

LETTER

Testing MacArthur's minimisation principle: do communities minimise energy wastage during succession?

Giulia Ghedini,^{1*} Michel Loreau,²
 Craig R. White¹ and
 Dustin J. Marshall¹

¹Centre for Geometric Biology,
 School of Biological Sciences,
 Monash University, Melbourne,
 Vic. 3800, Australia

²Centre for Biodiversity Theory and
 Modelling, Theoretical and Experi-
 mental Ecology Station, CNRS and
 Paul Sabatier University, 09200
 Moulis, France

*Correspondence: Email: giulia.
 ghedini@monash.edu.

Abstract

Robert MacArthur developed a theory of community assembly based on competition. By incorporating energy flow, MacArthur's theory allows for predictions of community function. A key prediction is that communities minimise energy wastage over time, but this minimisation is a trade-off between two conflicting processes: exploiting food resources, and maintaining low metabolism and mortality. Despite its simplicity and elegance, MacArthur's principle has not been tested empirically despite having long fascinated theoreticians. We used a combination of field chronosequence experiments and laboratory assays to estimate how the energy wastage of a community changes during succession. We found that older successional stages wasted more energy in maintenance, but there was no clear pattern in how communities of different age exploited food resources. We identify several reasons for why MacArthur's original theory may need modification and new avenues to further explore community efficiency, an understudied component of ecosystem functioning.

Keywords

Disturbance, energy, geometric biology, invasion, metabolism, stability, trophic interactions.

Ecology Letters (2018) 21: 1182–1190

INTRODUCTION

Among the seminal contributions to ecological competition theory, those of Robert MacArthur are some of the most notable. MacArthur extended Lotka–Volterra models to build a mechanistic model of competition that is broadly known as MacArthur's niche theory (MacArthur 1969; Loreau 2010). MacArthur's mechanistic approach to explaining ecological patterns overcomes the limitations of phenomenological models and allows us to explore both the structure and function of communities. MacArthur's niche theory has predicted patterns of interspecific competition and niche differentiation, and its importance in the field of community ecology should not be underestimated (Chesson 1990, 2000). Yet, surprisingly, there are major elements of MacArthur's theory that remain untested.

A key finding of MacArthur is that a competitive community obeying a number of assumptions (described in detail by Loreau 2010) has a unique globally stable equilibrium point, and this point has biologically interpretable structural and functional properties. In a series of papers, MacArthur (1969, 1970, 1972) and others since (Brew 1982; Chesson 1990; Gatto 1990; Tikhonov 2016) predicted that such a community obeys a Lyapunov function, i.e. a function that is always positive and whose time derivative is always negative, except at equilibrium where it is zero (see Gatto 1990; Loreau 2010 for mathematical details). A system that obeys a Lyapunov function will tend to converge to an equilibrium point where such function is minimised. Specifically, when expressed most simply, MacArthur's function has the form:

$$Q = U + B$$

where Q is a measure of community inefficiency that is determined by two components (U and B) and that will be minimised over time (Fig. 1).

The component U is defined as the difference between the maximum productivity of renewing food resources (measured by their rate of increase) and their total consumption across the community; in other words, U measures unutilised food resources. B is the maintenance energetic cost for the community, which is the amount of energy lost to basal metabolism and natural death per unit time. Both U and B may, thus, be viewed as different ways in which a community fails to capture or wastes available energy (Gatto 1990; Loreau 2010). MacArthur's theory predicts that a competitive community will minimise its total energy wastage Q over time. We therefore refer to Q as 'community inefficiency', to distinguish it from the many other measures that have been labelled as 'ecological efficiency' (Lindeman 1942, Odum 1956; Kozlovsky 1968). Importantly, MacArthur (1972) showed how his minimisation principle could be used to predict the composition and species relative abundances of competitive communities as well as their stability and invasibility (Loreau 2010).

