of effects between the two community response variables, the sign of effects as well as the relative importance of variables within models can still be compared among the two community responses.

While the taxonomic-group models on species richness were dominated by positive effects (71%) of higher stoichiometric availability, higher litter mass, pH and plant species richness, with fewer and overall weaker negative effects (29%), the biomass models exhibited a rather balanced ratio of positive to negative direct effects (44% and 56%, respectively). The strong role of litter mass and phosphorus in the species richness models was not reflected by the biomass models where, apart from a few strong single effects, sulphur dominated through its interactions with body mass. Depending on the consumer group and predictor variable in focus, there were cases where both species richness and biomass density were affected, cases where only one of them or none of the two was affected. Additionally, when both community response variables were affected, we found that the sign of species richness and biomass responses was matching in some cases and opposing in other cases. Specifically, increasing phosphorus concentration increased species richness and biomass density in ants, whereas higher nitrogen concentration decreased harvestmen species richness, but increased their biomass density. Furthermore, increasing Mg concentration showed a double-negative effect decreasing both species richness and biomass density of crickets. In contrast, higher potassium concentration increased millipede species richness, but decreased their biomass density. These results demonstrate that there is a variety of response patterns exhibited by consumer species richness and biomass density in response to varying resource stoichiometry and habitat

structure that calls for a mechanistic explanation.

5.4. Discussion

Our analysis of tropical litter macro-invertebrate communities indicates that consumer diversity and biomass density are both affected by several habitat structural and stoichiometric parameters of the local leaf litter and their interactions with body mass. Extending the approach of Ott *et al.* (2014a) from temperate forest systems, we found that macro-invertebrate taxa differed strongly in which habitat-structural and stoichiometric parameters they responded to, as well as in the direction and magnitude of their responses. While litter mass and P concentration had the strongest effect on consumer diversity, consumer biomass density was most heavily affected by interactions of population-averaged body mass with the other predictors; the latter result confirming previous findings from temperate forest floors (Ott *et al.*, 2014a,b). Our analyses provide support for all tested hypotheses. However, many predictors only affected either diversity or biomass density, or even had opposing effects on these two characteristics of consumer communities. In the following, we describe these patterns and relate them to potential underlying mechanisms. We discuss the tested hypotheses and compare the stoichiometric and habitat-structural effects on diversity and biomass density.

The ecosystem size hypothesis

The ubiquitous increase in species richness with increasing litter mass is in accordance with the ecosystem size hypothesis which posits that larger habitats can sustain higher species numbers (Post *et al.*, 2000; Post, 2002; Brose & Martinez, 2004; Kaspari & Yanoviak, 2009). Even though the strength of this effect differed between taxonomic groups, our results suggest that, across trophic groups, tropical consumer species richness increases with habitat size and basal resource mass. This is in line with results from tropical forest floors in Panama, where higher soil horizon dry mass also resulted in higher arthropod diversity (Sayer *et al.*, 2010). While other studies have shown arthropod density to increase with litter mass and depth (Yang *et al.*, 2007; Kaspari & Yanoviak, 2009), such responses have not been found for arthropod diversity in the tropics. Aside from the diversity effects in our study, litter mass also had direct positive effects on biomass density across several taxonomic groups. However, the interactions with body mass in spiders (negative), woodlice and beetles (positive) reveal differences between species of contrasting body size. For example, increasing litter mass appears to more strongly affect larger beetles yet smaller spiders. Termites exhibited the exact opposite pattern to spiders, whereby their biomass directly decreased but large-bodied species were more heavily affected by increasing litter mass. Such allometric differences were largely

absent in the temperate forest systems studied by Ott *et al.* (2014a), suggesting a higher importance of litter mass in tropical systems, which might be driven by the generally lower litter depth in our tropical, compared to their temperate forest sites (unpublished data). Our data therefore largely support the ecosystem size hypothesis (Post *et al.*, 2000; Post, 2002; Brose & Martinez, 2004; Kaspari & Yanoviak, 2009), and highlight the higher importance of litter mass for tropical versus temperate communities and a greater importance for consumer diversity than their biomass density. This finding suggests that, overall, tropical consumer diversity might be mainly driven by a heterogeneity-dependent species-area relationship, rather than being bottom-up controlled by nutrient availability, in which case consumer biomass would be more strongly affected.

The role of plant species richness

While it is under debate whether and how litter and plant diversity affect arthropod diversity (Brose, 2003; Wardle *et al.*, 2006; Scherber *et al.*, 2010), in our tropical litter data set, plant species richness had a positive effect on the diversity of at least some taxonomic groups (millipedes, termites, woodlice and harvestmen). Furthermore, plant species richness had positive direct effects (e.g., on harvestmen) and many negative interactions with body mass on biomass, resulting in increased biomass density but smaller consumers being more heavily affected by higher plant species richness. Woodlice were the only taxonomic group where large-bodied species were more heavily affected by higher plant species richness, along with an increase in biomass with increasing plant species richness. This result is directly comparable to temperate litter communities, where large-bodied woodlice were also more strongly affected by higher litter diversity (Ott *et al.*, 2014a). The negative interactions of plant species richness and body mass for the overall predator and omnivore data sets might be explained by habitat heterogeneity being more important for small species better able to move within the dense litter structures. In contrast, large consumers are generally more mobile and might rather utilize the litter surface, therefore being less constrained by local habitat structure.

The role of pH

The seemingly idiosyncratic response of different taxonomic groups to pH might reflect the response of decreasing fungal and increasing bacterial growth to increasing pH (Rousk *et al.*, 2009). The release of toxic elements at low pH (Rousk *et al.*, 2009) most likely imposes different constraints on consumer taxa, therefore leading to a diverse response pattern. However, the positive effect of increasing pH on the overall species richness in our study shows that at such low pH (4.1 – 4.8, mean 4.4), only a small increase leads to a positive effect on the overall consumer community, potentially due to microorganisms being released from their growth inhibition (Rousk *et al.*, 2009). The negative interaction

between body mass and soil pH in driving biomass densities (e.g., in spiders) could be explained by small-bodied species being more strongly constrained by soil acidity and the resulting effects of toxic elements, as their body surface is larger relative to their body volume compared to large-bodied consumer species. Alternatively, higher pH might more strongly affect small-bodied microbivore species that feed on bacteria as it increases bacterial biomass (Rousk *et al.*, 2009).

The growth rate and secondary productivity hypothesis

In accordance with the growth rate (Elser *et al.*, 2000b; Sterner & Elser, 2002) and secondary productivity hypothesis (Kaspari & Yanoviak, 2009), we found phosphorus to be a strong predictor of arthropod diversity. While species richness of some taxonomic groups (cockroaches, beetles, millipedes), as well as detritivores, was negatively affected by increasing P concentration, the effect of P on species richness remained positive in the overall model. Again, this was also found by Sayer *et al.* (2010) in their study on forest-floor communities in Panama, where P concentration was found to best predict arthropod diversity together with Ca and Na (Sayer *et al.*, 2010). In contrast, the biomass-density response provided only limited support for the P-based hypotheses, with only beetles, termites (both positive), cockroaches and ants (both negative) exhibiting interactions of P with population-averaged body mass. While in temperate forests, arachnids and woodlice responded to higher P availability (Ott *et al.*, 2014a), the spiders in our tropical samples did not show this effect. However, woodlice exhibited a slight positive direct effect of P on biomass density, in line with former results of woodlice abundance increasing with % P in tropical forests (Kaspari & Yanoviak, 2009). In the tropical communities that we sampled, P availability therefore affected consumer diversity much more strongly than their biomass density.

The structural elements hypothesis

The negative effect of Ca concentration on woodlice species richness and the lack of an effect on millipede species richness were very unexpected considering the dependence of these taxa on calcium, as suggested by the structural elements hypothesis (Kaspari & Yanoviak, 2009). While we did find a direct, positive effect of Ca on woodlice biomass, there was no interaction with population-averaged body mass. Millipedes even exhibited a negative direct biomass response to increasing Ca concentration. The positive woodlice response to Ca has also been found in other tropical (Kaspari & Yanoviak, 2009) and temperate (Ott *et al.*, 2014a) studies, whereas millipedes responded in temperate but not in tropical forests. These effects might point us to an important finding of our study; a factor that increases the growth and biomass of a consumer group can, but does not necessarily have to increase the diversity of this group and vice versa. Spider species

richness did increase with N concentration as predicted for their biomass by the structural elements hypothesis (Kaspari & Yanoviak, 2009). Spider biomass, however, was unaffected by N, with the interaction of N and body mass even excluded from the averaged model. Our data suggest that spider biomass in tropical communities might rather be driven by habitat structural variables than by stoichiometric parameters. Together, our analyses only partially support the structural elements hypothesis.

The sodium shortage hypothesis

In contrast to the predictions of the sodium shortage hypothesis (Kaspari *et al.*, 2009), sodium concentration did not increase termite or ant species richness or biomass density, but had a positive effect on woodlice species richness, whose biomass density has also been found to be controlled by Na in temperate forests (Ott et al. 2014a). For termites, small-bodied species were more strongly affected by higher Na concentration. Additionally, we found weak direct effects of sodium on cricket and spider biomass, which is in line with former research on tropical litter communities where sodium increased arthropod abundance (Sayer *et al.*, 2010). Overall, our results suggest Na to only be limiting for certain taxonomic groups of tropical litter arthropods.

The role of potassium

Our analysis indicated that potassium positively affects species richness in many taxonomic groups. As potassium is enriched in fungi (Sayer *et al.*, 2006), high potassium concentrations could point to higher fungal biomass in the leaf litter. Certain arthropod taxa consume such fungal biomass leading to higher potassium concentrations in their gut (Gist & Crossley, 1975). This mechanism is facilitated by coprophagy, which is relatively common in millipedes (McBrayer, 1973) and woodlice (Richardson & Araujo, 2015), two of the groups showing increased species richness with higher resource potassium. Among several weak negative interactions, there was an especially strong negative interaction between potassium and body mass on millipede biomass which could be explained by strong facilitation of small-bodied millipedes. Therefore, small-bodied species might be favoured by K through its high concentration in fungal biomass (Sayer *et al.*, 2006), which might be more easily accessible for smaller animals as their ability to move within dense decomposing litter structures might be higher.

The role of sulphur

Sulphur content has previously been related to enhanced nutritional quality of leaf litter (Kaspari & Yanoviak, 2009) and could explain the increased species richness in five taxonomic groups in response to increased sulphur concentration. Additionally, five taxonomic groups and two of the functional feeding guilds (omnivores and herbivores)

exhibited interactions of body mass with litter S concentration. The strong positive interaction of S with body mass in termites could be explained by higher plant nutritional value indicated by increased S content due to S-rich defence structures (Bloem *et al.*, 2005; Kaspari & Yanoviak, 2009). Sulphur might therefore be a good indicator of high-quality litter resources, at least for consumer groups that are not deterred by the S-based fungicidal plant defence structures. The resulting stronger effect of S on large-bodied termite species could thus be explained by these larger consumers being less constrained by fungicidal defence structures and the resulting effects on fungal biomass.

The role of magnesium

We found a strong increase in termite species richness in response to elevated Mg concentration. Additionally, Mg increased detritivore biomass and there was a stronger impact of Mg concentration on large-bodied detritivores. In a recent study on decomposition across biomes (Makkonen *et al.*, 2012), Mg was among the best predictors for the performance of this important ecosystem process. In the tropical litter systems investigated in this study, Mg might facilitate decomposition through higher detritivore biomass, body mass and additionally their species richness. This mechanism could be mediated by detritivore diversity affecting decomposition rates (Gessner *et al.*, 2010), although there is some debate on such results being driven by identity rather than diversity effects (Vos *et al.*, 2011).

The role of nitrogen

Aside from the largely positive effects of nitrogen on the species richness of five taxonomic groups, detritivores and the overall data set, N also interacted with population-averaged body mass exhibiting stronger effects of increasing N concentration on large-bodied compared to small-bodied termites and ants. This result could indicate a nitrogen facilitation of population biomass in large compared to small species within these taxa (Ott *et al.*, 2014b). In their temperate data set, Ott *et al.* (2014a,b) also found N to interact with body mass in driving biomass densities, although their data set did not include ants or termites. These results support the importance of nitrogen for heterotrophs consuming both detritus and animal tissue, as N content increases along the food chain from autotrophs to heterotrophs (Fanin *et al.*, 2013), as well as within heterotrophs with increasing trophic level (Fagan *et al.*, 2002).

Contrasts between diversity and biomass responses

While our ability to make direct, quantitative comparisons between the diversity and biomass-density models (e.g., comparing the effect sizes of certain parameters) is somewhat limited due to variability in sample size, we were still able to draw out general

striking patterns when interpreting the results of our joint analysis of both community characteristics. Ten taxonomic groups were tested for their response to variation in ten predictor variables (100 combinations). In 22% of these 100 tested combinations of predictor variables and taxonomic consumer groups, neither diversity, nor biomass density were affected, while in all other cases (78%) at least one of the two community response variables was impacted. However, we found many different response patterns ranging from double positive and double negative effects to opposing effects (one positive, the other negative) and also cases where change in a predictor variable altered one, but not the other community response variable.

In order to shed light on the potential mechanisms underpinning these various community responses, we developed a conceptual framework (Figure 5.4) that explains variable patterns in consumer diversity and biomass density responses. We assume a saturating response of biomass density and a hump-shaped response of diversity to increasing availability of a limiting resource (or more favourable habitat-structural parameters) (Figure 5.4, blue and red lines, respectively). As such, consumer biomass would monotonously increase with increasing availability of a limiting resource, whereas species richness would increase towards an optimum at the level of balanced consumer needs and resource availability but decrease towards higher and lower availability (Klausmeier *et al.*, 2004). Thus, when resource availability increases beyond consumer needs, consumer biomass might still increase, but diversity would decrease due to lower potential of species to coexist (Hillebrand & Lehmpfuhl, 2011) and stronger competition leading to competitive exclusion (Figure 5.4, phases I, II and III). At lower resource availability or at low habitat suitability, small improvements should therefore lead to parallel positive effects of consumer diversity and biomass density (Figure 5.4, phase I). Such parallel positive effects are not very surprising given that most of these tropical consumer groups are likely to be rather strongly constrained by low availability of the nutrients they depend on (Elser *et al.*, 2000a; McGroddy *et al.*, 2004). Therefore, increases in resource quality and habitat suitability are likely to facilitate biomass production via bottom-up forces. At the same time, this should lead to a more balanced ratio of consumer demand and resource supply (Klausmeier *et al.*, 2004), triggering higher diversity through increased potential for species coexistence (Figure 5.4, phase I) (Hillebrand & Lehmpfuhl, 2011). When reaching a balanced state of consumer demand and resource supply, consumer biomass would then further increase with increasing resource quality, but the diversity response would level out (Figure 5.4, phase II). Finally, when moving beyond the balanced state, consumer diversity would therefore decrease while biomass density could still monotonously increase with increasing resource supply (Figure 5.4, phase III). This conceptual framework explains patterns found across 80% of our taxonomic consumer groups (all except centipedes and millipedes) and in 27% of the combinations of predictor

variable and consumer group where at least one of the community response variables was impacted by the respective predictor variable.

Effect patterns that our framework cannot explain are potentially caused by simultaneously acting forces such as toxicity and allometric changes. As such, one possible explanation for decreasing biomass and increasing diversity would be the facilitation of small-bodied consumers. In this case, diversity could increase with small-bodied species coming in, but the higher metabolic demand of these small-bodied consumers would lead to a decrease in consumer biomass. Where higher elemental availability leads to parallel declines in diversity and biomass, the concentration of the focal element might be too high and therefore toxic for the respective consumer group. Alternatively, high elemental availability could lead to high population densities of competing consumer groups, resulting in the competitive exclusion of certain species. Thus, depending on the given combination of resource and consumer group, we would not expect a positive response of consumer diversity or biomass to increasing resource availability as this concept only applies to limiting resources and habitat parameters. Furthermore, although consumers are obviously limited by multiple factors in such tropical ecosystems (Sperfeld *et al.*, 2012), not all of these resources would necessarily have to trigger the diversity and biomass response patterns expected by our framework as consumers should not be limited by all possible resources but rather by a combination of a set of important factors. Taking into account these considerations, our conceptual framework successfully explains consumer responses to changing availability of limiting resources in tropical consumer communities.

Conclusions and future directions

In conclusion, our study on tropical macro-invertebrate responses to varying habitat structure and resource stoichiometry highlights the importance of a variety of stoichiometric and habitat-structural parameters for determining tropical litter arthropod consumer diversity and biomass density. All tested hypotheses received partial support, with different taxonomic groups and functional feeding guilds limited by different combinations of stoichiometric and habitat-structural variables. Our results confirm previous findings from temperate systems that consumers in leaf litter communities are constrained by multiple parameters rather than by single limiting elements. However, which variables have the strongest impact on which taxonomic group differs between biomes. Our analyses demonstrate that consumer diversity and biomass can exhibit a diverse array of responses to varying availability of different resources, which raises questions about the underlying mechanisms of such variable responses of consumer-community characteristics. Consequently, we introduce a conceptual framework that successfully explains diversity and biomass density responses found in 80% of the studied

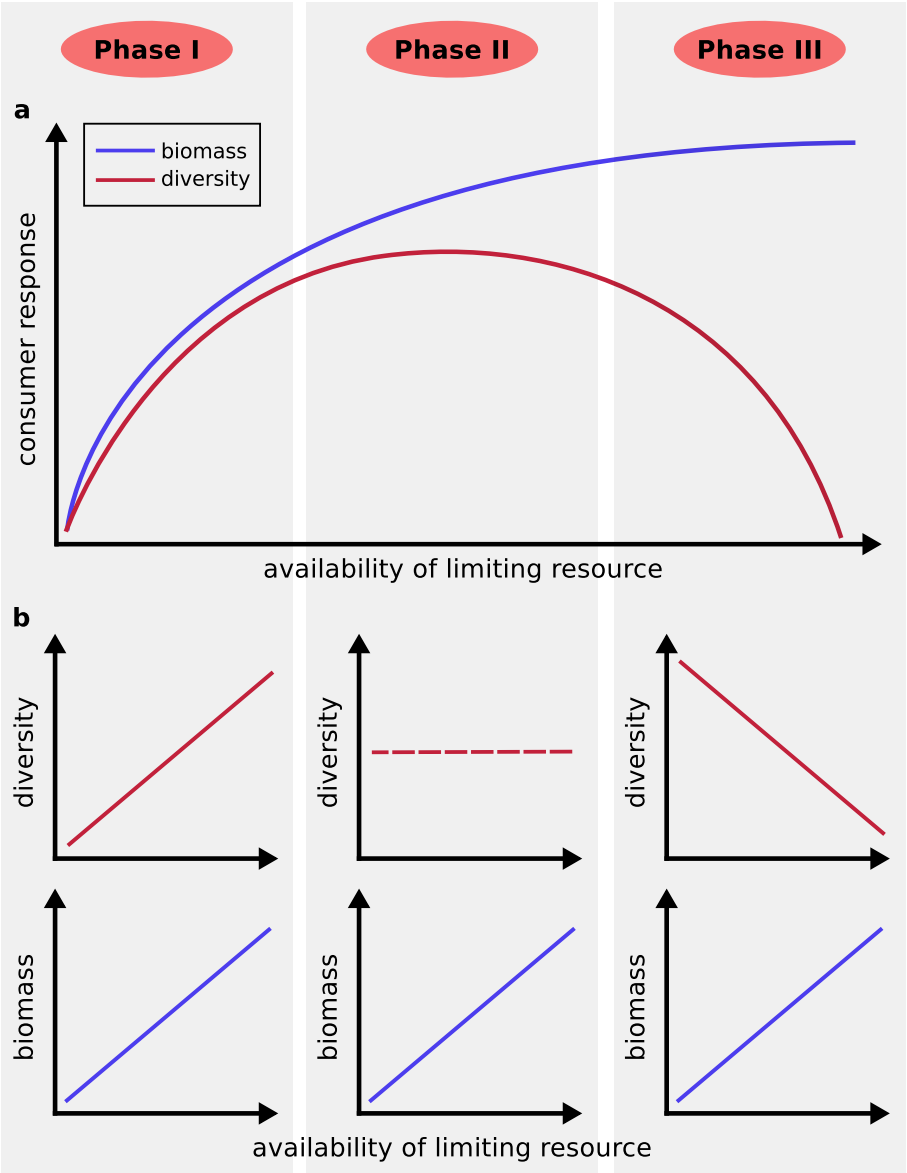

Figure 5.4 – Conceptual framework explaining three distinct response patterns of consumer diversity and biomass density to increasing resource availability. Hypothesized consumer response in diversity (red) and biomass (blue) to increasing availability of a limiting resource (a) and the resulting response patterns (b). Phase I shows a parallel positive response of diversity and biomass, phase II shows an increase in biomass, but no substantial change in diversity and phase III shows opposing effects with decreasing diversity but increasing biomass.

consumer groups. Thus, our study highlights promising directions for future research such as the simultaneous investigation of diversity and biomass-density responses in different biomes to assess the applicability of our conceptual framework across ecosystem types. Our study, therefore, represents a comprehensive extension of existing approaches using ecological stoichiometry in community-level consumer-resource research.

Acknowledgments

We thank Megawati, Rizky Nazarreta, Keisha Disa Putirama, Rosario Reza Valentino Lasse for assistance in the field and laboratory. Kara Allen and Bernhard Klarner provided pH and litter mass data, respectively. The Albrecht-von-Haller Intitute for Plant Sciences at Goettingen University conducted elemental analyses. This study was financed by the Deutsche Forschungsgemeinschaft (DFG) in the framework of the collaborative German-Indonesian research project CRC990. We also thank the village leaders, local plot owners, PT REKI, and Bukit Duabelas National Park for granting us access to and use of their properties. P.W. and D.O. acknowledge funding in the scope of the BEFmate project from the Ministry of Science and Culture of Lower Saxony. U.B. gratefully acknowledges the support of the German Centre for integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig funded by the German Research Foundation (FZT 118). This study was conducted using organisms collected based on Permit No. 2695/IPH.1/KS.02/XI/2012 recommended by the Indonesian Institute of Sciences (LIPI) and issued by the Ministry of Forestry (PHKA).

Part III.

General discussion

Chapter 6.

Synthesis

6.1. Synopsis

Earth's ecosystems are complex entities of organisms and their biotic and abiotic environment. To study the structure and functioning of such systems, several key drivers of ecological processes have been proposed. Body size has long been acknowledged to be a driving factor of biological and ecological processes across organisational scales affecting individual biological rates and interactions between organisms (Peters, 1983). Specifically, an organism's body mass affects its metabolic rate, the rate of energy uptake, transformation and allocation (Brown *et al.*, 2004). Furthermore, organism biomass, as well as the transfer of matter and energy through ecological networks, are tightly coupled to elemental stoichiometry of the organism and interacting trophic compartments (Sterner & Elser, 2002). When trying to understand the impacts of anthropogenic activities on natural ecosystems, it therefore seems imperative to take these key characteristics of individuals, populations and communities into account. Over the past decades, considerable advances have furthered our understanding of ecological processes in these complex systems. However, although a lot of research is being conducted on these core drivers of ecological processes, comprehensive attempts to jointly assess their impacts on ecosystem functioning across trophic levels are still scarce.

In the research chapters of this thesis, I investigated how body mass, metabolism and ecological stoichiometry can be jointly studied to gain a deeper understanding of ecological processes and especially of ecological responses to anthropogenic alteration of natural ecosystems. Specifically, I first reviewed previous research on body size and found that, despite their importance for many ecosystem processes and their overwhelming diversity and biomass, insects are underrepresented in body-size research (Chapter 2). I discussed research on allometric relationships such as the metabolic theory of ecology and recent advances on the integration of size- and non-size related information in the study of insect movement and behaviour and their effects on trophic interactions. Building on this knowledge base, in Chapter 3, I studied how land-use driven alterations of litter

macro-invertebrate communities affect ecosystem functioning across several systems of differing land-use intensity. Using metabolic- and food-web theory, I developed whole-community energy flux as a measure of multitrophic ecosystem functioning that can easily be calculated for sampled animal communities. Additionally, I found that the land-use driven loss in species richness lead to a severe reduction in multitrophic ecosystem functioning. In Chapter 4, I investigated multitrophic consumer responses to changing resource quality. In order to test three distinct hypotheses on consumer community responses, I altered the energy flux calculations from the previous chapter and calculated consumer feeding rates in response to varying resource quality, based on metabolic demand and assimilation efficiency. I found that, across trophic levels, consumer communities increased consumption in response to low-quality resources. Finally, I expanded the stoichiometric approach to investigate effects of multiple stoichiometric and habitat structural parameters on litter macro-invertebrate consumer diversity and biomass density (Chapter 5). I tested a set of distinct hypotheses and found that tropical consumers were co-limited by several parameters. Consequently, I synthesised the observed response patterns of contrasting diversity and biomass responses into a conceptual framework that explained patterns found in the vast majority of the tropical consumer groups.

6.2. Discussion

While body size has received a lot of attention in ecological research due to its implications for animal physiology and ecology, much of this research has focused on vertebrates and mammals (Damuth, 1981; Calder, 1983; Peters, 1983; Brown *et al.*, 2004). In Chapter 2, I reviewed existing research on body size with special attention to insect ecology. I found that, although insects have been underrepresented in early body-size research, more recently, they have been more intensively studied. Among other reasons, this development can be related to technological advances, for example in the field of insect telemetry (Kissling *et al.*, 2014), and growing availability of high-resolution data sets from empirical studies; for example on insect metabolic rates (Ehnes *et al.*, 2011) or functional responses (Kalinkat *et al.*, 2013). I payed special attention to the effect of body size on insect movement and behaviour as these two aspects of individual biology have far-reaching consequences for consumer-foraging success and thus determine the outcome and strength of trophic interactions. This relationship between individual-level physiological and behavioural processes and trophic interactions provides an important link that enables scaling up across levels of organisation from individuals to populations, communities and the flux of matter and energy through ecosystems. Thereafter, consumer body-size effects on prey-encounter rates seem to be driven by detection ability and temporal resolution of the consumer sensory system. Furthermore, while previous research on the integration

of allometry and functional morphology has mainly investigated animal migration and dispersal (Sacchi & Hardersen, 2012; Barnes *et al.*, 2015), similar research is needed for burst speed and acceleration potential because of their importance for foraging success. Insects allow extensive investigation of such topics as they occupy nearly all ecosystem types and exhibit various feeding modes. Recent advances in automated tracking methods will be crucial for further investigation of the relationship between individual movement and behaviour and higher levels of ecological organisation (Dell *et al.*, 2014a; Barnes *et al.*, 2015). By drawing on recent research on trophic interactions and the structure and functioning of ecological networks (Naisbit *et al.*, 2012; Eklöf *et al.*, 2013; Boukal, 2014), I furthermore discussed research on important non-size effects and concluded that including other parameters in addition to body size will improve the accuracy of ecological predictions. Thus, in order to develop more powerful ecological theory, size- and non-size effects such as temperature, phylogeny, stoichiometry and animal personality should be integrated into future approaches. In conclusion, because of their large body-size range, the diversity of feeding and movement types and their importance for ecological processes on the global scale, insects are an ideal group for further research on size and non-size effects on trophic interactions.

