A metabolic perspective of stochastic community assembly

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Abstract: Metabolism controls the pace of life driving major ecological patterns. We propose that the scaling of metabolism with temperature influences neutral processes of community assembly by controlling population dynamics independently of species identities. This perspective provides new insights into the prevalence of niche and neutral processes through universal energetic constraints.

How metabolism controls assembly processes

Current synthesis in community ecology recognizes the contribution of both, **niche** and **neutral processes** (see **Glossary**) in the assembly of ecological communities [1]. The niche perspective has traditionally focused on taxonomic identity and trait differences in shaping biotic interactions and environmental filtering. In contrast, the random birth, death, and dispersal of organisms within trophic levels have been the key factors in purely neutral perspective [2]. The future challenge in community ecology is thus to determine the factors that explain the relative contribution of niche and neutral processes during community assembly across environmental gradients [1]. Here, we address this challenge by integrating the metabolic theory of ecology [3] into the niche-neutral theories. We explain how considering the universal scaling of **mass-specific metabolic rates** (hereafter **metabolic rates**) with temperature casts a new light on how communities are organized in nature.

Metabolism encompasses the biological processing of material and energy by organisms via biochemical reactions. Due to an increased rate of molecular kinetics, metabolic rates increase predictably with temperature [3]. Consequently, environmental temperature is the most important abiotic driver of metabolism that propagates to all levels of biological organization [3]. The increased metabolism at higher temperature governs many natural processes, including the number of individuals within communities and the rates of biomass production in ecosystems [3]. Because temperature consistently changes along altitudinal, depth and especially latitudinal gradients, this should generate environmental gradients of metabolic rates. We argue that the universal influence of metabolism over biological processes could modulate the relative importance of niche and neutral processes during community assembly.

Hubbell's Neutral Theory of Biodiversity and Biogeography [2] assumes that organisms within a trophic level can be considered as approximately equivalent in their chances of birth, death and dispersal [2]. This implies that population abundances within trophic levels vary largely at random and similarly among species – i.e. negative density-dependency is equal among and within species and thus populations drift in time [2, 4]. Investigating the ecological equivalence of individuals and species is therefore pivotal for understanding community assembly [4] and metabolism could influence neutral processes in the following ways.

First, higher metabolic rates at high temperatures result in decreased longevity in ectotherms [3]. These changes in longevity are linked to extrinsic and intrinsic factors affecting population death rates [5]. Extrinsic factors are influenced by species niches as the chances of death increase in unfavourable environments. Intrinsic factors instead are driven by metabolic rates due to an increased accumulation of damage from oxidative reactions, telomere shortening and deleterious mutations impacting all individuals at higher temperatures [5]. We hypothesize a greater proportion of intrinsic to extrinsic deaths at higher temperatures (Figure 1) which could therefore reduce competitive differences and lead to higher species competitive equivalence. This would occur because intrinsic deaths are strongly controlled by cellular damages acting stochastically among individuals and consistently among species, possibly undermining their competitive differences. Consequently, populations would be under relatively weaker control of niche-based processes like competitive dominance (Figure 1). Accelerated death rates in organisms with high metabolic rates have been shown across a wide range of taxa indicating a strong intrinsic control [5], but extrinsic deaths could also be enhanced as ecological interactions are also faster with higher energetic demands (i.e. organisms became more susceptible to predation as they get more oxidative damages) [3]. Notwithstanding, increased deaths, independently of its causes, decrease population densities leading us to our second link between metabolism and neutral processes.

There is ample evidence that population densities decline with increasing metabolic rates, especially in ectotherms [3]. This relationship can be explained by the greater individual energetic demands at higher temperatures resulting in lower abundances under a fixed supply of resources [3] and by the faster biomass turnover due to shorter life cycles under these conditions [6]. In such lower densities, the relative importance of neutral processes is enhanced [7] (Figure 1). This happens because the influence of demographic stochasticity during community assembly is inversely proportional to population density [7] (Figure 1). Species with large competitive differences but with low densities can have equivalent chances of extinction since the effect of demographic stochasticity could overcome those of niche processes [7]. Whereas in communities with high densities the impacts of demographic stochasticity would be relatively weak compared to the population variation based on niche processes (Figure 1). Such predictable variation in neutral processes due to population size has been suggested theoretically [7] and demonstrated empirically [8]. Given a universal decrease in population densities under higher temperatures [3], this should entail consistent variation in neutral processes across temperature gradients.