However, as MacArthur postulated, partitioning Q into its components, U and B , does not lead to simple predictions regarding the ecological properties that are maximised or minimised in an ecological community (Loreau 2010). This is because the minimisation of U may conflict with the minimisation of B (Fig. 1). A small, species-poor community of highly efficient individuals might keep their maintenance energetic costs low, but leave plenty of food resources unutilised (Gatto 1990). On the other hand, an abundant and diverse late-stage community may more fully utilise food resources, but could expend more energy on maintenance and suffer more mortality (Gatto 1990). In the absence of empirical studies, however, it remains impossible to predict the outcome of such trade-offs or generalise the trajectory that any one community will take in minimising its energy wastage.

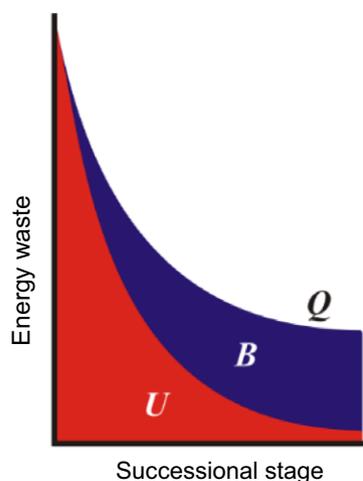


Figure 1 MacArthur's theory states that there are two main sources of energy waste in an ecological community: (1) one is given by the community failing to fully capture available food resources (U) and (2) the other is the energy lost to maintenance and mortality (B). MacArthur also predicts that the overall energy waste (Q) will be minimised (i.e. efficiency maximised) in a competitive community during succession. However, the minimisation of Q might not lead to simple predictions on how which ecological properties will change because the two components of Q vary idiosyncratically in that the minimisation of U might contrast with the minimisation of B .

An increasingly urgent goal of ecology is to understand the factors that determine whether a community is successfully invaded or not. One mechanism by which species diversity can reduce invasibility within the same trophic level is by decreasing resource availability (in MacArthur's framework, $1/U$), i.e. more diverse communities consume more of the available resources leaving less to support invaders (Stachowicz *et al.* 2002). Indeed, many studies have shown that more speciose communities are harder to invade where the invader competes for similar resources (Levine *et al.* 2004). A few other studies, however, have found the opposite – that more speciose communities are more invaded (Dunstan & Johnson 2004). The both positive and negative associations of diversity with invasion have come to be known as 'the invasion paradox' (Levine & D'Antonio 1999; Fridley *et al.* 2007; Clark & Johnston 2011). Several processes that can generate both patterns have been proposed to explain the conflicting results (Fridley *et al.* 2007), but MacArthur's minimisation principle could help resolve this paradox by directly addressing the resource use of communities over time. Specifically, MacArthur argues that diversity *per se* is less relevant to invasibility, rather it is the magnitude of U that determines whether a species can invade a community (MacArthur 1969; Loreau 2010). When U is very close to zero, there are so few unutilised food resources remaining in the system that invasion by an additional species becomes impossible. As Loreau (2010) notes, the relationship between U and diversity is unlikely straightforward or constant: if diversity is a poor proxy for U , then this may help explain some of the inconsistency in the relationship between diversity and invasibility.

Given MacArthur's massive and enduring impact on the study of ecology, it is remarkable that his predictions