In Chapter 3, I aimed to develop a framework allowing to calculate multitrophic ecosystem functioning across different ecosystems. Integrating metabolic theory (Brown *et al.*, 2004), previous advances in the field of food-web theory and the energetic view of ecosystem processes (de Ruiter *et al.*, 1993), I developed a measure of whole-community energy flux. This measure uses information on metabolic demand of consumer communities, network topology, assimilation efficiency, feeding preferences and energy loss to higher consumer levels. By combining individual-level data on metabolic rates with feeding-guild specific values for assimilation efficiency and consumer preferences, I was able to calculate energy flux across all present trophic levels. In contrast to earlier approaches, I used the metabolic demand rather than the biomass of consumers, as I was particularly interested in capturing the flux of energy through the ecological network. Therefore, I specifically assessed ecological processes instead of pools or stocks in order to study whole-ecosystem functioning (Ulanowicz, 2004). To test my novel measure of ecosystem functioning in complex, real-world ecosystems, I chose to investigate biodiversity and ecosystem functioning responses to anthropogenic land use in tropical lowland rainforest and a range of agriculturally used systems with varying land-use intensity, namely jungle rubber, rubber and oil-palm plantations. First, I established a consistent decline in species richness, density and biomass of the investigated litter macro-invertebrate communities from forest to oil-palm systems. This decline is directly comparable to reduced litter-ant diversity and abundance (Fayle *et al.*, 2010) as well as reduced bird and butterfly diversity (Koh & Wilcove, 2008) comparing forest and oil-palm communities. Detailing my analyses

for four functional feeding guilds provided clear indication of predators to be most heavily affected by land use, which might be explained by relatively higher extinction risk related to species of higher trophic levels (Purvis *et al.*, 2000). Second, I found that, in addition to these community responses, the summed metabolic demand of the macro-invertebrate consumer communities decreased from forest to oil-palm systems. Consequently, using the novel method, I calculated energy flux between the trophic compartments of the communities and constructed energy networks for the four land-use systems, depicting the differences between biomass and energy flux-responses to anthropogenic land use. I found that, while biomass did not decrease for all consumer feeding guilds from forest to oil palm, all guilds exhibited decreased energy flux in oil-palm systems. Thus, although stocks of biomass are often used in biodiversity ecosystem functioning research (Hooper *et al.*, 2005; Duffy *et al.*, 2007), they may not be an ideal proxy for the processing of energy and matter through ecological networks. Finally, I tested species-richness effects on whole-community ecosystem functioning (BEF relationships). The relationship was steepest in oil-palm communities, suggesting that in these highly-intensified systems any loss in species richness will lead to a higher loss in ecosystem functioning, compared to other land-use systems. A potential reason for this relatively high loss in function with decreasing species richness in oil palm plantations is the low functional redundancy found in these agriculturally intensified systems (Mumme *et al.*, 2015). Further analysis revealed that the relationship of species richness and ecosystem functioning was strongly dependent on the trophic group in focus. This has implications for future research on BEF, such as the need to assess BEF relationships across trophic groups instead of focusing on single trophic levels when trying to assess whole-community relationships (Hooper *et al.*, 2005). The whole-community energy flux framework developed in this chapter is a highly versatile measure of multitrophic ecosystem functioning and we have only started to test its application in different settings. While it clearly has the potential to be parameterised in many aspects, the application in Chapter 3 was more of a null-model approach. While working on Chapter 4, I became aware of a recently compiled database of assimilation efficiencies and was able to include that for the calculation of food-nitrogen driven assimilation efficiencies. To further optimize the approach, it seems promising to make extensive use of such databases on assimilation efficiency and feeding preferences for future application of the framework. In conclusion, this chapter provides strong evidence for the negative impact of anthropogenic land-use change on biodiversity and ecosystem functioning. It highlights the importance of trophic complexity in research on ecosystem functioning and, finally, offers a comprehensive framework for the standardised assessment of whole-community energy flux as a measure of multitrophic ecosystem functioning across ecosystems.

In Chapter 4, I studied multitrophic responses of macro-invertebrate consumer

communities to varying resource quality, combining ecological stoichiometry theory with the energetic advances from the previous chapter. I tested three distinct hypotheses expecting H1) consumer stoichiometric shift, H2) avoidance or H3) compensatory feeding in response to low-quality resources. Specifically, I tested for effects of increasing resource C:N ratios on consumer C:N ratios, consumer biomass and consumer feeding rates and I additionally investigated consumer species richness responses. Across trophic levels, I found that consumer feeding rates increased, but that consumer stoichiometry and biomass were not significantly altered in response to decreasing resource quality, as indicated by increasing C:N ratios. While previous research on compensatory feeding has predominantly focused on herbivores and their autotrophic resources (Cruz-Rivera & Hay, 2000; Hillebrand *et al.*, 2009), I investigated the response of detritivores and predators to changes in the quality of their respective resources. My results suggest that compensatory feeding is much more common across the trophic spectrum than could be assumed based on previous studies. Aside from this insightful result, I found detritivore species richness to decline with decreasing resource quality. One potential explanation for this consumer-diversity decline is that, in order to increase their feeding rates to take up higher amounts of limiting elements in low-quality food, consumers must deal with excess nutrients. Physiological pathways dealing with such excess nutrients are diverse, but not equally distributed across consumer taxa (Anderson *et al.*, 2005; Frost *et al.*, 2005b). This limited ability of consumers to increase feeding rates could therefore potentially decrease consumer species richness in response to low-quality resources. A third important aspect of this chapter is the method applied to calculate consumer feeding rates based on varying resource stoichiometry. Building on the energetic advances of the previous chapter, I calculated consumer feeding rates based on metabolic demand and assimilation efficiency. While metabolic rates were again calculated from individual body masses, assimilation efficiencies were inferred from previously published relationships between food nitrogen content and assimilation efficiency (Pandian & Marian, 1986). Combining empirically measured individual-level data and literature-based parameterisation of assimilation efficiency, this method allows for the calculation of consumer feeding rates without having to laboriously measure them under field conditions. Additionally, this chapter makes use of the assessment of consumer and resource stoichiometry across trophic levels in a community context, while many previous studies have only measured basal resource stoichiometry (Kaspari & Yanoviak, 2009; Sayer *et al.*, 2010; Ott *et al.*, 2014a). The body stoichiometry of heterotrophic consumers might be less flexible than that of low-level autotrophic resources (Sterner & Elser, 2002; Persson *et al.*, 2010). However, there still are consistent changes of elemental content along the food chain and between the upper trophic levels (Fagan *et al.*, 2002; Martinson *et al.*, 2008). While focusing on higher-level consumer responses to the general availability of certain elements in their environment

or in the basal resources of the given ecosystem can provide useful information, future studies should therefore make sure to measure organism stoichiometry across all trophic levels present in the focal system. This would enable investigation of ecological impact of varying stoichiometric mismatch between consumer and resource, rather than just changing resource stoichiometry. Additionally, it would be very interesting to test if relating consumer responses to changing stoichiometric mismatch rather than just resource stoichiometry yields more realistic results when studying consumer-resource interactions. In conclusion, this chapter expands previous knowledge on consumer-community responses to changes in resource quality across trophic levels and facilitates future research in the area by presenting a method to indirectly assess consumer feeding rates in response to varying resource quality.

In order to widen the stoichiometric perspective on the relationship between resource stoichiometry and consumer communities, in Chapter 5, I investigated the effects of basal resource stoichiometry and habitat structure on consumer biomass density and diversity. Following recent advances from temperate forest systems that established the joint effects of metabolic theory and ecological stoichiometry theory on consumer population biomass density (Ott *et al.*, 2014b,a), I tested a set of specific hypotheses on consumer community responses to changing resource stoichiometry (as indicated by carbon:element ratios) and habitat structure using my tropical leaf-litter macro-invertebrate data set. In contrast to these earlier approaches, I additionally investigated consumer-diversity responses to changing basal resource stoichiometry and habitat structure. While there exist theoretical predictions on changing consumer diversity in response to changing resource stoichiometry (Klausmeier *et al.*, 2004; Cardinale *et al.*, 2009), empirical support, especially from terrestrial systems, is limited (Sayer *et al.*, 2010). In order to gain comparable results between the two community characteristics and at the same time account for the potential co-limitation of ecological processes by multiple limiting resources (Kaspari *et al.*, 2008; Sperfeld *et al.*, 2012), I used an information theoretic approach to rank stoichiometric and habitat-structural predictor variables according to their importance within multiple models rather than one best-selected model (Burnham & Anderson, 2002; Grueber *et al.*, 2011). Following this model averaging procedure, I detailed my analysis to test for the effects of seven stoichiometric and three habitat-structural parameters on the biomass density and diversity of ten major taxonomic consumer groups and the four functional feeding guilds already studied in Chapters 3 and 4. Additionally, in the biomass-density models, I allowed for interactions of the ten predictor variables with population-averaged body mass following the approach of Ott *et al.* (2014a,b). Using this standardised model averaging framework, I found the tropical consumer groups to be co-limited by many, rather than single limiting factors. This result confirms previous findings of consumer communities (Sperfeld *et al.*, 2012) and ecological processes

(Kaspari *et al.*, 2008) being co-limited by multiple parameters, rather than controlled by a single limiting factor (Von Liebig, 1840). I found support for all tested hypotheses and discussed similarities and differences between other temperate and tropical studies and my findings. Additionally, I discussed contrasting results between the consumer diversity and biomass-density responses. While litter mass and phosphorus had the strongest effects on consumer diversity across consumer groups, the consumer biomass-density models showed strong interactions of population-averaged body mass with stoichiometric variables, such as nitrogen, potassium and sulphur. However, different consumer groups showed a variety of response patterns to different stoichiometric and habitat-structural parameters. Interestingly, consumer biomass density and diversity of a given group did not necessarily respond in the same way (with the same sign) to changes in a given predictor variable; there were parallel and opposing effects, as well as cases where one community characteristic would respond and the other one would not. Consequently, in order to explain this diversity of response patterns, I developed a conceptual framework assuming a saturating response of biomass density and a hump-shaped response of consumer diversity to increasing availability of a limiting resource. This framework successfully explained response patterns found in 80% of the studied tropical taxonomic consumer groups. While a lot of research has been conducted establishing stoichiometry effects on abundance and biomass density of consumer communities (Mulder *et al.*, 2004; Kaspari & Yanoviak, 2009; Ott *et al.*, 2014b), similarly broad research on consumer diversity reponses, as conducted in this chapter, seems to be largely missing. Especially given the established relationship of species richness and body mass (Brown *et al.*, 2004) and the fact that stoichiometry can interact with body mass to affect consumer biomass density (Ott *et al.*, 2014b), investigating interactive effects of resource stoichiometry and consumer body mass on consumer diversity seems a logical next step. Testing the conceptual framework developed in this chapter across different ecosystems comprising variation in resource stoichiometry and consumer body size structure should yield further insight into the mechanisms underpinning diverse responses of consumer biomass density and diversity to varying resource stoichiometry and habitat structure. In conclusion, this chapter provides an extensive investigation of basal resource stoichiometric and habitat structural effects on complex, diverse consumer communities. I applied a state-of-the-art statistical approach to further our understanding of diverse response patterns in two important consumer community characteristics and finally merged my findings into the development of a conceptual framework explaining these response patterns, that is now available to be tested for its validity in other ecosystems.

6.3. Future directions

This thesis is based on major areas of ecological research such as the metabolic theory of ecology, ecological stoichiometry theory, food web theory, global change ecology, and the energetic view of ecosystem processes. Building upon important advances made in these areas over the past decades, my thesis represents a significant advance in our understanding of how body mass, metabolism and stoichiometry can be jointly used to assess ecological processes and ecosystem consequences of anthropogenic alterations of the biotic and abiotic environment. The energetic view of ecosystem processes, as inspired by early work of Lindeman (1942) and adopted by de Ruiter *et al.* (1993), initially enabled the development of whole-community energy flux as a comprehensive and flexible measure of multitrophic ecosystem functioning and a method to calculate consumer feeding rates in response to varying resource quality. Together with the application of the state-of-the-art information theoretic approach in the last chapter, adopting this energetic view was essential for achieving the presented research results. However, the findings presented in the research chapters of this thesis also open up important questions that should be addressed by future ecological research.

The research chapters of this thesis have demonstrated the importance of taking a multitrophic approach when trying to capture ecosystem-level processes. While I have strictly adhered to the multitrophic approach throughout this thesis, my analyses were restricted to macro-invertebrate communities of tropical leaf-litter systems. While such litter communities are highly diverse and span a range of trophic levels (Hättenschwiler *et al.*, 2005; Digel *et al.*, 2014), these macrofauna-communities strongly depend on soil mesofauna animal groups as their prey and, in turn, provide a resource base for higher consumer groups, such as birds, mammals, reptiles and amphibians, in these ecosystems. Widening the scope of my previous analyses by including several key-groups of higher and lower trophic levels would be a highly attractive next step. Comparing the results of such extended investigations to my initial findings and especially testing the generality of the presented patterns would be insightful and additionally enable tests of how useful smaller-level data sets are to gain understanding and develop ecological theory on higher-level processes.

Essentially, my method of calculating community energy flux is meant to be an easy-to-assess measure of multitrophic ecosystem functioning. In the initial test presented in Chapter 3, I calculated community energy flux based on a rather coarse level of network topology and trophic grouping. With the increased availability of more highly resolved food webs, one could test if assessing ecosystem functioning based on coarse trophic groups and network topology yields comparable patterns to using a more fine-scale level. Additionally, there could likely be differences in the required resolution for capturing real

patterns between ecosystem types. Thus, if aquatic consumers, on average, tended to be less specialised than terrestrial consumers (Shurin *et al.*, 2006), investigation of these ecosystems might require less well-defined trophic structure and network topology than their terrestrial counterparts to detect the important patterns in ecosystem functioning.

Community energy flux and consumer feeding rates are based on consumer metabolic rates, which are highly dependent on environmental temperature and body size (Brown *et al.*, 2004), as well as on assimilation efficiencies, which are also affected by temperature (Lang *et al.*, in preparation). While the research chapters of this thesis were restricted to lowland tropical ecosystems that did not exhibit large variation in ground temperature, temperature should have a strong influence on the developed measures of energy flux and consumer feeding rates. It would therefore be highly desirable to compare energy flux and feeding rates between communities of similar size structure, but different environmental temperature. As it might turn out to be rather difficult to find communities of similar size structure that are exposed to significantly differing environmental temperature, given the reported effects of temperature on body size (Gardner *et al.*, 2011; Sheridan & Bickford, 2011), this might be an ideal case for an ecological modelling study, where it will be straightforward to establish communities of similar size structure and expose them to different environmental temperature to assess resulting changes in energy flux. Such comparison would further improve the precision of predictions on ecosystem-functioning consequences of climate change and the resulting alterations of global surface temperatures.

My method of calculating whole-community energy flux is only one example of how to approach the assessment of energy and matter flux through ecological networks. In the introduction of this thesis, I have introduced a few major approaches made in this field over the past decades (de Ruiter *et al.*, 1993; Bersier *et al.*, 2002; Ulanowicz, 2004; Reuman & Cohen, 2005). It would be a promising future goal to compare these approaches and especially to test their ability to capture the flux of matter and energy that is actually happening in the ecosystems they are trying to describe. Thus, measuring the energy flux along the food chain of a few example communities in different ecosystem types, calculating different energy flux measures and comparing their ability to depict major patterns would be a worthwile future project.

In a recent article on the functional consequences of logging tropical rainforests, Ewers *et al.* (2015) found the contribution of invertebrates to major ecosystem functions dramatically reduced. However, at the same time, they reported the level of functioning to be rather unaffected and related this finding to the increased abundance of small mammals, amphibians and birds. While these results suggest an astonishing resilience of ecosystem functioning to anthropogenic alterations, they might conceal the dimension of consequences triggered by the high losses of invertebrate diversity and biomass, as the

authors point out. As, in their study, the authors have measured three specific ecosystem functions (decomposition, seed disturbance and invertebrate predation), there are most likely other important functions that were not taken over by the higher-level taxa that profited from logging. It would therefore be compelling to use my method of assessing whole-community energy flux to quantify changes in the energy transferred through the ecological networks before and after logging and, thus, potentially capture changes in ecosystem multifunctionality that could not be detected by measuring specific ecosystem processes.

In an experimental test on consumer metabolic-rate responses to changes in the stoichiometric quality of consumed resources, Jeyasingh (2007) found differences in the allometric scaling exponent between consumers fed stoichiometrically balanced versus imbalanced diets. In the research chapters of this thesis, I have already made a first step towards integrating non-size effects into formerly body-size dominated research areas (as suggested in Chapter 2) by using phylogenetic-group specific regressions for calculating consumer metabolic rates (Ehnes *et al.*, 2011). However, incorporating the effect of resource stoichiometry on consumer metabolism would certainly add to the predictive power of the presented measures for ecosystem functioning and consumer feeding rates. Additionally, this would be a highly welcome step to further integrate the different research areas presented in my thesis and provide a perfect example of how to jointly use body mass, metabolism and stoichiometry to assess ecological impacts in a changing environment.

Given the severe anthropogenic alteration of Earth's ecosystems and natural global processes, the ability to make predictions on further ecological impact of these alterations is of striking importance to protect global biodiversity and maintain ecosystem functioning rates crucial for the human population. Based on a diverse range of ecological theories and concepts and integrating across levels of ecological organisation, the research chapters and synthesis of my thesis represent an important advance in our understanding of ecological processes crucial for improving future ecological approaches. My thesis has successfully furthered our understanding of how body mass, metabolism and stoichiometry can be used to assess ecological impacts in a changing environment and, at the same time, revealed important areas of further exploration and future ecological research. Thus, my thesis highlights the importance of these drivers of ecological processes and stimulates future ecological research in order to mitigate the negative impact of anthropogenic domination on planet Earth.

Part IV.

References

Literature cited

Achard, F., Eva, H.D., Stibig, H.J., Mayaux, P., Gallego, J., Richards, T. & Malingreau, J.P. (2002) Determination of deforestation rates of the world's humid tropical forests. *Science* **297**, 999–1002.

Allen, A.P. & Gillooly, J.F. (2009) Towards an integration of ecological stoichiometry and the metabolic theory of ecology to better understand nutrient cycling. *Ecology Letters* **12**, 369–384.

Allen, K., Corre, M.D., Tjoa, A. & Veldkamp, E. (2015) Soil nitrogen-cycling responses to conversion of lowland forests to oil palm and rubber plantations in Sumatra, Indonesia. *PLoS ONE* **10**, e0133325.

Andersen, K.H., Beyer, J.E. & Lundberg, P. (2009) Trophic and individual efficiencies of size-structured communities. *Proceedings of the Royal Society B: Biological Sciences* **276**, 109–114.

Andersen, T., Elser, J.J. & Hessen, D.O. (2004) Stoichiometry and population dynamics. *Ecology Letters* **7**, 884–900.

Anderson, T.R., Boersma, M. & Raubenheimer, D. (2004) Stoichiometry: linking elements to biochemicals. *Ecology* **85**, 1193–1202.

Anderson, T.R., Hessen, D.O., Elser, J.J. & Urabe, J. (2005) Metabolic stoichiometry and the fate of excess carbon and nutrients in consumers. *The American Naturalist* **165**, 1–15.

Angilletta, M.J., Steury, T.D. & Sears, M.W. (1996) Temperature, growth rate, and body size in ectotherms: Fitting pieces of a life-history puzzle. *Integrative and comparative biology* **509**, 498–509.

Bährmann, R. (2008) *Bestimmung wirbelloser Tiere*, vol. 5. Spektrum Akademischer Verlag, 5 edn.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D. & Schmid, B. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* **9**, 1146–56.

Banašek-Richter, C., Bersier, L.F., Cattin, M.F., Baltensperger, R., Gabriel, J.P., Merz, Y., Ulanowicz, R.E., Tavares, A.F., Williams, D.D., de Ruiter, P.C., Winemiller, K.O. & Naisbit, R.E. (2009) Complexity in quantitative food webs. *Ecology* **90**, 1470–1477.

Barnes, A.D., Jochum, M., Mumme, S., Haneda, N.F., Farajallah, A., Widarto, T.H. & Brose, U. (2014) Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning. *Nature Communications* **5**, 5351.

Barnes, A.D., Spey, I.K., Rohde, L., Brose, U. & Dell, A.I. (2015) Individual behaviour mediates effects of warming on movement across a fragmented landscape. *Functional Ecology* **29**, 1543–1552.

Barton, K. (2015) MuMIn: Multi-model inference. *R package version 1.15.1* .

Bawa, K.S. (1990) Plant-pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics* **21**, 399–422.

Begon, M. (2006) *Ecology : from individuals to ecosystems*, vol. 4. Wiley-Blackwell, 4th edn.

Benke, A.C., Huryn, A.D., Smock, L.A. & Wallace, J.B. (1999) Length-mass relationships for freshwater

macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society* **18**, 308–343.

Berlow, E.L., Dunne, J.A., Martinez, N.D., Stark, P.B., Williams, R.J. & Brose, U. (2009) Simple prediction of interaction strengths in complex food webs. *Proceedings of the National Academy of Sciences* **106**, 187–91.

Berlow, E.L., Neutel, A.M., Cohen, J.E., De Ruiter, P.C., Emmerson, M., Fox, J.W., Jansen, V.A.A., Jones, J.I., Kokkoris, G.D., Logofet, D.O., Mckane, A.J., Montoya, J.M. & Petchey, O. (2004) Interaction strength in food webs: issues and opportunities. *Journal of Animal Behavior* **73**, 585–598.

Bersier, L.F., Banašek-Richter, C. & Cattin, M.F. (2002) Quantitative descriptors of food-web matrices. *Ecology* **83**, 2394–2407.

Binzer, A., Guill, C., Rall, B.C. & Brose, U. (2015) Interactive effects of warming , eutrophication and size-structure: impacts on biodiversity and food-web structure. *Global Change Biology* **22**, 220–227.

Blakemore, R.J. (2010) Cosmopolitan earthworms, an eco-taxonomic guide to the peregrine species of the world.

Bloem, E., Haneklaus, S. & Schnug, E. (2005) Significance of sulfur compounds in the protection of plants against pests and diseases. *Journal of Plant Nutrition* **28**, 763–784.

Bocock, K.L. (1963) The digestion and assimilation of food by Glomeris. *Soil organisms* (ed. J. Doeksen, J. van der Drift), pp. 85–91, North-Holland Publ. Co., Amsterdam.

Boersma, M., Aberle, N., Hantzsche, F.M., Schoo, K.L., Wiltshire, K.H. & Malzahn, A.M. (2008) Nutritional limitation travels up the food chain. *International Review of Hydrobiology* **93**, 479–488.

Borer, E.T., Seabloom, E.W. & Tilman, D. (2012) Plant diversity controls arthropod biomass and temporal stability. *Ecology Letters* **15**, 1457–1464.

Boukal, D.S. (2014) Trait- and size-based descriptions of trophic links in freshwater food webs: current status and perspectives. *Journal of Limnology* **73**, 171–185.

Brose, U. (2003) Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? *Oecologia* **135**, 407–413.

Brose, U. (2010) Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Functional Ecology* **24**, 28–34.

Brose, U., Jonsson, T., Berlow, E.L., Warren, P., Banasek-Richter, C., Bersier, L.F., Blanchard, J.L., Brey, T., Carpenter, S.R., Blandenier, M.F.C., Cushing, L., Dawah, H.A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M.E., Martinez, N.D., Memmott, J., Mintenbeck, K., Pinnegar, J.K., Rall, B.C., Rayner, T.S., Reuman, D.C., Ruess, L., Ulrich, W., Williams, R.J., Woodward, G. & Cohen, J.E. (2006) Consumer-resource body-size relationships in natural food webs. *Ecology* **87**, 2411–2417.

Brose, U. & Martinez, N.D. (2004) Estimating the richness of species with variable mobility. *Oikos* **105**, 292–300.

Brose, U., Martinez, N.D. & Williams, R.J. (2003) Estimating species richness: sensitivity to sample coverage and insensitivity to spatial patterns. *Ecology* **84**, 2364–2377.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789.

Buddle, C.M. (2010) Photographic key to the pseudoscorpions of Canada and the adjacent USA. *Canadian Journal of Arthropod Identification* **10**, 1–77.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference*. Springer, 2nd edn.

Byrnes, J.E.K., Gamfeldt, L., Isbell, F., Lefcheck, J.S., Griffin, J.N., Hector, A., Cardinale, B.J., Hooper, D.U., Dee, L.E. & Duffy, J.E. (2014) Investigating the relationship between biodiversity and ecosystem multifunctionality: Challenges and solutions. *Methods in Ecology and Evolution* **5**, 111–124.

Calder, W.A. (1983) Ecological scaling: mammals and birds. *Annual Review of Ecology and Systematics* **14**, 213–230.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., A.Wardle, D., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67.

Cardinale, B.J., Harvey, C.T., Gross, K. & Ives, A.R. (2003) Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecology Letters* **6**, 857–865.

