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Metabolic scaling across succession: Do individual rates predict community-level energy use?

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Abstract

1. A major goal of metabolic ecology is to make predictions across scales such that individual metabolic rates might be used to predict the metabolic rates of populations and communities, but the success of these predictions is unclear given the rarity of tests.
2. Given that older communities tend to have species with slower life histories and larger body sizes, we hypothesized that the metabolism of whole communities should scale allometrically with their mass across successional stages.
3. We created experimental chronosequences of sessile marine invertebrate communities in the field. We then (1) determined the metabolic scaling of these whole communities across successional stages of different mass and (2) tested whether the sum of individual metabolic rates for the dominant species could predict overall community metabolism.
4. Contrary to what we expected based on metabolic theory and succession theory, community metabolism scaled isometrically with mass across succession, despite the mean body size of dominant individuals within the communities increasing over time. We resolved this paradox by estimating community metabolism based on individual metabolic rates for the dominant species in the community. We show that non-random changes in the membership of the species maintain mass-specific metabolic rates of the whole community invariant across succession despite changes in size structure.
5. These results suggest that simple assumptions about how community-level processes scale up from species are unlikely to be correct, because community turnover is non-random with respect to metabolic rate. Nevertheless, with the appropriate parametrization, the sum of individual species rates can predict the function of the community as a whole.

KEYWORDS
community ecology, competition, consumption, geometric biology, stability, trophic interactions

1 | INTRODUCTION

Metabolic rate determines the speed at which an organism uses resources and contributes to the flux of energy within a system. Metabolic rate per unit mass usually decreases with increasing body size across a wide range of multicellular species, for which metabolism scales with body mass with an exponent <1 (Brown, Gillooly, Allen, Savage, & West, 2004; Gillooly, Brown, West,

Savage, & Charnov, 2001; Glazier, 2005), whilst metabolism tends to scale isometrically for unicellular organisms (DeLong, Okie, Moses, Sibly, & Brown, 2010; Huete-Ortega, Cermeño, Calvo-Díaz, & Marañón, 2011). A consequence of the negative allometric relationship (<1) is that organismal size determines the efficiency and the rate of resource use within a community (Barneche et al., 2014; Persson & de Roos, 2013). As the total metabolic activity of a community is determined by the sum of individual rates within that community (but not necessarily of individuals taken alone, e.g. Ghedini, White, & Marshall, 2017), then changes in community size structure should influence overall metabolic scaling (Allen, Gillooly, & Brown, 2005). For instance, a community composed of a few large individuals should have cumulative, total metabolic rate that is lower than that of a community of equivalent biomass but composed of smaller individuals. Thus, knowing the size structure of a community (or population) might allow us to anticipate the rate at which the community utilizes resources (Cyr & Pace, 1993; Yvon-Durocher & Allen, 2012).

A major question regarding the role of metabolism in ecology is the extent to which relationships scale across levels of biological organization. Whilst body size is a good predictor of physiological rates across individuals and species, its role in whole communities is unclear. When considering complex systems, metabolic activity might be an emergent property where interactions among various components alter how organismal processes manifest at higher levels of ecological organization (DeLong, Hanley, & Vasseur, 2014; Ghedini et al., 2017). Resolving this uncertainty is not only theoretically interesting, but also practically significant to anticipate change in ecosystem functioning as human activities directly (e.g. fishing) and indirectly (e.g. warming) modify the size structure of populations and communities.

One of the most recurrent examples of changes in size structure in communities is observed during succession (Clements, 1916; Margalef, 1963). Succession occurs at a range of spatial and temporal scales, but is marked by a number of identifiable changes in community properties, most notably, increases in biomass resource use and productivity over time (Connell & Slatyer, 1977; Odum, 1969). These community-level changes are driven by changes in the presence and abundance of species that arise from species turnover (McCook, 1994). A distinguishing feature of ecological succession is the replacement of smaller, faster-growing species with species of larger size and longer life span (Tilman, 1988). Several models have been developed to account for patterns of succession, suggesting that they result from trade-offs in the allocation of metabolic expenditure to different physiological functions in different species (see McCook, 1994 for a review). Traits that confer an adaptive advantage to species dominating early-stages often contrast with traits of species dominating later stages (e.g. growth form, growth rate, reproductive traits). For example, faster "pace of life" species tend to invade and dominate early successional stages, whilst later stages are characterized by species with slower life histories. Ecological succession therefore entails a number of changes (in body size, abundance and traits of species) that may influence the mass-specific metabolic rate of a community.

The metabolic scaling, abundance and body size of the dominant species in a community should play a key role in determining the overall metabolism, as long as the contribution of subordinate species to total mass remains small. Based on metabolic theory and community succession theory, it is possible to predict how community metabolism should scale with total mass over time. If metabolism of the dominant species scales allometrically, then all else being equal, a prediction would be that community metabolism also scales allometrically with community mass. Furthermore, if the body size of the dominant species increases during succession, their metabolism per unit mass should decrease, resulting in later successional stages having a lower metabolic rate per unit mass than earlier stages (Dygert, 1981). This effect would be exacerbated if individuals reduce their metabolic activity as their conspecific density increases over time (DeLong et al., 2014; Ghedini et al., 2017). All of these inferences lead to the prediction that the total mass-specific metabolic rate of the community should decrease over time in a developing community, such that total community metabolic rate scales allometrically with total community mass. Tests of this prediction are rare. A few experimental studies on unicellular species found a range of scaling values: between 0.76 and 0.91 for the scaling of phytoplankton community respiration with community mass (Jensen, Sand-Jensen, Marcher, & Hansen, 1990); and scaling of 0.5 for microbial communities (Sinsabaugh, Shah, Findlay, Kuehn, & Moorhead, 2015). These studies, however, assessed the metabolic scaling of communities across gradients of resources or spatial scales, not across succession. Despite a substantial interest in using metabolic rate as a link between individual organisms and community or ecosystem level properties, there are remarkably few empirical tests of how community metabolism changes over succession in multicellular organisms (e.g. Boit & Gaedke, 2014).

