Biodiversity modulates the size-abundance relationship in changing environments

Vojsava Gjoni[*,1,2,3], Florian Altermatt[1,4], Aurélie Garnier[1,5] Gian Marco Palamara[1,6], Mathew Seymour[4,7], Mikael Pontarp[1,8], and Frank Pennekamp[1]

[1] *Department of Evolutionary Biology and Environmental Studies University of Zurich, Zurich, Switzerland*

[2] *Department of Biology, University of South Dakota, Vermillion, South Dakota, USA*

[3] *current address: Institute for Biological Resources and Marine Biotechnologies (IRBIM), National Research Council (CNR), Mazzara del Valo, Italy*

[4] *Department of Aquatic Ecology, EAWAG: Swiss Federal Institute of Aquatic Science and Technology, Dübendorf*

[5] *ECOBIO UMR CNRS 6553, University of Rennes, France*

[6] *Institute of Ecology and Evolution University of Bern, Bern, Switzerland*

[7] *School of Biological Sciences, The University of Hong Kong, Hong Kong SAR, China*

[8] *Department of Biology, Lund University, Lund, Sweden*

**Correspondence E-mail: vojsavagjoni@cnr.it*

Vojsava Gjoni: https://orcid.org/0000-0003-1740-6093
Florian Altermatt: https://orcid.org/0000-0002-4831-6958
Aurélie Garnier: https://orcid.org/0000-0002-3712-4301
Gian Marco Palamara: https://orcid.org/0000-0003-3517-9445
Mikael Pontarp: https://orcid.org/0000-0001-9045-7829
Mathew Seymour: https://orcid.org/0000-0002-3654-4857
Frank Pennekamp: https://orcid.org/0000-0003-0679-1045

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ABSTRACT

Organismal abundance tends to decline with increasing body size. Metabolic theory links this size structure with energy use and productivity across levels of biological organization, predicting a size-abundance slope of -0.75 that is invariant across environments. We tested whether the size-abundance relationship is robust to a gradient of protist species richness (1 to 6 species), temperature (15 to 25° C), and time. Our results support the expected slope of -0.75 for the size-abundance relationship, but we found interactive effects indicating that the size-abundance relationship is not invariant. In high-richness communities, temperature increased the abundance of small protists more than that of the large protists, leading to a steeper size abundance slope. Temperature and size-dependent species interactions were identified as potential drivers. Understanding variation in size-abundance relationship hence provides novel insight into the underlying mechanisms shaping the size structure of ecological communities under environmental change.

KEYWORDS: body size, protists, species richness, size-abundance relationship, temperature

INTRODUCTION

Smaller species are usually more abundant than larger species, that is, they have larger populations. The body size-abundance relationship, a well-established empirical pattern, describes this inverse relationship between the average body size of a species and its abundance (Damuth 1991; White *et al.* 2007). The slope of the size-abundance relationship is typically -0.75 (Brown *et al.* 2004; Nee *et al.* 1991). Body size-abundance relationships have become increasingly important in community ecology as they provide insights into the links between the size structure and abundance of communities (Arim *et al.* 2011; Enquist *et al.* 1998; Giometto *et al.* 2013; Gjoni *et al.* 2023; Jacquet *et al.* 2020; Li 2002; Long & Morin 2005; Meehan *et al.* 2004; Morán *et al.* 2010; White *et al.* 2004, 2007). The size-abundance relationship can also connect community-level ecological processes with the effect of various environmental factors and hence may be used to predict how communities will be reshaped by environmental change (Gjoni *et al.* 2023; Gjoni & Glazier 2020).

Theory postulates that size-abundance relationships link community size structure with ecosystem functioning through "energy equivalence" (Brown *et al.* 2004; Nee *et al.* 1991) when body size and abundance scale inversely to metabolic rate. This contrasting pattern was first recognized by Damuth (1981) who showed that abundance scaled with body size according to $\text{mass}^{-0.75}$, while metabolic rate is assumed to scale with mass with a power of 0.75. Energetic equivalence implies that the energy flux per unit area—calculated as the product of metabolic rate and abundance—remains constant and independent of body size. In other words, energy flux per unit area is independent of body size, i.e., mass^{0}, implying that population energy use is independent of body size. Energy equivalence is grounded in the notion that the abundance of a population directly depends on the availability of their resources. An increased resource input should thus lead to a corresponding increase in population abundance.

Despite these theoretical predictions, it remains unclear whether the expected size-abundance relationship is robust to environmental change and alterations in biodiversity. Body size and abundance are responsive to biotic and abiotic factors, which may lead to changes in the size-abundance scaling when either the abundance of small or large organisms is particularly affected (Gjoni *et al.* 2023). Indeed, deviations from the expected -0.75 slope for the size-abundance have been observed (Arim *et al.* 2011; Gjoni *et al.* 2017, 2023; Gjoni & Basset 2018; Gjoni & Glazier 2020; Long & Morin 2005; Meehan *et al.* 2004), suggesting that energy used may not be the same across all organism sizes (Nee *et al.* 1991) and that the size-abundance scaling is not as invariant as assumed. However, the abiotic and biotic drivers of size-abundance scaling are rarely systematically investigated.

Warming often leads to higher abundance of smaller organisms relative to larger ones, leading to a change in size-abundance scaling (Gjoni *et al.* 2023; Gjoni & Glazier 2020; Morán *et al.* 2010;

Pomeranz *et al.* 2022). The metabolic theory of ecology (MTE) predicts that increased temperatures accelerate biochemical reactions, speeding up metabolism exponentially and hence requiring more energy to maintain basic physiological functions (Brown *et al.* 2004; Gillooly *et al.* 2001). As a consequence, warmer conditions decrease the carrying capacity (i.e. biomass at equilibrium) because the same energy supply can only support a smaller number of individuals (Allen *et al.* 2002). If temperature affects all organisms similarly regardless of size, as assumed by the MTE, then temperature should not alter the size-abundance relationship (Fig. 1a). The temperature-size rule describes that organisms often exhibit smaller body sizes in warmer conditions (Adams *et al.* 2013; Atkinson 1995; Daufresne *et al.* 2009; Finkel *et al.* 2010; Gardner *et al.* 2011; Sheridan & Bickford 2011). This reduction in size leads to lower absolute energy requirements, hence more individuals can be supported by the same amount of energy. However, if all organisms shrink similarly due to temperature, as implied by the temperature-size rule, we do not expect any change in the size scaling. However, empirical evidence shows that the expected -0.75 slope in the size-abundance relationship often varies (Gjoni *et al.* 2023; Morán *et al.* 2010; Perkins 2022; Pomeranz *et al.* 2022; Saito *et al.* 2021). Furthermore, it is known that species interactions are sensitive to the environmental context (reviewed by Tylianakis *et al.* 2008), in particular, to temperature (Burnside *et al.* 2014) and size (Freckleton & Watkinson 2001).

Few studies on size-abundance relationships have so far explicitly considered the biotic context of, for example, community composition and species richness (but see Long *et al.* 2006; Long & Morin 2005). Biodiversity can play a critical role in shaping the size-abundance relationship due to species interactions that determine community resource use and structure. Research on biodiversity-ecosystem functioning has, for example, revealed that increased biodiversity, particularly species richness, consistently leads to higher community abundance (Hooper *et al.* 2005; Tilman *et al.* 2001). Higher community abundance can be driven by the selection effect where highly productive species are more likely to occur in species-rich communities, and the complementarity effect, where resource partitioning among species can reduce competition and lead to higher community biomass (Blackburn & Gaston 1996; Tilman *et al.* 2001). How community size structure is related to biodiversity effects is less well understood. Size variation of, for example, competitive communities is often small (Tilman *et al.* 2004) and there is little evidence that size structure is linked to complementarity or selection effects (but see Norkko *et al.* 2013) suggesting that size-abundance scaling should not be affected by species richness per se (Figure 1a). However, larger organisms are often competitively superior, as increased richness intensifies asymmetric resource competition, but the ecological context can mediate whether larger or smaller species are favored (Lawton & Hassell 1981; Gómez & González-Megías 2002). Therefore, high richness may lead to either a shallower or steeper size-abundance slope depending on whether larger or smaller species gain a competitive edge in more species-rich communities (Fig. 1c).

Temperature and diversity can also interactively shape the size-abundance relationship, if they disproportionally affect the interactions between larger and smaller organisms (Fig. 1b). Higher temperatures tend to reduce the number of larger individuals, due to their higher metabolic demands, creating a competitive advantage for smaller individuals due to their lower resource requirements (Petchey *et al.* 1999). Temperature may also counteract some of the positive biodiversity effects observed at higher richness due to direct negative physiological effects on biomass, leading to shallower or even negative biodiversity-abundance relationships (Parain *et al.* 2019; Pennekamp *et al.* 2018). Since interactive effects of temperature and diversity on the size-relationship are difficult to disentangle in observational data, dedicated experimental approaches are required to address this question.