regarding community energy use through time have not been tested. MacArthur published three separate considerations of community assembly (MacArthur 1969, 1970, 1972), the central theory of which has been the subject of continued theoretical refinement in subsequent years (Brew 1982; Chesson 1990; Gatto 1990; Loreau 2010), but the empirical testing of these ideas has lagged behind. This dearth of empirical studies is almost certainly explained by the formidable challenge that collecting such data represents, particularly using natural communities in the field. Here we make a first attempt to test MacArthur's predictions; specifically that (1) overall energy wastage (Q) will be minimised during community succession, and that (2) unutilised food resources (U) will decrease, whereas energy lost to metabolism and mortality (B) will increase over time (Fig. 1). To clarify the mechanisms driving changes in energy use, we quantify a number of community properties that are known to vary during succession, including biomass, richness, composition and size of organisms. We use communities of benthic sessile invertebrates as a model system (see Supporting Information: Appendix S1 for how our system matches MacArthur's assumptions). These communities of phytoplankton consumers provide an excellent system for studying processes of competition (Marshall & Keough 2009; Hart & Marshall 2013) and invasion within the same trophic level (Stachowicz 2001; Stachowicz *et al.* 2002). Phytoplankton availability drives the density-dependence of population growth in this system (Svensson & Marshall 2015) and increases consumer density cause more rapid decreases in resource availability even when space is not limiting (Ghedini *et al.* 2017). These sessile communities develop rapidly in the field (i.e. within a few weeks; Stachowicz *et al.* 2002), and can be used to create chronosequences of successional stages that are tractable to manipulation (Ghedini *et al.* 2018, in press), such that whole community metabolism and feeding rates can be tested in laboratory assays.

METHODS

Study site and system

Experimental communities were established using standard methods (detailed below) that generate fouling communities representative of those naturally found in their habitat (Hart & Marshall 2012). The study was carried out at the Royal Brighton Yacht Club, Melbourne, Australia (37°54'19.08" S, 144°58'51.94" E), an area of 200 × 400 m², and is 3–4 m deep. All experiments were conducted in the Austral summer of 2014–2015.

Ten experimental PVC panels (550 × 550 × 8 mm³) were suspended 1.2 m below the surface on floating pontoons. To create a chronosequence of succession, we attached five experimental PVC plates (100 × 100 × 6 mm³) to each panel every 3 weeks. This approach allowed us to develop a total of 150 communities representative of three successional stages (early, mid and late), 3 weeks apart from each other (3, 6 and 9 weeks old respectively). Each panel had 15 plates (5 plates for each successional stage) yielding 150 plates in total, with 50 plates that had been in the field for 9 weeks, 50 for 6 weeks and 50 for only 3 weeks. However, 16 plates were

lost during the field deployment (5 early stage, 1 mid stage and 10 late stage) so that we recovered 134 plates.

Nine weeks after the deployment of the first plates (i.e. late-stage communities), we photographed all the plates with a high-resolution digital camera and then re-photographed them 1 week later so as to estimate mortality rates (see 'Quantifying body size and mortality'). At this time, after 10 weeks in the field, we returned plates with the experimental communities to the laboratory in insulated aquaria where we estimated community metabolism and feeding. We repeated this process every day for 10 days and each day we returned plates from an entire panel (5 plates for each successional stage). The sampling time between the first panel and the last panel was a total of 10 days. Once community metabolism and feeding were estimated, each plate was weighed to the nearest milligram to determine wet weight of the community after being wiped and blotted dry with paper towel. We then dried the plates to constant weight (at 60 °C in a drying oven) and re-weighed them to the nearest milligram.

Feeding and metabolic chambers

To estimate the feeding rate and metabolic rate of the community, we placed each plate into its own metabolic chamber (see Ghedini *et al.* 2018, in press for details). All estimates of community feeding and metabolism were conducted in a constant temperature room at a temperature of 18 °C. We first estimated community feeding rates and then estimated community metabolic rate.

Community feeding

Once plates were returned from the field, we measured the feeding rate of each community plate ($N = 134$). We used ambient concentrations of phytoplankton from seawater collected from the field site on the same day as the experimental plates. When collecting the seawater, we first filtered it using a 100 micron mesh to remove planktonic animals that consume phytoplankton.

For each sample, we estimated the total abundance of phytoplankton in an 82 μL sample and then calculated phytoplankton concentrations using standard flow cytometer techniques (see Veldhuis & Kraay 2000). Field concentrations of phytoplankton varied over an order of magnitude from run to run, but did not show any systematic variation over time. Our estimates of field phytoplankton concentrations matched previously reported values for Port Phillip Bay (our average: 1.19×10^6 cells L^{-1} ; previous estimates range from 1×10^6 to 1×10^7 cells L^{-1} ; EPA 2010).

