response to Davidson *et al*. *Trends Ecol. Evol.* 36, 277–278
3. Greggor, A.L. *et al.* (2016) Seasonal changes in neophobia and its consistency in rooks: the effect of novelty type and dominance position. *Anim. Behav.* 121, 11–20
4. Davidson, G.L. *et al.* (2020) Diet induces parallel changes to the gut microbiota and problem solving performance in a wild bird. *Sci. Rep.* 10, 20783
5. Maurice, C.F. *et al.* (2015) Marked seasonal variation in the wild mouse gut microbiota. *ISME J.* 9, 2423–2434
6. Firth, J.A. and Sheldon, B.C. (2015) Experimental manipulation of avian social structure reveals segregation is carried over across contexts. *Proc. R. Soc. B Biol. Sci.* 282, 20142350
7. Liddicoat, C. *et al.* (2020) Naturally-diverse airborne environmental microbial exposures modulate the gut microbiome and may provide anxiolytic benefits in mice. *Sci. Total Environ.* 701, 134684
8. Bateson, P. *et al.* (2014) The biology of developmental plasticity and the Predictive Adaptive Response hypothesis. *J. Physiol.* 592, 2357–2368
9. Dufty, A.M. *et al.* (2002) Hormones, developmental plasticity and adaptation. *Trends Ecol. Evol.* 17, 190–196
10. Schmidt, K.L. *et al.* (2014) Developmental stress, condition, and birdsong: a case study in song sparrows. *Integr. Comp. Biol.* 54, 568–577

Forum

A Metabolic Perspective of Stochastic Community Assembly

Victor S. Saito [1,*,@], Daniel M. Perkins,[2,@] and Pavel Kratina[3]

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 Community 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 a purely neutral perspective [2]. The current 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 concepts from 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 latitudinal gradients, this should generate environmental gradients of metabolic rates. Because metabolism influences fundamental biological processes, we argue that it modulates the importance of neutral processes during community assembly.

The Unified 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 densities within trophic levels vary largely at random and similarly among species; that is, 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

Glossary

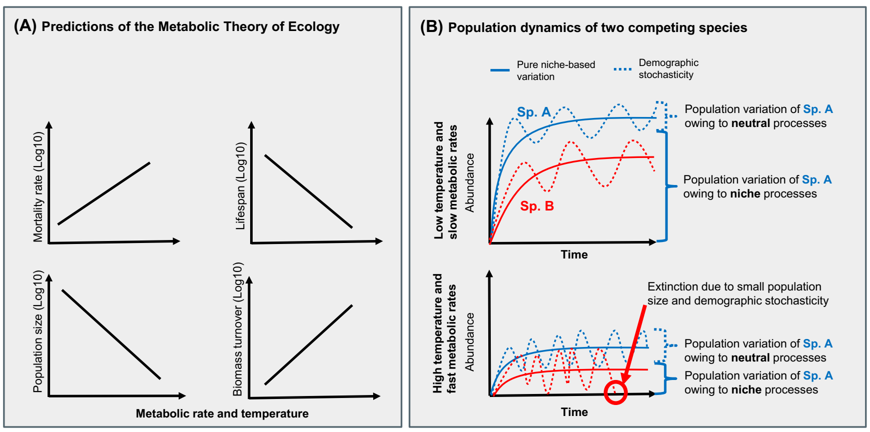
Mass-specific metabolic rates: demands of energy per unit of body mass per time in order to maintain biological functions inherent to survival. The difference from absolute metabolic rate is important, given that body size also tends to decrease with higher environmental temperatures [3], sustaining a trade-off along temperature gradients. In other words, individuals demand more energy under higher temperatures but also tend to 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 (and considered in this study) as basal metabolic rate of a resting or inactive organism. This basal metabolic rate is generally correlated with the mean daily metabolic rate of organisms under active periods [6].

Metabolic rates: 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 [3].

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 Unified 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 whereby species differences determine ecological outcomes. For example, prey differences in antipredator behavior 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 midpoint of the size class. The negative slope of the size spectrum summarizes energy allocation and transfer through the food web, for which a rich body of theory exists (e.g., [3,6]).



Trends in Ecology & Evolution

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 warming due to molecular kinetics. At the individual level, mortality rates increase but lifespan decreases with increasing temperature. At the population level, density decreases but biomass turnover increases with temperature. (B) At high temperatures and fast metabolic rates, population densities are low due to a faster pace of life and higher mortality rate. In this scenario, the relative influence of demographic stochasticity increases (blue broken brackets), whereas those of niches differences (blue unbroken brackets) for community assembly decreases (here represented as competition between two species). Given the low population densities, species in warmer environments are more prone to random extinctions (red circle).

could influence neutrality in the ways described next.