Effects of biotic and abiotic factors on the size-abundance scaling may further vary through time, since ecological communities are complex, adaptive systems which exhibit temporal dynamics in response to both biotic and abiotic factors (McGrady-Steed *et al.* 1997). Over time, changes in temperature and biodiversity may alter the relative proportions of organisms of different sizes within a community. Due to the equilibrium assumptions of the energy equivalence (Brown *et al.* 2004; Nee *et al.* 1991), we would expect the slope to converge to -0.75 in the long run. Indeed, experimental studies have shown that closed communities with controlled species richness (e.g., low vs. high richness) converge to a stable size-abundance relationship (Fig. 1d; Long & Morin 2005). In contrast, natural communities can exhibit fluctuating size-abundance relationships over time, driven by dynamic species interactions and environmental variability (Fig. 1e; White *et al.* 2004) that deviate from the expected slope. Whether temporal changes in the size-abundance scaling are further modulated by environmental change is currently unknown.

Here, we investigated the size-abundance relationship across temperature and biodiversity (i.e., initial species richness) in controlled experimental microcosms over a six-week period (Pennekamp *et al.* 2017, 2018). All protist communities were initially started from the same set of species, thus changes in size and abundance were integrating both phenotypic change in size and abundance. Based on a null model informed by the MTE, we hypothesize the following (1) size-abundance relationship follows a slope of -0.75, (2) this slope remains unchanged regardless of temperature or species richness, with only the intercepts varying, and (3) the slope converges to -0.75 over time. To test these predictions, we tracked the cross-community size relationship across communities varying in richness (from 1 to 6 species) and temperature (from 15 to 25°C). We examined cross-community size relationships that aggregate size and abundance at the community level, by relating the average individual size of a community with its total abundance across different communities (White *et al.* 2007). We assessed the role of species interactions by comparing experimentally assembled multi-species communities to simulated "communities without species interactions," where single-species data were pooled to match the richness and composition of the

experimental communities. Unlike previous observational studies, this controlled approach allowed us to directly test how temperature and diversity jointly shape size-abundance scaling. Our results confirmed that the initial slope of the size-abundance relationship approximated -0.75, but temperature and diversity interactively altered it, challenging its assumed invariance. Notably, the slope was stable at first but became shallower over time, suggesting that species interactions mediate the effects of temperature, diversity, and temporal dynamics on size-abundance scaling.

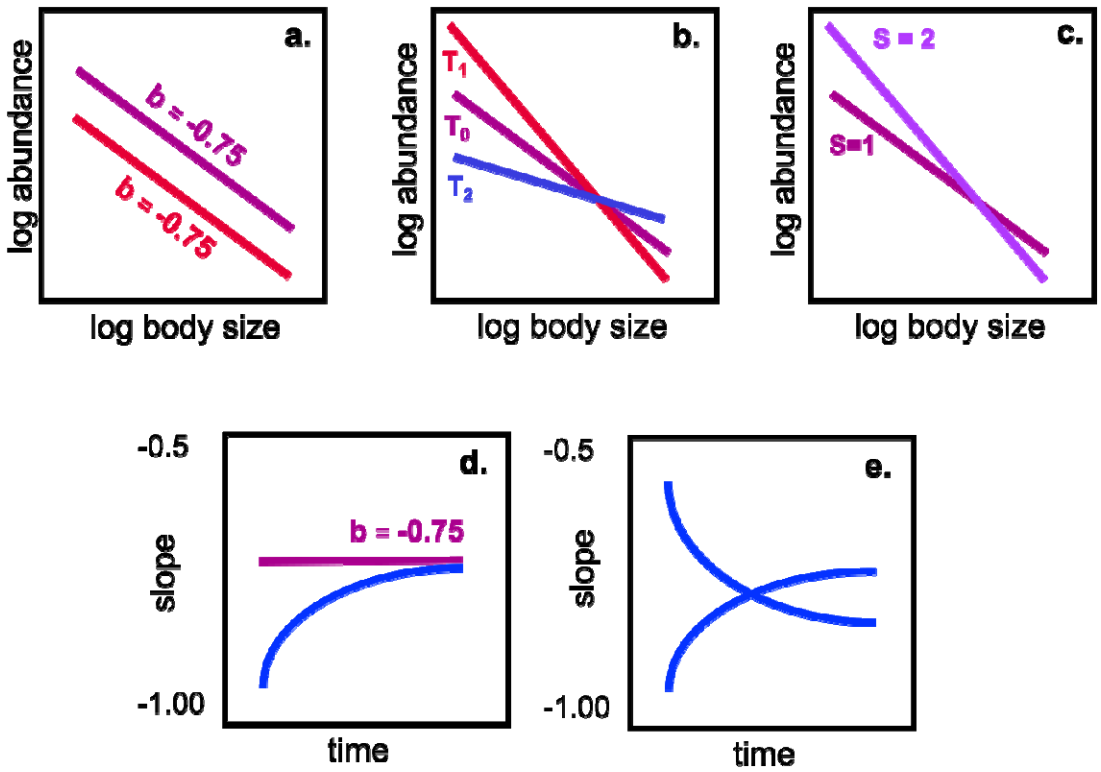


Figure 1 Conceptual overview of size-abundance relationships across temperature and diversity. a) Temperature and diversity may affect abundance and size regardless of the size of individuals, which may lead to changes in the intercept, but not the scaling. In contrast, smaller or larger individuals may be favored at b) higher (T1) or lower temperature (T2), or c) lower or higher species richness, leading to changes in the size-abundance scaling. Over time, the size-abundance relationship may be stable or converge to the expected slope of -0.75 (d), or show more variable trajectories with endpoints that differ from the expected slope.

MATERIALS & METHODS

We used microcosms to test the effect of temperature and species richness on size-abundance scaling. To this end, we factorially manipulated temperature (15, 17, 19, 21, 23, and 25 °C) and species richness (1 to 6 species) in communities of six bacterivorous ciliate species: *Colpidium striatum*, *Dexiostoma campylum*, *Loxocephalus* sp., *Paramecium caudatum*, *Spirostomum teres*, and *Tetrahymena thermophila*. These species span a cell length gradient ranging from ~30 μm to 400 μm.

The species were cultured in organic protist pellet medium on which the freshwater bacterium *Serratia fonticola* was inoculated as the sole protist food source. Due to the non-sterile handling of cultures, additional bacteria may have colonized the microcosms throughout the experiment. The organic medium consisted of protist pellets (Carolina Biological Supplies, Burlington, NC) at a concentration of 0.55 g per L of Chalkley's medium, and two wheat seeds for slow nutrient release (for details on cultivation and experimental procedures, see also Altermatt *et al*. (2015)). Stocks of protist cultures (monocultures) were established before the start of the experiment to inoculate the microcosms. Single species cultures (richness = 1) were started at a density of three individuals per mL in 100 mL medium kept in 250 mL Duran bottles. Multispecies communities with species richness ranging from 2 to 6 species were initiated as a fixed fraction of the species-specific carrying capacity. Therefore, communities were assembled at fixed initial richness. Since communities were closed to dispersal, richness can only decrease, and species may be lost due to extinctions. We replicated each level of species richness and composition at least twice for all levels including an additional replicate for the lowest and additional three replicates for the highest levels of species richness resulting in 115 experimental units per temperature. Cultures communities were randomly assigned to their temperature level and placed in climate-controlled incubators (Pol-Eko Aparatura, Wodzislaw, Poland) set to 15, 17, 19, 21, 23, or 25 °C. We used two independent incubators for each temperature level.

To measure abundance and size of individual cells, we sampled each experimental unit every day for the first 7 days, then 3 times per week for the following 50 days, and a final sampling 7 days later. Each sample was analyzed with automated video species classification analysis (Pennekamp *et al.* 2015, 2017) where we measured the abundance and size of every population using five-second videos (at 25 frames per second). Using the video microscopy data we calculated the average size (i.e., volume) and abundance of each species (Supplementary material section S1). We calculated individual cell volume based on cell length and width measurements using the following equation: cell volume = 4/3 * pi * width /2) ^ 2 * length/2 (Laakso *et al.* 2003). Volume is reported in microlitre. Abundance was calculated by counting the number of individuals of a given species on the 50th frame of a video, thus avoiding double counting of individuals, and then upscaled to density per mL.

