

Allometry – Relations to Energy and Abundance

Zur Erlangung des Grades eines Doctor rerum naturalium (Dr. rer. nat.)
genehmigte Dissertation von Dipl. Biol. Roswitha B. Ehnes aus Fulda
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Allometry – Relations to Energy and Abundance

Vom Fachbereich Biologie genehmigte Dissertation von Dipl. Biol. Roswitha B. Ehnes aus Fulda

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Wir sind so gerne in der freien Natur, weil diese keine Meinung über uns hat.

— Friedrich Nietzsche

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1 Aims and Scope

The species in assemblages are linked by interactions. Many of these are trophic interactions, indicating who eats what and thus, also, the flow of energy through the system. These feeding interactions constitute the food web and are themselves determined by the attributes of the interacting organisms.

The complexity of such a food web cannot be understood using only a single methodology. Different concepts must be used to gain insight into the structure of the system. Likewise, the system cannot be well understood by examining only a single level and several levels have to be taken into account. I therefore concentrated on several different aspects and attributes of the organisms interacting in food webs.

It is enormously demanding to derive detailed descriptions of feeding interactions by laboratory study. However, such studies do provide precise information on the strengths of the interactions. Obtaining such precise information for large systems of interacting organisms is, unfortunately, logistically impossible. It is therefore necessary, for large assemblages, to obtain estimations of interaction strengths. I therefore used different approaches during my thesis. In the laboratory, I investigated specific feeding interactions and determined how they are driven by predator body mass and by temperature. Then, I focused on the metabolic needs of different invertebrates differentiating their phylogenetic group and feeding type. I then combined these findings with a field study to test different theories of food-web structure.

2 Introduction

Natural ecosystems consist of many organisms, large or small, rare or abundant. How do all these organisms relate to each other and how is this assemblage structured? The structure of these species communities can be characterized by the feeding interactions between the species. The majority of these organisms are heterotrophs feeding on different resources such as plants (i.e. herbivores), detritus (i.e. detritivores), or other animals (i.e. predators). The question of their coexistence engages ecologists and it cannot be answered exclusively by concentrating on one individual organism as it involves factors inherent to the many organisms and also depends on the habitat. For example, each organism needs to take up certain amounts of energy, according to certain intrinsic factors, and can conversely be fed on by other organisms. These intrinsic factors include for example body mass of the organism, its physiology, feeding type, phylogeny, and activity level (Fig. 2.1). However, also the environment with its specific properties influences the energetic demand of an organism via temperature effects, or factors like habitat type, possible disturbances (human land use), or properties of the occurring resources (for instance their type, body mass, availability, Fig. 2.1).

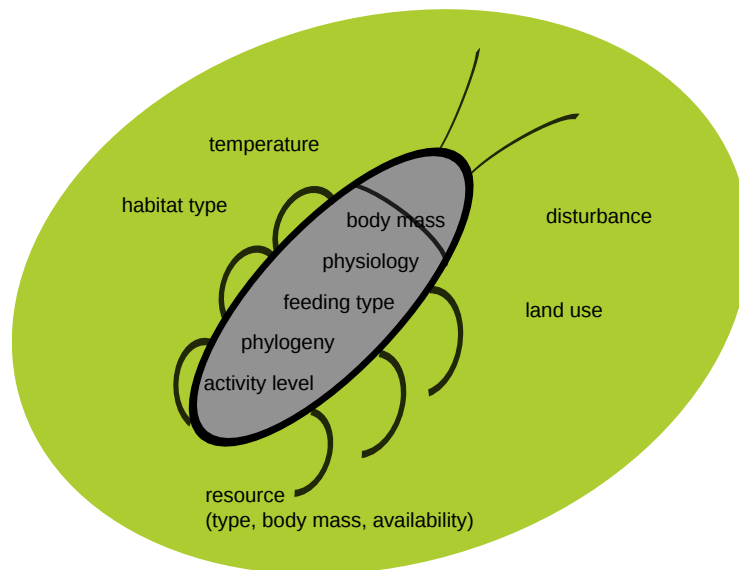


Figure 2.1: Factors that influence the metabolic demand of an organism. Green background represents the environment and its influences on the organism, the intrinsic factors are given inside the organism.

Animal communities consist of many organisms which belong to different species and show different abundances. As it is not an easy task to determine the energy demand of one organism, it is not trivial to determine how much energy the whole community needs. A species energy demand is influenced by several factors the interplay of which makes its assessment even more complicated (Humphries and McCann, 2013). While a lot of studies on energy demand or metabolism focused on mammals little is known about invertebrates. Communities consist of many species and small species are generally more abundant than large ones. These different organisms possess different energy demands, feeding types, trophic levels and abundances. However, all of them need to – at least – balance their energy demands. Thus, every organism, basically, needs to absorb energy (sun

light, plant material, prey organisms, dead organic matter, etc.) for metabolism, growth and reproduction. I concentrated on invertebrate organisms to investigate their energetic demand and the consequences of different energetic needs of various organisms (different phylogenetic groups) for communities. Invertebrates are poikilothermic animals and thus are of a different metabolic type than mammals and birds. Their body temperature depends on the environmental temperature and follows environmental temperature changes, but this dependency can be modified by the behaviour of the animal. Thus, body temperature of poikilothermic animals is much more variable than that of mammals or birds. As a consequence of this temperature dependency, the body temperature of poikilothermic animals can be estimated by measuring environmental temperature. However, the biochemical reactions, the determinants of metabolism and, thereby energy demand, proceed more easily in warmer environments (Arrhenius, 1889) and less activation energy is needed when it is warmer. Furthermore, the life stage of the organism also has an important effect: is the animal growing or a full-grown adult? Is the animal moving – fast or slow – is it sitting, resting or even hibernating? All these factors influence metabolic rates and accordingly energy demand.

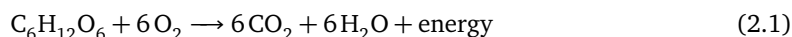
To be able to answer the questions of coexistence and energy distribution in natural communities several other questions have to be answered first. The questions I want to answer in my thesis are: What determines the metabolic rate and hence, the demand of an organism, is it body mass or the environmental temperature? Are there applicative models for this description? What further influences have to be accounted for? In what way does the energetic demand of an individual affect the structure of communities? What is the impact of these energetic restrictions on the distribution of animals and may it be affected by human land use?

Some of these questions cannot be answered in the field, because there are no methods for direct measurement. Thus, we need data from laboratory work to be able to draw conclusions about what may happen in the field, especially if it is a "field" that is difficult to observe like soil-animal communities. In the following, I will introduce some theories and models which aim to explain various factors that, put together, are able to explain the metabolic constraints that shape food-web assemblages.

2.1 Metabolism

Every organism needs energy for survival (sustain the vital functions) and furthermore for growth, movement, and reproduction. Metabolism is the sum of all processes that allow organisms to obtain energy for their functioning. Thus, metabolic rates can be described as the combined rates of energy uptake, transformation and allocation (Brown *et al.*, 2004; Hickman and Weber, 2008). Phototrophic organisms (plants, algae and some bacteria) use energy from (sun-) light, carbondioxide, and water to generate carbohydrates and oxygen. Heterotrophic organisms on the other hand use chemical compounds (carbohydrates, lipids, and proteins) and oxygen for aerobic organisms, to yield energy and set free carbondioxide and water. Nutrients are digested to generate smaller compounds which will be processed further. Thus, passing through different metabolic steps, like digestion, glycolysis, tricarboxylic acid cycle and respiratory chain, resources are digested, energy rich compounds like ATP (Adenosine-5'-triphosphate) are produced (Hickman and Weber, 2008) and indigestible residues are excreted. Energy from organic compounds are transferred to energy-rich compounds in stepwise enzymatic reactions for storage and for transportation to allow usage in different parts. The most important energy-storage compounds are ATP and NADPH (Nicotinamide adenine dinucleotide phosphate). The products of the cellular respiration, that needs carbohydrates and oxygen (for aerobic organisms) are carbondioxide and water (Brown *et al.*,

2004). The overall reaction of glucose and oxygen to carbondioxide and water can be summarized as follows:



However, this reaction is not possible in a single reaction, but requires multiple steps. The different steps are associated with specific cellular compartments in eukaryotes.

At first, in the glycolysis, which takes place in the cytosol, glucose is degraded to pyruvate. In a second step acetyl-CoA is formed from degraded pyruvate in the mitochondria. The third part is the tricarboxylic acid cycle, which with its small number of reactions makes up the core of metabolism (Morowitz *et al.*, 2000) and leads to the creation of energy-rich compounds (ATP, NADH or NADPH), water, and carbondioxide. During these reactions electrons are transported across the inner mitochondrial membrane which leads to the creation of a proton gradient across the membrane which is then used to synthesize ATP. The nascent energy is stored as energy-rich molecules. While ATP is relatively stable in a physiological environment, it can easily be hydrolyzed in a catalytic cycle to set free the contained energy.

Thus, a breathing animal ‘consumes’ the amount of oxygen needed for the chemical reactions and releases the ‘used’ oxygen as carbon dioxide. The oxygen content of the respiratory air is reduced and the carbondioxide content is enriched compared to before breathing. The consumption of oxygen and the production of carbondioxide enables external measurement of energy used by an heterotrophic organism. As the stoichiometry of respiratory gas exchange and the rate of oxygen consumption is fixed, estimating the decrease in oxygen concentration or the increase in carbondioxide concentration will enable calculation of the metabolic demand. Different methods have been developed for measurement of the oxygen reduction and carbondioxide accumulation. For the measurements in this thesis an automated electrolytic microrespirometer (Scheu, 1992) has been used (Chapter 3, 4, 5).

Basal, standard or resting metabolic rate describe the energy an organism needs for mere survival. Thus, basal metabolic rate is the minimum value of metabolic rate. If an organism moves, the metabolic rate increases. Two types of metabolic rates above basal metabolic rates are common: field and maximum metabolic rate. Field metabolic rate can be described as the mean metabolic rate of an animal that moves and rests alternately. Whereas maximum metabolic rate is a description for a continuously running (heavily respiring) animal. Therefore, field metabolic rate is somewhat intermediate between basal and maximum metabolic rate, and quite complicated to determine. Caused by the difficulty to control for the movement of an organism, metabolic rates are often determined from animals at rest. These resting animals show a relatively constant metabolic rate without large or abrupt fluctuations and provide information about the basal energetic needs of an inactive organism in the laboratory and thus, its essential energy demand.

Measured oxygen uptake of an organism can be transferred into energetic equivalents by using the relationship described by Peters (1983):

$$1431.03 \mu\text{g O}_2 \equiv 20.1 \text{ J} \quad (2.2)$$

This conversion allows the estimation of the energy demand of an organism at rest from the amount of oxygen it uses per unit time. Measured oxygen use of an organism at different temperatures can be used to gain values for basal metabolic rate of an individual with a determined body mass. From this, the metabolic rate per unit mass of different organisms can be calculated to allow further comparison.

2.2 Body-mass effect

Large animals need more energy than small ones, this is questionless acknowledged (Kleiber, 1932). The importance of body mass in specifying the amount of energy (food) demand was acknowledged a long time ago. However, the relation of body mass and energy needed is not easily captured. With increasing body mass the energetic demand increases, but it does not increase unitarily.

The fact that small animals use relatively more resources (per unit body mass) than large animals has been known for more than a century (Chossat, 1843; Regnault and Reiset, 1849; Reiset, 1863). However, body mass was not recognized as a major determining factor for metabolism until the work of Rubner (1883). He stated that the amount of heat produced by dogs of different body masses was approximately the same per body-surface area. Furthermore, he proposed that metabolism was not only influenced by surface area but affected by more factors like amount of food consumed, state of the animal (active or at rest), growth (still growing or full grown) and species considered. Whole-body metabolic rate of fasting dogs was directly proportional to their surface area. The equation that summarizes these findings is the following, where the metabolic rate, I , scales with body mass, M , to the power of two thirds, which represents the scaling of surface to volume, and a normalization constant, a .

$$I = a * M^{\frac{2}{3}} \quad (2.3)$$

Rubner tried to keep as many factors constant as possible. Thus, he focused on full grown dogs that were all fasting, furthermore he tried to keep the conditions for the measurements constant (15 °C) (Rubner, 1883). Rubner favoured the influence of ambient temperature as an explanation for the differences as small and large animals tolerate the same temperature differently. This point of view was supported by the examination of the distribution of animals of different body masses across the world, later known as Bergmann's rule (Bergmann, 1848). Homeotherm animals tend to be larger in cooler environments as an increase in size involves a more rapid increase of the volume of an animal than of its surface area. Thus, larger (higher volume) animals will be able to produce more heat while they will lose relatively less heat due to the relatively smaller surface area (Bergmann, 1848; Meiri and Dayan, 2003). Thus, Rubner (1883) concluded that heat loss via the surface area determined the minimal metabolism of an organism, even though this might be influenced by fur, subcutaneous fat and posture. Surface area was seen as a main determinant of metabolic rate by Rubner (1883) and others (Burton, 1934; DuBois, 1937; Hardy *et al.*, 1938).

This surface-area-to-volume argument, also known as Rubner's surface law (Eqn. 2.3, Rubner, 1883), became criticized as new data on different animals became available. Data analysis was accompanied by a new theory: Kleiber's law (Fig. 2.2, Kleiber, 1932, 1947).

A linear correlation between the logarithm of metabolic rate and the logarithm of body weight demonstrated metabolic rate to be proportional to a three-quarter power function of body mass (Kleiber, 1947). Furthermore Kleiber had no impediment for applying this three-quarter power law to intraspecific data as well.

$$I = a * M^{\frac{3}{4}} \quad (2.4)$$

Additional data suggested a broad generality of the three-quarter power law or Kleiber's law (Kleiber, 1947; Peters, 1983; Savage *et al.*, 2004b). Critique on the two-third and three-quarter power law proposed by Rubner (1883) and Kleiber (1932; 1947), respectively, highlighted the

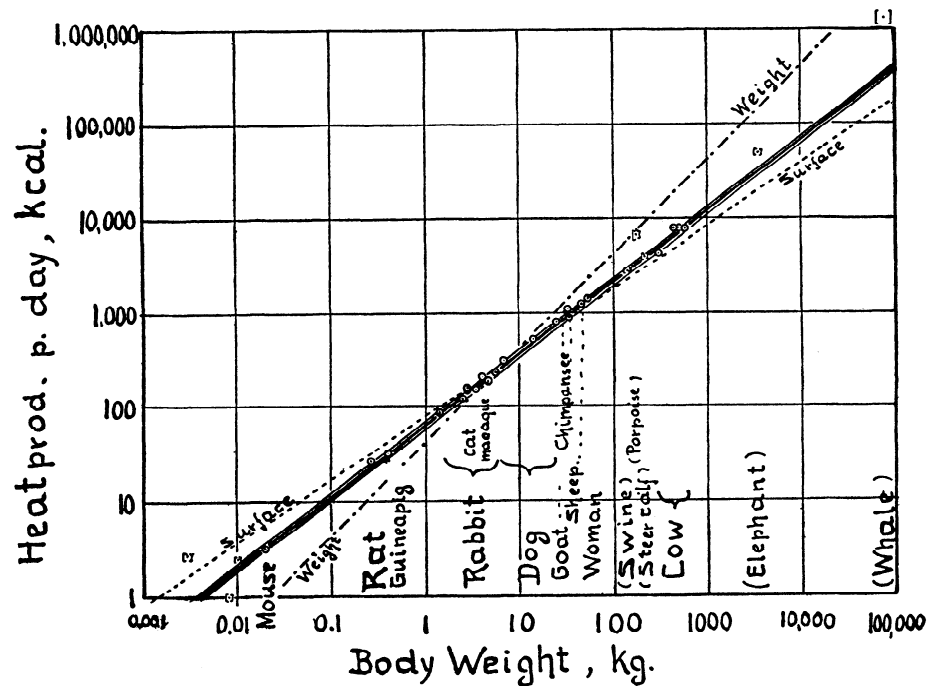


Fig. 1. Log. metabol. rate/log body weight

Figure 2.2: Log. metabolic rate / log body weight, as given in (Kleiber, 1947)

differences in the studies (Wieser, 1984). Wieser (1984) claimed that each of these two scaling exponents is justified but has to be applied to different types of datasets. As the two-third exponent was derived from an intraspecific comparison of dogs it should only be applied to intraspecific data, while the three-quarter exponent originated from interspecific comparisons of different mammals and should only be applied to interspecific data. Ontogeny and phylogeny should affect scaling differently and thus cause these different scaling behaviours of inter- and intraspecific metabolic rate (Wieser, 1984). The three-quarter power law, even though it was empirically supported, was doubted due to the lack of a theoretical basis to explain this scaling exponent. This gap seemed to be filled by the model presented by West, Brown and Enquist (WBE, West *et al.*, 1997) stating that the three-quarter exponent is caused by optimized fractal transport networks within organisms such as the cardiovascular system of vertebrates (West *et al.*, 1997). However, the reasons for the allometric scaling of metabolism with organism body mass as well as the value of the power-law exponent of this relationship have been debated extensively (White, 2010). I will get more into detail and present a variety of different theories that aim to explain the scaling relationships in a following section (part 2.4). Yet, one fact is doubtless recognised: energy needed by an organism depends to a large proportion on the body mass of the organism and is – especially for ectothermic organisms – affected by environmental temperature.

2.3 Temperature effect

The effect of temperature on chemical rates was realized roughly at the same time as the main effect of body mass on metabolic rates. This influence was conspicuous as ectotherm animals move faster in warm environments than in cold ones. However, the combination of these two findings did not take place for a long time. The easier progression of chemical reactions with increasing temperature has been described by van't Hoff (1884) and some years later by Arrhenius (1889).

The amount of energy needed to start a reaction becomes smaller with increasing temperature and chemical reactions progress more easily (van't Hoff, 1884; Arrhenius, 1889). Thus, increasing temperature will affect whole body metabolic rates via increased speed of chemical reactions which in turn increases turnover of food and thus the need for food. Therefore, energy demand of endothermic animals increases with increasing temperature. Following these findings the Q_{10} values were developed. This unitless quantity describes how the speed of a reaction changes if the ambient temperature increases by 10 °C (van't Hoff, 1884). It relates the rates, R , at two temperatures T_1 and T_2 , where temperature may be given in °C or K:

$$Q_{10} = \left(\frac{R_2}{R_1} \right)^{\left(\frac{10}{T_2 - T_1} \right)} \quad (2.5)$$

For biological systems the Q_{10} value ranges usually between two and four. The larger the temperature difference between T_1 and T_2 the less accurately the temperature coefficient predicts the change and thus should not be applied for large temperature differences. Some years later the establishment of the Arrhenius equation (Arrhenius, 1889) advanced the predictability of the temperature dependence of chemical processes. The exponential factor, respectively Boltzmann's factor, in Arrhenius' equation is the term that describes the temperature dependence of a reaction.

The temperature term by Arrhenius (1889) ($e^{\epsilon_a/RT}$) is based on two relationships that were already known: van't Hoff's findings of the temperature dependence (van't Hoff, 1884) and the law of mass action (which relates the equilibrium constant and equilibrium concentrations (more general: activities) of the different compounds of a chemical reaction). Arrhenius created an equation describing the temperature dependence of a reaction. The equation of the rate constant k' comprises the preexponential factor A , the activation energy, $-\epsilon_a$, the gas constant, R , and T temperature in K:

$$k' = A * e^{\left(\frac{-\epsilon_a}{RT} \right)} \quad (2.6)$$

This equation shows that molecules need a certain amount of energy, $-\epsilon_a$, to be able to react. As $\ln k'$ and T are inversely proportional plotting will result in a straight line with the slope $-\epsilon_a/R$, if $\ln k'$ and inverse temperature $[1/K]$ are plotted. Multiplying ϵ_a and RT with Avogadro's number leads to the Arrhenius' temperature term in the form usable for metabolism

$$e^{\left(\frac{-E_a}{kT} \right)} \quad (2.7)$$

with E_a the activation energy, k Boltzmann's constant [$energy/K$] and T the temperature in K. For metabolic rates, E_a is usually expressed in electron Volt [eV] and Boltzmann's constant would be [$8.62 \times 10^{-5} eV/K$]. This predicts an exponential scaling of metabolic rate with temperature where the activation energy represents the exponent of this relationship. Adding this temperature term to the three-quarter power law of the metabolic equation significantly enhanced the quality and stressed the interacting effect of body mass and temperature on metabolic rates. Including this universal temperature dependence (Gillooly *et al.*, 2001) into the power-law equation describing the metabolic rate led to the development of the Metabolic Theory of Ecology (MTE, Gillooly *et al.*, 2001; Brown *et al.*, 2004). This MTE is a combination of the WBE model (West *et al.*, 1997, 1999a) (which has the same value for the allometric exponent as Kleiber's law, but provides a possible explanation for this scaling) and Arrhenius' temperature term as the universal temperature

dependence (Gillooly *et al.*, 2001)). However, usability of the Arrhenius' equation for predicting the temperature effect was criticized (Wolfe and Bagnall, 1980; Knies and Kingsolver, 2010).

One critique stated that a straight-line fit would not represent the 'real' temperature dependence as there were obvious 'breaks' in the line at certain 'critical' temperatures for plants and homeothermic animals (Wolfe and Bagnall, 1980). Thus, the correct representation of the temperature dependence would be a curve with a continuously decreasing slope (Wolfe and Bagnall, 1980) while Arrhenius' kinetics would only apply over narrow temperature range for ectotherms (Knies and Kingsolver, 2010). Another critique went beyond the problem of the straight-line fit. This time the universal temperature dependence (based on the Arrhenius equation, Gillooly *et al.*, 2001), was criticized for its basic assumption that the rate limiting enzyme (for the reaction in question) is 100% in active conformation and does not vary within the physiologically relevant temperature range (Knies and Kingsolver, 2010). If the probability of active conformation would decline at high or low temperatures the relationship would become curved (Knies and Kingsolver, 2010). For multicellular animals metabolic fluxes may be limited by oxygen supply but not one single enzyme might be limiting across the complete temperature range (Knies and Kingsolver, 2010). Furthermore, the temperature range affects the type of temperature dependence found so that a large dataset is better fit by a second order polynomial, whereas for very small temperature ranges the linear model performed best (Knies and Kingsolver, 2010). Thus, the physiologically relevant temperature range measured should always be as large as possible to avoid the problems formulated by Wolfe and Bagnall (1980) and Knies and Kingsolver (2010).

Different ranges for the activation energy have been proposed. While Gillooly *et al.* (2001) predicted activation energies to vary between 0.2 and 1.2 eV, Brown *et al.* (2004) stated a range of 0.6 to 0.7 eV. Empirical studies cast doubt on the narrow as well as on the large distribution of average activation energies predicted by the MTE and universal temperature dependence, respectively (Meehan, 2006b; Terblanche and Chown, 2007; Downs *et al.*, 2008; Irlich *et al.*, 2009). A range of intermediate size (0.46–0.96 eV) which represents Q_{10} values between 2 to 3 for temperatures between 0 to 40 °C has been proposed (Downs *et al.*, 2008). However, temperature is not a trait of the environment the animal has to tolerate. Animals are, in certain ranges, able to adjust to temperatures not that favourable to them. Via metabolic cold adaptation (MCA) organisms are able to survive in cold habitats (Addo-Bediako *et al.*, 2002). While this remains controversial, the MCA has been supported for insects (Addo-Bediako *et al.*, 2002) and might have acted as a source for variation in metabolic rates. To evaluate a possible effect of the MCA on the variation in metabolic rates the life histories of species have to be paid further attention (Addo-Bediako *et al.*, 2002). The MCA may as well be partly responsible for the large-scale asymmetry of insects associated with the occupied hemisphere (Addo-Bediako *et al.*, 2002 and references therein). The temperature within a habitat also affects the possible body size of an ectothermic organism via physiology. Terrestrial poikilotherms have been shown to grow bigger the warmer the habitat is (Makarieva *et al.*, 2005e) as already predicted by Bergmann (1848). The study by Makarieva and colleagues (Makarieva *et al.*, 2005e) showed that the world's largest poikilotherms in the warmest habitats grew 3.2 and 5.7 times bigger than their counterparts from Great Britain and Wrangel Island, respectively (extreme minimum temperature of warmest month 18, 6 and -5 °C, respectively).

2.4 Allometric Scaling – current Debate

The explanation by West, Brown and Enquist (WBE, West *et al.*, 1997) for the $3/4$ scaling states that it is a result of the fractal nature of transport networks in organisms. The paradigm of the later formulated MTE, based on the WBE, was criticized from various sides. Alternative models challenged

the causal explanation of metabolic scaling and the theoretical basis, the fractality of the transport networks (the WBE model) and predicted different ranges of exponents, curved deviations from the predicted relationships, lacking universality of the exponent across different groups of species. The WBE model and therefore also the MTE is only applicable to organisms that possess a closed vascular network. Furthermore, the generality of the MTE has to be questioned as it is not able to explain why metabolic rates of insects, amphibians, reptiles, and unicells should scale with a three-quarter power law as well as these animals do not possess such transport networks that are claimed to build the basis for the $3/4$ scaling (Kozłowski and Konarzewski, 2004, 2005; O'Connor *et al.*, 2007). Further on, it is not able to explain the differences in the scaling of basal and maximum metabolic rates (Glazier, 2010), especially if these are dominated by different tissues (Demetrius, 2006; O'Connor *et al.*, 2007). Some studies showed that increases in basal metabolic rate with body mass on a log-log scale are not always represented best by a straight line. A curvature was found for mammalian data on basal metabolic rates and with a different model for eutherian basal metabolic rates by adding a second order polynomial term which significantly increased the fit (Hayssen and Lacy, 1985; Painter, 2005; Isaac and Carbone, 2010; Kolokotronis *et al.*, 2010). Another critique refers to the rationale and assumptions of the MTE. The branching mode proposed in the MTE is mathematically the same as one single vessel (Apol *et al.*, 2008). Whole body metabolic rate would be proportional to total volume flow, thus, the total size of the network has to be fixed (Apol *et al.*, 2008). Furthermore Apol *et al.* (2008) claimed that West *et al.* (1997) stopped the optimization of their model too early as wall-thickness vessel-radius ratio could be obtained from optimization and would not have to be stated as an independent assumption (Apol *et al.*, 2008). Isometric scaling of blood volume and the steady flow stated by the MTE model (West *et al.*, 1997; Brown *et al.*, 2004) has been criticized as well. While minimizations of pulsatile flow in combination with a generalized space-filling concept would result in an isometric scaling of metabolic rate with body mass (Apol *et al.*, 2008), evolution optimizes individuals within species, which would explain the observed isometric scaling if metabolic rate is considered intraspecifically. In contrast to the isometric intraspecific scaling the scaling of interspecific metabolic rate should show a lower value for the allometric scaling (Apol *et al.*, 2008). As the service volume is not free to vary with body size length, radius, and flow velocity would be the same for all organisms of different body mass. This flaw could be solved by relaxing this assumption and allowing radius and length to increase with increasing body mass of the animal (Kozłowski and Konarzewski, 2005). Thus, a plethora of alternative metabolic-scaling models were established. All these models have one thing in common: they relax the rigorous prediction of $3/4$ for the allometric exponent. I will concentrate on those published in this century, mainly in the last ten years. These alternative models include the Arrhenius fractal supply model (Downs *et al.*, 2008), the metabolic level boundaries hypothesis (Glazier, 2010), the explosion model (Banavar *et al.*, 2010), the quantum metabolism model (Demetrius, 2006), the ecophysiological model (Kozłowski *et al.*, 2003) and the allometric cascade model (Darveau *et al.*, 2002).

The Arrhenius fractal supply model (Downs *et al.*, 2008), is based on the same assumptions as the MTE, but avoids fixing the allometric exponent. Fixing the allometric exponent might potentially mislead the analysis of the temperature dependence. For the temperature dependence, this model predicts a broader range for the activation energy of 0.46 to 0.96 eV.

The metabolic level boundaries hypothesis (MLB, Glazier 2010) states that ecological lifestyle and activity level influence the overall metabolic intensity of a specific organism which in turn affects the relative influence of basic physical boundary constraints. Thus, the MLB hypothesis distinguishes between two extreme idealized boundary constraints: (1) surface-area limits on fluxes of metabolic resources, wastes or heat causing allometric scaling with a $2/3$ power law, and (2) vol-

ume limits on energy use or power production yielding isometric scaling. These constraints act as boundary limits for the metabolic-scaling exponent, depending on the relative importance of supply and demand, allometric exponents can thus vary between $2/3$ and 1 (Glazier, 2010). For bursts of maximal activity the allometric-scaling exponent should approach unity because in this case metabolic rate is primarily driven by resource demand of metabolism (Glazier, 2010). This idea was complemented by Makarieva and colleagues (2005a; 2005b) who stated that mass-specific metabolic rates should have a scaling exponent of 1 for maximal and minimal metabolic rates as these states represent extreme mass independent limits.

model	author	predicted scaling (range)
Metabolic Theory of Ecology	(Brown <i>et al.</i> , 2004)	$3/4$
Arrhenius fractal supply model	(Downs <i>et al.</i> , 2008)	$3/4$ expected, but not fixed
Metabolic Level Boundaries	(Glazier, 2010)	$2/3$ and 1 as boundaries
Explosion	(Banavar <i>et al.</i> , 2010)	$2/3$ and $3/4$ as upper boundaries, depending on velocity
Quantum Metabolism	(Demetrius, 2006)	$2/3$ to $3/4$ as boundaries for animals
Ecophysiological	(Kozłowski <i>et al.</i> , 2003)	$2/3$ and 1 as boundaries, depending on the way of mass increase
Allometric Cascade	(Darveau <i>et al.</i> , 2002)	Sum of ATP-utilizing processes, each scale with mass

The explosion model suggests that a network with lines radiating from a central source yields allometric scalings with $3/4$ as an upper bound if blood velocity scales as body mass to the power of one twelfth (Banavar *et al.*, 2010). The $3/4$ power emerges from resource-distribution networks no matter if they branch hierarchically or like a radial explosion. An explosion network thus represents the simplest centralized network with minimized transport distances. Routes would be straight lines and the number of routes would be proportional to metabolic rate. The centralized branched network is deduced from the WBE model, but with variable length routes. This model also yields a $3/4$ scaling exponent as an upper bound if blood velocity scales as one twelfth to the power of body mass. However, deviations towards a $2/3$ scaling are likely if velocity does not vary with body mass, deviations towards a linear scaling are likely if the organism does not possess a vascular system or if the range of body masses is sufficiently small that blood volume scales super-linearly. Thus, both models would result in an exponent of $2/3$ or $3/4$ if blood velocity remains constant as animal body mass increases or blood velocity scales with body mass to the power of one twelfth, respectively.

The quantum metabolism model employs fundamental mechanisms of transduction of energy across cell membranes to predict allometric scaling of animals with exponents ranging between $2/3$ and $3/4$ (Demetrius, 2006). Demetrius (2006) criticizes the WBE model (West *et al.*, 1997, 1999a) for disregarding metabolic efficiency and the differences in the scaling of basal and maximum metabolic rate and furthermore for its incapability to explain the differences between endothermic and ectothermic or large and small individuals. This quantum metabolism theory relates metabolic energy demand generated by a cell with metabolic cycle time, the turnover of oxidation-reduction reactions. Therefore, transport efficiency as described by type and composition of nutrients, and the geometry of the internal branching network, as well as proton conductance and electrochemical proton gradient are important factors determining metabolic rates of organisms. Thus, according to the quantum metabolism model (Demetrius, 2006), metabolic rate is regulated by three factors: (1) metabolic efficiency, (2) membrane composition, and (3) the structure of the circulatory network for transporting the nutrients. Furthermore, actual scaling values depend on evolutionary constraints whether the organism is an equilibrium or an opportunistic species. Equilibrium species are mainly large animals and characterized by a high basal metabolic rate which causes an allo-

metric scaling of three quarters. In contrast to the equilibrium species an opportunistic species is a small organism and displays a minimal basal metabolic rate, their resulting allometric exponent would be two thirds. For one special case, when metabolic efficiency as well as proton motive force are one, the quantum metabolism model will be the same as the MTE model (Demetrius, 2006). Thus, the three-quarter exponent acts as an upper bound in these models (Demetrius, 2006; Banavar *et al.*, 2010).

The ecophysiological model (Kozłowski *et al.*, 2003) distinguishes whether individual growth primarily depends on increases in cell number or cell expansion leading to allometric exponents of 1 or $2/3$, respectively. Increasing body mass solely due to increasing cell size would result in an allometric exponent of two thirds because metabolic rate of larger cells would decrease due to surface-to-volume ratio (Kozłowski *et al.*, 2003). Body expansion exclusively due to increasing cell number would result in an allometric exponent of one. Usually an increase in body size would be due to a combination of both processes which would result in exponents lying inbetween. Moreover the contributions of these processes will differ between lineages (Kozłowski *et al.*, 2003). Thus, no single exponent but rather a distribution of allometric scaling exponents with a mode somewhere between two thirds and one would be expected.

The allometric cascade model predicts that allometric scaling is the sum of different allometric scaling relationships that interactively determine the overall relationship (Darveau *et al.*, 2002). This concept arises from the layering of functions at different levels in an organism. Each step in ATP turnover possesses an own scaling behaviour at different sites of the body. Thus, the basal metabolic rate is a result of interacting scaling exponents at different 'functional units' (Darveau *et al.*, 2002). The allometric cascade model is able to explain differences between basal and maximal metabolic rates as these differences can not be explained by a single cause. However, an application of a multi-site model to basal metabolic rate is more difficult as little is known about the different steps important in the energy-demand processes. Especially, as not only intrinsic factors but also extrinsic factors like temperature, pressure or humidity affect allometric behaviour as well. Furthermore, basal and maximum metabolic rate are differently affected by oxygen delivery steps. Whereas oxygen-delivery steps contribute almost nothing to the global allometric-scaling exponent when metabolism is at the basal level, it significantly increases the global allometric-scaling exponent in times of maximum metabolic rates (Darveau *et al.*, 2002). The allometric cascade model has been used with data on mammalian metabolic rates, parameters have been determined based on relationships for organs, patterns of cell organization in animal tissues, and on relationships between cell metabolic rates and body mass (Painter, 2005). This multicompartiment model predicted positive curvature for mammalian data on basal metabolic rates (Painter, 2005). The curvature in mammalian basal metabolic rates was documented and partly explained by Kolokotronis *et al.* (2010). Overall, these alternative models relax the assumption of universal scaling exponents and predict allometric exponents that vary between $2/3$ and $3/4$ (explosion and quantum metabolism model) or $2/3$ and 1 (MLB and ecophysiological model). This lack of a universal exponent is consistent with recent data analyses, where this was partly explained by variance in factors such as phylogenetic groups, life styles, activity state or developmental stage (Dodds *et al.*, 2001; White and Seymour, 2003; Glazier, 2005; Makarieva *et al.*, 2005c,d; Niven and Scharlemann, 2005; White *et al.*, 2007; McNab, 2008; Glazier, 2009; Isaac and Carbone, 2010 and Chapter 5).

One of the central assumptions of the MTE is that the fractal nature of the metabolic transport network is invariant across organisms and body sizes (West *et al.*, 1997; Brown *et al.*, 2004). While this assumption appears reasonable for vertebrates with cardiovascular systems, it is certainly violated for comparisons amongst invertebrates that are much more diverse in the size and shape

of their bodies and the structure, openness, or even lack of tracheal and body-fluid transport systems across phylogenetic groups. In consequence, the few studies comprising metabolic data of invertebrates found substantial variation in their metabolic scaling across phylogenetic groups and deviations from MTE predictions (Niven and Scharlemann, 2005; Meehan, 2006b; Chown *et al.*, 2007; White *et al.*, 2007; Isaac and Carbone, 2010). Much of the differences in scaling exponents documented across studies could be explained by a convex curvature of the mammalian metabolism-mass relationship on a log-log scale (Hayssen and Lacy, 1985; Savage *et al.*, 2008; Kolokotronis *et al.*, 2010). While this curvature challenges the general assumption of a power-law scaling between metabolism and body mass, it can be reconciled with the fractal transport network model of the MTE by modifications to the vascular system architecture assumed (Kolokotronis *et al.*, 2010).

Another study tested the MTE model with a dataset on different mammal species (Duncan *et al.*, 2007). They proposed that closely related taxa share evolutionary history and thus their deviations from the three-quarter scaling of the MTE will be correlated with phylogeny. Fitting different models showed a strong phylogenetic signal resulting in a best fit model that estimated separate scaling exponents and normalization constants for each order (Duncan *et al.*, 2007). This result again confirmed that there is no single universal scaling exponent suitable for all organisms and that phylogenetic effects are of major importance when modelling allometric scaling relationships even though there is still some uncertainty in details of phylogeny of mammals (Duncan *et al.*, 2007).

2.5 Metabolic Theory of Ecology for endotherms and ectotherms?

Many theories exist that try to describe the relationship of metabolism to body mass and temperature. Some of these give a range of expected allometric exponents, some give an explicit value. So, why not stick to a theory that is based on basic principles and fits to many observations and seems to be quite general. The MTE (West *et al.*, 1997, 1999a; Brown *et al.*, 2004) as many other theories has been build upon observations of a specific group of organisms, mostly mammals. My focus was on invertebrates and I expected deviations from the 'general' theories as invertebrates in contrast to mammals are quite small animals, ectothermic and the phylogeny is much more widely branched and diverse than for mammals. Even mammals that are mainly larger animals and endothermic differ strongly in their metabolic needs depending on their phylogeny and feeding type. An organism's metabolism is not only influenced by the previously described factors temperature and body mass, but also by physiology, feeding type and phylogeny (also, as a surrogate for body architecture, etc.) and its way to regulate body temperature (ectothermic or endothermic). Thus, a theory that has been built upon observations of mammals is not necessarily suitable for such very differential organisms like invertebrates.

The way an organism controls its body temperature, actively or more or less passively, is an important factor for its metabolic rate at different environmental temperatures. While an endothermic organism (like mammals and birds) always has a relatively constant body temperature and needs energy to keep it constant by warming up or cooling, body temperature of ectotherms (invertebrates, amphibians, and reptiles) generally follows the ambient temperature. Even though some ectotherms passively control body temperature by sunbathing or seeking shelter in cooler places, they are not independent of the environment surrounding them. While this reliance on external heat sources may have disadvantages by restricting the times of activity, it is a very effective way to run on less energy. Ectothermic organisms generally are active when they are warm, but when they are cold all their reactions are reduced, thus they need less energy than an endotherm of the

same size. The trait of very low metabolic rate in cold environments is a fact that is likely to cause a metabolic scaling different from those of endotherms. Furthermore, the reliance of ectotherms on environmental heat sources facilitates measurement of metabolic rates of these animals at different specific temperatures. All metabolic measurements in the chapters of this thesis took advantage of this feature of ectothermic organisms.

2.6 Food balances metabolic demand

So far, I have shown that movement, growth, reproduction – in short: living – burns up energy. Hence, each organism has to at least balance its basic energy demand to stay alive or absorb even more energy to be able to grow and reproduce. Animals take up energy by consuming food and oxygen. In order to balance their energetic demand, animals have to feed. Depending on the type of resource and its energetic content, different groups of animals can be distinguished by what they feed on, for example plant material (herbivores), other animals (predators), detritus (detritivores), or on more than one resource (omnivores). Different types of resources may provide different amounts of energy to the consumer due to the size of the resource item, its nutritiousness or the existence of large indigestible parts. Thus, the amount of consumed resource will be affected by the resource type and vary according to the previously mentioned factors of resources. Furthermore, depending on the type of resource, a different amount of energy may be assimilated from the consumed resource. These assimilation efficiencies differ between consumer types (Peters, 1983). A high assimilation efficiency means that the consumer is able to use a high proportion of the absorbed biomass for own metabolism, growth, movement and reproduction. While the relation of the assimilation efficiency to temperature and body mass is ambiguous (Hamilton, 1985; Mathavan, 1990), it is supposed to increase with trophic level (Kozlovsky, 1968).