Cardinale, B.J., Hillebrand, H., Harpole, W.S., Gross, K. & Ptacnik, R. (2009) Separating the influence of resource 'availability' from resource 'imbalance' on productivity-diversity relationships. *Ecology Letters* **12**, 475–487.

Cardinale, B.J., Srivastava, D.S., Emmett Duffy, J., Wright, J.P., Downing, A.L., Sankaran, M. & Jouseau, C. (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* **443**, 989–992.

Cebrian, J. (1999) Patterns in the fate of production in plant communities. *The American Naturalist* **154**, 449–468.

Centre for Land and Biological Resources Research (1993) *Hymenoptera of the world: an identification guide to families*. Research Branch, Agriculture Canada, Ottowa, Ontario.

Chown, S.L., Marais, E., Terblanche, J.S., Klok, C.J., Lighton, J.R.B. & Blackburn, T.M. (2007) Scaling of insect metabolic rate is inconsistent with the nutrient supply network model. *Functional Ecology* **21**, 282–290.

Chown, S.L. & Gaston, K.J. (2010) Body size variation in insects: a macroecological perspective. *Biological Reviews* **85**, 139–169.

Chu, H.F. (1949) *How to know the immature insects*. W. C. Brown Co., Dubuque, Iowa.

Cloudsley-Thompson, J.L. (1958) *Spiders scorpions centipedes and mites*. Pergamon Press Ltd.

Cohen, J.E., Pimm, S.L., Yodzis, P. & Saldaña, J. (1993) Body sizes of animal predators and animal prey in food webs.

Coleman, D.C. (2013) Soil biota, soil systems, and processes. *Encyclopedia of Biodiversity* (ed. S. Levin), vol. 6, pp. 580–589, Academic Press, 2nd edn.

Coley, P.D. & Barone, J.A. (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* **27**, 305–335.

Cross, W.F., Benstead, J.P., Frost, P.C. & Thomas, S.A. (2005) Ecological stoichiometry in freshwater benthic systems: recent progress and perspectives. *Freshwater Biology* **50**, 1895–1912.

Crutzen, P.J. (2002) Geology of mankind. *Nature* **415**, 23.

Cruz-Rivera, E. & Hay, M.E. (2000) Can quantity replace quality? Food choice, compensatory feeding, and fitness of marine mesograzers. *Ecology* **81**, 201–219.

CSIRO Division of Entomology (1991) *The insects of Australia*. Cornell University Press, Ithaca, New York, 2 edn.

Damuth, J. (1981) Population density and body size in mammals. *Nature* **290**, 699–700.

Darwin, C.R. (1859) *On the origin of species by means of natural selection; or the preservation of favoured races in the struggle for life*. John Murray, London.

Daufresne, M., Lengfellner, K. & Sommer, U. (2009) Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences* **106**, 12788–12793.

De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., Hampel, H., Denys, L., Vanhecke, L., Van der Gucht, K., Van Wichelen, J., Vyverman, W. & Declerck, S.A.J. (2012) Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecology Letters* **15**, 740–747.

de Ruiter, P.C., Neutel, A.M. & Moore, J.C. (1995) Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* **269**, 1257–1260.

de Ruiter, P.C., Van Veen, J.A., Moore, J.C., Brussaard, L. & Hunt, H.W. (1993) Calculation of nitrogen mineralization in soil food webs. *Plant and Soil* **157**, 263–273.

de Ruiter, P.C., Neutel, A.M. & Moore, J.C. (1994) Modelling food webs and nutrient cycling in agro-ecosystems. *Trends in Ecology & Evolution* **9**, 378–383.

DeFries, R.S., Foley, J.A. & Asner, G.P. (2004) Land-use choices: balancing human needs and ecosystem function. *Frontiers in Ecology and the Environment* **2**, 249–257.

Dell, A.I., Pawar, S. & Savage, V.M. (2011) Systematic variation in the temperature dependence of physiological and ecological traits. *Proceedings of the National Academy of Sciences* **108**, 10591–10596.

Dell, A.I., Bender, J.A., Branson, K., Couzin, I.D., de Polavieja, G.G., Noldus, L.P.J.J., Pérez-Escudero, A., Perona, P., Straw, A.D., Wikelski, M. & Brose, U. (2014a) Automated image-based tracking and its application in ecology. *Trends in Ecology and Evolution* **29**, 417–428.

Dell, A.I., Pawar, S. & Savage, V.M. (2014b) Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *Journal of Animal Ecology* **83**, 70–84.

Dell, A.I., Zhao, L., Brose, U., Pearson, R.G. & Alford, R.A. (2015) Population and community body size structure across a complex environmental gradient. *Advances in Ecological Research*, vol. 52, pp. 115–167.

DeLong, J.P. (2011) Energetic inequivalence in eusocial insect colonies. *Biology Letters* **7**, 611–614.

Dial, K.P., Greene, E. & Irschick, D.J. (2008) Allometry of behavior. *Trends in Ecology and Evolution* **23**, 394–401.

Díaz, S., Fargione, J., Chapin, F.S. & Tilman, D. (2006) Biodiversity loss threatens human well-being. *PLoS Biology* **4**, 1300–1305.

Dickinson, M.H., Farley, C.T., Full, R.J., Koehl, M.A.R., Kram, R. & Lehman, S. (2000) How animals move: an integrative view. *Science* **288**, 100–106.

Digel, C., Curtsdotter, A., Riede, J.O., Klarner, B. & Brose, U. (2014) Unravelling the complex structure of forest soil food webs: higher omnivory and more trophic levels. *Oikos* **123**, 1157–1172.

Digel, C., Riede, J.O. & Brose, U. (2011) Body sizes, cumulative and allometric degree distributions across natural food webs. *Oikos* **120**, 503–509.

Domenici, P. (2001) The scaling of locomotor performance in predator-prey encounters: From fish to killer whales. *Comparative Biochemistry and Physiology Part A* **131**, 169–182.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B.,

Schurr, F.M. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* **30**, 609–628.

Dossena, M., Yvon-Durocher, G., Grey, J., Montoya, J.M., Perkins, D.M., Trimmer, M. & Woodward, G. (2012) Warming alters community size structure and ecosystem functioning. *Proceedings of the Royal Society B: Biological Sciences* **279**, 3011–3019.

Dudley, R. & Srygley, R.B. (1994) Flight physiology of Neotropical butterflies: allometry of airspeeds during natural free flight. *Journal of Evolutionary Biology* **191**, 125–39.

Duffy, J.E. (2002) Biodiversity and ecosystem function: the consumer connection. *Oikos* **99**, 201–219.

Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thébault, E. & Loreau, M. (2007) The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* **10**, 522–538.

Dunne, J.A. (2006) The network structure of food webs. *Ecological networks: linking structure to dynamics in food webs* (eds. M. Pascual & J. Dunne), pp. 27–86, Oxford University Press, New York.

Ebeling, A., Meyer, S.T., Abbas, M., Eisenhauer, N., Hillebrand, H., Lange, M., Scherber, C., Vogel, A., Weigelt, A. & Weisser, W.W. (2014) Plant diversity impacts decomposition and herbivory via changes in aboveground arthropods. *PLoS ONE* **9**, e106529.

Edwards, C.A. (1959) Keys to the genera of the Symphyla. *Journal of the Linnean Society of London* **44**, 164–169.

Edwards, R. (1996) Estimating live spider weight using preserved specimens. *Journal of Arachnology* **24**, 161–166.

Ehnes, R.B., Pollierer, M.M., Erdmann, G., Klarner, B., Eitzinger, B., Digel, C., Ott, D., Maraun, M., Scheu, S. & Brose, U. (2014) Lack of energetic equivalence in forest soil invertebrates. *Ecology* **95**, 527–537.

Ehnes, R.B., Rall, B.C. & Brose, U. (2011) Phylogenetic grouping, curvature and metabolic scaling in terrestrial invertebrates. *Ecology Letters* **14**, 993–1000.

Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N.P., Dalsgaard, B., de Sassi, C., Galetti, M., Guimarães, P.R., Lomáscolo, S.B., Martín González, A.M., Pizo, M.A., Rader, R., Rodrigo, A., Tylianakis, J.M., Vázquez, D.P. & Allesina, S. (2013) The dimensionality of ecological networks. *Ecology Letters* **16**, 577–583.

Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, A., Interlandi, S., Kilham, S.S., McCauley, E., Schulz, K.L., Siemann, E.H. & Sterner, R.W. (2000a) Nutritional constraints in terrestrial and freshwater food webs. *Nature* **408**, 578–580.

Elser, J.J., Sterner, R.W., Gorokhova, E., Fagan, W.F., Markow, T.A., Cotner, J.B., Harrison, J.F., Hobbie, S.E., Odell, G.M. & Weider, L.J. (2000b) Biological stoichiometry from genes to ecosystems. *Ecology Letters* **3**, 540–550.

Elser, J.J., Bracken, M.E., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B. & Smith, J.E. (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* **10**, 1135–1142.

Elser, J.J., Dobberfuhl, D.R., Mackay, N.A. & Schampel, J.H. (1996) Organism size, life history, and N:P stoichiometry - Toward a unified view of cellular and ecosystem processes. *BioScience* **46**, 674–684.

Elton, C. (1927) *Animal ecology*. Macmillan Co., New York.

Enghoff, H. (2005) *Myriapoda*. Natural History Museum of Denmark (Zoological Museum).

Enquist, B.J., Kerkhoff, A.J., Stark, S.C., Swenson, N.G., McCarthy, M.C. & Price, C.A. (2007) A general integrative model for scaling plant growth, carbon flux, and functional trait spectra. *Nature* **449**, 218–222.

Ewers, R.M., Boyle, M.J.W., Gleave, R.A., Plowman, N.S., Benedick, S., Bernard, H., Bishop, T.R., Bakhtiar, E.Y., Chey, V.K., Chung, A.Y.C., Davies, R.G., Edwards, D.P., Eggleton, P., Fayle, T.M., Hardwick, S.R., Homathevi, R., Kitching, R.L., Khoo, M.S., Luke, S.H., March, J.J., Nilus, R., Pfeifer, M., Rao, S.V., Sharp, A.C., Snaddon, J.L., Stork, N.E., Struebig, M.J., Wearn, O.R., Yusah, K.M. & Turner, E.C. (2015) Logging cuts the functional importance of invertebrates in tropical rainforest. *Nature Communications* **6**, 6836.

Fagan, W.F. & Denno, R.F. (2004) Stoichiometry of actual vs. potential predator-prey interactions: insights into nitrogen limitation for arthropod predators. *Ecology Letters* **7**, 876–883.

Fagan, W.F., Siemann, E., Mitter, C., Denno, R.F., Huberty, A.F., Woods, H.A. & Elser, J.J. (2002) Nitrogen in insects: implications for trophic complexity and species diversification. *The American Naturalist* **160**, 784–802.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology and Systematics* **34**, 487–515.

Fanin, N., Fromin, N., Buatois, B. & Hättenschwiler, S. (2013) An experimental test of the hypothesis of non-homeostatic consumer stoichiometry in a plant litter-microbe system. *Ecology Letters* **16**, 764–772.

Fayle, T.M., Turner, E.C., Snaddon, J.L., Chey, V.K., Chung, A.Y., Eggleton, P. & Foster, W.a. (2010) Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. *Basic and Applied Ecology* **11**, 337–345.

Ferry-Graham, L.A., Bolnick, D.I. & Wainwright, P.C. (2002) Using functional morphology to examine the ecology and evolution of specialization. *Integrative and Comparative Biology* **42**, 265–277.

Fitzherbert, E., Struebig, M., Morel, A., Danielsen, F., Bruhl, C., Donald, P. & Phalan, B. (2008) How will oil palm expansion affect biodiversity? *Trends in Ecology & Evolution* **23**, 538–545.

Foley, J.A., S, D.R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global consequences of land use. *Science* **309**, 570–574.

Foster, W.A., Snaddon, J.L., Turner, E.C., Fayle, T.M., Cockerill, T.D., Ellwood, M.D.F., Broad, G.R., Chung, A.Y.C., Eggleton, P., Khen, C.V. & Yusah, K.M. (2011) Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of South East Asia. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 3277–3291.

Frausto da Silva, J.J.R. & Williams, R.J.P. (2001) *The biological chemistry of the elements: The inorganic chemistry of life*. Oxford University Press.

Frost, P.C. & Elser, J.J. (2002) Growth responses of littoral mayflies to the phosphorus content of their food. *Ecology Letters* **5**, 232–240.

Frost, P.C., Cross, W.F. & Benstead, J.P. (2005a) Ecological stoichiometry in freshwater benthic ecosystems: an introduction. *Freshwater Biology* **50**, 1781–1785.

Frost, P.C., Evans-White, M.A., Finkel, Z.V., Jensen, T.C. & Matzek, V. (2005b) Are you what you eat? Physiological constraints on organismal stoichiometry in an elementally imbalanced world. *Oikos* **109**, 18–28.

Full, R.J., Zuccarello, D.A. & Tullis, A. (1990) Effect of variation in form on the cost of terrestrial locomotion. *Journal of Experimental Biology* **150**, 233–246.

Fussmann, K.E., Schwarzmüller, F., Brose, U., Jousset, A. & Rall, B.C. (2014) Ecological stability in response to warming. *Nature Climate Change* **4**, 2ß6–21ß.

Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L. & Heinsohn, R. (2011) Declining body size: a third universal response to warming? *Trends in Ecology & Evolution* **26**, 285–291.

Gaveau, D., Wandono, H. & Setiabudi, F. (2007) Three decades of deforestation in southwest Sumatra: Have protected areas halted forest loss and logging, and promoted re-growth? *Biological Conservation* **134**, 495–504.

Gere, G. (1956) The examination of the feeding biology and the humificative function of Diplopoda and Isopoda. *Acta Biologica Academiae Scientiarum Hungaricae* **6**, 257–271.

Gergs, A. & Ratte, H.T. (2009) Predicting functional response and size selectivity of juvenile Notonecta maculata foraging on Daphnia magna. *Ecological Modelling* **220**, 3331–3341.

Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H. & Hättenschwiler, S. (2010) Diversity meets decomposition. *Trends in Ecology and Evolution* **25**, 372–380.

Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N. & Foley, J.A. (2010) Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences* **107**, 16732–16737.

Gilbert, N. (2012) Palm-oil boom raises conservation concerns. *Nature* **487**, 14–15.

Gist, C.S. & Crossley, D.A. (1975) The litter arthropod community in a southern Appalachian hardwood forest: numbers , biomass and mineral element content. *The American Midland Naturalist* **93**, 107–122.

Glazier, D.S. (2015) Is metabolic rate a universal 'pacemaker' for biological processes? *Biological Reviews* **90**, 377–407.

Gould, S.J. (1966) Allometry and size in ontogeny and phylogeny. *Biological Reviews* **41**, 587–638.

Gouws, E.J., Gaston, K.J. & Chown, S.L. (2011) Intraspecific body size frequency distributions of insects. *PLoS ONE* **6**, e16606.

Gouyon, A., de Foresta, H. & Levang, P. (1993) Does 'jungle rubber' deserve its name? An analysis of rubber agroforestry systems in southeast Sumatra. *Agroforestry Systems* **22**, 181–206.

Gowing, G. & Recher, H.F. (1984) Length-weight relationships for invertebrates from forests in south-eastern New South Wales. *Australian Journal of Ecology* **9**, 5–8.

Grace, J.B. (2006) *Structural equation modeling and natural systems*. Cambridge University Press.

Gross, K. & Cardinale, B.J. (2007) Does species richness drive community production or vice versa? Reconciling historical and contemporary paradigms in competitive communities. *The American Naturalist* **170**, 207–220.

Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. (2011) Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology* **24**, 699–711.

Gruner, D.S. (2003) Regressions of length and width to predict arthropod biomass in the Hawaiian Islands. *Pacific Science* **57**, 325–336.

Haddad, N.M., Haarstad, J. & Tilman, D. (2000) The effects of long-term nitrogen loading on grassland insect communities. *Oecologia* **124**, 73–84.

Hale, C.M., Reich, P.B. & Frelich, L.E. (2004) Allometric equations for estimation of ash-free dry mass from length measurements for selected European earthworm species (Lumbricidae) in the Western Great Lakes Region. *The American Midland Naturalist* **151**, 179–185.

Hamilton, A.J., Basset, Y., Benke, K.K., Grimbacher, P.S., Miller, S.E., Novotný, V., Samuelson, G.A., Stork, N.E., Weiblen, G.D. & Yen, J.D.L. (2010) Quantifying uncertainty in astimation of tropical arthropod species richness. *The American Naturalist* **176**, 90–95.

Hamilton, A.J., Basset, Y., Benke, K.K., Grimbacher, P.S., Miller, S.E., Novotný, V., Samuelson, G.A., Stork, N.E., Weiblen, G.D. & Yen, J.D.L. (2011) Correction. *The American Naturalist* **177**, 544–545.

Handa, I.T., Aerts, R., Berendse, F., Berg, M.P., Bruder, A., Butenschoen, O., Chauvet, E., Gessner, M.O., Jabiol, J., Makkonen, M., McKie, B.G., Malmqvist, B., Peeters, E.T.H.M., Scheu, S., Schmid, B., van Ruijven, J., Vos, V.C.A. & Hättenschwiler, S. (2014) Consequences of biodiversity loss for litter decomposition across biomes. *Nature* **509**, 218–221.

Hansen, H.J. (1903) The genera and species of the order Symphyla. *Quaterly Journal of Microscopical Science* **47**, 1–101.

Harrison, J.F., Klok, C.J. & Waters, J.S. (2014) Critical PO2 is size-independent in insects: implications for the metabolic theory of ecology. *Current Opinion in Insect Science* **4**, 54–59.

Hättenschwiler, S. & Jørgensen, H.B. (2010) Carbon quality rather than stoichiometry controls litter decomposition in a tropical rain forest. *Journal of Ecology* **98**, 754–763.

Hättenschwiler, S., Tiunov, A.V. & Scheu, S. (2005) Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics* **36**, 191–218.

Healy, K., McNally, L., Ruxton, G.D., Cooper, N. & Jackson, A.L. (2013) Metabolic rate and body size are linked with perception of temporal information. *Animal Behaviour* **86**, 685–696.

Hector, A. & Bagchi, R. (2007) Biodiversity and ecosystem multifunctionality. *Nature* **448**, 188–190.

Heiman, D.R. & Knight, A.W. (1975) The influence of temperature on th ebioenergetics of the carnivorous stonefly nymph Acroneuria california Banks (Plecoptera: Perlidae). *Ecology* **56**, 105–116.

Hein, A.M., Hou, C. & Gillooly, J.F. (2012) Energetic and biomechanical constraints on animal migration distance. *Ecology Letters* **15**, 104–110.

Hessen, D.O. (1992) Nutrient element limitation of zooplankton production. *The American Naturalist* **140**, 799–814.

Hillebrand, H., Borer, E.T., Bracken, M.E.S., Cardinale, B.J., Cebrian, J., Cleland, E.E., Elser, J.J., Gruner, D.S., Stanley Harpole, W., Ngai, J.T., Sandin, S., Seabloom, E.W., Shurin, J.B., Smith, J.E. & Smith, M.D. (2009) Herbivore metabolism and stoichiometry each constrain herbivory at different organizational scales across ecosystems. *Ecology Letters* **12**, 516–527.

Hillebrand, H., Cowles, J.M., Lewandowska, A., Van de Waal, D.B. & Plum, C. (2014) Think ratio! A stoichiometric view on biodiversity–ecosystem functioning research. *Basic and Applied Ecology* **15**, 465–474.

Hillebrand, H. & Lehmpfuhl, V. (2011) Resource stoichiometry and consumers control the biodiversity-productivity relationship in

pelagic metacommunities. *The American Naturalist* **178**, 171–181.

Hirst, A.G., Glazier, D.S. & Atkinson, D. (2014) Body shape shifting during growth permits tests that distinguish between competing geometric theories of metabolic scaling. *Ecology Letters* **17**, 1274–1281.

Höfer, H. & Ott, R. (2009) Estimating biomass of Neotropical spiders and other arachnids (Araneae, Opiliones, Pseudoscorpiones, Ricinulei) by mass-length regressions. *Journal of Arachnology* **37**, 160–169.

Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E. & Spiegel, O. (2008) Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences* **105**, 19060–19065.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**, 3–35.

Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L. & O'Connor, M.I. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* **486**, 105–108.

Hudson, L.N., Emerson, R., Jenkins, G.B., Layer, K., Ledger, M.E., Pichler, D.E., Thompson, M.S.A., O'Gorman, E.J., Woodward, G. & Reuman, D.C. (2013) Cheddar: analysis and visualisation of ecological communities in R. *Methods in Ecology and Evolution* **4**, 99–104.

Hunt, H.W., Coleman, D.C., Ingham, E.R., Ingham, R.E., Elliott, E.T., Moore, J.C., Rose, S.L., Reid, C.P.P. & Morley, C.R. (1987) The detrital food web in a shortgrass prairie. *Biology and Fertility of Soils* **3**, 57–68.

Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis, H.M., Olesen, J.M., van Veen, F.F., Warren, P.H. & Woodward, G. (2009) Ecological networks - beyond food webs. *Journal of Animal Ecology* **78**, 253–269.

IPCC (2014) *Climate change 2014: synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change*. IPCC, Geneva.

Ives, A.R., Cardinale, B.J. & Snyder, W.E. (2004) A synthesis of subdisciplines: predator-prey interactions, and biodiversity and ecosystem functioning. *Ecology Letters* **8**, 102–116.

Jacob, U., Thierry, A., Brose, U., Arntz, W.E., Berg, S., Brey, T., Fetzer, I., Jonsson, T., Mintenbeck, K., Möllmann, C., Petchey, O.L., Riede, J.O. & Dunne, J.A. (2011) The role of body size in complex food webs. *Advances in Ecological Research* **45**, 181–223.

Jetz, W., Carbone, C., Fulford, J. & Brown, J.H. (2004) The scaling of animal space use. *Science* **306**, 266–268.

Jeyasingh, P.D. (2007) Plasticity in metabolic allometry: the role of dietary stoichiometry. *Ecology Letters* **10**, 282–289.

Jochum, M., Schneider, F.D., Crowe, T.P., Brose, U. & O'Gorman, E.J. (2012) Climate-induced changes in bottom-up and top-down processes independently alter a marine ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**, 2962–2970.

Jocqué, R. & Dippenaar-Schoeman, A. (2007) *Spider families of the world*. Royal Museaum for Central Africa, 2 edn.

Johnson, M.D. & Strong, A.M. (2000) Length-weight relationships of Jamaican

arthropods. *Entomological News* **111**, 270–281.

Johnson, N.F. & Triplehorn, C.A. (2004) *Borror and DeLong's introduction to the study of insects*. Brooks Cole, 7 edn.

Kalinkat, G. (2014) Bringing animal personality research into the food web arena. *Journal of Animal Ecology* **83**, 1245–1247.

Kalinkat, G., Rall, B.C., Vucic-Pestic, O. & Brose, U. (2011) The allometry of prey preferences. *PLoS ONE* **6**, e25937.

Kalinkat, G., Schneider, F.D., Digel, C., Guill, C., Rall, B.C. & Brose, U. (2013) Body masses, functional responses and predator-prey stability. *Ecology Letters* **16**, 1126–1134.

Kaspari, M. (2012) Stoichiometry. *Metabolic ecology: A scaling approach* (eds. R. Sibly, J. Brown & A. Kodric-Brown), pp. 34–47, Wiley.

Kaspari, M., Clay, N.A., Donoso, D.A. & Yanoviak, S.P. (2014) Sodium fertilization increases termites and enhances decomposition in an Amazonian forest. *Ecology* **95**, 795–800.

Kaspari, M., Garcia, M.N., Harms, K.E., Santana, M., Wright, S.J. & Yavitt, J.B. (2008) Multiple nutrients limit litterfall and decomposition in a tropical forest. *Ecology Letters* **11**, 35–43.

Kaspari, M. & Yanoviak, S.P. (2009) Biogeochemistry and the structure of tropical brown food webs. *Ecology* **90**, 3342–3351.

Kaspari, M., Yanoviak, S.P., Dudley, R., Yuan, M. & Clay, N.A. (2009) Sodium shortage as a constraint on the carbon cycle in an inland tropical rainforest. *Proceedings of the National Academy of Sciences* **106**, 19405–19409.

Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., Boit, A., Joppa, L.N., Lafferty, K.D., Williams, R.J., Martinez, N.D., Menge, B.A., Blanchette, C.A., Iles, A.C. & Brose, U. (2012) More than a meal... integrating non-feeding interactions into food webs. *Ecology Letters* **15**, 291–300.

Kelt, D.A. & Van Vuren, D.H. (2001) The ecology and macroecology of mammalian home range area. *The American Naturalist* **157**, 637–645.

Kiltie, R.A. (2000) Scaling of visual acuity with body size in mammals and birds. *Functional Ecology* **14**, 226–234.

Kirchner, T.B. (1977) The effects of resource enrichment on the diversity of plants and arthropods in a shortgrass prairie. *Ecology* **58**, 1334–1344.

Kissling, W.D., Pattemore, D.E. & Hagen, M. (2014) Challenges and prospects in the telemetry of insects. *Biological Reviews* **89**, 511–530.

Klarner, B., Ehnes, R.B., Erdmann, G., Eitzinger, B., Pollierer, M.M., Maraun, M. & Scheu, S. (2014) Trophic shift of soil animal species with forest type as indicated by stable isotope analysis. *Oikos* **123**, 1173–1181.

Klausmeier, C.A., Litchman, E., Daufresne, T. & Levin, S.A. (2004) Optimal nitrogen-to-phosphorus stoichiometry of phytoplankton. *Nature* **429**, 171–174.

Klecka, J. & Boukal, D.S. (2013) Foraging and vulnerability traits modify predator-prey body mass allometry: freshwater macroinvertebrates as a case study. *Journal of Animal Ecology* **82**, 1031–1041.

Kleiber, M. (1947) Body size and metabolic rate. *Physiological reviews* **27**, 511–541.

Kleiber, M. (1932) Body size and metabolism. *Hilgardia* **6**, 315–351.

Koh, L.P. & Ghazoul, J. (2010) Spatially explicit scenario analysis for reconciling agricultural expansion, forest protection, and carbon conservation in Indonesia. *Proceedings of the National Academy of Sciences* **107**, 11140–11144.