Experimental tests on succession are problematic for many systems because community development can take decades to centuries and involve long-lived or wide-ranging species. We address this problem using fouling assemblages as a model system; these communities are experimentally tractable and develop rapidly in the field (i.e. a few weeks to months) (Marshall & Keough, 2009). Using this experimental system, we quantify metabolic scaling of communities at different successional stages. By identifying the species driving differences between early and late-stage communities, we use changes in their abundance and body size to reconstruct the metabolic rate of the community and test whether this predicted metabolic rate well approximates the observed metabolic scaling for the community as a whole.

2 | MATERIALS AND METHODS

2.1 | Generating community chronosequences

To measure community metabolism across succession, we generated communities of different age on a standardized substratum

that could be transported to the laboratory for measurement. We used settlement plates (11 × 11 × 0.5 cm) that had been roughened with sandpaper to encourage development of fouling communities from local settlers in the field. We affixed the settlement plates to PVC backing panels (55 × 55 × 0.8 cm), which were suspended face-down from floating pontoons at a depth of 1.5 m below the mean low water mark at our field site (Blairgowrie, Victoria, Australia). This standard method results in a representative community after six weeks in the field (Marshall & Keough, 2009). Algal growth on these shaded plates is minimal.

We established four successional "stage" treatments that determined the time communities were left to develop in the field (3.5, 4, 4.5 and 5 months, from September 2013 to January 2013) and assigned four replicate plates to each of them. These plates were replicated spatially on four panels so that we had a maximum of 16 plates per panel and a total of 64 plates. Plates assigned to each age treatment were deployed every two weeks such that communities of different ages could be retrieved at the same time (January 2013). At the time of retrieval, one plate assigned to the 5-month treatment was missing, so we had a total of n = 63 plates (15 plates with 5-month-old communities and 16 plates for each of the other age treatments).

We chose these successional stages because pilot studies indicated that sessile communities at this field site exhibited the greatest changes in both size and composition of species within the first few months of colonization. Indeed, this approach allowed us to obtain a fivefold increase in community biomass from early to late stages (see Results).

Pilot data collected from invertebrate communities naturally growing on pilings indicated that the metabolism of these communities scales isometrically with their biomass (b = 0.996, CI: 0.923–1.07), well beyond the range of mass we established. Indeed, these natural communities had a much larger biomass (and were much older) than the communities we generated experimentally—with their weight being up to two orders of magnitude that of our experimental communities. Of course, natural communities may be of different ages or mass which may covary with local environmental conditions. Thus, the experimental communities we established here span less of a mass range, but avoid the potential historical and spatial confounding factors that could drive differences in natural communities.

2.2 | Measuring community metabolism

Communities were kept in the laboratory in aerated tanks for 2–3 days prior to measuring metabolic rates. Mortality of individuals within the communities was minimal during this period. Metabolic rates were measured using hermetic flow-through chambers at constant temperature that approximated seawater temperatures at the time of plate retrieval (19°C). Each respirometer chamber (~4 L) was completely filled with sterilized filtered seawater and, after removing any eventual air bubble, was sealed with a lid after the plate with animals was put inside. The exact volume of seawater in each chamber was calculated precisely by weight. Water within the chambers was recirculated using a peristaltic pump in a closed loop, and changes in % oxygen saturation were determined using an optical oxygen meter (FireStingO2, Pyro Science GmbH, Germany) and flow-through cells with oxygen sensor (Pyro Science GmbH, Germany) placed in the tubing connecting the bath to the peristaltic pump. Communities were left to acclimate for 15–20 min prior to starting the measurements which ran for 3 hr. The rate of oxygen consumption (V_{O2}, ml/hr) was calculated following Ferguson, White, and Marshall (2013) using the equation:

$$V_{O2} = -1 \times [(m_b - m_c)/100] \times V \times \beta_{O2}$$

where m_b is the slope of the line relating oxygen saturation to time for the chambers containing experimental communities (% air saturation/hr), m_c is the slope for the control chambers filled just with water (% air saturation/hr, n = 7 controls), V is the water volume in the chambers minus that taken up by the community on the plate (litres), and βO_2 is the oxygen capacitance of air-saturated seawater (5.31 ml/L; Cameron, 1986) at the specific temperature (19°C) and salinity of the run (35 ppt). The wet biomass of the community on each plate (minus the known mass of the plate) was determined at the end of metabolic measurements.

2.3 | Community size structure and estimates of community metabolism

For each plate, we identified each organism present in the community to the species level and the percentage of space occupied on the plate to detect differences in species richness and community composition during succession. Community composition was used to identify the species driving differences between early and late successional stages (see "*Community composition and size structure*" in Results). We identified three dominant species (or species groups): the solitary ascidian *Pyura dalbyi*, the encrusting colonial bryozoan *Watersipora subtorquata* and two species of tube-forming polychaetes, that is *Pomatoceros taeniata* and *Hydroides elegans*, which will be referred to as "tubeworms" from this point forward.