However, independent of the type of resources consumed the organism has to – at least – fulfill its basic needs. To balance the metabolic costs the minimum amount of energy taken up via feeding has to be the same as the minimum metabolic rate of an organism. Thus, an equation in the form of the allometric scaling theory of metabolism is also able to predict the amount of resources needed:

$$C_i = c_0 * M^b \quad (2.8)$$

where C_i is consumption, c_0 is a normalization constant, M body mass and b the allometric exponent. For mammals this has been shown to be valid (Carbone *et al.*, 2007). This equation does not capture the amount a consumer would take up of a specific resource, it provides information about the necessary energy input of an individual. While exact determination of the consumption of a consumer in the field would need very elaborate methods and would be very costly, the determination of its needs via its body mass and the metabolic-rate scaling would result in the specification of the lower level of the energy input. Thus, knowing the energy demand of organisms in a certain area provides information about the energy content of the system. An organism will only be able to survive in a certain area if enough resources are present to fulfill its energetic needs. For field data, even more components are important: the nutritiousness of a resource and also its abundance as well as the abundance of possible alternative resources, and the structure of the habitat in which both, consumer and resources, occur (Fig. 2.3).

The number of prey individuals eaten is commonly described via a so called functional response (Holling, 1959a; Berlow *et al.*, 2004; Rall *et al.*, 2008; Kalinkat *et al.*, 2013a).

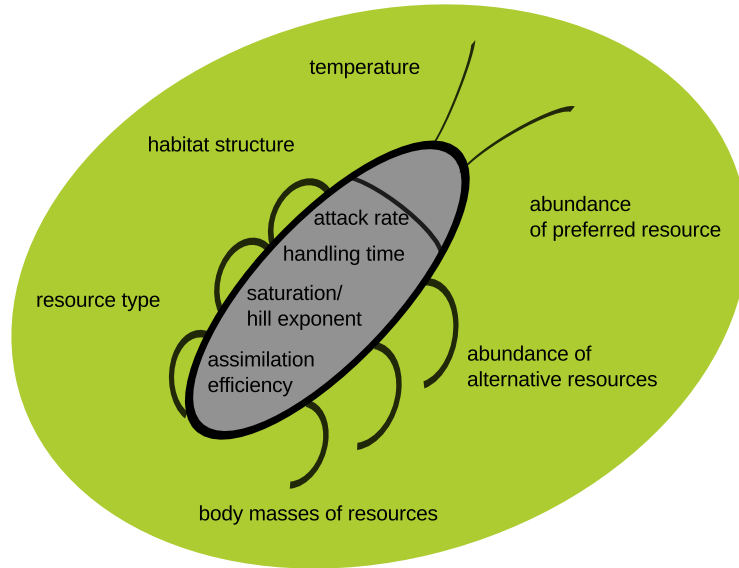


Figure 2.3: Organismal and environmental factors that influence consumption by the predator

$$F(N) = \frac{aN^{q+1}}{1 + ahN^{q+1}} \quad (2.9)$$

It quantifies per capita consumption rates of a predator in dependence on the number of available prey, N , the capture rate a (rate of encounter and success of attacks on prey individuals per unit time), and handling time h (how much time a predator needs to kill, ingest and digest a prey item). Depending on the hill exponent (h or the generalized formulation $q + 1$) the relationship between prey abundance and number of prey eaten may take on different shapes, hyperbolic type II ($q = 0$) or a sigmoid type III ($q = 1$) (Rall *et al.*, 2008; Vucic-Pestic *et al.*, 2010b; Kalinkat *et al.*, 2013a). All of the different types of the equation describe that with increasing abundance of the prey the predator will consume more prey until the constraints of handling time and capture rate limit a further increase in ingestion. Even if prey abundance keeps increasing the consumption will not increase further and stay on a constant maximum ingestion level (type II and III). The type of the functional response is very important for the stability of a whole community (Williams and Martinez, 2004; Rall *et al.*, 2008).

Furthermore, functional response is also influenced by temperature. The amount of energy needed by a predator will increase with increasing temperature (as already described in part 2.3) via increased turn-over rates, thereby increasing the need to ingest. Moreover, the reactions of the animals are affected by temperature, thus altering the parameters of the functional response as a consumer will be moving faster as well as handle a prey item faster.

2.7 Diversity of invertebrates

My research focused on soil invertebrates, which is a large animal group and very diverse in view of the size and shape of their bodies and the structure and openness of their tracheal and body-fluid transport systems. Invertebrates are the largest and most diverse group of organisms of the animal kingdom (Ricklefs, 1997; Hickman and Weber, 2008). Insects alone constitute most of the invertebrates (Ricklefs, 1997; Hickman and Weber, 2008). The body-mass range of invertebrates, from small mites to large earthworms, is huge and spans several orders of magnitude (nine orders

for the invertebrates I worked with). However, not only their size, but also their body architecture (structure, composition, shape) differs. Slender elongated forms like earthworms, centipedes or millipedes clearly differ from short, round bodied species like spiders and mites and of course there are a lot of intermediate body shapes to be found. And there are still more differences amongst others type of outer layer and preferred habitat. The outer layer of earthworms is soft while that of millipedes, mites and beetles is shielded and thus makes the animal more or less vulnerable to predatory attack. Earthworms and centipedes need a humid habitat (mostly in the deeper litter and soil layers) while beetles, spiders and millipedes are not thus restricted and can be found in the uppermost layers and on the (litter) surface. All these differences between invertebrate species that occur in the soil and litter layer make it necessary to account for the different phylogenetic groups when considering the metabolism. This importance has been shown already by Meehan (2006b) and Chown *et al.* (2007), who reported different scaling exponents as well as different activation energies for different animal groups. Though some groups display the same scaling behaviour with body mass and temperature they differed in their normalization constants (Meehan, 2006b). Furthermore, studies dealing with metabolic data of invertebrates found substantial variation in their metabolic scaling across phylogenetic groups and deviations from the $3/4$ power-law prediction (Farrell-Gray and Gotelli, 2005; Niven and Scharlemann, 2005; Meehan, 2006b; White *et al.*, 2007; Isaac and Carbone, 2010). This was also shown by Chown *et al.* (2007) with a superior fit of a model that accounted for phylogenetic nonindependence. However, there are even more distinctive features for distinguishing animals in communities which are generally connected with the relations of the species. Species might be grouped into feeding types by their resources. This differentiation is useful regarding metabolic rate as predators usually have a higher metabolic rate which results in a lower density due to the higher energetic demand (Damuth, 1987; Marquet *et al.*, 2005). Especially in phylogenetic groups that entail a diversity of feeding types this differentiation is able to explain some of the variance found within these groups. The soil organisms I worked with differ in their feeding type. While spiders, some beetles, centipedes and some mites are predatory, earthworms, isopods and millipedes feed on various types of litter or detritus in different stages of decay. However, despite their many differences they also share a uniform feature, they are all ectothermic.

2.8 Community energy use

The MTE (Brown *et al.*, 2004) predicts the metabolic rate to scale with body mass to the power of three quarters. Thus, mass-specific metabolic rate has to scale with body mass to a negative one-quarter power. Besides these power-law scalings of metabolic rate, many other biological rates also showed a power-law scaling of one quarter or multiples of one quarter with body mass. Examples of these quarter power-law scalings are heart rate, developmental rate, turnover times, biomass production, mortality, and equilibrium number of individuals or carrying capacity (Brown *et al.*, 2004). Heart rate, mortality, and developmental rate scale with body mass to the power of a negative quarter while turnover times scale with a positive quarter power. Biomass production and fluxes of elements are found to scale in the same manner as metabolic rate with body mass to the three-quarter power. Contrasting this, equilibrium number of individuals or carrying capacity is supposed to scale inversely, with a negative three-quarter power law.

The observation that broad animal groups (birds, mammals, invertebrates, reptiles and amphibians) show an abundance scaling with body mass to the power of $-3/4$ (Damuth, 1991) in combination with the prediction of metabolism scaling with body mass to the $3/4$ power (Kleiber, 1947; Peters, 1983) led to the perception that the resulting scaling of energy use of all populations

in a community should be independent of body mass (Damuth, 1981, 1991; Nee *et al.*, 1991). To achieve this equal distribution of energy use in a natural community, both metabolic rate and abundance have to scale directly inverse. This prediction was formulated in the energetic equivalence rule (EER, Damuth, 1991; Nee *et al.*, 1991) and tested with global abundance data that verified the predicted inverse scaling of metabolic rate and abundance (Meehan *et al.*, 2006; Buckley *et al.*, 2008).

In the previous sections, I have shown that descriptions of what is happening in field communities first need a lot of laboratory work to learn something about energy demand of the different organisms (part 2.2 to 2.6). This knowledge drawn from laboratory work (Chapter 5 and 6) can then be used for calculations of interactions in the field (Chapter 7 and 8).

2.9 Investigating animals in the soil

Evaluating animal assemblages in the soil is a challenging task as these animals cannot be observed directly. It is not clear how soil animals are affected by the usage or type of habitat (managed vs. unmanaged) they are living in (Wall *et al.*, 2010). Moreover, as soil animals are so diverse, it is likely that different animals are differently affected by land use. Certain species might be threatened by land use while others may seem to be unaffected. The assemblage might be able to recover from the impact of the usage after a certain period of time if the habitat is unmanaged and allowed to develop freely. Such questions may be answered in field studies, where different land-use types can be compared. A special research facility for such large-scale comparisons are the Biodiversity Exploratories (Fischer *et al.*, 2010b). There are three research regions (exploratories) in which long-term field studies in grassland and forest are performed (Fig. 2.4). Additionally, different land-use types are replicated in all regions and enable a comparison. My field work was performed in the forest and compared the different land-use types that are replicated in all regions: coniferous forest, young beech forest (about 30 years old), old beech forest (about 70 years old) and natural beech forests (about 120 years old, unmanaged).

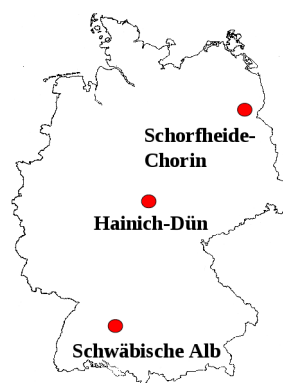


Figure 2.4: Locations of the three areas of the Biodiversity Exploratories in Germany

However, research on soil organisms is difficult as these organisms with their encrypted life style impede direct monitoring. Therefore, organisms have to be extracted from litter and soil to be accessible for investigation. Mobile animals, like earthworms, that react to a certain stimulus with moving up and out of the soil, can be trapped without removal of soil. Other organisms are more likely to move to deeper soil layers when interference occurs and can only be gathered by removal of soil cores that contain them. These soil cores are then taken to the lab, the animals extracted and determined. Thus, information about abundance of soil-dwelling species can only be inferred from the known surface (or volume) of the soil cores and the designated number of animals in

this small sample but cannot be determined directly in the field. Another method for investigating organisms of the litter layer is litter sieving. From a defined surface area all litter is removed and sieved with a coarse mesh to capture mobile organisms. Additionally, the bare soil is observed and all emerging animals are caught and together with the sieved organisms represent the assemblage of this researched area. Abundances will be given per square meter or another metric of area, as the area is the relevant unit for the energy input by leaf litter, even though the litter and soil layers could also provide a three-dimensional habitat. Thus, such samplings yield information about which species are present in which abundance per area, as well as the mean body mass of each species (or mean body masses of different life stages). With this information the biomass of each species can be determined. These data form the foundation for proceeding calculations of energy use of a specific organism with the estimated body mass as well as the calculation of the energy use of the different populations of species in a soil-animal community. Such knowledge about energy use of the populations allows an assessment of the energy that is present in this system and how it is distributed among the different populations.

2.10 Short outline

During my thesis, I worked on different aspects of energy demand and supply of litter and soil living invertebrate species in forests. These are so diverse in terms of physiology, phylogeny and body architecture that they are likely to show differences in scaling of their rates. I used laboratory experiments on consumption at different temperatures to evaluate possible effects on the strength of feeding interactions, the resulting stability of the community, and their ingestion efficiency (Chapter 3 and Chapter 4). Metabolic demand of the different phylogenetic groups showed strong variation (Chapter 3 and 4). Therefore, I closely examined the effect of body mass, temperature and phylogenetic affiliation on the scaling of metabolic rates (Chapter 5). I gathered data on metabolic rates, calculated specific scaling relationships for the different phylogenetic groups, thereby showing that phylogenetic group has a major influence on metabolic scaling (Chapter 5). By complementing the metabolic-rates dataset with data on assimilation efficiencies, I was able to compare the changes with body mass or temperature for different consumer types (Chapter 6). Furthermore, I calculated maintenance consumption rates which represent the energy demand required for maintenance of life. Hence, with this study I made it possible to predict how different consumer types might be affected by increasing temperature (Chapter 6). Then, I applied my previous results from the laboratory study (Chapter 5) to field data for scrutinizing different hypotheses. I used estimated metabolic rate and density as a surrogate for resource supply and analysed its effect on the type of reproduction in mites (Chapter 7). The proportion of asexually reproducing species should be higher in energy rich bottom-up controlled systems, while systems poor in resources should favour sexually reproducing species as these are able to adapt more easily (Chapter 7). And finally, I applied the previous findings of differences in metabolic rate scalings on a field study on a diverse soil-animal community in different land-use types. Thereby, I tested different hypotheses about the distribution of energy in an assemblage and how abundances and biomasses of the different species are distributed in dependence on their body masses (Chapter 8). With the data on abundance and body mass obtained by a field survey, I calculated the metabolic rates of the species in the litter and soil communities. Furthermore, I considered the population energy use of the different phylogenetic groups and their biomass. For my analyses I differentiated not only between the phylogenetic groups, but also between the land-use types and the feeding types (Chapter 8).

2.11 Contributions to the publications

Chapter 3

Temperature, predator-prey interaction strength and population stability

Authors: Rall, B.C., Vucic-Pestic, O., Ehnes, R.B., Emmerson, M.C. and Brose, U.

Published in: *Global Change Biology* (2010) 16, 2145–2157

Author Contributions: Idea by B.C.R., laboratory work by B.C.R., O.V.P., R.B.E. and U.B.; statistical analyses and theoretical analysis by B.C.R.; the text was written mainly by B.C.R., M.C.E. and U.B..

Chapter 4

Warming up the system: higher predator feeding rates but lower energetic efficiencies

Authors: Vucic-Pestic, O., Ehnes, R.B., Rall, B.C. and Brose, U.

Published in: *Global Change Biology* (2011) 17, 1301–1310

Author Contributions: Idea by O.V.P., B.C.R., R.B.E. and U.B., laboratory work by all authors, but mainly by O.V.P. and R.B.E.; statistical analyses by O.V.P. and B.C.R.; the text was written mainly by O.V.P. and U.B. with minor contributions of B.C.R. and R.B.E..

Chapter 5

Phylogenetic grouping, curvature and metabolic scaling in terrestrial invertebrates

Authors: Ehnes, R.B., Rall, B.C. and Brose, U.

Published in: *Ecology Letters*, (2011) 14: 993–1000,

Author Contributions: R.B.E. collected literature data and ran the respiration measurements. R.B.E. and U.B. designed the study and wrote the manuscript. All authors carried out the statistical analysis, interpreted and discussed the results and commented on the manuscript.

Chapter 6

Respiration rates, assimilation efficiencies and maintenance consumption rates depend on consumer types: energetic implications of environmental warming

Authors: Lang, B., Ehnes R.B., Rall, B.C. and Brose, U.

Manuscript in preparation

Author Contributions: Idea and analyses by all authors, database work by R.B.E. and B.L., text by B.L., B.C.R. and U.B.

Chapter 7

Positive correlation of density and parthenogenetic reproduction in oribatid mites (Acari) supports the ‘Structured Resource Theory of Sexual Reproduction’

Authors: Maraun, M., Norton, R.A., Ehnes R.B., Scheu, S. and Erdmann, G.

Published in: *Evolutionary Ecology Research*, (2012) 14: 311–323,

Author Contributions: Idea by M.M. and S.S.; empirical data from M.M. and G.E.; analysis by M.M., G.E. and R.B.E.; text written by M.M., S.S. and G.E.

Chapter 8

Lack of energetic equivalence in forest soil invertebrates

Authors: Ehnes R.B., Pollierer, M.M., Erdmann, G., Klarner, B., Eitzinger, B., Digel, C., Ott, D., Maraun, M., Scheu, S. and Brose, U.

Accepted manuscript in Ecology

Author Contributions: Idea by R.B.E., U.B. and S.S.; Laboratory and field work by R.B.E., M.M.P, G.E., B.K., B.E., C.D., D.O., M.M.; statistical analysis by R.B.E. and U.B.. The text was written by R.B.E. and U.B. and all authors commented on the manuscript.

3 Temperature, predator-prey interaction strength and population stability

3.1 Abstract

Warming could strongly stabilize or destabilize populations and food webs by changing the interaction strengths between predators and their prey. Predicting the consequences of warming requires understanding how temperature affects ingestion (energy gain) and metabolism (energy loss). Here, we studied the temperature dependence of metabolism and ingestion in laboratory experiments with terrestrial arthropods (beetles and spiders). From this data, we calculated ingestion efficiencies (ingestion/metabolism) and per capita interaction strengths in the short and long term. Additionally, we investigated if and how body mass changes these temperature dependencies. For both predator groups, warming increased metabolic rates substantially, whereas temperature effects on ingestion rates were weak. Accordingly, the ingestion efficiency (the ratio of ingestion to metabolism) decreased in all treatments. This result has two possible consequences: on the one hand, it suggests that warming of natural ecosystems could increase intrinsic population stability, meaning less fluctuations in population density; on the other hand, decreasing ingestion efficiencies may also lead to higher extinction risks because of starvation. Additionally, predicted long-term per capita interaction strengths decreased with warming, which suggests an increase in perturbation stability of populations, i.e., a higher probability of returning to the same equilibrium density after a small perturbation. Together, these results suggest that warming has complex and potentially profound effects on predator-prey interactions and food-web stability.

3.2 Introduction

Understanding the impact of global warming on the stability of populations and critical ecosystem processes is one of the most important scientific challenges we currently face (Mann *et al.*, 1999; Hughes, 2000). Warming may affect a species by changing the strength of its interactions (e.g., competition or predator-prey interactions) with coexisting species. By modifying interaction strength warming may not only directly affect population densities, but it may also indirectly affect the population size of coexisting species (Berlow *et al.*, 2009). Indirect effects occur when a species affects the per capita population growth rate of a non-adjacent species within an ecological network such as a food web. These indirect effects among species can be more important than direct effects in driving the outcomes of perturbations (Abrams, 1995; Menge, 1997; Yodzis, 2000; Ives and Cardinale, 2004). Moreover, the pattern and strength of species interactions determine the stability of populations and food webs (May, 1972; de Ruiter *et al.*, 1995; Emmerson and Yearsley, 2004; Brose *et al.*, 2006b; Otto *et al.*, 2007; Neutel *et al.*, 2007; Brose, 2008). Thus, understanding how temperature affects interaction strengths is of vital importance for predicting consequences of global warming for the stability of populations, communities and ecosystem processes (Hughes, 2000). Two important aspects of population stability (McCann, 2000) are (1) intrinsic stability expressed as the inverse of variability in population density over time (Brose *et al.*, 2006b), inversely related to predator ingestion efficiencies (Yodzis and Innes, 1992; Vasseur

and McCann, 2005; Rall *et al.*, 2008), which are defined as the ratio of ingestion to metabolism; and (2), perturbation stability, quantifying the resistance of a population to a small perturbation measured as the probability of returning to the same equilibrium density (Emmerson and Raffaelli, 2004). Perturbation stability decreases with increasing per capita interaction strength (hereafter: interaction strength) expressing the effects of a predator individual on the abundance of prey populations (May, 1972; de Ruiter *et al.*, 1995). Often, interaction strength is measured as the log ratio between prey density in treatments with predators versus prey density in treatments without predators (Berlow *et al.*, 1999, 2004). The time scales used to calculate interaction strength varies between short term experiments of some days (Emmerson and Raffaelli, 2004) or weeks (Sanford, 1999) and longer experiments over several months (Berlow, 1999). These differences in time scales may result in different outcomes and interpretations of experiments (Walther, 2007). In particular, interaction strengths on a short time scale (days) depend primarily on predator ingestion rates while ignoring numerical responses in predator and prey abundances. However, on a long time scale (months, years), interaction strengths are also influenced by the rates of prey growth and prey abundance (Berlow *et al.*, 2009). Therefore, predicting the consequences of warming requires an understanding of temperature effects on the rates of ingestion and metabolism of the predators (with implications for short term interaction strengths) and the growth rates and abundances of the prey species (with additional implications for long term interaction strengths). The Metabolic Theory of Ecology (MTE) offers a general framework for tackling these questions by suggesting: (i) three-quarter power-law increases in the rates of metabolism, ingestion and growth with organism body mass, (ii) a three-quarter power-law decrease in abundance with body mass within a single trophic level, and (iii) exponential scaling of these rates and abundance with temperature, where the strength of these scaling relationships is determined by an activation energy, E (Gillooly *et al.*, 2001; Brown and Gillooly, 2003; Brown *et al.*, 2004; Meehan, 2006a). Despite an intensive debate on the exact exponents, the power-law (body mass) and the exponential (temperature) scaling of metabolism find broad empirical support (Clarke, 2004; Kozłowski and Konarzewski, 2004; Savage *et al.*, 2004b; Brown *et al.*, 2004; Makarieva *et al.*, 2005b). In the case of ingestion, the scaling with body mass and temperature remains hotly debated (see: Peters, 1983; Brown *et al.*, 2004; Vasseur and McCann, 2005; Carbone *et al.*, 2007; Brose *et al.*, 2008; Vucic-Pestic *et al.*, 2010b; Brose, 2010; and references therein). In contrast to MTE predictions (Peters, 1983), recent foraging studies have documented a hump-shaped relationship between ingestion rates and predator-prey body-mass ratios (Wahlström *et al.*, 2000; Vonesh and Bolker, 2005; Brose *et al.*, 2008; Vucic-Pestic *et al.*, 2010b). This implies that handling and digestion constrain predator ingestion rates at low predator-prey body-mass ratios (i.e. when prey species are relatively large), whereas catching efficiencies limit predator ingestion rates at high ratios (i.e. when prey species are relatively small). While some prior studies showed that ingestion increases with temperature (Thompson, 1978; Kingsolver and Woods, 1997) others concluded that ingestion is not effected by warming (Woodward and Hildrew, 2002). Unfortunately, studies that include both, temperature-dependent ingestion and metabolism of predators, are scarce (Vasseur and McCann, 2005; Abrahams *et al.*, 2007; but see Kingsolver and Woods, 1997 for an example), and it remains unknown whether the different processes leading to handling and catching limitation of large (left side of the hump-shaped relationship, (Brose *et al.*, 2008)) and small prey (right side of the hump-shaped relationship), are similarly influenced by temperature. Here, we address these deficiencies by quantifying the temperature dependence of metabolism and ingestion (of small and large prey) of terrestrial arthropods (beetles and spiders) across a range of body masses. The predator and prey species of our experiments were chosen to reflect the predator-prey body-mass ratios of natural food webs (Brose *et al.*, 2006a) and both sides of the hump-shaped relationship

between ingestion and body-mass ratios documented in a prior study with the same species (Brose *et al.*, 2008; Vucic-Pestic *et al.*, 2010b). All experiments were replicated at three environmental temperatures (8 °C, 15 °C and 22 °C) representing the natural gradient of spring and summer temperatures in central Germany (Deutscher Wetterdienst, 2007). Based on these experiments, we quantified how temperature affects ingestion efficiencies, short term and long term interaction strengths, which provides the information required to address the effect of temperature on both intrinsic and perturbation stability of populations and food webs.

3.3 Material and Methods

3.3.1 Respiration and ingestion experiments

We investigated how predator metabolism varied with temperature. Specifically, we measured the oxygen consumption of eight carabid beetle species (*Abax parallelepipedus*, *Carabus auratus*, *Harpalus affinis*, *Notiophilus biguttatus*, *Platynus dorsalis*, *Poecilus versicolor*, *Pseudophonus rufipes* and *Pterostichus oblongopunctatus*) and six species of lycosid and pisaurid spiders (*Alopecosa cuneata*, *Pardosa lugubris*, *Pardosa palustris*, *Pirata latitans*, *Pirata piraticus* and *Pisaura mirabilis*). Oxygen consumption of the beetles and spiders was measured in an automated electrolytic microrespirometer (Scheu, 1992). We converted the individual oxygen (O₂) consumption [ml/s] into energetic equivalents of metabolism I [J/s] by assuming that 1ml O₂ equals 20.1 J (Peters, 1983). For a subset of these predators we investigated how ingestion varied with predator and prey body mass, and temperature. Logistic constraints restricted our study to five beetle species (*Abax parallelepipedus*, *Carabus auratus*, *Platynus dorsalis*, *Poecilus versicolor* and *Pseudophonus rufipes*) and four spider species (*Alopecosa cuneata*, *Pardosa palustris*, *Pirata latitans* and *Pisaura mirabilis*). For each predator species, the experiments were replicated six times: with large prey (beetle prey: fly larvae *Lucilia caesar*, spider prey: cricket *Gryllus sigillatus*) and with small prey (beetle prey: fruit fly *Drosophila hydei*, spider prey: springtail *Heteromurus nitidus*) in climatic chambers at three temperature levels (8 °C, 15 °C and 22 °C). These two prey size groups represent the whole range of body size ratios found in nature (Brose *et al.*, 2006a), including the left and right side of the hump-shaped relationship between predation rates and predator-prey body-mass ratios documented in a prior study (Brose *et al.*, 2008). For both predator groups, we used two prey species with similar escape behaviour. Crickets and springtails avoid spider predation by jump-escaping in the case of emergency. Flightless fruit flies and the fly larvae escape beetle predation by crawling. Ingestion experiments were performed in 0.04m² perspex arenas lined with dental cast to hold moisture during experimental time of 24 h. Initially, we added 2.35 g of re-moistened dry moss (*Polytrichum formosum*) as habitat structure, 30 prey individuals, N_i , and one predator individual to each arena. The number of the remaining prey individuals was counted after 24 h to calculate the number of prey individuals eaten (N_e). The full-factorial combination of the independent variables (nine predators, two prey sizes, three temperatures) with six replicates per combination resulted in a total of 324 experimental units. For every combination of predator j and prey i , we calculated the ingestion rate, J_{ij} [J/s],

$$J_{ij} = \frac{N_e M_i \varepsilon}{t_F} \quad (3.1)$$

where M_i is the individual body mass of a prey individual [g/Ind.] and t_F is the experimental duration in [s], we assume an energy content ε of 7000 J/g wet mass (Peters, 1983). Subsequently, we calculated the dimensionless ingestion efficiency, y_{ij} , (Vasseur and McCann, 2005) as

$$y_{ij} = \frac{\omega_{ij} J_{ij}}{\lambda I - j} \quad (3.2)$$

where ω_{ij} is the dimensionless assimilation efficiency ((ingestion – faeces)/ingestion). We assumed a constant assimilation efficiency ($\omega_{ij} = 0.85$, (Lawton, 1970; Peters, 1983; Yodzis and Innes, 1992)) that does not vary with environmental temperature as documented in most empirical studies, e.g. of carnivorous insects (Lawton, 1970), caterpillars (Kingsolver and Woods, 1998) and lizards (Chen *et al.*, 2003; McConnachie and Alexander, 2004). λ is a dimensionless constant converting basal metabolic rate into field metabolic rate ($\lambda = 3$ (Savage *et al.*, 2004b)), and I_j is the metabolic rate of predator j (calculated according to Eqn. 3.4 below). The ingestion efficiency expresses the ingestion gain of a consumer relative to its metabolic loss, and it is thus closely related to biomass gains or losses. Although there is a wide range of different metrics that can be used to calculate per capita interaction strengths (Berlow *et al.*, 1999, 2004), we focused on the most widely used: the log response ratio, (Berlow *et al.*, 1999; Emmerson and Raffaelli, 2004):

$$\alpha_{ij} = \left| \frac{\ln \left(\frac{(N_i - N_e)}{N_i} \right)}{t} \right| \quad (3.3)$$

where t [d] is the experimental duration, N_i [Ind.] is the initial prey abundance and N_e [Ind.] is the number of prey eaten. In our case, the short term interaction strength is the log ratio between the prey abundances at the end and at the start of the experiment. This approach assumes that prey abundance without predators equals the initial prey density, and that thus natural mortality of the prey species is negligible. This assumption was supported by the lack of mortality in controls without predators.

3.3.2 Statistical analysis of experimental data

All data were analysed by ANCOVAs with the statistical software R 2.9.0 (R Development Core Team, 2010) to distinguish between effects of the factors (1) predator group (beetle or spider) and (2) prey size (large or small, only for ingestion experiments), (3) level of environmental temperature (8 °C, 15 °C, 22 °C), and the continuous variable (4) predator mass [ln(g)]. Subsequently, we generated multiple regression models following the MTE (Brown *et al.*, 2004) predicting that per capita rates of metabolism, I_j [J/s], and ingestion, J_{ij} [J/s], of an ectotherm organism depend on its body mass, M [g], and the environmental temperature, T [K] as:

$$I_j = i_0 M_j^{b_I} e^{\frac{-E_I}{kT}} \quad (3.4)$$

$$J_{ij} = j_0 M_j^{b_J} e^{\frac{-E_J}{kT}} \quad (3.5)$$

where i_0 and j_0 are normalisation constants, b is an allometric exponent, k is Boltzman's constant ($8.62 \times 10^{-5} \text{ eV/K}$) and E [eV] is the activation energy. In the same vein, we analysed the temperature and body-mass dependence of ingestion efficiencies and interaction strengths as:

$$y_{ij} = y_0 M_j^{b_y} e^{\frac{-E_y}{kT}} \quad (3.6)$$

$$e^{\alpha_{ij}} = \alpha_0 M_j^{b_\alpha} e^{\frac{-E_\alpha}{kT}} \quad (3.7)$$

Note that due to the fact that the per capita interaction strength is calculated as the natural logarithm (Eqn. 3.3), we used the exponential functions for investigating the mass and temperature dependence of per capita interaction strength (Eqn. 3.7). Consistent with prior studies (Brown *et al.*, 2004; Meehan, 2006a,b), we made multiple linear least-squares regressions with the GLM-procedure of the statistical software R 2.9.0 (R Development Core Team, 2010) to estimate the parameters of equation (3.4–3.7) after ln-transformation.

3.3.3 Long term interaction strength

Calculations of long term interaction strengths were based on a population dynamic model (Yodzis and Innes, 1992; Vasseur and McCann, 2005; Rall *et al.*, 2008) of prey density, N [$\text{Ind.}/\text{m}^2$], and predator density, P [$\text{Ind.}/\text{m}^2$]:

$$\frac{dN}{dt} = r \left(1 - \frac{N}{K} \right) N - c_F J_{ij} NP \quad (3.8)$$

$$\frac{dP}{dt} = \frac{c_J J_{ij} NP}{\omega_{ij}} - c_1 I_j P, \quad (3.9)$$

where t [d] is time, r [$1/d$] is the intrinsic growth rate, and K [$\text{Ind.}/\text{m}^2$] is the carrying capacity of the prey species. The feeding interaction follows a linear functional response, where J_{ij} [J/s] is the ingestion rate of a single predator, c_J [sN/dJ] is a correction factor that converts the ingestion rate from Joules per second into prey individuals per day. I_j [J/s] is the metabolic rate of the predator and c_1 is a correction factor that converts metabolism from Joules per second into predator individuals per day [sP/dJ]. The temperature and mass dependent intrinsic growth rate r in (Eqn. 3.8) is calculated by

$$r = r_0 M_j^{b_r} e^{\frac{E_r}{kT}}, \quad (3.10)$$

where r_0 ($r_0 = e^{32.39}$, Savage *et al.*, 2004a) is a normalisation constant, M is the mass [μg], b_r ($b_r = -0.25$) is a constant exponent, k is Boltzmann's constant ($8.62 \times 10^{-5} \text{ eV/K}$) and E_r (-0.84 eV) is the activation energy for insects (Savage *et al.*, 2004a). The carrying capacity K in (Eqn. 3.8) depends on environmental temperature, body mass, the trophic level of the prey and the net primary production of the habitat (Allen *et al.*, 2002; Meehan, 2006a) following

$$K = K_0 M_j^{b_K} e^{\frac{E_K}{kT}} \sigma^z e^{tl_0(tl-1)}, \quad (3.11)$$

where K_0 is a normalisation constant, b_K is a constant exponent, E_K is the activation energy, σ is the annual net primary productivity of the habitat [$\text{g(C)}/\text{m}^2\text{y}$], z is a constant exponent, tl_0 is a constant and tl the trophic level. We used constants found in other studies with similar soil invertebrates as in our study: $K_0 = e^{-31.15}$; $b_K = -0.72$; $E_K = 0.71$; $tl_0 = -2.68$; $z = 1.03$; $tl = 1.5$ for decomposers, fungivores and herbivores (Meehan, 2006a). The net primary productivity in equation 3.11 is temperature dependent (Allen *et al.*, 2005):

$$\sigma = \sigma_0 e^{\frac{E_\sigma(T_0 - T)}{kT T_0}} \quad (3.12)$$

where σ_0 is the net primary productivity at the temperature T_0 [K] and E_σ is the activation energy (-0.35 eV, of the net primary production that is mechanistically derived from the activation energy of photosynthesis (Allen *et al.*, 2005)). We assumed an average net primary production, σ_0 , of $600 \text{ g(C)}/\text{m}^2\text{y}$ for temperate regions (Cramer *et al.*, 1999) at an average temperature T_0 of 9.5°C (282.65 K) which is approximately equal to the annual average temperature in Germany since 2000 (Deutscher Wetterdienst, 2007). The long-term population densities of equations 3.8 and 3.9 are calculated assuming that the system is at equilibrium (i.e. $dN/dt = 0$; $dP/dt = 0$), which yields equilibrium densities (P' , N') of

$$P' = \frac{(K - N')r}{c_F J_{ij} K}, \quad (3.13)$$

$$N' = \frac{\omega_{ij} c_I I_j}{c_F J_{ij}}. \quad (3.14)$$

Subsequently, the long term per capita interaction strength between i and j , A_{ij} , is calculated according to the log ratio interaction strength used in prior studies (also known as dynamic index) (Berlow *et al.*, 1999; Emmerson and Raffaelli, 2004):

$$A_{ij} = \left| \frac{\ln\left(\frac{N^+}{N^-}\right)}{Y} \right|, \quad (3.15)$$

where N^+ is the prey abundance when the predator is present and N^- is the prey abundance when the predator is absent and Y is the predator abundance. We can replace N^+ by N' and Y by P' (see Eqn. 3.13, 3.14). Moreover, in absence of a predator the prey is growing to its carrying capacity (Eqn. 3.11), and we can replace N^- with K , which yields

$$A_{ij} = \left| \frac{\ln\left(\frac{N'}{K}\right)}{P'} \right|. \quad (3.16)$$

Inserting the equations 3.13 and 3.14 in equation 3.16 and using the temperature dependencies of I (Eqn. 3.4), J_{ij} (Eqn. 3.5), K (Eqn. 3.11) and r (Eqn. 3.10) yields the long-term interaction strengths depending on environmental temperature.

3.4 Results

3.4.1 Respiration and ingestion experiments

The metabolic rates of the predators, beetles and spiders, increased significantly with their body mass and temperature (Fig. 3.1a, b; ANCOVA, Table 3.1). The significant interaction term between predator mass and predator group (Table 3.1) suggests that the exponent for beetles ($b_1 = 0.72$; Table 3.2; Fig. 3.1a, circles) is higher than the exponent for spiders ($b_1 = 0.46$; Table 3.2; Fig. 3.1a,

Table 3.1: ANCOVA tables of metabolism, ingestion, ingestion efficiency and interaction strength

	DF	metabolism		ingestion		ingestion efficiency		short term interaction strength	
		F	p	F	p	F	p	F	p
1: <i>Predator mass</i> ($\ln(M)$)	1	1012.23	< 0.001	341.43	< 0.001	13.61	< 0.001	1.23	0.27
2: Temperature (8 °C, 15 °C, 22 °C)	2	326.35	< 0.001	6.38	< 0.01	63.87	< 0.001	1.43	0.24
3: Prey size (large/small)	1			1385.96	< 0.001	341.83	< 0.001	18.04	< 0.001
4: Predator group (beetles/spiders)	1	56.97	< 0.001	175.4	< 0.001	0.9	0.34	33.15	< 0.001
<i>Predator mass</i> x Temperature	2	0.08	0.92	1.36	0.25	2.27	0.11	2.39	0.09
<i>Predator mass</i> x Prey size	1			189.24	< 0.001	14.54	< 0.001	130.14	< 0.001
Temperature x Prey size	2			4.41	0.01	32.29	< 0.001	2.68	0.07
<i>Predator mass</i> x Predator group	1	26.04	< 0.001	7.35	< 0.01	0.04	0.84	28.14	0.001
Temperature x Predator group	2	0.88	0.41	1.53	0.22	0.68	0.51	3.53	0.03
Prey size x Predator group	1			47.32	< 0.001	1.68	0.2	< 0.01	0.96
1 x 2 x 3	2			0.06	0.95	3.21	0.04	0.75	0.47
1 x 2 x 4	2	0.13	0.88	0.59	0.56	0.62	0.54	1.5	0.23
1 x 3 x 4	1			0.42	0.52	0.02	0.89	20.53	< 0.001
2 x 3 x 4	2			0.97	0.38	0.26	0.77	3.39	0.04
1 x 2 x 3 x 4	2			0.83	0.44	0.41	0.66	1.61	0.2

Continuous variables in italic and factors in bold.

The metabolism ANCOVA does not include the factor "prey size".

Residual standard errors are: metabolism (333), ingestion, ingestion efficiency and short term interaction strength (270)

crosses). In contrast, the interaction term between temperature and predator group was not significant (Table 3.1) suggesting that the activation energy was similar for beetles ($E_1 = 0.87$; Table 3.2; Fig. 3.1b, circles) and spiders ($E_1 = 0.80$; Table 3.2; Fig. 3.1b, crosses).

We found significant effects of predator body mass and temperature on ingestion rates (ANCOVA, Table 3.1). Significant interaction terms with predator mass indicate that the allometric exponents differ for predator groups and prey size (Table 3.1): exponents were higher for beetles than for spiders and while ingestion increased with predator body mass when prey were large ($b_J = 0.82$ and $b_J = 0.6$ for beetles and spiders, respectively; Table 3.2; Fig. 3.1c), it decreased with predator body mass when prey were small ($b_J = -0.25$ and $b_J = -0.63$ for beetles and spiders, respectively; Table 3.2; Fig. 3.1e). Temperature effects on ingestion were similar for both predator groups (no significant interaction term between temperature and predator group) while they differed with respect to prey size (Table 3.1). Ingestion increased with temperature when prey were large ($E_1 = 0.24$ and $E_1 = 0.30$ for beetles and spiders, respectively; Table 3.2; Fig. 3.1d), whereas it did not vary significantly when prey were small (Table 3.2; Fig. 3.1f).