Koh, L.P., Miettinen, J., Liew, S.C. & Ghazoul, J. (2011) Remotely sensed evidence of tropical peatland conversion to oil palm. *Proceedings of the National Academy of Sciences* **108**, 5127–5132.

Koh, L.P. & Wilcove, D.S. (2007) Cashing in palm oil for conservation. *Nature* **448**, 993–994.

Koh, L.P. & Wilcove, D.S. (2008) Is oil palm agriculture really destroying tropical biodiversity? *Conservation Letters* **1**, 60–64.

Kotowska, M.M., Leuschner, C., Triadiati, T., Meriem, S. & Hertel, D. (2015) Quantifying above- and belowground biomass carbon loss with forest conversion in tropical lowlands of Sumatra (Indonesia). *Global Change Biology* **21**, 3620–3634.

Kram, R. & Taylor, C.R. (1990) Energetics of running: a new perspective. *Nature* **346**, 265–267.

Krebs, C.J. (2009) *Ecology : the experimental analysis of distribution and abundance*. Pearson.

Laliberté, E., Wells, J.A., Declerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., Aubin, I., Bonser, S.P., Ding, Y., Fraterrigo, J.M., McNamara, S., Morgan, J.W., Merlos, D.S., Vesk, P.A. & Mayfield, M.M. (2010) Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters* **13**, 76–86.

Lang, A., Krooss, S. & Stumpf, H. (1997) Mass length relationships of epigeal arthropod predators in arable land (Araneae, Chilopoda, Coleoptera). *Pedobiologia* **41**, 327–333.

Lang, B., Ehnes, R.B., Brose, U. & Rall, B.C. (in preparation) From databases to a global model: warming induced shifts of biotic and abiotic carbon pools .

Lang, B., Rall, B.C., Scheu, S. & Brose, U. (2013) Effects of environmental warming and drought on size-structured soil food webs. *Oikos* **123**, 1224–1233.

Langel, R. & Dyckmans, J. (2014) Combined 13C and 15N isotope analysis on small samples using a near-conventional elemental analyzer/isotope ratio mass spectrometer setup. *Rapid Communications in Mass Spectrometry* **28**, 1019–1022.

Laumonier, Y., Uryu, Y., Stüwe, M., Budiman, A., Setiabudi, B. & Hadian, O. (2010) Eco-floristic sectors and deforestation threats in Sumatra: identifying new conservation area network priorities for ecosystem-based land use planning. *Biodiversity and Conservation* **19**, 1153–1174.

Laurance, W.F., Sayer, J. & Cassman, K.G. (2014) Agricultural expansion and its impacts on tropical nature. *Trends in Ecology & Evolution* **29**, 107–116.

Lewis, S.L., Edwards, D.P. & Galbraith, D. (2015) Increasing human dominance of tropical forests. *Science* **349**, 827–832.

Lindeman, R.L. (1942) The trophic-dynamic aspect of ecology. *Ecology* **23**, 399–417.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D., Huston, M.a., Raffaelli, D., Schmid, D., Tilman, D. & Wardle, D. (2001) Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. *Science* **294**, 804–808.

Lotka, A.J. (1925) *Elements of physical biology*. Williams and Wilkins Company, Baltimore.

Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., Garcia-Gomez, M., Bowker, M.A., Soliveres, S., Escolar, C., Garcia-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., Conceicao, A.A., Cabrera, O., Chaieb, M., Derak, M., Eldridge, D.J., Espinosa, C.I., Florentino, A., Gaitan, J., Gatica, M.G., Ghiloufi, W., Gomez-Gonzalez, S., Gutierrez, J.R., Hernandez, R.M., Huang, X., Huber-Sannwald, E., Jankju, M., Miriti, M., Monerris, J., Mau,

R.L., Morici, E., Naseri, K., Ospina, A., Polo, V., Prina, A., Pucheta, E., Ramirez-Collantes, D.A., Romao, R., Tighe, M., Torres-Diaz, C., Val, J., Veiga, J.P., Wang, D. & Zaady, E. (2012) Plant species richness and ecosystem multifunctionality in global drylands. *Science* **335**, 214–218.

Makkonen, M., Berg, M.P., Handa, I.T., Hättenschwiler, S., van Ruijven, J., van Bodegom, P.M. & Aerts, R. (2012) Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. *Ecology Letters* **15**, 1033–1041.

Malzahn, A.M., Aberle, N., Clemmesen, C. & Boersma, M. (2007) Nutrient limitation of primary producers affects planktivorous fish condition. *Limnology and Oceanography* **52**, 2062–2071.

Maraun, M., Alphei, J., Beste, P., Bonkowski, M., Buryn, R., Migge, S., Peter, M., Schaefer, M. & Scheu, S. (2001) Indirect effects of carbon and nutrient amendments on the soil meso- and microfauna of a beechwood. *Biology and Fertility of Soils* **34**, 222–229.

Markow, T.A., Raphael, B., Dobberfuhl, D., Breitmeyer, C.M., Elser, J.J. & Pfeiler, E. (1999) Elemental stoichiometry of Drosophila and their hosts. *Functional Ecology* **13**, 78–84.

Martinson, H.M., Schneider, K., Gilbert, J., Hines, J.E., Hambäck, P.a. & Fagan, W.F. (2008) Detritivory: stoichiometry of a neglected trophic level. *Ecological Research* **23**, 487–491.

Matson, P.A., Parton, W.J., Power, A.G. & Swift, M.J. (1997) Agricultural intensification and ecosystem properties. *Science* **277**, 504–509.

McBrayer, J.F. (1973) Exploitation of deciduous leaf litter by Apheloria montana (Diplopoda: Eurydesmidae). *Pedobiologia* **13**, 90–98.

McFeeters, B.J. & Frost, P.C. (2011) Temperature and the effects of elemental food quality on Daphnia. *Freshwater Biology* **56**, 1447–1455.

McGill, B.J. & Mittelbach, G.C. (2006) An allometric vision and motion model to predict prey encounter rates. *Evolutionary Ecology Research* **8**, 691–701.

McGroddy, M.E., Daufresne, T. & Hedin, L.O. (2004) Scaling of C:N:P stoichiometry in forests worldwide: implications of terrestrial Redfield-type ratios. *Ecology* **85**, 2390–2401.

McPeek, M.A., Schrot, A.K. & Brown, J.M. (1996) Adaptation to predators in a new community: swimming performance and predator avoidance in damselflies. *Ecological Society of America* **77**, 617–629.

Mercer, R.D., Gabriel, A., Barendse, J., Marshall, D. & Chown, S. (2001) Invertebrate body sizes from Marion Island. *Antarctic Science* **13**, 135–143.

Modlmeier, A.P., Keiser, C.N., Wright, C.M., Lichtenstein, J.L.L. & Pruitt, J.N. (2015) Integrating animal personality into insect population and community ecology. *Current Opinion in Insect Science* **9**, 77–85.

Moe, S.J., Stelzer, R.S., Forman, M.R., Harpole, W.S., Daufresne, T. & Yoshida, T. (2005) Recent advances in ecological stoichiometry: insights for population and community ecology. *Oikos* **109**, 29–39.

Moore, J.C., de Ruiter, P.C. & Hunt, H.W. (1993) Influence of productivity on the stability of real and model ecosystems. *Science* **261**, 906–908.

Mulder, C., Cohen, J.E., Setälä, H., Bloem, J. & Breure, A.M. (2004) Bacterial traits, organism mass, and numerical abundance in the detrital soil food web of Dutch agricultural grasslands. *Ecology Letters* **8**, 80–90.

Mulder, C. & Elser, J.J. (2009) Soil acidity, ecological stoichiometry and allometric scaling in grassland food webs. *Global Change Biology* **15**, 2730–2738.

Mulder, C., Van Wijnen, H.J. & Van Wezel, A.P. (2005) Numerical abundance and biodiversity of below-ground taxocenes along a pH gradient across the Netherlands. *Journal of Biogeography* **32**, 1775–1790.

Mulder, C., Vonk, J.A., Den Hollander, H.A., Hendriks, A.J. & Breure, A.M. (2011) How allometric scaling relates to soil abiotics. *Oikos* **120**, 529–536.

Muller-Landau, H.C., Condit, R.S., Chave, J., Thomas, S.C., Bohlman, S.A., Bunyavejchewin, S., Davies, S., Foster, R., Gunatilleke, S., Gunatilleke, N., Harms, K.E., Hart, T., Hubbell, S.P., Itoh, A., Kassim, A.R., LaFrankie, J.V., Lee, H.S., Losos, E., Makana, J.R., Ohkubo, T., Sukumar, R., Sun, I.F., Nur Supardi, M.N., Tan, S., Thompson, J., Valencia, R., Munoz, G.V., Wills, C., Yamakura, T., Chuyong, G., Dattaraja, H.S., Esufali, S., Hall, P., Hernandez, C., Kenfack, D., Kiratiprayoon, S., Suresh, H.S., Thomas, D., Vallejo, M.I. & Ashton, P. (2006) Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. *Ecology Letters* **9**, 575–588.

Mumme, S., Jochum, M., Brose, U., Haneda, N.F. & Barnes, A.D. (2015) Functional diversity and stability of litter-invertebrate communities following land-use change in Sumatra, Indonesia. *Biological Conservation* **191**, 750–758.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–8.

Naisbit, R.E., Rohr, R.P., Rossberg, A.G., Kehrli, P. & Bersier, L.F. (2012) Phylogeny versus body size as determinants of food web structure. *Proceedings of the Royal Society B: Biological Sciences* **279**, 3291–3297.

Nakagawa, S. & Freckleton, R.P. (2011) Model averaging, missing data and multiple imputation: a case study for behavioural ecology. *Behavioral Ecology and Sociobiology* **65**, 103–116.

Neutel, A.M., Heesterbeek, J.A.P. & de Ruiter, P.C. (2002) Stability in real food webs: weak links in long loops. *Science* **296**, 1120–1123.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Borger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S., Echeverria-Londono, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W. & Purvis, A. (2015) Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45–50.

Nielsen, U.N., Ayres, E., Wall, D.H. & Bardgett, R.D. (2011) Soil biodiversity and carbon cycling: a review and synthesis of studies examining diversity-function relationships. *European Journal of Soil Science* **62**, 105–116.

Novotny, V., Basset, Y., Auga, J., Boen, W., Dal, C., Drozd, P., Kasbal, M., Isua, B., Kutil, R., Manumbor, M. & Molem, K. (1999) Predation risk for herbivorous insects on tropical vegetation: a search for enemy-free space and time. *Australian Journal of Ecology* **24**, 477–483.

O'Gorman, E.J., Pichler, D.E., Adams, G., Benstead, J.P., Cohen, H., Craig, N., Cross, W.F., Demars, B.O.L., Friberg, N., Gíslason, G.M., Gudmundsdóttir, R., Hawczak, A., Hood, J.M., Hudson, L.N., Johansson, L., Johansson, M.P., Junker, J.R., Laurila, A., Manson, J.R., Mavromati, E., Nelson, D., Ólafsson, J.S., Perkins, D.M., Petchey, O.L., Plebani, M., Reuman, D.C., Rall, B.C., Stewart, R., Thompson, M.S.A. & Woodward, G.

(2012) Impacts of warming on the structure and functioning of aquatic communities. Individual- to ecosystem-level responses. *Advances in Ecological Research*, vol. 47, pp. 81–176.

Olff, H., Alonso, D., Berg, M.P., Eriksson, B.K., Loreau, M., Piersma, T. & Rooney, N. (2009) Parallel ecological networks in ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 1755–1779.

Ollerton, J., Winfree, R. & Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos* **120**, 321–326.

Orians, G.H. & Milewski, A.V. (2007) Ecology of Australia: the effects of nutrient-poor soils and intense fires. *Biological Reviews* **82**, 393–423.

Ott, D., Rall, B.C. & Brose, U. (2012) Climate change effects on macrofaunal litter decomposition: the interplay of temperature, body masses and stoichiometry. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**, 3025–3032.

Ott, D., Digel, C., Klarner, B., Maraun, M., Pollierer, M., Rall, B.C., Scheu, S., Seelig, G. & Brose, U. (2014a) Litter elemental stoichiometry and biomass densities of forest soil invertebrates. *Oikos* **123**, 1212–1223.

Ott, D., Digel, C., Rall, B.C., Maraun, M., Scheu, S. & Brose, U. (2014b) Unifying elemental stoichiometry and metabolic theory in predicting species abundances. *Ecology Letters* **17**, 1247–1256.

Otto, S.B., Berlow, E.L., Rank, N.E., Smiley, J. & Brose, U. (2008) Predator diversity and identity drive interaction strength and trophic cascades in a food web. *Ecology* **89**, 134–144.

Otto, S.B., Rall, B.C. & Brose, U. (2007) Allometric degree distributions facilitate food-web stability. *Nature* **450**, 1226–1229.

Pandian, T.J. & Marian, M.P. (1985) Nitrogen content of food as an index of absorption efficiency in fishes. *Marine Biology* **85**, 301–311.

Pandian, T.J. & Marian, M.P. (1986) An indirect procedure for the estimation of assimilation efficieny of aquatic insects. *Freshwater Biology* **16**, 93–98.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, vol. 37, pp. 637–669, Annual Reviews, Palo Alto.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42.

Pawar, S., Dell, A.I. & Savage, V.M. (2014) From metabolic constraints on individuals to the dynamics of ecosystems. *Aquatic Functional Biodiversity: An Eco-Evolutionary Approach* (eds. A. Belgrano, G. Woodward & U. Jacob), pp. 3–36, Elsevier Academic Press Inc.

Pawar, S., Dell, A.I. & Van M. Savage (2012) Dimensionality of consumer search space drives trophic interaction strengths. *Nature* **486**, 485–489.

Persson, J., Fink, P., Goto, A., Hood, J.M., Jonas, J. & Kato, S. (2010) To be or not to be what you eat: regulation of stoichiometric homeostasis among autotrophs and heterotrophs. *Oikos* **119**, 741–751.

Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2008) Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences* **105**, 4191–4196.

Petchey, O.L., Gaston, K.J., Downing, A.L., Mittelbach, G.G., Persson, L., Steiner, C.F., Warren, P.H. & Woodward, G. (2004) Species loss and the structure and functioning of multitrophic aquatic systems. *Oikos* **104**, 467–478.

Peters, R.H. (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge.

Pimm, S.L. (1982) *Food webs*. Chapman and Hall, London.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Development Core Team (2014) Nlme: linear and nonlinear mixed effects models. *R package version 3.1-122* .

Poboszny, M. (1997) Vergleichende Untersuchungen des Konsums bei Männchen und Weibchen von Diplopoden. *Opuscula Zoologica Budapest* pp. 29–30.

Pontzer, H. (2007) Effective limb length and the scaling of locomotor cost in terrestrial animals. *Journal of Experimental Biology* **210**, 1752–1761.

Post, D.M. (2002) The long and short of food-chain length. *Trends in Ecology and Evolution* **10**, 269–277.

Post, D.M., Pace, M.L. & Hairston, N.G. (2000) Ecosystem size determines food-chain length in lakes. *Nature* **405**, 1047–1049.

Prus, T. (1971) The assimilation efficiency of Asellus aquaticus L. (crustacea, isopoda). *Freshwater Biology* **1**, 287–305.

Purvis, A., Gittleman, J.L., Cowlishaw, G. & Mace, G.M. (2000) Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences* **267**, 1947–1952.

R Core Team (2014) R: a language and environment for statistical computing. URL `http://www.r-project.org/`.

R Core Team (2015) R: a language and environment for statistical computing. URL `http://www.r-project.org/`.

Raine, N.E. & Chittka, L. (2008) The correlation of learning speed and natural foraging success in bumble-bees. *Proceedings of the Royal Society B: Biological Sciences* **275**, 803–808.

Rall, B.C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmuller, F., Vucic-Pestic, O. & Petchey, O.L. (2012) Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**, 2923–2934.

Rall, B.C., Kalinkat, G., Ott, D., Vucic-Pestic, O. & Brose, U. (2011) Taxonomic versus allometric constraints on non-linear interaction strengths. *Oikos* **120**, 483–492.

Redfield, A.C. (1958) The biological control of chemical factors in the environment. *American Scientist* **46**, 205–221.

Reiners, W.A. (1986) Complementary models for ecosystems. *The American Naturalist* **127**, 59.

Reiss, J., Bridle, J.R., Montoya, J.M. & Woodward, G. (2009) Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology and Evolution* **24**, 505–514.

Reuman, D.C. & Cohen, J.E. (2005) Estimating relative energy fluxes using the food web, species abundance, and body size. *Advances In Ecological Research* **36**, 137–182.

Richardson, A. & Araujo, P.B. (2015) Lifestyles of terrestrial crustaceans. *Lifestyles and Feeding Biology* (eds. M. Thiel & L. Watling), vol. 1, pp. 299–336, Oxford University Press.

Riede, J.O., Brose, U., Ebenman, B., Jacob, U., Thompson, R., Townsend, C.R. & Jonsson, T. (2011) Stepping in Elton's footprints: a general scaling model for body masses and trophic levels across ecosystems. *Ecology Letters* **14**, 169–178.

Riveros, A. & Enquist, B. (2011) Metabolic scaling in insects supports the predictions of the WBE model. *Journal of Insect Physiology* **57**, 688–693.

Rizopoulos, D. (2006) ltm: an R package for latent variable modeling and item response theory analyses. *Journal of Statistical Software* **17**, 1–25.

Rousk, J., Brookes, P.C. & Baath, E. (2009) Contrasting soil pH effects on fungal

and bacterial growth suggest functional redundancy in carbon mineralization. *Applied and Environmental Microbiology* **75**, 1589–1596.

Rubner, M. (1883) Über den Einfluss von Körpergrösse auf Stoff- und Kraftwechsel. *Zeitschrift für Biologie* **19**, 536–562.

Rudolf, V.H.W. & Rasmussen, N.L. (2013) Population structure determines functional differences among species and ecosystem processes. *Nature Communications* **4**, 1–7.

Sacchi, R. & Hardersen, S. (2012) Wing length allometry in Odonata: differences between families in relation to migratory behaviour. *Zoomorphology* **132**, 23–32.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, Rodolfo, Hubner-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Global biodiversity scenarios for the year 2100. *Science* **287**, 1770–1774.

Sample, B.E., Cooper, R.J., Greer, R.D. & Whitmore, R.C. (1993) Estimation of insect biomass by length and width. *The American Midland Naturalist* **129**, 234–240.

Savage, V.M., Deeds, E.J. & Fontana, W. (2008) Sizing up allometric scaling theory. *PLoS Computational Biology* **4**, e1000171.

Sayer, E.J., Tanner, E.V.J. & Lacey, A.L. (2006) Effects of litter manipulation on early-stage decomposition and meso-arthropod abundance in a tropical moist forest. *Forest Ecology and Management* **229**, 285–293.

Sayer, E.J., Sutcliffe, L.M.E., Ross, R.I.C. & Tanner, E.V.J. (2010) Arthropod abundance and diversity in a lowland tropical forest floor in Panama: the role of habitat space vs. nutrient concentrations. *Biotropica* **42**, 194–200.

Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.D., Roscher, C., Weigelt, A., Allan, E., Beß ler, H., Bonkowski, M., Buchmann, N., Buscot, F., Clement, L.W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., Klein, A.M., Koller, R., König, S., Kowalski, E., Kummer, V., Kuu, A., Lange, M., Lauterbach, D., Middelhoff, C., Migunova, V.D., Milcu, A., Müller, R., Partsch, S., Petermann, J.S., Renker, C., Rottstock, T., Sabais, A., Scheu, S., Schumacher, J., Temperton, V.M. & Tscharntke, T. (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* **468**, 553–556.

Scheu, S. & Falca, M. (2000) The soil food web of two beech forests (Fagus sylvatica) of contrasting humus type: stable isotope analysis of a macro- and a mesofauna-dominated community. *Oecologia* **123**, 285–296.

Schmidt-Nielsen, K. (1984) *Scaling: Why is animal size so important?* Cambridge University Press.

Schneider, F.D. & Brose, U. (2013) Beyond diversity: how nested predator effects control ecosystem functions. *Journal of Animal Ecology* **82**, 64–71.

Schneider, F.D., Scheu, S. & Brose, U. (2012) Body mass constraints on feeding rates determine the consequences of predator loss. *Ecology Letters* **15**, 436–443.

Schramski, J.R., Dell, A.I., Grady, J.M., Sibly, R.M. & Brown, J.H. (2015) Metabolic theory predicts whole-ecosystem properties. *Proceedings of the National Academy of Sciences* **112**, 201423502.

Seastedt, T.R. & Crossley, D.A. (1984) The influence of arthropods on ecosystems. *BioScience* **34**, 157–161.

Sheridan, J.A. & Bickford, D. (2011) Shrinking body size as an ecological response to climate change. *Nature Climate Change* **1**, 401–406.

Shurin, J.B., Gruner, D.S. & Hillebrand, H. (2006) All wet or dried up? Real

differences between aquatic and terrestrial food webs. *Proceedings of the Royal Society B: Biological Sciences* **273**, 1–9.

Simpson, S.J. & Raubenheimer, D. (2000) The hungry locust. *Advances in the Study of Behavior, Vol. 29* (eds. P. Slater, J. Rosenblatt, C. Snowdon & T. Roper), vol. 29, pp. 1–44, Academic Press.

Smith, V.H., Tilman, G.D. & Nekola, J.C. (1999) Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environmental Pollution* **100**, 179–196.

Sodhi, N.S., Koh, L.P., Brook, B.W. & Ng, P.K. (2004) Southeast Asian biodiversity: an impending disaster. *Trends in Ecology & Evolution* **19**, 654–660.

Sperfeld, E., Martin-Creuzburg, D. & Wacker, A. (2012) Multiple resource limitation theory applied to herbivorous consumers: Liebig's minimum rule vs. interactive co-limitation. *Ecology Letters* **15**, 142–150.

Srivastava, D.S. & Vellend, M. (2005) Biodiversity-ecosystem function research: is it relevant to conservation? *Annual Review of Ecology, Evolution, and Systematics* **36**, 267–294.

Steffen, W., Grinevald, J., Crutzen, P. & McNeill, J. (2011) The Anthropocene: conceptual and historical perspectives. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **369**, 842–867.

Stehr, F.W. (2005) *Immature insects*. Kendall Hunt Publishing, Dubuque, Iowa, 1 edn.

Steigen, A.L. (1975) Energetics in a population of Pardosa palustris (L.) (Araneae, Lycosidae) on Hardangervidda. *Fennoscandian Tundra Ecosystems, Ecological Studies Volume 17* (ed. F.E. Wiegolaski), pp. 129–144, Springer Berlin Heidelberg.

Sterner, R.W. & Elser, J.J. (2002) *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton University Press.

Sterner, R.W. (1997) Modelling interactions of food quality and quantity in homeostatic consumers. *Freshwater Biology* **38**, 473–481.

Stevens, V.M., Trochet, A., Van Dyck, H., Clobert, J. & Baguette, M. (2012) How is dispersal integrated in life histories: a quantitative analysis using butterflies. *Ecology Letters* **15**, 74–86.

Tansley, A.G. (1935) The use and abuse of vegetational concepts and terms. *Ecology* **16**, 284–307.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* **31**, 79–92.

Tho, Y.P. (1992) *Termites of peninsular Malaysia*. Forest Research Institute Malaysia.

Tilman, D., Isbell, F. & Cowles, J.M. (2014) Biodiversity and ecosystem functioning. *Annual Review of Ecology Evolution and Systematics* **45**, 471.

Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R. & Polasky, S. (2002) Agricultural sustainability and intensive production practices. *Nature* **418**, 671–7.

Tilman, D., Reich, P.B. & Knops, J.M.H. (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**, 629–632.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H. & Westphal, C. (2012) Landscape moderation

of biodiversity patterns and processes - eight hypotheses. *Biological Reviews* **87**, 661–685.

Ulanowicz, R.E. (2004) Quantitative methods for ecological network analysis. *Computational Biology and Chemistry* **28**, 321–339.

Ulanowicz, R.E. & Scharler, U.M. (2008) Least-inference methods for constructing networks of trophic flows. *Ecological Modelling* **210**, 278–286.

Urabe, J. & Sterner, R.W. (1996) Regulation of herbivore growth by the balance of light and nutrients. *Proceedings of the National Academy of Sciences* **93**, 8465–8469.

Vitousek, P.M., Mooney, H.A., Lubchenko, J. & Melillo, J.M. (1997a) Human domination of Earth's ecosystems. *Science* **277**, 494–499.

Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W., Schlesinger, W.H. & Tilman, D.G. (1997b) Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* **7**, 737–750.

Vogel, S. (2008) Modes and scaling in aquatic locomotion. *Integrative and Comparative Biology* **48**, 702–712.

Von Liebig, J. (1840) *Die Organische Chemie in Ihrer Answendung auf Agrikultur und Physiologie.* Vieweg und Sohn, Braunschweig.

Vos, V.C.A., van Ruijven, J., Berg, M.P., Peeters, E.T.H.M. & Berendse, F. (2011) Macro-detritivore identity drives leaf litter diversity effects. *Oikos* **120**, 1092–1098.

Wardhaugh, C.W. (2013) Estimation of biomass from body length and width for tropical rainforest canopy invertebrates. *Australian Journal of Entomology* **52**, 291–298.

Wardle, D.A., Yeates, G.W., Barker, G.M. & Bonner, K.I. (2006) The influence of plant litter diversity on decomposer abundance and diversity. *Soil Biology and Biochemistry* **38**, 1052–1062.

Warren, A.P.H. & Lawton, J.H. (1987) Invertebrate predator-prey body size relationships : an explanation for upper triangular food webs and patterns in food web structure? *Oecologia* **74**, 231–235.

West, G.B., Brown, J.H. & Enquist, B.J. (1999) A general model for the structure, and algometry of plant vascular systems. *Nature* **400**, 122–126.

West, G.B., Brown, J.H. & Enquist, B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122–126.

White, C.R. (2010) There is no single p. *Nature* **464**, 691–693.