Metabolism and the assembly of stream metacommunities

Metabolism influences community assembly in several additional ways and the relative importance of individual mechanisms may differ among ecosystems. We illustrate our ideas using short-lived ectotherms, as the smaller abundance with rising temperature should be less important for long-lived organisms [3, 6]. Stream metacommunities represent a good example because a central part of these food webs encompasses insects with short life spans. Adult insects emerge into terrestrial ecosystems and recolonize the streams via oviposition, completing the life cycles in months to up to few years. In tropical communities, stream insect abundances have been found to be approximately five times lower than in high-latitude streams [8], likely due to high metabolism and fast biomass turnover, making communities strongly affected by demographic stochasticity [8]. In addition to the general effects of increased mortality and lower densities, other mechanisms should operate in these communities. For example, predation could enhance neutrality in prey communities because an increased metabolic rate in predator fish generally leads to more generalist and omnivorous feeding. This occurs because faster metabolism requires organisms to feed more often, less selectively and on high carbon content prey [9]. This shift in feeding behaviour could result in less predictable feeding interactions with a higher stochasticity in preys consumed, reinforcing neutrality in prey communities.

The fast biomass turnover of aquatic insects entails frequent dispersal of adults among streams, given that tropical insects often have more generations per year than temperate species [6]. Since tropical community composition would be driven by neutral processes, dispersal and recolonization is less predictable as well [8]. At the metacommunity level, neutrality is thus enhanced by the frequent colonization of organisms with variable body sizes and taxonomic identities that could ultimately influence the whole metacommunity structure [10].

In summary, differences in metabolism should lead to predictable variation in the relative importance of neutral processes in stream communities. This variation can also alter the way energy flows through ecosystems, explaining food web structure that stems from energetic constraints, such as relationships between abundance and body mass.

Niche and neutral mass-abundance relationships

Size spectra have long been used to investigate relationships between body mass and abundance, and understand energy allocation and transfer in ecosystems. These relationships depict the frequency distribution of individual body sizes and allow comparisons of communities in different environmental settings, irrespective of their taxonomic composition (Figure 2). Metabolic scaling theory predicts a negative power law relationship [3] as a function of two main parameters: the transfer efficiency of energy across trophic levels and the relative size of predators and prey (Figure 2). We propose that the fitted parameters of the size spectrum vary with temperature and the relative influence of niche and neutral processes (Figure 2). First, the variation in abundance explained by body mass (i.e. R^2 value) should be smaller at higher temperatures (and under neutral community assembly) due to enhanced importance of demographic stochasticity and the frequent random dispersal of organisms, relaxing energetic constraints [10] (Figure 2). Second, the intercept should be lower in warm regions because of the lower population abundances and community biomass [3, 6] (Figure 2). Size spectra provide an excellent tool to test these and other hypotheses (Figure 2), as they directly represent energy fluxes and constraints across multiple trophic levels.

Towards a metabolic niche-neutral theory

Whereas the mechanisms described here suggest a weaker role of niche processes under higher temperatures, variation among systems should occur. For example: i) a fast pace of life could strengthen interspecific differences if population size is strongly constrained by carrying capacity and limiting resources are scarcer under high temperature [11] because faster metabolism could lead to accelerated deterministic competitive exclusions. ii) Predators with higher metabolism could also specialise and selectively feed on more nutritious prey, as observed in lizards [12], in contrast to increased generalism found for fish [9]. Our key point is not to imply a singular direction of the metabolism-stochasticity relationship, but rather to emphasize that the metabolic perspective provides a general biological framework to investigate variation in niche and neutral community assembly.

Our ideas represent the first steps towards linking metabolic constraints with niche and neutral processes to understand community assembly across multiple trophic levels. Future empirical tests of this framework will be pivotal to test whether niche-neutral theories and the metabolic theory of ecology can be viewed as two sides of the same coin.