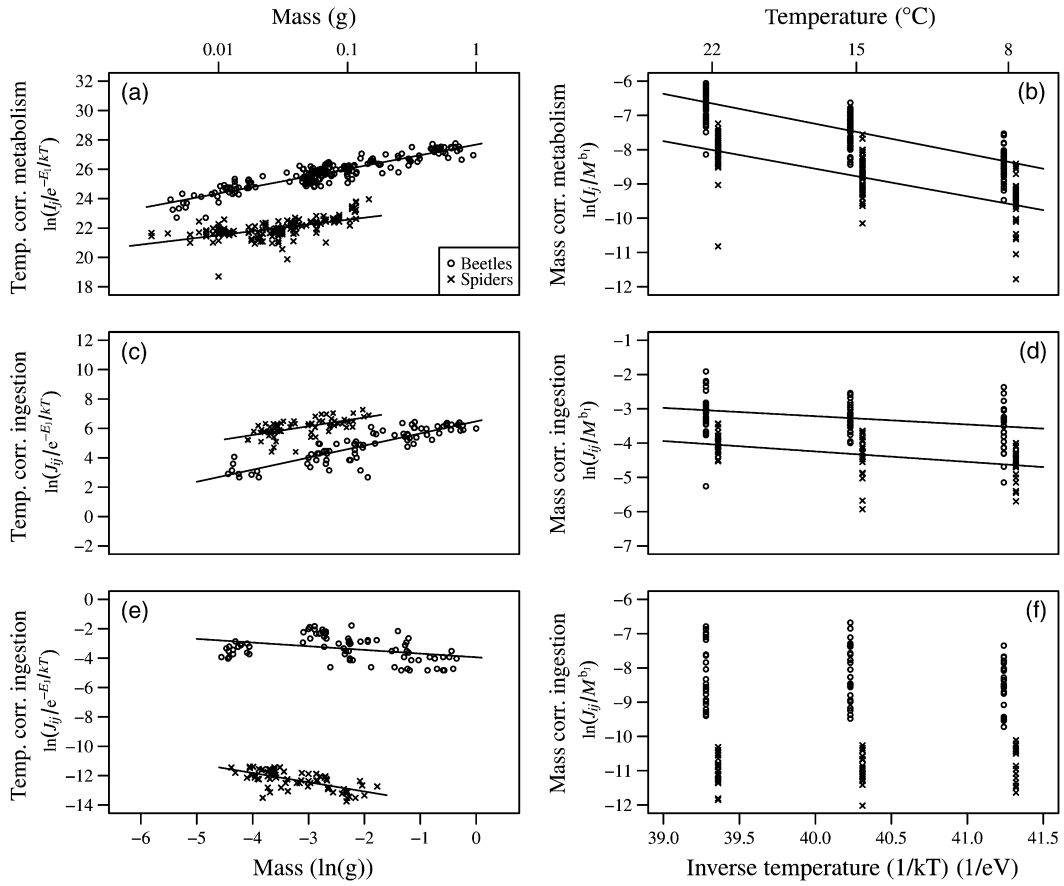


Figure 3.1: Beetle (circles) and spider (crosses) metabolism I_j (a, b), ingestion J_{ij} of the larger (c, d) and the smaller prey (e, f) depending on predator body mass (a, c, e) and environmental temperature (b, d, f). Data are ln-transformed and the dependent variables are normalized by their temperature dependence (a, c, e) or their mass dependence (b, d, f). Upper axes show untransformed body mass (g) and temperature [°C] scales. Offsets of -0.04 (beetles) and 0.04 (spiders) were applied to temperature data in panels (b), (d) and (f). Note the inverse scaling of the lower temperature axes.

Table 3.2: Regression results for the body-mass and temperature dependence of metabolism, ingestion, ingestion efficiency and interaction strength.

	ln(c)	p	lower CI	upper CI	b	p	lower CI	upper CI	E	p	lower CI	upper CI	r ²	AIC	n
<i>metabolism</i>															
beetles	27.68	***	24.72	30.64	0.72	***	0.68	0.77	0.87	***	0.80	0.95	0.89	192.19	183
spiders	23.62	***	19.17	28.07	0.46	***	0.36	0.55	0.80	***	0.69	0.91	0.64	265.06	162
<i>ingestion of large prey</i>															
beetles	6.47	*	0.13	12.82	0.82	***	0.71	0.93	0.24	**	0.09	0.40	0.75	142.11	80
spiders	7.93	*	2.05	13.81	0.60	***	0.40	0.79	0.30	***	0.16	0.45	0.42	96.26	67
<i>ingestion of small prey</i>															
beetles	-3.94	-	-12.86	4.97	-0.25	**	-0.39	-0.11	0.11	-	-0.11	0.33	0.14	193.17	79
spiders	-14.34	***	-20.19	-8.48	-0.63	***	-0.80	-0.46	-0.09	-	-0.23	0.06	0.44	97.04	68
<i>ingestion efficiency – large prey</i>															
beetles	-22.40	***	-28.74	-16.05	0.10	-	-0.01	0.21	-0.63	***	-0.79	-0.47	0.47	142.23	80
spiders	-16.88	***	-22.77	-10.99	0.14	-	-0.06	0.33	-0.50	***	-0.64	-0.36	0.45	96.48	67
<i>ingestion efficiency – small prey</i>															
beetles	-32.84	***	-41.76	-23.92	-0.97	***	-1.11	-0.83	-0.76	***	-0.99	-0.54	0.74	193.28	79
spiders	-39.18	***	-45.03	-33.32	-1.09	***	-1.26	-0.91	-0.89	***	-1.03	-0.74	0.81	97.17	68
<i>absolute interaction strength with large prey</i>															
beetles	3.33	***	1.46	5.20	0.16	***	0.13	0.19	0.07	**	0.02	0.11	0.58	-53.29	80
spiders	3.62	***	2.19	5.05	0.15	***	0.11	0.20	0.07	***	0.04	0.11	0.44	-92.85	67
<i>absolute interaction strength with small prey</i>															
beetles	2.80	*	0.22	5.39	-0.04	-	-0.08	0.00	0.07	*	0.00	0.13	0.09	-2.55	79
spiders	-5.13	*	-8.95	-1.31	-0.36	***	-0.48	-0.25	-0.11	*	-0.21	-0.02	0.4	38.99	68

c = normalization constant; p = level of significance; CI = confidence interval; b = allometric exponent; E = activation energy; # = zero values omitted for ln transformation.
 Level of significance: *** p < 0.001; ** p < 0.01; * p < 0.05.

3.4.2 Ingestion efficiency

From the metabolism and ingestion measures, we calculated the ingestion efficiency (ingestion / metabolism) for each predator. We found significant effects of temperature and predator body mass on ingestion efficiencies (ANCOVA, Table 3.1). Significant interaction terms indicated that these effects depend on prey type, whereas non-significant interaction terms suggest similar mass and temperature effects for both predator groups (ANCOVA, Table 3.1).

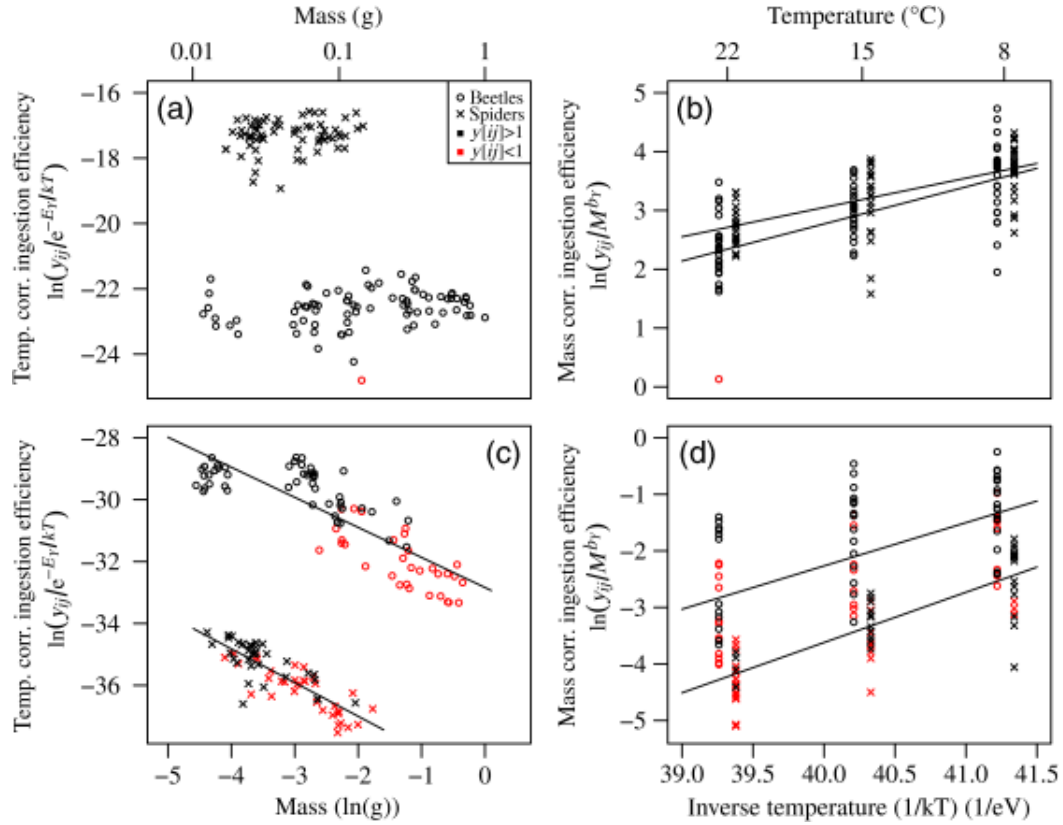


Figure 3.2: Beetle (circles) and spider (crosses) ingestion efficiency y_{ij} in treatments with the larger (a, b) and the smaller prey (c, d) depending on predator body mass (a, c) and environmental temperature (b, d). Data are ln-transformed and the dependent variables are normalized by their temperature dependence (a, c) or their mass dependence (b, d). Upper axes show untransformed body mass (g) and temperature [°C] scales. Offsets of -0.04 (beetles) and 0.04 (spiders) were applied to temperature data in panels (b) and (d). Note the inverse scaling of the lower temperature axes. Red coloured circles and crosses indicate where the ingestion efficiency was below the critical threshold of unity ($y_{ij} < 1$).

For both predator groups, ingestion efficiencies did not vary with predator mass in treatments with large prey (Fig. 3.2a; Table 3.2), whereas they decreased in treatments with small prey (Fig. 3.2c; Table 3.2). Eventually, ingestion efficiencies fell below unity indicating that metabolism exceeded ingestion (Fig. 3.2c, red symbols). For both predator groups and both prey sizes, increasing temperature generally decreased the ingestion efficiency, which increased the number of predator individuals that could not balance their metabolic demands (Fig. 3.2b, d, red symbols; 8 °C: 11 individuals, 15 °C: 20 individuals, 22 °C: 34 individuals). Thus, the critical boundary, at which predator ingestion was insufficient to balance metabolic loss ($y_{ij} < 1$, Eqn. 3.2) shifted to a range of lower predator body masses when temperature increased.

3.4.3 Short-term interaction strength

Effects of predator mass and temperature on short-term interaction strengths exhibited a significant dependence on predator group and prey size (significant three-way interaction terms in Table 3.1). Short-term interaction strengths increased significantly with predator body mass in treatments with large prey irrespective of the predator group (Fig. 3.3a).

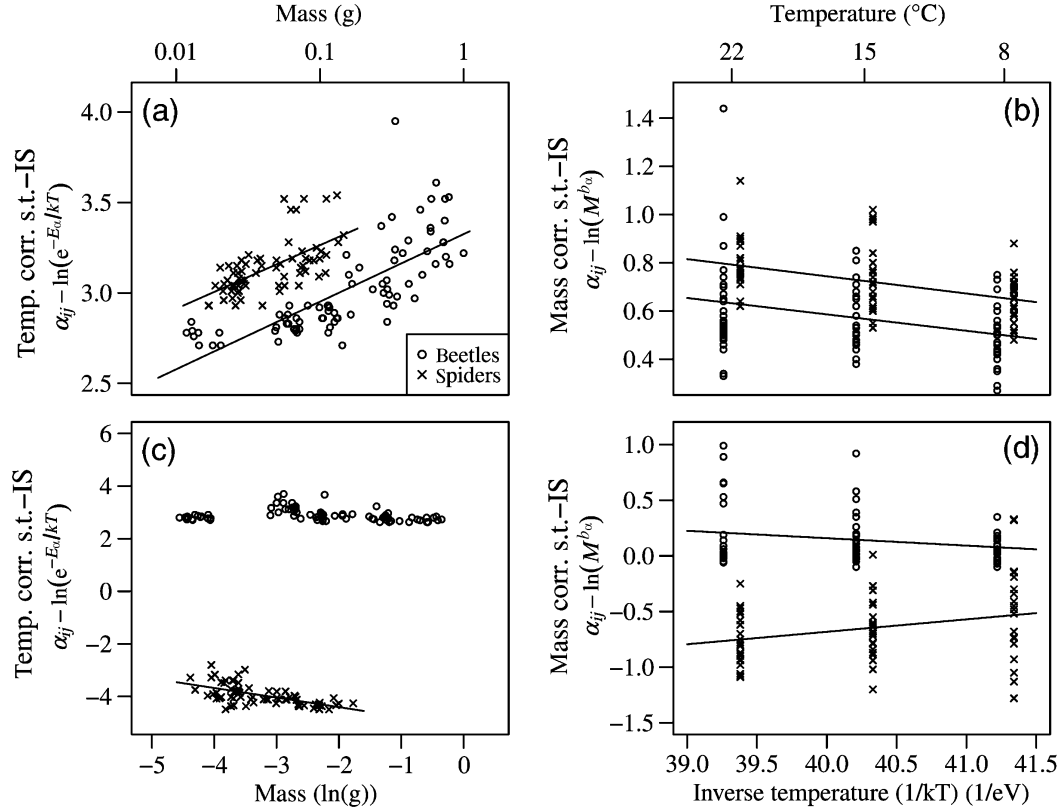


Figure 3.3: Beetle (circles) and spider (crosses) absolute short-term per capita interaction strength α_{ij} in treatments with the larger (a, b) and the smaller prey (c, d) depending on predator body mass (a, c) and environmental temperature (b, d). Data are ln-transformed and the dependent variables are normalized by their temperature dependence (a, c) or their mass dependence (b, d). Upper axes show untransformed body mass (g) and temperature [°C] scales. Offsets of -0.04 (beetles) and 0.04 (spiders) were applied to temperature data in panels (b) and (d). Note the inverse scaling of the lower temperature axes.

In treatments with small prey, short-term interaction strengths decreased slightly with predator mass for spiders, but they remained constant for beetles (Fig. 3.3c; Table 3.2). Moreover, short-term interaction strengths increased with warming when predators fed on large prey (Fig. 3.3b; Table 3.2) and when beetles fed on small prey (Fig. 3.3d, circles; Table 3.2). In contrast, short-term interaction strengths decreased slightly with warming when spiders fed on small prey (Fig. 3.3d, crosses; Table 3.2).

3.4.4 Prediction of long-term interaction strength

Calculated long-term interaction strength generally decreased with increasing temperature across all combinations of predator groups, predator masses and prey sizes (Fig. 3.4). Large predators have a higher impact on the large prey and smaller predators have a higher impact on the small

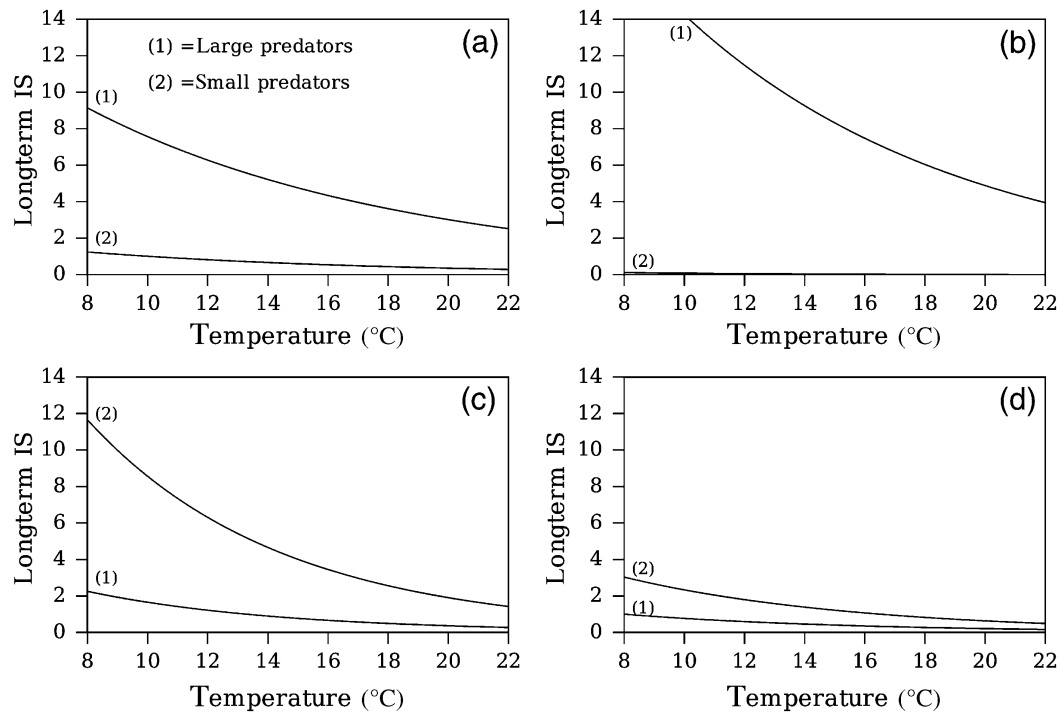


Figure 3.4: Beetle (b, d) and spider (a, c) long-term per capita interaction strength A_{ij} in treatments with the larger (a, b) and the smaller prey (c, d) in dependence on environmental temperature. Lines marked with (1) denote largest predators in our experiments (beetles: 1000 mg, spiders: 170 mg) and lines marked with (2) denote smallest predators in our experiments (beetles: 11 mg, spiders: 13 mg).

prey (Fig. 3.4a, b vs. Fig. 3.4c, d). In all cases, the total decrease in long-term interaction strength is stronger when the long-term interaction strength is generally strong (Fig. 3.4).

3.5 Discussion

Consistent with the MTE (Brown *et al.*, 2004), our experiments demonstrate that the metabolism of beetles and spiders followed a power-law increase with their body mass and an exponential increase with temperature. However, we did not find similar relationships for predator ingestion rates. As expected based on recent foraging studies documenting hump-shaped relationships between ingestion and predator-prey body-mass ratios (Wahlström *et al.*, 2000; Vonesh and Bolker, 2005; Brose *et al.*, 2008), we found differences in warming effects on ingestion rates between treatments with small prey (constant rates) and treatments with large prey (increasing rates). In contrast to our initial expectation based on the MTE, activation energies of ingestion were lower than those of metabolism, and thus ingestion efficiencies (the ratio of ingestion to metabolism) generally decreased with warming. Moreover, short-term interaction strengths (only accounting for ingestion) increased with warming in all treatments except for the treatment with spiders and small prey, whereas the long-term interaction strengths (additionally accounting for temperature effects on prey abundance) generally decreased. Together, these results demonstrate that warming may have complex and profound implications for predator-prey interaction strengths, population dynamics and food-web stability.

3.5.1 Metabolism

The MTE predicts a $3/4$ power-law increase in metabolism with body mass and an exponential increase with temperature, where the activation energy should be in the range of biochemical reactions between 0.2 and 1.4 eV (Gillooly *et al.*, 2001; Clarke, 2004). Generally, most of our results corroborate the predictions of the MTE. The exception is spider metabolism, which exhibited a particularly low allometric exponent ($b_1 = 0.46 \pm 0.09$). The low spider exponent may be caused by factors limiting metabolism other than the circulatory transport network (e.g. the relative metabolic tissue is larger in small than in large spiders; but see Brose *et al.* (2008) for more examples), but a mechanistic explanation of allometric exponents is beyond the scope of this study.

3.5.2 Body-mass effects on ingestion

Following assumptions of the MTE, the allometric exponents and the activation energies for ingestion should be similar to those for metabolism (Brown *et al.*, 2004). Consistent with this assumption, the allometric exponents for metabolism were within the 95 % confidence intervals of those for ingestion in treatments with large prey. Moreover, the confidence intervals of the allometric exponents of both predator groups in treatments with large prey include the $3/4$ exponent predicted by models based on MTE (Brown *et al.*, 2004). Contrary to the assumptions of the MTE, however, the allometric exponents of ingestion in treatments with small prey were negative, indicating that ingestion rates decreased with increasing predator body mass. The pattern of increasing and decreasing ingestion rates documented here is consistent with hump-shaped relationships between ingestion and predator-prey body-mass ratios documented by foraging theory (Wahlström *et al.*, 2000; Vonesh and Bolker, 2005; Brose *et al.*, 2008; Vucic-Pestic *et al.*, 2010b; Brose, 2010). On the left side of the hump at low body-mass ratios (e.g., large prey in our experiments), predator effects on prey are limited by handling-time constraints and ingestion rates increase with body-mass ratios due to decreasing handling time (i.e. the disparity in predator and prey body mass increases and large predators are able to handle small prey with ease). On the right side of the hump, when body-mass ratios are large (e.g. small prey in our experiments), predator ingestion is constrained by the rate at which they can catch small prey and ingestion rates decrease with body-mass ratios, because the predators' attacks become increasingly inefficient (Aljetlawi *et al.*, 2004; Brose *et al.*, 2008). Predators may either not perceive prey, or there is a trade off between the time taken to capture a very small prey item and the energetic benefit derived from the interaction. Thus, the effects of increasing predator body-mass on ingestion should deviate from a simple power law when a wider range of predator and prey body masses is considered. As in prior studies over a more limited range of body-mass ratios (Peters, 1983; Emmerson and Raffaelli, 2004), we found that the increasing slope of this hump-shaped relationship at low body-mass ratios (i.e. large prey) is well described by an increasing power function. However, documentation of a hump-shaped relationship required extension of the range of body-mass ratios studied to include decreasing ingestion rates at high body-mass ratios (i.e. small prey in our study).

3.5.3 Temperature effects on ingestion, ingestion efficiencies and interaction strengths

The activation energies of ingestion were more than two times smaller than those of metabolism. Thus, the response of ingestion to warming is much weaker than the increase in metabolism. Contrary to expectations based on the MTE, ingestion efficiencies (i.e. ingestion relative to metabolism) thus decreased with warming independent of the prey size and predator group. Eventually, warm-

ing leads to ingestion efficiencies below unity (ingestion lower than metabolic demands, see Figure 3.2, red symbols), which causes predator starvation. This suggests that many predator-prey interactions could become infeasible under warming. The activation energies of ingestion were slightly positive in treatments with large prey where predators were limited by handling time, which includes biochemical digestion processes (van Rijn *et al.*, 2005). Warming can accelerate these biochemical processes (Gillooly *et al.*, 2001), which leads to faster handling time thus explaining higher ingestion rates in our experiments with large prey. Interestingly, the activation energies of ingestion were not significantly different from zero in treatments with small prey, where predators were constrained by their ability to catch prey, and ingestion was independent of digestion and satiation (van Rijn *et al.*, 2005). Warming does not affect the catching efficiency, which is primarily driven by constraints such as detectability and mobility. If warming had an equal effect on predator and prey mobility, the net effect of warming on the catching efficiency of predators would be neutral, which could explain the lack of warming effects in our treatments with small prey. Generally, absolute short-term per capita interaction strengths increased with temperature except for the treatment of spiders with small prey. This corroborates a prior field study documenting positive effects of temperature on interaction strengths in a marine intertidal food web (Sanford, 1999). Our study demonstrates that these positive temperature effects are driven by increasing ingestion rates. While comprehensive field studies investigating temperature and body-mass effects on interaction strengths are scarce, based on metabolic arguments our study suggests the broad generality of positive correlations between temperature and short-term interaction strengths. Interestingly, the absolute values of the long-term interaction strengths (not taking its sign into account) decrease with warming. This is caused by differences between the activation energies of predator metabolism and ingestion (see Eqn. 3.14) yielding higher prey population densities at higher temperatures in simple predator-prey systems. Moreover, the carrying capacity of the prey decreases because abundances of natural populations embedded in a complex network generally decrease with warming (Allen *et al.*, 2002; Meehan, 2006a). The long-term interaction strengths (Eqn. 3.15) are proportional to the ratio of the equilibrium prey density (increasing with warming) to the prey carrying capacity (decreasing with warming). Consequently, this ratio increases with warming, yielding less negative values, and decreases in absolute strength. Additionally, due to the differences in prey growth rates and predator ingestion rates, the predator density increases with warming causing an additional decrease in absolute per capita interaction strength with warming (Eqn. 3.13). While short-term interaction strengths were determined by increases in predator ingestion rates under warming (see Eqn. 3.3), temperature effects on predator and prey densities outweigh these increasing ingestion rates and yield decreasing long-term interaction strengths under warming. This disparity between different measurements of interaction strength on different time scales is a general problem in ecological sciences, especially in experiments exploring aspects of climate change (Walther, 2007). The approach adopted in this study to calculate long-term interaction strengths might offer a solution to this problem.

3.5.4 Temperature effects on population stability

In our experiments, ingestion rates and short-term interaction strengths with large prey (low body-mass ratios) increased with warming. This may result in a stronger short-term top-down control of prey populations under warming when prey growth rates and densities are negligible. However, long-term interaction strengths generally decrease with warming. As decreasing interaction strengths are inversely correlated with perturbation stability (May, 1972), our results suggest that the perturbation stability of natural communities should increase with warming. Additionally, our


results demonstrate decreases in ingestion efficiencies with warming, which should lead to higher intrinsic population stability for all predator-prey interactions irrespective of the body-mass ratio (Yodzis and Innes, 1992; Vasseur and McCann, 2005; Rall *et al.*, 2008). However, decreased ingestion efficiencies combined with higher predator density may lead to starvation of the predator population, even if the prey population also has increased in density. Consistent with this conclusion, warming of microcosm food webs caused an increase in biomass of bacteria and bacterivorous consumers whereas larger predators and herbivores became extinct and the biomass of producers increased (Petchey *et al.*, 1999). Our results indicate that predator-prey interactions characterised by high body-mass ratios (small prey in our experiments) are particularly prone to this predator-starvation effect of warming. Analyses of the body-mass structure of natural food webs (Brose *et al.*, 2006a) may thus facilitate predictions of their sensitivity to global warming. Global warming may also increase the productivity of ecosystems because of increasing CO₂ levels (Emmerson *et al.*, 2005), which may counteract the direct temperature effects studied here due to increased net primary productivity. Eventually, these two global warming effects need to be reconciled to achieve accurate forecast models.

3.6 Caveats

As any laboratory study, our approach was based on some simplifying assumptions: (1) simple predator-prey pairs ignore potentially more complex feeding behaviour of predators when multiple prey or predator species or multiple predator individuals coexist (e.g., prey switching or interference competition, compensatory effects of alternative predators); (2) constant prey densities across all ingestion experiments do not account for non-linearly saturating responses of ingestion to high prey densities. Future more complex extensions of our laboratory approach will need to address effects of these simplifying assumptions. However, our assumption of constant assimilation efficiencies across the temperature gradient is supported by empirical studies of carnivorous insects (Lawton, 1970), caterpillars (Kingsolver and Woods, 1998) and lizards (Chen *et al.*, 2003; McConnachie and Alexander, 2004). As most prior warming experiments, our approach did not account for thermal adaptation of the species, which can reduce their physiological responses to warming (Lenski and Bennett, 1993; Clarke and Johnston, 1999). However, a 76 % lower activation energy of metabolism as documented for fish species after thermal adaptation (Clarke and Johnston, 1999) would not affect the qualitative conclusions of the present study. Nevertheless, our approach presents a simplistic, mechanistic null model of temperature effects on predator-prey interactions in which thermal adaptation effects remain to be included. In contrast, prior, long-term field studies on the effects of warming avoid some of these simplifying assumptions at the cost of lacking mechanistic explanations. Future studies will need to bridge the gap between simplified but mechanistic laboratory studies and more complex field studies.

3.7 Conclusions

Four conclusions arise from our results: warming of natural ecosystems may cause (1) higher feeding rates and short-term interaction strengths yielding higher impacts on a prey population over a short period of time, (2) higher perturbation stability of the populations (higher probability of returning to the same equilibrium density after a small perturbation) due to lower absolute long-term per capita interaction strengths, (3) a higher intrinsic population stability (less fluctuations in population density) due to reduced ingestion efficiencies, and (4) higher extinction risks due to predator starvation. As species interactions provide the mechanistic link between global warming



and ecosystem functions (Hughes, 2000), our results suggest that predicting the consequences of climate change may be far from trivial. Nevertheless, future extensions of our approach may provide a mechanistic understanding of how warming affects population dynamics, species' extinction risks and ecosystem functions.

4 Warming up the system: higher predator feeding rates but lower energetic efficiencies

4.1 Abstract

Predictions on the consequences of the rapidly increasing atmospheric CO₂ levels and associated climate warming for population dynamics, ecological community structure and ecosystem functioning depend on mechanistic energetic models of temperature effects on populations and their interactions. However, such mechanistic approaches combining warming effects on metabolic (energy loss of organisms) and feeding rates (energy gain by organisms) remain a key, yet elusive, goal. Aiming to fill this void, we studied the metabolic rates and functional responses of three differently sized, predatory ground beetles on one mobile and one more resident prey species across a temperature gradient (5, 10, 15, 20, 25 and 30 °C). Synthesizing metabolic and functional-response theory, we develop novel mechanistic predictions how predator-prey interaction strengths (i.e., functional responses) should respond to warming. Corroborating prior theory, warming caused strong increases in metabolism and decreases in handling time. Consistent with our novel model, we found increases in predator attack rates on a mobile prey, whereas attack rates on a mostly resident prey remained constant across the temperature gradient. Together, these results provide critically important information that environmental warming generally increases the direct short-term per capita interaction strengths between predators and their prey as described by functional-response models. Nevertheless, the several fold stronger increase in metabolism with warming caused decreases in energetic efficiencies (ratio of per capita feeding rate to metabolic rate) for all predator-prey interactions. This implies that warming of natural ecosystems may dampen predator-prey oscillations thus stabilizing their dynamics. The severe long-term implications; however, include predator starvation due to energetic inefficiency despite abundant resources.

4.2 Introduction

The world's ecosystems are exposed to a rapid global change including increasing atmospheric CO₂ levels and associated climate warming. Eventually, this may cause severe changes in population dynamics, ecological community structure and ecosystem functioning at a global scale (Hughes, 2000; Parmesan, 2006). Many direct effects of warming on organismal physiology and population abundances depend on metabolic rates that are, as all thermodynamic processes, determined by specific activation energies (Gillooly *et al.*, 2001). However, relatively limited attention has been paid to understanding the consequences of warming for interactions between species, which can have the most profound implications for ecosystem structure and functioning (Sala *et al.*, 2000; Tylianakis *et al.*, 2008). Any change in interaction strengths and their distributions across species can severely impact food-web stability (McCann *et al.*, 1998; Rooney *et al.*, 2006; Neutel *et al.*, 2007; Berlow *et al.*, 2009; O'Gorman and Emmerson, 2009). Nevertheless, a mechanistic understanding of temperature effects on interaction strengths remains a critically important yet to be

realized step towards predicting the consequences of global warming for natural ecosystems (Abrahams *et al.*, 2007). A simple mechanistic model of nonlinear predator-prey interaction strengths is provided by functional responses of per capita feeding rates, F , depending on prey density, N :

$$F(N) = \frac{aN}{1 + ahN} \quad (4.1)$$

where a is the attack rate (i.e., instantaneous rate of discovery or successful capture, hereafter attack rate) and h is the handling time needed to ingest and digest a resource (Holling, 1959a). Dynamically, limited variation in these parameters can have dramatic consequences for population and food-web stability (Williams and Martinez, 2004; Brose *et al.*, 2006b; Rall *et al.*, 2008). Specifically, warming can stabilize or destabilize population dynamics depending on its effects on metabolic and feeding rates (Vasseur and McCann, 2005). Maximum feeding rates should exhibit a similar temperature dependence as metabolic rates (Brown *et al.*, 2004) suggesting exponential decreases in handling time (inverse of maximum feeding rate) with warming. While this negative relationship between handling time and warming found broad support, the scaling of attack rates with warming can follow linear, power-law, sigmoid, hyperbolic or dome-shaped functions, or it can be entirely absent (Thompson, 1978; Dreisig, 1981; Gresens *et al.*, 1982; Bergman, 1987; Bailey, 1989; Cave and Gaylor, 1989; Song and Heong, 1997; McCoull *et al.*, 1998; Zhang *et al.*, 1998, 1999; Xia *et al.*, 2003; Gilioli *et al.*, 2005; García-Martín *et al.*, 2008). This plethora of scaling relationships precluded any general conclusions on how warming affects interaction strengths. Some confusion arises from the compound character of attack rates comprising encounter and suc-

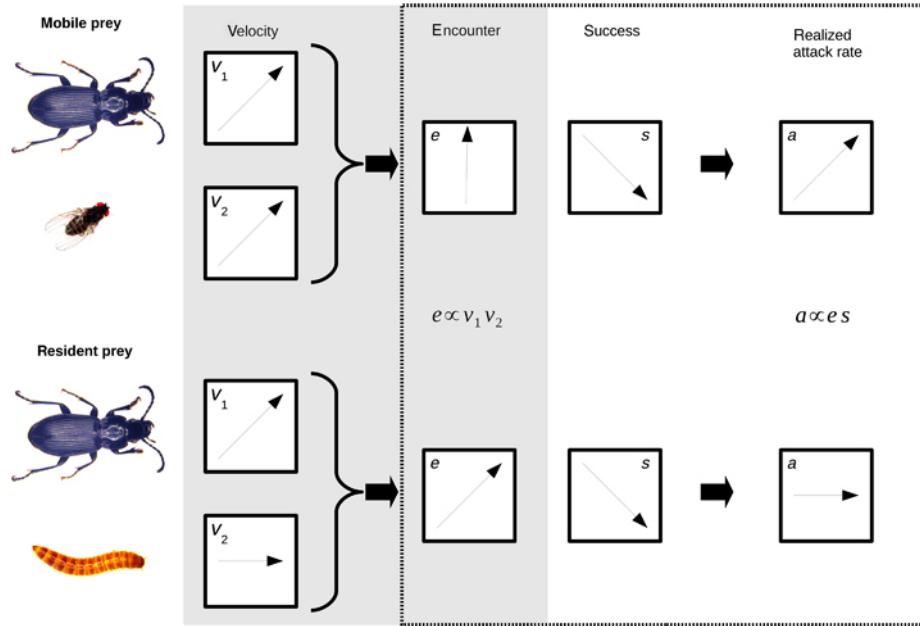


Figure 4.1: Simple conceptual model of temperature effects on attack rates depending on prey mobility.

cess rates (Gergs and Ratte, 2009). Here, we propose the following concept (see Fig. 4.1 for an overview): (1) attack rates equal the product of encounter rates, e and success rates, s (assuming that encounters lead to attacks) ($a \propto es$), (2) encounter rates depend on predator and prey movement speed, ($e = v_i v_j$), (3) success rates are inversely proportional to prey escape efficiencies, ε , ($s = 1/\varepsilon$) and (4) $v_{i,j}$, and ε follow exponential temperature scaling, which yields:

$$a = es = \frac{v_i v_j}{\varepsilon} \approx e^{\frac{-E_1}{kT}} e^{\frac{-E_2}{kT}} e^{\frac{E_3}{kT}} = e^{\frac{-E_1 - E_2 + E_3}{kT}} \quad (4.2)$$

where k is Boltzmann's constant ($8.62 \times 10^{-5} \text{ eV/K}$), T is temperature [K], and E_1 , E_2 and E_3 [eV] are the activation energies of v_i , v_j and ε , respectively. Together, this suggests that warming has a twofold positive effect on encounter rates via predator and prey mobility (E_1 , E_2 ; note that negative terms in the nominator cause positive relationships, because the temperature term is in the denominator of the exponent) and a simple negative effect on success rates (E_3), which should result in increases in attack rates under warming (if $E_1 + E_2 > E_3$, Fig 4.1). However, a different prediction arises if the prey species (or the predator) is of limited mobility (hereafter: resident) and does not respond to warming ($E_2 \approx 0$), which should yield attack rates that are roughly independent of temperature (if $E_1 \approx E_3$, Fig. 4.1). The present study provides an empirical test of this novel prediction that prey mobility should constrain warming effects on attack rates. Recently, we demonstrated systematic effects of predator and prey body masses on functional-response parameters for terrestrial invertebrate predators (Brose *et al.*, 2008; Vucic-Pestic *et al.*, 2010b). Our results suggest that handling time follows simple power-law increases and decreases with prey and predator mass, respectively, whereas attack rates follow more complex hump-shaped relationships with predator-prey body-mass ratios. Attack rates are constrained by movement, high detectability and encounter at small body-mass ratios, when predator and prey species are of similar size, and by low detectability and attack success at high body-mass ratios, when predators are much larger than their prey (Brose *et al.*, 2008; Vucic-Pestic *et al.*, 2010b). Certainly, warming can have different effects on these different processes constraining attack rates at high and low predator-prey body-mass ratios. To account for these constraints in the present study, we chose three of these predators along the same body-mass gradient to study effects of warming on their metabolic rates, functional responses and energetic efficiencies (ratio of feeding to respiration). In a prior study, we used replicated feeding experiments at constant prey densities to show that warming increases short-term per capita interaction strengths, whereas it decreases long-term interaction strengths (Rall *et al.*, 2010). Here, we extend this approach by (1) generalizing the findings across a gradient of prey abundance, (2) providing mechanistic explanations for the patterns, and (3) adding a concept how species mobility (here: mobile vs. resident prey) can modify these warming effects.

4.3 Methods

4.3.1 Experiments

We studied the functional responses of three differently sized predators (*Pterostichus melanarius*, *Harpalus rufipes*, *Calathus fuscipes*; Coleoptera: Carabidae) on one mobile (flightless adults of *Drosophila hydei*; Diptera: Drosophilidae, hereafter: *Drosophila*) and one resident prey (larvae of *Alphitobius diaperinus*; Coleoptera: Tenebrionidae; hereafter: *Alphitobius*). We chose these prey, because *Drosophila* individuals were constantly moving around (not flying) in the arena, whereas *Alphitobius* often remained at the same place for the entire time of the experiments (most individuals remain at the same place, whereas few moved over very short distances of few centimeters). The predators' feeding rates were compared with their standard metabolic rates to calculate their energetic efficiencies. All experiments were replicated across a temperature gradient (5, 10, 15, 20, 25 and 30 °C). We used an automated electrolytic microrespirometer (Scheu, 1992) to measure standard metabolic rates of individuals. All species were sampled in the field by pitfall trapping. To

standardize their feeding status, all individuals were first fed ad libitum with commercial dog food and subsequently starved for 3 d in incubators at a constant temperature of 15 °C. The length of the starvation period was chosen to allow digestion of prior meals while avoiding metabolic down regulation due to extended starvation. While this approach does not account for thermal acclimation to the different temperature treatments or evolutionary adaptation to environmental temperature (see Terblanche *et al.*, 2005 for an example), it provides information on temperature effects on metabolic rates under standardized conditions, because the dietary status is independent of the temperature treatment. Respiration measurements over 12 h were carried out in closed chambers under constant partial oxygen pressure (see Scheu, 1992 for details) to avoid confounding effects of oxygen depression. The automated electrolytic microrespirometer releases oxygen pulses to balance any reduction in oxygen pressure by animal respiration (increases in CO₂ are buffered). This yields a time series of oxygen pulses corresponding to the intensity of animal respiration. We averaged the measurements between 8 and 12 h of our experiments (J/h , 1 mL O₂ \equiv 20.1 J, Peters, 1983) while excluding replicates with animal activity indicated by sudden peak increases in oxygen pulses. These measurements were carried out with five replicates for each predator at each of the six temperatures (5, 10, 15, 20, 25 and 30 °C). Each functional-response experimental unit comprised one predator individual and prey individuals at different initial densities (6 *replicates/density*) varying between low densities and high prey densities (specific for each predator-prey combination to reach saturation in per capita feeding rates). Before feeding experiments, the predator individuals were similarly treated as before the respiration experiments. Experiments were carried out in Perspex[®] arenas (L20 × W20 × H10 cm equaling a surface area of 400 cm²). The ground was covered with moist dental cast (200 g dry weight) to provide constant moisture during the experiments. Moss (*Polytrichum formosum*, 2.35 g dry weight) was used as habitat structure in the arenas. It was first dried for several days at 40 °C to exclude other animals and then remoisturized. Prey individuals were placed in the arenas half an hour in advance of the predators to allow them to adjust to the arenas. The experiments ran for 24 h with a day/night rhythm of 12/12 h dark/light. Initial and final prey densities were used to calculate the number of prey eaten. Control experiments without predators showed that prey mortality or escape did not influence our experiments.