Monocultures and polycultures had different starting densities; therefore, we aligned the time series to make the dynamics directly comparable. To do so, we only consider monoculture time series after reaching 20% of their carrying capacity, in correspondence with the polyculture time series as done previously (Pennekamp *et al.* 2018). The alignment did not influence the qualitative patterns observed over the full experimental period. Time series were cut to have a maximum length of 42 days. Alignment of mono- and polyculture time series led to differences in the time points where abundance and size were measured. We used cubic hermite splines to interpolate the mean abundance and mean volume of species in each experimental microcosm. We manually checked that

interpolations closely agreed with the size and abundance dynamics observed. In rare cases, when either negative abundances or volumes resulted from the interpolation, we discarded the observation. For all subsequent analyses (size-abundance scaling and its temporal dynamics), we only considered every second time point to minimize temporal autocorrelation and to not artificially increase the sample size due to the interpolation. We then calculated the cross-community size relationship relating total community abundance (sum of the abundance of all species in the community) and the weighted mean size of an individual in the community (White *et al.* 2007).

We used a regression approach to quantify the relationship between abundance (response) and size, richness and temperature in our controlled microcosm communities. We scaled size, temperature and richness treatments (by subtracting the respective mean from all values) to facilitate the interpretation of model coefficients (Schielzeth 2010). The random structure for all models consisted of a random intercept for community composition and a random intercept for incubator. We then perform four analyses: 1) we estimated the overall cross-community scaling relationship across protist communities, regressing total abundance on mean individual size (White *et al*. 2007). 2) We regressed total abundance on mean individual size, temperature, and richness as well as all interactions between main effects averaged over time. We included all possible interactions of the 3-way interactions models (cell volume x temperature x richness). 3) We fitted the previous model (3 main effects and all possible interactions, same random effects) to each time point to understand how estimates change through time. 4) To understand the role of species interactions on the size-abundance scaling relationship, we simulated polycultures without interactions by pooling monoculture data with the same richness and composition as the real polycultures that we studied experimentally. We then used the same model as 3) to compare the effects of size, richness, and temperature, as well as their interactions between the simulated and real communities. Deviations in coefficient estimates would be putatively driven by species' interactions. All analyses were performed in the statistical computing environment R (version 3.6.1).

RESULTS

Interacting temperature and richness effects on size-abundance relationship

Averaging over time, we found a strong negative relationship between total abundance and average cell volume (b = -0.71, CI = -0.777 to -0.644) across community richness and temperature treatments, undistinguishable from the expected value of b = -0.75 (Fig. 2A). Although deviations from the linear fit are visible, they disappear when data was stratified by richness (Fig. 2B).

Including temperature and richness in the model (Table 1), the size-abundance slope (b = -0.749 CI = -0.813 to -0.685) perfectly matched the expected value. However, temperature and richness jointly changed the effect of size on abundance (volume:temperature coefficient = -0.015, CI = -0.024 to -0.005 and volume:richness coefficient = -0.055, CI = -0.100 to -0.010). The effect of size on abundance was furthermore mediated by a three-way interaction (volume:temperature:richness

coefficient = -0.012, CI = -0.018 to -0.007). In other words, at low richness, the abundance of small and large protists was not affected by temperature (similar slope), whereas in more species rich communities, temperature increased the abundance of smaller protists relative to larger ones, resulting in a steeper size-abundance scaling (Fig. 3, Table 1). For a complementary view, stratifying by richness within temperature, refer to section S2 of the supplementary material.

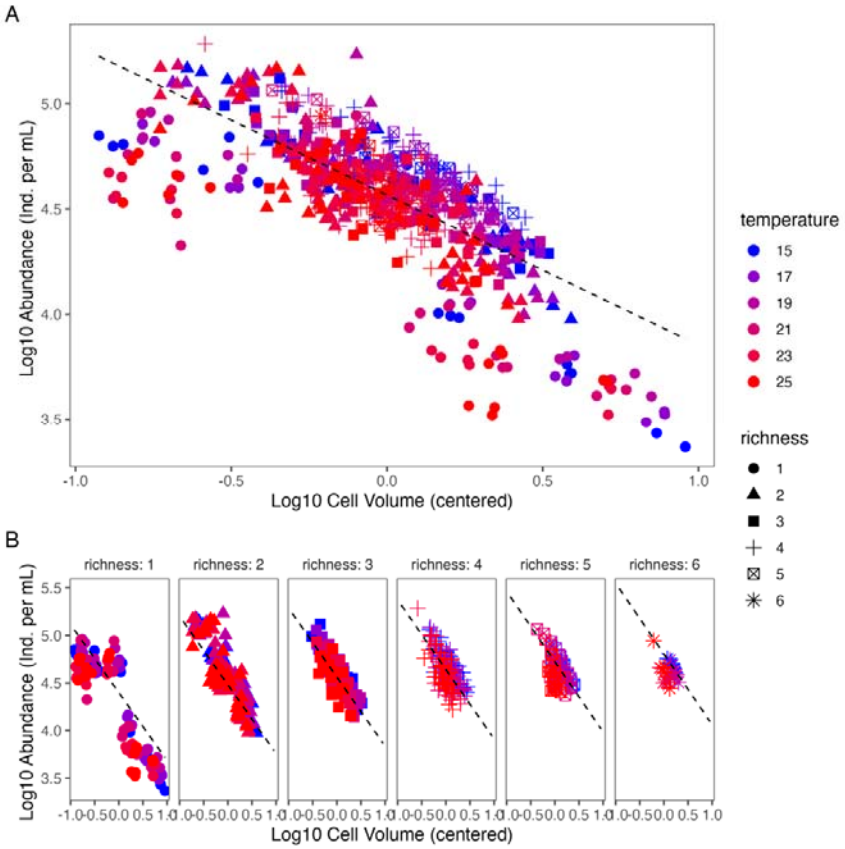


Figure 2 The relationship between centered average log10 cell volume (µm µL^{-1}) and average $\log_{10}$ total abundance of protist communities approximated with a simple linear fit (A). Deviations are visible at the lowest (< -0.5 log cell volume) and largest average cell sizes (> 0.5 log cell volume) but disappear when we stratify by richness (B).

Table 1 Temperature and species richness interact to affect the size-abundance relationship across protist communities. All predictors were mean centered for the analysis. Confidence intervals (CI) not overlapping with zero are significant. All terms including the effect of volume on abundance are shown in bold.

Term	Estimate [95% CI]
Intercept	4.564 [4.524, 4.603]
volume	-0.749 [-0.813, -0.685]
temperature	-0.019 [-0.023, -0.014]
richness	0.080 [0.051, 0.109]

volume:temperature	-0.015 [-0.024, -0.005]
volume:richness	-0.055 [-0.100, -0.010]
richness:temperature	-0.003 [-0.004, -0.001]
volume:temperature:richness	-0.012 [-0.018, -0.007]