Half of the plates across all successional stages (n = 32) were photographed to determine the size structure of the dominant species at each successional stage and to quantify their exact contribution to community metabolism (i.e. based on their abundance and individual mass). For each photograph, we measured the exact area covered by each individual *Pyura* or *Watersipora* colony using ImageJ and recorded their abundance (i.e. number of individuals or colonies), whilst for tubeworms, we measured the overall area and quantified abundance as percentage cover as it was impractical to determine the size of each individual tubeworm from photographs of the community. Each of these dominant species occupied up to 25% of the total area of the community at least at one stage across succession.

We then converted these measures of area to mass. To do so, we determined the relationship between area and wet mass for each of

the dominant species (or species groups) using specimens of various sizes collected in the field (n = 35 for *Pyura*; n = 25 for *Watersipora*; n = 75 for tubeworms, see Figure S1). We then estimated the metabolic rate of these focal organisms for a range of masses (wet mass), for each species separately (Figure 4). As these species differed in mass by four orders of magnitude, we used two different respirometry systems to accurately measure their oxygen consumption following methods used in Lagos, White, and Marshall (2017). Specifically, for *Pyura* (n = 23 individuals, one per chamber) we used the flow-through respirometry system that we also used for the communities (see above). For the smaller *Watersipora* (n = 20 colonies, one per chamber) and tubeworms (n = 18 colonies, one per chamber), we used 20 ml closed vials mounted on a 24-channel sensor dish reader (Sensor Dish Reader SDR; PreSens, Aachen, Germany). All metabolic measurements were taken at the same temperature (19°C) and were conducted for 12 hr for *Pyura* and 3 hr for *Watersipora* and tubeworms depending on their rate of oxygen depletion. These differences in approach (chamber size, water movement) inevitably will introduce slight differences in estimates of metabolic rate, but they also reflect the specific water flow conditions experienced by these taxa—whilst *Pyura* often protrudes into the water column, *Watersipora* and tubeworms live on the benthic boundary layer. The different-sized equipment was necessary to accommodate the large differences in mass among species and measure accurately their metabolism. Critically, these differences in methodology are unlikely to substantially alter our estimates as we were interested in relative scaling of respiration.

We then used the species-specific metabolic scaling exponents (Figure 4) to estimate the metabolic rate for each individual of *Pyura* and *Watersipora* on our experimental communities based on its mass (individual metabolism = species-specific intercept × individual mass$^{\text{species-specific exponent}}$). The total metabolism for each species was then calculated from their abundance (i.e. total species metabolism = Σ individual metabolism of n individuals). As tubeworms typically form colonial structures composed by multiple tubes attached to each other, their metabolic scaling was determined for a range of biomasses obtained manipulating the abundance of similarly sized tubes (n = 18 colonies of tubeworms). This method allowed us to quantify how tubeworm metabolism varied with total mass, so that we could use the total mass of tubeworms on our experimental plates to determine their total metabolism (total tubeworm metabolism = species-specific intercept × total tubeworm mass$^{\text{species-specific exponent}}$). Finally, we reconstructed community metabolism by summing the total metabolic rate of each dominant species: community metabolism = *Pyura* metabolism + *Watersipora* metabolism + tubeworms metabolism. This predicted metabolic rate is thus calculated from the size structure and abundance of the three dominant species in each community.

2.4 | Data analyses

We used GLM to test the relationship between community metabolism and mass, including stage and panel as fixed categorical effects. Panel was treated as fixed effect because of its low replication level (Bolker, 2008), but was not of intrinsic interest; rather it was an experimental convenience that allowed greater replication. Four plates (three from stage 2 and one from stage 1) were excluded from this analysis because of a nonlinear decrease in oxygen consumption (suggesting equipment failure), so the total number of replicates was n = 59. Estimates of community metabolism and mass obtained from size structure analysis (n = 32) were analysed in the same way with the only difference that panel had only two levels instead of four. Community metabolism and mass were $\log_{10}$-transformed for the first suite of analyses, but we then used nonlinear models to estimate the parameters of metabolic scaling with mass on untransformed data (Hayes & Shonkwiler, 2006; Hui & Jackson, 2007). The metabolic scaling exponents of the dominant species were also calculated on untransformed data using nonlinear models. To test whether our predicted metabolic rates from the sum of the dominant species metabolic rates were a good predictor of overall observed metabolic rate, we regressed predicted metabolic rate against observed. We used linear regression because the relationship between predicted and observed was linear.

A two-factor analysis of variance was used to test for differences in species richness among developmental stages across panels. Differences in community composition were analysed using the same design in a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001). In order to reduce the contribution of quantitatively dominant taxa, data on abundance were square-root (x + 1)-transformed prior to the construction of Bray–Curtis similarity matrices. A non-metric multidimensional scaling (nMDS) plot was constructed from the Bray–Curtis matrices to graphically represent the data. The species contributing the most to differences between early and late successional stages were identified with a similarity percentage analysis (SIMPER).