To estimate initial phytoplankton concentrations, we took a sample before placing the field seawater into the feeding chamber. To estimate feeding rates of the communities, we then placed our plates into their feeding chambers, switched on the aquarium pumps and estimated the abundance of phytoplankton after two hours and five hours. Samples were kept in the refrigerator for a maximum of one hour between being drawn from the chamber and placed in the flow cytometer. We then determined how much phytoplankton concentrations

had decreased over the run of the experiment (relative to control runs free of settlement plates).

Community metabolism

To estimate oxygen saturation within the chambers, we used standard methods as described in Ghedini *et al.* (2018, in press). We estimated dissolved oxygen concentration every 30 s for 6 h, removed the plates from the chambers and weighed the water in the chamber. We combined the water volume measures with the rate of decline in oxygen saturation to calculate the rate of oxygen usage or VO_2 of our communities (see Ferguson *et al.* 2013 for details). Care was taken to quantify VO_2 at around 80% oxygen saturation as previous studies show this range is well away from the critical PO_2 of sessile marine invertebrates and therefore reflects VO_2 in the absence of hypoxia stress (Lagos *et al.* 2017). All plates showing a nonlinear decrease in metabolism were eliminated from analyses so that we had a total of 113 plates.

Quantifying body size and mortality

To quantify changes in body size during community development, we calculated the area cover of 20 individuals (or the total number of individuals/colonies present if less than 20) for each of the dominant taxa at each successional stage. Since body size varies naturally across the different taxa, we standardised our measurements of area cover by subtracting the sample mean from each value and then dividing by the sample standard deviation.

To quantify mortality rates within our communities, we marked the position and recorded the identity of every organism on each experimental plate on the first photograph of each plate. For a subsample within each panel, we also measured the size of colonies or individuals as appropriate. We then digitally overlaid the second photograph of each plate to determine which individuals were still present and which had disappeared (removal of an individual almost always results in death in sessile marine invertebrates that cannot re-attach to a new substrate). Thus, we tracked the fate of over 25 000 individuals over a single week across all of our experimental plates. MacArthur's predictions rest on instantaneous rates of mortality, so our short time interval was appropriate. We then estimated the species-specific and total loss rates (measured in terms of cover) for each plate. The abundance data collected at the beginning of the week were also used to check for differences in community composition across successional stages.

Estimates of energy waste for U , B and Q

The unutilised energy from food resources (U) was determined as the difference between the initial energy available based on initial phytoplankton abundance and the energy captured as phytoplankton consumed after 5 h of feeding (J h^{-1}). Phytoplankton concentration was converted to energy (J h^{-1}) based on the conversion of 2.85×10^{-8} mg of carbon cell^{-1} (Ghedini *et al.* 2017) and that 1 mg of carbon approximates 47.7 J (Platt & Irwin 1973).

The energy lost to maintenance (B) was estimated as energy lost to metabolism and energy lost to mortality within the community. To estimate energy lost to metabolism, we converted respiration rates to energy values (J h^{-1}) based on the conventionally assumed thermal equivalent of oxygen exchange with proteins as main metabolic substrate (i.e. 19 kJ L^{-1} ; Walsberg and Hoffman 2005). To estimate the energy lost to mortality, we obtained from the literature the average energetic content for each species of the community for which we estimated mortality rates (Norrbín & Båmstedt 1984; Wacasey & Atkinson 1987; Brey *et al.* 1988). We then averaged the energy content across species (10.83 J per mg of dry weight) and calculated rough estimates of energy lost to mortality (J h^{-1}) based on the biomass that each species lost to death (mg of dry weight).

Total energy waste (Q , J h^{-1}) was calculated for each age class as the sum of average unutilised food resources (U), average metabolic and mortality costs (which together determine B). Since there was a significant effect of initial phytoplankton concentration on food consumption, and thus on the U component of Q , we compared the energy wastage of communities separately for different levels of initial food concentration; these were divided into three categories of low ($0\text{--}1.49 \text{ cells } \mu\text{L}^{-1}$), medium ($1.5\text{--}2.89$) and high concentration ($2.9\text{--}4.15$).