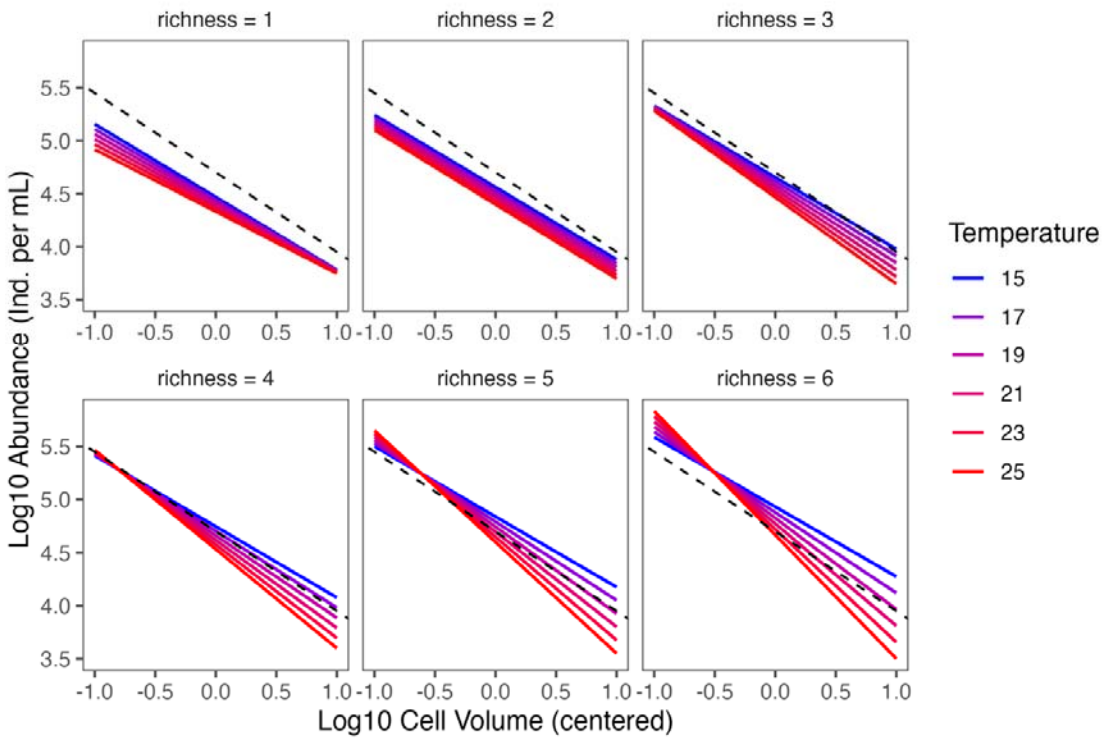
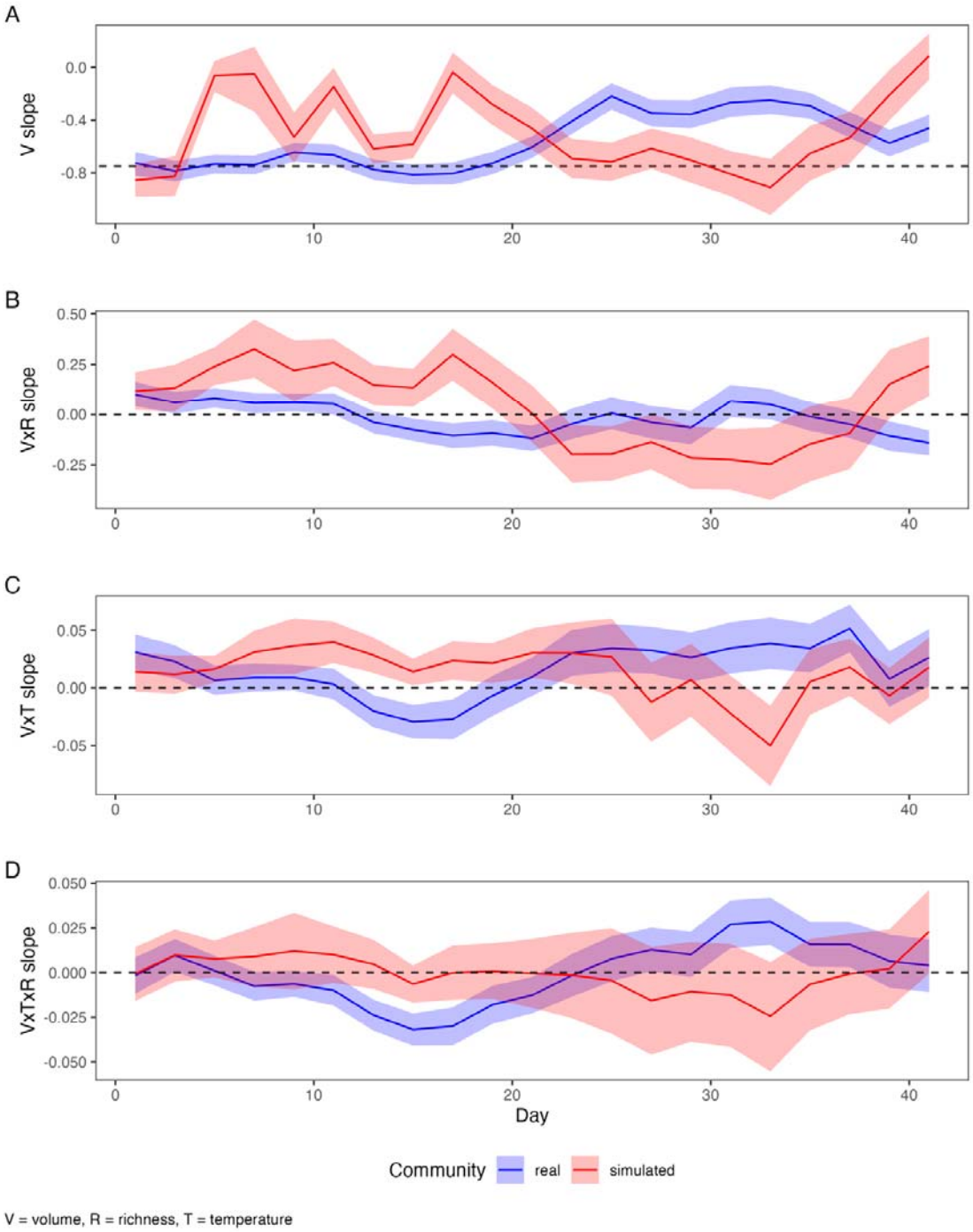


Figure 3 Temperature and richness interact to alter size-abundance relationships of protist communities. The dashed line indicates the expected size-abundance scaling of -0.75. The figure shows the fitted size-abundance scaling based on the model presented in Table 1.

The size-abundance relationship through time

At the beginning of the experiment, the size abundance slope was steeper (b = -0.9) than expected but then stabilized around the expected slope of b=0.75 until day 20. Afterwards the size-abundance slope became considerably shallower than expected (b = -0.35). Similar temporal patterns were observed when we used community evenness accounting for species extinctions and changes in relative abundance (see Section S3). In other words, initially, communities with small average individual size tended to have higher abundance, then, average community size led to expected abundance, while at the end, communities with higher average size had higher abundance than expected (Fig. 4A).



V = volume, R = richness, T = temperature

Figure 4: Temporal dynamics of effect sizes (and 95% confidence intervals) of a linear mixed-effects model where abundance is modelled as a function size (V = volume), temperature (= T) and richness (= R) and their interactions for the real (observed) and simulated communities (in blue and red, respectively). The x-axis shows the day. A) Effect of cell size (V) on abundance, B–C) effect of two-way interactions between size and temperature (V x T), size and richness (V x R) on abundance. D) Three-way interaction between size, temperature and richness (V x T x R) on abundance. The dashed lines indicate a slope of -0.75 in panel A and zero in panels B–D (a deviation from zero would indicate a slope modification).

Temporal analysis of the size-abundance slope revealed that temperature (V x T) initially promoted larger organism sizes (Figure S3). However, after day 15, higher temperatures favored smaller organisms. By the end of the experiment, the temperature effect was no longer significant. In contrast, species richness (V x R) initially reduced the effect of cell size. After day 20, the effect reversed, with richness promoting larger organisms. Finally, the interactive effect of temperature and species richness (V x T x R) on size structure was negative after day 10, became positive from days 14 to 20 and 25 to 35, and was non-significant in between. These changes resulted in changes in the predicted slopes through time, with high richness communities being more strongly affected by temperature than low richness communities (see section S4). Finally, we compared the temporal dynamics of the real, observed polycultures in which species engage in positive or negative interactions, with simulated polycultures without such species interactions (Fig. 4). At the beginning of the experiment, simulated communities had a steeper size-abundance slope than expected, indicating a higher relative abundance of smaller organisms. After day 14, the slope of simulated communities became shallower, approaching -0.40 by day 20, in contrast to the real communities that maintained a slope of -0.75 until day 20 (Fig. 4A). By day 30, the slope of simulated communities returned to the expected value, while real communities became increasingly shallow. The combined effect of temperature and richness (V x R x T) showed no significant influence throughout the experiment, indicating that the impact of temperature on the size-abundance slope was not dependent on community richness, unlike the more dynamic responses seen in real protist communities (Fig. 4D).

DISCUSSION

Our study revealed that the size-abundance relationship of protist communities is mediated by temperature, biodiversity (i.e., initial species richness), and time. The shift in the size-abundance slope with temperature and diversity challenges the widely held assumption that size-abundance relationships remain stable within a trophic level across time and space (Damuth 1981; Enquist & Niklas 2001; Niklas & Enquist 2001). As expected, we found a negative relationship (b ~ -0.75) between abundance and body size across species richness, and temperature, in line with the expected slope of the energy equivalence (Damuth 1991; Nee *et al.* 1991). This is consistent with other studies that have used cross-community size scaling to test energetic equivalence and found the same slope value across phytoplankton (Li 2002), macroinvertebrate, amphibian, and fish (Arim *et al.* 2011) communities, as well as across rodent (White *et al.* 2004) and tree communities (Enquist *et al.* 1998). The size-abundance relationship is typically mirrored by the metabolic rate, which follows a 0.75 scaling exponent with mass (Brown *et al.* 2004), implying a slope of -0.75 for the size-abundance relationship. This alignment is seen in natural and experimental phytoplankton communities, where the scaling slope is close to -0.75 (Malerba *et al.* 2017; Perkins *et al.* 2019). In contrast, an

experimental study using protist communities initially divided into low and high species richness showed no change over time with a cross-community size scaling of -1, which converged over time (Long & Morin 2005).