To determine changes in abundance, mass and proportion of the dominant species to total community, we used linear regression with stage as continuous factor. The area–mass relationship for *Watersipora* and tubeworms was well represented by a linear regression (R^2 = .97 and .72, respectively), whilst for *Pyura*, we used a power function estimated using log–log-transformed data (R^2 = .94, Figure S1) because measurements of area would otherwise underestimate the mass of each individual *Pyura* (as the area photographed from the top tends to increase less than the mass of the individual). All multivariate analyses were performed using PRIMER-E v6 software package (PRIMER-E). All other analyses were performed in SYSTAT (Systat Software, San Jose, CA).

3 | RESULTS

3.1 | Observed community metabolic scaling

Both community biomass and community metabolic rate increased during succession resulting in late-stage communities having greater mass ($F_{3,43}$ = 13.91, p < .001) and metabolic rate ($F_{3,43}$ = 11.02,

$p < .001$) than early stages (Figure S2, Table S1). Despite changes in total metabolism, mass-specific metabolic rate remained stable across successional stages (effect of stage: $F_{3,43} = 0.40$, $p = .76$; Figure S2, Table S1), indicating that increases in biomass and metabolism occurred proportionally during succession. Indeed, we found that community metabolism scaled isometrically with community mass (Figure 1) with a scaling exponent significantly different from 0.75 (Wald's test: $t = 0.005$) but not significantly different from 1 ($t = 0.67$). There was no significant effect of successional stage ($F_{3,51} = 0.58$, $p = .63$) or panel ($F_{3,51} = 1.61$, $p = .20$), but only an effect of mass (Logmass: $F_{1,51} = 41.02$, $p < .001$) on the relationship between metabolic rate and biomass (Table S2). The scaling exponent estimated from log-transformed data (b = 0.94) led to the same results as it was also significantly different from 0.75 (Wald's test: $t = 0.047$) but not different from 1 ($t = 0.53$).

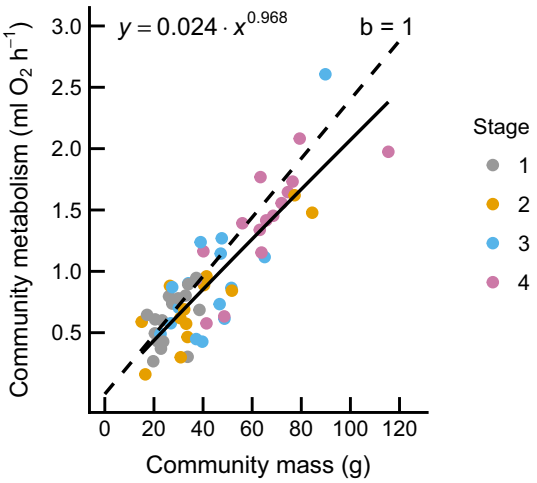

FIGURE 1 Community metabolism scales isometrically with community mass with a scaling exponent of 0.968. The dotted line shows the metabolic scaling predicted with an exponent (b) of 1

3.2 | Community composition and size structure

Community composition differed among successional stages across all panels (PERMANOVA, "Stage × Panel" Pseudo-$F_{9,47} = 1.33$, P-perm = 0.03; Figure 2a), but maintained comparable species richness ($F_{3,47} = 0.18$; $p = .91$). Differences in community composition were driven by a shift in species dominance with *Watersipora* dominating early-stage communities and *Pyura* dominating late-stage communities (Figure 2b). These two species contributed the most to differences between successional stages, together representing more than 20% of the difference between early (stage 1) and late-stage (stage 4) communities (percentage contribution to dissimilarity: *Pyura* = 13.35%, *Watersipora* = 8.97%, cumulative contribution = 22.32%). In addition, we identified tubeworms as a third taxon that might have significantly influenced the scaling of community metabolism because of their higher proportion of non-metabolizing mass relative to other species (i.e. calcareous tubes) and their changing relative abundance across succession (Figure 3). Other subordinate species were present on the plates, but they represented a much lower percentage of the community and, most importantly, their abundance did not show any strong pattern of change during succession (Figure S3).

The abundance of *Watersipora* colonies did not change significantly during succession ($F_{1,30} = 0.001$, $p = .97$), but colonies decreased in size in later stages ($F_{1,262} = 20.14$, $p < .001$). Consequently, the proportion of *Watersipora* mass relative to total community mass declined during succession ($F_{1,30} = 23.12$, $p < .001$, $R^2 = .42$, Figure 3). Similarly, the abundance of tubeworms (measured as percentage cover) and their total mass did not differ among successional stages (percentage cover: $F_{1,30} = 0.001$, $p = .98$, mass: $F_{1,30} = 0.001$, $p = .98$), but their contribution to total community mass declined during succession ($F_{1,30} = 21.42$, $p < .001$, $R^2 = .40$, Figure 3). *Pyura* showed the opposite pattern, with abundance and mass of individuals increasing during