Data analysis

We used linear mixed-effects models to test the effect of succession stage (fixed effect, categorical) on community mass and metabolism where retrieval date and experimental panel (recall that each panel was retrieved on a separate date) were random categorical effects. We also tested for the effects of succession stage on mass-corrected metabolism by including community mass as a covariate. We used LMM to test for the effect of successional stage on richness and mortality rates including panel as a random factor. To test for significant differences between successional stages, we used Fisher least significant difference post-hoc tests.

To test for the effect of successional stage on community feeding rate, we used repeated-measures ANCOVA where initial phytoplankton concentration was a fixed covariate, and reduction in phytoplankton abundance after 2 and 5 h were repeated measures, including panel as categorical effect. To explore the interaction between algal concentration and successional stage we plotted the final community feeding rates for each stage against initial food availability. We used a MANOVA test to determine whether average body size increased or decreased for the six dominant species across successional stages. Differences in community composition among successional stages were analysed with PERMANOVA. To reduce the contribution of quantitatively dominant taxa, abundance data were square-root ($x + 1$) transformed prior to the construction of Bray–Curtis similarity matrix, which was then used to construct a non-metric multidimensional scaling (nMDS) plot. A similarity percentage analysis (SIMPER) was done on transformed data to determine the species contributing the most to differences among successional stages.

RESULTS

Biomass and community composition

Community biomass measured as both wet and dry weight was greatest in the intermediate successional stage ($F_{2,109} = 81.56$ for wet, $F_{2,109} = 93.28$ for dry, $P < 0.001$; see Fig. S1a in Supporting Information). The relationship between dry and wet mass was shallowest in the later successional stage ($F_{2,106} = 85.82$, $P < 0.001$; Fig. S1b), probably unitary species with heavy calcareous exoskeletons (such as barnacles) were largely absent from this later stage. Barnacles contributed more than 60% to the similarity among early-stage communities, but only 15% among late-stage communities (Fig. S2a, Table S1).

Overall community composition changed significantly across succession (PERMANOVA, Pseudo- $F_{2,88} = 43.6$, P-perm = 0.0001, Fig. S2b) and richness increased steadily with successional stage, from between 5 and 6 species per plate to almost 10 species per plate on 3-week old and 9-week-old communities respectively ($F_{2,116} = 29.90$, $P < 0.001$, Fig. S2c). The average size of individuals or colonies increased significantly (MANOVA: Pillai Trace = 1.259, $F_{12,106} = 15.004$, $P < 0.0001$) in all of the largest taxa (*Bugula* spp., *Sycon*) across succession as well as in the most numerically abundant taxa (*Hydroïdes*, *Pomaceros*, *Elminius*; Fig. S3).

Community feeding rates

The amount of food captured by communities was determined by an interaction between initial phytoplankton concentration and successional age (Fig. 2, Table 1). Communities in the early successional stage consumed the least across all initial algal concentrations. Similarly, late-stage communities consumed few food resources but had slightly better consumption rates when phytoplankton concentration was low. Mid-stages performed better overall, particularly when initial food concentration was high (Fig. 2). Overall, we found that food capture improved from early to mid-stages according to MacArthur's predictions, but it did not improve further in late-stages, on the contrary it decreased from mid- to late-stages. When consumption was standardised by wet-mass, consumption per gram of mass was similar across successional stages ($F_{2,121} = 0.65$, $P = 0.52$) and was overall affected by initial phytoplankton concentration (i.e. higher consumption when more food was available; $F_{1,121} = 17.87$, $P < 0.001$). We obtained the same result when considering dry mass (effect of age: $F_{2,121} = 0.64$, $P = 0.53$; effect of initial phytoplankton concentration: $F_{1,121} = 7.87$, $P < 0.01$).