Our experiment revealed a size-abundance scaling close to -0.75, suggesting that the scaling of metabolic rate with body size may be a possible explanation. However, when we explicitly considered the abiotic and biotic context of communities, we found that the size-abundance relationship of protist communities is mediated by temperature, biodiversity and their interaction. Interacting effects between size-abundance scaling and temperature as well as diversity, are inconsistent with energetic equivalence. In our high-richness communities, small organisms were favored (more abundant than expected) with high temperature, whereas large organisms were favored (more abundant than expected) when the temperature was low. Smaller organisms have lower absolute resource requirements (Gillooly *et al.* 2001; Reuman *et al.* 2014), allowing for a higher number of smaller organisms to be sustained (Li *et al.* 2006; Morán *et al.* 2010). Temperature may lead to smaller organisms on average according to the temperature-size rule (Atkinson *et al.* 2003), however, this physiological effect will affect organisms regardless of their size. Therefore, this cannot explain the observed changes in size-abundance scaling, requiring additional explanations. Species richness increased abundance, which is in line with experimental evidence that increasing the number of species (i.e., in this case, competing for the same resources, such as bacteria) increases the total acquisition of resources due to complementarity (Gómez & González-Megías 2002). However, richness did not interact with size, suggesting that complementarity and selection effects are not size-dependent in our communities. So how can we explain changes in size-abundance scaling across temperature and species richness gradients?

Species interactions are major determinants of community structure and have been found to be strongly temperature-dependent (Burnside *et al.* 2014; Jiang & Morin 2004). The observed interactions may hence be driven by temperature-dependent size asymmetries in resource competition (Cotgreave 1993; Nee *et al.* 1991; Russo *et al.* 2003), since high richness communities with stronger interactions were particularly affected. Asymmetric competition results from the differential ability of species to occupy higher positions in a competitive hierarchy (Freckleton & Watkinson 2001). Competitive asymmetries between small and large species further depend on various biotic and abiotic ecological factors (Gjoni & Glazier 2020; Morán *et al.* 2010; Pomeranz *et al.* 2022). Resource acquisition is fueled by metabolism, and the metabolism increases with higher temperatures by accelerating the rates of biochemical reactions (Brown *et al.* 2004). Temperature hence may intensify competition and also affect which species is the dominant competitor for resources (Carson & Root 2000; Clements *et al.* 2014; Gillooly *et al.* 2001; Jiang & Morin 2004; Long & Morin 2005; Reuman *et al.* 2014; Schmitz 2003). Consequently, these processes may drive the observed dominance of smaller organisms in more species rich communities at high temperature, while larger organisms

dominate in communities at low temperature, where they remain competitively superior due to larger access to resources.

Previous analyses on protist communities have indeed shown that species interactions become more asymmetric when temperatures rise. Tabi et al. (2020) have shown that this leads to lower coexistence of protist communities and a decoupling between abundance in isolation and abundance in communities. We provide indirect evidence of this process by comparing the temporal dynamics of size-abundance scaling in simulated communities and observed polycultures. In real polycultures, the initial slope aligned with the expected slope of -0.75, and over time, there was an interactive effect of size, temperature and richness. In contrast, this pattern did not occur in simulated polycultures, as they lack the influence of species interactions. Maynard et al. (2020) estimated coefficients that describe temperature effects on species interactions, showing mostly negative effects of temperature and decreasing coefficients across the temperature gradient. Jointly, this suggests that the observed steepening of the size-abundance scaling in high richness communities at high temperature is driven by species interactions that are both temperature-dependent and size asymmetric.

Our results revealed that size-abundance scaling is dynamically changing through time. Contrary to our expectations, the slope of the size-abundance relationship was remarkably stable during the first half of the experiment but deviated from the value of -0.75 by the end of the experiment, hence indicating a higher proportion of larger individuals in the community. These results are inconsistent with the MTE which predicts that given a sufficient amount of time, communities should converge on a line of constant yield and energy use should be independent of body size (Brown *et al.* 2004; Brown & Gillooly 2003). Our findings showing variation in the size-abundance relationship over time implies that larger individuals acquire more energy than smaller individuals after sufficient time for community development. These findings align with previous research, which proposed that larger individuals may gain greater access to resources compared to the smaller ones when resources become scarce in protist communities (Tabi *et al.* 2019). Furthermore, in experiments with phytoplankton conducted over time, larger individuals tend to show a higher proportion relative to the smaller ones (Malerba & Marshall 2019). The dominance of larger protists relative to smaller ones may be explained by their ability to efficiently store resources (e.g., food intake), enabling them to better endure periods of resource scarcity (Fenchel 1980; Thurman *et al.* 2010). The hypothesis (Millar & Hickling 1990) that larger species may have more endurance under fasting conditions and their ability to accumulate more resources, provides a compelling explanation for the deviation from the -0.75 slope observed towards the end of the experiment. This hypothesis is plausible because experimental studies have shown that larger cells, relative to smaller ones, promote the use of storing resources in microbial organisms (Malerba *et al.* 2018). Thus, they maintain resource use efficiency even as nutrient level change over time (Marshall *et al.* 2022). Similar findings were reported for a field study, where changes in the average size of individual species and changes in species composition influenced the evolving size-abundance relationship over time (White *et al.* 2004).

Our study system differs in certain ways from natural systems, which should be considered when interpreting the results. First, we do not assess community turnover as an important mechanism affecting community size structure under warming (Khaliq *et al.* 2024), since we did not allow for colonization by warm-adapted species/genotypes. Second, microcosms are closed systems whose supply of energy, despite replenishment, is not constant through time. While all microcosms have initially received the same amount of resources, protist feed on bacteria, which could influence the composition of the ciliate communities (Saleem *et al.* 2013) and hence potentially their dynamics. The temporal effects observed therefore needed to be judged cautiously; in contrast to changing temperature and biodiversity, they hence do not provide strong evidence against energetic equivalence. Third, we do not know whether the observed changes in size-abundance scaling are only driven by short-term responses (i.e., phenotypic plasticity), or also include evolutionary responses that may have occurred over the timescale of the experiment. Despite these differences, our approach provides important complementary insights to analyses of size-abundance scaling in natural communities.

CONCLUSION

Our experiments suggest that temperature and species richness play an important role in shaping the size structure of ecological communities through time. We hence caution against assuming that energy flux is size-independent in dynamic ecosystems, as changes in the biotic and abiotic environment may change community size structure and hence the flow of energy. Testing these assumptions with experimental communities provided new insights into the mechanisms driving community size responses to environmental change, improving our ability to predict how biodiversity may influence the size structure of communities in the face of global environmental change.

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REFERENCES

Allen, A.P., Brown, J.H. & Gillooly, J.F. (2002). Global Biodiversity, Biochemical Kinetics, and the Energetic-Equivalence Rule. *Science*, 297, 1545–1548.

Altermatt, F., Fronhofer, E.A., Garnier, A., Giometto, A., Hammes, F., Klecka, J., *et al.* (2015). Big answers from small worlds: a user's guide for protist microcosms as a model system in ecology and evolution. *Methods Ecol Evol*, 6, 218–231.

Arim, M., Berazategui, M., Barreneche, J.M., Ziegler, L., Zarucki, M. & Abades, S.R. (2011). Determinants of Density–Body Size Scaling Within Food Webs and Tools for Their Detection. In: *Advances in Ecological Research*, The Role of Body Size in Multispecies Systems (ed. Belgrano, A.). Academic Press, pp. 1–39.

Atkinson, D., Ciotti, B.J. & Montagnes, D.J.S. (2003). Protists decrease in size linearly with temperature: ca. 2.5% per degree Celsius. *Proceedings of the Royal Society of London B: Biological Sciences*, 270, 2605–2611.

Bierbaum, T.J., Mueller, L.D. & Ayala, F.J. (1989). DENSITY-DEPENDENT EVOLUTION OF LIFE-HISTORY TRAITS IN DROSOPHILA MELANOGASTER. *Evolution*, 43, 382–392.

Brown, J.H. & Gillooly, J.F. (2003). Ecological food webs: High-quality data facilitate theoretical unification. *Proceedings of the National Academy of Sciences*, 100, 1467–1468.

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

Burnside, W.R., Erhardt, E.B., Hammond, S.T. & Brown, J.H. (2014). Rates of biotic interactions scale predictably with temperature despite variation. *Oikos*, 123, 1449–1456.