First, greater metabolic rates at higher temperatures result in decreased longevity of 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 unfavorable environmental conditions. Intrinsic factors instead are driven by metabolic rates due to an increased accumulation of damage from oxidative reactions, telomere shortening, and deleterious mutations [5]. We hypothesize a greater proportion of intrinsic to extrinsic deaths at higher temperatures (Figure 1), which could therefore reduce competitive differences among species and lead to a higher competitive equivalence. This would occur because intrinsic deaths are controlled by 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 such as competitive dominance (Figure 1). Higher death rates in organisms with high metabolism have been found across a wide range of taxa, indicating a strong control of intrinsic factors [5]. However, extrinsic factors may also increase death rates as biotic interactions change predictably with warming (i.e., organisms become more susceptible to predation as their oxidative damages accumulate) [3,6]. Whether increased rates of total deaths are predominantly driven by intrinsic or extrinsic factors remains an area of future research. In any case, increased death rates reduce population densities and lead us to the second major link between individual metabolisms and neutral processes of community assembly.

There is ample evidence that population densities decline with increasing metabolic rates, especially in ectotherms [3]. This is due to the increased death rates and can be explained by the greater individual energetic demands at higher temperatures resulting in lower densities under a fixed supply of resources [3] and by the faster biomass turnover due to shorter life cycles under these conditions [7]. At lower densities, the relative importance of neutral processes is enhanced [8] (Figure 1), because the influence of demographic stochasticity during community assembly is inversely proportional to population density [8] (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 [8]. In communities with high densities, the impacts of demographic stochasticity would be relatively weak compared with the population variation caused by niche processes (Figure 1). Such predictable variation in neutral processes due to population density has been suggested theoretically [8] and demonstrated empirically [9]. Given the predicted decrease in population densities under higher temperatures [3], this should entail consistent variation in neutral processes across temperature gradients.

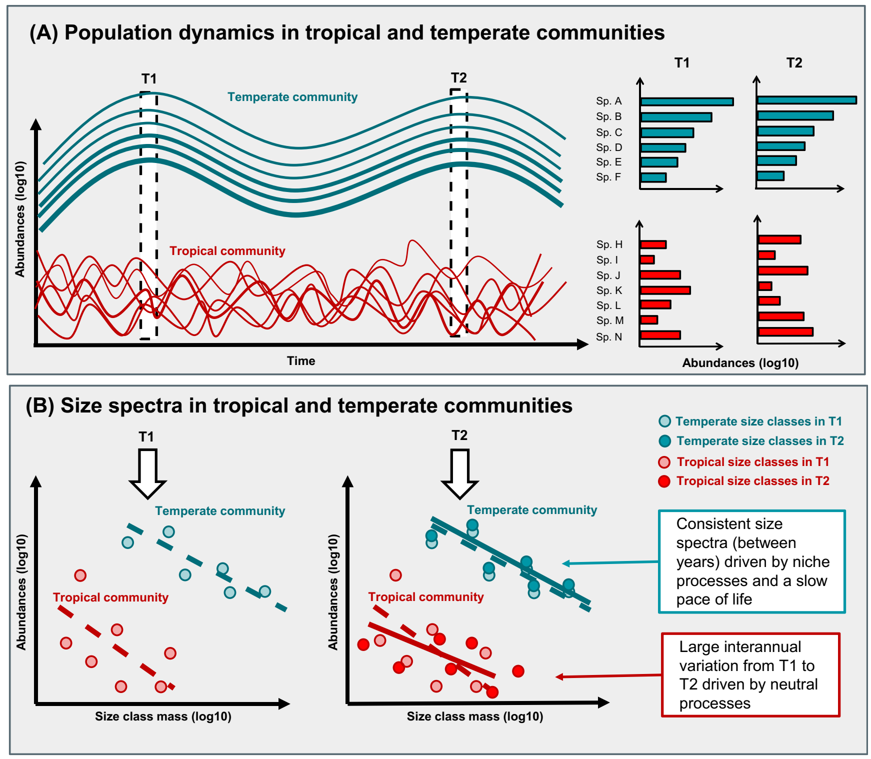
Metabolism and the Assembly of Stream Metacommunities

Metabolism influences community assembly in several additional ways, and the importance of individual mechanisms may differ among ecosystems. We illustrate our ideas using short-lived stream insects, as the lower densities with rising temperature should be less important for long-lived organisms [3,7]. Adult insects emerge into terrestrial ecosystems and recolonize the streams via oviposition, completing the life cycles in months to up to a few years. In tropical communities, insect densities have been found to be approximately five times lower than in high-latitude streams [9], likely due to the accelerated metabolism and biomass turnover in the warmer tropics, making communities strongly affected by demographic stochasticity [9]. 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 [10]. This occurs because faster metabolism requires organisms to feed more often, less selectively, and on prey with high carbon content [10], potentially leading to a higher stochasticity in size and identity of consumed prey, reinforcing neutrality in prey communities.

The fast biomass turnover of aquatic insects entails frequent dispersal of adults among streams, with more dispersal events for tropical insects, given they have more generations per year than temperate species [7]. Since tropical communities are more neutrally assembled, dispersal and recolonization are less predictable as well [9]. At the metacommunity level, neutral processes prevail due to the frequent colonization of organisms with variable body sizes and taxonomic identities that could ultimately influence neutrality at the metacommunity level [11].