Community metabolism

As predicted by MacArthur, the metabolic costs of the community increased progressively during succession as later stage communities had around twice the metabolic rates of early-stage communities ($F_{2,92} = 16.93$, $P < 0.0001$, Fig. 3a). Post hoc tests revealed significant increases between the earliest successional stage and the latter two, but no difference between mid- and late-successional stages. Differences in wet mass between stages meant that mass-corrected metabolic rates also increased in late-stage communities, but with a

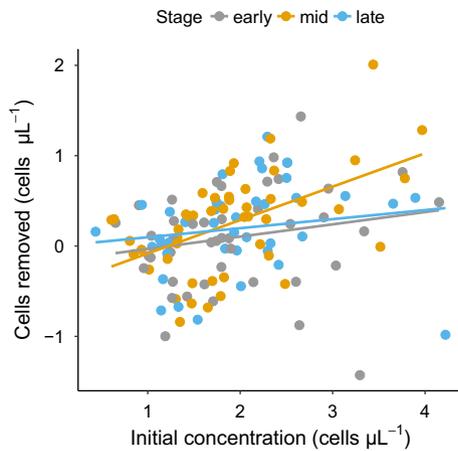


Figure 2 There was an interaction between initial algal concentration and successional age on community feeding rate. Early-stage communities consumed the least across all initial algal concentrations, with late-stage communities showing a similar pattern but higher consumption rates when resources were low. Mid-stages captured the most food when initial food concentration was higher. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 1 Repeated-measure ANCOVA of community feeding rate across successional stages with initial algal concentration as covariate

Source	SS	d.f.	MS	F-ratio	P-value
Between subjects					
Panel	20.774	9	2.308	8.906	0.000
Successional stage	1.765	2	0.882	3.405	0.036
Initial algal concentration	11.493	1	11.493	44.346	0.000
Successional stage × Initial algal concentration	3.134	2	1.567	6.046	0.003
Error	30.841	119	0.259		
Within subjects					
Feeding rate	0.011	1	0.011	0.136	0.712
Feeding rate × Panel	2.369	9	0.263	3.325	0.001
Feeding rate × Age	0.148	2	0.074	0.937	0.395
Feeding rate × Initial algal conc.	0.043	1	0.043	0.545	0.462
Feeding rate × Age × Initial algal conc.	0.139	2	0.07	0.88	0.418
Error	9.418	119	0.079		

weaker pattern. Indeed, there was a significant increase from mid- to late-stage communities but no difference between early- and late-stages (Fig. 3b). Early- and late-stage communities had the same scaling of metabolism with wet-mass, whereas mid-stage communities had a lower metabolic scaling (as their mass-specific metabolic rate was lower; Fig. 3c).

Community mortality rates

Community mortality rates, measured as total cover lost across species, increased during succession as predicted by MacArthur's theory ($F_{2,116} = 6.23$, $P = 0.003$); specifically, mortality rates in mid- and late-stage communities were higher than in early stages, but did not differ between them (Fig. 4a). Mortality per unit of wet mass was similar among successional stages ($F_{2,124} = 0.1$, $P = 0.9$), although there was a trend of higher mortality in late-stage communities (Fig. 4b). Mortality

Table 2 Summary table of observed and predicted changes in the sources of community energy wastage during succession

Metric	Successional stage (observed responses)			Direction of change	
	Early	Mid	Late	Observed	Predicted
Unutilised food sources (U)	High	Low	High	Variable and context-dependent	Decreased
Metabolic rate	Low	Medium	High	Increased	Increased
Mortality rate	Low	High	High	Increased	Increased
Maintenance (B)	Low	Medium	High	Increased	Increased
Overall waste (Q)	High	Low	High	Variable and context-dependent	Decreased

of individual taxa varied across successional stage, but no pattern was apparent except that mortality was generally higher in later successional stages (Fig. S4).