Carson, W.P. & Root, R.B. (2000). Herbivory and Plant Species Coexistence: Community Regulation by an Outbreaking Phytophagous Insect. *Ecological Monographs*, 70, 73–99.

Clements, C.F., Collen, B., Blackburn, T.M. & Petchey, O.L. (2014). Effects of directional environmental change on extinction dynamics in experimental microbial communities are predicted by a simple model. *Oikos*, 123, 141–150.

Cotgreave, P. (1993). The relationship between body size and population abundance in animals. *Trends in Ecology & Evolution*, 8, 244–248.

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

Damuth, J. (1991). Of size and abundance. *Nature*, 351, 268–269.

Enquist, B.J., Brown, J.H. & West, G.B. (1998). Allometric scaling of plant energetics and population density. *Nature*, 395, 163–165.

Enquist, B.J. & Niklas, K.J. (2001). Invariant scaling relations across tree-dominated communities. *Nature*, 410, 655–660.

Fenchel, T. (1980). Suspension feeding in ciliated protozoa: Functional response and particle size selection. *Microb Ecol*, 6, 1–11.

Freckleton, R.P. & Watkinson, A.R. (2001). Asymmetric competition between plant species. *Functional Ecology*, 15, 615–623.

Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. & Charnov, E.L. (2001). Effects of Size and Temperature on Metabolic Rate. *Science*, 293, 2248–2251.

Giometto, A., Altermatt, F., Carrara, F., Maritan, A. & Rinaldo, A. (2013). Scaling body size fluctuations. *Proceedings of the National Academy of Sciences*, 110, 4646–4650.

Gjoni, V. & Basset, A. (2018). A Cross-community Approach to Energy Pathways Across Lagoon Macroinvertebrate Guilds. *Estuaries and Coasts*, 41, 2433–2446.

Gjoni, V., Cozzoli, F., Rosati, I. & Basset, A. (2017). Size–Density Relationships: a Cross-Community Approach to Benthic Macroinvertebrates in Mediterranean and Black Sea Lagoons. *Estuaries and Coasts*, 40, 1142–1158.

Gjoni, V. & Glazier, D.S. (2020). A Perspective on Body Size and Abundance Relationships across Ecological Communities. *Biology*, 9, 42.

Gjoni, V., Glazier, D.S., Wesner, J.S., Ibelings, B.W. & Thomas, M.K. (2023). Temperature, resources and predation interact to shape phytoplankton size–abundance relationships at a continental scale. *Global Ecology and Biogeography*, 32, 2006–2016.

Glazier, D.S. (2022). Variable metabolic scaling breaks the law: from 'Newtonian' to 'Darwinian' approaches. *Proceedings of the Royal Society B: Biological Sciences*, 289, 20221605.

Gómez, J.M. & González-Megías, A. (2002). Asymmetrical Interactions Between Ungulates and Phytophagous Insects: Being Different Matters. *Ecology*, 83, 203–211.

Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., *et al.* (2005). Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge. *Ecological Monographs*, 75, 3–35.

Jacquet, C., Gounand, I. & Altermatt, F. (2020). How pulse disturbances shape size-abundance pyramids. *Ecology Letters*, 23, 1014–1023.

Jiang, L. & Morin, P.J. (2004). Temperature-Dependent Interactions Explain Unexpected Responses to Environmental Warming in Communities of Competitors. *Journal of Animal Ecology*, 73, 569–576.

Khaliq, I., Rixen, C., Zellweger, F., Graham, C.H., Gossner, M.M., McFadden, I.R., *et al.* (2024). Warming underpins community turnover in temperate freshwater and terrestrial communities. *Nat Commun*, 15, 1921.

Laakso, J., Löytynoja, K. & Kaitala, V. (2003). Environmental noise and population dynamics of the ciliated protozoa Tetrahymena thermophila in aquatic microcosms. *Oikos*, 102, 663–671.

Li, W.K.W. (2002). Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean. *Nature*, 419, 154–157.

Li, W.K.W., Glen Harrison, W. & Head, E.J.H. (2006). Coherent assembly of phytoplankton communities in diverse temperate ocean ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, 273, 1953–1960.

Long, Z.T. & Morin, P.J. (2005). Effects of organism size and community composition on ecosystem functioning. *Ecology Letters*, 8, 1271–1282.

Long, Z.T., Steiner, C.F., Krumins, J.A. & Morin, P.J. (2006). Species Richness and Allometric Scaling Jointly Determine Biomass in Model Aquatic Food Webs. *Journal of Animal Ecology*, 75, 1014–1023.

Malerba, M.E. & Marshall, D.J. (2019). Size-abundance rules? Evolution changes scaling relationships between size, metabolism and demography. *Ecology Letters*, 22, 1407–1416.

Malerba, M.E., Palacios, M.M. & Marshall, D.J. (2018). Do larger individuals cope with resource fluctuations better? An artificial selection approach. *Proc Biol Sci*, 285, 20181347.

Malerba, M.E., White, C.R. & Marshall, D.J. (2017). Phytoplankton size-scaling of net-energy flux across light and biomass gradients. *Ecology*, 98, 3106–3115.

Marshall, D.J., Malerba, M., Lines, T., Sezmis, A.L., Hasan, C.M., Lenski, R.E., *et al.* (2022). Long-term experimental evolution decouples size and production costs in Escherichia coli. *Proceedings of the National Academy of Sciences*, 119, e2200713119.

Maynard, D.S., Miller, Z.R. & Allesina, S. (2020). Predicting coexistence in experimental ecological communities. *Nature Ecology & Evolution*, 4, 91–100.

McGrady-Steed, J., Harris, P.M. & Morin, P.J. (1997). Biodiversity regulates ecosystem predictability. *Nature*, 390, 162–165.

Meehan, T.D., Jetz, W. & Brown, J.H. (2004). Energetic determinants of abundance in winter landbird communities. *Ecology Letters*, 7, 532–537.

Millar, J.S. & Hickling, G.J. (1990). Fasting Endurance and the Evolution of Mammalian Body Size. *Functional Ecology*, 4, 5–12.

Morán, X.A.G., López-Urrutia, Á., Calvo-Díaz, A. & Li, W.K.W. (2010). Increasing importance of small phytoplankton in a warmer ocean. *Global Change Biology*, 16, 1137–1144.

Mueller, L.D. & Ayala, F.J. (1981). Trade-off between r-selection and K-selection in Drosophila populations. *Proc Natl Acad Sci U S A*, 78, 1303–1305.

Nee, S., Read, A.F., Greenwood, J.J.D. & Harvey, P.H. (1991). The relationship between abundance and body size in British birds. *Nature*, 351, 312–313.

Niklas, K.J. & Enquist, B.J. (2001). Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proc Natl Acad Sci U S A*, 98, 2922–2927.

Norkko, A., Villnäs, A., Norkko, J., Valanko, S. & Pilditch, C. (2013). Size matters: implications of the loss of large individuals for ecosystem function. *Sci Rep*, 3, 2646.

Parain, E.C., Rohr, R.P., Gray, S.M. & Bersier, L.-F. (2019). Increased Temperature Disrupts the Biodiversity–Ecosystem Functioning Relationship. *The American Naturalist*, 193, 227–239.

Pennekamp, F., Griffiths, J.I., Fronhofer, E.A., Garnier, A., Seymour, M., Altermatt, F., *et al.* (2017). Dynamic species classification of microorganisms across time, abiotic and biotic environments-A sliding window approach. *PLoS One*, 12, e0176682.

Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, Y., *et al.* (2018). Biodiversity increases and decreases ecosystem stability. *Nature*, 563, 109–112.

Pennekamp, F., Schtickzelle, N. & Petchey, O.L. (2015). BEMOVI, software for extracting behavior and morphology from videos, illustrated with analyses of microbes. *Ecology and Evolution*, 5, 2584–2595.

Perkins, D.M. (2022). Temperature effects on community size structure: The value of large-scale biomonitoring programs. *Global change biology*.

Perkins, D.M., Perna, A., Adrian, R., Cermeño, P., Gaedke, U., Huete-Ortega, M., *et al.* (2019). Energetic equivalence underpins the size structure of tree and phytoplankton communities. *Nat Commun*, 10, 255.

Petchey, O.L., McPhearson, P.T., Casey, T.M. & Morin, P.J. (1999). Environmental warming alters food-web structure and ecosystem function. *Nature*, 402, 69–72.

Pianka, E.R. (1970). On r- and K-Selection. *The American Naturalist*, 104, 592–597.

Pomeranz, J.P.F., Junker, J.R. & Wesner, J.S. (2022). Individual size distributions across North American streams vary with local temperature. *Global Change Biology*, 28, 848–858.