4.3.2 Statistical analyses

To account for prey depletion (decreasing N during the time course of the experiments), we used Rogers's random predator equation (Rogers, 1972):

$$N_e = N_0 \left(1 - e^{aN(hN_e - t)} \right) \quad (4.3)$$

where N_e is the number of prey eaten, t is the total experimental time and N_0 is the initial prey density. We solved this recursive function of N_e with a maximum likelihood method using the additional packages 'BBMLE' and 'EMDBOOK' provided by Ben Bolker for the statistical software package R (Bolker, 2008; R Development Core Team, 2009). This yields:

$$N_e = N_0 - \frac{W(ahN_0e^{-a(t-hN_0)})}{ah} \quad (4.4)$$

where W is the Lambert W function (see Bolker, 2008 and references therein for a detailed description). Fitting of more complex type-III functional-response models (see Vucic-Pestic *et al.*, 2010b for examples) yielded nonsignificant trends in attack rates with prey density, which rendered

their application in the present study unnecessary. Our experiments resulted in 90 measurements of standard metabolic rates I [J/h], and 18 independent estimates of attack rates a [$0.04m^2$] and handling times h [h/Ind] for each of the two prey species (three predators across six temperatures). Based on metabolic scaling theory (Brown *et al.*, 2004; Glazier, 2010), these variables should depend on body mass, M [mg] and environmental temperature, T [K].

$$I = I_0 M^{b_I} e^{\frac{-E_I T_0 - T}{k T T_0}} \quad (4.5)$$

$$h = h_0 M^{b_h} e^{\frac{-E_h T_0 - T}{k T T_0}} \quad (4.6)$$

$$a = a_0 M^{b_a} e^{\frac{-E_a T_0 - T}{k T T_0}} \quad (4.7)$$

where I_0 , h_0 and a_0 are intercepts at temperature T_0 of 17.5 °C (= 290.65 K) equal to the mean of our experimental temperature gradient (5, 10, 15, 20, 25 and 30 °C), b_I , b_h , b_a are allometric exponents, E_I , E_h , E_a are activation energies [eV], k is Boltzmann's constant (8.62×10^{-5} eV/K). These constants were estimated by fitting linear, least-squares regressions to the double ln-transformed data. For the subsequent energetic evaluation of the predator-prey interactions, we had to convert the units of the per capita feeding rates from 'prey individuals per hour' into 'Joule per hour'. First, we multiplied the per capita feeding rates [$Ind./h$] by individual prey weights [$mg/Ind.$] (Table 4.1) to yield per capita biomass feeding rates [mg/h]. Secondly, we multiplied these rates by a weight-energy conversion factor (1 kg wet mass = 7×10^6 J; Peters, 1983) to yield per capita energy feeding rates [J/h]. These rates were used to calculate dimensionless energetic efficiencies, y , of the predators by:

$$y = \frac{\omega F}{\lambda I} \quad (4.8)$$

where F is the per capita energy feeding rate (Eqn. 4.1), I is metabolism (Eqn. 4.5), ω is a temperature-independent assimilation efficiency (0.85 for carnivores, see Rall *et al.*, 2010 for details) and λ is a constant converting standard metabolic rate into field metabolic rate ($\lambda = 3$, Savage *et al.*, 2004b). By inserting the mass- and temperature-dependent models of handling time and attack rate (Eqns. 4.6 and 4.7) into the functional-response model (Eqn. 4.1), and subsequently inserting the functional-response model (Eqn. 4.1) and the metabolic model (Eqn. 4.5) into equation 4.8, we obtained a model of energetic efficiencies depending on predator mass and environmental temperature. Additionally, F depends on prey density, N , which can be predicted by:

$$N = n_0 M^{b_N} e^{\frac{-E_N}{k T}} \sigma^z e^{t l_0 (t l - 1)} \quad (4.9)$$

where n_0 is a normalization constant, b_N , z and $t l_0$ are constants, E_N [eV] is the activation energy, σ is the annual net primary productivity of the habitat (gC/m^2y), and $t l$ is the trophic level (Allen *et al.*, 2005; Meehan, 2006a). For soil animals, these constants are: $n_0 = e^{-31.15}$, $b_N = -0.72$, $E_N = -0.71$, $t l_0 = -2.86$, $z = 1.03$ and $t l = 1.5$ for decomposers, fungivores and herbivores (Meehan, 2006a). The net primary productivity in equation 4.9 equals:

$$\sigma = \sigma_0 e^{\frac{-E_\sigma T_0 - T}{k T T_0}} \quad (4.10)$$

where σ_0 is the net primary productivity at temperature T_0 [K] and E_σ is the activation energy (0.35 eV, Allen *et al.*, 2005). We assumed a net primary production, σ_0 , of 600 gC/m²y for temperate regions (Cramer *et al.*, 1999) at a T_0 of 9.5 °C (282.65 K), which equals the average annual temperature in Germany.

4.4 Results

We tested for significant trends in predator metabolic rates, handling times and attack rates depending on predator body mass and environmental temperature.

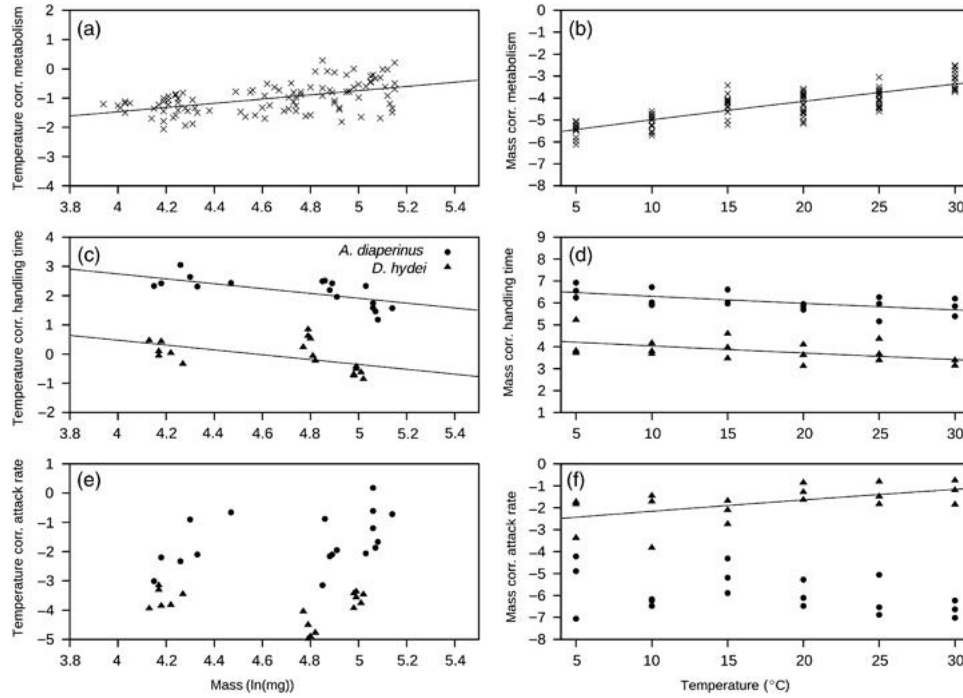


Figure 4.2: Predator metabolism I (a, b), handling time h (c, d) and attack rate a (e, f) depending on predator body mass [mg] (a, c, e) and the environmental temperature [°C] (b, d, f). Data are ln-transformed and the dependent variables are normalized by their temperature dependence (a, c, e) or their body-mass dependence (b, d, f). Temperature axes are untransformed. Untransformed data is shown in Table 4.1. Note that only significant regression lines are shown. Regression models (parameters and standard errors in brackets) for (a, b) metabolism (Eqn. 4.5): $I_0 = -3.91$ (0.59), $b_I = 0.62$ (0.13), $E_I = 0.61$ (0.04), $r^2 = 0.75$, $p < 0.001$, $n = 90$; (c, d) handling time (Eqn. 4.6): *Alphitobius* $h_0 = 6.85$ (1.18), $b_h = -1.0$ (0.25), $E_h = -0.23$ (0.07), $r^2 = 0.63$, $p < 0.001$, $n = 18$; *Drosophila* $h_0 = 2.99$ (1.57), $b_h = -0.66$ (0.34), $E_h = -0.24$ (0.1), $r^2 = 0.4$, $p = 0.022$, $n = 18$; (e, f) attack rate (Eqn. 4.7): *Alphitobius* $a_0 = -5.94$ (2.83), $b_a = 0.91$ (0.59), $E_a = -0.27$ (0.18), $r^2 = 0.24$, $p = 0.13$, $n = 18$; *Drosophila* $a_0 = -1.77$ (2.33), $b_a = -0.48$ (0.5), $E_a = 0.37$ (0.15), $r^2 = 0.33$, $p = 0.049$, $n = 18$.

For the three predator species of our study, we found significant increases in metabolism with predator mass (Fig. 4.2a) and temperature (Fig. 4.2b). Subsequently, the functional-response model (Eqn. 4.3 and 4.4) was fitted separately to the feeding data for each combination of predator–prey interaction and temperature, which yielded substantial variance in handling times [$0.37 \leq h \leq 18.24$ (h/ind)] and attack rates [$0.002 \leq a \leq 0.84$ (0.04 m²/h)] (Table 4.1). Our analyses show significant decreases in handling time with increasing predator mass (Fig. 4.2c) and warming (Fig. 4.2d) for both prey species. Interestingly, the absolute values of the activation energies (i.e., the exponents, E , in Eqn. 4.6) of handling time were much lower (*Alphitobius*: -0.23 eV;

Drosophila: -0.24 eV, Fig. 4.2d) than those of metabolism (0.61 eV, Fig. 4.2b). The attack rates of the predators on the mobile prey, *Drosophila*, decreased with predator body mass and increased with warming, whereas the attack rates of the same predators on the resident prey, *Alphitobius*, were influenced neither by predator body mass nor by environmental temperature (Fig. 4.2e, f).

Table 4.1: Estimates of handling time, h [h/ind] and attack rate, a [$0.04m^2/h$], and their standard errors (SE) obtained by fitting 36 independent functional response models to the data for the full-factorial combination of three predators (*Calathus fuscipes*, *Harpalus rufipes*, *Pterostichus melanarius*), two prey species (*Drosophila*, *Alphitobius*) and six environmental temperatures

Predator	Temperature [°C]	Mass [mg]	N	h	SE	a	SE	r^2
Prey: <i>Drosophila</i>		1.91						
<i>C. fuscipes</i>	5	65.02	48	1.44	0.17	0.022	0.000	0.40
<i>C. fuscipes</i>	10	64.69	61	1.41	0.15	0.025	0.003	0.65
<i>C. fuscipes</i>	15	62.01	58	1.73	0.21	0.017	0.002	0.52
<i>C. fuscipes</i>	20	71.81	54	0.66	0.06	0.036	0.003	0.57
<i>C. fuscipes</i>	25	65.65	56	1.23	0.11	0.031	0.004	0.52
<i>C. fuscipes</i>	30	67.79	48	0.71	0.06	0.041	0.004	0.79
<i>H. rufipes</i>	5	119.93	55	3.54	0.86	0.004	0.001	0.33
<i>H. rufipes</i>	10	122.77	54	1.21	0.61	0.002	0.000	0.51
<i>H. rufipes</i>	15	121.82	55	1.87	0.37	0.007	0.001	0.63
<i>H. rufipes</i>	20	117.57	55	1.17	0.11	0.020	0.003	0.52
<i>H. rufipes</i>	25	120.68	55	1.49	0.15	0.016	0.002	0.40
<i>H. rufipes</i>	30	124.53	64	0.55	0.07	0.016	0.002	0.64
<i>P. melanarius</i>	5	151.23	63	0.65	0.07	0.016	0.002	0.68
<i>P. melanarius</i>	10	145.70	67	0.64	0.06	0.022	0.002	0.74
<i>P. melanarius</i>	15	145.91	65	0.52	0.06	0.017	0.002	0.57
<i>P. melanarius</i>	20	147.23	62	0.61	0.04	0.039	0.004	0.68
<i>P. melanarius</i>	25	146.61	66	0.48	0.03	0.042	0.004	0.77
<i>P. melanarius</i>	30	150.53	65	0.37	0.02	0.043	0.003	0.76
Prey: <i>Alphitobius</i>		23.26						
<i>C. fuscipes</i>	5	87.17	33	17.28	2.69	0.84	1.43	0.09
<i>C. fuscipes</i>	10	63.60	40	13.21	2.62	0.07	0.04	0.14
<i>C. fuscipes</i>	15	65.11	36	12.25	1.99	0.12	0.08	0.17
<i>C. fuscipes</i>	20	75.59	32	9.34	2.29	0.11	0.09	0.28
<i>C. fuscipes</i>	25	73.44	32	11.05	1.78	0.31	0.33	0.2
<i>C. fuscipes</i>	30	70.82	31	14.32	3.71	0.06	0.05	0.23
<i>H. rufipes</i>	5	127.74	37	18.24	3.96	0.07	0.06	0.1
<i>H. rufipes</i>	10	132.74	36	14.37	2.34	0.16	0.11	0.08
<i>H. rufipes</i>	15	129.10	49	13.29	1.79	0.46	0.61	0.09
<i>H. rufipes</i>	20	135.64	37	6.58	0.95	0.13	0.06	0.47
<i>H. rufipes</i>	25	152.30	37	8.12	1.18	0.1	0.04	0.32
<i>H. rufipes</i>	30	131.36	34	6.07	0.92	0.07	0.02	0.42
<i>P. melanarius</i>	5	169.97	36	0.83	0.79	0.79	0.85	0.34
<i>P. melanarius</i>	10	158.98	42	0.54	0.21	0.21	0.07	0.48
<i>P. melanarius</i>	15	158.02	36	0.58	1.31	1.31	2.01	0.47
<i>P. melanarius</i>	20	157.97	36	0.45	0.5	0.5	0.3	0.6
<i>P. melanarius</i>	25	161.11	40	0.24	0.14	0.14	0.03	0.71
<i>P. melanarius</i>	30	157.88	39	0.33	0.19	0.19	0.06	0.77

The fitted regression models of handling time and attack rate depending on predator body mass and environmental temperature (Fig. 4.2) are inserted in the functional-response model (Eqn. 4.1). The resulting synthetic model predicts the per capita feeding rates of the predators depending on predator body mass, environmental temperature and prey density (the model is illustrated as the

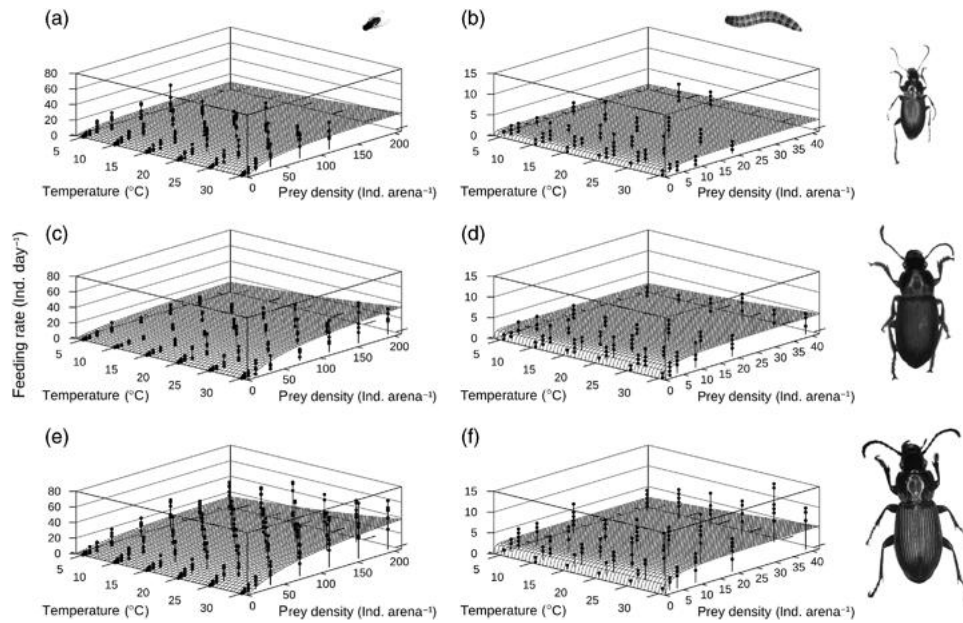


Figure 4.3: Experimental per capita feeding rates depending on environmental temperature [°C] and prey density (N). The planes show the predictions of the synthetic functional response model based on the allometric and temperature scaling relationships in Fig. 4.2 for (a) *C. fuscipes* and *Drosophila*, (b) *C. fuscipes* and *Alphitobius*, (c) *H. rufipes* and *Drosophila*, (d) *H. rufipes* and *Alphitobius* and (e) *P. melanarius* and *Drosophila*, (f) *P. melanarius* and *Alphitobius*.

planes in Fig. 4.3, where the data points are the results of our feeding experiments). The statistically significant fits of our models (Fig. 4.2) are supported by a visual inspection how the synthetic model relates to the data points (Fig. 4.3): across all predator-prey combinations in our study, the per capita feeding rates were well described by the synthetic model except for slight underestimations of feeding rate for the largest predators (*P. melanarius*) at the highest prey densities (Fig. 4.3e and f). The synthetic model and the data demonstrated increases in per capita feeding rates with warming across all predator-prey interactions. For all predators, these increases were steeper when preying on *Drosophila* and shallower when preying on *Alphitobius* (Fig. 4.3).

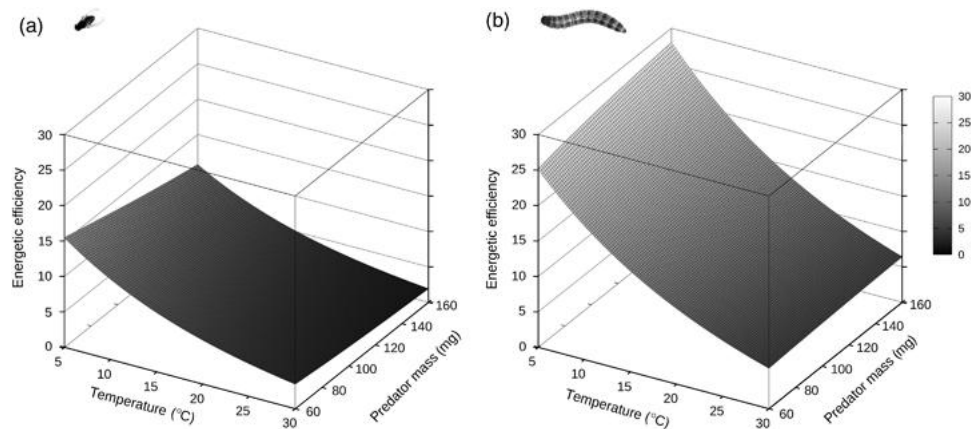


Figure 4.4: Predator energetic efficiency y in treatments with (a) *Drosophila* as prey and (b) *Alphitobius* as prey depending on predator mass [mg] and environmental temperature [°C].

Accounting for the trends in the per capita rates of feeding and metabolism yields decreases in energetic efficiencies with increasing temperature (Fig. 4.4). While feeding exceeded the metabolic loss roughly 10- to 30-fold at the lowest experimental temperatures of 5 °C, we found much lower ratios (one- to eightfold) at the highest temperature of 30 °C. In addition, the energetic efficiencies increased and decreased with predator body mass when preying on *Alphitobius* (Fig. 4.4a) and *Drosophila* (Fig. 4.4b), respectively. This pattern is consistent with similar trends in attack rates (Fig. 4.2).

4.5 Discussion

The metabolic rates and functional responses of three common terrestrial predators of different body masses on one mobile (*Drosophila*) and one resident prey (*Alphitobius*) depended on environmental temperature in ways that were consistent with expectations. We found exponential and power-law increases in metabolism with warming and body mass, respectively (Brown *et al.*, 2004; Glazier, 2010). A decrease in handling time with warming and predator body mass was also found in prior studies (Thompson, 1978; Dreisig, 1981; Gresens *et al.*, 1982; Bergman, 1987; Bailey, 1989; Cave and Gaylor, 1989; Song and Heong, 1997; McCoull *et al.*, 1998; Zhang *et al.*, 1998, 1999; Xia *et al.*, 2003; Gilioli *et al.*, 2005; García-Martín *et al.*, 2008), which indicates the broad generality of these scaling relationships. However, these prior studies documented a plethora of temperature scaling models for attack rates. Consistent with our initial concept, we demonstrate for the first time that attack rates increase with warming when predators feed on mobile prey, whereas they are independent of environmental temperature if the same predators feed on resident prey. We suggest the following explanation for the different warming effects on attack rates. The net effect of warming on attack rates depends on the twofold positive effect on encounter rates via increased predator and prey mobility and the simple negative effect via prey escape efficiency (Fig. 4.1). Accordingly, the twofold positive effect on encounter rates with mobile prey such as *Drosophila* should outweigh the negative effect on prey escape efficiencies to result in a positive net effect of warming on attack rates. In contrast, warming did not increase the mobility of the resident prey, *Alphitobius*, and the positive effect of warming on predator mobility was counteracted by the negative effect via increased prey escape efficiency, which prevented a warming effect on attack rates (Fig. 4.1). Observations during the experiments support this interpretation: *Alphitobius* individuals did not increase their movement, but they twitched more strongly under increased temperature, which led to more unsuccessful attacks. To minimize the complexity of the fitted models we have excluded effects of prey body mass from the present study. We caution that being based on only two prey species it is impossible to disentangle effects of prey body mass from those of prey type in the present study. Addressing these differences would require replicating our experiments for mobile and sessile prey across different body-mass classes, which would exceed the scope of our study with 36 functional responses. While we have focused the interpretation of our results on differences between mobile and sessile prey species, potential effects of the different prey masses cannot be ruled out entirely. However, our interpretation is based on a clear a priori hypothesis that attack rates should only increase with warming when prey are mobile (see Fig. 4.1), whereas potentially confounding effects of prey body mass remain unsupported by theoretical background. The present study thus enables predictions on temperature effects on functional response across gradients in predator body mass and across different categories of prey mobility, whereas any predictions across gradients in prey body mass require combination of the present results with those of prior studies (Brose *et al.*, 2008; Vucic-Pestic *et al.*, 2010b). Interactions between prey mass and temperature in affecting functional responses remain to be addressed in subsequent studies. De-

spite different effects on attack rates, our results document that per capita feeding rates generally increase with warming. This increase was shallower when the predators fed on *Alphitobius*, which is explained by the lack of a warming effect on attack rates. The broad generality of increasing per capita feeding rates suggest that short-term per capita predator-prey interaction strengths (those that are independent of changes in predator and prey abundances) should increase with warming. A similar prior result was obtained under the simplifying assumption of constant prey density (Rall *et al.*, 2010). The novelty of the present study lies (1) in generalizing this result across a gradient in prey density and (2) in mechanistic links to warming effects on handling times and attack rates. Specifically, this study contributes towards the general understanding of warming effects on predator-prey interaction strengths by presenting a concept that differentiates between metabolically driven effects on handling time and behavioral effects on attack rates. In addition, we extend prior models of body-mass constraints on functional responses (Aljetlawi *et al.*, 2004; Brose *et al.*, 2008; Gergs and Ratte, 2009; Vucic-Pestic *et al.*, 2010b). These results allow including warming effects in an allometric modelling framework addressing the stability of populations, food webs and ecosystem functioning, which will be critically important for a mechanistic understanding of the consequences of global warming for natural ecosystems (Abrahams *et al.*, 2007). Moreover, interest in functional-response parameters has been recently invigorated by their central importance for an allometric model predicting the network structure of food webs (Petchey *et al.*, 2008), which was recently extended to include temperature effects on food-web connectance (Petchey *et al.*, 2010). This study employed temperature-scaling models for handling time and attack rate to predict the network structure of food webs across a temperature gradient. In combination with our novel temperature-scaling models in the present study this provides an opportunity for predicting warming effects on food-web structure.

As for any laboratory study, some caveats have to be mentioned: we did not take into account more complex aspects of interactions such as interference competition or thermal adaptation. In particular, it is quite likely that thermal adaptation could change the response in metabolism and feeding to warming. Any longer acclimation treatment before the experiments would have accounted for thermal adaptation at the cost of losing standardized conditions. For instance, starving the predators at different temperature levels would have led to different levels of hunger at the beginning of the experiments as a consequence of the positive correlation between temperature and metabolism. In the present study, we chose to maintain standardized conditions (similar level of hunger across temperature treatments) to obtain a simplistic model of warming effects (see illustration in Fig. 4.1). We think that this simplistic model will provide an important baseline for subsequent experiments accounting for thermal adaptation. Moreover, logistic constraints prevented additional experiments addressing warming effects on functional responses including resident predators (e.g., sessile filter feeders) or resources without escape efficiencies (e.g., detritus). However, we are confident that the successful test of theory presented here indicates the broad generality of the model, which should be confirmed by subsequent studies. Generally, the scaling models for metabolic rates, feeding rates, handling times and attack rates presented here and in prior studies (Brose *et al.*, 2008; Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2010a,b) provide a mechanistic support for dynamic population models (Vasseur and McCann, 2005; Rall *et al.*, 2008), dynamic models of complex food webs (Loeuille and Loreau, 2005; Brose *et al.*, 2006b; Brose, 2008; Berlow *et al.*, 2009; Romanuk *et al.*, 2009) and topological models (Petchey *et al.*, 2008, 2010) that are based on allometric and temperature scaling. Generally, this research agenda will benefit tremendously from a closer linkage between empirical and theoretical approaches (Woodward *et al.*, 2005; Brose, 2008; Ings *et al.*, 2009), and future extensions should scale up our results for predator-prey systems to more complex networks of feeding interactions in size-structured commu-

nities. Eventually, this should lead to critically important knowledge how the structural persistence and functioning of complex natural ecosystems may be affected by global warming (Montoya and Raffaelli, 2010). Our results provide strong evidence that warming imposes energetic restrictions on predators by decreasing their energetic efficiencies (i.e., the ratio of feeding to metabolism). This result rests on the conservative assumption that the field metabolic rate is three times higher than the standard metabolic rate when animals rest. Alternative assumptions that field metabolic rates are five to 40 times higher than the standard metabolic rates would only strengthen the trend of decreasing energetic efficiencies presented here. In consequence of these decreasing energetic efficiencies, warming should increase population stability with less fluctuations in population densities over time (Vasseur and McCann, 2005; Rall *et al.*, 2008). Consistent with a prior study of linear interaction strengths (Rall *et al.*, 2010), our results also suggest that decreasing energetic efficiencies impose the risk of predator starvation in natural ecosystems, which may explain severe consumer extinctions in warmed microcosms (Petchey *et al.*, 1999). Eventually, the mechanistic functional-response framework of the present study may allow detailed predictions on the consequences of warming on predator-prey interaction strengths depending on metabolic and behavioral constraints.

4.6 Acknowledgement

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5 Phylogenetic grouping, curvature and metabolic scaling in terrestrial invertebrates

5.1 Abstract

For more than a century the scaling of animal metabolic rates with individual body masses and environmental temperature has predominantly been described by power-law and exponential relationships, respectively. Many theories have been proposed to explain these scaling relationships, but were challenged by empirically documented curvatures on double-logarithmic scales. In the present study, we present a novel dataset comprising 3661 terrestrial (mainly soil) invertebrate respiration rates from 192 independent sources across a wide range in body masses, environmental temperatures and phylogenetic groups. While our analyses documented power-law and exponential scaling with body masses and temperature, respectively, polynomial models identified curved deviations. Interestingly, complex scaling models accounting for phylogenetic groups were able to remove curvatures except for a negative curvature at the highest temperatures ($>30^{\circ}\text{C}$) indicating metabolic down regulation. This might indicate that the tremendous differences in invertebrate body architectures, ecology and physiology may cause severely different metabolic scaling processes.

5.2 Introduction

For more than a century, the reasons for the allometric scaling of metabolism with organism body mass and the value of the power-law exponent of this relationship have been debated extensively (White, 2010). While early concepts employed a surface-area-to-volume argument to advocate a general power exponent of $2/3$ also known as Rubner's surface law (Rubner, 1883), subsequent data analyses suggested the broad generality of a $3/4$ power law or Kleiber's law (Kleiber, 1947; Peters, 1983; Savage *et al.*, 2004b). The empirically dominating $3/4$ exponent was explained by the optimized, fractal transport networks within organisms such as the cardiovascular system of vertebrates (West *et al.*, 1997). This fractal model together with the universal temperature dependence of metabolism that is, as any thermodynamic process, determined by specific activation energies (i.e., the exponents of the exponential scaling terms, Gillooly *et al.*, 2001) served as a basis for the metabolic theory of ecology (hereafter: MTE, Brown *et al.*, 2004). Hence, the MTE predicts that metabolism follows a $3/4$ power-law scaling with individual body masses (West *et al.*, 1997; Brown *et al.*, 2004; Savage *et al.*, 2004b) and an exponential scaling with environmental temperature with an exponent (hereafter: activation energy) ranging between 0.6 and 0.7 eV (Gillooly *et al.*, 2001, 2006; Allen and Gillooly, 2007). The generality of this MTE paradigm was challenged by (1) alternative metabolic scaling models predicting different ranges of exponents, (2) lacking universality of the exponents across different groups of species, and (3) curved deviations from the predicted relationships. Alternative metabolic scaling models relax the assumption of universal scaling exponents and predict allometric exponents varying between $2/3$ and $3/4$ (e.g., explosion

and quantum metabolism models) or $2/3$ and 1 (metabolic level boundaries (MLB) hypothesis and cell-size model; for detailed descriptions see Darveau *et al.*, 2002; Kozłowski *et al.*, 2003; Glazier, 2005, 2010; Demetrius, 2006; Banavar *et al.*, 2010 or overview by Glazier, 2005 and references therein). This lack of a universal exponent is consistent with recent data analyses, which was partly explained by variance in factors such as phylogenetic groups, lifestyles, activity state or developmental stage (McNab, 1988; Dodds *et al.*, 2001; White and Seymour, 2003; Glazier, 2005; Makarieva *et al.*, 2005c,d; Niven and Scharlemann, 2005; White *et al.*, 2007; McNab, 2008; Glazier, 2009; Isaac and Carbone, 2010). One of the central assumptions of the MTE is that the fractal nature of the metabolic transport network is invariant across organisms and body sizes (West *et al.*, 1997; Brown *et al.*, 2004). While this assumption might appear adequate for vertebrates with cardiovascular systems, it is certainly violated for comparisons amongst invertebrates that are much more diverse in the size and shape of their bodies and the structure, openness, or presence of tracheal and body-fluid transport systems across phylogenetic groups. In consequence, the few studies comprising metabolic data of invertebrates found substantial variation in their metabolic scaling across phylogenetic groups and deviations from linear scaling (Zeuthen, 1953; Meehan, 2006b; Niven and Scharlemann, 2005; Chown *et al.*, 2007; White *et al.*, 2007; Isaac and Carbone, 2010). Similarly, empirical studies have also cast doubt on the narrow distribution of average activation energies predicted by the MTE (Meehan, 2006b; Terblanche *et al.*, 2007; Irlich *et al.*, 2009), and suggested a wider range between 0.46 and 0.96 eV (Downs *et al.*, 2008). Some prior studies tried to explain differences in scaling exponents documented across studies by their focus on different body-mass ranges (according to the phylogenetic groups chosen) across a curved metabolism-mass relationship on a log-log scale (Zeuthen, 1953; Hayssen and Lacy, 1985; Glazier, 2005; Savage *et al.*, 2008; Kolokotronis *et al.*, 2010 and references therein). In this study, we use the largest dataset on invertebrate standard metabolic rates compiled so far to examine power-law and exponential scaling of the metabolic rates with organism body mass and temperature, respectively. The fitted exponents are tested for deviations from the MTE and alternative models. Subsequently, we test for curvatures in these scaling relationships. Finally, we address variability in these exponents across phylogenetic groups to analyze whether accounting for phylogenetic differences removes these curvatures.

5.3 Methods

To address the interspecific scaling of standard metabolic rates of terrestrial invertebrates (with an emphasis on soil invertebrates) with individual body masses (wet weight) and environmental temperature, we combined data from different sources: (1) the dataset of Meehan (2006b), (2) the dataset of Chown *et al.* (2007), (3) additional data from miscellaneous prior publications, and (4) our own measurements (see Appendix). The data-selection criteria of the first two datasets are described in the materials and methods in Meehan (2006b) and Chown *et al.* (2007). Additionally, published literature on the standard metabolic rates of soil invertebrates dating back as far as 1910 with a major emphasis on the past 50 years (ending in 2010), was examined. Data were included if they contained measurements of standard metabolic rates (oxygen consumption per unit mass or per individual), individual body masses and the environmental temperature. Measurements of stressed animals or animals that were cultivated or reared in the laboratory, feeding trials, fluctuating temperature regimes, thermal acclimation or conditions that were not standardized across weight classes and temperature levels were not included into the dataset. Furthermore, we excluded measurements of starving animals to avoid effects of increased searching behavior or down regulation of respiration. Data were transformed into units of joule per hour [J/h] for metabolism,

Kelvin [K] for temperature and milligram [mg] for wet weight (see Appendix). To ensure that our data cover the natural range of body masses and a similar temperature range for each phylogenetic group (see Table 5.1 for an overview), we added our own respiration measurements to the data base. Oxygen consumption by individuals was quantified with an automated electrolytic microrespirometer (Scheu, 1992). Animals for the measurements were either collected by pitfall traps or caught by hand on different field sites (i.e., field plots of the Biodiversity Exploratories, Germany). The animals were stored in climatic chambers (constant 15 °C), and they were fed adequately but fasted for some time prior to the respiration measurement to avoid down regulation of metabolism due to starvation. Using fasted (not fed directly before the experiment) but not starved (not deprived of food over a longer period of time) animals seemed an adequate compromise, but we cannot entirely exclude a possible effect of digestion on metabolism such as specific dynamic action. Each individual was weighed with a precision scale prior to the measurement. Our measurements of oxygen consumption lasted for 12 h at each of six temperatures (5, 10, 15, 20, 25, and 30 °C) and were conducted in a closed system with oxygen supply to avoid oxygen depletion.

Table 5.1: Overview of body mass and temperature range (minimum and maximum) for each phylogenetic group (n = number of measurements)

Phylogenetic group	Body mass [mg]		Temp. [°C]		n	Minimum no. of species [†]	lower taxonomic groups included
	Min	Max	Min	Max			
Arachnida	0.72	1000	3	40	378	45	Araneae
Chilopoda	0.75	187.46	4	30	387	2	Geophilomorpha, Lithobiomorpha
Clitellata	0.02	10500	5	36	340	17	Enchytraeida, Lumbricida
Insecta*	0.00279	7285	-2	30	1826	415	Blattodea, Coleoptera, Collembola, Diptera, Grylloidea, Hemiptera, Hymenoptera, Isoptera, Lepidoptera, Odonata, Orthoptera
Isopoda	1.11	108.04	5	35	245	13	Isopoda
Mesostigmata	0.0044	0.582	0	25	28	10	Mesostigmata
Oribatida	0.0017	0.781	0	29	216	41	Oribatida
Progoneata	4.4425	293.49	5	30	204	3	Juliformia, Pentazonia, Polydesmida
Prostigmata	0.000035	0.0302	0	25	37	6	Prostigmata

* Insecta also includes Archaeognatha, Dermaptera, Megaloptera, Mantodea, Mantophasmatodea, Siphonaptera with single and Thysanura with three data points.

[†] In some taxonomic groups, individuals were not identified to the species' level; minimum no. of species assumes that all these individuals are from identical species.

The respiration between the 8th and the 12th hour was averaged to obtain the standard metabolic rate per hour ($[J/h]$, $1 \text{ ml O}_2 \equiv 20.1 \text{ J}$, Peters, 1983) as respiration had usually saturated at constantly low respiration levels indicative of standard metabolic rates. Details on the respiration measurement are provided in the Appendix. Our analyses focus on effects of body masses (wet weight) and temperature while not accounting for differences between species, which favours generality in the scaling relationships for phylogenetic groups at the cost of ignoring differences between species-specific scaling relationships within phylogenetic groups. We applied three models to the dataset to test their ability of predicting standard metabolic rates of invertebrates. We started with the linear model (Downs *et al.*, 2008), which is similar to the MTE but without fixed values for the allometric exponent, a or the activation energy, E :

$$I = i_0 M^a e^{\frac{-E}{kT}} \quad (5.1)$$

where I is the metabolic rate, a is the allometric exponent, E the activation energy [eV], k is Boltzmann's constant ($8.62 \times 10^{-5} \text{ eV/K}$), T temperature in Kelvin and i_0 a normalization factor. Natural-logarithm transformation yields:

$$\ln I = \ln i_0 + a \ln M - E \left(\frac{1}{kT} \right) \quad (5.2)$$

We added polynomial terms to the mass and temperature terms of this linear model. An n^{th} order polynomial form would be represented by:

$$\ln I = \ln i_0 + \sum_{i=1}^{i=n} a_i \ln M^i - \sum_{j=1}^{j=n} E_j \left(\frac{1}{kT} \right)^j \quad (5.3)$$

Subsequently, the polynomial model with the lowest AIC was chosen. In a third approach, we accounted for the different phylogenetic groups included in the dataset. As no appropriate phylogenetic tree is available for these phylogenetic groups we refrained from using phylogenetic contrasts. As surrogates, genera of invertebrates were merged into broader groups in accordance with a current phylogeny (Westheide and Rieger, 2003). These phylogenetic groups represent relatively homogeneous body architectures (see Table 5.1). The phylogenetic model included direct effects of body mass, temperature and phylogenetic group and two-way interactions terms between phylogenetic group on the one side and body mass or temperature on the other side, which yielded group-specific intercepts, i_{PG} , allometric exponents, a_{PG} , and activation energies, E_{PG} :

$$\ln I = \ln i_{\text{PG}} + a_{\text{PG}} \ln M - E_{\text{PG}} \left(\frac{1}{kT} \right) \quad (5.4)$$

We fitted the three models (Eqn. 5.2, 5.3 and 5.4) to our data employing linear mixed effects models with maximum likelihood (function 'lme' with 'method = ML' in the nlme package (Pinheiro *et al.*, 2009) of the statistics program R (R Development Core Team, 2010)). To account for systematic differences among studies, the study identity was entered as a random effect in these models. We compared the goodness of fit of the three models by their AIC values. We tested for curvatures in these relationships by analyzing the distribution of the residuals against the independent variables, the natural logs of body mass and temperature term (inverse of temperature multiplied with Boltzmann's constant; $1/(kT)$), utilizing the function 'loess' in the stats package of R. Loess is a locally weighted polynomial regression method that uses weighted least squares, giving more weight to points near the point whose response is being estimated and less weight to points further away and is plotted against the independent variable. We calculated the model confidence bands for the linear model. In this two-parameter model, confidence calculations yield planes across the dimensions of body mass and temperature. Compression of these planes in two-dimensional figures results in confidence bands. Loess fits outside these confidence bands were interpreted as indicators of curvatures. For the sake of simplicity, we refrained from calculating similar confidence bands for the higher dimensional polynomial and phylogenetic models (e.g., the phylogenetic model would yield independent confidence limits for each combination of phylogenetic group with body mass or temperature). Instead, we compared the deviation of the residual loess fits from the zero line of the model prediction.