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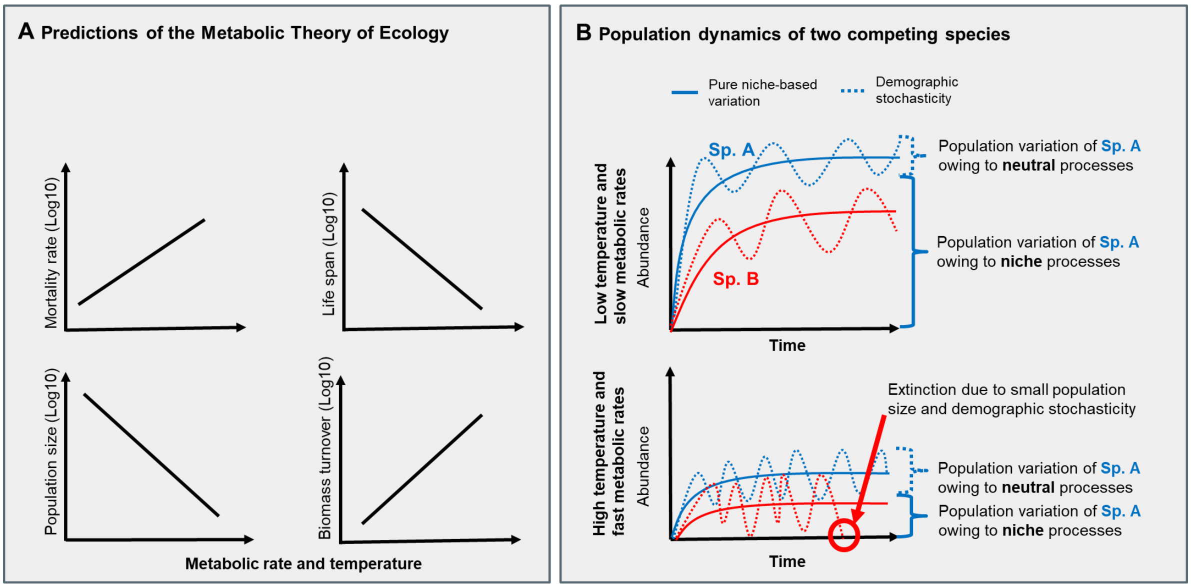

Figure 1. The influence of temperature and metabolism on the relative importance of niche and neutral processes. A) Predictions based on the universal acceleration of mass-specific metabolic rates with increasing temperature due to molecular kinetics. At the individual-level, mortality rates increase whilst life span decrease with increasing temperature. At the population level, densities decreases whilst biomass turnover increases with temperature. B) At high temperatures and fast metabolic rates, densities are low due to a faster pace of life and higher mortality rate. In these cases, the relative influence of demographic stochasticity increases (blue dashed brackets), whereas those of niches differences (blue solid brackets) for community assembly decreases (here represented as competition between two species). Given the low densities, species in warmer conditions are more prone to random extinctions (red circle).