Reuman, D.C., Holt, R.D. & Yvon-Durocher, G. (2014). A metabolic perspective on competition and body size reductions with warming. *J Anim Ecol*, 83, 59–69.

Russo, S.E., Robinson, S.K. & Terborgh, J. (2003). Size-Abundance Relationships in an Amazonian Bird Community: Implications for the Energetic Equivalence Rule. *The American Naturalist*, 161, 267–283.

Saito, V.S., Perkins, D.M. & Kratina, P. (2021). A Metabolic Perspective of Stochastic Community Assembly. *Trends in Ecology & Evolution*, 36, 280–283.

Saleem, M., Fetzer, I., Harms, H. & Chatzinotas, A. (2013). Diversity of protists and bacteria determines predation performance and stability. *ISME J*, 7, 1912–1921.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1, 103–113.

Schmitz, O.J. (2003). Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecology Letters*, 6, 156–163.

Tabi, A., Pennekamp, F., Altermatt, F., Alther, R., Fronhofer, E.A., Horgan, K., *et al.* (2020). Species multidimensional effects explain idiosyncratic responses of communities to environmental change. *Nature Ecology & Evolution*, 4, 1036–1043.

Tabi, A., Petchey, O.L. & Pennekamp, F. (2019). Warming reduces the effects of enrichment on stability and functioning across levels of organisation in an aquatic microbial ecosystem. *Ecol Lett*, 22, 1061–1071.

Thurman, J., Parry, J.D., Hill, P.J. & Laybourn-Parry, J. (2010). The Filter-Feeding Ciliates Colpidium striatum and Tetrahymena pyriformis Display Selective Feeding Behaviours in the Presence of Mixed, Equally-Sized, Bacterial Prey. *Protist*, 161, 577–588.

Tilman, D., HilleRisLambers, J., Harpole, S., Dybzinski, R., Fargione, J., Clark, C., *et al.* (2004). Does Metabolic Theory Apply to Community Ecology? It's a Matter of Scale. *Ecology*, 85, 1797–1799.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, 294, 843–845.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, 11, 1351–1363.

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

White, E.P., Ernest, S.K.M. & Thibault, K.M. (2004). Trade-offs in Community Properties through Time in a Desert Rodent Community. *The American Naturalist*, 164, 670–676.

SUPPLEMENTARY MATERIAL for

Biodiversity modulates the size-abundance relationship in changing environments

Materials & methods

S1: Video microscopy and processing to calculate abundance and individual size

The videos were taken using a stereomicroscope (Leica M205 C) with a 16-times magnification mounted with a digital CMOS camera (Hamamatsu Orca C11440, Hamamatsu Photonics, Japan). We used the BEMOVI package (Pennekamp *et al.* 2015, version 1.0.2) to process the 18,720 videos collected during the experiment and extract the raw trajectories. Global segmentation and tracking parameters were defined for the automated processing of videos (Pennekamp *et al.* 2017). The difference lag was defined to be 2 seconds, particle size was restricted to 5 to 2000 pixels, and the grey threshold was set to an intensity value of 10. For particle linking, we specified a link range of 3 frames and a displacement of 20 pixels. These settings were optimized using a subset of videos (spanning sampling dates of all single, two, and six species combinations at 15 °C, 21 °C, and 25 °C). Video settings were optimized to rather include false positives rather than exclude true positives at this step, and exclude false positives later in the processing pipeline. For further details regarding video processing, please refer to (Pennekamp *et al.* 2017). After tracking, trajectories were filtered to remove artifacts such as spurious trajectories (e.g., floating debris). Trajectories for analysis were required to show a minimum net 7 displacement of at least 50 μm, a duration greater than 0.2 seconds, and a detection rate of 80 percent (for a trajectory with a duration of 10 frames the individual has to be detected on at least 8 frames), a median step length greater than 2 μm and a minimum mean speed of 50 pixels per second.

We applied machine learning (random forest classification) on quantitative properties such as cell size and shape to predict to which species an individual belongs. We thus identified individuals from all species automatically from the videos and quantified their cell size. Details of the procedure can be found in the supplement (Pennekamp *et al.* 2017) for a detailed description of the experimental design, setup of micro-ecosystems, and sampling regime.

Results

Section S2: Predicting size-abundance scaling across temperature and richness gradients

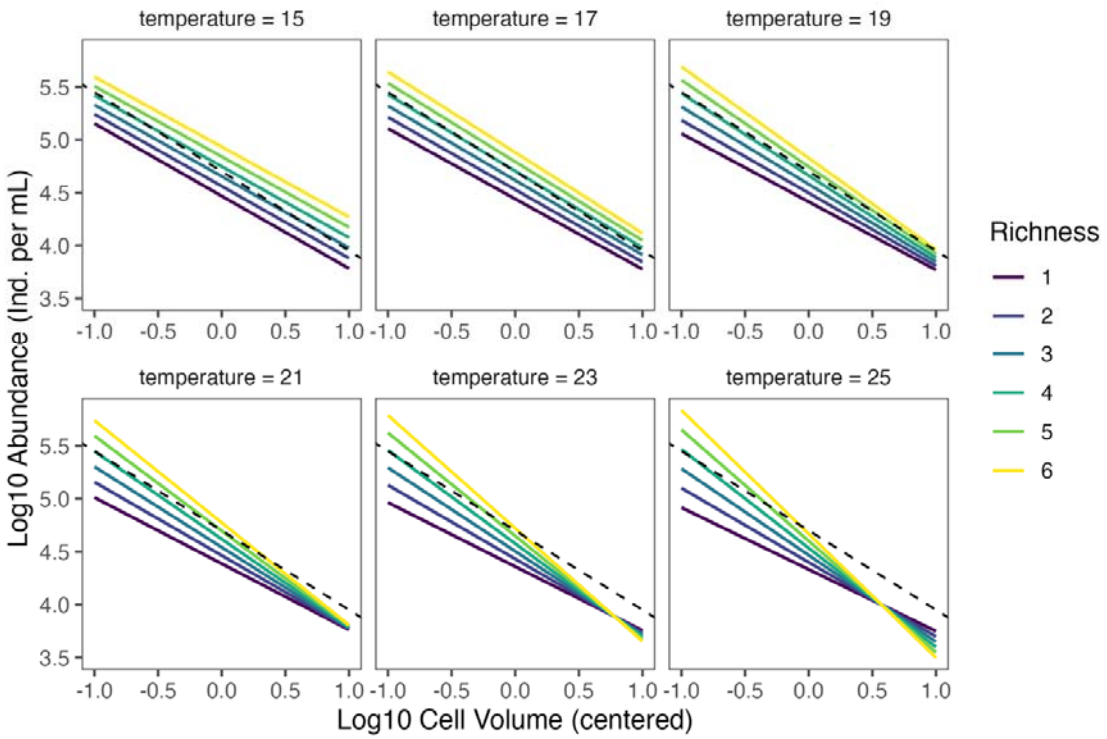

Figure S1 Temperature and richness interact to alter size-abundance relationships across protist communities. This figure is another visualization (see Figure 2) of the mixed model predicting total log10 abundance (number of individuals) with mean log10 cell volume (µm µL-1), temperature (15 °C, 17 °C, 19 °C, 21 °C, 23 °C, and 25 °C), and community richness (1, 2, 3, 4, 5, and 6 species), as well as interactions between those predictors based on the model presented in table 1. The dashed line indicates the expected slope of -0.75.

Section S3: Using evenness as a proxy of realized species richness

We experimentally manipulated initial species richness, but since community assembly and coexistence are dynamic processes where abundances change through time and even extinctions may occur, we also calculated species evenness as a proxy of realized species richness. Since some species may not go extinct, but only reach very low densities, this measure is more appropriate than species richness which turned out to be pretty stable over the duration of the experiment, although some extinctions did occur. Figure S2 shows qualitatively similar trajectories when realized species richness is used rather than initial species richness.