5.4 Results

The dataset compiled for this analysis includes 3661 metabolic rate measurements of 580 taxa (mostly species and some higher taxa) and 192 independent published sources (see Appendix). The body masses of the invertebrate species ranged over almost nine orders of magnitude from the smallest mites of 0.000035 mg body weight (Prostigmata) to the largest earthworms of 10,500 mg body weight (Clitellata), and our data base covered temperatures between -2 and 40 °C (Table 5.1).

Table 5.2: Results of the fits of the three models: linear, polynomial and phylogenetic model.

	Estimate	Std. Error	<i>p</i>
Linear Model[†] (AIC: 7069)			
$\ln i_0$	23.055335	0.4467264	< 0.001
<i>a</i>	0.695071	0.0070217	< 0.001
<i>E</i>	0.68642	0.0111510	< 0.001
Polynomial Model[‡] (AIC: 6975)			
$\ln i_0$	-2475.2739	448.8304	< 0.001
<i>a</i> ₁	0.7335	0.0130	< 0.001
<i>a</i> ₂	-0.01341	0.0029	< 0.001
<i>a</i> ₄	0.0002	0.0000	< 0.001
<i>a</i> ₅	-9.23×10^{-6}	0.0000	0.0092
<i>E</i> ₁	-184.123	33.6544	< 0.001
<i>E</i> ₂	4.5538	0.8408	< 0.001
<i>E</i> ₃	-0.0374	0.0070	< 0.001
Phylogenetic Model[§] (AIC: 6112)			
$\ln i_0$ (Arachnida)	24.581475	1.427089	< 0.001
$\ln i_0$ (Chilopoda)	28.252911	1.738555	< 0.001
$\ln i_0$ (Clitellata)	12.441891	1.860958	< 0.001
$\ln i_0$ (Insecta)	21.97205	1.548440	< 0.001
$\ln i_0$ (Isopoda)	23.168652	1.956933	< 0.001
$\ln i_0$ (Mesostigmata)	9.674023	7.124471	0.0175
$\ln i_0$ (Oribatida)	22.02277	2.564171	< 0.001
$\ln i_0$ (Progoneata)	22.347024	1.939854	< 0.001
$\ln i_0$ (Prostigmata)	10.281495	6.189070	0.097
<i>a</i> (Arachnida)	0.5652537	0.021186	< 0.001
<i>a</i> (Chilopoda)	0.5580991	0.031299	< 0.001
<i>a</i> (Clitellata)	0.8006928	0.030859	< 0.001
<i>a</i> (Insecta)	0.7588950	0.023176	< 0.001
<i>a</i> (Isopoda)	0.5544768	0.042168	< 0.001
<i>a</i> (Mesostigmata)	0.6904864	0.088527	< 0.001
<i>a</i> (Oribatida)	0.6793706	0.037195	< 0.001
<i>to be continued . . .</i>			

... table continued

	Estimate	Std. Error	<i>p</i>
<i>a</i> (Progoneata)	0.5713411	0.036623	<0.001
<i>a</i> (Prostigmata)	0.6599399	0.067537	<0.001
<i>E</i> (Arachnida)	0.7093476	0.035668	<0.001
<i>E</i> (Chilopoda)	0.8030069	0.043370	<0.001
<i>E</i> (Clitellata)	0.4432832	0.046141	<0.001
<i>E</i> (Insecta)	0.6574038	0.038672	<0.001
<i>E</i> (Isopoda)	0.6867293	0.049441	<0.001
<i>E</i> (Mesostigmata)	0.3792541	0.175105	0.031
<i>E</i> (Oribatida)	0.7060855	0.063551	<0.001
<i>E</i> (Progoneata)	0.6700449	0.048703	<0.001
<i>E</i> (Prostigmata)	0.4125318	0.153008	0.008

p-values indicate significant difference of the parameter estimates from zero.

$$^{\dagger} \ln I = \ln i_0 + a \ln M - E \left(\frac{1}{kT} \right) \quad \text{linear model} \quad (\text{Eqn. 5.2})$$

$$^{\ddagger} \ln I = \ln i_0 + \sum_{i=1}^{i=n} a_i \ln M^i - \sum_{j=1}^{j=n} E_j \left(\frac{1}{kT} \right)^j \quad \text{polynomial model} \quad (\text{Eqn. 5.3})$$

$$^{\S} \ln I = \ln i_{\text{PG}} + a_{\text{PG}} \ln M - E_{\text{PG}} \left(\frac{1}{kT} \right) \quad \text{phylogenetic model} \quad (\text{Eqn. 5.4})$$

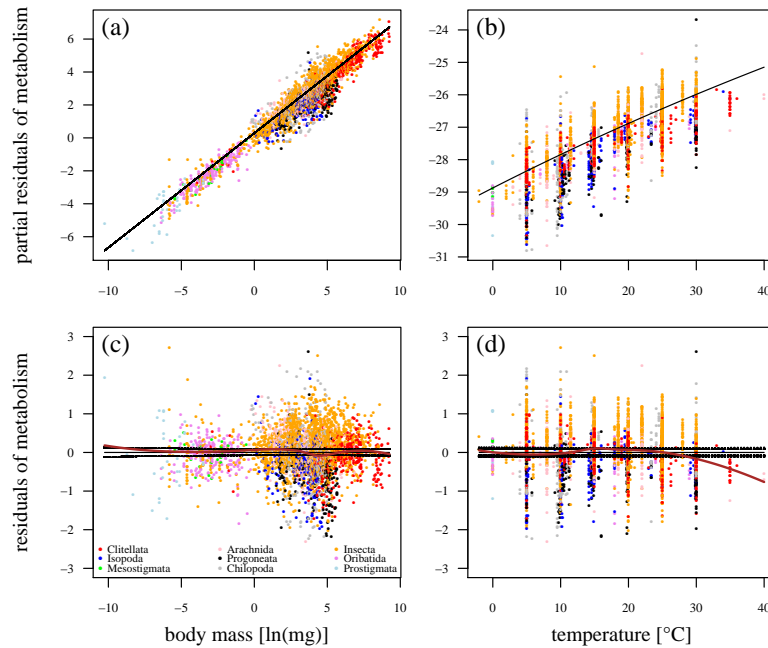


Figure 5.1: Metabolic scaling according to the linear model: dependence of partial residuals of the natural logarithm of metabolism on (a) the natural logarithm of body mass and (b) temperature with the fitted multiple linear model (Eqn. 5.2, black line). In these partial residual plots, metabolism is plotted against one of the independent variables while accounting for the effect of the other. Distributions of the linear model's residuals (deviation of data points from black line in panels a and b) across (c) the natural logarithm of body mass and (d) temperature characterized by deviations of the loess fit (brown curves) from the 95% confidence bands (dotted black bands). See Table 5.2 for parameters of the fitted linear model (Eqn. 5.2). Note that statistical fits employed inverse temperature terms (Eqn. 5.2, 5.3, 5.4), whereas figure axes were labelled with temperature.

Across these ranges covered by our data, the standard metabolic rates increase with increasing body mass and temperature (Fig. 5.1). Fitting of the linear model (Eqn. 5.2) resulted in an allometric exponent, a , of 0.695 ± 0.007 , Table 5.2, Fig. 5.1a) differing significantly from the $3/4$ exponent predicted by the MTE (t -test, $p < 0.001$), whereas the activation energy, E , of 0.686 eV (std error ± 0.011 , Table 5.2, Fig. 5.1b) was within the predicted range ($0.6 - 0.7 \text{ eV}$). Some phylogenetic groups such as mites (Oribatida, Mesostigmata), isopods and earthworms exhibited metabolic rates systematically lower than the prediction of the linear model (Fig. 5.1a, b). In contrast, Chilopoda and Arachnida had higher metabolic rates than predicted (Fig. 5.1a, b). Interestingly, the groups with respiration rates higher than the linear model's prediction represent active hunters, whereas the groups with lower respiration rates mostly consist of detritivores. To assess curvatures in the relationships, we analyzed the dependence of the linear model residuals on the natural logarithms of body mass and temperature ($1/(kT)$) and tested for deviation from linearity by 'loess fits' (see Methods). The closer the loess fit is to the zero (optimum) line the higher is the quality of the model. Note that positive residuals and a positive loess fit indicate underestimation of the standard metabolic rate by the model, whereas negative residuals and a negative loess fit suggest overestimation. Our residual analyses indicate significant deviations from the model (i.e., loess line outside the 95 % confidence bands) at low and intermediate body masses (Fig. 5.1c) and strong negative deviations at high temperatures (over 30°C , Fig. 5.1d). Together, these patterns clearly suggest non-linear deviations from the linear model (Eqn. 5.2). We repeated these analyses with nine subsets of the data that each excluded one of the phylogenetic groups. In all analyses, the residuals of the model fit against the natural logarithm of body mass and temperature exhibited similar curvatures. This suggests that the curvature was not driven by a single phylogenetic group and characterized the compound dataset.

We accounted for these non-linearities by fitting polynomial models (Eqn. 5.3). The polynomial model we used here contained polynomials of 2nd, 4th and 5th degree for the body-mass term (Table 5.2). While removing any of these polynomials decreased the quality of the model (i.e., yielding higher AIC values), the 3rd order polynomial could be omitted. Comparisons of the 'loess fits' between the linear model (Fig. 5.1c, d) and the polynomial model (Fig. 5.2a, b) show that polynomials removed most of the curvature. The polynomial model (AIC: 6975) was much more parsimonious than the linear model (AIC: 7069). Together, the significance of the polynomial terms and the lower AIC of the polynomial models suggest that the curvatures in the metabolic scaling should be considered.

Subsequently, we replicated these analyses with a model including nine phylogenetic groups (Eqn. 5.4, Table 5.1). We fitted an overall linear model to the data accounting for differences in allometric exponents, activation energies and normalization constants among these groups (see Table 5.2 and Fig. 5.3 for parameter estimates). Overall, this model including phylogenetic groups yielded the lowest AIC value (AIC: 6112) of all three models, which suggests that it has substantially superior support compared to the simpler linear and polynomial models (Burnham and Anderson, 2001). Interestingly, this superior fit of the phylogenetic model was accompanied by removing most of the curvatures in the relationships as indicated by smaller deviations of the loess fits from the zero-optimum line (Fig. 5.2c, d vs. Fig. 5.1c, d). However, the overestimation of metabolic rates at the highest temperatures (indicated by the negative loess fits in Fig. 5.2d) remained, which suggests that they cannot be explained by phylogenetic effects. To ensure that our results are not driven by the statistical methodology chosen, we repeated the analyses with linear least squares models (ANCOVA) thus incorrectly ignoring effects of different study designs. The results were qualitatively similar to those obtained with linear mixed effects models with significant interaction terms and heterogeneity of slopes for the different phylogenetic groups, which

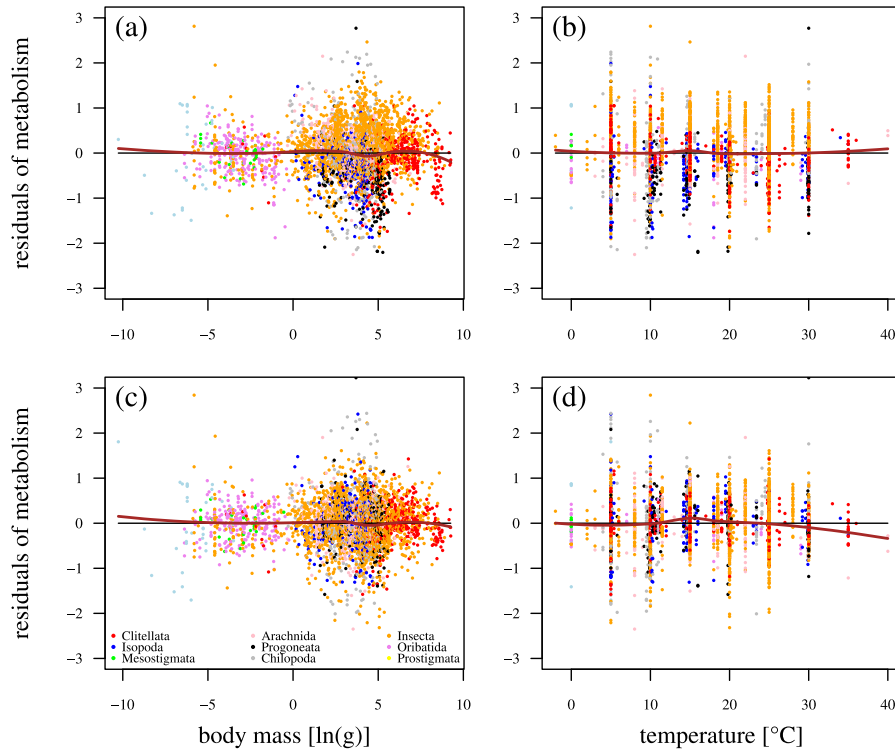


Figure 5.2: Accuracy of polynomial and phylogenetic models: distributions of the residuals for the polynomial (a, b) and the phylogenetic model (c, d) across the natural logarithms of body mass (a, c) and temperature (b, d). Systematic deviations of the data from model predictions are characterized by loess fits (brown curves). See Table 5.2 for parameters of the fitted polynomial (Eqn. 5.3) and phylogenetic model (Eqn. 5.4).

indicates the independence of our conclusions from statistic methodology. To disentangle intra- and interspecific metabolic scaling, we replicated our analyses for 100 random subsamples of the dataset including only one data point per species (excluding data of higher taxonomic levels) per temperature. These interspecific scaling analyses supported our prior results: (1) We found significant polynomial terms for allometric exponents (a_2 and a_4 , $p < 0.05$, with four subsamples having higher p -values for a_4) and activation energies (E_2 and E_3 , $p < 0.05$) indicating curvatures in the metabolic scaling relationships; (2) The AICs of the phylogenetic model were much lower than the AICs of the linear and the polynomial model in all subsamples suggesting the phylogenetic as the preferred model; (3) The phylogenetic models removed most of the curvatures in all subsamples. The allometric exponents (a) of the nine phylogenetic groups varied substantially in a range between 0.554 for Isopoda and 0.801 for Clitellata (Table 5.2, Fig. 5.3b). The exponents of four phylogenetic groups were significantly lower than the predicted $3/4$ exponent of the MTE (95 % confidence intervals do not include the dashed line in Fig. 5.3b). Interestingly, the exponents of Arachnida and Chilopoda were even lower than the lower boundary ($2/3$) of the exponent range predicted by alternative models (see discussion below for comparison with higher exponents in prior studies). The activation energies (E , [eV]) of the different groups display a wide range from 0.379 for Mesostigmata to 0.803 for Chilopoda (Table 5.2, Fig. 5.3c). Despite this substantial variation in mean activation energies, our results suggest that the range between 0.6 and 0.7 predicted by the MTE is within all 95 % confidence limits.

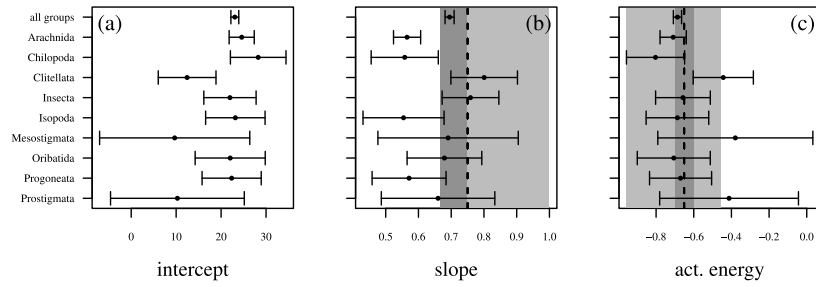


Figure 5.3: Distribution of fitted metabolic scaling parameters and their 95 % confidence limits in the phylogenetic model across phylogenetic groups: (a) intercepts, (b) allometric exponents and (c) activation energies. Parameters of the linear model (all groups) have been included. Indications of model predictions: (b) dashed line equals $3/4$ (MTE); gray and dark gray areas indicate ranges $2/3 - 1$ and $2/3 - 3/4$ respectively (alternative models); (c) the dark gray area indicates range -0.6 to -0.7 eV and the dashed line the mean 0.65 eV (MTE); the light gray area depicts range -0.46 to -0.96 eV.

5.5 Discussion

We examined three models in their ability to predict standard metabolic rates of terrestrial invertebrates: a power-law model deduced from the metabolic theory of ecology that was linearized by natural logarithms (linear model), a model with additional polynomial terms added to the linear model (polynomial model), and a model allowing specific intercepts, allometric slopes and activation energies for each of nine phylogenetic groups (phylogenetic model). Overall, we found that all three models fit the data significantly. The fitted linear model estimated an allometric exponent of $0.695 (\pm 0.007 \text{ standard error})$ that is significantly different from the $3/4$ exponent predicted by the MTE (West *et al.*, 1997; Brown *et al.*, 2004), and an activation energy, E of $0.686 \text{ eV} (\pm 0.011)$ that is in the predicted range of 0.6 to 0.7 eV (Gillooly *et al.*, 2001, 2006; Allen and Gillooly, 2007). Together, these results support the universal thermodynamic temperature-dependence of metabolism while rejecting the universal power-law scaling with body mass (West *et al.*, 1997). Consistent with prior studies on the metabolic rates of mammals (Hayssen and Lacy, 1985; Kolokotronis *et al.*, 2010), residual analyses revealed curvatures in the relationship of the linear model that could be removed by the polynomial and the phylogenetic model. Overall, the phylogenetic model has the highest statistical quality (i.e., the lowest AIC), because it removes most of the curvature found for the linear model and – in contrast to the polynomial model – it allows for mechanistic interpretation of the fitted parameters. Together, these results suggest that the phylogenetic model should be preferred over the linear and polynomial models and that the assumptions of the MTE are not appropriate for invertebrates. Similarly, Kozłowski and Konarzewski (2005) found variance in scaling exponents across various mammalian groups suggesting a broader generality of the phylogenetic signatures in metabolic scaling. Alternative metabolic scaling models such as the explosion model (Banavar *et al.*, 2010), the allometric cascade model (Darveau *et al.*, 2002), quantum metabolism (Demetrius, 2006), the MLB hypothesis (Glazier, 2010) and the cell-size model by Kozłowski *et al.* (2003) relax the strict $3/4$ power law and predict scaling exponents that vary within the range between $2/3$ and $3/4$ or 1 (MLB hypothesis and cell-size model). While seven allometric exponents fell within this predicted range, two of the phylogenetic groups of the present study exhibited exponents with 95 % confidence limits lower than $2/3$ (see discussion below) thus suggesting that none of the models might be able to explain their metabolic scaling. Moreover, the non-linearities detected in our analyses suggest more complex mechanistic relationships between body masses and standard metabolic rates accounting for differences among organisms concern-

ing their morphology, ecology, lifestyle and physiology. Here, we followed prior studies (Meehan, 2006b; Chown *et al.*, 2007; Irlich *et al.*, 2009; White *et al.*, 2007; Isaac and Carbone, 2010) and aggregated these differences in phylogenetic signals included in metabolic scaling relationships. Our analyses indicate that the incorporation of phylogenetic groups is essential for predicting the standard metabolic rates of different groups of invertebrates, because the phylogenetic model provided the best fit to the data and removed curvatures in the scaling relationship. We explain our results with the different body architectures and metabolic strategies of the invertebrates included in our study. Invertebrates possess (1) partially or entirely open tracheal and body-fluid transport systems that are heterogeneous across their body parts, and dramatically different across differently sized species from different phylogenetic groups, and (2) different ecological lifestyles and habitats. Together, these two characteristics may be responsible for the different scaling exponents of the phylogenetic groups, and they prevent a general scaling relationship across phylogenetic groups. Similarly, prior studies have also documented the importance of phylogenetic signals in the metabolic scaling relationships (Kozłowski and Konarzewski, 2005; Meehan, 2006b; White *et al.*, 2007; Chown *et al.*, 2007; Irlich *et al.*, 2009; Isaac and Carbone, 2010). However, until more complex metabolic scaling models accounting for phylogenetic differences in body architecture as well as ecological lifestyle or habitat are developed the fitted exponents of our phylogenetic model remain descriptive. Nevertheless, we anticipate that the dataset sampled for the present study may provide an important benchmark against which such more complex metabolic models should be tested. The allometric exponents of some phylogenetic groups reported here are lower than those of prior studies (e.g., Meehan, 2006b; Pennington and Meehan, 2007; Glazier, 2010, but see the lower exponent for oribatid mites by Wood and Lawton, 1973). In case of the chilopods, we caution that this might be caused by the low species number in our study. However, as the data of Meehan (2006b) and Wood and Lawton (1973) are included in our dataset, other differences in fitted exponents are more likely to be explained by (1) the larger range in body-masses, and (2) parameter estimation via mixed effect models with maximum likelihood in our study. Re-analyses of our data with sums of squares statistics yielded higher estimates of the exponents more consistent with prior publications, which suggests differences in statistical methodology as the main explanation for the disparity in exponents between studies. However, more detailed analyses of allometric exponents for individual phylogenetic groups were beyond the scope of this study. For six of nine invertebrate groups the activation energies for the temperature dependence of invertebrate standard metabolic rates lay within the range of 0.46 to 0.96 eV (Downs *et al.*, 2008). However, only three phylogenetic groups exhibited activation energies in the more narrow range for metabolic processes between 0.6 and 0.7 eV (Gillooly *et al.*, 2001). This is consistent with the substantial variation in metabolic activation energies found in prior studies (Meehan, 2006b; Terblanche *et al.*, 2007; Irlich *et al.*, 2009; Isaac and Carbone, 2010). However, even the narrow range for metabolic activation energy is within the confidence limits of the parameter estimates of our analyses for each of the nine phylogenetic groups as well as for the linear model. This suggests that despite substantial variation in activation energies across phylogenetic groups the universal temperature dependence of metabolic processes as predicted by the MTE (Gillooly *et al.*, 2001) is not rejected by our analyses. In addition to testing for curvature in the body-mass scaling, we have documented non-linearities in the scaling of invertebrate standard metabolic rates with the environmental temperature. We found the most pronounced deviations from the predictions of the linear model at high temperatures, where the linear model overestimated the invertebrate standard metabolic rates drastically. In part, this severe overestimation might be overcome by thermal adaptation processes (Terblanche *et al.*, 2005; Lachenicht *et al.*, 2010; Terblanche *et al.*, 2009). While such thermal adaptation processes may be important for our understanding of temperature effects on metabolism, we chose to focus the

present study on standard metabolic rates excluding possible acclimation effects. One important aspect of the standardization involved in our own study was to start the metabolic measurements with organisms of the same standardized initial conditions (see Appendix for details). This implied keeping them at the same temperature prior to the measurement. Consistent with a prior study (Knies and Kingsolver, 2010), a polynomial model provided a better fit to the data than the simple linear model. While the phylogenetic model could remove most of the curvature in the metabolic scaling relationship, a systematic negative deviation of the metabolic data from the model predictions at the highest temperatures ($> 30^{\circ}\text{C}$) remained. These temperatures are probably close to the edge of the species' thermal windows (Pörtner *et al.*, 2006; Pörtner and Farrell, 2008) or the 'biologically relevant' temperature range (Gillooly *et al.*, 2001), which causes down regulation of the metabolism when approaching lethal temperatures. Metabolic down regulation at high temperatures (Gillooly *et al.*, 2001) is thus the reasonable explanation for the non-linearities remaining in the temperature scaling of the phylogenetic model.

5.6 Conclusions

A comparison of the three tested models clearly shows that the linear and the polynomial model do not fit the metabolic data equally well as the phylogenetic model. The linear model employs the least parameters, which came at the cost of curved residuals across the body-mass and temperature axes. Hence, the linear model sacrifices detail for the sake of generality (i.e., residual variation of the linear model was 12 % higher than that of the phylogenetic model). In contrast, the introduction of polynomials removed most of the curvature in the residuals while lacking a mechanistic basis. Our analyses demonstrated that a phylogenetic model accounting for differences in allometric exponents, activation energies and normalization constants between phylogenetic groups provided the best fit to the data and also removed most of the curvature in the residuals. Although this does not provide the critically needed, novel mechanistic model for the scaling of invertebrate metabolic rates, our analyses suggest that differences in body architectures as well as ecological lifestyles and habitats among phylogenetic groups could be centrally important to such novel models.

5.7 Acknowledgements

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6 Respiration rates, assimilation efficiencies and maintenance consumption rates depend on consumer types: energetic implications of environmental warming

6.1 Abstract

With the world continuously warming, a mechanistic understanding how food webs react to climate change gains importance. Biological rates fundamental to the energy distribution in food webs such as respiration rates and consumption rates are accelerated by warming but no studies so far investigated if this temperature dependency differs between trophic levels or consumer types. Here, we performed a meta-analysis of published studies on respiration rates and assimilation efficiencies to investigate how the influence of temperature and body mass differs between consumer types. Based on that we calculated the maintenance consumption rates (i.e. amount of energy required to balance life maintenance) in dependence on temperature, body mass and consumer type by dividing respiration rates by assimilation efficiencies.

The scaling of respiration rates and assimilation efficiencies with temperature and body mass differed between consumer types. Respiration rates increased with temperature and body mass for all consumer types with the strongest impact of temperature on carnivores and the strongest body-mass effect for herbivores. While assimilation efficiencies of herbivores increased with warming, they were not affected by temperature for all other consumer types. Moreover, body mass did not affect assimilation efficiencies except for a decrease that we found for detritivores. The resulting maintenance consumption rates increased with temperature and body mass for all consumer types with the strongest increase with temperature for carnivores whereas the body-mass effect was most pronounced for detritivores.

Overall, our results suggest non-trivial effects of temperature on food-web stability and biomass distribution in food webs. Climate change will have profound energetic consequences for natural communities (1) by increasing turnover rates at the detritivore level due to their accelerated consumption rates and (2) by strongly increasing maintenance consumption rates of carnivores. Interestingly, consumption rates of lower trophic levels increased less under warming than experimentally measured consumption rates published in literature. In contrast, calculated predator maintenance consumption rates increased stronger under environmental warming than realized consumption rates. This suggests that lower trophic levels should be able to increase their biomass under warming whereas predators should struggle to consume enough energy for maintenance and have no resources left for population growth.

6.2 Introduction

Species in natural communities are linked to one another by their feeding interactions which drive the flow of energy and nutrients, thus forming a highly complex network with hundreds of species

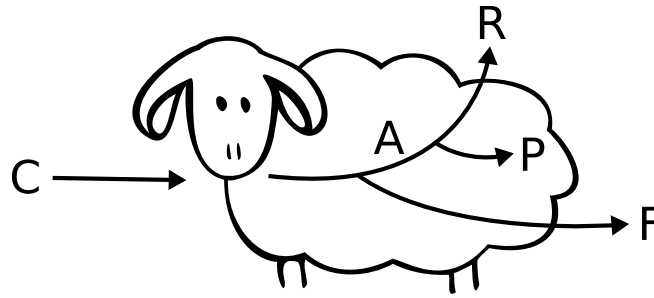


Figure 6.1: Schematic diagram of the energy pathways through an organism. Part of the consumed energy, C , is assimilated, A . The part which cannot be utilized is egested as faeces, F . The assimilated energy is used for production P and the organism's respiration R . Assimilation efficiency describes the proportion of assimilation to consumption (A/C).

and thousands of links between these species. Natural food webs display a characteristic body-mass structure which may account for the specific link structure defining who eats whom and determines the stability and dynamics of ecological systems (Brose *et al.*, 2006b; Otto *et al.*, 2007; Rall *et al.*, 2008; Brose, 2010; Riede *et al.*, 2011; Yvon-Durocher *et al.*, 2011; Heckmann *et al.*, 2012).

As the world is continuously warming due to climate change (IPCC, 2007; Sanderson *et al.*, 2011), a mechanistic understanding how food webs react to environmental warming is a major challenge for ecologists. Warming directly accelerates chemical reactions and thereby alters biological processes fundamental to the energy distribution in food webs, such as respiration rates (Gillooly *et al.*, 2001; Brown *et al.*, 2004; Ehnes *et al.*, 2011) or consumption rates (Brose, 2008; Vucic-Pestic *et al.*, 2010b; Lang *et al.*, 2012; Ott *et al.*, 2012; Rall *et al.*, 2012) with higher trophic levels being more sensitive to climatic conditions (Daufresne *et al.*, 2009; Sentis *et al.*, 2012).

Understanding how food webs and ecosystem functions are affected by environmental warming requires a combined knowledge of food-web structure and interaction strengths (i.e. the magnitude of energy flowing from resource to consumer) which are fundamental to food-web stability (Berlow *et al.*, 2004). The patterns of interaction strengths within communities are determined by the distribution of energy (de Ruiter *et al.*, 1998; Brose, 2008), with weak interactions having a stabilizing effect (Berlow, 1999). The idea of treating nature as an energy-flow system is deeply rooted in early history of science (Elton, 1927; Lindeman, 1942; Odum, 1968; Reichle, 1968; de Ruiter *et al.*, 1998). Classical quantitative food-web models estimated the annual consumption rates C of a population by assuming that it needs to balance its respiration, its biomass loss due to consumption by predators and its change in biomass by natural death and population growth (Hunt *et al.*, 1987; de Ruiter *et al.*, 1994a,b). In a steady-state system (i.e. without biomass change), the consumption necessary to balance the metabolic demand (i.e. equilibrium energy flow) therefore can be calculated by

$$C \propto \frac{R}{A_{\%}} \quad (6.1)$$

where C is the organism's consumption, R its respiration rate and $A_{\%}$ the assimilation efficiency. The respiration rate describes the rate at which an organism transforms energy and material and may be the most fundamental biological rate as it determines the demands an organism places on its environment (Brown *et al.*, 2004). Assimilation efficiency expresses how much energy is being extracted from the food consumed and can be used for metabolism and production (Fig. 6.1).

Biological rates depend on body mass and due to the underlying chemical reactions on temperature. The metabolic theory of ecology (Brown *et al.*, 2004) explains how body mass and temperature affect respiration rates. Originally, a fixed allometric exponent (0.75) was used, but

Downs *et al.* (2008) enhanced the model by allowing group-specific allometric exponents and activation energies:

$$I = i_0 M^a e^{\frac{-E}{kT}} \quad (6.2)$$

where I is the respiration rate, i_0 a normalization factor, M the body mass [mg], a the allometric exponent, E the activation energy [eV], k the Boltzmann's constant (8.62×10^{-5} eV/K) and T environmental temperature [K]. Respiration rates increase with temperature and body mass (Gillooly *et al.*, 2001; Brown *et al.*, 2004), but these scaling relationships differ between phylogenetic groups (Downs *et al.*, 2008; Isaac and Carbone, 2010; Ehnes *et al.*, 2011). As phylogenetic groups often comprise animals of the same consumer type we expected to also find a correlation between respiration rates and consumer types as proposed by Ehnes *et al.* (2011) who observed higher respiration rates in groups consisting mainly of active hunters and lower respiration rates in detritivorous groups. By re-analyzing their database on standard respiration rates of terrestrial invertebrates we explored how the allometric and temperature scaling of respiration rates differs between consumer types.

Assimilation efficiencies vary between consumer types (e.g. carnivores, herbivores, detritivores) depending on the amount of material which cannot be utilized such as chitinous exoskeletons and lignin (Odum, 1968; Peters, 1983). Usually, it is calculated by dividing the assimilated energy by the consumed energy (Fig. 6.1):

$$A_{\%} = \frac{R + P}{C} \quad (6.3)$$

or

$$A_{\%} = \frac{C - F}{C}. \quad (6.4)$$

Equation 6.3 assumes that the assimilated energy becomes available for metabolism R (life maintenance, activity) and production P (growth and reproduction). A second way of calculating the assimilated energy is by subtracting the excreted energy F (faeces) from the consumed energy (Eqn. 6.4). Some studies investigating assimilation efficiencies found an impact of temperature (Heiman and Knight, 1975; Mathavan, 1990) whereas others found assimilation efficiencies to be temperature independent (Richardson, 1975; Hamilton, 1985; Pandian and Marian, 1985, 1986). Furthermore, body mass showed no effect on assimilation efficiencies (Buhr, 1976; Gerald, 1976; Pandian and Marian, 1985, 1986). However, most of these studies were conducted for a small set of species and replicated over small temperature or body-mass gradients. Metastudies so far concentrated on the influence of nitrogen content on assimilation efficiencies of aquatic insects and fish (Pandian and Marian, 1985, 1986) and consumer types of birds (Castro *et al.*, 1989; Hilton *et al.*, 1999) while not accounting for temperature and body mass. Generally, assimilation efficiencies are assumed to increase with trophic level (Kozlovsky, 1968) which indicates differences between consumer types (Odum, 1968; Peters, 1983). Here, we compiled a database for assimilation efficiencies using literature research to investigate the impact of temperature, body mass and consumer type over a broader range.

Knowledge on how respiration rates and assimilation efficiencies for different consumer types are affected by temperature and body mass allowed us to calculate the consumption rates which exactly balance energy loss (i.e. maintenance consumption rates). Prior studies using a functional-response approach (Holling, 1959b) showed that consumption rates increase with temperature and body mass (Brose, 2008; Vucic-Pestic *et al.*, 2010a, 2011; Ott *et al.*, 2012; Rall *et al.*, 2012). Our

approach allows investigation of the impact of climate change on food webs by assigning consumer types to species and accounting for consumer-type specific scaling with temperature and body mass.

The questions we address in this study are (1) whether the impact of temperature and body mass on respiration rates differs between consumer types and (2) if assimilation efficiencies are affected by temperature, body mass and consumer type. Based on these results we then (3) investigated how maintenance consumption rates which exactly balances energy loss scale with temperature depending on consumer types.

6.3 Materials and methods

6.3.1 Datasets

To address the scaling of standard respiration with temperature and body mass for different consumer types, we used the database of terrestrial invertebrates by Ehnes *et al.* (2011). For our analysis, only species which could be clearly categorized into a consumer type were included, resulting in a database with 2683 experimental observations (see Appendix). Data were transformed into joule per hour [J/h] for respiration rates, Kelvin [K] for temperature and milligram [mg] for body mass (wet weight).

For assimilation efficiencies, we combined data from 53 published studies with 376 experimental observations where assimilation efficiencies were measured under a controlled temperature regime (see Appendix). Studies using the Conover ash-ratio method or radioactive labelling of the resource were excluded as they seemed to be unreliable (Prus, 1971; Lasenby and Langford, 1973; Richardson, 1975; Nielsen and Olsen, 1989). If no information on body mass was provided, we used average body masses from secondary literature. Dry weight of body mass was converted into wet weight by a conversion factor of 4 (Peters, 1983). Data were transformed into Kelvin [K] for temperature and milligram [mg] for wet weight.

Species were classified by their consumer type as carnivores, herbivores or detritivores. Bacterivores and fungivores were not included in the analyses as the data records were poor.

6.3.2 Statistical analyses

Data were analysed using the statistical program R (R Development Core Team, 2010) with the additional package ‘nlme’ (Pinheiro *et al.*, 2010) employing linear mixed effects models with maximum likelihood (function ‘lme’ with ‘method=ME within the ‘nlme’ package). Study identity was entered as a random effect in these models to account for systematic differences among studies. Assimilation efficiencies were arcsine square-root transformed (Sokal and Rohlf, 1995) as they are a percentage.

To analyse the influence of temperature and body mass on respiration rates for different consumer types, we included consumer type and the two-way interaction terms between consumer type and body mass and consumer type and temperature in the linear model (Eqn. 6.2, Ehnes *et al.* 2011). Temperature was normalized to a standard temperature of 20 °C (293.15 K) by incorporation of an extended Arrhenius term (Gillooly *et al.*, 2001; Vasseur and McCann, 2005; Rall *et al.*, 2010). Natural-logarithm transformation of the consumer-type model allowed calculation of consumer-type specific intercepts, allometric exponents and activation energies

$$\ln I = \ln i_{0C} + a_C \ln M - E_C \frac{T - T_0}{k T T_0} \quad (6.5)$$

where I is the respiration rate, i_{0C} , a_C and E_C are the consumer-type specific intercepts, allometric exponents and activation energies, respectively, M is the body mass [mg], k the Boltzmann's constant ($8.62 \times 10^{-5} \text{ eV/K}$), T the absolute temperature [K] and T_0 the standard temperature [K].

For investigation of the influence of temperature and body mass on assimilation efficiencies $A_{\%}$ a linear model was used with temperature normalized as above, yielding

$$\arcsin \sqrt{A_{\%}} = i_{0C} + a_C \ln M + E_C \frac{T - T_0}{k T T_0}. \quad (6.6)$$

6.3.3 Simulation of maintenance consumption rates

The values estimated by fitting of respiration rates and assimilation efficiencies were used to simulate 1000 hypothetical data points of maintenance consumption. We sampled 1000 body mass (\ln) and temperature values using a normal distribution (function 'rnorm', R Development Core Team 2010) with a mean of zero and a standard deviation of 3 for natural logarithmic body mass, and a mean of 20 °C with a standard deviation of 5 for temperature. To create reproducible data, the random number generator used to generate the 1000 hypothetical data points was initialised with a fixed seed of 667 (function 'set.seed', R Development Core Team 2010). Subsequently, we used the intercepts, slopes and activation energies from the fittings of respiration rates and assimilation efficiencies and their standard errors to calculate the 1000 corresponding respiration rates and assimilation efficiencies. The resulting respiration rates were multiplied by 3 for approximate conversion into field respiration rates (Savage *et al.*, 2004b).

Finally, we calculated maintenance consumption rates C following equation 6.1 by fitting a multiple linear model to obtain consumer-type specific intercepts, allometric exponents and activation energies:

$$C = i_{0C} + a_C \ln M + E_C \frac{T - T_0}{k T T_0}. \quad (6.7)$$

6.4 Results

6.4.1 Respiration rates

Respiration rates increased with temperature and body mass with activation energies and allometric exponents depending on the consumer type (Table 6.1). For herbivores, the temperature relationship was not significant as only a small temperature range was covered by the data (19 °C–25 °C). Respiration rates of carnivores were higher than respiration rates of detritivores and showed the strongest increase with temperature (Fig. 6.2a). The influence of body mass on respiration rates was highest for herbivores and least pronounced for carnivores (Fig. 6.2b).

6.4.2 Assimilation efficiencies

Assimilation efficiencies differed widely between consumer types. Carnivores had the highest assimilation efficiencies ($88\% \pm 6.4$, mean \pm STD) and detritivores the lowest ($19.9\% \pm 13.3$, mean \pm STD) whereas herbivores showed a large variance between 14 and 95 % ($55.3\% \pm 19.2$, mean \pm STD). Assimilation efficiencies of carnivores and detritivores were independent of temperature but

Table 6.1: Results of the fits for consumer-type specific respiration rates (Eqn. 6.5) and assimilation efficiencies (Eqn. 6.6) with intercepts normalized to 20 °C.