Estimates of energy wastage (Q) as a function of unutilised productivity and maintenance

Energy wasted as unutilised food resources (U) contributed the most to overall energy wastage (Q) and varied across successional stages. Instead of declining during succession as predicted, U varied across successional stages depending on food availability (initial food concentration × stage: $F_{4,7} = 74.7$, $P < 0.001$; Fig. 5a). Mid-stage communities were the most effective at capturing food resources as these increased, but late-stage communities were similar to early-stage communities. When resources were low, all communities left a similar amount of unutilised resources, with late-stage communities leaving slightly less than the other stages (Fig. 5a). The B component of Q , i.e. the energy wasted in maintenance costs of metabolism and mortality, progressively increased during succession as predicted, although its quantitative contribution to Q was minimal (Fig. 5b).

Overall, total energy wastage (Q) varied among successional stages depending on the availability of algal food, following the same pattern of U (Fig. 5c), and was not minimised across succession. When initial food concentration was low, there was no difference in overall energy wastage among successional stages, although late-stage communities tended to have the lowest energy waste. When food concentration was intermediate or high, mid-stage communities reduced their energy wastage, whereas early- and late-stage communities wasted similar amounts of energy. The energy wastage of mid-stage communities was further reduced by increasing food availability, whereas for mid- and late-stages the opposite was true (i.e. energy wastage increased with increasing food availability).

When accounting for differences in mass among successional stages, we found that early stage communities had significantly higher energy wastage per unit mass than both mid- and late-stages across all food concentrations (Fig. 5d). Similar to total energy wastage Q , waste per unit mass also increased for both early- and late-stages with increasing food availability, whereas it decreased for mid-stages.

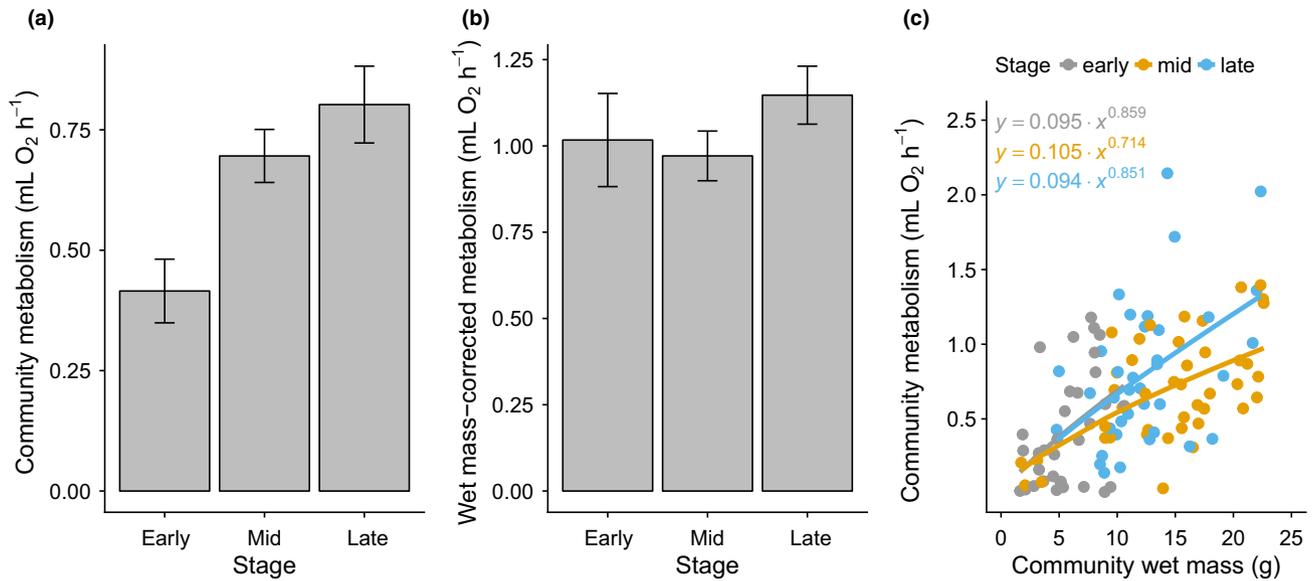


Figure 3 (a) Community metabolism increases with successional stage. (b) When wet-mass is taken into account (as a covariate) mass-corrected metabolic rate increased in late-stage communities, with a significant increase from mid- to late-stage communities but no difference between early- and late-stages. (c) Early- and late-stage communities had the same metabolic scaling, whereas mid-stage communities had a lower metabolic scaling.