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 structures that stem from energetic constraints, such as relationships between abundance and body mass.



Trends in Ecology & Evolution

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 small population densities (red color) compared with large population 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 tend to be, on average, smaller in warmer tropical communities [3] (indicated by the thickness of lines), even though the opposite relationship exists for some taxa. The relatively higher influence of neutral processes entails greater variation in rank-abundance patterns in tropical communities. This is illustrated 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). Broken and unbroken lines indicate size spectra in T1 and T2, respectively.

Niche and Neutral Mass–Abundance Relationships

Size spectra have long been used to investigate relationships between body mass and abundance and to 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, regardless 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), providing a way to test predictions across trophic levels. 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 [11] (Figure 2). Under these conditions, higher temporal and spatial variation in size-spectra slopes would also be expected for communities in warmer conditions (Figure 2). Finally, the intercept should be lower in warm regions because of the lower population densities and community biomass [3,7] (Figure 2). Size spectra provide an excellent tool to test these and other hypotheses (Figure 2) as they directly represent energy fluxes across trophic levels.

Toward a Metabolic Niche Theory

Whereas the mechanisms described here suggest a weaker role of niche processes in community assembly under higher temperatures, variation among systems could occur. For example, a fast pace of life could increase interspecific differences if population density is strongly constrained by carrying capacity and limiting resources are scarcer at high temperatures (e.g., green food webs) [12]. In such conditions, a faster metabolism could lead to greater importance of niche differences accelerating deterministic competitive exclusions. Also, predators with higher metabolism could also specialize and selectively feed on more nutritious prey, as observed in lizards [13], in contrast to increased generalism found for fish [10]. 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 for understanding variation in niche and neutral community assembly.

Our ideas represent the first steps toward linking metabolic constraints with neutral processes to understand community assembly within and across 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.

Acknowledgments

We thank Tadeu Siqueira, Raul Costa Pereira, Luís Schiesari, two reviewers, and the editor for comments that improved our perspective. This manuscript was initiated through discussions held during a British Council–FAPESC funded Early Career workshop (RLWK8-10592) in Florianopolis, Brazil. We gratefully acknowledge the following grants: a Newton Fund/São Paulo Research Foundation (FAPESP) grant (2019/05464-1) to D.M.P., a Royal Society grant (NAF\R2\180791) to P.K., and an FAPESP grant (2019/06291-3) to V.S.S.

Declaration of Interests

No interests are declared.

[1]Environmental Sciences Department, Federal University of São Carlos, São Carlos/SP 13565-905, Brazil
[2]Life Sciences Department, University of Roehampton, London SW15 4JD, UK
[3]School of Biological and Chemical Sciences, Queen Mary University of London, London E1 4NS, UK

*Correspondence:
victor.saito@gmail.com (V.S. Saito).
[@]Twitter: @vs_saito (V.S. Saito) and @drDanPerkins (D.M. Perkins).

https://doi.org/10.1016/j.tree.2021.01.003

References

1. Shoemaker, L.G. *et al.* (2020) Integrating the underlying structure of stochasticity into community ecology. *Ecology* 101, e02922
2. Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*, Princeton University Press
3. Brown, J.H. *et al.* (2004) Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789
4. McPeek, M.A. and Siepielski, A.M. (2019) Disentangling ecologically equivalent from neutral species: the mechanisms of population regulation matter. *J. Anim. Ecol.* 88, 1755–1765
5. McCoy, M.W. and Gillooly, J.F. (2008) Predicting natural mortality rates of plants and animals. *Ecol. Lett.* 11, 710–716
6. Brown, J.H. *et al.* (2018) Equal fitness paradigm explained by a trade-off between generation time and energy production rate. *Nat. Ecol. Evol.* 2, 262–268
7. Munch, S.B. and Salinas, S. (2009) Latitudinal variation in lifespan within species is explained by the metabolic theory of ecology. *Proc. Natl. Acad. Sci. U. S. A.* 106, 13860–13864
8. Orrock, J.L. and Watling, J.I. (2010) Local community size mediates ecological drift and competition in metacommunities. *Proc. Biol. Sci.* 277, 2185–2191
9. Siqueira, T. *et al.* (2020) Community size can affect the signals of ecological drift and niche selection on biodiversity. *Ecology* 101, e03014
10. González-Bergonzoni, I. *et al.* (2012) Meta-analysis shows a consistent and strong latitudinal pattern in fish omnivory across ecosystems. *Ecosystems* 15, 492–503
11. Perkins, D.M. *et al.* (2018) Bending the rules: exploitation of allochthonous resources by a top-predator modifies size-abundance scaling in stream food webs. *Ecol. Lett.* 21, 1771–1780
12. Bernhardt, J.R. *et al.* (2018) Metabolic theory and the temperature-size rule explain the temperature dependence of population carrying capacity. *Am. Nat.* 192, 687–697
13. Bestion, E. *et al.* (2019) Altered trophic interactions in warming climates: consequences for predator diet breadth and fitness. *Proc. Biol. Sci.* 286, 2019–2227