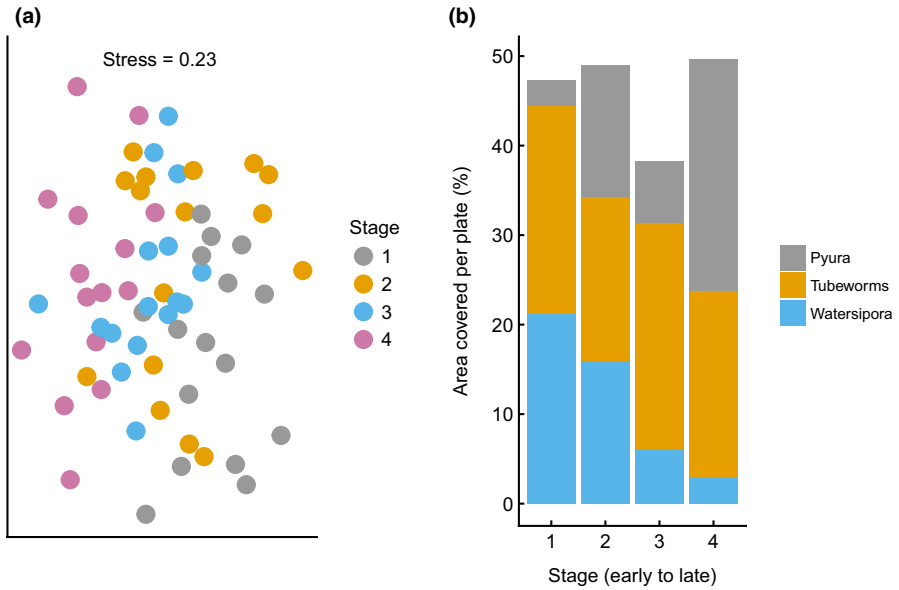

FIGURE 2 (a) Non-metric multidimensional scaling plot (nMDS) of species composition among successional stages; it shows that community composition changes during succession with early (grey) and late-stage communities (magenta) grouping separately. (b) Changes in community composition were mostly driven by a shift in species dominance (i.e. changes in area cover), with *Watersipora* dominating the early stages (1) and *Pyura* the late-stage communities (4). Tubeworms are consistently present across succession and represent an important part of the community, but their relative contribution to total community mass declines over time (see Figure 3)

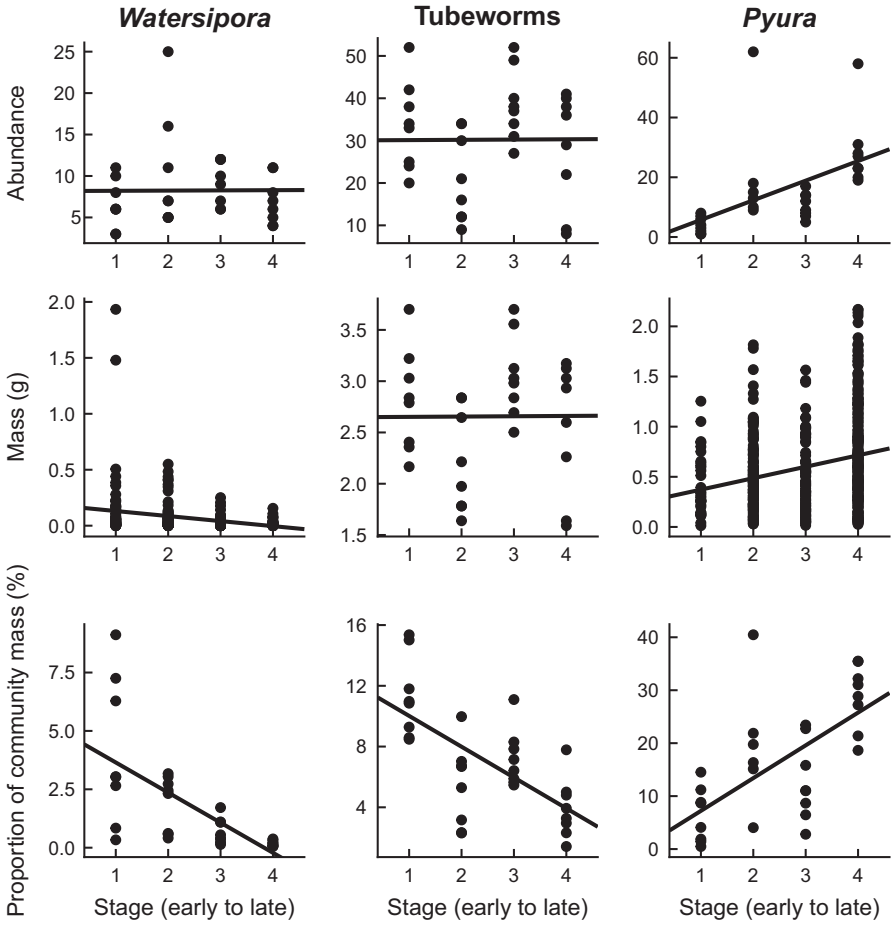

FIGURE 3 Changes in community composition are driven by changes in abundance (top) and individual mass (middle) of a few main species (*Watersipora*, tubeworms, *Pyura*) whose contribution to total community mass changes during succession (bottom) with *Watersipora* and tubeworms representing a decreasing proportion of the community mass, whilst *Pyura* an increasing proportion

succession (abundance: $F_{1,28} = 10.76$, $p < .01$, mass: $F_{1,472} = 32.17$, $p < .001$), such that the proportion of *Pyura* mass relative to community mass increased in late-stage communities ($F_{1,28} = 18.95$, $p < .001$, $R^2 = .38$, Figure 3).