White, E.P., Ernest, S.M., Kerkhoff, A.J. & Enquist, B.J. (2007) Relationships between body size and abundance in ecology. *Trends in Ecology & Evolution* **22**, 323–330.

Wilcove, D.S., Giam, X., Edwards, D.P., Fisher, B. & Koh, L.P. (2013) Navjot's nightmare revisited: Logging, agriculture, and biodiversity in Southeast Asia. *Trends in Ecology and Evolution* **28**, 531–540.

Wilcove, D.S. & Koh, L.P. (2010) Addressing the threats to biodiversity from oil-palm agriculture. *Biodiversity and Conservation* **19**, 999–1007.

Wilson, E.O. (1987) The little things that run the world (The importance and conservation of invertebrates). *Conservation Biology* **1**, 344–346.

Woods, H.A., Fagan, W.F., Elser, J.J. & Harrison, J.F. (2004) Allometric and phylogenetic variation in insect phosphorus content. *Functional Ecology* **18**, 103–109.

Woodward, G., Speirs, D.C. & Hildrew, A.G. (2005) Quantification and resolution of a complex, size structured food web. *Advances in Ecological Research* **36**, 85–135.

Wootton, J.T. (1994) The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* **25**, 443–466.

Wootton, J.T. & Emmerson, M. (2005) Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution, and Systematics* **36**, 419–444.

Wulff, F., Field, J.G. & Mann, K.H. (1989) *Network analysis in marine ecology: methods and applications*. Springer, Berlin.

Xu, Z., Lenaghan, S.C., Reese, B.E., Jia, X. & Zhang, M. (2012) Experimental studies and dynamics modeling analysis of the swimming and diving of whirligig beetles (Coleoptera: Gyrinidae). *PLoS Computational Biology* **8**, e1002792.

Yang, L.H. (2000) Effects of body size and plant structure on the movement ability of a predaceous stinkbug, Podisus maculiventris (Heteroptera: Pentatomidae). *Oecologia* **125**, 85–90.

Yang, L.H. & Gratton, C. (2014) Insects as drivers of ecosystem processes. *Current Opinion in Insect Science* **2**, 1–7.

Yang, X., Warren, M. & Zou, X. (2007) Fertilization responses of soil litter fauna and litter quantity, quality, and turnover in low and high elevation forests of Puerto Rico. *Applied Soil Ecology* **37**, 63–71.

Yodzis, P. & Innes, S. (1992) Body size and consumer-resource dynamics. *The American Naturalist* **139**, 1151–1175.

Zalasiewicz, J., Williams, M., Haywood, A. & Ellis, M. (2011) The Anthropocene: a new epoch of geological time? *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **369**, 835–841.

Zuur, A., Ieno, E.N. & Smith, G.M. (2007) *Analysing ecological data*. Springer.

Part V.

Appendix

Chapter 7.

Supplementary information to chapter 3

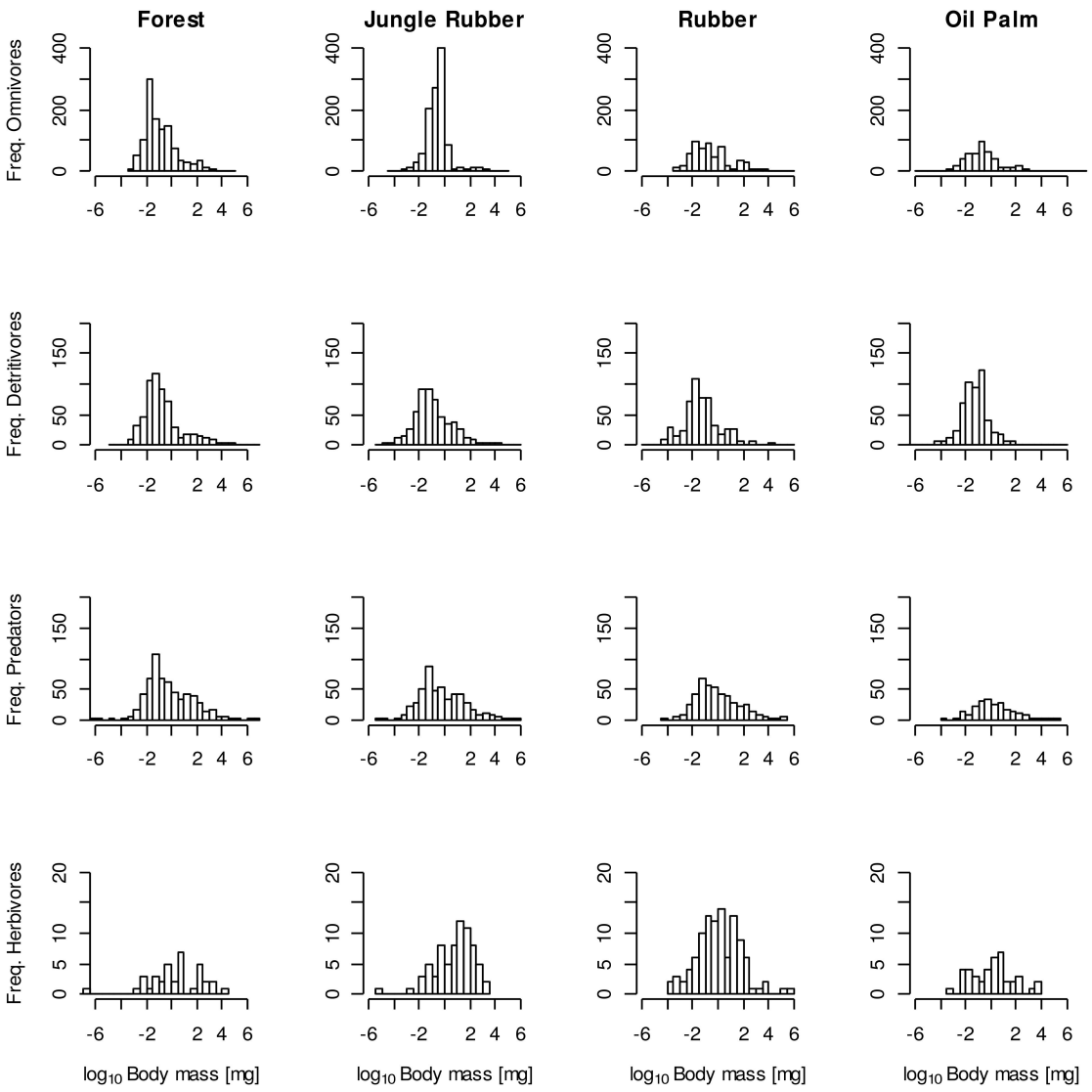

Figure 7.1 – Body mass distributions across the four transformation systems for each of the four functional feeding guilds: omnivores (3209 individuals), detritivores (2242 individuals), predators (1766 individuals), and herbivores (255 individuals).

Table 7.1 – Summary and ANOVA tables from the best-fit generalized linear mixed effects models as selected by AIC: (a) negative binomial model testing the effects of transformation system (TrSys) and functional feeding guild (FFG) on species richness (SpRichness); (b) gaussian models testing the effects of transformation system (TrSys) and functional feeding guild (FFG) on density, biomass, and community metabolism (CM). Asterisks denote significance levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

(a) Model	Fixed effects	Estimate	Std. Error	z value	Pr	
SpRichness ∼ TrSys * FFG	Intercept	3.088	0.127	24.29	0	***
	Jungle rubber	0.054	0.179	0.299	0.766	
	Oil palm	-0.556	0.19	-2.921	0.003	**
	Rubber	-0.275	0.184	-1.491	0.135	
	Omnivores	0.168	0.101	1.668	0.096	
	Herbivores	-1.759	0.194	-9.065	0	***
	Predators	0.606	0.092	6.553	0	***
	Jungle rubber : Omnivores	-0.399	0.149	-2.685	0.007	**
	Oil palm : Omnivores	-0.087	0.168	-0.52	0.603	
	Rubber : Omnivores	-0.099	0.154	-0.644	0.519	
	Jungle rubber : Herbivores	0.346	0.254	1.361	0.174	
	Oil palm : Herbivores	0.641	0.274	2.337	0.019	*
	Rubber : Herbivores	0.953	0.246	3.876	0	***
	Jungle rubber : Predators	-0.253	0.132	-1.912	0.056	
	Oil palm : Predators	-0.235	0.156	-1.51	0.131	
	Rubber : Predators	-0.078	0.141	-0.556	0.578	

(b) Model	Fixed effects	numDF	denDF	F-value	Pr	
Density ∼ TrSys * FFG	TrSys	3	27	0.363	0.78	
	FFG	3	84	77.611	0	***
	TrSys : FFG	9	84	3.432	0.001	**
Biomass ∼ TrSys + FFG	TrSys	3	27	3.57	0.027	*
	FFG	3	93	38.759	0	***
CM ∼ TrSys + FFG	TrSys	3	27	3.456	0.03	*
	FFG	3	93	64.825	0	***

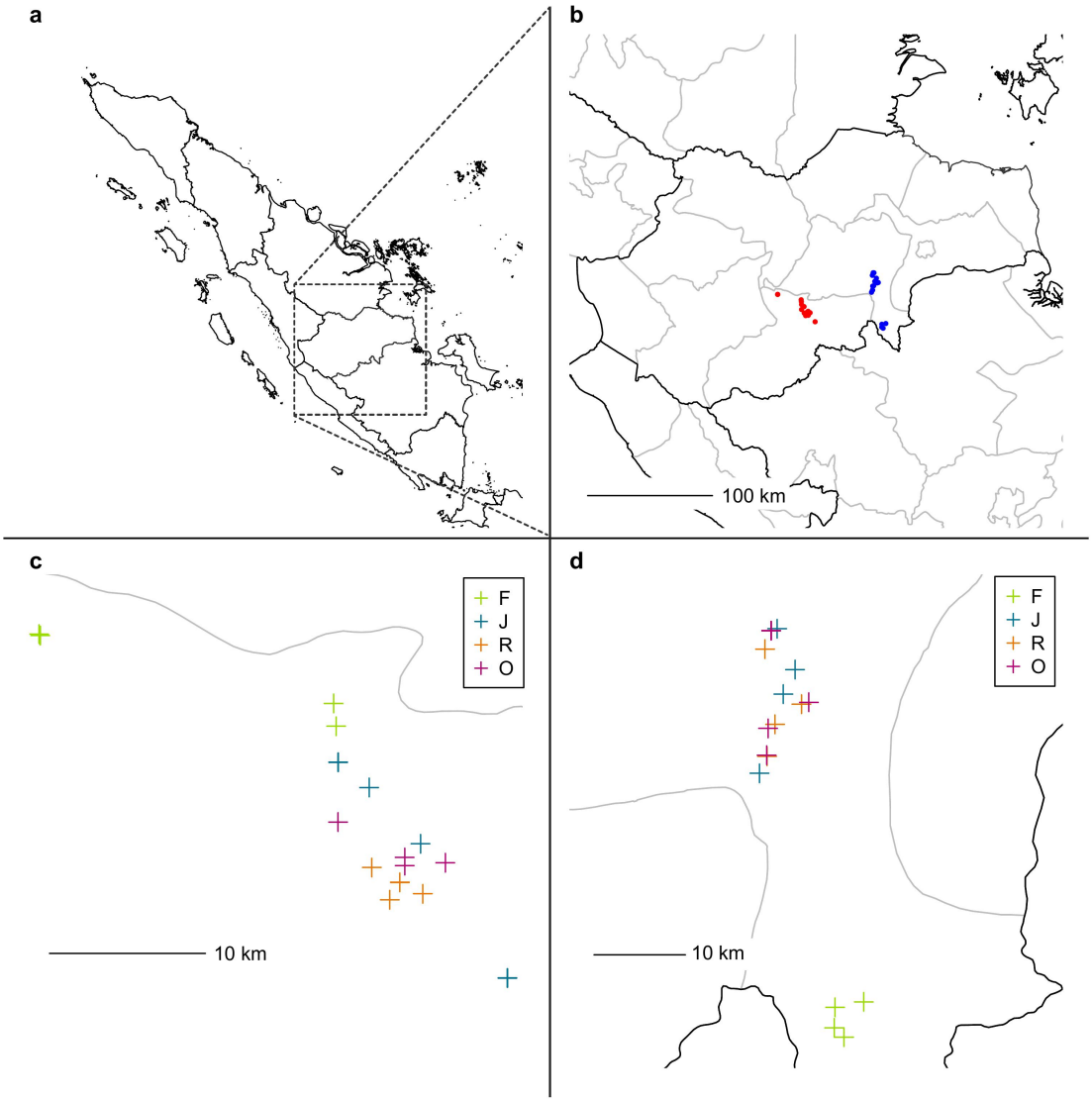

Figure 7.2 – Map of the study region with an overview of Sumatra (a) and Jambi Province (b) with red and blue points denoting the 16 sites in Bukit Duabelas landscape and the 16 sites in Harapan landscape, respectively. Additionally, the spatial layout of the sampling sites in Bukit Duabelas landscape (c) and Harapan landscape (d) is represented by coloured crosses for forest (F), jungle rubber (J), rubber (R) and oil palm (O).

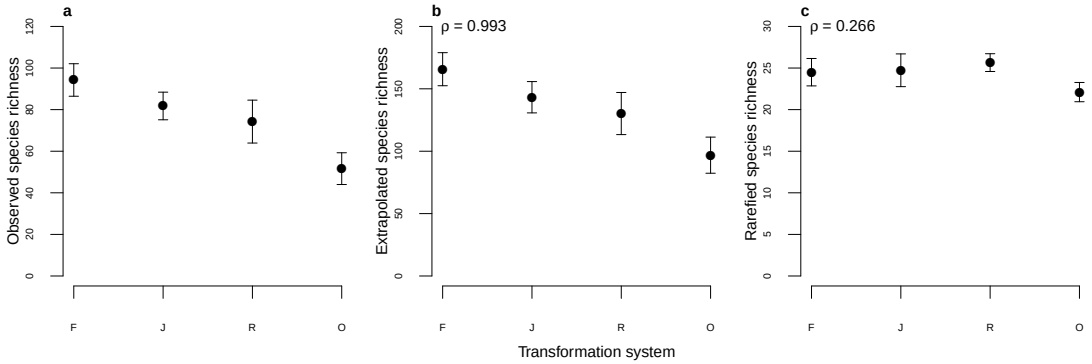

Figure 7.3 – Mean (± SE) observed species richness (a), 2nd order jacknife extrapolated species richness (b) and rarefied species richness (c) for the four land-use transformation systems: forest (F), jungle rubber (J), rubber (R) and oil palm (O). p-values denote Pearson correlation coefficients between observed species richness and extrapolated (b) and rarefied species richness (c) for the 32 sites ($n = 32$), respectively.

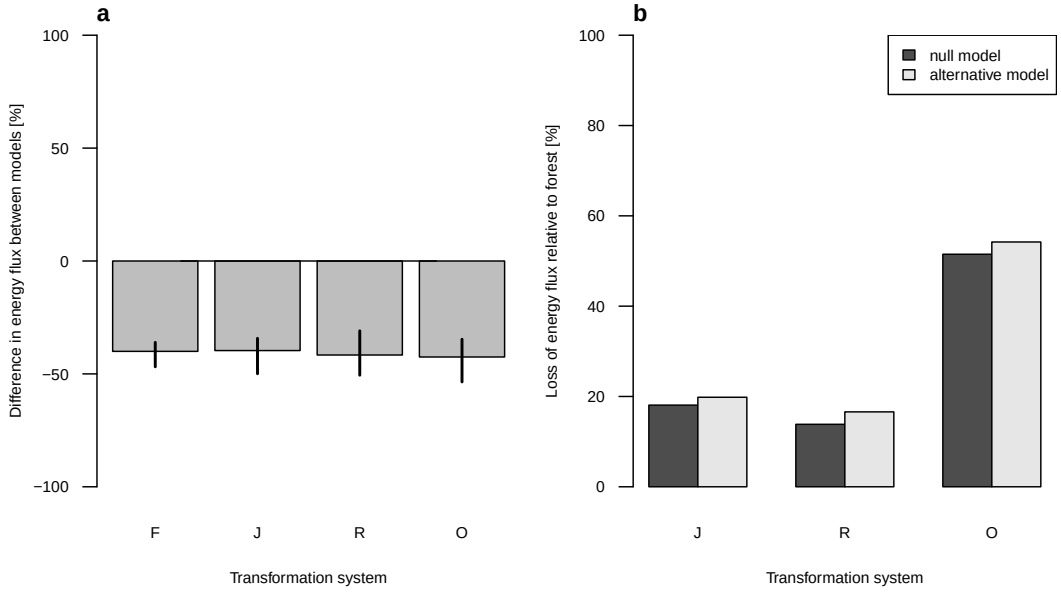

Figure 7.4 – (a) Comparative mean percentage change in total energy flux for the four transformation systems between our feeding link assumption null-model (Supplementary Methods) and an alternative flux calculation with omnivores consuming only live plant material and detritus (50% each). Error bars denote upper and lower limits of absolute deviation from the mean. (b) Mean percentage loss in energy flux of the three agriculturally used transformation systems compared to the forest system. Dark grey and light grey bars denote the null model and alternative model calculations, respectively. Transformation system abbreviations are: forest (F), jungle rubber (J), rubber (R) and oil palm (O)

Table 7.2 – Energy flux and fresh biomass values for the four functional feeding guilds (FFG) and four transformation systems. Energy flux is expressed as kg fresh mass [ha^{-1} yr^{-1}] using a conversion factor (Peters, 1983): 1 kg wet mass = 7 * 10^6 J.

FFG	Transformation system	Energy flux [kg ha^{-1} yr^{-1}]	Biomass [kg ha^{-1}]
Omnivore	Forest	61.900	0.629
Omnivore	Jungle rubber	52.313	0.494
Omnivore	Rubber	55.880	0.751
Omnivore	Oil palm	32.531	0.766
Detritivore	Forest	200.187	1.039
Detritivore	Jungle rubber	160.165	0.558
Detritivore	Rubber	164.194	0.504
Detritivore	Oil palm	94.440	0.352
Predator	Forest	66.816	1.664
Predator	Jungle rubber	53.248	0.976
Predator	Rubber	55.454	0.954
Predator	Oil palm	30.697	0.424
Herbivore	Forest	87.537	0.093
Herbivore	Jungle rubber	75.389	0.139
Herbivore	Rubber	83.288	0.319
Herbivore	Oil palm	44.316	0.076

Table 7.3 – ANOVA tables from the generalized linear mixed effects models testing the effects of transformation system (TrSys), species richness (SpRichness), and their interaction on energy flux (EF) for the total community data set and also separated into functional feeding guilds (FFG). All models displayed are those that were selected as the best-fit model from the stepwise AIC selection procedure. Asterisks denote significance levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Model	Fixed effects	numDF	denDF	F-value	Pr	
Total Community	TrSys	3	23	5.226	0.007	**
EF ~ TrSys * SpRichness	SpRichness	1	23	4.965	0.036	*
	TrSys : SpRichness	3	23	4.637	0.011	*
Omnivores	SpRichness	1	29	42.842	0	***
EF ~ SpRichness						
Detritivores	TrSys	3	26	3.103	0.044	*
EF ~ TrSys + SpRichness	SpRichness	1	26	22.285	0	***
Predators	TrSys	3	23	5.507	0.005	**
EF ~ TrSys * SpRichness	SpRichness	1	23	5.813	0.024	*
	TrSys : SpRichness	3	23	4.618	0.011	*
Herbivores	TrSys	3	26	5.944	0.003	**
EF ~ TrSys + SpRichness	SpRichness	1	26	9.436	0.005	**

Table 7.4 – Length-mass regression parameters for calculation of individual body masses from measured body lengths. For damaged individuals where body length could not be measured (66 of 7472 individuals), body mass was substituted by species median body mass or order median body mass (for species with single individuals). 'Taxon', 'Group' and 'Further grouping' specify which animals the presented regression has been used for in this study. Regressions were available from the literature that estimate both dry (DM) and fresh mass (FM) ('Mass type') for different taxa. Table b presents the dry-to-fresh mass conversions from the literature (Mercer *et al.*, 2001) for transformation of dry body masses (from length-dry-mass regression calculations) to fresh mass. The equations and regression parameters, 'a' and 'b', are presented, as well as the size range the regressions were calculated from ('Min' and 'Max'). All regressions were taken from the literature ('Reference'), with different specific definitions of how body length was measured ('Details of body length measurement') and specificity of the given regression ('Regression specificity').

(a) Taxon	Group	Mass type	Equation M[mg], L[mm]	a	b	Min (mm)	Max (mm)	Reference	Details of body length measurement	Regression specificity
Annelida	All	ash free DM	M = 1000*exp(a + b * log(L))	-11.8423	2.3225			(Hale *et al.*, 2004)	Total length	General Lumbricidae
Araneae	Araneae < 2.5 mm	FM	M = exp(a + b * log(L))	-1.958	2.746	0.56	2.5	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Group specific
Araneae	hunting	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Group specific
Araneae	web-building	FM	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Group specific
Araneae	spiders random	FM	M = exp(a + b * log(L))	-1.844	2.711	1.8	21.5	(Edwards, 1996)	clypeus to tip of spinnerets	Group specific
Araneae	Anapidae	FM	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, web-building
Araneae	Araneidae	FM	M = exp(a + b * log(L))	-1.923	2.923	2.1	21.2	(Edwards, 1996)	clypeus to tip of spinnerets	Group specific
Araneae	Barychelidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, hunting spiders
Araneae	Clubionidae	FM	M = exp(a + b * log(L))	-2.156	2.653	2.5	9	(Edwards, 1996)	clypeus to tip of spinnerets	Group specific
Araneae	Corinnidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, hunting spiders
Araneae	Ctenidae	FM	M = exp(a + b * log(L))	-1.758	2.894	1.3	36	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Group specific
Araneae	Deinopidae	FM	M = exp(a + b * log(L))	-1.844	2.711	1.8	21.5	(Edwards, 1996)	clypeus to tip of spinnerets	inferred, spiders random sample
Araneae	Gnaphosidae	FM	M = exp(a + b * log(L))	-2.83	3.055	3	13.1	(Edwards, 1996)	clypeus to tip of spinnerets	Group specific
Araneae	Hexathelidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, hunting spiders

Araneae	Lamponidae	FM	M = exp(a + b * log(L))	-2.83	3.055	3	13.1	(Edwards, 1996)	clypeus to tip of spinnerets	inferred, Gnaphosidae
Araneae	Linyphiidae	FM	M = exp(a + b * log(L))	-1.892	2.754	1.5	5.5	(Edwards, 1996)	clypeus to tip of spinnerets	Group specific
Araneae	Lycosidae	FM	M = exp(a + b * log(L))	-2.043	2.842	2	23.5	(Edwards, 1996)	clypeus to tip of spinnerets	Group specific
Araneae	Micropholcommatidae	FM	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, web-building
Araneae	Miturgidae	FM	M = exp(a + b * log(L))	-2.83	3.055	3	13.1	(Edwards, 1996)	clypeus to tip of spinnerets	inferred, Gnaphosidae
Araneae	Mysmenidae	FM	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, web-building
Araneae	Nemesiidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, hunting spiders
Araneae	Nephilidae	FM	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, web-building
Araneae	Ochyroceratidae	FM	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, web-building
Araneae	Oonopidae	FM	M = exp(a + b * log(L))	-2.039	2.666	0.67	2.5	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Group specific
Araneae	Oxyopidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, hunting spiders
Araneae	Palpimanidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, hunting spiders
Araneae	Pararchaeidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, hunting spiders
Araneae	Philodromidae	FM	M = exp(a + b * log(L))	-1.985	2.94	2.5	8.6	(Edwards, 1996)	clypeus to tip of spinnerets	Group specific
Araneae	Pholcidae	FM	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, web-building
Araneae	Prodidomidae	FM	M = exp(a + b * log(L))	-2.83	3.055	3	13.1	(Edwards, 1996)	clypeus to tip of spinnerets	inferred, Gnaphosidae
Araneae	Salticidae	FM	M = exp(a + b * log(L))	-2.184	2.901	4	13	(Edwards, 1996)	clypeus to tip of spinnerets	Group specific
Araneae	Scytodidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, hunting spiders
Araneae	Segestriidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, hunting spiders

Araneae	Sparassidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, hunting spiders
Araneae	Stenochilidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, hunting spiders
Araneae	Symphytognathidae	FM	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, web-building
Araneae	Telemidae	FM	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, web-building
Araneae	Tetrablemmidae	FM	M = exp(a + b * log(L))	-2.039	2.666	0.67	2.5	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, Oonopidae
Araneae	Tetragnathidae	FM	M = exp(a + b * log(L))	-2.615	2.574	3.5	9	(Edwards, 1996)	clypeus to tip of spinnerets	Group specific
Araneae	Theridiidae	FM	M = exp(a + b * log(L))	-1.577	2.907	1.5	7.5	(Edwards, 1996)	clypeus to tip of spinnerets	Group specific
Araneae	Theridiosomatidae	FM	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, web-building
Araneae	Thomisidae	FM	M = exp(a + b * log(L))	-1.644	2.973	1.8	8	(Edwards, 1996)	clypeus to tip of spinnerets	Group specific
Araneae	Uloboridae	FM	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, web-building
Araneae	Unidentifiable < 1.8	FM	M = exp(a + b * log(L))	-1.958	2.746	0.56	2.5	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, Araneae < 2.5 mm
Araneae	Unidentifiable > 1.8	FM	M = exp(a + b * log(L))	-1.844	2.711	1.8	21.5	(Edwards, 1996)	clypeus to tip of spinnerets	inferred, spiders random sample
Araneae	Zodariidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, hunting spiders
Archaeognatha	All	DM	M = exp(a + b * log(L))	-3.628	2.494	2.13	54.51	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, all insect taxa
Blattodea	Blaberidae	DM	M = exp(a + b * log(L))	-3.98	2.76	2.2	14	(Wardhaugh, 2013)	front of labrum to tip of abdom. (excl. cerci or ovipos.) or tip of elytra (longest)	inferred, Blattodea
Blattodea	Blattellidae	DM	M = exp(a + b * log(L))	-3.98	2.76	2.2	14	(Wardhaugh, 2013)	front of labrum to tip of abdom. (excl. cerci or ovipos.) or tip of elytra (longest)	inferred, Blattodea
Blattodea	Blattidae	DM	M = exp(a + b * log(L))	-3.98	2.76	2.2	14	(Wardhaugh, 2013)	front of labrum to tip of abdom. (excl. cerci or ovipos.) or tip of elytra (longest)	inferred, Blattodea
Blattodea	Unidentifiable	DM	M = exp(a + b * log(L))	-3.98	2.76	2.2	14	(Wardhaugh, 2013)	front of labrum to tip of abdom. (excl. cerci or ovipos.) or tip of elytra (longest)	inferred, Blattodea
Chilopoda	Ballophilidae	DM	M = exp(a + b * log(L))	-4.049	2.18	4	47	(Gowing & Recher, 1984)	not mentioned	inferred, Chilopoda