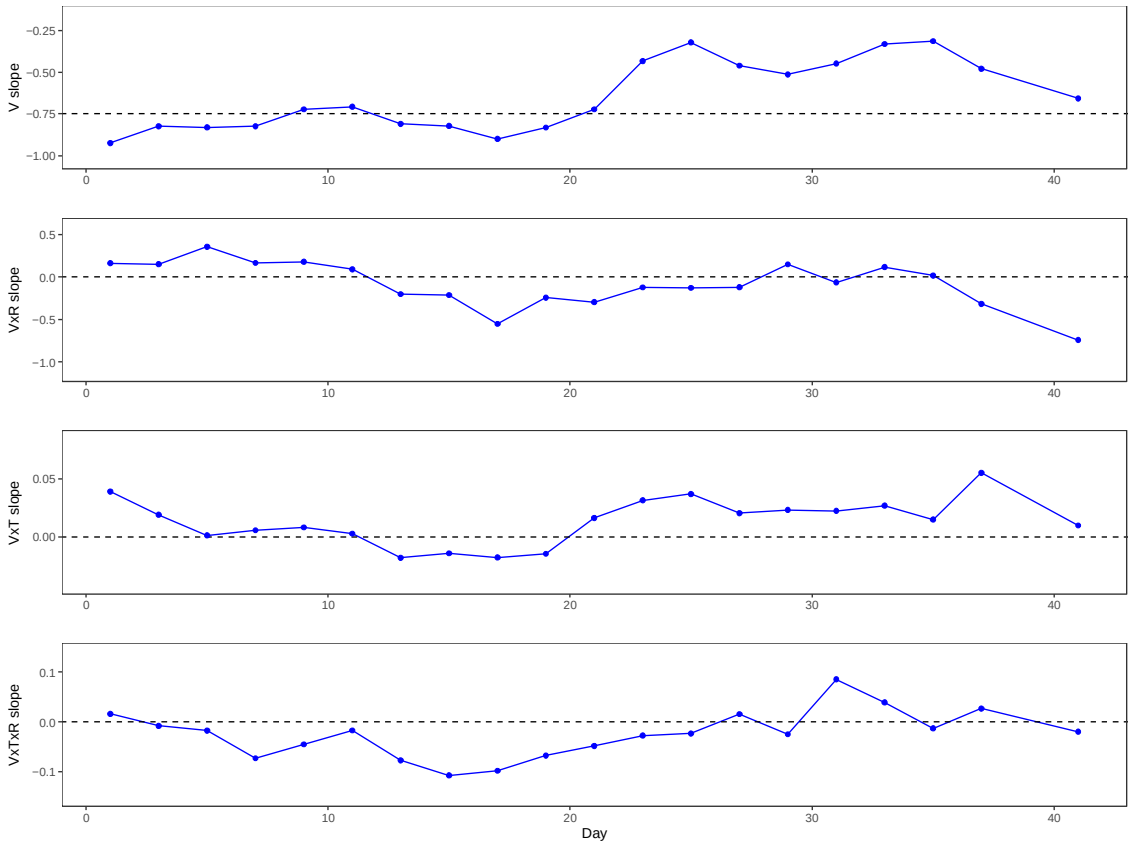

Figure S2: Temporal dynamics of effect sizes (and 95% confidence intervals) of a linear mixed-effects model where abundance is modelled as a function size (V = volume), temperature (= T) and realized richness (= R) and their interactions for the observed communities. The x-axis shows the day. A) Effect of cell size (V) on abundance, B-C) effect of two-way interactions between size and temperature (V x T), size and realized richness (V x R) on abundance. D) Three-way interaction between size, temperature and realized richness (V x T x R) on abundance. The dashed line indicates a slope of -0.75 in panel A and zero in panels B–D.

Section S4: Interactions between size, temperature and richness through time

Temperature and richness influenced the size-abundance relationship in distinct, time-dependent ways when comparing low- and high-richness communities. On day 11, the slope and intercept of the relationship remained stable in both low- and high-richness communities, suggesting that temperature had minimal influence on the relative abundance of small vs. large protists (i.e., no interaction, Fig. S3A). By day 17, temperature caused a steeper slope, indicating a relative increase in smaller protist abundance compared to larger ones, especially across high richness communities (i.e., negative interaction, Fig. S3C). On day 23, size-abundance scaling became shallower with higher temperatures, increasing the abundance of larger individuals compared to smaller individuals in low but not high richness communities (Fig. S3B). On day 29, this pattern was apparent in both low and high richness communities (i.e., positive interaction, Fig. S3D). These shifts highlight the dynamic influence of

temperature and richness on community structure, where the balance between small and large protist abundance is regulated by time-dependent physiological and ecological processes (i.e., species interactions).

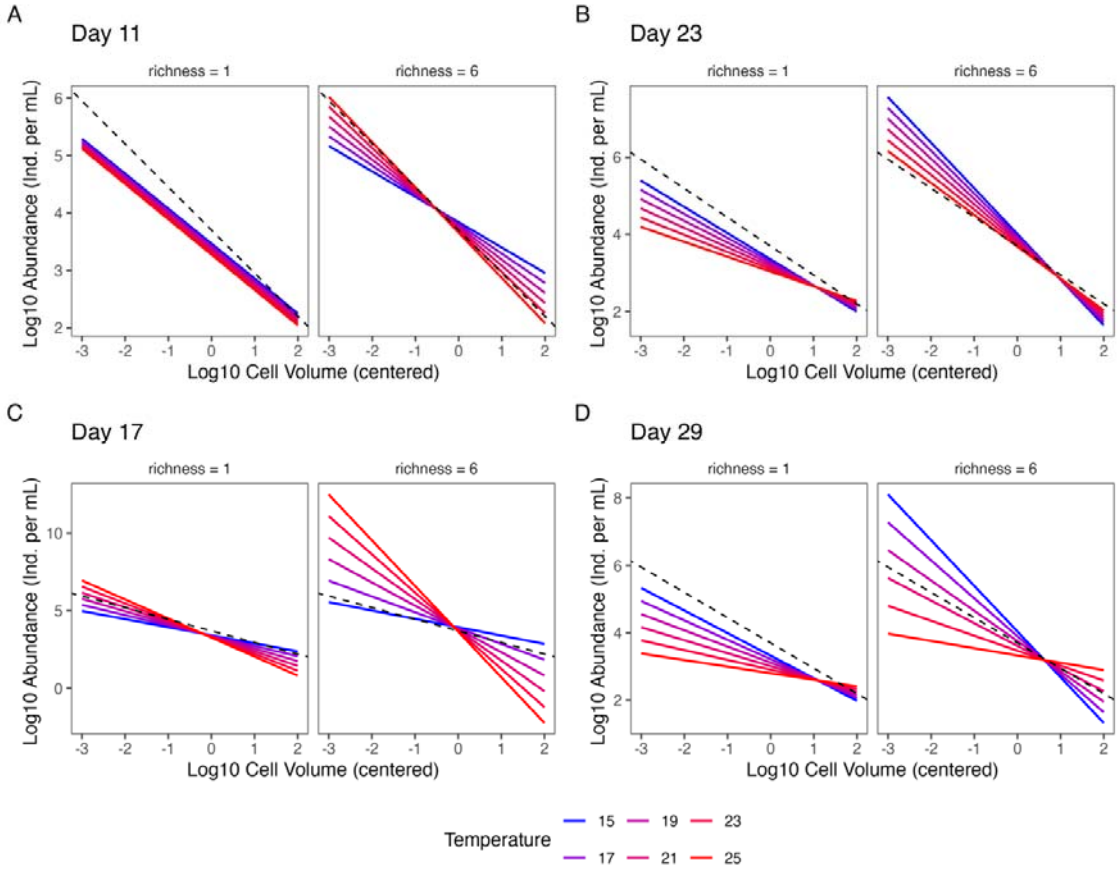

Figure S3: Temperature and community richness alter size-abundance relationships of protist communities across time. This figure is a visualization of the mixed model predicting total log10 abundance with mean log10 cell volume (μm μL^{-1}), temperature (15 °C, 17 °C, 19 °C, 21 °C, 23 °C, and 25 °C), and richness (low = 1 and high = 6 species number), as well as interactions between those predictors across time (A. day = 11, B. day = 17, C. day = 23 and D. day = 29; see Fig. 4D). All predictors were mean-centered for the analysis, but here the actual richness and temperature values are shown). The dashed line indicates the expected slope of -0.75.

Interpretation:

It seems that in warm environments under intense competition, smaller individuals have higher resource-use efficiency in the short-term, whereas, in the long-term, this is true for the larger ones, potentially in combination with higher survival due to the ability to store resources. Previous work has shown that intense competition selects for high resource efficiency and lower metabolism, leading larger individuals to a competitive advantage (Bierbaum *et al.* 1989; Mueller & Ayala 1981; Pianka 1970). In contrast, our study showed that this is true only in cooler conditions and the long-term. This implies that in the short-term and with increased temperature smaller individuals gain a competitive

advantage due to their lower resource demands. Smaller organisms require less energy for growth, reproduction, and activity, allowing them to efficiently acquire resources and outcompete larger individuals. In contrast, larger individuals experience higher resource demands that escalate with temperature, making them less efficient. However, in the long term, larger individuals may survive better compared to smaller ones, being able to exploit available resources. This suggests that, over time, larger organisms are better able to balance resource use under elevated temperatures.