3.3 | Metabolic scaling of dominant species and predicted community metabolism

The metabolic rate for each of the dominant species groups scaled allometrically with mass, with exponents of 0.56 for *Watersipora* (CI: 0.28–0.83), 0.74 for tubeworms (CI: 0.11–1.36) and 0.47 for *Pyura* (CI: 0.13–0.81) (Figure 4). We used these species-specific relationships to estimate the metabolism of each individual in our experimental communities based on the size structure of these three dominant groups of species (i.e. *Watersipora*, tubeworms and *Pyura*). We then obtained estimates of community metabolism by summing the respiration rate of all individuals of these three species. We found that predicted community metabolism estimated from changes in the size and abundance of the dominant species was a good predictor of the observed community metabolism: VO_2 observed = 0.917 × VO_2 estimated + 0.299 ($n = 29$, adjusted $R^2 = .58$; Figure 5). Calculations of total community metabolism from the average size of individual tubeworms, rather than their total mass, did not alter the relationship between observed and estimated metabolism: VO_2 observed = 0.918 × VO_2 estimated + 0.355 ($n = 29$, adjusted $R^2 = 0.58$).

Two data points were excluded from this analysis because these two communities had an unusually high density of *Pyura* (more than double that of other communities), which was a strong predictor of community metabolism (Figure S4). Our estimates of community metabolism matched well-observed community metabolism across all *Pyura* densities, except for these two data points for which estimates overestimated actual metabolic rates (Figure S4).

4 | DISCUSSION

Contrary to straightforward assumptions based on the allometry of metabolic scaling and patterns of community development, we found that community metabolism scaled isometrically with community mass during succession. That metabolism scaled isometrically was surprising because, for each of the dominant species measured, metabolism scaled allometrically with individual mass (between 0.47 and 0.74). Furthermore, the mean size of the most abundant species (*Pyura*) and its abundance increased over time and larger and denser individuals are both predicted to decrease individual's mass-specific energy use and thereby decrease community metabolism per gram of total biomass (DeLong et al., 2014;

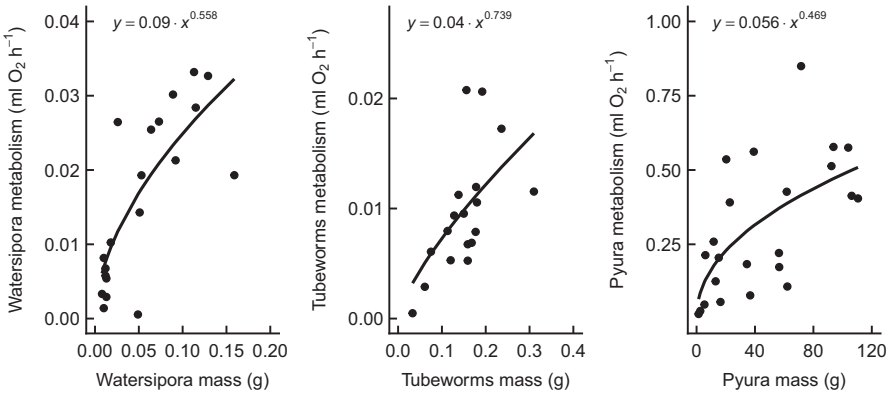

FIGURE 4 Metabolic scaling for *Watersipora*, tubeworms and *Pyura*

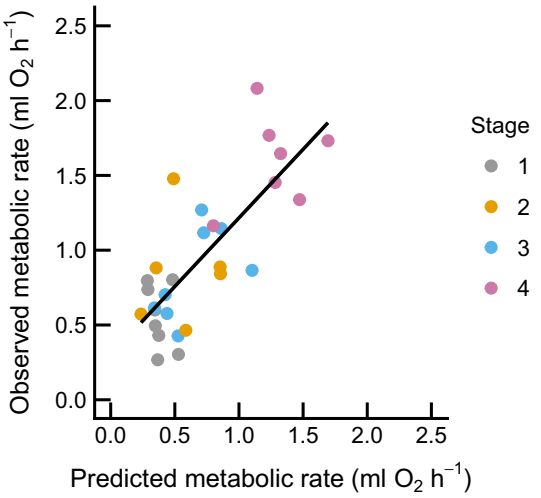

FIGURE 5 Predicted community metabolic rates, obtained from the size structure, abundance and metabolic scaling relationships for the dominant species in the community, are good predictors of observed community metabolic rates (n = 29, adjusted R^2 = .58)

Ghedini et al., 2017; Gillooly et al., 2001). Yet, we resolved this paradox by reconstructing overall community metabolism from the size structure of the dominant members in the community and showed that individual metabolism was ultimately a good predictor of whole community metabolism.

A scaling of 1 for overall community metabolism means that at any point in time changes in size structure (i.e. combinations of abundance and body size of individuals among species) maintained total community metabolism directly proportional to total community mass. So, whilst variation in body size during succession affected individual physiological rates (e.g. an increase in the size of an individual results in a decrease in mass-specific metabolic rate because the scaling exponent is <1), changes in size structure (body size, abundance and species composition) left community-level mass-specific metabolic rate unaltered. We suspect isometric metabolic scaling was driven by species turnover during succession. In other words, the specific combination of abundances and body sizes of individual organisms at each successional stage, together with their species-specific scaling relationships, yielded constant mass-specific energy use of the entire community across succession (Figure 6). For instance, communities in early successional stages were dominated by *Watersipora*, which had a higher mass-specific metabolism (Figure 4), but individuals decreased in size during succession (Figure 3), such that mass-specific energy use of this species increased over time. Early successional stages were also dominated by tubeworms, which had the lowest intercept and mass-specific metabolic rate probably due to their metabolically inactive calcareous tube (Figure 4). These two groups of species were gradually replaced by *Pyura* that had a higher intercept and intermediate mass-specific metabolism (Figure 4), but increased in size and abundance during succession (i.e. decreasing mass-specific metabolism) (Figure 3). Therefore, species with high mass-specific metabolic rate (*Watersipora*) and very low mass-specific metabolic rates (tubeworms) were replaced with species with intermediate mass-specific metabolic rates but with higher mass and abundance (*Pyura*), maintaining an isometric relationship overall.