Chilopoda	Cryptopidae	DM	M = exp(a + b * log(L))	-4.049	2.18	4	47	(Gowing & Recher, 1984)	not mentioned	inferred, Chilopoda
Chilopoda	Henicopidae	DM	M = exp(a + b * log(L))	-4.049	2.18	4	47	(Gowing & Recher, 1984)	not mentioned	inferred, Chilopoda
Chilopoda	Lithobiomorpha	DM	M = exp(a + b * log(L))	-4.049	2.18	4	47	(Gowing & Recher, 1984)	not mentioned	inferred, Chilopoda
Chilopoda	Mecistocephalidae	DM	M = exp(a + b * log(L))	-4.049	2.18	4	47	(Gowing & Recher, 1984)	not mentioned	inferred, Chilopoda
Chilopoda	Scolopendridae	DM	M = exp(a + b * log(L))	-4.049	2.18	4	47	(Gowing & Recher, 1984)	not mentioned	inferred, Chilopoda
Chilopoda	Unidentifiable	DM	M = exp(a + b * log(L))	-4.049	2.18	4	47	(Gowing & Recher, 1984)	not mentioned	inferred, Chilopoda
Coleoptera	Anobiidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Anthicidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Bostrichidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Byrrhidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Carabidae	DM	M = a * L^b	0.0237	2.7054	2.88	24	(Lang *et al.*, 1997)	Measured from anterior tip of head to posterior of abdom. excl. append.	Group specific
Coleoptera	Cerylonidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Chelonariidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Chrysomelidae	DM	M = exp(a + b * log(L))	-2.427	2.171	3.34	7.84	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	Group specific
Coleoptera	Ciidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Cleridae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Coccinellidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Colydiidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Curculionidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Dermestidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Discolomidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Elateridae	DM	M = a * L^b	0.0138	2.595	1.65	10.3	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, slender beetles
Coleoptera	Endomychidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Histeridae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera

Coleoptera	Hydrophilidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Languriidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Larvae	DM	$M = a * L^b$	0.0035	2.4033	1.5	25.27	(Lang *et al.*, 1997)	Measured from anterior tip of head to posterior of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Leiodidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Lucanidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Melyridae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Mordellidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Mycetophagidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Pselaphidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Ptiliidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Scarabaeidae	DM	M = exp(a + b * log(L))	-2.448	2.494	4.24	24.79	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	Group specific
Coleoptera	Scydmaenidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Silvanidae	DM	$M = a * L^b$	0.0138	2.595	1.65	10.3	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, slender beetles
Coleoptera	Staphylinidae	DM	$M = a * L^b$	0.0134	2.26	2.2	13.6	(Lang *et al.*, 1997)	Measured from anterior tip of head to posterior of abdom. excl. append.	Group specific
Coleoptera	Tenebrionidae	DM	M = exp(a + b * log(L))	-0.043	1.2	5.65	13.39	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	Group specific
Coleoptera	Throscidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Trogossitidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Unidentifiable	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Coleoptera	Zopheridae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Coleoptera
Dermaptera	Anisolabididae	DM	M = exp(a + b * log(L))	-3.628	2.494	2.13	54.51	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, all insect taxa
Dermaptera	Forficulidae	DM	M = exp(a + b * log(L))	-3.628	2.494	2.13	54.51	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, all insect taxa
Diplopoda	Chordeumatida	DM	M = exp(a + b * log(L))	-4.591	2.543	11	47	(Gowing & Recher, 1984)	not mentioned	inferred, Diplopoda
Diplopoda	Glomerida	DM	M = exp(a + b * log(L))	-4.591	2.543	11	47	(Gowing & Recher, 1984)	not mentioned	inferred, Diplopoda

Diplopoda	Polidesmatidae	DM	M = exp(a + b * log(L))	-4.591	2.543	11	47	(Gowing & Recher, 1984)	not mentioned	inferred, Diplopoda
Diplopoda	Polydesmatida	DM	M = exp(a + b * log(L))	-4.591	2.543	11	47	(Gowing & Recher, 1984)	not mentioned	inferred, Diplopoda
Diplopoda	Polydesmida	DM	M = exp(a + b * log(L))	-4.591	2.543	11	47	(Gowing & Recher, 1984)	not mentioned	inferred, Diplopoda
Diplopoda	Polydesmidae	DM	M = exp(a + b * log(L))	-4.591	2.543	11	47	(Gowing & Recher, 1984)	not mentioned	inferred, Diplopoda
Diplopoda	Polyxenida	DM	M = exp(a + b * log(L))	-4.591	2.543	11	47	(Gowing & Recher, 1984)	not mentioned	inferred, Diplopoda
Diplopoda	Siphonophorida	DM	M = exp(a + b * log(L))	-4.591	2.543	11	47	(Gowing & Recher, 1984)	not mentioned	inferred, Diplopoda
Diplopoda	Spirobolida	DM	M = exp(a + b * log(L))	-4.591	2.543	11	47	(Gowing & Recher, 1984)	not mentioned	inferred, Diplopoda
Diplura	Heterojapygidae	DM	M = a * L^b	0.034	2.191	0.9	17.6	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, general arthropod
Diptera	Larvae	DM	M = a * L^b	0.029	1.73	1.7	16.65	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, holomet. Larvae
Diptera	Adults	DM	M = a * L^b	0.0153	2.573	1.75	8.6	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	Group specific, Diptera adult
Diptera	Agromyzidae	DM	M = a * L^b	0.029	1.73	1.7	16.65	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, holomet. Larvae
Diptera	Cecidomyiidae	DM	M = a * L^b	0.035	2.173	0.9	17.6	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, all insect taxa
Diptera	Ceratopogonidae	DM	M = a * L^b	0.029	1.73	1.7	16.65	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, holomet. Larvae
Diptera	Chironomidae	DM	M = a * L^b	0.029	1.73	1.7	16.65	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, holomet. Larvae
Diptera	Drosophilidae	DM	M = a * L^b	0.029	1.73	1.7	16.65	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, holomet. Larvae
Diptera	Muscidae	DM	M = a * L^b	0.0153	2.573	1.75	8.6	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	Group specific, Diptera adult
Diptera	Mycetophilidae	DM	M = a * L^b	0.029	1.73	1.7	16.65	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, holomet. Larvae
Diptera	Phoridae	DM	M = a * L^b	0.0153	2.573	1.75	8.6	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	Group specific, Diptera adult

Diptera	Pipunculidae	DM	$M = a * L^b$	0.029	1.73	1.7	16.65	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, holomet. Larvae
Diptera	Sciaridae	DM	$M = a * L^b$	0.0153	2.573	1.75	8.6	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	Group specific, Diptera adult
Diptera	Simuliidae	DM	$M = a * L^b$	0.0153	2.573	1.75	8.6	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	Group specific, Diptera adult
Diptera	Syrphidae	DM	$M = a * L^b$	0.029	1.73	1.7	16.65	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, holomet. Larvae
Diptera	Tachinidae	DM	$M = a * L^b$	0.0153	2.573	1.75	8.6	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	Group specific, Diptera adult
Diptera	Tephritidae	DM	$M = a * L^b$	0.029	1.73	1.7	16.65	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, holomet. Larvae
Diptera	Thaumaleidae	DM	$M = a * L^b$	0.035	2.173	0.9	17.6	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, all insect taxa
Gastropoda	All	DM	M = exp(a + b * log(L*W))	-2.75	1.59	2.1	18	(Wardhaugh, 2013)	front of labrum to tip of abdom. (excl. cerci or ovipos.) or tip of elytra (longest)	inferred, Gastropoda
Hemiptera	Acanthosomatidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	Group specific, Hemiptera
Hemiptera	Anthocoridae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	Group specific, Hemiptera
Hemiptera	Aradidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	Group specific, Hemiptera
Hemiptera	Ceratocombidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	Group specific, Hemiptera
Hemiptera	Cicadellidae	DM	M = exp(a + b * log(L))	-3.735	2.561	2.13	13.25	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	Group specific
Hemiptera	Cimicidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Hemiptera
Hemiptera	Cydnidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Hemiptera
Hemiptera	Delphacidae	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	Inferred, Homoptera
Hemiptera	Dipsocoridae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Hemiptera
Hemiptera	Enicocephalidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Hemiptera

Hemiptera	Eurybrachyidae	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	Inferred, Homoptera
Hemiptera	Hebridae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Hemiptera
Hemiptera	Hydrometridae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Hemiptera
Hemiptera	Lophopidae	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	Inferred, Homoptera
Hemiptera	Lygaeidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Hemiptera
Hemiptera	Meenoplidae	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	Inferred, Homoptera
Hemiptera	Membracidae	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	Inferred, Homoptera
Hemiptera	Mesoveliidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Hemiptera
Hemiptera	Miridae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Hemiptera
Hemiptera	Nabidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Hemiptera
Hemiptera	Pentatomidae	DM	M = exp(a + b * log(L))	-4.197	3.053	6.35	16.73	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	Group specific
Hemiptera	Reduviidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Hemiptera
Hemiptera	Schizopteridae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, Hemiptera
Hemiptera	Triozidea	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	Inferred, Homoptera
Hymenoptera	Bethylidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher, 1984)	not mentioned	inferred, Hym. excl Form.
Hymenoptera	Diapriidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher, 1984)	not mentioned	inferred, Hym. excl Form.
Hymenoptera	Eucoilidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher, 1984)	not mentioned	inferred, Hym. excl Form.
Hymenoptera	Eupelmidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher, 1984)	not mentioned	inferred, Hym. excl Form.
Hymenoptera	Figitidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher, 1984)	not mentioned	inferred, Hym. excl Form.
Hymenoptera	Formicidae	DM	M = exp(a + b * log(L))	-3.996	2.489	2	18	(Gowing & Recher, 1984)	not mentioned	Group specific

Hymenoptera	Mymaridae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher, 1984)	not mentioned		inferred, Hym. excl Form.
Hymenoptera	Scelionidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher, 1984)	not mentioned		inferred, Hym. excl Form.
Hymenoptera	Specidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher, 1984)	not mentioned		inferred, Hym. excl Form.
Hymenoptera	Trichogrammatidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher, 1984)	not mentioned		inferred, Hym. excl Form.
Hymenoptera	Unidentifiable	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher, 1984)	not mentioned		inferred, Hym. excl Form.
Isopoda	All	DM	M = exp(a + b * log(L))	-4.81	3.44	2.7	8	(Wardhaugh, 2013)	front of labrum to tip of abdom. (excl. cerci or ovipos.) or tip of elytra (longest)		Group specific, Isopoda
Isoptera	Rhinotermitidae	DM	$M = e^a * L^b$	-5.802	3.177	3.3	5.6	(Johnson & Strong, 2000)	head to end of abdom.		inferred, Isoptera
Isoptera	Termitidae	DM	$M = e^a * L^b$	-5.802	3.177	3.3	5.6	(Johnson & Strong, 2000)	head to end of abdom.		inferred, Isoptera
Isoptera	Unidentifiable	DM	$M = e^a * L^b$	-5.802	3.177	3.3	5.6	(Johnson & Strong, 2000)	head to end of abdom.		inferred, Isoptera
Lepidoptera	Alucitidae	DM	M = exp(a + b * log(L))	-5.909	2.959	6.26	44.62	(Sample *et al.*, 1993)	frons to tip of abdom. (excl. ovipos., wings etc.)	antennae,	inferred, Lepidoptera Larvae
Lepidoptera	Arctiidae	DM	M = exp(a + b * log(L))	-5.909	2.959	6.26	44.62	(Sample *et al.*, 1993)	frons to tip of abdom. (excl. ovipos., wings etc.)	antennae,	inferred, Lepidoptera Larvae
Lepidoptera	Arctiidae	DM	M = exp(a + b * log(L))	-3.755	2.658	5.05	20.06	(Sample *et al.*, 1993)	frons to tip of abdom. (excl. ovipos., wings etc.)	antennae,	inferred, Lepidoptera
Lepidoptera	Gelechiidae	DM	M = exp(a + b * log(L))	-5.909	2.959	6.26	44.62	(Sample *et al.*, 1993)	frons to tip of abdom. (excl. ovipos., wings etc.)	antennae,	inferred, Lepidoptera Larvae
Lepidoptera	Geometridae	DM	M = exp(a + b * log(L))	-5.493	2.625	7.66	29.5	(Sample *et al.*, 1993)	frons to tip of abdom. (excl. ovipos., wings etc.)	antennae,	Group specific
Lepidoptera	Hesperiidae	DM	M = exp(a + b * log(L))	-5.909	2.959	6.26	44.62	(Sample *et al.*, 1993)	frons to tip of abdom. (excl. ovipos., wings etc.)	antennae,	inferred, Lepidoptera Larvae
Lepidoptera	Lasiocampidae	DM	M = exp(a + b * log(L))	-5.909	2.959	6.26	44.62	(Sample *et al.*, 1993)	frons to tip of abdom. (excl. ovipos., wings etc.)	antennae,	inferred, Lepidoptera Larvae

Lepidoptera	Lymantriidae	DM	M = exp(a + b * log(L))	-5.909	2.959	6.26	44.62	(Sample *et al.*, 1993)	frons to tip of abdom. (excl. antennae, ovipos., wings etc.)	inferred, Lepidoptera Larvae
Lepidoptera	Noctuidae	DM	M = exp(a + b * log(L))	-5.424	2.845	7.96	42.8	(Sample *et al.*, 1993)	frons to tip of abdom. (excl. antennae, ovipos., wings etc.)	Group specific
Lepidoptera	Nolidae	DM	M = exp(a + b * log(L))	-5.909	2.959	6.26	44.62	(Sample *et al.*, 1993)	frons to tip of abdom. (excl. antennae, ovipos., wings etc.)	inferred, Lepidoptera Larvae
Lepidoptera	Pterophoridae	DM	M = exp(a + b * log(L))	-5.909	2.959	6.26	44.62	(Sample *et al.*, 1993)	frons to tip of abdom. (excl. antennae, ovipos., wings etc.)	inferred, Lepidoptera Larvae
Lepidoptera	Pyralidae	DM	M = exp(a + b * log(L))	-5.909	2.959	6.26	44.62	(Sample *et al.*, 1993)	frons to tip of abdom. (excl. antennae, ovipos., wings etc.)	inferred, Lepidoptera Larvae
Lepidoptera	Pyralidae	DM	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	(Sample *et al.*, 1993)	frons to tip of abdom. (excl. antennae, ovipos., wings etc.)	inferred, Lepidoptera
Mantodea	Mantidae	DM	M = exp(a + b * log(L))	-6.34	3.01	6	66	(Wardhaugh, 2013)	front of labrum to tip of abdom. (excl. cerci or ovipos.) or tip of elytra (longest)	Group specific
Neuroptera	Chrysopidae	DM	M = exp(a + b * log(L))	-4.483	2.57	3.45	54.51	(Sample *et al.*, 1993)	frons to tip of abdom. (excl. antennae, ovipos., wings etc.)	inferred, Neuroptera
Opiliones	All	FM	M = exp(a + b * log(L))	-0.899	2.984	0.57	6.9	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, Opiliones
Orthoptera	Acrididae	DM	M = exp(a + b * log(L))	-3.17	2.61	2.3	33	(Wardhaugh, 2013)	front of labrum to tip of abdom. (excl. cerci or ovipos.) or tip of elytra (longest)	inferred, Orthoptera
Orthoptera	Eumastacidae	DM	M = exp(a + b * log(L))	-3.17	2.61	2.3	33	(Wardhaugh, 2013)	front of labrum to tip of abdom. (excl. cerci or ovipos.) or tip of elytra (longest)	inferred, Orthoptera
Orthoptera	Gryllidae	DM	M = exp(a + b * log(L))	-3.17	2.61	2.3	33	(Wardhaugh, 2013)	front of labrum to tip of abdom. (excl. cerci or ovipos.) or tip of elytra (longest)	inferred, Orthoptera
Orthoptera	Tetrigidae	DM	M = exp(a + b * log(L))	-3.17	2.61	2.3	33	(Wardhaugh, 2013)	front of labrum to tip of abdom. (excl. cerci or ovipos.) or tip of elytra (longest)	inferred, Orthoptera
Plecoptera	All	DM	M = a * L^b	0.0094	2.754	1.95	3.232	(Benke *et al.*, 1999)	Total length	Group specific
Plecoptera	Austroperlidae	DM	M = a * L^b	0.0094	2.754	1.95	3.232	(Benke *et al.*, 1999)	Total length	Group specific
Plecoptera	Gripopterygidae	DM	M = a * L^b	0.0094	2.754	1.95	3.232	(Benke *et al.*, 1999)	Total length	Group specific
Plecoptera	Notonemouridae	DM	M = a * L^b	0.0094	2.754	1.95	3.232	(Benke *et al.*, 1999)	Total length	Group specific
Pseudoscorp.	All	FM	M = exp(a + b * log(L))	-1.892	2.515	0.86	2.1	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Group specific
Psocoptera	Archipsocidae	DM	M = a * L^b	0.014	3.115	1.5	3.15	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, Psocoptera
Psocoptera	Caeciliidae	DM	M = a * L^b	0.014	3.115	1.5	3.15	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, Psocoptera
Psocoptera	Ectopsocidae	DM	M = a * L^b	0.014	3.115	1.5	3.15	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, Psocoptera
Psocoptera	Elipsocidae	DM	M = a * L^b	0.014	3.115	1.5	3.15	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, Psocoptera
Psocoptera	Epipsocidae	DM	M = a * L^b	0.014	3.115	1.5	3.15	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, Psocoptera

Psocoptera	Hemipsocidae	DM	$M = a * L^b$	0.014	3.115	1.5	3.15	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, Psocoptera
Psocoptera	Lepidopsocidae	DM	$M = a * L^b$	0.014	3.115	1.5	3.15	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, Psocoptera
Psocoptera	Pachytroctidae	DM	$M = a * L^b$	0.014	3.115	1.5	3.15	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, Psocoptera
Psocoptera	Psocidae	DM	$M = a * L^b$	0.014	3.115	1.5	3.15	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, Psocoptera
Psocoptera	Psyllipsocidae	DM	$M = a * L^b$	0.014	3.115	1.5	3.15	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, Psocoptera
Psocoptera	Unidentifiable	DM	$M = a * L^b$	0.014	3.115	1.5	3.15	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, Psocoptera
Schizomida	Hubbardiidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott, 2009)	edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	inferred, hunting spiders
Symphyla	Scutegerillidae	DM	$M = a * L^b$	0.035	2.173	0.9	17.6	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, all insect taxa
Thysanoptera	Aeolothripidae	DM	$M = a * L^b$	0.035	2.173	0.9	17.6	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, all insect taxa
Thysanoptera	Phlaeothripidae	DM	$M = a * L^b$	0.035	2.173	0.9	17.6	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, all insect taxa
Thysanoptera	Thripidae	DM	$M = a * L^b$	0.035	2.173	0.9	17.6	(Gruner, 2003)	tip of abdom. to end of head or carap., excl. append.	inferred, all insect taxa
Thysanura	Nicoletiidae	DM	M = exp(a + b * log(L))	-3.628	2.494	2.13	54.51	(Sample *et al.*, 1993)	From frons to tip of abdom. excl. append.	inferred, all insect taxa

(b) Taxon	Equation FM [mg], DM [mg]	a	b	Reference	Regression specificity
Annelida	FM = exp(a + b * log(DM))	0.9282	1.0899	(Mercer *et al.*, 2001)	Oligochaeta
All other groups with dry-mass length-mass regressions, (see Table 7.4 a)	FM = exp(a + b * log(DM))	0.6111	1.0213	(Mercer *et al.*, 2001)	Insects

Table 7.5 – Regression parameters for individual metabolic rate calculation from the literature (Ehnes *et al.*, 2011) and unpublished data (Roswitha Ehnes). Phylogenetic model: ln I = ln i_{PG} + a_{PG} ln M – E_{PG} (1/kT) ; Linear model: ln I = ln i_o + a ln M – E (1/kT). I is the metabolic rate, a is the allometric exponent, E is the activation energy, k is the Boltzmann constant, T the temperature in Kelvin (in our models taken as local mean soil temperature) and i_o a normalisation factor.

Regression group	Applied to taxa	ln i_o / ln i_{PG}	a / a_{PG}	E / E_{PG}	Model
Arachnida	Araneae, Opiliones, Pseudoscorpionida, Schizomida	24.581	0.565	0.709	phylogenetic
Chilopoda	Chilopoda	28.253	0.558	0.803	phylogenetic
Clitellata	Clitellata	12.442	0.801	0.443	phylogenetic
Coleoptera	Coleoptera	21.418	0.738	0.639	phylogenetic
General invertebrates	Gastropoda	23.055	0.695	0.686	linear
Hymenoptera	Hymenoptera	22.013	0.742	0.668	phylogenetic
Insecta	Arachaeognatha, Blattodea, Dermaptera, Diplura, Diptera, Hemiptera, Isoptera, Lepidoptera, Mantodea, Neuroptera, Orthoptera, Plecoptera, Psocoptera, Symphyla, Thysanoptera, Thysanura	21.972	0.759	0.657	phylogenetic
Isopoda	Isopoda	23.169	0.554	0.687	phylogenetic
Progoneata	Diplopoda	22.347	0.571	0.67	phylogenetic

7.1. Supplementary methods to chapter 3

Calculation of energy fluxes (F) from community metabolism (X), assimilation efficiencies (e) and losses to predation (L). O, P, D, H, Pl and Dt denote omnivores, predators, detritivores, herbivores, plants and detritus. We denote total flux to a node I as F_I and the flux from node J to I as F_{IJ}. For example, F_O is the total flux to omnivores and F_{OP} is the flux from predators to omnivores. Assilimation efficiencies of animal food (0.60), plant food (0.45) and detritus food (0.25) (de Ruiter *et al.*, 1993) are given as e_a, e_p and e_d, respectively.

$$F_O = F_{OP} + F_{OH} + F_{OD} + F_{OPl} + F_{ODt} \tag{7.1}$$

We assume that predators, herbivores and detritivores each contribute to 1/4 of the omnivore diet and plants and detritus equally contribute to the remaining 1/4.

$$F_{OP} = F_{OH} = F_{OD} = \frac{1}{4}F_O \tag{7.2}$$

$$F_{OPl} = F_{ODt} = \frac{1}{8}F_O \tag{7.3}$$

The community metabolism X of a node is given as:

$$X = (F \cdot e) - L. \tag{7.4}$$

Thus, the energy entering the omnivore node is given as:

$$X_O + L = e_a \cdot (F_{OP} + F_{OH} + F_{OD}) + e_p \cdot F_{OPl} + e_d \cdot F_{ODt} = (\frac{3}{4}e_a + \frac{1}{8}e_p + \frac{1}{8}e_d) \cdot F_O, \tag{7.5}$$

where equations 7.2 and 7.3 were used to replace single fluxes with the fraction of the overall flux.
The efficiency with which omnivores assimilate resources is

$$e_O = (\frac{3}{4}e_a + \frac{1}{8}e_p + \frac{1}{8}e_d). \tag{7.6}$$

Now, to express F_O, e_O needs to be replaced by equation 7.6, which yields

$$F_O = \frac{1}{e_O} \cdot (X_O + \frac{F_P}{3}). \tag{7.7}$$

The equation for predators is similar but with the e_a assimilation efficiency, yielding

$$F_P = \frac{1}{e_a} \cdot (X_P + \frac{F_O}{4}). \tag{7.8}$$

We then solve for F_P by inserting equation 7.7 into 7.8:

$$F_P = \frac{12 \cdot e_O \cdot X_P + 3 \cdot X_O}{12 \cdot e_a \cdot e_O - 1} \tag{7.9}$$

Now we can calculate F_O using equation 7.7 and, with F_P and F_O we can calculate F_H and F_D using equations

$$F_H = \frac{1}{e_p} \cdot (X_H + \frac{F_P}{3} + \frac{F_O}{4}) \tag{7.10}$$

and

$$F_D = \frac{1}{e_d} \cdot (X_D + \frac{F_P}{3} + \frac{F_O}{4}). \tag{7.11}$$

Chapter 8.

Supplementary information to chapter 4

Table 8.1 – Taxonomic resolution, species numbers, individual numbers (ind.) and body mass of sampled higher taxa (Chapter 4) in the overall data set of 7,472 macro-invertebrates. After hand-collecting all animals visible to the naked eye, we excluded species belonging to the mesofauna (such as collembolans and mites), due to the limitations of the sampling method (sieving) regarding these groups. FG denotes the four feeding guilds: Detritivores (Det, 2242 individuals, 192 species), Herbivores (Her, 255 ind., 90 spec.), Omnivores (Omn, 3209 ind., 159 spec.) and Predators (Pre, 1766 ind., 430 spec.). Masses are minimum, maximum and median fresh body mass (mg), calculated from length-mass regressions (see Chapter 7). For some groups, order and family denote other higher and lower taxa, respectively.