	Estimate	Standard error	<i>p</i>
<i>Respiration rate</i>			
$\ln i_0$ (Carnivore)	-4.1417	0.095	< 0.001
$\ln i_0$ (Herbivore)	-3.9353	0.576	< 0.001
$\ln i_0$ (Detritivore)	-4.9138	0.106	< 0.001
<i>a</i> (Carnivore)	0.6944	0.01	< 0.001
<i>a</i> (Herbivore)	0.8158	0.061	< 0.001
<i>a</i> (Detritivore)	0.7216	0.013	< 0.001
<i>E</i> (Carnivore)	0.6997	0.014	< 0.001
<i>E</i> (Herbivore)	0.5373	0.818	0.511
<i>E</i> (Detritivore)	0.6074	0.02	< 0.001
<i>Assimilation efficiency</i>			
i_0 (Carnivore)	69.219	3.178	< 0.001
i_0 (Herbivore)	46.1244	2.377	< 0.001
i_0 (Detritivore)	37.1643	3.226	< 0.001
<i>a</i> (Carnivore)	-0.0209	0.326	0.949
<i>a</i> (Herbivore)	0.2762	0.258	0.286
<i>a</i> (Detritivore)	-2.3806	0.73	0.012
<i>E</i> (Carnivore)	1.3351	0.9	0.139
<i>E</i> (Herbivore)	5.2132	1.03	< 0.001
<i>E</i> (Detritivore)	1.6425	1.689	0.332

Note that values for assimilation efficiencies were arcsine square root transformed.

herbivores exhibited a strong increase in their assimilation efficiencies with warming (Table 6.1, Fig. 6.3a). Body mass did not affect assimilation efficiencies of carnivores and herbivores but influenced detritivorous assimilation efficiencies negatively (Table 6.1, Fig. 6.3b).

6.4.3 Maintenance consumption rates

Maintenance consumption rates increased with temperature across all consumer types (Table 6.2). For carnivores and detritivores, assimilation efficiencies were temperature independent (Table 6.1) and the increasing maintenance consumption rates under warming are only caused by their increasing respiration rates (Table 6.1). Carnivorous maintenance consumption rates showed a stronger reaction to warming as their respiration rates increased rapidly with temperature whereas consumption rates of detritivores increased at a lower rate as their respiration rates increased more slowly. Herbivorous maintenance consumption rates showed the lowest increase with temperature as their assimilation efficiencies increased with temperature. In contrast, investigation of body-mass effects showed a stronger increase of detritivorous maintenance consumption rates with increasing body mass as assimilation efficiencies decreased with body mass and thereby intensified the effect of higher respiration rates with increasing body mass.

6.5 Discussion

In this study, we used a literature research to investigate the impact of temperature and body mass on respiration rates and assimilation efficiencies and subsequently calculated maintenance consumption rates of different consumer types. Based on that, we discuss implications of environmental warming for the distribution of energy flows and stability of food webs. Especially

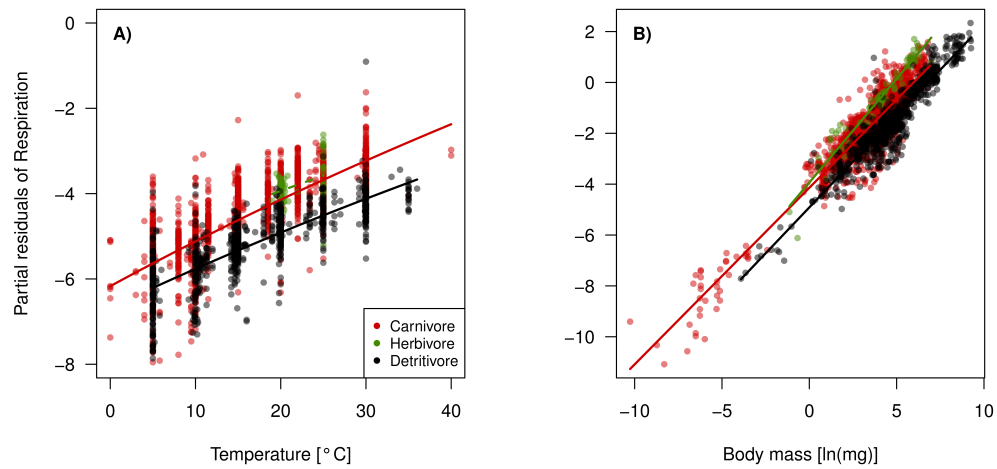


Figure 6.2: Partial residual plots of the natural logarithm of respiration rates in dependence on (a) temperature and (b) body mass. In these plots, respiration rates are plotted against one of the independent variables while accounting for the effect of the other. Dotted lines indicate non-significant regressions.

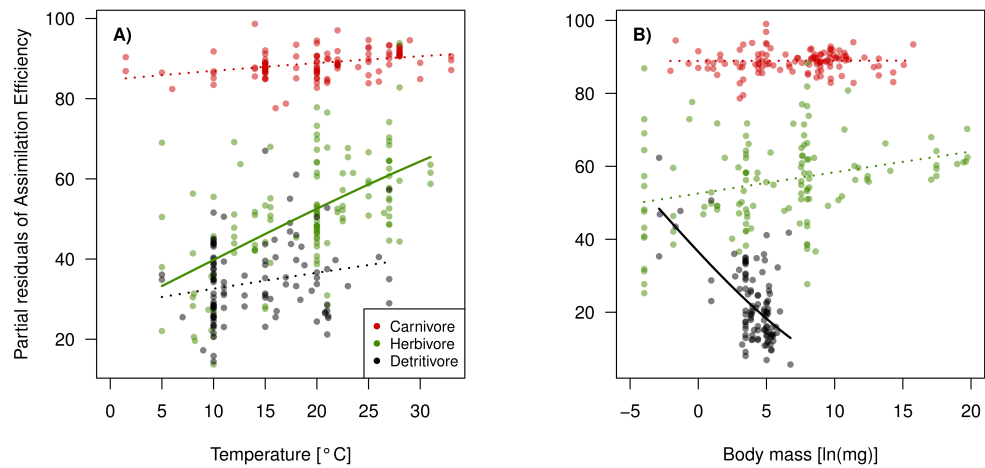


Figure 6.3: Partial residual plots of assimilation efficiencies in dependence on (a) temperature and (b) body mass. Dotted lines are not significant. Note: Table 6.1 shows the arcsine square root transformed assimilation efficiency but plotted here are the regressions and residuals of the actual values.

Table 6.2: Simulated group-specific intercepts, activation energies and allometric exponents for maintenance consumption rates of carnivores, herbivores and detritivores.

	Estimate	Standard error	<i>p</i>
i_0 (Carnivore)	-2.9014	0.016	< 0.001
i_0 (Herbivore)	-2.1669	0.016	< 0.001
i_0 (Detritivore)	-2.7561	0.016	< 0.001
a (Carnivore)	0.6967	0.006	< 0.001
a (Herbivore)	0.8038	0.006	< 0.001
a (Detritivore)	0.8334	0.006	< 0.001
E (Carnivore)	0.6811	0.024	< 0.001
E (Herbivore)	0.3611	0.024	< 0.001
E (Detritivore)	0.5013	0.024	< 0.001

carnivores showed a strong reaction to environmental warming which may substantially change food-web structure and dynamics.

For respiration rates, we found activation energies and allometric exponents to differ between consumer types, thus supporting the hypothesis of Ehnes *et al.* (2011) of lower respiration rates in detritivorous groups in comparison to actively hunting animals. Respiration rates of carnivores showed the strongest reaction to temperature as they expend much more energy for active searching and hunting than herbivores and detritivores feeding on immobile resources (Table 6.1, Fig. 6.2a). The values of activation energies for carnivores and detritivores lie well in the expected range between 0.6 and 0.7 eV (Gillooly *et al.*, 2001), whereas herbivores exhibited somewhat lower activation energies lying in the wider range of 0.46 to 0.96 eV proposed by Downs *et al.* (2008). Our database only contains data of resting animals, measurements of stressed or feeding animals were not included. However, the physiology of actively hunting animals is still reflected in their increased respiration rates. This energy consuming life strategy is balanced by carnivores preying on food of higher quality as animal tissue is of higher calorific value than plants or detritus (Golley, 1961) resulting in significantly higher assimilation efficiencies (Table 6.1).

Assimilation efficiencies of carnivores and detritivores were independent of temperature thus supporting other studies (Richardson, 1975; Hamilton, 1985; Pandian and Marian, 1985, 1986) whereas herbivorous assimilation efficiencies were scattered over a broad range and increased with temperature (Fig. 6.3a). Depending on the habitat and light or nutrient limitation within a habitat, plants can differ widely in their stoichiometry (Frost *et al.*, 2005; Fink *et al.*, 2006). Aquatic primary producers contain a higher amount of nutrient-rich (high nitrogen and phosphorous content) photosynthetic material in comparison to terrestrial plants with their carbon-rich structural and transport tissues (Elser *et al.*, 2000; Shurin *et al.*, 2006). As heterotrophs have high nitrogen and phosphorous demands, terrestrial herbivores face a greater nutritional imbalance than aquatic consumers (Elser *et al.*, 2000; Frost *et al.*, 2005; Shurin and Seabloom, 2005). However, animals have the ability to change their ingestion rate and degree of food selectivity to alter the balance of elements and may also reduce their assimilation efficiencies for elements ingested in excess (Logan *et al.*, 2004; Frost *et al.*, 2005; Frost and Tuchman, 2005). This explains the high variability in herbivorous assimilation efficiencies and may also be responsible for the temperature dependency if the plant's stoichiometry is changed under environmental warming (Aerts *et al.*, 2009; Finkel *et al.*, 2010; Sardans *et al.*, 2012). To disentangle effects of different nutrient quality on assimilation efficiencies, future research should therefore include the resource's stoichiometry.

Investigation of the impact of body mass on respiration rates showed the strongest body-mass effect in herbivores and the lowest in carnivores (Table 6.1, Fig. 6.2b). For assimilation efficiencies

we found a different pattern: the assimilation efficiencies of detritivores decreased with increasing body mass but we found no body-mass relationship for carnivores and herbivores (Table 6.1, Fig. 6.3b). We propose an explanation for the body-mass relationship of detritivores based on the smooth transition between primary decomposers feeding on litter and secondary decomposers feeding on fragmented litter and microorganisms (Scheu and Falca, 2000; Schneider *et al.*, 2004; Chahartaghi *et al.*, 2005; Pollierer *et al.*, 2009). Most studies did not sterilize detritus prior to experiments, therefore decomposers could directly feed on litter and also on bacteria and fungi. Only recent studies were able to disentangle the trophic ecology of small organisms (Scheu and Falca, 2000; Schneider *et al.*, 2004; Chahartaghi *et al.*, 2005; Crotty *et al.*, 2011; Maraun *et al.*, 2011) showing that a high number of detritivores mainly feed on microorganisms. Our literature research did not reveal sufficient data of bacterivorous and fungivorous assimilation efficiencies to include them in the analysis, but the small number available showed distinctly higher assimilation efficiencies for both consumer types in comparison to detritivores, with $(68\% \pm 19.1 \text{ (mean} \pm \text{STD, } n = 16))$ and $(71.8\% \pm 13.1 \text{ (mean} \pm \text{STD, } n = 12))$ for bacterivores and fungivores, respectively. The decrease of detritivorous assimilation efficiencies with body mass in our dataset is mainly caused by few very small oribatid mites which were identified as secondary decomposers also feeding on fungi (Maraun *et al.*, 2011) and thus exhibit high assimilation efficiencies. To figure out whether detritivorous assimilation efficiencies truly decrease with body mass or if this effect is completely mediated by additional feeding on fungi, additional measurements of primary and secondary decomposers over a broader body-mass range are needed.

Knowledge of the dependency of respiration rates and assimilation efficiencies on temperature and body mass of different consumer types enabled us to simulate maintenance consumption rates. The increased energetic demand metabolism places on any ectothermic organism under warming resulted in increased maintenance consumption rates of all consumer types (Table 6.2) with higher consumption rates (i.e. higher intercepts) at the detritivore and herbivore level due to their low assimilation efficiencies and high respiration rates, respectively. Simulated maintenance consumption rates of carnivores showed the strongest reaction to temperature due to the strong temperature dependency of their respiration rates with their assimilation efficiencies staying on the same level. Therefore, their consumption has to increase rapidly under environmental warming thus confirming the high sensitivity of higher trophic levels to climate change (Daufresne *et al.*, 2009; Sentis *et al.*, 2012). However, comparison with experimentally measured consumption rates shows that the simulated high activation energies are not fulfilled by actual consumption rates for carnivores (Table 6.3). In contrast, herbivorous and detritivorous consumption rates increased faster with temperature than their energetic demand (Table 6.2, Table 6.3). This resulting net-energy gain may cause population growth (Ott *et al.*, 2012) whereas carnivores fail to cover their increasing demand and thus face a higher risk of extinction under environmental warming (Petchey *et al.*, 1999; Brose *et al.*, 2012; Kratina *et al.*, 2012; Rall *et al.*, 2012). The increased maintenance consumption rates of detritivores should cause accelerated decomposition rates under warming and may create positive or negative feedbacks to global climate change as carbon-dioxide fluxes to the atmosphere are stimulated as well as primary productivity due to higher nutrient availability (Aerts, 2006; Davidson and Janssens, 2006; Kutsch *et al.*, 2009; Nielsen *et al.*, 2011; Dossena *et al.*, 2012).

The theoretical approach we have chosen here focussed on calculation of maintenance consumption rates in a steady-state system and completely ignored changes in biomass due to consumption by higher trophic levels, natural death and population growth, which are important parts of energy flows in natural systems and can be integrated by estimation of biomass changes over time (mirroring biomass losses due to consumption and natural death and biomass accumulation by population

growth, de Ruiter *et al.* 1998). This more precise calculation of non-equilibrium energy flows, however, can only be achieved for specific communities if data on food-web topology (i.e. the links defining who is consuming whom), and biomass densities replicated in time are available for all populations (de Ruiter *et al.*, 1994b). While studies based on these non-equilibrium energy flows have unraveled astonishing patterns in the energetic structure of natural communities (de Ruiter *et al.*, 1998; Neutel *et al.*, 2002, 2007), approximation of energy flows based on equilibrium assumptions such as in our study allows generalizing energy-flow patterns across communities and ecosystems. Our approach thus enables broad, large-scale predictions at the cost of precision in predicting specific energy flows.

Additionally, in complex food webs a large number of other factors play a role which were not taken into account here, such as habitat structure, multiple prey (preference, switching) or predator interference which can modify consumption rates (Kratina *et al.*, 2009; Vucic-Pestic *et al.*, 2010a; Kalinkat *et al.*, 2011; Lang *et al.*, 2012; Sentis *et al.*, 2012). As these factors may also be influenced by temperature and body mass (Kalinkat *et al.*, 2011; Lang *et al.*, 2012) they may be of high importance for energy distribution in food webs and food-web stability.

Overall, we have shown that the impact of temperature and body mass on respiration rates and assimilation efficiencies differs between consumer types which has important implications for the distribution of energy flows in food webs. Approximation of energy flows based on equilibrium assumptions such as in our study allows generalizing energy-flow patterns across communities and ecosystems. In this vein, we have shown how environmental warming changes the energetic requirements of organisms of different consumer types which have to be met for survival. The high maintenance consumption rates of detritivores due to low assimilation efficiencies may strongly affect carbon and nutrient turnover and thus feed back to global climate change. Carnivorous maintenance consumption rates showed the strongest reaction to increasing temperature as their respiration rates were strongly temperature dependent. This may have strong implications for food-web stability due to changed interaction strengths under environmental warming. However, as natural populations are subject to biomass changes, the actual energy flows for the populations to persist have to be higher than the calculated maintenance consumption rates. Our results thus represent lower boundaries of energy flows and how they are affected by warming. Comparison of the temperature relationship of estimated consumption rates and experimental data strongly stresses the importance of environmental warming for ecosystems as higher trophic levels fail to increase their consumption rates strong enough to counterbalance increased metabolic demands.

6.6 Acknowledgements

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Table 6.3: Realized maximum consumption rates for different consumer types.

Consumer	Resource	Temp.	E_C	Source	Comments
Carnivores					
Carabid beetles	<i>Alphitobius diaperinus</i> larvae	5–30	0.230	Vucic-Pestic <i>et al.</i> (2011)	
Carabid beetles	flightless <i>Drosophila hydei</i>	5–30	0.240	Vucic-Pestic <i>et al.</i> (2011)	
<i>Coleomegilla maculata lengi</i>	<i>Myzus persicae</i>	13.9–32.8	0.900	Sentis <i>et al.</i> (2012)	
<i>Ischnura elegans</i>	<i>Daphnia magna</i>	5–27.5	0.709	Thompson (1978); Petchey <i>et al.</i> (2010)	
<i>Amblyseius longispinosus</i>	<i>Aponychus corpuzae</i>	15–35	0.226	Zhang <i>et al.</i> (1998); Petchey <i>et al.</i> (2010)	
<i>Amblyseius longispinosus</i>	<i>Schizotetranychus nanjingensis</i>	10–35	0.439	Zhang <i>et al.</i> (1999); Petchey <i>et al.</i> (2010)	
<i>Coccinella septempunctata</i>	<i>Aphis gossypii</i>	15–35	0.133	Xia <i>et al.</i> (2003); Petchey <i>et al.</i> (2010)	
Herbivores					
<i>Tintinnopsis</i> sp.	phytoplankton	5–25	0.711	Verity (1985); Hansen <i>et al.</i> (1997)	calculated by Q_{10}
<i>Acartia hudsonica</i>	<i>Thalassiosira constricta</i>	4.5–16	0.606	Durbin and Durbin (1992); Hansen <i>et al.</i> (1997)	calculated by Q_{10}
<i>Ostrea edulis</i>	<i>Pavlova lutheri</i>	10–20	0.876	Crisp <i>et al.</i> (1985); Hansen <i>et al.</i> (1997)	calculated by Q_{10}
<i>Mytilus edulis</i>	<i>Isochrysis galbana</i>	6–18	0.770	Sprung (1984); Hansen <i>et al.</i> (1997)	calculated by Q_{10}
<i>Centropages hamatus</i>	<i>Ditylum brightwellii</i>	1–15	0.927	Kjørboe <i>et al.</i> (1985); Hansen <i>et al.</i> (1997)	calculated by Q_{10}
<i>Manduca sexta</i>	low-protein artificial diet	14–34	0.906	Kingsolver and Woods (1998)	data from Fig. 1
<i>Manduca sexta</i>	high-protein artificial diet	14–34	0.798	Kingsolver and Woods (1998)	data from Fig. 1
<i>Manduca sexta</i>	low-protein artificial diet	14–34	0.541	Kingsolver and Woods (1998)	data from Fig. 2
<i>Manduca sexta</i>	high-protein artificial diet	14–34	0.589	Kingsolver and Woods (1998)	data from Fig. 2
<i>Malacosoma disstria</i>	<i>Acer saccharum</i>	18–30	0.456	Levesque <i>et al.</i> (2002)	re-analysed from Tab. 1, data from 1997
<i>Malacosoma disstria</i>	<i>Acer saccharum</i>	18–30	0.275	Levesque <i>et al.</i> (2002)	re-analysed from Tab. 1, data from 1998
Detritivores					
<i>Oniscus asellus</i>	<i>Carpinus betulus</i>	10–20	0.860	Ott <i>et al.</i> (2012)	
<i>Oniscus asellus</i>	<i>Fraxinus excelsior</i>	10–20	1.360	Ott <i>et al.</i> (2012)	
<i>Porotermes adamsoni</i>	<i>Eucalyptus regans</i>	11.5–24	0.740	Lenz <i>et al.</i> (1982); Dell <i>et al.</i> (2011)	
<i>Porotermes adamsoni</i>	<i>Eucalyptus viminalis</i>	11.5–24	0.650	Lenz <i>et al.</i> (1982); Dell <i>et al.</i> (2011)	
<i>Porotermes adamsoni</i>	<i>Pinus radiata</i>	9–26	0.770	Lenz <i>et al.</i> (1982); Dell <i>et al.</i> (2011)	

Temp. gives the temperature range in °C and E_C the activation energy of maximum consumption. In some cases, activation energies were calculated from Q_{10} -values by $E_C = 0.1kT_0^2 \ln Q_{10}$, where k is the boltzman's constant and T_0 the arithmetic mean of the temperature range (Vasseur and McCann, 2005).

7 Positive correlation between density and parthenogenetic reproduction in oribatid mites (Acari) supports the structured resource theory of sexual reproduction

7.1 Abstract

A number of theories have been proposed to explain the dominance of sexual reproduction in Metazoa. Using oribatid mites (Acari, Oribatida) as model organisms, we test the validity of the ‘structured resource theory of sexual reproduction’ (SRTS) which suggests that limited resources result in the dominance of sexual processes, whereas ample resources favour parthenogenesis. Oribatid mites are mainly soil living animals that reproduce either sexually or by thelytoky.

Resource supply is reflected by animal density. Populations are controlled predominantly by bottom-up rather than top-down forces, such as predation, which is likely to be true for oribatid mites.

The relationship between oribatid mite density and the frequency of parthenogenetic reproduction was investigated at two spatial scales (1) regionally using data on oribatid mites from two different forests in Germany, and (2) globally compiling data on 38 oribatid mite communities from different habitats.

Predictions of the SRTS were supported at both scales, indicating that ample resources (as indicated by high population densities) in fact favour parthenogenetic reproduction.

7.2 Introduction

The perceived disadvantages of sexual compared to parthenogenetic reproduction are manifold and include, for example, the break-up of favourable gene combinations and the need to both find mating partners and produce male offspring (Maynard Smith, 1978). Despite these disadvantages, most species of animals reproduce sexually (Bell, 1982). Theories proposed to explain advantages and disadvantages of parthenogenetic and sexual reproductive modes might be viewed as either genetic (based on mutations) or ecological (based on species-environment interactions, including those with other species). Mutational theories state that parthenogens either accumulate detrimental mutations (Kondrashov’s hatchet; Kondrashov, 1988), or that in parthenogenetic populations mutation-free genotypes are more quickly lost than in sexual populations (Muller’s ratchet; Muller, 1964). Another genetic theory assumes beneficial mutations to spread more quickly in sexual than parthenogenetic populations (Fisher-Muller-accelerated-evolution; Fisher, 1930; Muller, 1932). Ecological theories propose that strong biotic interactions foster sexual reproduction (Red Queen hypothesis; Jaenike, 1978; Hamilton, 1980), or that spatially variable niches favor sexually produced offspring (Tangled Bank hypothesis; Ghiselin, 1974; Bell, 1982). These different and mutually exclusive theories led some authors to propose that multiple theories are needed to explain the various aspects associated with sexual reproduction (West *et al.*, 1999b). However, the recent

‘structured resource theory of sexual reproduction’ (SRTS; Scheu and Drossel, 2007) proposes an overarching explanation, that sexual reproduction favors the exploitation of complex resources that are in short supply. According to the SRTS, outcrossing and mixing shuffle new genotypes, allowing a more complete exploitation of local resources. Conversely, it predicts that the availability of ample resources favours parthenogenetic reproduction since parthenogenetic species exploit these resources more quickly. The SRTS resembles the Tangled Bank theory in that it relates advantages of sexual reproduction to variations in niche space, but it focuses on food resources rather than on abiotic conditions (Song *et al.*, 2011). Thus, the SRTS incorporates sib-competition models in which sexually produced offspring benefit from being genetically different by relaxing intraspecific competition (Williams, 1966, 1975; Bell, 1982). In addition, the SRTS integrates aspects of the Red Queen theory, since parasites may be experienced by the host as aggravation of shortage of resources (Scheu and Drossel, 2007). Whether or not the SRTS is sufficient to explain all evolutionary aspects of these issues, we believe that it is a powerful predictor of the local distribution of reproductive modes – that is, of the relative dominance of sexual and parthenogenetic reproduction in local communities. This idea is best tested in environments where parthenogenetic taxa are frequent and widespread, where we can assume that mechanisms promoting the general dominance of sexual reproduction are more relaxed. Below-ground communities are ideally suited for investigating the relative merits of sexual and parthenogenetic reproduction, since parthenogenetic or asexual reproduction is common in protozoans, nematodes, enchytraeid worms, earthworms, collembolans, isopods and oribatid mites (Bell, 1982, 1988; Palmer and Norton, 1991; Christensen *et al.*, 1992; Sbordoni *et al.*, 1997; Doroszuk *et al.*, 2006; Terhivuo and Saura, 2006; Chahartaghi *et al.*, 2009; Fischer *et al.*, 2010a). Sexual taxa are also common, and often co-exist with parthenogenetic taxa that are both closely related and ecologically similar. Thus understanding the high incidence of parthenogenetic reproduction in soil may help to identify unifying concepts responsible for the maintenance and general dominance of sexual reproduction. Oribatid mites are among the most suited animal group for investigating mechanisms responsible for the maintenance of sexual reproduction in soil animal taxa. They are ubiquitous, occurring in high numbers in virtually all ecosystems (Maraun and Scheu, 2000). Of the approximately 10,000 species described today, nearly 10 % reproduce by parthenogenetic development of females, i.e. by thelytoky (Palmer and Norton, 1991; Norton and Palmer, 1991; Norton, 1994), and parthenogenetic species can comprise up to 80 % of oribatid mite individuals in local faunas (Fischer *et al.*, 2010a). Using oribatid mites as model organisms, we tested the prediction of the SRTS that the proportion of parthenogenetic individuals is positively correlated with resource availability. The prediction was investigated at two spatial scales: regional (two forest systems in Germany) and global. Oribatid mite density was taken as a proxy for resource availability, since all current information shows that oribatid mites are controlled predominantly by bottom-up forces. Indeed, due to an array of defense mechanisms including strong cuticle, protective structures and body forms, and chemical repellants (Sanders and Norton, 2004; Heethoff *et al.*, 2011) oribatid mites have been shown to be resistant to predation (Peschel *et al.*, 2006). Using density as a proxy for resource availability is too simplistic, as it ignores changes in metabolism with body size. Allometric scaling predicts that smaller organisms have higher metabolic rates per unit body mass (Brown *et al.*, 2004) and reach higher densities than larger organisms (Damuth, 1981). Therefore, at the regional scale we also investigated the relationship of oribatid mite reproductive mode to metabolism (i.e. respiration). The respiration of oribatid mites has been estimated to be equivalent to 16 % of the energy ingested (Luxton, 1975; Wallwork, 1983). Our regional sites comprised mull (Schwäbische Alb) and moder forests (Schorfheide) varying in macrofaunal density (Schaefer and Schauer mann, 1990). Soil macrofauna is known to affect mesofauna (including oribatid mite) communities through mechanical

disturbance, resource competition, predation and destruction of habitable space (Maraun *et al.*, 2003; Eisenhauer, 2010; Erdmann *et al.*, 2012). Therefore, we expected the relationship between reproductive mode of oribatid mites and density and/or respiration to be most pronounced in the macrofauna-poor moder systems of the Schorfheide. On the global scale, we compiled data on the density of parthenogenetic oribatid mite species from 38 sites ranging from temperate and tropical forests, to fields and meadows, to the bark of trees. According to the SRTS, we expected the density of oribatid mites to be positively correlated with the frequency of parthenogenetic individuals in both datasets.

7.3 Materials and Methods

7.3.1 Regional scale

The sites of the regional dataset comprised forests in the southwest (Swabian Alb; 460 – 860 m a.s.l.) and the northeast (Schorfheide; 3 – 140 m a.s.l.) of Germany. They form part of the ‘Biodiversity Exploratories’, a long-term monitoring and experimental study project (Fischer *et al.*, 2010b). The Schwäbische Alb is dominated by European beech (*Fagus sylvatica*) growing on Jurassic limestone parent rock; the sampled forest types were on cambisols or leptosols (pH of 4.51 ± 0.72) at about 700 m above sea level. The Schorfheide is located on glacial till, which often is covered by sand; the accompanying soil types are mostly dystric cambisols (pH 3.3 ± 0.19), but occasionally podsoles occur (for details see Fischer *et al.*, 2010b). Mean annual precipitation in the Swabian Alb is 700 – 1000 mm and in the Schorfheide 500 – 600 mm, with a mean annual temperature of 6.0 – 7.0 °C and 8.0 – 8.5 °C, respectively (Fischer *et al.*, 2010b). Four forest types were studied in each region: 30-year-old beech forests, 70-year-old beech forests, 120-year-old unmanaged beech forests and 70-year-old coniferous forests (consisting of *Picea abies* in the Schwäbische Alb and *Pinus sylvestris* in the Schorfheide). In spring 2008, four soil samples were taken from each forest in each of the two regions. The 32 samples were taken with a corer (5 cm diameter) each separated into organic (L/F material) and soil (4 cm thick) layers, from which soil arthropods were extracted by heat (MacFadyen, 1961); mite data from these two layers were subsequently pooled for all analyses. Adult oribatid mites were identified following Weigmann (2006) and the gender of each individual was determined by examining genitalia (Grandjean, 1955, 1956). Suctobelbidae and Brachychthoniidae were identified only to family level. The mode of reproduction (sexual or parthenogenetic) was inferred from sex ratios in combination with data in the literature (Palmer and Norton, 1991; Cianciolo and Norton, 2006). For each species, fresh weight (M) was calculated from dry weight (M_{dry}) of individuals (Hadley, 1994) as $M = 4 \times M_{\text{dry}}$ or from the mean body length L [mm] given in Weigmann (2006) and the correlation constants a and b given in Huhta and Koskenniemi (1975) as $\log M = b \log L + a$, with $a = 2.386$ and $b = 2.519$. Respiration I [$\text{J}/\text{h} \times \text{ind.}$] was calculated from fresh weight M [mg] using a linear model (Brown *et al.*, 2004; Downs *et al.*, 2008). The values i_0 , a and E are specific for oribatid mites and were adopted from Ehnes *et al.* (2011):

$$I = i_0 M^a e^{\frac{-E}{kT}} \quad (7.1)$$

with the normalization constant $i_0 = e^{22.02277 \text{ J}/\text{h} \times \text{mg}}$, the allometric exponent $a = 0.6793706$, the activation energy $E = 0.7060855 \text{ eV}$, the Boltzmann’s constant $k = 8.62 \times 10^{-5} \text{ eV/K}$ and T = mean annual temperature (Schwäbische Alb = 279.7 K; Schorfheide = 281.4 K). The calculated respiration per individual was multiplied by the density per square meter of each species; summing

the respiration rates of all species present per square meter resulted in an estimate of the energy use of the whole oribatid mite community [$J/h \times m^2$].

7.3.2 Global scale

The 38 sites investigated included a wide range of habitats: raw humus forests, moder forests, mull forests, riparian forests, peat bogs, meadows, fields, and lichen patches on the bark of trees (for details see Table 7.1). Most habitats were from temperate regions but we also included tropical forest sites. Sites strongly influenced by man such as agricultural systems were not included, as in such systems oribatid mites are unlikely to be controlled by resource availability.

7.3.3 Statistical analysis

The data (oribatid mite density, respiration, proportion of parthenogenetic individuals, and the respective residuals) were inspected using Kolmogorov-Smirnov test. Data were normally distributed ($p > 0.2$). For the regional scale dataset, the relationships between the proportion of parthenogenetic individuals and oribatid mite density, oribatid mite respiration and site (Schorfheide and Schwäbische Alb) were examined using stepwise linear regression. Similarly, for the global scale dataset, the relationships between the proportion of parthenogenetic individuals or taxa and oribatid mite density or habitat type (the seven different habitats where the oribatid mites were collected; see Table 7.1) were examined with stepwise linear regression. Prior to the analysis data on the proportion of parthenogenetic individuals and taxa were arcsin square-root transformed. Regressions between the proportion of parthenogenetic individuals and oribatid mite density were calculated with untransformed and log-transformed data; only results of the latter are presented as the logarithmic regression explained more variation in the dataset. Statistical analyses were carried out using STATISTICA v.9 (StatSoft Inc., Tulsa, OK) and SAS 9.13 (SAS Institute Inc., Cary, NC).

Table 7.1: Habitat type, site characteristics, soil type (if known) , country of the study site, oribatid mite abundance in $ind./m^2$, percentage of parthenogenetic individuals of oribatid mites, percentage of parthenogenetic taxa of oribatid mites, and references for the 38 sites used for the meta-analysis of this study

site no.	habitat type	site characteristics	humus form (if known)	country of study	abundance [$ind./m^2$]	% parthen. Individuals	% parthen. Taxa	publication
1	bark	Western redcedar trees (<i>Thuja plicata</i>)		Canada	323	27	18	(Lindo and Winchester, 2007)
2	meadow	brown earth on loess		Germany	1482	8	27	(Toschki, 2008)
3	bark	oak trees (<i>Quercus robur</i>)		Germany	1940	2	13	(Woltemade, 1982)
4	bark	lime trees (<i>Tilia cordata</i>)		Germany	5000	1	19	(Weigmann and Jung, 1992)
5	forest soil	tropical montane rainforest (3000 m)	raw humus	Ecuador	5769	4	17	(Eiðsfeller, 2007)
6	bark	oak trees (<i>Quercus robur</i>)		Poland	6000	2	15	(Erdmann, 2004)
7	forest soil	tropical montane rainforest (3000 m)	raw humus	Ecuador	6004	25	18	(Fronczek, 2010)
8	field	brown earth on loess		Germany	6179	23	35	(Hülsmann and Wolters, 1998)
9	forest soil	beech forest (Carpathians)	mull	Romania	9200	6	21	(Fabian, 1997)
10	riverine forest	sandy soils with mainly grey alder (<i>Alnus incana</i>)		Austria	11100	17	13	(Totschnig and Schatz, 1997)
11	peat bog	Ledo-Spagnetum with <i>Calamagrostis stricta</i>	mor	Germany	12200	43	35	(Kehl, 1997)
12	forest soil	tropical montane rainforest (1000 m)	moder	Ecuador	13677	43	31	(Fronczek, 2010)
13	forest soil	tropical montane rainforest (1000 m)	moder	Ecuador	15015	36	35	(Eiðsfeller, 2007)
14	forest soil	beech forest on limestone	mull	Germany	22134	36	44	(Schulz, 1991)
15	lichens	on limestone walls		Sweden	23500	24	50	(Fröberg <i>et al.</i> , 2003)
16	forest soil	beech forest	mull	Denmark	34515	38	40	(Luxton, 1981)
17	forest soil	beech forest	mull	Germany	40373	19	23	(Alberti <i>et al.</i> , 1996)
18	forest soil	Scots pine forest	moder	France	42400	65	40	(Garay, 1981)
19	forest soil	mixed hardwood forest	moder	USA	44200	37	59	(Lamoncha and Crossley, 1998)
20	forest soil	mixed beech/spruce (Schwäbische Alb)	mull	Germany	53451	55	73	(Erdmann, 2012)
21	forest soil	mixed beech/spruce (Hainich)	mull/moder	Germany	59814	43	68	(Erdmann, 2012)
22	forest soil	beech forest	moder	Germany	61981	68	40	(Wunderle, 1992)
23	peat bog	Ledo-Spagnetum <i>magellanic</i>	moder	Germany	65000	77	43	(Kehl, 1997)
24	forest soil	beech forest, lined (Solling)	moder	Germany	66277	72	67	(Heiligenstadt, 1988)
25	forest soil	beech forest (Hainich)	moder	Germany	73980	68	58	(Bayer, 2008)
to be continued ...								

... table continued

site no.	habitat type	site characteristics	humus form (if known)	country of study	abundance [<i>ind./m²</i>]	% parthen. Individuals	% parthen. Taxa	publication
26	forest soil	mixed beech/pine (Schorfheide)	moder	Germany	84690	82	77	(Erdmann, 2012)
27	forest soil	coniferous forest	hemimor	Canada	91904	87	75	(Berch <i>et al.</i> , 2007)
28	meadow	Galio-Molinietum		Germany	95500	80	42	(Kehl, 1997)
29	forest soil	beech forest, not limed (Solling)	moder	Germany	101301	84	77	(Heiligenstadt, 1988)
30	forest soil	pine forest with earthworms	moder	Canada	102013	45	54	(McLean and Parkinson, 1998)
31	forest soil	mixed oak, beech and hornbeam forest	moder	Germany	133000	74	51	(Schneider, 2001)
32	forest soil	pine forest without earthworms	mull	Canada	150447	50	56	(McLean and Parkinson, 1998)
33	forest soil	120y old spruce forest (Solling)	moder	Germany	165264	85	62	(Migge, 1996; Migge <i>et al.</i> , 1998)
34	forest soil	Sessile oak forest	moder	France	182900	87	40	(Garay, 1981)
35	forest soil	coniferous forest (Tuusula)	raw humus	Finland	185800	85	71	(Huhta <i>et al.</i> , 1986)
36	forest soil	mixed beech and spruce stand (Solling)	moder	Germany	196137	90	60	(Migge, 1996; Migge <i>et al.</i> , 1998)
37	forest soil	coniferous forest (Tammela)	raw humus	Finland	276700	79	67	(Huhta <i>et al.</i> , 1986)
38	forest soil	coniferous forest (Saarijärvi)	raw humus	Finland	351500	78	66	(Huhta <i>et al.</i> , 1986)

7.4 Results

7.4.1 Regional scale

There were more parthenogenetic individuals in the Schorfheide than in the Schwäbische Alb (stepwise linear regression; $r^2 = 0.65$, $F_{2,29} = 56.24$, $p < 0.0001$). Furthermore, the proportion of parthenogenetic individuals correlated positively with oribatid mite density ($r^2 = 0.76$, $F_{2,29} = 14.82$, $p = 0.0006$) which was significant in the Schorfheide ($r^2 = 0.37$, $F_{1,14} = 8.12$, $p = 0.013$) and marginally significant in the Schwäbische Alb ($r^2 = 0.21$, $F_{1,14} = 3.72$, $p = 0.074$) (Fig. 7.1a). The proportion of parthenogenetic individuals also correlated positively with community respiration of oribatid mites (Fig. 7.1b) which was significant in the Schorfheide ($r^2 = 0.25$, $F_{1,14} = 4.68$, $p = 0.048$) but not in the Schwäbische Alb ($r^2 = 0.17$, $F_{1,14} = 2.92$, $p = 0.109$). However, including community respiration did not markedly increase the explained variance in the stepwise regression analysis, which was due to the high correlation between oribatid mite density and community respiration ($r^2 = 0.85$).

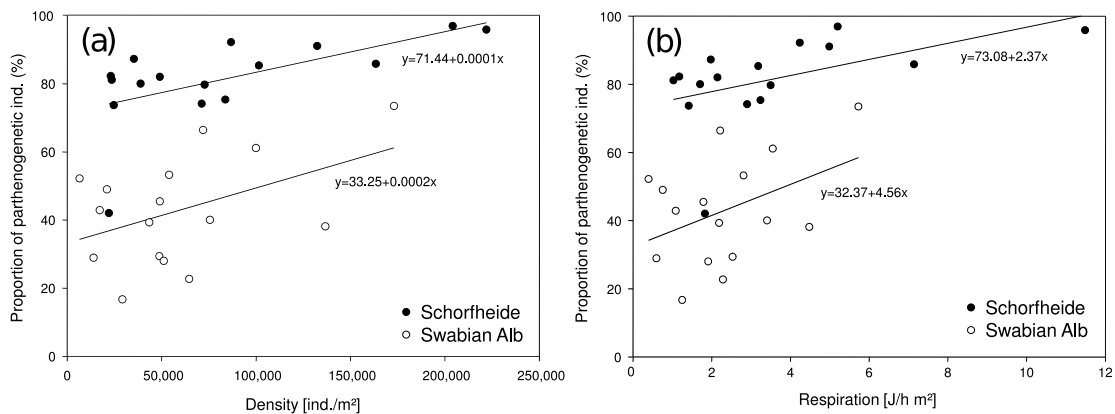


Figure 7.1: Relationship between the proportion of parthenogenetic individuals and oribatid mite density (a) and oribatid mite respiration (b) in Schwäbische Alb and Schorfheide.