It is important to note that succession caused an overall increase in community biomass accompanied by significant increases in total energy use and, consequently, in area-specific energy use during succession (the area of our communities did not change over time). Indeed, both community mass and respiration rates increased threefold, meaning that the same area (i.e. experimental plate) supported much higher biomasses and energy use during late-stages compared to early stages. Therefore, area-specific energy usage increased across succession but mass-specific energy usage remained constant. Is isometry maintained even at older stages of succession? Whilst we did not formally test this hypothesis, results from a pilot study indicate that mass-specific energy use remains independent of community age and biomass even at later stages of succession. Tests of metabolic scaling in much older communities, up to two orders of magnitude heavier than those considered here, showed that metabolism keeps increasing proportionally to community biomass with a scaling exponent of 0.996.

The community metabolic rate reconstructed from the sum of individual metabolic rates from three key species groups successfully predicted overall community metabolism. Thus, it appears that community rates are largely the sum of their parts with respect to metabolism (i.e. the effects of species-specific metabolic rates are additive). However, we found that the predictive power of additive

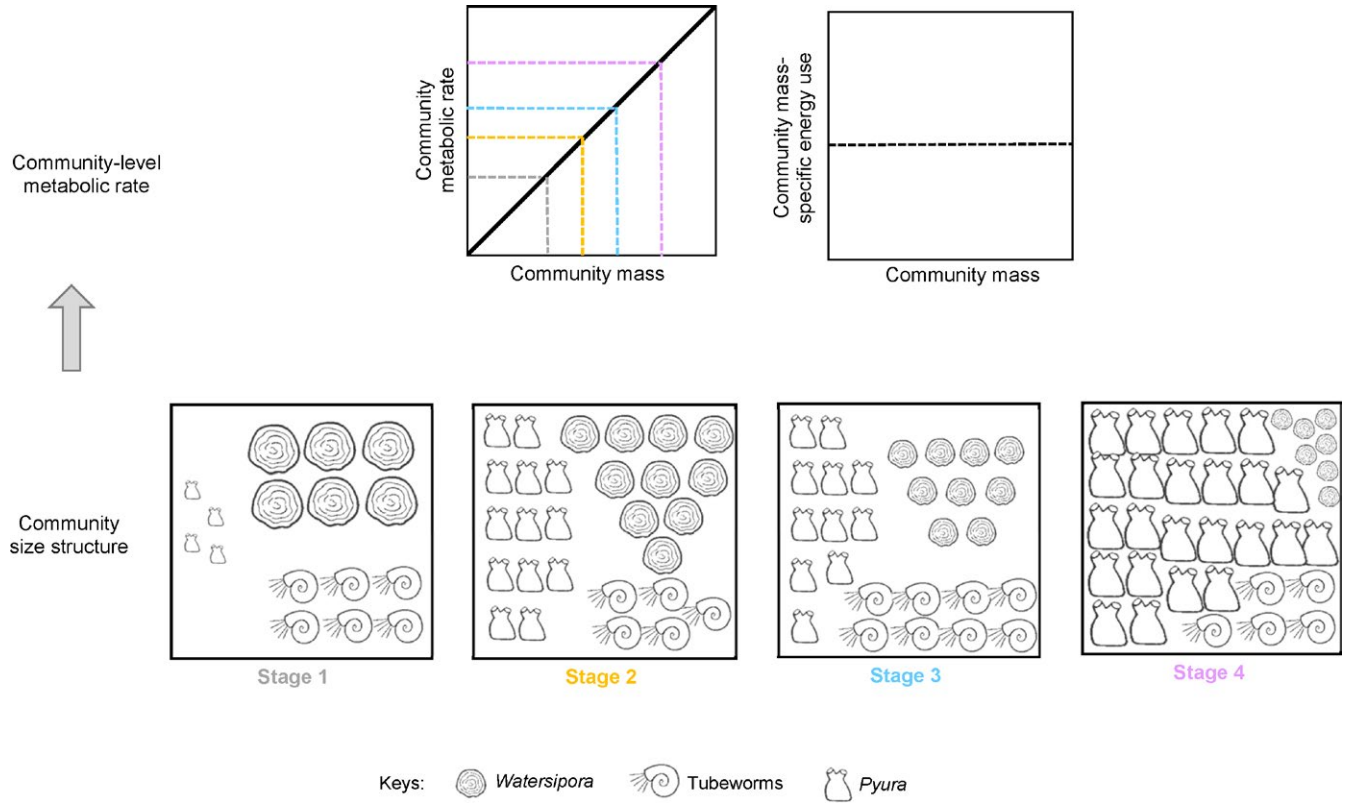

FIGURE 6 Schematic showing how changes in community mass driven by species replacements and changes in individual size might have maintained an overall isometric scaling of community metabolism across successional stages

