The cost of living
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The most fundamental biological rate is the metabolic rate of organisms, the rate at which organisms uptake, transform and expend energy and material. Differences in the basal metabolic rate of organisms can explain variations in population ecology up to ecosystems. Therefore the basal metabolic rate of individual organisms is a central issue for ecology. The Metabolic Theory of Ecology (MTE) was presented with the ambition to be a quantitative theory on the metabolic rate, applicable for all organisms. The MTE presumes that differences in the basal metabolic rate of organisms are described by its biomass and temperature dependence. As consequence of evolutionary differences in the transporting network of all organisms the metabolic rate scales to biomass by $3/4$. The impact of temperature is presumed to be described by the impact of temperature on enzymatic reactions given by the Arrhenius relation. Thus the basal metabolic rate ($B$) should be described by the master equation

$$B = b_0 \cdot M^{3/4} \cdot e^{-E/kT},$$

where, $b_0$ is the species-specific normalization constant, the term $M^{3/4}$ describes the scaling on biomass ($M$) and the Arrhenius-term ($e^{-E/kT}$) is a formalization of the thermodynamic effect of temperature effect on the metabolic reaction rate of key-enzymes. The presented thesis provides an important contribution to the enormous debate, enrolled by the MTE.

In MTE the biomass dependence of the metabolic rate results from evolutionary optimization, while the temperature dependence is based on the physical impact on enzymatic reactions, is unaffected by evolutionary optimization. The Arrhenius relation explains the short-term respiratory temperature-dependence, but upon extended temperature exposure duration the metabolic rate becomes relatively independent of the prevailing temperature. By acclimation (intraspecific) and adaptation (interspecific) organisms adjust for the thermodynamic effect of temperature on key-enzymatic reaction. In addition our results show that the short-term temperature-dependence, reflected by the activation energy varies between species, while the MTE considers a fixed activation energy. Furthermore for animals the activation energy is positively related to biomass indicating that for big animals the metabolic rate is more sensitive to changes in temperature.

Focusing on the biomass-dependence of the metabolic rate, differences in the building plan of the variety of organisms might result in different construction of the transporting network. In consequence the scaling of the metabolic rate might differ for animals and plants. Further, differences in biomass allocation might play an important role for differences in the metabolic rate of plants, as biomass allocation scales on biomass and different tissues vary in metabolic activity. We show that biomass-dependent differences in the metabolic rate of plants result from morphological properties, such as biomass allocation patterns as well as exposed leaf area and pigment content, which are related to photosynthetic capacity. Therefore the metabolic rate can
not simply be predicted from first principles, like assumed by the MTE, although, the observed scaling exponent is similar to their prediction.

Thermal acclimation and adaptation could possibly impact the morphology of plants. Within the phenotypic (acclimation) and/or genotypic (adaptation) plasticity organisms adjust, so that metabolic processes become relatively independent of temperature where else morphological properties are affected by temperature. Thermal acclimation has an impact on the specific leaf area (SLA), leaf area per unit leaf biomass and leaf area index, exposed leaf area per unit plant biomass, indicating the plastic response of leaves to changing environment. From the absences of morphological differences of adapted ecotypes it seems that plant species only adjust by acclimation, reflecting the importance of phenotypic plasticity. But the dependence of phenotypic plasticity on genotypes shows that adaptive differences also occur. Such temperature dependent morphological variations within the phenotypic and genotypic plasticity might impact scaling relations. However, the biomass-dependence of physiological and morphological features is unchanged.

Leaf construction has a high impact on metabolic rate of plants, so that temperature-dependent variations in leaf parameters might compensate for the thermodynamic effect induced by short-term temperature exposure. Here we show that climatic differences in the SLA lead have a compensatory effect on the metabolic rate. This applies for both, thermal acclimation (within species) and adaptation (between species). However at the intraspecific level, the effect of climate, which is the sum of the effects of temperature, solar radiation, precipitation, wind, etc. could not be reduced to specific environmental variables. To determine the effect of temperature on the specific leaf area (SLA), we additionally applied data of plants exposed to different temperatures, while other climatic parameters were kept stable, like given for some greenhouse studies. The temperature-dependence of the SLA is contrivers to the SLA-dependence of climate (latitude), so that temperature dependent changes in leaf construction enforce high metabolic rates in warm climates, while other climatic parameters counterbalance and overcompensate the effect of temperature on SLA.

Conclusively, describing the basal metabolic rate by the $3/4$ scaling on biomass and the Arrhenius-relation is too simplistic. A formulization of the various effects of biomass, temperature and leaf construction is presented in the synthesis, showing that the dependence of the basal metabolic rate is much more complex than assumed.