FG	order (higher taxon)	families (lower taxa)	species	ind.	median mass	min mass	max mass
Det	Annelida		6	58	1.283	0.015	319.373
	Blattodea		25	326	1.363	0.012	395.080
		Blaberidae					
		Blattellidae					
		Blattidae					
	Coleoptera		42	110	0.366	0.042	36.948
		Anobiidae					
		Anthicidae					
		Bostrichidae					
		Curculionidae					
		Dermestidae					
		Elateridae					
		Hydrophilidae					
		Leiodidae					
		Mordellidae					
		Scarabaeidae					
		Silvanidae					
		Staphylinidae					
		Tenebrionidae					
	Diplopoda		27	150	1.593	0.009	798.488
		Chordeumatida					
		Glomeridae					
		Polydesmidae					
		Polyxenida					
		Siphonophorida					
		Spirobolida					
	Diptera		14	99	0.287	0.033	0.626
		Cecidomyiidae					
		Ceratopogonidae					
		Chironomidae					
		Drosophilidae					
		Phoridae					
		Sciaridae					
	Isopoda		36	128	0.571	0.006	126.799
	Isoptera		14	778	0.274	0.002	7.070
		Rhinotermitidae					

		Termitidae					
	Orthoptera		3	5	4.476	1.021	36.239
		Acrididae					
		Tetrigidae					
	Plecoptera		6	46	0.67	0.07	6.449
		Austroperlidae					
		Gripopterygidae					
		Notonemouridae					
	Psocoptera		17	507	0.127	0.003	0.623
		Archipsocidae					
		Caeciliidae					
		Ectopsocidae					
		Elipsocidae					
		Epipsocidae					
		Hemipsocidae					
		Lepidopsocidae					
		Pachytroctidae					
		Psocidae					
		Psyllipsocidae					
	Symphyla		2	35	0.46	0.107	1.095
		Scutegerillidae					
Her	Coleoptera		14	18	1.108	0.028	42.241
		Byrrhidae					
		Chrysomelidae					
		Curculionidae					
		Elateridae					
		Lucanidae					
		Melyridae					
		Scarabaeidae					
	Diptera		6	29	0.387	0.004	0.943
		Agromyzidae					
		Simuliidae					
		Tephritidae					
		Thaumaleidae					
	Hemiptera		27	42	0.803	0.04	149.672
		Anthocoridae					
		Aradidae					
		Cicadellidae					
		Cydnidae					
		Delphacidae					
		Eurybrachyidae					
		Lophopidae					
		Lygaeidae					
		Meenoplidae					
		Membracidae					
		Miridae					

		Pentatomidae					
		Triozidea					
	Lepidoptera		41	163	2.642	0.001	299.725
		Alucitidae					
		Arctiidae					
		Gelechiidae					
		Geometridae					
		Hesperiidae					
		Lasiocampidae					
		Lymantriidae					
		Noctuidae					
		Nolidae					
		Pterophoridae					
		Pyralidae					
	Orthoptera		1	1	46.391	46.391	46.391
		Eumastacidae					
	Thysanoptera		1	2	0.087	0.048	0.127
		Thripidae					
Omn	Archaeognatha		3	20	4.081	0.569	15.170
		Meinertellidae					
	Dermaptera		5	34	3.54	0.421	24.346
		Anisolabididae					
		Forficulidae					
	Diplura		1	13	1.524	0.733	5.136
		Heterojapygidae					
	Diptera		1	1	4.45	4.45	4.450
		Muscidae					
	Gastropoda		12	29	18.53	0.062	1213.95
	Hymenoptera		111	2985	0.426	0.003	56.907
		Bethylidae					
		Diapriidae					
		Eucoilidae					
		Eupelmidae					
		Figitidae					
		Formicidae					
		Mymariidae					
		Scelionidae					
		Trichogrammatidae					
	Opiliones		3	3	31.611	9.758	108.468
	Orthoptera		21	122	1.744	0.093	315.642
		Gryllidae					
	Thysanoptera		1	1	0.17	0.17	0.170
		Aeolothripidae					
	Thysanura		1	1	0.517	0.517	0.517
		Nicoletiidae					

Pre	Araneae		252	1079	0.803	0.02	769.383
		Anapidae					
		Araneidae					
		Barychelidae					
		Clubionidae					
		Corinnidae					
		Ctenidae					
		Deinopidae					
		Gnaphosidae					
		Hexathelidae					
		Lamponidae					
		Linyphiidae					
		Lycosidae					
		Micropholcommatidae					
		Miturgidae					
		Mysmenidae					
		Nemesiidae					
		Nephilidae					
		Ochyroceratidae					
		Oonopidae					
		Oxyopidae					
		Palpimanidae					
		Pararchaeidae					
		Philodromidae					
		Pholcidae					
		Prodidomidae					
		Salticidae					
		Scytodidae					
		Segestriidae					
		Sparassidae					
		Stenochilidae					
		Symphytognathidae					
		Telemidae					
		Tetrablemmidae					
		Tetragnathidae					
		Theridiidae					
		Theridiosomatidae					
		Thomisidae					
		Uloboridae					
		Zodariidae					
	Chilopoda		15	136	3.279	0.109	163.176
		Ballophilidae					
		Cryptopidae					
		Henicopidae					
		Lithobiomorpha					
		Mecistocephalidae					

	Scolopendridae					
Coleoptera		95	318	0.317	0.02	44.247
	Carabidae					
	Chelonariidae					
	Ciidae					
	Coccinellidae					
	Dermestidae					
	Histeridae					
	Pselaphidae					
	Scydmaenidae					
	Silvanidae					
	Staphylinidae					
	Trogossitidae					
Diptera		1	1	0.943	0.943	0.943
	Syrphidae					
Hemiptera		44	104	0.271	0.002	99.920
	Acanthosomatidae					
	Ceratocombidae					
	Dipsocoridae					
	Enicocephalidae					
	Hebridae					
	Hydrometridae					
	Mesoveliidae					
	Nabidae					
	Reduviidae					
	Schizopteridae					
Hymenoptera		1	1	5.325	5.325	5.325
	Sphecidae					
Mantodea		4	15	0.4	0.112	19.827
	Mantidae					
Neuroptera		1	4	0.94	0.47	1.741
	Chrysopidae					
Opiliones		11	60	2.351	0.407	25.475
Pseudoscorpionida		5	46	0.238	0.026	5.242
Schizomida		1	2	6.01	4.06	7.960
	Hubbardiidae					
total		871	7472			

Table 8.2 – Literature and online resources used for the identification of the 7,472 animal individuals to family (orother lower taxon) and morphospecies, listed per order (or other higher taxon). Individuals were first sorted into higher taxa and, from there, further identified to morphospecies by experts within the team. All individuals of one order (higher taxon) have therefore been identified by only one team member, additionally using an internal data base, to warrant consistency within taxa. Animals, as well as the internal data base containing the morphospecies descriptions, are stored and treated according to the rules of the EFForTS project.

order (higher taxon)	resources used for identification
Annelida	Blakemore (2010)
Araneae	Jocqué & Dippenaar-Schoeman (2007)
Archaeognatha, Blattodea, Coleoptera, Dermaptera, Diplura, Diptera, Hemiptera, Lepidoptera, Mantodea, Neuroptera, Orthoptera, Plecoptera, Psocoptera, Thysanoptera, Thysanura	Chu (1949); CSIRO Division of Entomology (1991); Johnson & Triplehorn (2004); Stehr (2005) http:anic.ento.csiro.au/insectfamilies/
Chilopoda, Diplopoda	Cloudsley-Thompson (1958); Enghoff (2005)
Gastropoda	Bährmann (2008)
Hymenoptera	CSIRO Division of Entomology (1991); Centre for Land and Biological Resources Research (1993)
Isopoda	Bährmann (2008)
Isoptera	CSIRO Division of Entomology (1991); Tho (1992); Johnson & Triplehorn (2004)
Opiliones, Schizomida	Cloudsley-Thompson (1958)
Pseudoscorpionida	Buddle (2010)
Symphyla	Hansen (1903); Edwards (1959); Enghoff (2005)

Table 8.3 – Number of leaf types sampled on each of the 32 sites. Sites are coded as "landscape-land use system-replicate", where the two landscapes are Harapan rainforest (H) and Bukit Duabelas (B), the land-use systems are forest (F), jungle rubber (J), oil palm (O), and rubber (R), and the replicates are coded 1-4.

site	no of leaf types
BF1	8
BF2	9
BF3	7
BF4	7
BJ1	6
BJ2	7
BJ3	7
BJ4	7
BO1	7
BO2	4
BO3	3
BO4	3
BR1	2
BR2	2
BR3	1
BR4	3
HF1	6
HF2	10
HF3	7
HF4	9
HJ1	10
HJ2	9
HJ3	6
HJ4	9
HO1	2
HO2	2
HO3	4
HO4	3
HR1	1
HR2	3
HR3	1
HR4	4

Table 8.4 – Number of animal individuals per feeding type analyzed for C:N content for each of the 32 sites (overall $n = 391$). Missing values for herbivores were substituted by the average C:N ratio of herbivores in the other three sites of the same land-use system and in the same landscape. Sites are coded as "landscape-land use system-replicate", where the two landscapes are Harapan rainforest (H) and Bukit Duabelas (B), the land-use systems are forest (F), jungle-rubber (J), oil palm (O), and rubber (R), and the replicates are coded 1-4.

site	predators	omnivores	detritivores	herbivores
BF1	6	4	3	2
BF2	7	7	2	2
BF3	4	5	4	1
BF4	6	4	4	1
BJ1	6	1	3	1
BJ2	7	5	3	1
BJ3	3	4	4	2
BJ4	6	2	4	1
BO1	2	3	6	1
BO2	3	2	3	2
BO3	5	2	3	2
BO4	3	3	2	1
BR1	3	2	3	2
BR2	3	2	3	2
BR3	4	5	4	2
BR4	3	3	3	2
HF1	4	2	3	1
HF2	6	2	3	1
HF3	3	4	5	0
HF4	3	1	4	2
HJ1	3	4	5	2
HJ2	5	4	2	0
HJ3	3	2	4	1
HJ4	6	3	3	1
HO1	4	3	6	2
HO2	3	3	3	0
HO3	3	1	4	2
HO4	4	2	2	1
HR1	3	2	3	2
HR2	4	4	6	1
HR3	6	3	3	2
HR4	5	3	4	1
total	136	97	114	44

Table 8.5 – Litterfall weighting for the 32 sites. For forest sites, we averaged over the C : N ratios of all leaf types to gain the site-specific litter-quality measure. For jungle rubber and rubber sites, we applied site-specific data on relative litter fall (Kotowska *et al.*, 2015) of rubber and other leaf types to weight the C : N ratios of the local rubber leaves against an average of all other leaf types per site. Missing litter-fall data for single sites was substituted by means from the respective land-use system in the same landscape. For the oil-palm sites, we assumed an overall importance of 50% for the oil palm C : N ratio and 50% for the average of the remaining local leaf types. Sites are coded as "landscape-land use system-replicate", where the two landscapes are Harapan rainforest (H) and Bukit Duabelas (B), the land-use systems are forest (F), jungle-rubber (J), oil palm (O), and rubber (R), and the replicates are coded 1-4.

site	landscape	land-use system	percent rubber	percent oil palm	percent other
BF1	B	F	0	0	100
BF2	B	F	0	0	100
BF3	B	F	0	0	100
BF4	B	F	0	0	100
BJ1	B	J	7	0	93
BJ2	B	J	7	0	93
BJ3	B	J	10	0	90
BJ4	B	J	3	0	97
BO1	B	O	0	50	50
BO2	B	O	0	50	50
BO3	B	O	0	50	50
BO4	B	O	0	50	50
BR1	B	R	74	0	26
BR2	B	R	73	0	27
BR3	B	R	87	0	13
BR4	B	R	91	0	9
HF1	H	F	0	0	100
HF2	H	F	0	0	100
HF3	H	F	0	0	100
HF4	H	F	0	0	100
HJ1	H	J	20	0	80
HJ2	H	J	8	0	92
HJ3	H	J	10	0	90
HJ4	H	J	7	0	93
HO1	H	O	0	50	50
HO2	H	O	0	50	50
HO3	H	O	0	50	50
HO4	H	O	0	50	50
HR1	H	R	70	0	30
HR2	H	R	82	0	18
HR3	H	R	70	0	30
HR4	H	R	61	0	39

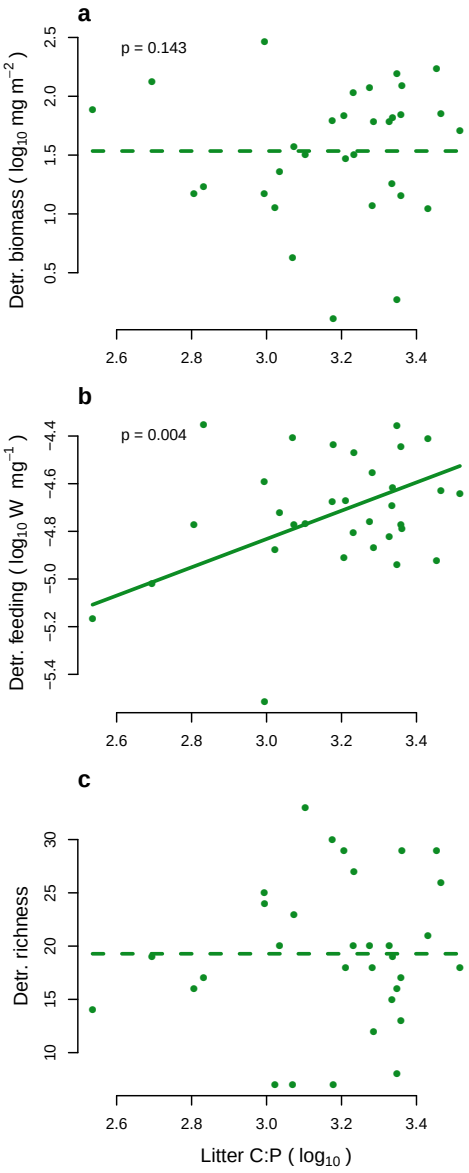

Figure 8.1 – Effects of resource quality depletion (higher C : P ratios) on macro-invertebrate detritivores. Linear mixed effects models for (green lines and points) detritivore biomass (a), feeding (b) and species richness (3 m^2) (c) in response to increasing litter C : P for each site ($n = 32$). The three relationships correspond to Figure 4.2 c, e and g where litter C : N effects are tested. Model selection was done as described in Supplementary methods 2. Litter C : P values are site-specific litter-fall weighted averages (see Table 8.5). Elemental carbon and phosphorus content was measured as milligram per gram dry weight from litter specimens using a CHNSO analyzer and an ICP-OES setup. Feeding is per-unit-biomass detritivore feeding per site. Relationships shown and p-values presented are for just resource C : P from the best models according to AICc that also included resource C : P. Regression fit for b) was plotted as the effect of C : P on feeding while holding litter mass constant at its mean. Dashed lines in a) and c) show the average response value for not significant relationships. Where indicated, data were log_{10}-transformed to meet the assumptions of normality.

Table 8.6 – The temperature values used in the calculation of individual metabolic rates are site-specific annual mean temperatures from measurements of soil temperature at 30 *cm* depth from 2014. Two missing values were replaced my mean temperature of the three other sites from the same land-use system within the same landscape. Minimum and maximum annual mean site temperatures were 24.5 °C (forest) and 27.3 °C (oil palm), respectively. The table shows means for the four different transformation systems: forest (F), jungle rubber (J), rubber (R) and oil palm (O) ($n = 8$ each).

Land-use system	Mean temperature (°C)
F	25.2
J	25.4
R	26.0
O	26.2

Table 8.7 – Literature-values of food nitrogen (foodN) content and assimilation efficiency (e_a) for 46 consumer-resource pairs of arthropod detritivore ($n = 19$) and predator consumers ($n = 27$) and their resources, with "ecotype" coding for terrestrial and freshwater ecosystem types and "ftype" giving consumer feeding types. The consumer order is given in the first column. The two last columns provide information on the references for food nitrogen content and assimilation efficiencies for the respective consumer-resource pairs. Information on consumer-resource pairs has been taken from Pandian & Marian (1986) and an unpublished data base (Lang *et al.*, in preparation). In order to obtain realistic relationships between food nitrogen content and assimilation efficiency, a literature survey was performed looking for data on arthropod assimilation efficiency measurements in response to resource quality. From the available resources, we only used data on arthropod detritivores and predators. The values represent typical values for arthropod detritivores and predators.

consumer order	consumer	resource	foodN (percent)	e_a (percent)	ecotype	ftype	reference foodN	reference e_a
Araneida	*Pardosa palustris*	*Drosophila*	8.00	89.04	terrestrial	predator	Markow *et al.* (1999)	Steigen (1975)
Araneida	*Pardosa palustris*	*Drosophila*	8.00	80.92	terrestrial	predator	Markow *et al.* (1999)	Steigen (1975)
Araneida	*Pardosa palustris*	*Drosophila*	8.00	79.55	terrestrial	predator	Markow *et al.* (1999)	Steigen (1975)
Araneida	*Pardosa palustris*	*Drosophila*	8.00	79.35	terrestrial	predator	Markow *et al.* (1999)	Steigen (1975)
Araneida	*Pardosa palustris*	*Drosophila*	8.00	79.26	terrestrial	predator	Markow *et al.* (1999)	Steigen (1975)
Araneida	*Pardosa palustris*	*Drosophila*	8.00	77.25	terrestrial	predator	Markow *et al.* (1999)	Steigen (1975)
Araneida	*Pardosa palustris*	*Drosophila*	8.00	83.10	terrestrial	predator	Markow *et al.* (1999)	Steigen (1975)
Coleoptera	*Melanotus rufipes*	Dipteran larvae	9.70	90.00	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)
Diplopoda	*Chromatojulus projectus*	oak leave litter	0.71	16.00	terrestrial	detritivore	Ott et al. unpublished	Gere (1956)
Diplopoda	*Chromatojulus projectus*	oak leave litter	0.71	12.50	terrestrial	detritivore	Ott et al. unpublished	Gere (1956)
Diplopoda	*Cylindroiulus luridus*	ash litter	1.17	16.40	terrestrial	detritivore	Ott et al. unpublished	Poboszny (1997)
Diplopoda	*Glomeris hexasticha*	oak leave litter	0.71	11.90	terrestrial	detritivore	Ott et al. unpublished	Gere (1956)
Diplopoda	*Glomeris hexasticha*	oak leave litter	0.71	5.00	terrestrial	detritivore	Ott et al. unpublished	Gere (1956)
Diplopoda	*Glomeris marginata*	ash litter	1.17	8.30	terrestrial	detritivore	Ott et al. unpublished	Bocock (1963)
Diplopoda	*Megaphyllum projectum*	ash litter	1.17	19.10	terrestrial	detritivore	Ott et al. unpublished	Poboszny (1997)
Diplopoda	*Protracheoniscus politus*	oak leave litter	0.71	13.30	terrestrial	detritivore	Ott et al. unpublished	Gere (1956)
Diplopoda	*Unciger foetidus*	ash litter	1.17	30.50	terrestrial	detritivore	Ott et al. unpublished	Poboszny (1997)
Diptera	*Simulium ornatum*	Detritus	0.40	5.00	freshwater	detritivore	Pandian & Marian (1986)	Pandian & Marian (1986)
Ephemeroptera	*Hexagenia limbata*	Sediment	0.05	18.00	freshwater	detritivore	Pandian & Marian (1986)	Pandian & Marian (1986)
Ephemeroptera	*Hexagenia limbata*	Sediment	0.08	20.00	freshwater	detritivore	Pandian & Marian (1986)	Pandian & Marian (1986)
Ephemeroptera	*Hexagenia limbata*	Sediment	0.40	8.00	freshwater	detritivore	Pandian & Marian (1986)	Pandian & Marian (1986)
Ephemeroptera	*Hexagenia limbata*	Sediment	0.90	23.00	freshwater	detritivore	Pandian & Marian (1986)	Pandian & Marian (1986)
Ephemeroptera	*Hexagenia limbata*	Sediment	1.00	36.00	freshwater	detritivore	Pandian & Marian (1986)	Pandian & Marian (1986)
Hemiptera	*Sphaerodema annulatus*	*Culex larva*	8.50	97.00	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)
Hemiptera	*Sphaerodema annulatus*	*Culex larva*	8.50	95.00	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)
Hemiptera	*Sphaerodema annulatus*	*Culex larva*	8.50	96.00	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)
Hemiptera	*Sphaerodema annulatus*	*Culex larva*	8.50	93.00	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)
Hemiptera	*Sphaerodema annulatus*	*Culex larva*	8.50	94.00	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)
Isopoda	*Asellus aquaticus*	alder leaves	1.48	26.30	freshwater	detritivore	Ott et al. unpublished	Prus (1971)
Odonata	*Pyrrhosoma nymphula*	*Chironomus*	9.70	84.00	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)
Odonata	*Pyrrhosoma nymphula*	*Cleon*	9.10	91.00	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)
Odonata	*Pyrrhosoma nymphula*	*Asellus*	8.20	77.00	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)
Odonata	*Pyrrhosoma nymphula*	*Daphnia*	8.50	86.00	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)
Odonata	*Pyrrhosoma nymphula*	*Daphnia*	8.50	87.00	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)
Odonata	*Pyrrhosoma nymphula*	*Daphnia*	8.50	88.30	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)

Odonata	*Diplacodes trivialis*	*Artemisia salina*	9.80	91.00	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)
Odonata	*Brachythemis contaminata*	*Artemisia salina*	9.80	89.00	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)
Odonata	*Orthetrum sabina*	*Artemisia salina*	9.80	89.50	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)
Odonata	*Pantala flavescens*	*Culex fatigans*	8.50	91.50	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)
Plecoptera	*Pteronarcys scotti*	leaves (detritus)	0.40	11.00	freshwater	detritivore	Pandian & Marian (1986)	Pandian & Marian (1986)
Plecoptera	*Acroneuria pacifica*	Midge larvae	9.70	83.00	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)
Plecoptera	*Acroneuria californica*	Midge larvae	9.70	83.00	freshwater	predator	Pandian & Marian (1986)	Pandian & Marian (1986)
Plecoptera	*Acroneuria californica*	*Hydropsyche sp.*	9.20	88.10	freshwater	predator	Pandian & Marian (1986)	Heiman & Knight (1975)
Plecoptera	*Acroneuria californica*	*Simulium sp.*	9.20	90.00	freshwater	predator	Pandian & Marian (1986)	Heiman & Knight (1975)
Trichoptera	*Arctopsyche irrorata*	vascular plant detritus	0.40	10.00	freshwater	detritivore	Pandian & Marian (1986)	Pandian & Marian (1986)
Trichoptera	*Arctopsyche irrorata*	fine detritus	0.40	10.00	freshwater	detritivore	Pandian & Marian (1986)	Pandian & Marian (1986)

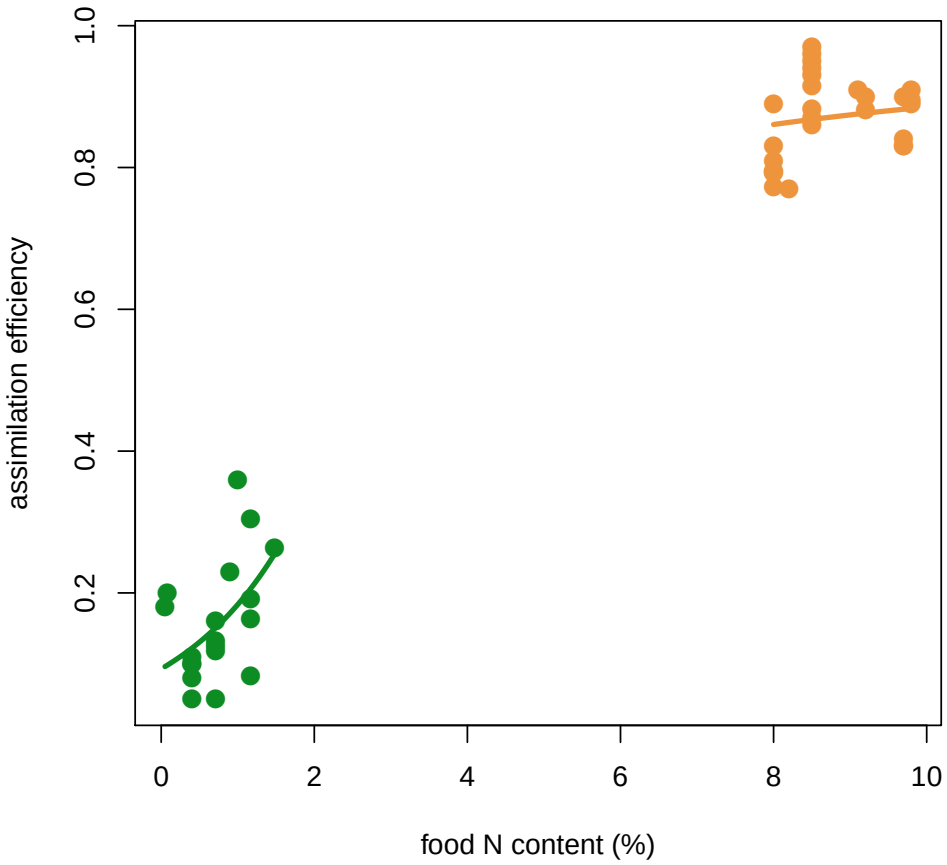

Figure 8.2 – Relationship of food nitrogen (N) content and assimilation efficiency for detritivores (green) and predators (orange) for the literature data (see Table 8.7). The green line represents the best-fit exponential model for the detritivore assimilation efficiency (eDet, $mean = 0.16$) and the orange line represents the best-fit Michaelis-Menten model for the predator assimilation efficiency (ePre, $mean = 0.87$) against their food nitrogen content. Assimilation efficiencies are presented as a ratio between 0 and 1. Regression parameters are presented in Supplementary methods 1.