7.4.2 Global scale

The density of oribatid mites was significantly positively correlated with the percentage of parthenogenetic species and also with the percentage of parthenogenetic individuals (stepwise linear regression with log-transformed data; $r^2 = 0.61$, $F_{1,36} = 57.93$, $p < 0.0001$, and $r^2 = 0.66$, $F_{1,36} = 72.90$, $p < 0.0001$, respectively) (Fig. 7.2). Including habitat type did not increase the explained variance significantly.

7.5 Discussion

7.5.1 Parthenogenetic reproduction in oribatid mites

Results of our study suggest that the percentage of parthenogenetic individuals in oribatid mite communities is positively correlated with density, at both the regional and the global scale. The relationship also holds for metabolism as indicated by our regional scale dataset. Assuming that

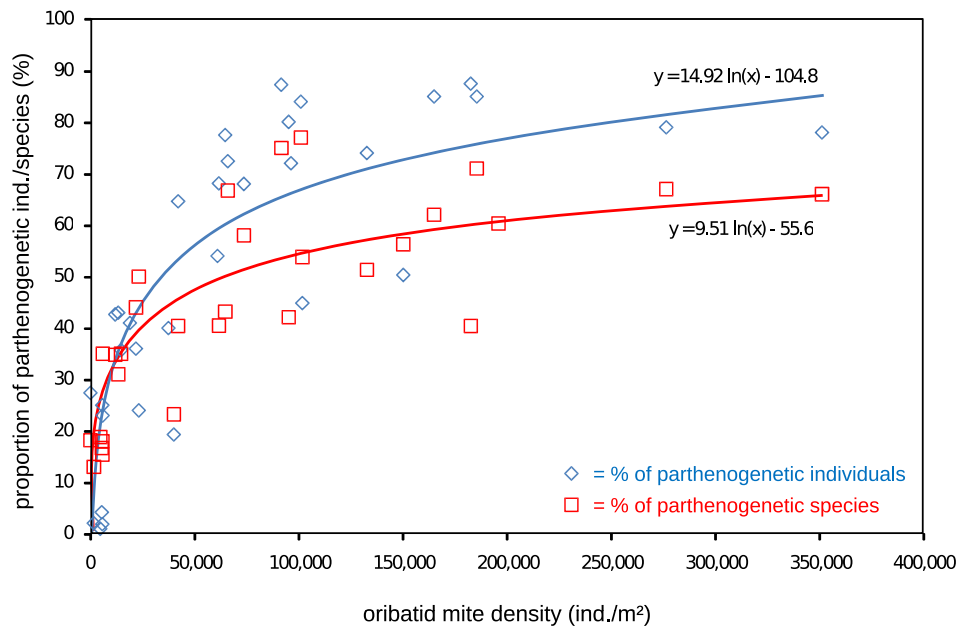


Figure 7.2: Relationship between the proportion of parthenogenetic individuals/proportion of parthenogenetic species and oribatid mite density on a global scale. For details see text.

density and metabolism reflect the availability of resources, these relationships are consistent with predictions of the SRTS (Scheu and Drossel, 2007; Song *et al.*, 2011). Oribatid mites were considered especially well-suited to test predictions of the SRTS, as they are little affected by top-down forces and therefore their density likely reflects resource availability (Schneider and Maraun, 2009; Heethoff *et al.*, 2011). Although this may apply less strictly to soil invertebrates that are more subject to predation (Salamon *et al.*, 2006; Schneider and Maraun, 2009), it would be interesting to investigate correlations between density and reproductive mode in a large range of soil invertebrate taxa, including in particular nematodes and collembolans.

7.5.2 Regional scale

Irrespective of the indicator of the resources available to oribatid mite communities (density or respiration), or of the soil type at the two sites (mull or moder) the proportion of individuals of parthenogenetic oribatid mite species correlated positively with the resource proxy. However, the correlation was weaker in mull (Schwäbische Alb) than in the moder forests (Schorfheide) and less strong for respiration than for density. The mull and moder forests studied differed both in the proportion of individuals of parthenogenetic oribatid mite species and in oribatid mite density (43 % vs. 82 % and 59,800 vs. 84,700 individuals per m², respectively). The lower proportion of individuals of parthenogenetic species in the mull forests of the Schwäbische Alb, where oribatid mite density was lower, conforms to our expectations and is consistent with predictions of the SRTS. However, differences in habitat characteristics may also have contributed to the lower proportion of individuals of parthenogenetic oribatid mite species, since at this site the parthenogenetic Brachychthoniidae were rare. Low abundance of Brachychthoniidae is typical for mull forests and is likely to be due to disturbances by earthworms (Maraun and Scheu, 2000; Eisenhauer, 2010). Macrofauna activity, in particular that of earthworms, has a detrimental effect on mesofauna com-

munities, including those of the slow-developing long-lived oribatid mites, weakening bottom-up control via resource availability.

7.5.3 Global scale

On the global scale, the proportion of parthenogenetic taxa (as well as parthenogenetic individuals) fitted best with density on a logarithmic scale. This reflects the high proportion (typically > 60 %) of parthenogenetic taxa in temperate and boreal forests where the density of oribatid mites spans a wide range from moderate to high (Behan-Pelletier, 1999). The shape of the curve further shows that the high incidence of parthenogenetic species (and individuals) in temperate forests is in contrast with that elsewhere, where parthenogenetic species are much less abundant, such as tropical forests, meadows and the bark of trees. According to the SRTS, the high proportion of parthenogenetic oribatid mites in temperate forests should be due to high availability of resources. Both above- and belowground inputs of resources (i.e. leaf litter and root derived resources) are likely to contribute to this high resource pool (Pollierer *et al.*, 2007). Low densities of oribatid mites in tropical systems are probably related to poor litter quality; indeed, it is increasingly recognized that, compared with temperate and boreal forests, litter in tropical forests decomposes slowly (Hättenschwiler *et al.*, 2011). This is consistent with the finding that tropical forests lack true decomposer animal taxa (Illig *et al.*, 2005). The low density of oribatid mites on the bark of trees (and associated high proportion of sexual species) presumably relates to the fact that many bark-living oribatid mites feed on lichens which are well defended by secondary compounds (Fischer *et al.*, 2010a). Overall, the results indicate a somewhat counterintuitive interrelationship, i.e., with increasing oribatid mite density the importance of resource limitation declines. Presumably, in temperate and boreal forests oribatid mites are structured predominantly by density-independent factors such as cold winters but also by pulsed resource inputs via litter and root deposits. In contrast, in habitats where sexual reproduction of oribatid mites dominates, i.e., on the bark of trees and in soil of tropical forests, resources likely are limiting. Again this is counterintuitive, as animal communities on the bark of trees are exposed to harsh environmental conditions, suggesting that bark living communities are structured by density independent factors. In fact, oribatid mites are well adapted to cold winter conditions and, by feeding predominantly on lichens, presumably are regulated by the availability of food resources that are well defended (e.g., by producing secondary compounds such as usnic acid) (Seyd EL, 1984). Also, the low density of oribatid mites in tropical forest soils suggests a predominance of resource control, reflecting that tropical soils are poor in nutrients and leaves of tropical trees are of low food quality. Low densities of oribatid mites on the bark of trees and in tropical forests therefore also conform to the predictions of the SRTS.

7.5.4 The structured resource theory of sexual reproduction as an integrative theory

Compared with other theories that attempt to explain the predominance of sexually reproducing species, the SRTS focuses on resource availability as the main factor responsible for the mode of reproduction (Scheu and Drossel, 2007; Song *et al.*, 2011). Results of the present study support this view by providing evidence that oribatid mite communities of low density and with a high proportion of sexual species are controlled predominantly by density-dependent factors (i.e. the availability of food resources). In contrast, resources presumably are of limited importance as regulating factor of oribatid mite populations in soils of temperate and boreal forests where they reach high densities and where parthenogenetic species and individuals prevail. We propose that these somewhat counterintuitive relationships explain one of the most striking patterns in oribatid

mite ecology, i.e., the dominance of parthenogens in certain ecosystems, such as temperate and boreal forests. This view is consistent with the assumption that the reproductive mode in oribatid mites is not controlled by biotic interactions (Cianciolo and Norton, 2006). Overall, both the regional and global scale datasets analyzed in this study are consistent with predictions of the SRTS, suggesting that the high incidence of parthenogenetic reproduction in soil-animal taxa is related to periods of relaxed resource competition allowing parthenogenetic taxa to outgrow sexual ones. Experiments manipulating the resource supply of soil animal communities are needed to prove these conclusions. Soil animal communities are well suited for such experiments, as many parthenogenetic species of different taxonomic affiliation co-exist on small spatial scales, allowing tests of the generality of the SRTS in explaining sexual versus parthenogenetic reproduction in Metazoa.

7.6 Acknowledgements

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8 Lack of energetic equivalence in forest soil invertebrates

8.1 Abstract

Ecological communities consist of small abundant, and large rare species. The energetic-equivalence rule is an often observed pattern which could be explained by equal energy usage among many small organisms and rare large organisms. To generate this pattern metabolism as an indicator of individual energy use and abundance have to scale inversely with body mass and cancel out. In contrast, the pattern referred to as biomass equivalence states that biomasses of all species in an area should be constant across the body-mass range. In this study, we investigated forest-soil communities in respect to metabolism, abundance, population energy use and biomass. We focused on four land-use types in three different landscape blocks ('Biodiversity Exploratories'). The soil samples contained 870 species across twelve phylogenetic groups. Our results indicate positive sublinear metabolic scaling and negative sublinear abundance scaling with species' body masses. The relationships varied mainly due to differences among phylogenetic groups or feeding types and only marginally due to land-use type. However, these scaling relationships were not exactly inverse to each other resulting in increasing population energy use and biomass with increasing body mass for most combinations of phylogenetic group or feeding type with land-use type. Thus, our results are mostly inconsistent with the classic perception of energetic equivalence and reject the biomass-equivalence hypothesis while documenting a specific and non-random pattern how abundances, energy use and biomasses are distributed across size classes. However, these patterns are consistent with two alternative predictions: the resource-thinning hypothesis stating that abundances decrease with trophic level and the allometric-degree hypothesis holding that population energy use should increase with population average body mass due to correlations with the number of links of consumers and resources. Overall, our results suggest that a synthesis of food-web structures with metabolic theory may be most promising to predict natural patterns of abundances, biomasses and energy use.

8.2 Introduction

As a general pattern, ecological communities comprise small species of high abundance as well as large species that are rare. The resulting negative relationships between abundance and body mass were ascribed to the energy use (i.e., the metabolic rate) of differently sized individuals. A special case of the opposite scaling of abundance and energy use is the energetic-equivalence rule (EER, Damuth 1981; Nee *et al.* 1991), which holds that population energy use (PEU, the product of population abundance and individual metabolic rate) should be independent of population body mass. For this special case, the scaling of abundances with body masses matches the inverse of the scaling of metabolism with body masses. In this case, PEU is unrelated to population average body mass. Subsequent model analyses suggested that the PEU exponent converges to energetic equivalence (i.e., PEU exponents of zero), because negative or positive exponents yield species with lower than average energy use and consequently a high extinction risk. These extinctions cause a

return of the system to energetic equivalence (Damuth, 2007). Assuming a general $3/4$ power law between metabolic rates and body masses as predicted by metabolic theory (Peters, 1983; Brown *et al.*, 2004) requires a negative $3/4$ exponent for the abundance-mass relationship to support the EER. This concept found empirical support (Damuth, 1981, 1991; Mulder *et al.*, 2005; Meehan *et al.*, 2006; Meehan, 2006a,b) as well as rejection (Peters and Wassenberg, 1983; Silva and Downing, 1995; Jennings and Mackinson, 2003; Long *et al.*, 2006; Reuman *et al.*, 2008; Hayward *et al.*, 2009; DeLong, 2011; Munn *et al.*, 2013). However, the EER in a strict sense assumes that all populations of a community share a common energy resource. In contrast, the populations of natural communities are distributed across trophic levels of complex food webs and thus feed on different resources (e.g., herbivores feed on living plants, and predators consume animals). In these trophic networks, inefficiencies in exploitation, assimilation and biomass-production processes cause decreasing resource availability with increasing trophic level, which should decrease the abundances of high trophic-level populations (Brown and Gillooly, 2003). This resource-thinning hypothesis found some empirical support (Armstrong, 1997; Long *et al.*, 2006). In aquatic ecosystems, abundances often scale with population average body mass raised to a -1 power and thus total population biomass is invariant with body mass (e.g. Sheldon *et al.*, 1977; Cohen *et al.*, 2003). This body-mass independent scaling of biomasses has been proposed as a general rule of biomass equivalence (Polishchuk, 1994). Alternatively, structural analyses of natural food webs have documented that the number of resources exploited increases with population average body masses, whereas the number of consumers simultaneously decreases (Digel *et al.*, 2011). These relationships have been referred to as allometric-degree distributions (Otto *et al.*, 2007). Assuming that abundances increase with bottom-up resource availability expressed by the number of resources and decrease with top-down control expressed by the number of consumers, this suggests that allometric-degree correlations create a positive effect of population average body mass on abundances. Consequently, this should cause shallower abundance-mass relationships and positive PEU-mass relationships (hereafter: allometric-degree hypothesis), which is also supported by some empirical studies (Cohen *et al.*, 2003; Reuman *et al.*, 2008). In this study, we address these alternative ideas as (1) the energetic-equivalence rule (population-energy use, PEU, is invariant with population average body mass), (2) the biomass-equivalence hypothesis (population biomass is invariant with population average body mass), (3) the resource-thinning hypothesis (abundances decrease with trophic levels) and (4) the allometric-degree hypothesis (PEU increases with population average body mass). We use a large data base on abundances and population average body masses for 870 species distributed across 48 forest-soil communities. Previous EER studies assumed a $3/4$ power-law scaling of metabolic rates with body mass (Damuth, 1981, 1987, 2007; Nee *et al.*, 1991; Blackburn *et al.*, 1993), whereas recent metabolic-scaling studies suggested different scaling exponents, non-linear relationships and differences among phylogenetic groups (Kozłowski and Konarzewski, 2005; Meehan, 2006a; Isaac and Carbone, 2010; Ehnes *et al.*, 2011). We follow a novel approach by measuring the metabolic rates (Ehnes *et al.*, 2011) and employing specific metabolism-mass relationships for each phylogenetic group (different in exponent and intercept), which allows predicting their metabolic rates more precisely. Moreover, we follow previous studies (Mulder *et al.*, 2005, 2011) in accounting for possible effects of land use, phylogenetic group of species and feeding type on scaling relationships of abundances, PEU and biomasses with population average body masses.

8.3 Methods

We investigated invertebrate forest-soil communities along a land-use gradient to evaluate possible impacts in three different landscape blocks, the Biodiversity Exploratories (Fischer *et al.*, 2010b) located in the south, centre and north of Germany: (1) The Schwäbische Alb is a mountain range in the state of Baden-Württemberg in SW-Germany; forest types range from natural old-growth beech forests over mixed forests to managed coniferous monocultures. (2) The Hainich-Dün region is situated in the west of Thuringia; it is characterised by unmanaged pure or mixed beech forests. (3) The Schorfheide is located in the lowlands of northern Germany within the boundaries of the biosphere reserve Schorfheide-Chorin; forests range from natural old-growth beech forests with trees older than 100 years over mixed forests to intensively managed coniferous monocultures. We focused on four land-use types present in each of the landscapes: Coniferous forests as the most intensively used forest type and beech forests of different ages, i.e. young (approximately 30 years old), old (about 70 years old) and natural beech forests (about 120 years old) as increasingly more extensively used forest types. Each combination of the four land-use types with the three landscape blocks was replicated four times resulting in a total of 48 plots. On each of the 48 plots, we applied four sampling methods to include animals of different phylogenetic groups and size classes: (1) soil sampling with a small soil corer (Ø 5 cm, two samples per plot), (2) soil sampling with a large soil corer (Ø 20 cm, two samples per plot), (3) earthworm extraction using mustard solution, and (4) sieving of leaf litter. To extract all soil animals accurately we separated each soil sample into two smaller subsamples: litter and mineral soil (0 – 5 cm) yielding eight subsamples per plot (litter and mineral for two small and two large soil cores) and a total of 384 soil samples (eight subsamples times 48 plots). The small soil cores were used for extraction of the mesofauna as these animals are more likely to be fully extracted from a smaller soil sample where the organisms only need to move short distances. The large soil cores were used for extraction of the smaller macrofauna to ensure that the sample is sufficiently large. Animals were extracted from each of the 384 soil samples individually by heat using a high gradient extractor (Kempson *et al.*, 1963) as this method is the most efficient in terms of recovering high abundances (Smith *et al.*, 2008). Heat extraction ran for ten days and temperature was increased daily up to a maximum temperature of 50 °C which was kept constant for additional three days. Extracted animals were collected in ethylene-glycol solution. Earthworms were sampled using a mustard solution (100 g ground mustard seeds and 10 l of water; for detailed description see Eisenhauer *et al.*, 2008). A steel frame of 50 cm by 50 cm was placed on the ground, all litter material and small herbs were removed and 10 l of a mustard solution were poured on the ground in two rounds with a 15 min break in-between. This method is most effective at sampling endogeic and anecic earthworms (Eisenhauer *et al.*, 2008). Additionally to these extraction methods, leaf litter was sieved to capture the highly mobile larger macrofauna. On four subplots per plot, litter was sieved using a steel frame of 50 cm by 50 cm. The frame was placed on the ground and all litter inside the frame was put on a coarse sieve (1 cm mesh size) and all sieved animals were captured. Additionally, the bare ground was observed for animals emerging out of the soil until no further animal occurred for 30 min.

In combination, the four different sampling methods employed provide a comprehensive picture of the litter-soil animal community including mesofauna, small macrofauna, large, mobile macrofauna and earthworms. The animals were stored in ethanol (70 %), identified to species level wherever possible, and abundances per plot were counted for each species individually. Body lengths were measured, and body masses [mg] of soil animals were calculated via mass-length regressions (see Appendix). All samples of each plot (small and large soil cores, litter sieving and mustard extraction) were pooled to yield one sample per plot, and abundances were rescaled to

the unit of individuals per square meter. The combination of these four sampling methods enabled a quantitative sample of the animals. Although the soil represents a three-dimensional habitat, we expressed the densities relative to the surface area, because (1) the animals live mainly in the upper layers, and (2) the densities are maintained by the resource input that is proportional to surface area. However, density data could also be expressed relative to volume without changing the conclusions of our study. The resulting dataset contains species' identities, abundances per square meter and population average body masses. These measurements were obtained for each of the 48 plots independently. Animals were grouped into twelve phylogenetic groups (Arachnida, Chilopoda, Coleoptera, Collembola, Diplopoda, Diplura, Gastropoda, Isopoda, Lumbricidae, Mesostigmata, Prostigmata and Oribatida) and also into five feeding types (detritivores, fungivores, herbivores, omnivores and predators). We calculated the metabolic rates [W_{ind}] of an average individual for each species, the population energy use [W/m^2] and biomass [mg/m^2] on each plot (i.e., for each population) separately. These calculations were based on a large database on metabolic rates spanning wide ranges in body mass and temperature for eleven of our phylogenetic groups (Ehnes *et al.*, 2011). Note that the groups Coleoptera, Collembola and Diplura were aggregated into the broader group Insecta in the prior study (Ehnes *et al.*, 2011). This data base was updated with published data on metabolic rates of gastropods as the twelfth group of our analyses (Liebsch, 1928; Müller, 1943). Then, we employed the metabolic scaling equations of this prior study including specific normalization constants, allometric exponents and activation energies for each phylogenetic group to calculate the population-specific individual metabolic rate for each population on each plot independently accounting for the population average body masses of the species, the mean annual temperature of the growing season in each landscape block and the phylogenetic group (Ehnes *et al.*, 2011). Note that we could not use these laboratory measurements of metabolic rates, because the individuals of the prior laboratory study differed slightly in body mass from the population average body masses in the field that we use in the present study. To account for this difference in body mass we entered the population average body masses of the field communities in the metabolic-scaling relationships of the prior study, which yielded calculated metabolic rates. Subsequently, the energy use of the different populations (PEU) of soil animals was calculated by multiplying population-specific individual metabolic rate (the energy use of an individual) with the abundance (the number of individuals of a population) on the each plot individually. Biomass per square meter was calculated by multiplying population average body mass per plot with the abundance of the respective species on each plot individually.

Then, all data were log-transformed. With these log-transformed data we analysed the dependence of (1) population-specific individual metabolism, (2) abundance, (3) population energy use (PEU) and (4) biomass on the population average body mass of the species (also measured for each species on each plot independently) employing independent linear mixed effects models with restricted maximum likelihood (function 'lme' with 'method = REML' in the nlme package (Pinheiro *et al.*, 2009)) of the statistics program R (R Development Core Team, 2010) with exploratory (i.e., the landscape block) as a random factor. We tested for the scaling of the four dependent variables with population average body mass and how these relationships were modified by fixed factors: the land-use type of the plots and either the phylogenetic group of the species (first series of models) or their feeding type (second series of models).

8.4 Results

The samples included 870 species across twelve phylogenetic groups and 48 plots yielding a total of 5284 populations. Their body masses ranged over nine orders of magnitude from the

smallest juvenile mites (Oribatida) with a body mass of 736×10^{-9} g to the largest earthworms (*Lumbricus terrestris*) with a body mass of 11 g. The phylogenetic groups Diplura and Prostigmata rarely occurred, and they were not well-replicated across the land-use types and exploratories (the landscape blocks). Hence, we excluded their data from all analyses separating the populations into their phylogenetic groups reducing the total number of populations to 5245 in these analyses. The calculated metabolic rates increased with population average body mass with an allometric exponent of $0.824 (\pm 0.005 \text{ standard error})$. However, differences among the phylogenetic groups occurred: allometric exponents ranged between $0.552 (\pm 0.006)$ for isopods and $0.929 (\pm 0.005)$ for gastropods (Table 8.1, Fig. 1a).

Table 8.1: ANOVA results of the linear mixed effects models for the four scaling relationships of metabolism (W_{ind}), abundance (ind/m^2), population energy use (PEU in W/m^2) and biomass (mg/m^2) depending on body mass (mg), phylogenetic group (categorical) and land-use type (categorical).

	num DF	F-value	
<i>Source of Variation: metabolism</i>			
intercept	1	72765	***
body mass	1	5113512	***
phylogenetic group	9	94401	***
land use	3	3	*
body mass x phylogenetic group	9	1751	***
body mass x land use	3	1	
phylogenetic group x land use	27	1	
body mass x phylogenetic group x land use	27	1	
<i>Source of Variation: abundance</i>			
intercept	1	22418.674	***
body mass	1	19458.916	***
phylogenetic group	9	427.654	***
land use	3	3.878	*
body mass x phylogenetic group	9	21.06	***
body mass x land use	3	12.79	***
phylogenetic group x land use	27	2.365	**
body mass x phylogenetic group x land use	27	1.573	*
<i>Source of Variation: PEU</i>			
intercept	1	17860.48	***
body mass	1	858.445	***
phylogenetic group	9	543.011	***
land use	3	3.478	*
body mass x phylogenetic group	9	43.837	***
body mass x land use	3	12.511	***
phylogenetic group x land use	27	2.395	**
<i>to be continued ...</i>			

... table continued

	num DF	F-value	
body mass x phylogenetic group x land use	27	1.602	*
<i>Source of Variation: biomass</i>			
intercept	1	11881.799	***
body mass	1	4270.034	***
phylogenetic group	9	427.654	***
land use	3	3.878	*
body mass x phylogenetic group	9	21.06	***
body mass x land use	3	12.79	***
phylogenetic group x land use	27	2.365	**
body mass x phylogenetic group x land use	27	1.573	*

Asterisks indicate level of significance: *** $p < 0.0001$; ** $p < 0.001$; * $p < 0.05$. Note that the denominator (error) degrees of freedom are 5163 in all cases.

Except for gastropods, all allometric exponents were shallower than the overall exponent of 0.824. The phylogenetic signatures in these metabolic-scaling relationships were addressed in a prior study (Ehnes *et al.*, 2011) and will thus not be re-analysed in detail here. The land-use types did not affect the metabolic rates (Table 8.1, Fig. 8.1b), whereas we found a highly significant effect of the feeding types on the scaling of metabolic rates with population average body masses (Table 8.2). The allometric exponents varied between 0.759 (± 0.008) for detritivores and 0.957 (± 0.013) for omnivores (Fig. 8.1c). Abundance decreased with increasing population average body mass with an overall exponent of $-0.681 (\pm 0.006 \text{ standard error})$. The exponent varied mainly due to the phylogenetic group (Fig. 8.1d) and feeding type (Fig. 8.1f) and only marginally due to land-use type (Fig. 8.1e) as indicated by their significant two-way interaction terms with body mass (Table 1). The exponent was lowest for isopods (-0.729 ± 0.077 , Fig. 8.1d) and shallowest for gastropods (-0.021 ± 0.064). Interestingly, the scaling exponents of all phylogenetic groups except collembolans (-0.698 ± 0.072) and isopods (see above) were shallower than the overall exponent (Fig. 8.1d). This indicates that abundances decrease less strongly with population average body masses within the phylogenetic groups than across the groups. The abundance-mass relationships for the four land-use types regardless of phylogenetic group indicated different exponents for the different types with coniferous forests exhibiting the steepest exponent (-0.757 ± 0.019) and natural beech forests showing the shallowest exponent (-0.643 ± 0.018 , Fig. 8.1e). The five feeding types had different exponents: detritivores had the shallowest (-0.538 ± 0.011) and predators had the steepest exponent (-0.753 ± 0.015). Generally, the abundances of predators and omnivores were lower than those of detritivores and fungivores (Fig. 8.1f), which supports the resource-thinning hypothesis. The PEU increased significantly with increasing population average body mass with an overall exponent of $0.143 (\pm 0.007)$ (Table 8.1, Fig. 8.1g, h, i) indicating deviations from the special case of energetic equivalence. In contrast, this result is consistent with the allometric-degree hypothesis implying that PEU should increase with population average body mass. Moreover, the PEU exponents were strongly influenced by the phylogenetic group (Fig. 8.1g), the feeding type (Fig. 8.1i) and only marginally by the land-use type (Fig. 8.1h). For isopods, the PEU even decreased with an exponent of $-0.177 (\pm 0.077)$, whereas gastropods showed the strongest increase with an exponent of $0.907 (\pm 0.064)$. The old beech forests showed the highest exponent (0.175 ± 0.019), whereas coniferous stands showed the lowest exponent (0.077 ± 0.020). Interestingly, this suggests a negative relationship between

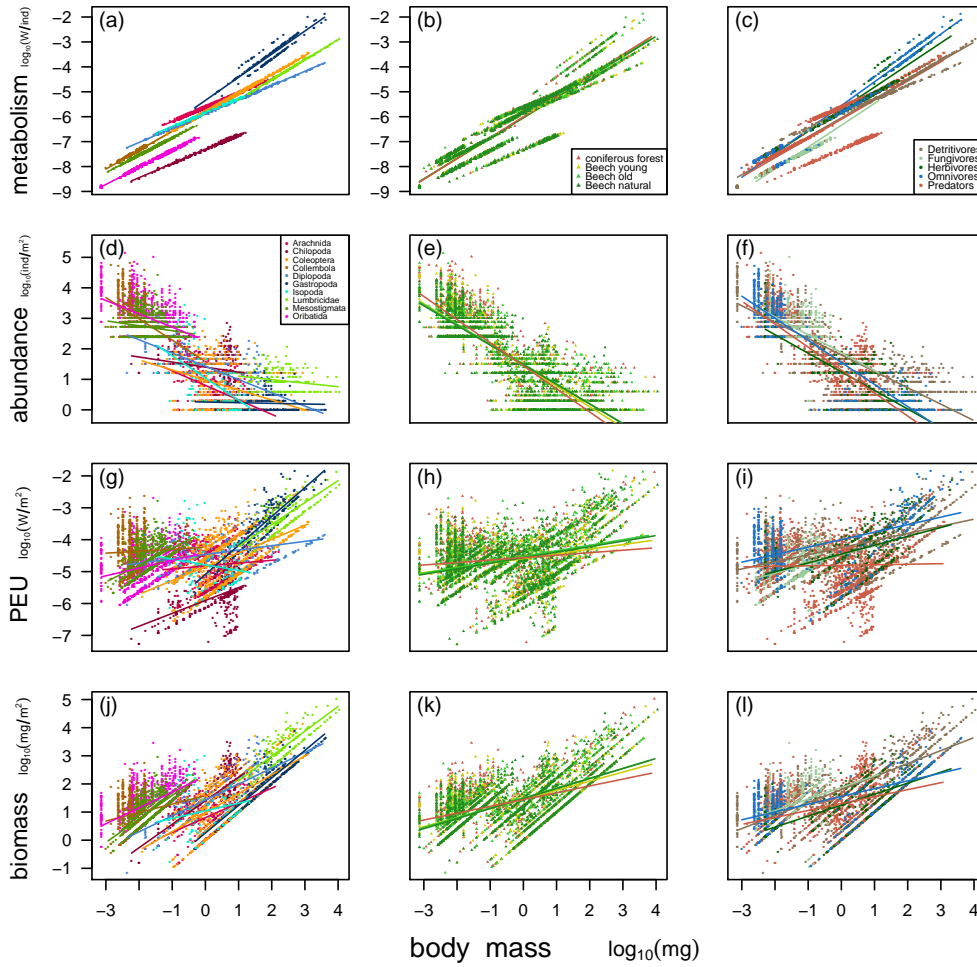


Figure 8.1: Relationships of metabolism (a–c), abundance (d–f), population energy use (g–i) and biomass (j–l) with the population average body mass across phylogenetic groups (a, d, g, j), land-use types (b, e, h, k) or feeding types (c, f, i, l).

land-use intensity and the exponent of the PEU. Considering feeding types, predators showed the lowest exponent (0.016 ± 0.015) and fungivores the highest exponent (0.289 ± 0.047) (Fig. 8.1i). Biomass increased significantly with population average body mass with an overall exponent of $0.319 (\pm 0.006)$ (Table 8.1, Fig. 8.1j, k, l) indicating a lack of biomass equivalence in these forest-soil systems. In consequence, the biomass-equivalence hypothesis has to be rejected. The biomass exponents were strongly affected by phylogenetic group (Fig. 8.1j) as well as by feeding type (Fig. 8.1l) and only marginally affected by land-use type (Fig. 8.1k). Isopods showed the lowest exponent with $0.270 (\pm 0.077)$ and gastropods the highest exponent with a value of $0.979 (\pm 0.064)$. Considering the land-use type, natural beech forests and coniferous forests showed the highest and lowest exponents with $0.356 (\pm 0.018)$ and $0.242 (\pm 0.019)$, respectively. Regarding feeding types, the detritivores showed the steepest exponent (0.462 ± 0.011) and predators the lowest exponent (0.247 ± 0.015).

Table 8.2: ANOVA results of the linear mixed effects models for the four scaling relationships metabolism (W_{ind}), abundance (ind/m^2), population energy use (PEU in W/m^2) and biomass (mg/m^2) depending on body mass (mg), feeding type (categorical) and land-use type (categorical).

	num DF	F-value	
<i>Source of Variation: metabolism</i>			
intercept	1	25638.78	***
body mass	1	38747.45	***
feeding type	4	250.81	***
land use	3	1.6	
body mass x feeding type	4	76.79	***
body mass x land use	3	0.92	
feeding type x land use	12	1.97	*
body mass x feeding type x land use	12	0.49	
<i>Source of Variation: abundance</i>			
intercept	1	40636.31	***
body mass	1	12577.57	***
feeding type	4	121	***
land use	3	1.24	
body mass x feeding type	4	58.54	***
body mass x land use	3	17.88	***
feeding type x land use	12	2.4	*
body mass x feeding type x land use	12	1.29	
<i>Source of Variation: PEU</i>			
intercept	1	10401.423	***
body mass	1	515.268	***
feeding type	4	170.201	***
land use	3	2.783	*
body mass x feeding type	4	69.974	***
body mass x land use	3	11.632	***
feeding type x land use	12	1.41	
body mass x feeding type x land use	12	1.529	
<i>Source of Variation: biomass</i>			
intercept	1	21937.201	***
body mass	1	2792.879	***
feeding type	4	121.001	***
land use	3	1.24	
body mass x feeding type	4	58.536	***
body mass x land use	3	17.876	***
<i>to be continued ...</i>			

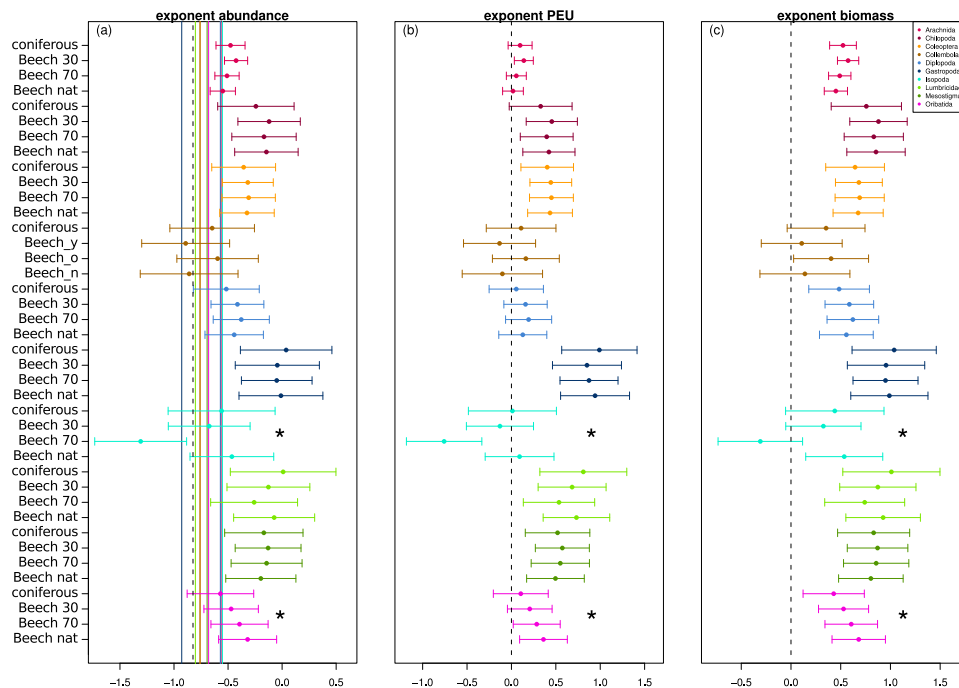


Figure 8.2: Exponents of the abundance-mass (a), the PEU-mass (b) and the biomass-mass (c) scaling relationships for all combinations of phylogenetic groups and land-use types. Error bars represent the 95 % confidence intervals. Vertical lines represent theoretical predictions according to the energetic-equivalence rule (dashed lines in panel a and b using the general metabolism-mass exponent and coloured lines in panel a using phylogenetic-group specific exponents; line colours correspond to those of the phylogenetic groups in the legend) and the biomass-equivalence hypothesis (dashed line in panel c). Land-use types are Beech 30 = young beech (approximately 30 years old), Beech 70 = old beech (about 70 years old), Beech nat = natural beech forests and coniferous forest. Asterisks indicate a significant effect of land-use type within the phylogenetic group.

... table continued

	num DF	F-value	
feeding type x land use	12	2.402	*
body mass x feeding type x land use	12	1.292	

Asterisks indicate level of significance: *** $p < 0.0001$; ** $p < 0.001$; * $p < 0.05$.

Note that the denominator (error) degrees of freedom are 5242 in all cases.

In these analyses, we have addressed the effects of land-use type and species groups (either phylogenetic or feeding type) on the scaling of the dependent variables with population average body masses separately. However, all three-way interaction terms for the analyses with phylogenetic groups were significant (Table 8.1) indicating that these effects are not independent. In contrast, in the analyses of the feeding types only for PEU a significant three-way interaction term was found (Table 8.2). Subsequently, we have carried out more detailed analyses of the allometric exponents for each of the combinations of land-use type with phylogenetic groups (Fig. 8.2).

Consistently for all scaling relationships, the differences between phylogenetic groups (differences between points of different colours in Fig. 8.2) were larger than the differences between land-use types (differences between points of the same colour in Fig. 8.2). Only isopods and oribatids were significantly influenced by land-use type (as indicated by the asterisks in Fig. 8.2), whereas all other phylogenetic groups exhibited a similar abundance-mass scaling across the dif-

ferent land-use types. These phylogenetic groups were thus responsible for the significant three-way interaction terms (Table 8.1). Subsequently, we re-visited our four initial hypotheses for these more detailed scaling relationships. As predictions for the abundance exponents based on energetic equivalence (Fig. 8.2a), we used the inverse of the overall metabolism exponent for the relationship pooling all phylogenetic groups (-0.824) and, for a more detailed view, the inverse of the metabolism exponents of each phylogenetic group to show deviations from energetic equivalence since these exponents should have the same value but different signs. Only eight of the 40 combinations (20 %) of phylogenetic group and land-use type included the predicted overall exponent of -0.824 in their confidence intervals (dashed line in Fig. 8.2a). However, the phylogenetic group-specific predictions (inverse of the allometric exponent of the metabolism-mass relationship for the same phylogenetic group) were included in the confidence intervals in seventeen cases (42.5 %, see Fig. 8.2a for groups). In consequence, only the same 42.5 % of combinations of phylogenetic group and land-use type corroborated the energetic-equivalence rule, because they included the prediction of zero (energetic equivalence) in their confidence intervals (see Fig. 8.2b). Regarding the scaling of biomass with population average body mass, only six (15 %) of the more detailed relationships as combinations of phylogenetic group and land-use type included the predicted exponent of zero in their confidence intervals (Fig. 8.2c). Together, these results suggest that the more specific results for individual combinations of phylogenetic groups and land-use types (Fig. 8.2) differ from those obtained by assuming general scaling relationships (Fig. 8.1), but they also support the overall conclusions that energetic equivalence and biomass equivalence are rarely found in nature, whereas most abundance patterns are consistent with the energy-thinning hypothesis, and the positive PEU exponents support the allometric-degree hypothesis.