effects of species identity and mass is limited. For two of our experimental communities, which contained unusually high densities of one species (*Pyura*), our predicted metabolic rates (assuming additive effects) were much higher than the observed metabolic rate (Figure S4). We suspect that a lower-than-expected metabolic rate may have been driven by metabolic suppression in response to a high density of conspecifics. This hypothesis is supported by recent studies, which have shown that *per capita* metabolic rates are reduced in dense populations (DeLong et al., 2014; Malerba, White, & Marshall, 2017), where conspecific density reduces energy use beyond the constraints of body size (Ghedini et al., 2017). Therefore, the overestimation of community metabolism could result from the high densities of *Pyura* reducing *per capita* metabolic rates in this species. These densities might have altered the scaling exponent in a way that could not be predicted from our data on metabolic scaling of single *Pyura* individuals and that did not occur at lower densities (see Ghedini et al., 2017 for details). Nevertheless, whilst our results suggest that the use of physiological rates and individual body size might have limitations and likely exceptions, overall we found that they were good proxy of total community metabolism. It is possible that, when density of any one species is low, conspecific interactions that suppress metabolic rate are sufficiently diffuse so as to prevent density-dependent metabolic suppression.

Does the fact that the scaling relationship is around 1 have particular significance? Theory that considers metabolic scaling for groups of organisms is scarce (Glazier, 2014; Kooijman, 2010), and too few studies have experimentally assessed metabolic scaling at the community level to make clear generalizations about how metabolism could be expected to change with total mass (Boit & Gaedke, 2014; Sinsabaugh et al., 2015). Studies that seek to predict community or ecosystem respiration typically consider these higher-level rates to be the sum of the individual rates (Allen et al., 2005; Enquist et al., 2003). Given the typically inverse relationship between abundance of individuals and their body size, a general prediction is that ecological rates of energy use should be independent of size structure (Damuth, 1981). Thus, communities of different-sized organisms should over time converge to have similar rates of energy use and differences between communities should be driven by species identity effects (or richness) rather than by size structure (Enquist et al., 2003). Whilst some studies found evidence for these patterns (Huete-Ortega et al., 2011; Long & Morin, 2005), others found that altering the size structure of communities alters ecosystem rates of energy use (Norkko, Villnäs, Norkko, Valanko, & Pilditch, 2013) and that ecological interactions can reduce the predictive power of body size when scaling from physiological to ecological rates, that is populations or communities (Barneche, Kulbicki, Floeter, Friedlander, & Allen, 2016; Cyr & Pace, 1993). Our results are intermediate between these extremes. We found that changes in size structure during succession affected total energy use, but did not alter mass-specific rates of energy use (i.e. scaling exponent ~1).

A further consideration is that the metabolic scaling of communities across spatial scales or resource environments might

differ from the metabolic scaling of communities developing during succession, similar to how interspecific scaling across a range of body sizes differs from metabolic scaling during ontogeny (Glazier, 2005; Persson & de Roos, 2013). The classic theory of community succession predicts that changes in species traits and size should lead to increased energy efficiency during succession, with the amount of standing biomass supported by the available energy flow increasing in mature communities (Odum, 1969). In a study of secondary succession in a lake system, Boit and Gaedke (2014) found that increases in average body size and shifts to K-strategist species caused overall mass-specific metabolic activity to decrease during succession. Conversely, our results do not provide support for increased metabolic efficiency in later successional stages.

However, measurements of metabolism alone do not estimate ecological efficiency, rather only a part of it. Ecological efficiency is quantified as both energy expenditure for maintenance (e.g. metabolism) and the ability to exploit available resources (Loreau, 2010; MacArthur, 1969). Mature systems might have equal or higher mass-specific maintenance costs relative to younger systems, but might increase their efficiency by utilizing available resources more completely (e.g. greater storage capacity of organisms, increased niche differentiation) (Gatto, 1990). Furthermore, a mature community might have a greater capacity to entrap external nutrients and materials within the system, for example because of a more complex structure. Through these mechanisms, open systems may sustain elevated productivity throughout succession (Odum, 1969). Our experimental communities can also be considered open systems that during succession transitioned from a predominant 2D developmental mode to a 3D developmental mode; this shift in structure might explain how the same area was able to support higher levels of biomass and metabolic activity. The development in height into the water column might have allowed greater access to food (plankton) and might have increased oxygen flow within the community. Hence, whilst knowledge of the size structure of a community can offer some insights into the overall rates of energy use, simultaneous measurements of changes in maintenance rates (metabolism) and assimilation of resources (feeding) need to be evaluated to determine changes in energy flux (efficiency).

Changes in ecological rates of energy use have long been identified as an indicator of change in ecosystem functions (Odum, 1985). As the formal introduction of the metabolic theory of ecology (Brown et al., 2004), metabolic scaling relationships have sparked considerable interest for their potential predictive power at larger ecological scales. In this study, we found that under most circumstances and with the appropriate parametrization, species-specific individual metabolic rates can approximate overall community metabolic rates but there are important exceptions.

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AUTHORS' CONTRIBUTIONS

All authors helped with collecting data. G.G. performed data analysis and drafted the manuscript. The authors declare no competing interests.

DATA ACCESSIBILITY

The datasets supporting this article are deposited in the Figshare repository: https://figshare.com/s/d1b7fd290c32cfac593b. https://doi.org/10.4225/03/5aa1d20d4e544 (Ghedini, White, & Marshall, 2018).

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