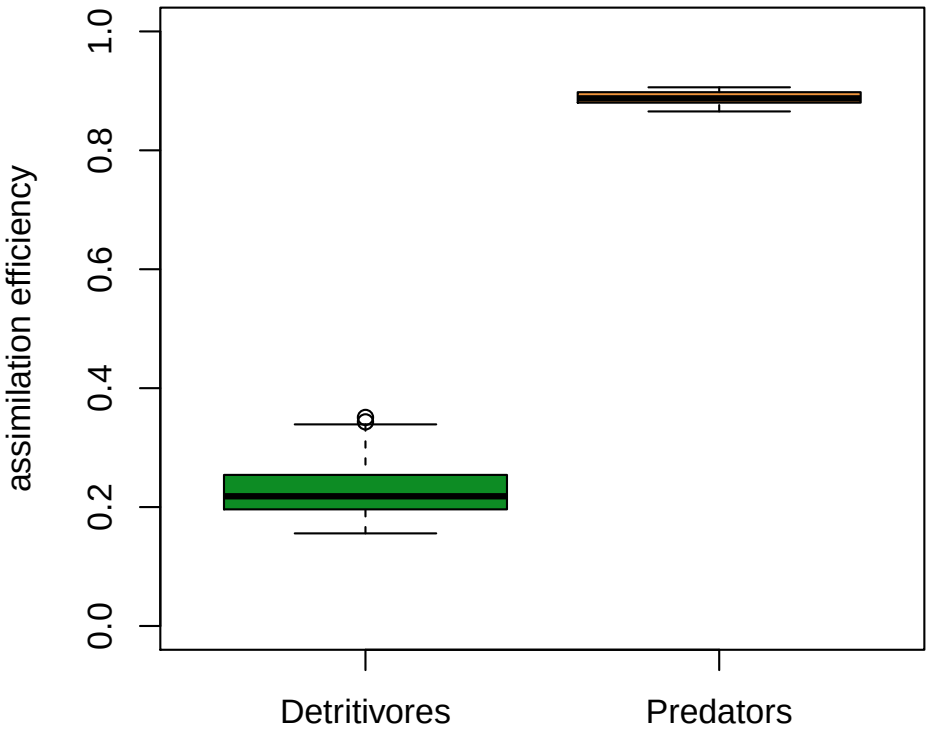

Figure 8.3 – Boxplots of calculated values for detritivore (green) and predator (orange) assimilation efficiencies (eDet and ePre) for each site (n = 32) calculated in response to the site-specific resource nitrogen content. Values have been calculated using the best-fit models from the literature values (see Supplementary methods 1, Table 8.7 and Figure 8.2). As resources, we used the site-specific nitrogen content of the weighted leaf litter specimen (see Table 8.5) for detritivores and the nitrogen content of herbivores, omnivores and detritivores weighted by their relative abundance among the possible prey organisms for predators (see Table 8.8) to account for different prey types in their diet. Assimilation efficiencies are presented as a ratio between 0 and 1.

Table 8.8 – Relative abundance (%) of detritivores, omnivores and herbivores among the possible prey organisms for predators on each of the 32 sites. Sites are coded as "landscape-land use system-replicate", where the two landscapes are Harapan rainforest (H) and Bukit Duabelas (B), the land-use systems are forest (F), jungle-rubber (J), oil palm (O), and rubber (R), and the replicates are coded 1-4.

site	detritivores	omnivores	herbivores
BF1	49	46	5
BF2	14	84	2
BF3	21	78	2
BF4	27	71	2
BJ1	57	39	3
BJ2	36	56	8
BJ3	28	71	1
BJ4	38	47	15
BO1	57	40	3
BO2	72	25	3
BO3	40	55	5
BO4	39	48	13
BR1	27	64	9
BR2	56	30	14
BR3	54	36	10
BR4	39	55	7
HF1	45	52	3
HF2	36	63	1
HF3	17	82	1
HF4	57	43	1
HJ1	23	67	10
HJ2	19	80	1
HJ3	57	37	6
HJ4	50	45	5
HO1	61	36	3
HO2	22	69	8
HO3	63	33	3
HO4	28	70	2
HR1	64	33	2
HR2	48	40	12
HR3	24	68	8
HR4	49	48	2

8.1. Supplementary methods 1 to chapter 4

In order to select the best fit for the relationship of the food nitrogen content ($foodN$) and assimilation efficiency (e_a) data from Table 8.7, we tested four different models for each of the two feeding guilds: a) a linear model, b) a power law, c) a Michaelis-Menten model, and d) an exponential relationship:

a)

$$e_a = a \cdot foodN + b \tag{8.1}$$

b)

$$e_a = a \cdot foodN^b \tag{8.2}$$

c)

$$e_a = \frac{1 \cdot foodN}{a + foodN} \tag{8.3}$$

d)

$$e_a = a \cdot e^{(b \cdot foodN)} \tag{8.4}$$

We then performed a two-step model selection approach, first choosing the best models by AIC (delta AIC < 2 from the lowest value),

detritivore model	AIC	predator model	AIC
a) linear	**-39.110**	a) linear	**-74.206**
b) power law	-36.290	b) power law	**-74.416**
c) Michaelis Menten	-36.180	c) Michaelis Menten	**-75.933**
d) exponential	**-39.920**	d) exponential	**-74.142**

and subsequently selecting the most significant one of these AIC-selected best models:

model	model parameter	estimate	std. Error	t-value	p-value
Det e_a a)	a	0.095	0.046	2.055	0.056
	b	0.090	0.038	2.368	0.030
Det e_a d)	a	0.093	0.027	3.476	**0.003**
	b	0.682	0.289	2.362	**0.030**
Pre e_a a)	a	0.024	0.016	1.468	0.155
	b	0.662	0.143	4.633	9.65e-05
Pre e_a b)	a	0.507	0.181	2.809	0.010
	b	0.250	0.164	1.522	0.140
Pre e_a c)	a	1.295	0.124	10.44	**8.52e-11**
Pre e_a d)	a	0.690	0.113	6.119	2.14e-06
	b	0.027	0.019	1.432	0.165

This procedure resulted in choosing the exponential model (d) for the detritivore relationship and the Michaelis-Menten model (c) for the predator relationship. Figure 8.2 and 8.3 show the two fits for the literature data and the calculated assimilation efficiencies for detritivores and predators from this study, respectively.

8.2. Supplementary methods 2 to chapter 4

In order to decide if resource C : N is still important even if habitat structure and resource biomass are also included in the linear mixed effects models, we implemented the following model selection procedure:

Firstly, a full model was established. This included litter C : N and litter mass (both, habitat structure and resource biomass) for detritivore (Det) responses as well as detritivore C : N, litter mass (habitat structure) and detritivore biomass (resource biomass) for predator (Pre) responses. Secondly, for each of the consumer community response parameters (C : N (CN), biomass (B), feeding (F) and species richness (S)), we analyzed all possible factor combinations for their AICc using the "dredge" function in the R package "MuMIn" (Barton, 2015). We employed linear mixed effects models (lme) with land- use system nested within the landscape used as a random factor for all models to account for the study design. The model selection table results are given below. Bold AICc and delta AICc values indicate models within 2 delta AICc units from the best model (top-ranked models). From these top-ranked models, we then chose the best model (lowest AICc) that included resource C : N to account for the questions we aim to answer in our study. When resource C : N was not included in any top-ranked model, we chose the model with the best AICc. The resulting chosen models are indicated by an asterisk, their summary outputs are presented in Table 4.1 and, where significant responses to resource C : N were among the top-ranked models, these are plotted in Figure 4.2.

Response and model formula	Intercept	Slope resource C : N	Slope littermass	Slope DetB	DF	AICc	Delta	Best model
detritivore C/N	5.299		-3.968		5	**70.8**	**0.00**	*
DetCN ~ log10(litterCN) + littermass	4.943				4	**71.9**	**1.15**	
	3.919	0.90570	-4.479		6	73.3	2.55	
	5.046	-0.06547			5	74.7	3.97	
predator C/N	0.6230				4	**-112.1**	**0.00**	
log10(PreCN) ~ log10(DetCN) + log10(DetB) + littermass	0.7293	-0.1539			5	**-111.0**	**1.10**	*
	0.6257			-0.001748	5	-109.3	2.81	
	0.6217		0.01407		5	-109.3	2.81	
	0.7409	-0.1605		-0.004606	6	-108.1	4.01	
	0.7434	-0.1672	-0.05571		6	-108.1	4.01	
	0.6246		0.02281	-0.002363	6	-106.2	5.84	
	0.7483	-0.1683	-0.04206	-0.003455	7	-104.8	7.25	
detritivore biomass	1.077		5.092		5	**53.9**	**0.00**	
log10(DetB) ~ log10(litterCN) + littermass	2.951	-1.2290	5.786		6	**55.4**	**1.46**	*
	1.534				4	60.9	7.01	
	1.859	-0.2058			5	63.7	9.81	
predator biomass	1.539		3.590		5	**33.9**	**0.00**	
log10(PreB) ~ log10(DetCN) + log10(DetB) + littermass	2.850	-1.803	2.861		6	**34.4**	**0.55**	*
	3.309	-2.097			5	**34.7**	**0.84**	
	1.299		2.946	0.1940	6	**34.9**	**1.07**	
	3.010	-2.108		0.2003	6	**35.0**	**1.12**	
	1.862				4	**35.4**	**1.52**	

	1.543			0.2079	5	**35.6**	**1.73**	
	2.603	-1.732	2.248	0.1648	7	36.0	2.12	
detritivore feeding	-6.783	1.413	-1.845		6	**4.5**	**0.00**	*
log10(DetF) ~ log10(litterCN) + littermass	-6.307	1.006			5	7.8	3.31	
	-4.723				4	9.6	5.13	
	-4.629		-1.048		5	10.6	6.07	
predator feeding	-2.923e-06	9.244e-06	-1.104e-05		6	**-767.8**	**0.00**	*
PreF ~ log10(DetCN) + log10(DetB) + littermass	-3.700e-06	9.405e-06	-1.411e-05	6.142e-07	7	**-766.5**	**1.36**	
	3.754e-06		-1.431e-05		5	**-766.2**	**1.65**	
	3.124e-06		-1.729e-05	5.851e-07	6	-764.6	3.19	
	-6.741e-06	1.334e-05			5	-764.1	3.75	
	-6.575e-06	1.322e-05		-5.534e-08	6	-761.0	6.79	
	2.470e-06				4	-759.2	8.67	
	2.547e-06			-5.072e-08	5	-756.3	11.49	
detritivore species richness	79.94	-38.52			5	**216.6**	**0.00**	*
DetS ~ log10(litterCN) + littermass	70.32	-35.36	51.65		6	**217.0**	**0.37**	
	14.57		52.47		5	219.8	3.15	
	19.28				4	220.9	4.21	
predator species richness	9.301		120.3	7.101	6	**249.9**	**0.00**	
PreS ~ log10(DetCN) + log10(DetB) + littermass	51.200	-57.74	100.8	6.922	7	**250.0**	**0.11**	*
	60.100	-59.59	134.3		6	**250.4**	**0.50**	
	17.100		154.9		5	**250.4**	**0.55**	
	70.990	-81.84		10.770	6	253.9	4.01	
	15.080			10.370	5	256.0	6.18	
	84.710	-77.78			5	258.0	8.09	
	31.000				4	259.3	9.44	

Chapter 9.

Supplementary information to chapter 5

Table 9.1 – Model averaging results for the body mass-biomass relationship: For each animal set (taxonomic groups, functional feeding guilds and the overall data set), the table shows the number of populations in the data set, the number of best candidate models (top mod.) within ΔAICc 4 from the model with the lowest AICc, and for each predictor (structural and stoichiometric variables) the number of models within the set of best candidate models that it was included in (n) and the importance of the variable within the set of best candidate models (imp.). The importance gives the "sum of Akaike weights over all models including the explanatory variable" (Barton, 2015). NA's denote variables not included in any of the best candidate models. Abbreviations: LM (litter mass), prich (plant species richness), CX (C:element ratio) and M (population-averaged body mass). Asterisks denote interactions.

group	ants	cockroaches	centipedes	beetles	millipedes	woodlice	termites	harvestmen	crickets	spiders	detritivores	predators	omnivores	herbivores	all
no. populations	459	128	67	272	64	71	55	37	89	590	617	992	630	175	2414
no. top mod.	249	92	55	478	20	105	54	20	95	66	132	325	400	127	182
LM [n]	153	15	8	138	2	40	53	3	52	66	32	186	296	34	72
LM [imp.]	0.62	0.14	0.11	0.27	0.09	0.35	0.99	0.11	0.50	1.00	0.23	0.55	0.74	0.24	0.39
prich [n]	58	26	8	264	2	66	5	15	20	64	120	276	161	69	32
prich [imp.]	0.20	0.24	0.12	0.55	0.08	0.66	0.06	0.83	0.19	0.98	0.91	0.87	0.37	0.50	0.15
pH [n]	117	24	10	179	2	48	15	2	47	60	39	139	112	32	27
pH [imp.]	0.48	0.25	0.14	0.35	0.08	0.48	0.24	0.07	0.46	0.92	0.27	0.41	0.27	0.21	0.13
CN [n]	126	34	17	92	2	9	20	4	32	7	19	94	82	23	39
CN [imp.]	0.50	0.36	0.35	0.17	0.08	0.07	0.40	0.17	0.38	0.09	0.12	0.26	0.18	0.15	0.18
CP [n]	95	16	11	217	2	27	17	2	13	16	26	69	153	18	42
CP [imp.]	0.35	0.14	0.19	0.43	0.08	0.20	0.31	0.09	0.12	0.19	0.17	0.19	0.37	0.12	0.20
CK [n]	74	25	13	146	19	8	5	2	10	14	21	94	100	20	28
CK [imp.]	0.26	0.23	0.18	0.30	0.98	0.06	0.06	0.06	0.09	0.19	0.13	0.27	0.22	0.14	0.13
CCa [n]	32	8	10	128	11	87	54	1	11	10	131	196	58	19	75
CCa [imp.]	0.11	0.07	0.14	0.25	0.42	0.87	1.00	0.04	0.09	0.13	1.00	0.63	0.12	0.12	0.40
CMg [n]	31	9	5	265	2	8	5	2	19	63	107	56	55	17	30
CMg [imp.]	0.11	0.08	0.08	0.53	0.08	0.06	0.10	0.07	0.18	0.97	0.82	0.15	0.11	0.10	0.14
CNa [n]	38	17	7	118	2	6	5	1	31	64	71	162	66	16	33
CNa [imp.]	0.13	0.15	0.11	0.22	0.08	0.05	0.08	0.05	0.28	0.98	0.52	0.48	0.14	0.11	0.15
CS [n]	156	24	7	158	2	45	51	1	25	12	15	57	241	87	57
CS [imp.]	0.62	0.23	0.10	0.31	0.10	0.47	0.96	0.07	0.28	0.16	0.09	0.14	0.59	0.67	0.30
M*LM [n]	15	NA	NA	37	NA	14	39	NA	4	49	3	57	167	4	7
M*LM [imp.]	0.05	NA	NA	0.08	NA	0.14	0.75	NA	0.03	0.78	0.02	0.15	0.42	0.02	0.03
M*prich [n]	1	1	3	101	NA	39	1	3	1	17	25	270	47	6	2
M*prich [imp.]	< 0.01	0.01	0.03	0.21	NA	0.44	0.01	0.11	0.01	0.22	0.18	0.86	0.10	0.03	0.01
M*pH [n]	13	3	3	136	NA	5	2	NA	4	11	3	109	35	2	3
M*pH [imp.]	0.04	0.03	0.04	0.28	NA	0.05	0.03	NA	0.03	0.17	0.02	0.33	0.07	0.01	0.01
M*CN [n]	89	1	1	10	NA	NA	17	1	2	NA	NA	9	8	3	4
M*CN [imp.]	0.35	0.01	0.02	0.02	NA	NA	0.36	0.03	0.02	NA	NA	0.02	0.02	0.02	0.02
M*CP [n]	12	1	1	180	NA	1	2	NA	NA	1	2	18	43	NA	3
M*CP [imp.]	0.04	0.01	0.02	0.37	NA	0.01	0.04	NA	NA	0.01	0.01	0.05	0.10	NA	0.01
M*CK [n]	12	7	1	109	19	NA	1	NA	NA	1	2	94	8	NA	2
M*CK [imp.]	0.04	0.06	0.01	0.23	0.98	NA	0.01	NA	NA	0.01	0.01	0.27	0.01	NA	0.02
M*CCa [n]	NA	NA	1	16	1	9	4	NA	NA	4	17	183	7	1	11
M*CCa [imp.]	NA	NA	0.01	0.03	0.03	0.07	0.05	NA	NA	0.06	0.11	0.60	0.01	0.01	0.05
M*CMg [n]	1	NA	NA	42	NA	NA	NA	1	1	8	21	7	3	3	3

M*CMg [imp.]	< 0.01	NA	NA	0.07	NA	NA	NA	0.03	0.01	0.10	0.14	0.02	< 0.01	0.02	0.01
M*CNa [n]	1	NA	NA	10	NA	NA	1	NA	2	9	8	34	5	NA	3
M*CNa [imp.]	< 0.01	NA	NA	0.02	NA	NA	0.02	NA	0.01	0.11	0.05	0.09	0.01	NA	0.01
M*CS [n]	61	19	NA	32	NA	5	8	NA	2	1	NA	4	172	57	29
M*CS [imp.]	0.24	0.18	NA	0.06	NA	0.04	0.11	NA	0.02	0.01	NA	0.01	0.44	0.43	0.15

Table 9.2 – Correlation table for the predictor variables used in the statistical analysis: Upper diagonal part contains Pearson correlation coefficient estimates and lower diagonal part contains the corresponding p-values. Abbreviations: LM (litter mass), prich (plant species richness) and C:element ratios. The table has been created using the "ltm" package (Rizopoulos, 2006) in R.

*****	LM	prich	pH	CN	CP	CK	CCa	CMg	CNa	CS
LM	*****	0.692	-0.572	0.103	0.425	-0.067	0.302	-0.094	0.274	-0.161
prich	<0.001	*****	-0.491	-0.112	0.278	-0.338	0.613	0.056	-0.069	-0.032
pH	0.001	0.004	*****	0.197	0.046	0.083	-0.416	-0.295	-0.098	-0.037
CN	0.574	0.541	0.279	*****	0.556	0.199	-0.029	-0.097	0.036	0.300
CP	0.015	0.123	0.805	0.001	*****	0.366	0.308	-0.204	0.273	0.249
CK	0.715	0.059	0.651	0.274	0.040	*****	-0.023	0.032	0.335	0.130
CCa	0.093	<0.001	0.018	0.876	0.086	0.901	*****	0.327	-0.019	0.462
CMg	0.609	0.759	0.101	0.599	0.263	0.862	0.068	*****	0.144	0.162
CNa	0.129	0.708	0.594	0.846	0.130	0.061	0.920	0.433	*****	0.004
CS	0.378	0.863	0.841	0.096	0.170	0.480	0.008	0.377	0.981	*****

Table 9.3 – Model averaging results for species richness: For each animal set (taxonomic groups, functional feeding guilds and the overall data set), the table shows the number of best candidate models (top mod.) within ΔAICc 4 from the model with the lowest AICc, and for each predictor (structural and stoichiometric variables) the number of models within the set of best candidate models that it was included in (n) and the importance of the variable within the set of best candidate models (imp.). The importance gives the "sum of Akaike weights over all models including the explanatory variable" (Barton, 2015). NA's denote variables not included in any of the best candidate models. Abbreviations: LM (litter mass), prich (plant species richness) and CX (C:element ratio).

group	ants	cockroaches	centipedes	beetles	millipedes	woodlice	termites	harvestmen	crickets	spiders	detritivores	predators	omnivores	herbivores	all
no. top mod.	19	18	33	21	38	13	31	23	17	9	9	15	9	21	15
LM [n]	19	14	3	21	6	7	5	5	17	9	9	15	9	8	15
LM [imp.]	1.00	0.83	0.08	1.00	0.13	0.64	0.12	0.15	1.00	1.00	1.00	1.00	1.00	0.30	1.00
prich [n]	2	3	3	2	9	7	3	21	3	1	1	1	1	10	1
prich [imp.]	0.07	0.12	0.05	0.05	0.22	0.40	0.10	0.94	0.22	0.07	0.07	0.04	0.07	0.45	0.05
pH [n]	3	6	3	4	3	1	4	2	2	1	1	8	1	2	4
pH [imp.]	0.10	0.25	0.06	0.16	0.05	0.03	0.08	0.07	0.07	0.11	0.10	0.61	0.07	0.06	0.25
CN [n]	2	2	18	19	20	NA	3	2	2	1	9	1	1	2	4
CN [imp.]	0.08	0.08	0.56	0.92	0.60	NA	0.07	0.06	0.09	0.07	1.00	0.04	0.07	0.05	0.20
CP [n]	10	7	5	9	5	5	3	8	2	9	1	14	9	3	13
CP [imp.]	0.54	0.33	0.11	0.45	0.10	0.43	0.06	0.33	0.06	1.00	0.08	0.97	1.00	0.12	0.89
CK [n]	2	1	3	3	27	6	3	1	13	1	1	3	1	7	2
CK [imp.]	0.13	0.04	0.06	0.08	0.73	0.48	0.06	0.03	0.82	0.09	0.07	0.11	0.07	0.35	0.08
CCa [n]	2	1	3	2	4	13	12	8	1	1	1	2	1	1	2
CCa [imp.]	0.07	0.04	0.06	0.09	0.06	1.00	0.43	0.32	0.06	0.07	0.08	0.08	0.08	0.04	0.07
CMg [n]	2	2	6	3	5	NA	18	4	9	1	1	3	1	18	2
CMg [imp.]	0.07	0.06	0.19	0.07	0.08	NA	0.57	0.12	0.54	0.07	0.12	0.12	0.07	0.86	0.13
CNa [n]	2	14	15	5	8	6	3	5	2	1	1	3	1	15	3
CNa [imp.]	0.06	0.87	0.43	0.23	0.20	0.54	0.08	0.15	0.07	0.10	0.07	0.20	0.08	0.75	0.16
CS [n]	3	2	5	2	9	13	4	12	1	1	1	1	1	2	1
CS [imp.]	0.14	0.15	0.13	0.05	0.20	1.00	0.11	0.53	0.03	0.07	0.08	0.05	0.13	0.08	0.04

Acknowledgements / Danksagungen

Ich möchte mich zunächst bei Uli Brose bedanken. Danke, Uli, für die Chance, in deinem EcoNetLab wissenschaftliches Arbeiten lernen und meine eigenen Ideen und Interessen einbringen zu dürfen. Danke für dein Vertrauen, deine Unterstützung, deinen Rat und nicht zuletzt dafür, dass du eine Gruppe von Leuten um Dich versammelt hast, mit denen wissenschaftlicher Fortschritt UND Spaß an der Arbeit möglich war und über die letzten vier Jahre zu meinem Alltag geworden ist ;-)

Herzlichen Dank an den Rest meines PhD thesis committee's: Prof. Dr. Stefan Scheu und Prof. Dr. Teja Tscharntke für die Bereitschaft, meine Arbeit über die vergangenen 4 Jahre wohlwollend und beratend zu begleiten!

This brings me to my PhD-sibling (I will not comment on the husband/wife issue, here) Andrew Barnes. Unfortunately, I have to refrain from using the correct terminology to describe how awesome it was working with you both here in Germany and in Indonesia, but as you know, I am a father now and, as you tried teaching me, it is very important to stick to adequate language, especially when children are around. So, thank you very much, Andrew, for working next to me in Indonesia's moist heat and Germany's dry cold. Thanks for teaching me many sciency things along with useful english grammar! Thanks for sharing the bad and annoying as well as the awesome and enlightening moments of four years of working on our PhD's. I am very grateful to have had a colleague and found a friend like you.

Thank you EcoNetLab gang! Thanks for your support and friendship from the early student days on up to the final days of my PhD. Thanks for answering a million questions and always offering your help! Thank you Amrei for your early modelling support! Thank you Flo for co-supervising my diploma project! Thank you David for introducing me to the stoichiometric world view! Thank you Flo and Tony and Mimi for the climbing fun we had! Thanks Steffen, Lucas and Esra for being awesome masters students =) Thanks to all the HiWi's supporting our scientific work!

Thank you co-authors of the research chapters and proofreaders of this thesis! It has been

a pleasure working with you.

Thank you EFForTS PhD's and PostDocs for a lot of fun while being in Bogor and Jambi! Thanks for sharing the awesome and not so awesome parts of our Southeast Asian experience, for being awesome house- and roommates and supportive colleagues whenever I needed one.

Thank you EFForTS and EcoNetLab staff! Rita, Wolfram, Barbara, Ivonne, Kerstin for your very very helpful assistance in solving the administrative issues related to my work! Thank you Bogor- and Jambi-office crew! Thank you Mega, Keisha, Rizky and Reza for your assistance in Jambi! Thank you Ibu Noor, Pak Achmad and Pak Tri Heru for being incredibly friendly and helpful counterparts!

Thank you DFG for funding my PhD!

Thank you Eoin for inviting me over to Iceland to get my head off the PhD issues when I needed it!

Besonderer Dank geht an alle Freunde, egal ob in Bickenbach, Darmstadt, Hamburg, Göttingen oder irgendwo sonst verteilt! Danke für eure Unterstützung und die super Zeit, die ich immer wieder mit euch haben darf! Ohne euch wäre ich nie in der Lage gewesen, Arbeit und Freizeit und Familie unter einen Hut zu bekommen!

Herzlichen Dank an meine Familie! Doro, Uli, Lisa, Tobi, Enno, Vivi, Daniel, Charlotte, Beate, Wolfgang, Tanten, Onkels, Cousins und Cousinen, Großeltern! Ohne euch wäre ich nicht der, der ich heute bin. Danke, dass ihr mich immer unterstützt habt, ein glückliches, selbstbestimmtes Leben zu führen, meine Meinung zu sagen, eigene Standpunkte zu vertreten und verteidigen, aber auch andere Meinungen zu akzeptieren, anderen zuzuhören und zu vertrauen! Danke, dass ich bei euch lernen durfte, meinem Kopf und meinem Herz zu vertrauen und meinen eigenen Weg zu gehen!

Zuletzt möchte ich mich bei Delila und Timea bedanken. Danke, dass ich mit euch leben darf! Danke für jedes Lachen, alles Verständnis und alle Unterstützung, die ihr mir entgegen bringt. Ich bin unendlich dankbar für die Zeit, die wir schon miteinander hatten und freue mich auf alles, was noch vor uns liegt!

Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Arbeit selbstständig und ohne Zuhilfenahme anderer als der angegebenen Hilfsmittel angefertigt habe. Weiterhin erkläre ich, bisher noch keinen Promotionsversuch unternommen oder die vorliegende Arbeit einer anderen Prüfungsbehörde vorgelegt zu haben.

Malte Jochum
Göttingen,