8.5 Discussion

In this study, we addressed (1) the scaling of metabolic rates, abundances, the total population energy use (PEU) and biomasses of soil organisms with their population average body masses and (2) how these scaling relationships vary across ten phylogenetic groups, five feeding types and four forest land-use types across three landscape blocks (i.e., 'Biodiversity Exploratories'). Our results corroborate the general pattern that the metabolic rate of an individual and the abundance of the population (i.e., the density of individuals) increases and decreases, respectively, with the population average body mass. However, our results show variable scalings of population energy use. While the special case of the energetic-equivalence rule (EER), where the metabolism-mass and abundance-mass scalings cancel out is found in 42.5 % of the cases, in most cases (57.5 % of the combinations of land-use type and phylogenetic group) the two scaling exponents did not cancel out thus preventing constant population energy use across populations of different average body masses. Decreases in abundance with trophic level are consistent with the resource-thinning hypothesis. The mostly positive exponents of the PEU-mass relationships support the allometric-degree hypothesis (systematic changes in in- and out-going links with body masses cause positive PEU scaling). However, both, resource-thinning and allometric-degree hypotheses, are unable to predict the whole range of PEU scaling exponents found in this study, especially those close to zero, while the body-size dependent consumer-resource model (DeLong and Vasseur, 2012a,b) would allow for such a huge range in scaling relationships. Yet, this consumer-resource model requires additional parameters that are not easily determined for a large dataset with many different phylogenetic groups as well as feeding types. Moreover, the prediction of the biomass-equivalence hypothesis that the population biomass should be independent of population average body masses is also inconsistent with our results as all except one combination of land-use type and phyloge-

netic group showed a positive exponent and only 15 % of these combinations included zero in their confidence intervals. These general conclusions hold for the large majority of combinations of phylogenetic groups, feeding types and land-use types. Hence, the large species of the forest communities accumulated abundance and biomass, which caused increasing PEU with increasing body mass of the species. This stresses the important role of large-bodied species in the energetic functioning of natural communities. In contrast to previous studies on energetic equivalence, we did not assume a general $3/4$ power-law scaling of metabolic rates with body masses, but employed empirical scaling relationships for each of the phylogenetic groups. This was motivated by previous studies (Meehan, 2006a; Meehan *et al.*, 2006; Isaac and Carbone, 2010; Ehnes *et al.*, 2011) suggesting that differences among phylogenetic groups cause different metabolic scaling exponents. Assuming a $3/4$ power-law scaling of metabolic rates (Peters, 1983; Brown *et al.*, 2004) instead of the differing, empirically-determined exponents for the specific phylogenetic groups (Ehnes *et al.*, 2011) would have led to an overestimation of metabolic rates for small individuals and an underestimation for the large ones. Utilization of the $3/4$ power law as a prediction for the abundance scaling would have increased the number of combinations of feeding type and land-use type that include the inverse in their confidence intervals from 20 % (include inverse of overall exponent -0.824 in confidence interval) to 22.5 % (include $-3/4$ in confidence interval), which in turn would have led to incorrectly supporting energetic equivalence in more cases.

The overall exponent of -0.681 we found for the general abundance-mass scaling is steeper than those of many prior studies on invertebrates (-0.54 , Peters and Wassenberg, 1983), soil invertebrates (-0.2 to -0.6 ; Mulder *et al.*, 2011) and natural aquatic rock-pool communities (-0.32 , Hayward *et al.*, 2009), but shallower than those of estuarine food webs ranging from -0.78 to -0.91 (Hechinger *et al.*, 2011). On the one hand, this illustrates that the decrease in abundance with increasing population average body mass documented in our study is a general pattern. On the other hand, this also documents substantial differences in scaling exponents between communities and species groups suggesting that there is no universal scaling relationship. In our analyses, we have addressed whether such differences could depend on the land use of the ecosystem, phylogenetic groups or feeding types of the species included, which will be discussed below. We characterized all species according to their phylogenetic group as they have strong impacts on the allometric scaling of metabolism (Ehnes *et al.*, 2011) and also capture many aspects of biological organization including morphology, behaviour and feeding ecology. These differences among phylogenetic groups should thus also cause differences in abundances even for populations of the same body mass. In our analyses, abundance decreased in all phylogenetic groups with increasing body mass. Phylogenetic group as well as land-use type affected the abundance scaling significantly and interactively, but the effect of land-use type was smaller than the effect of the phylogenetic group. Considering each phylogenetic group separately showed that only oribatid mites and isopods were significantly affected by the land-use type and thus created the significant interaction term. In contrast to isopods, the abundance-mass exponent of oribatid mites became shallower from coniferous to beech forests showing that species especially of small sizes had highest abundances in the coniferous forest (smaller body-mass range than in the other land-use types). This may be an indirect effect of the thicker litter layers in coniferous forests (Maraun and Scheu, 2000), where the resource input per surface area is enabled to accumulate as the low soil pH causes low abundance of earthworms that process the litter in other ecosystems (Eisenhauer, 2010). This thicker litter layer provides more habitat volume for all micro-invertebrates and a higher resource density for litter-feeding oribatid mites, which may explain their higher abundance in coniferous forests. Our interpretation of the differences between the ten phylogenetic groups corroborates prior conclu-

sions that they may be caused by their different diets (Silva and Downing, 1995) or trophic levels (Long *et al.*, 2006; Hechinger *et al.*, 2011).

Thus, we also classified the different species according to their feeding types. These additional analyses showed a similarly steep decrease of abundances with population average body mass for all feeding types. The abundances generally decrease with trophic levels: detritivores and fungivores showed the shallowest decrease in abundance with population average body mass, herbivores had an intermediate exponent and predators and omnivores showed the steepest decreases (Fig. 8.1f). One potential explanation might be that the abundances of small decomposers and fungivores such as collembolans are lowered by strong top-down control by predators and omnivores. In contrast, the large-bodied decomposers and fungivores such as many diplopods and isopods are usually well defended against predation by their hard exoskeletons. The resulting decrease in top-down control with increasing population average body mass of decomposers and fungivores likely explains their shallower decrease in abundances with body masses. This explanation is highlighting the potential importance of allometric-degree distributions in shaping the abundance patterns of the community, which will be discussed in more detail below. This result is supporting prior conclusion that mixing of trophic levels blurs abundance-body mass relationships by thinning of resources with increasing trophic levels (Brown *et al.*, 2004; Hechinger *et al.*, 2011). As an exception to this pattern, however, the abundances of herbivores on the second trophic level of the food web were as low or lower than those of predators and omnivores that compose the higher trophic levels. With the exception of herbivores, our results thus support the resource-thinning hypothesis stating that resource availability and abundances should decrease with trophic levels.

We found energetic equivalence in 42.5 % of the combinations of phylogenetic group and land-use type as in the other cases abundance and metabolic rates did not follow inverse scaling relationships with population-averaged body masses in our study, which caused increasing PEU in the majority of combinations of land-use types with phylogenetic groups. This positive scaling of PEU with population average body mass is consistent with a growing number of studies on birds and mammals (Damuth, 1991), birds, mammals and fish (Brown and Maurer, 1986), aquatic meio-invertebrates (Hayward *et al.*, 2009), eusocial insects (DeLong, 2011) and marsupials (Munn *et al.*, 2013). However, it deviates from a prior study on soil micro- and macro-arthropods in an aspen-conifer stand showing the pattern of energetic equivalence (Meehan *et al.*, 2006). This is surprising because the latter study is the most similar concerning the soil species groups included. Potential explanations for this disparity include the smaller size range covered by the abundance-mass data, and the application of metabolic models that are pooled across phylogenetic groups (Meehan *et al.*, 2006). A previous study (Ehnes *et al.*, 2011) clearly showed that phylogeny has a significant effect on metabolism even after accounting for population average body masses. Consistently, our analyses demonstrated that including phylogeny into the statistical models improved the predictions of abundance and population energy use substantially (shown by lower AIC values of the phylogenetic model compared to the linear model). Even though body mass remained the most important factor determining metabolic rates, abundances and PEU, these relationships were modified by the phylogeny of the species.

The scaling of PEU with population-averaged body masses also differed between the land-use types: it was shallowest in the coniferous forests and the scaling exponents increased with increasing age of the beech forests with natural beech forests showing the steepest scaling relationships. Thus, human land use affects the energy partitioning in soil-animal communities: more intensively used (more strongly modified) forests show a shallow PEU scaling (more evenly distributed energy use), which steepens (becoming asymmetrically distributed) with the transition to more natural conditions and longer time periods since the last disturbance by cutting trees (when comparing

the beech forests). More precisely, the more natural and old-grown forests developed into a state in which the populations with large-bodied individuals dominated the energy processing of the communities.

One explanation for the consistent deviations of our and prior studies from the pattern of energetic equivalence is that this pattern might not apply to entire communities with multiple trophic levels, where organisms do not share a common resource (Jennings and Mackinson, 2003). Hence, we repeated our analysis with the species sorted into feeding types. This analysis supported the results of phylogenetic-group analysis. Especially, fungivores and herbivores showed strong increases in PEU with population average body mass. These increases were driven by the high abundances of larger species in the groups of coleoptera and gastropoda that are often outside the feeding range of predators (Brose *et al.*, 2008).

Our results demonstrate that the idea of biomass equivalence (Polishchuk, 1994) should be rejected for a diversity of north temperate soil invertebrates. However, our results show a wide range of PEU scalings which sometimes conform and mostly do not conform to the pattern of the energetic equivalence (Damuth, 1981; Nee *et al.*, 1991). Furthermore, they document abundance, energetic and biomass patterns that are in most cases consistent with the allometric-degree hypothesis that is derived from food-web theory and could possibly be explained by applying body-size dependent consumer-resource models (DeLong and Vasseur, 2012a,b). Food-web ecologists have documented a variety of trivariate patterns how abundances, body masses and trophic links of populations are related in the complex networks of natural communities (Cohen *et al.*, 2003; Jonsson *et al.*, 2005). Generally, the allometric-degree relationships characterizing the correlation between the number of out-going links to consumers and in-going links from resource populations with population average body masses are determining the strengths of the top-down and bottom-up links surrounding a population (Brose *et al.*, 2005; Berlow *et al.*, 2009; Rall *et al.*, 2011), which should have feedback effects on its abundance. This allometric-degree distribution exhibits systematic patterns: the number of links to consumers and resources of a population decreases and increases, respectively, with body mass (Otto *et al.*, 2007; Digel *et al.*, 2011; Riede *et al.*, 2011). In consequence, with increasing body mass the availability of alternative resources increases, and the risk of top-down control by predators decreases. These two beneficial effects of increasing body mass should lead to higher abundances and positive deviations of abundance-mass and population-energy use relationships from energetic equivalence. Our results generally confirm these expectations thus supporting the allometric-degree hypothesis in most cases.

Moreover, the systematic relationships of the allometric-degree distribution with the population average body masses are important drivers of community stability (Brose *et al.*, 2006b; Rall *et al.*, 2008; Heckmann *et al.*, 2012). Accordingly, neither constant PEU nor constant biomass may necessarily be a prerequisite of community stability. Instead, the size structure of natural communities that promotes stability might simultaneously yield a positive relationship between PEU and population-averaged body mass just as between biomass and population-averaged body mass.

8.6 Conclusions

Reviewing the ideas of biomass and energetic equivalence using field data of soil-inhabiting invertebrates from different land-use types led to a refusal of these patterns as they were seldom found. Thus, these ideas are unable to predict the energy partitioning among co-occurring species whether they share a common resource or not. As metabolism and abundance scaling with population average body mass were not directly inverse the resulting population energy use increased with increasing body mass of the species instead of being equal. Therefore, our results support two

more recent alternatives to predict abundances, biomasses and population energy use: consistent with the resource-thinning hypothesis abundances decreased with trophic level and corroborating the allometric-degree hypothesis the population energy use increased with the population average body mass. However, even these models are unable to fully predict the whole range of energy partitioning among co-occurring species, and this gap might be filled by body-size dependent consumer-resource models (DeLong and Vasseur, 2012a,b). Our results also suggest that human land use can affect these patterns how biomasses and population energy use are distributed across size classes. Together, these results call for a closer integration of approaches addressing abundance or energy-use patterns with food-web theory.

8.7 Acknowledgements

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9 General Discussion

The chapters of my thesis elucidate different aspects of metabolic scaling, its consequences and influencing factors. Organisms as well as the assemblages they form (e.g., food webs, communities and, ecosystems) are highly organized systems. A basic feature responsible for these highly organized structures and for determining the rate of energy transformation and other energy related steps is the metabolic rate. Ecology can be seen as governed by metabolism and may be described via metabolic constraints (Sibly *et al.*, 2012). Especially in times when natural ecosystems are threatened by severe changes, like climate change, changes in human land use or habitat loss, assessment of possible consequences of these changes becomes increasingly important. Enhancing current food-web models with parameters that shape the energy partitioning in a community will allow more precise descriptions of natural systems (Wall *et al.*, 2010; Sibly *et al.*, 2012). I focused on questions of allometric and temperature effects on metabolic demand, consumption and assimilation efficiency and factors that influence them. Furthermore, I provide a detailed description of the constraints of metabolic rates. Together, this enables a prediction of consequences for entire communities.

Body mass as an important determinant for metabolism, as well as the relevant effect of temperature have been acknowledged (Rubner, 1883; van't Hoff, 1884; Arrhenius, 1889; Kleiber, 1947). However, not until recently a general law for metabolism that includes both effects has been proposed (Gillooly *et al.*, 2001; Brown *et al.*, 2004). In my thesis, I emphasize the importance of body mass and temperature for the determination of metabolic rate. Furthermore, I stress the importance of parameters depending on metabolism for structuring entire communities (e.g., energetic demand, ingestion efficiency, assimilation efficiency and energy use of individuals and populations).

In the first four studies of my thesis (Chapter 3 to 6), I could show that metabolic rates generally increase with increasing body mass of the organism as well as with its body temperature, matching the expectations of metabolic theory. Increasing body mass as well as increasing temperature will amplify the metabolic demand of an organism. However, the scaling clearly deviated from the proposed $3/4$ power-law scaling of body mass and the activation-energy range predicted by the Metabolic Theory of Ecology (Brown *et al.*, 2004). For a detailed study of metabolic rates, I compiled a dataset consisting of 3661 measurements of basal metabolic rate, body mass, measurement temperature and phylogenetic information of the organisms (Chapter 5). These data, ranging over several terrestrial invertebrate groups and a large body-mass as well as temperature range, exhibited strong deviations. These deviations point to the limited ability of this theory to predict the metabolic-rate scaling of invertebrates and to factors influencing these scalings that do not relate to body mass.

However, as metabolism generally increases with temperature, it puts pressure on an organism to increase its energetic consumption. With the experiments in chapter 3 and 4, I demonstrated this increased energetic demand with increased temperature. The experiments in chapter 3 corroborate the effect of the prey size on the consumption by causing a hump-shaped consumption rate in relation to predator-prey body-mass ratio (Vonesh and Bolker, 2005; Brose *et al.*, 2008; Kalinkat *et al.*, 2013b). Furthermore, I could show that handling time and attack rate and therefore also the predatory consumption is affected by prey mobility (Chapter 4). This effect of rising temperature on the movement speed will make it harder for predators, especially those feeding on resident

prey to balance their metabolic demand. In a similar direction points the study on assimilation efficiencies of organisms utilizing different resources (Chapter 6). In this chapter, I demonstrated that assimilation efficiency depends on the consumer type (e.g., herbivore, detritivore, predator) and the effects of body mass and temperature differ between them. For predatory organisms assimilation efficiency is generally high and influenced neither by body mass nor by temperature. Detritivores and herbivores generally show lower assimilation efficiencies, which increase with rising temperature for herbivores. This result points to the importance of accounting for the feeding type of the considered organisms.

However, there are even more factors influencing these metabolic-scaling relationships that are neither depending on the body mass of an organism nor its temperature and which are not considered in the Metabolic Theory of Ecology. The large dataset on invertebrate metabolic rates exhibited a curved relationship between basal metabolic rates and individual body mass, a pattern so far only known for mammals (Hayssen and Lacy, 1985; Kolokotronis *et al.*, 2010). Adding a polynomial to the model removed the curvature in the data for mammals as well as for my data on invertebrates. Yet, such curved deviations may point to a causal factor that does not relate to body mass (Glazier, 2013). Consequently, I applied another model which regarded the phylogenetic groups of the species separately, thereby not only removing the curvature, but also providing an explanation for the observed deviation. This phylogenetic model had the highest quality (Chapter 5) and furthermore emphasized the importance of accounting for the phylogenetic signal, a necessity that has recently been asked for (Chown *et al.*, 2007; Irlich *et al.*, 2009; Kozłowski and Konarzewski, 2005; Meehan, 2006b; White *et al.*, 2007; Isaac and Carbone, 2010). Hence, distinguishing between phylogenetic groups is of great importance for understanding results of metabolic scaling studies. As these different effects of various groups may have profound consequences on the interaction strength between a consumer and its resource. The two broadly based laboratory studies of this thesis (Chapters 5 and 6) point to the severe influence of factors like feeding type or phylogenetic group on metabolic rates. Thus, differentiating investigated species regarding their feeding type or phylogenetic group is particularly advisable for sound interpretation of studies on allometric scaling.

Therefore, metabolic constraints on species assemblages should be viewed separately for the various groups as the effects on them may differ severely. In a field study, I concentrated on detritivore oribatid mites (Chapter 7). Within this specific phylogenetic group based on one resource, the parameters affecting energy uptake may impair the ability to balance the metabolic need, thereby altering the community assembly. Hence, the quantity (or quality) of the consumed resource can have profound effects. Oribatid mite communities are mostly influenced by the provision of food resource, which is an abiotic parameter (Chapter 7). The amount of accessible resource affects the oribatid mite assembly not only regarding their population density, but also changes the proportion of parthenogenetic species and individuals. The proportion of asexually reproducing species and individuals was higher in habitats with ample resources, hence corroborating the predictions of the Structured Resource Theory of Sexual Reproduction (Scheu and Drossel, 2007). This theory regards resource availability as the main factor responsible for the mode of reproduction. In times of lessened resource competition parthenogenetic species are able to outgrow sexual ones, while they suffer from inferior modulation abilities, especially, when resources are scarce. These oribatid mites are a distinct example of community variations of sexual reproduction driven entirely by the effect of resource availability and the resulting competition (Chapter 7).

However, natural systems consist of many feeding and phylogenetic types, mainly structured by feeding interactions. These interactions may then again be differently affected by their metabolic constraints besides body mass and temperature, resulting in complex consequences. The studies I

presented in chapter 3 and 4 yield detailed information on specific predator-prey pairs, but most importantly provide results that are transferable to future scenarios of climate change. Thus, studies like these allow predicting changes of food-web structure due to warming. These chapters demonstrate that warming imposes an increased metabolic demand on predators which may result in increased feeding to compensate it or, if unable to fulfill it, even starvation. Starvation of predators would be caused by their inability to balance the increased metabolic demand which is furthermore modified by the body size of the prey (Chapter 3) and also by prey mobility (Chapter 4). Yet, the long term effects on a whole food web or on ecosystem functions are still more complex.

The effect of a predator on a prey population might differ due to the observed time scale. Generally, interaction strength is calculated by the log ratio of prey abundance in presence of the predator and prey abundance in the absence of the predator. For short-term interaction strengths the reactions primarily depend on the ingestion rates of the predator, while the numerical responses in predator and prey abundance is ignored. However, the long-term interactions are also influenced by prey growth and abundance (Berlow *et al.*, 2009). A population dynamic model of prey and predator density (Yodzis and Innes, 1992; Vasseur and McCann, 2005; Rall *et al.*, 2008) provided the basis for calculating long term interaction strengths. Furthermore, known relationships can be used to infer changes in metabolism, ingestion, growth and abundance. All these parameters are supposed to scale with body mass and with temperature, determined by the activation energy (Gillooly *et al.*, 2001; Brown and Gillooly, 2003; Meehan, 2006a; Brown *et al.*, 2004).

Due to the resulting lower long-term per capita interaction strengths of a predator on its prey, the food web might be rendered more resilient, hence returning to the same equilibrium density after a small perturbation. Furthermore, warming may result in higher intrinsic population stability (less fluctuating densities) caused by the lower ingestion efficiencies and, additionally, higher extinction risks of predators due to starvation. A broader approach, moving from these two studies on predator-prey interactions to a more general view of consumer-resource interactions, was tested in Chapter 6. As previously described, metabolic rate is influenced by body mass and temperature, but these dependencies are greatly modified by the feeding type of the organism. With the results of this study, I could show that these feeding types differ in their assimilation efficiencies. The combination of the large dataset on metabolic rates and the dataset on assimilation efficiencies additionally enabled the calculation of maintenance consumption (i.e. energy required to balance life maintenance, Chapter 6). Generally maintenance consumption increases with warming, hence corroborating the findings for predators of Chapter 3 and 4. Contrasting this, warming may result in stronger increases in consumption rates than in metabolic rates for detritivores and herbivores causing a net energy gain and higher population densities for these two feeding types. Thus, these studies generally show the importance of different factors (e.g., phylogenetic affiliation, feeding type, resource parameters) on the interactions structuring complex food webs of natural ecosystems. Furthermore, these laboratory studies allow predictions of warming effects on these feeding interactions. Hence, the results point to the importance of including factors like phylogenetic affiliation, feeding type, resource size, mobility, and quantity besides body mass and environmental temperature for predicting the effects of resource and demand on the structure of natural systems. All these parameters that affect individual metabolic rate and therefore, the interaction between a consumer and a resource may – if put altogether – have profound effects on the structure of the whole food web.

Yet, more precise descriptions of energy use in natural soil systems are scarce. I proceeded to a study where I applied the previously determined metabolic-scaling parameters on data of natural systems. Using field data of soil-inhabiting invertebrates from different land-use types (Chapter 8) and complementing these with previous findings on metabolic rates (Chapter 5) enabled

me to test hypotheses of energy and biomass distribution. The prediction of biomass equivalence (Polishchuk, 1994) was not confirmed for these field data and it was impossible to predict the distribution of biomasses in natural ecosystems. I also refused the energetic equivalence (Damuth, 1981; Nee *et al.*, 1991) as my results were generally quite ambiguous and most relations between energy use of the populations and body mass did not suit to this predicted pattern. This inability to correctly predict energy partitioning was independent of shared resource use among the species. Scaling of metabolism, abundance and biomass with population average body mass were not directly inverse, thereby causing increasing energy use with body mass instead of showing a body-mass independence. Yet, the observed scaling relationships support more recent, alternative predictions. Abundances decreased with trophic level, thus corroborating predictions of the resource-thinning hypothesis (Brown and Gillooly, 2003). Furthermore, population energy use increased with the population average body mass which is consistent with the allometric-degree hypothesis (Otto *et al.*, 2007; Digel *et al.*, 2011). With increasing body mass the availability of alternative resources increases just as the top-down control by predators decreases. This would produce the observed biomass accumulation for organisms of large body mass causing positive deviations of abundance-mass and population-energy use relationships. While the documented patterns of abundance, energetic and biomass distribution are consistent with these hypotheses derived from food-web theory. These are even unable to explain the whole range of energy partitioning among co-occurring species. The body-size dependent consumer-resource model (DeLong and Vasseur, 2012a,b) might be able to fill this gap by allowing for a huge range in scaling relationships. However, this model requires the determination of even more parameters. Nevertheless, positive population energy use and biomass scaling in relation to increasing average body mass may be a prerequisite of community stability. Just as much as allometric-degree distributions are important drivers of it (Brose *et al.*, 2006b; Rall *et al.*, 2008; Heckmann *et al.*, 2012). Hence, in natural communities the structure of body masses that favours stability might, at the same time, produce positive population energy use and biomass scalings with population-averaged body mass. Furthermore, the results of this study suggest that human land use can affect the distributions of biomasses and population energy use across size classes. Together, these results call for a closer integration of approaches addressing abundance or energy-use patterns with food-web theory.

The questions I asked in the beginning of my thesis have been answered. Metabolic rate and therefore the energetic demand of an organism is jointly determined by its body mass and temperature. Yet allometric models are not able to correctly predict the whole spectrum of observed relations. This points to the importance of causal factors influencing the relationship between metabolism, body mass and temperature. I have shown that models including phylogenetic information are of superior quality and allow precise predictions. The energetic constraints imposed by temperature on handling time and capture rate, the resulting interaction strengths as well as the varying assimilation efficiencies of different feeding types will have profound effects on animal assemblages. Communities should be more resilient, however, predators might be more prone to extinction following starvation. In my field studies, I demonstrated that energetic demand of individuals and the resulting competition is able to affect the species assemblage by changing not only the density, but also the proportion of reproductive mode. With my final study, I could show that these previously determined energetic restrictions shape the distribution of animals in natural systems. Neither biomass nor energy is equally distributed across the differently sized organisms. Furthermore, these distributions can be modified by human land use.

The chapters of my thesis suggest that predicting the consequences of climate change may be very complex and stress the need to integrate several levels, from individuals and populations to whole ecosystems and their functions. While determining effects of warming onto species interac-

tions is a difficult task, their transferable results may provide the mechanistic link between warming and ecosystem functions (Hughes, 2000). The possible starvation of predators with warming and thus, their increased risk of extinction might be counteracted by increased primary productivity of ecosystems because of increasing CO₂ levels (Emmerson *et al.*, 2005). Furthermore, detritivores may cause accelerated decomposition rates (Chapter 6) and affect carbon and nutrient turnover rates under warming and thus, possibly causing a feedback to global climate change. Such effects of global warming need to be reconciled to achieve accurate forecast models.

Allometry has proven to be a useful tool in analysing and predicting feeding interactions (Chapter 3 and 4, Kalinkat *et al.*, 2013b). The allometric approach allows to detect regularities in the relative changes of any depending parameter in relation to body mass (Glazier, 2013). Deviations from such general scaling relationships may point to parameters that affect these scalings (Chapter 5). However, even though allometric relationships are able to explain a great proportion of the observed patterns within food webs, they are no panacea for solving all aspects of complex systems (Schneider *et al.*, 2012). The huge dataset on the metabolic rates of invertebrates allowed the detection of phylogeny as an important factor, that affects the allometric scaling (Chapter 5). However, there are even more factors than phylogeny that have to be integrated when regarding the consumption effects of species like feeding type or human land use (Chapter 6 and 8). Then finally, such integrated models will allow successful predictions of links between predator and prey, trophic level and hence, the structure of complex food webs. Moreover, my thesis provides insights into the energy demand at various levels that can hardly be investigated directly.

In conclusion, my thesis provides information on how climate change might affect predators consuming different prey and the different effects of land use on different (phylogenetic or feeding type) groups. Thus, the results of my thesis add to the studies concerned with the possible effects of climate change on food-web stability. Furthermore, the allometric scalings controlling metabolic need, feeding interactions (capture rate, handling time), and assimilation efficiency determined in this thesis, can be integrated into dynamic models. Hence, this will improve food-web theory and dynamic models of soil habitats as has already been shown for an aquatic habitat (Boit *et al.*, 2012). Such enhanced models may improve decisions for conservation and management of these habitats.

To put my main findings into a nutshell: Allometric theory has proven useful for predicting metabolic rates, consumption rates, assimilation efficiencies. However, including effects of temperature (Chapters 3 and 4) and also phylogenetic or consumption type (Chapters 5, 6 and 8) thoroughly enhances its predictive power.

Approaches integrating physiology of the consumers allow for an enhanced understanding of their energetic demand on the individual (Chapters 3, 4, 5 and 7) as well as on the community level (Chapters 6 and 8).

10 General Summary

During my PhD, I focused on metabolic rates of litter- and soil-dwelling invertebrates, parameters that exert influence on them or are influenced by metabolism. I started with consumption experiments, comparing the estimated amounts of energy taken up with the energetic demand estimated via metabolic-rate measurements. These experiments showed that, generally, ingestion as well as metabolic rates increase for beetle and spider species with increasing temperature. However, while ingestion increased only slightly with increasing temperature, metabolic demand increased strongly thus reducing the ingestion efficiency with increasing temperature (Chapter 3). This might have strong effects on the whole food web in a natural system. Populations might depict a higher stability but on the other hand, due to the lowered ingestion efficiencies, predators might become more prone to starvation and even extinction (Chapter 3). In the next study again metabolic rates and consumption rates (functional responses) were compared across a temperature range, but with a different focus. Here, ground beetles in combination with a more resident and a mobile prey type were used to examine the different effects of temperature on these predator-prey pairs (Chapter 4). Generally, increasing temperature led to an increase in metabolic rate, a decrease in energetic efficiency and a decrease in handling time. However, the effect of increased temperature on attack rate differed for the two prey types. For mobile prey the attack rate increased with temperature, while it was not affected for the more resident prey. This implies that an increase in temperature might stabilize population dynamics. Since the first two studies had shown that the metabolic rate of different organisms is differently affected by body mass and temperature, I focused on the effects of body mass and temperature on metabolic rates for my next study. Therefore, I compiled a large dataset on metabolic rates of mainly soil-dwelling invertebrates by performing measurements of respiration and by literature research (Chapter 5). With this dataset I tested a very prominent theory (Metabolic Theory of Ecology) on how metabolism depends on body mass and temperature. As this theory uses a fixed three-quarter allometric exponent (fixed body-mass dependence), which the results of chapter 3 and 4 proved not to be useful, I also used a relaxed version (unrestricted body-mass and temperature dependence). Finally, I tested a model, similar to the relaxed one but incorporating phylogenetic information, thus each phylogenetic group would be fit independently. This phylogenetic model obtained the highest quality thus emphasizing the importance of accounting for the phylogenetic affiliation of an organism (Chapter 5). Thus, the results of this study allow a conservative energy-demand estimation for different terrestrial invertebrate species.

Having seen that metabolic rates of organisms as well as their consumption rates increase with temperature, the question remains how the assimilation efficiencies change. The effect of temperature on the assimilation efficiencies of different consumer types (carnivore, detritivore, herbivore) had not been studied yet. For filling this gap, a database on assimilation efficiencies for different consumer types was used and the database on metabolic rates (Chapter 5). Metabolic rates increased with temperature for all consumer types while the assimilation efficiency only increased for herbivores and was independent of temperature for the other two consumer types (Chapter 6). From this it follows that maintenance consumption rates increase with temperature, however the amount of increase differs between the consumer types. For carnivores the metabolic rates increased stronger with increasing temperature than did their consumption rates, which might lead to starvation. Accelerated consumption rates of detritivores could lead to increased turnover rates and might result in increasing biomass of the populations (Chapter 6).

Aside from using the metabolic-rate data with other laboratory data, it may also provide information on the energy distribution in natural systems while its direct measurement is not possible. For testing the Structured Resource Theory of Sexual Reproduction (SRTS) abundance and body-mass data on oribatid mites in differently used habitats were used to estimate the metabolic demand of the oribatid community (Chapter 7). The SRTS suggests that limited resources favor sexually reproducing consumers while ample resources would be superiorly exploited by parthenogenetically reproducing species. Abundance and metabolic demand served as a surrogate for resource supply. The data supported the predictions of the SRTS as in habitats with a high amount of resources (as indicated by high population densities or high metabolic rates) parthenogenetic reproduction occurred in a higher proportion (Chapter 7). Finally, I used the metabolic parameters to estimate the energetic demand of soil-invertebrate communities in differently used forests. Abundances and body masses (via body lengths) were obtained by field sampling. Based on these data I calculated the metabolic demand, the population energy use (PEU) and the biomass of the different species present (Chapter 8). Thus, this dataset allowed testing different patterns that have been described to apply to energy or biomass distribution in a community. The energetic equivalence is observed if populations of small and large organisms use the same amount of energy. The biomass equivalence on the other hand states that the biomasses are independent of body mass. I compared the results with these patterns. Generally, metabolic rates increased with body mass of the species and abundances declined independently of phylogenetic group, land-use type or feeding type. Biomasses increased in all cases thus clearly rejecting the biomass-equivalence hypothesis. Population energy use mostly increased with body mass. Furthermore, a more detailed analysis (phylogenetic groups separately in each land-use type) showed that the energetic equivalence is sometimes met and sometimes not. However, the data support predictions of the resource-thinning hypothesis, which states that abundances should decrease with trophic level, and mostly the allometric-degree hypothesis stating that PEU should increase with increasing body mass. Thus, predictions from food-web theory regarding the structure of natural communities are met and further integration of metabolic and food-web theory might help to explain the natural community structures.

11 Zusammenfassung

Im Verlauf meiner Dissertation habe ich mich mit den verschiedenen Aspekten des Metabolismus von wirbellosen Tieren und dessen Beeinflussung durch andere Faktoren beschäftigt. Beginnend mit vergleichenden Untersuchungen der Energieaufnahme und des Energieverbrauchs bei verschiedenen Wirbellosen, besonders im Hinblick auf unterschiedliche Umgebungstemperaturen, habe ich mich mit den unterschiedlichen Parametern beschäftigt, die die Fraßbeziehungen zwischen Räuber und Beute modifizieren können, sowie deren Auswirkungen auf die Energiebilanz des Räubers. Welchen Einfluss hat eine Temperaturerhöhung auf das Fraßverhalten des Räubers und wie verändert sich dabei seine Effizienz? Diese Frage und die, der daraus resultierenden Konsequenz für die Stabilität von Nahrungsnetzen konnten, mit Hilfe von Fraßversuchen bei unterschiedlichen Temperaturen geklärt werden (Kapitel 3). Daran anschließend rückten die Parameter der funktionellen Antwort (Fraßverhalten des Räubers in Abhängigkeit von der Beutedichte, engl: functional response) und deren Temperaturabhängigkeiten in den Fokus. Hierbei zeigte sich, dass die Fangrate (Fangen und Fressen der Beute, engl.: capture rate) abhängig von der Mobilität der Beute sich bei steigender Temperatur unterschiedlich verhält (Kapitel 4). So steigt die Fangrate mit der Temperatur für mobile Beutetiere, während sie für stationäre Beutetiere gleich bleibt. Zusammen mit einem durch die Temperatur erhöhten Stoffwechsel ergeben sich für einen Räuber daraus eine abnehmende Energieeffizienz, was im Extremfall die Deckung des Nahrungsbedarfs unmöglich machen könnte.

Da die Wirkung der Temperatur auf die bisher untersuchten Wirbellosen unterschiedlich ausfiel, habe ich mich in einer weiteren Untersuchung auf die Effekte von Körpermasse und Temperatur sowie der phylogenetischen Zugehörigkeit auf die Stoffwechselraten beschäftigt. Mit Hilfe von Respirationmessungen und Literaturrecherche entstand ein großer Datensatz, der die separate Ermittlung der Parameter, allometrischer (körpermassenabhängiger) Exponent, Aktivierungsenergie sowie eines Korrekturfaktors für neun verschiedene phylogenetische Gruppen der streu- und bodenbewohnenden Wirbellosenfauna ermöglichte. In dieser Studie habe ich mich mit markanten Theorien zum Verhältnis von Stoffwechsel zu Körpergröße und Temperatur beschäftigt. Der, in der metabolischen Theorie der Ökologie (Metabolic Theory of Ecology), postulierte universale Exponent zeigte sich dabei als nicht passend. Die Analyse zeigte, dass die Einbeziehung phylogenetischer Informationen die Qualität des Modells stark erhöhen kann, was deren Wichtigkeit für weitere Untersuchungen unterstreicht (Kapitel 5). Es gibt also nicht einen allometrischen Exponenten, der alle Organismen gleich gut beschreibt, sondern für unterschiedliche Tiergruppen unterschiedliche. Anwendung fanden die so gewonnenen Parameter in verschiedenen weiteren Untersuchungen. Zusammengefasst mit Daten zur Aufnahmeeffizienz (engl: assimilation efficiency) lassen sich so Schlüsse ziehen über diese Abhängigkeit von Temperatur und Körpermasse. Dabei wird, im Gegensatz zu den Kapiteln 3 und 4, nicht nur der Konsum eines Tieres mit seinem Stoffwechsel ins Verhältnis gesetzt, sondern zusätzlich noch die Menge an Energie, die ein Konsument aus seiner Resource zu ziehen in der Lage ist, betrachtet. Respiration und Assimilation hängt je nach Konsumententyp unterschiedlich stark von Temperatur ab. Bemerkenswert ist, wie sich der Instandhaltungskonsum (überlebensnotwendige Nahrungsaufnahme, engl: maintenance consumption), mit steigender Temperatur für verschiedene Konsumententypen verhält. Während Herbivore und Detritivore in der Lage sind mehr Energie als nötig aufzunehmen, was zu Popula-

tionswachstum führen kann, so sind Carnivore kaum in der Lage ihren rapide steigenden Bedarf zu decken, was zu Hungern oder dem Aussterben der Population führen kann (Kapitel 6).

Es folgten zwei weitere Studien, in denen die Parameter der Stoffwechselraten Anwendung fanden um mit Hilfe von Felddaten unterschiedliche Theorien zu testen. Die Theorie, nach der begrenzte Ressourcen sexuelle, reichliche Ressourcen jedoch asexuelle Fortpflanzung begünstigen ('Structured Resource Theory of Sexual Reproduction') wurde mit Daten über die Häufigkeit von Oribatiden (Milben) bzw. deren Stoffwechsel und dem Verhältnis von asexuell bzw. sexuell sich fortpflanzenden Arten bzw. Individuen getestet (Kapitel 7). Bei dieser Theorie wird davon ausgegangen, dass in Tiergemeinschaften, in denen die Ressourcen knapp sind eher sexuelle Fortpflanzung vorherrscht, da diese die immer neue Anpassung an neue oder wechselnde Arten von Ressourcen besser ermöglicht. In Tiergesellschaften, in denen ein hohes Übermaß an Ressourcen zu finden ist, so wie es bei Gesellschaften, dieser auf Detritus beruhenden Arten der Fall war, ist die asexuelle Fortpflanzung im Vorteil, da Ressourcen effektiver ausgebeutet werden können. Die Daten über die Verteilung der Asexuellen bestätigte die Theorie. Wobei nicht allein die Quantität der Resource, sondern auch ihre Qualität eine große Rolle spielen. So ist die Menge an Ressourcen in tropischen Wäldern vergleichsweise groß, die Qualität für zersetzende Organismen allerdings gering, was das geringe Auftreten asexueller Arten bestätigt.

Mit einem größeren Datensatz mit Abundanz von verschiedenen bodenbewohnender Wirbelloser in Kombination mit den phylogenetisch spezifischen Parametern für die Bestimmung des Stoffwechsels konnte der Energieverbrauch von Artengemeinschaften in verschieden stark genutzten Wäldern bestimmt werden (Kapitel 8). Die vorherrschenden Theorien zu Abundanz und Biomasse wurden dabei betrachtet. Die Theorie der Biomasse, die besagt, dass über alle Größenklassen die Biomasse unverändert bleibt, konnte widerlegt werden. Unklarer waren allerdings die Ergebnisse hinsichtlich der Theorie der energetischen Gleichverteilung. Dieses Muster bezeichnet eine gleichmäßig verteilte Energienutzung über die verschiedenen Körpergrößenklassen. Die Ergebnisse waren variabel, teils mit dem Muster zu vereinbaren, teils nicht. Allerdings bestätigen die Ergebnisse Funde anderer Studien zur Nahrungsnetztheorie, die zeigen, dass eine Monopolisierung der Energie durch größere Tiere stattfindet und für die Stabilität von Nahrungsnetzen von Bedeutung ist.

So zeigt meine Arbeit die verschiedenen Aspekte in denen der Stoffwechsel eine entscheidende Rolle spielt und wie er auf mannigfache Weise beeinflusst wird, sowie deren Effekte auf die Interaktionen zwischen Organismen in komplexen natürlichen Systemen.

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12 Appendix

All data (tables, figures) can be found on an attached data medium.

Erklärung zur Dissertation

Hiermit versichere ich, die vorliegende Dissertation ohne Hilfe Dritter nur mit den angegebenen Quellen und Hilfsmitteln angefertigt zu haben. Alle Stellen, die aus Quellen entnommen wurden, sind als solche kenntlich gemacht. Diese Arbeit hat in gleicher oder ähnlicher Form noch keiner Prüfungsbehörde vorgelegen.

Darmstadt, den

(R. Ehnes)



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14 Curriculum Vitae



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More than any time in history, mankind now faces a crossroads. One path leads to despair and utter hopelessness, the other to total extinction. Let us pray that we have the wisdom to choose correctly.

— Woody Allen, "Side Effects"