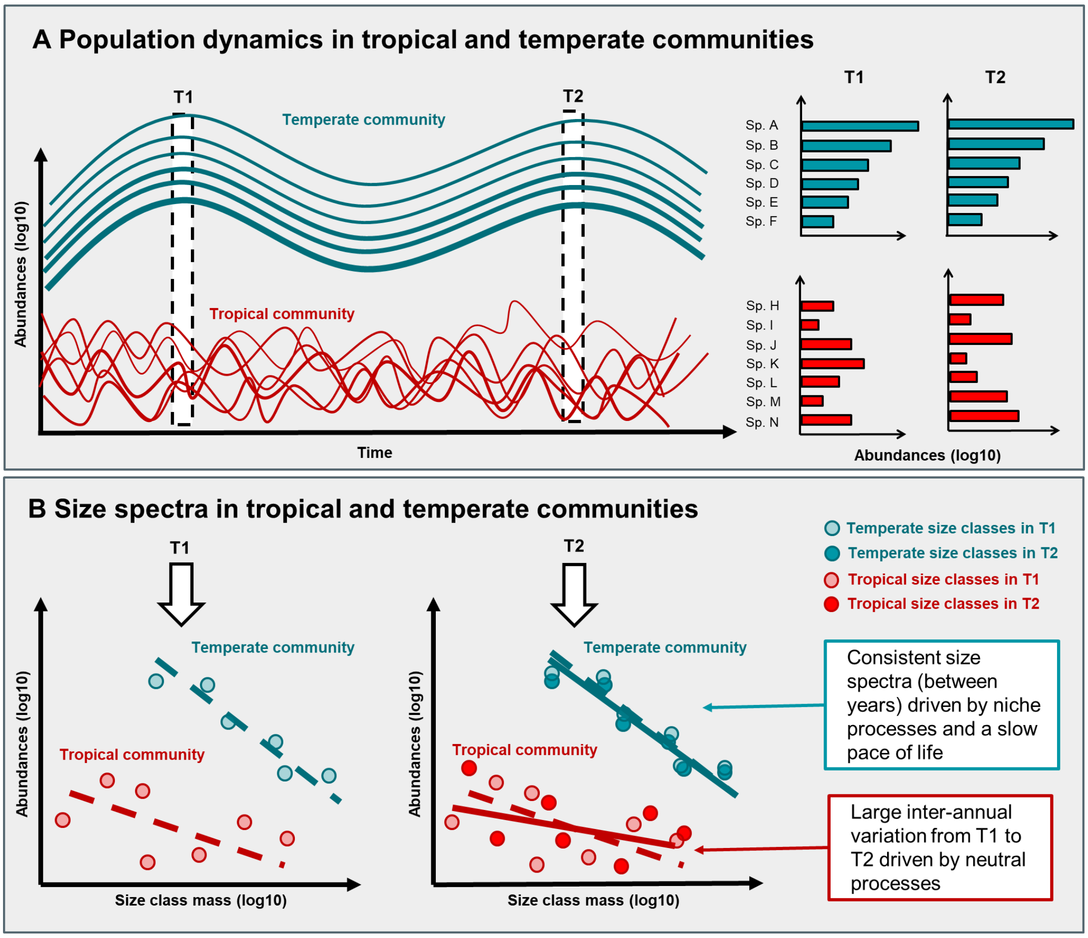

Figure 2. The relative influence of niche and neutral processes on local community size spectra. **A)** Tropical and temperate communities have distinct patterns of population dynamics. In warm tropical communities, populations (individual lines) are more strongly influenced by demographic stochasticity due to lower densities (red colour) compared to high densities in cool temperate communities (blue lines). A higher number of generations per year also enhances the number of demographic events increasing the importance of stochastic population dynamics in tropical communities. Due to energetic constraints, organisms can be on average smaller in warmer tropical communities (indicated by the thickness of lines). The relatively higher influence of neutral processes entail greater variation in rank-abundance patterns in tropical communities. This is shown by the bar plots where species have higher abundance variation from T1 to T2 in tropical than in temperate communities. **B)** Hypothetical local size spectra depicting the distribution of abundance among different size classes in tropical and temperate communities. In tropical communities, the higher relative importance of neutral processes results in greater variation of data around the regression line, with size classes with higher and lower abundances than predicted based on steady-state energetic conditions. Under these conditions, higher temporal and spatial variation in size spectra parameters are expected in tropical communities (variation in size spectra from T1 to T2). Dashed and solid lines indicate size spectra in T1 and T2, respectively.

Glossary:

Mass-specific metabolic rate: Demands of energy per unit of body mass per time in order to maintain biological functions inherent to survivorship but not including expenditure to reproduction. The difference from absolute metabolic rate is important, given that body size can decrease with warming, sustaining a potential trade-off along temperature gradients. In other words, individuals demand more energy under higher temperatures, but also can be smaller, demanding less energy per individual. Mass-specific metabolic rate reflects the higher energetic expenditure per unit of body mass at higher temperatures and is commonly measured as basal metabolic rate of a resting or inactive organism This basal metabolic rate is in general correlated with the average daily metabolic rate of organisms under active periods.

Metabolic rate: Individual demands of energy in time to maintain biological functions inherent to survivorship. In heterotrophs metabolism is aerobic respiration, whereas photosynthesis is the main contributor to the metabolic rates in autotrophs.

Neutral processes: A combination of processes that can be specifically stochastic at the population level. These processes include stochastic rates of birth and death, dispersal and the introduction of evolutionary novelty via mutation and speciation. The Neutral Theory of Biodiversity and Biogeography [2] assumes that these processes are similar among species within a trophic level at a first approximation.

Niche processes: A combination of processes where species differences determine ecological outcomes. For example, prey differences in anti-predator behaviour can determine predation pressure, or differences in species tolerances can determine community composition along a gradient of salinity.

Size spectra: Relationship between organism body size and abundance, which commonly encompasses multiple trophic levels. The relationship is depicted by plotting (on double logarithmic scales) the number of individuals within body size (or mass) classes against the mean size of the size class. The negative slope of the size spectrum summarises energy allocation and transfer through the food web, for which a rich body of theory exists (e.g. [3]).