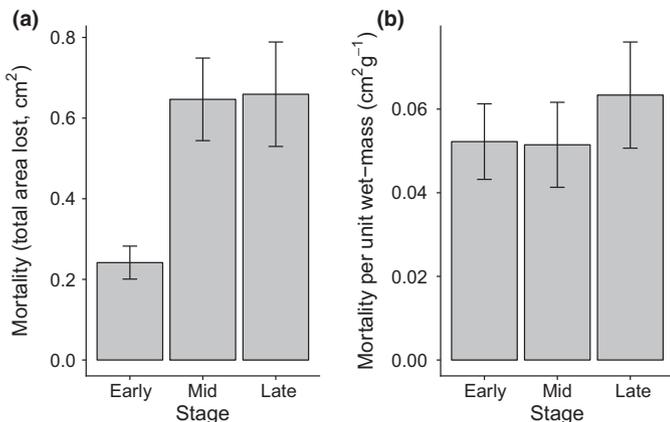


Figure 4 (a) Total cover lost due to mortality (area in cm²) increased from early- to mid-stage communities, but remained the same between mid- and late-stage communities. (b) However, mortality per unit mass tended to increase, although not significantly, in late-stage communities as these had on average a lower mass than mid-stage communities.

DISCUSSION

Do communities minimise the wastage of energy over time as Robert MacArthur predicted? We found mixed support for MacArthur's minimisation principle. As predicted, energy lost to maintenance (the *B* component) increased during succession, as older communities sustained higher costs of metabolism and mortality. However, *U*, the component that measures unutilised food resources, showed less straightforward patterns. Both MacArthur's minimisation principle (MacArthur 1969; Loreau 2010) and biodiversity theory (Naeem *et al.* 1994; Tilman *et al.* 1996; Loreau 1998; Hector *et al.* 1999) predict that the more mature, species-rich late-stages would be the most effective at capturing food resources because of

complementarity effects among species. We found, instead, that food capture varied idiosyncratically across successional stages and depended on the initial availability of phytoplankton. Whilst mid-stage communities became more effective at capturing food as its abundance increased, both early and late-stages performed poorly and left more unutilised phytoplankton. Under low food availability, all communities performed poorly but our results suggest that late-stage communities were slightly better at capturing resources when these were low (Fig. 2 and 5a). When food concentrations are very low and in low flow systems with poorly mixed boundary layers (such as this; Lagos *et al.* 2017), the resources adjacent to the feeders can be depleted completely and so feeding success drops. Yet, it seems that late-stage communities might be better than earlier stages at exploiting food resources when these are scarce and this ability might be partly due to their greater diversity (Whalen & Stachowicz 2017). Hence, whilst it is well-known that food availability influences consumption rates (McNaughton *et al.* 1989; Kooijman 2013), our results further suggest that food availability mediates the performance of a competitive community differently among successional stages.

Why were mid-stage communities better at capturing food than later successional stages when food was abundant? First, late-stage communities had lower biomasses than mid-stage, meaning there were fewer consumers overall. Second, the benthic cnidarian *Hydra sp.* was only present in the late stage communities; this predatory species took up space that other phytoplankton-feeding species would have otherwise occupied – thus there were fewer consumers of the focal resource. Third, barnacles (*Elminius modestus*) were more abundant in mid-stage communities than in late-stages (Table S1) and their feeding cirri may have broken up the boundary layer, creating greater access to food for other organisms. These three reasons highlight the importance of species identity effects in the

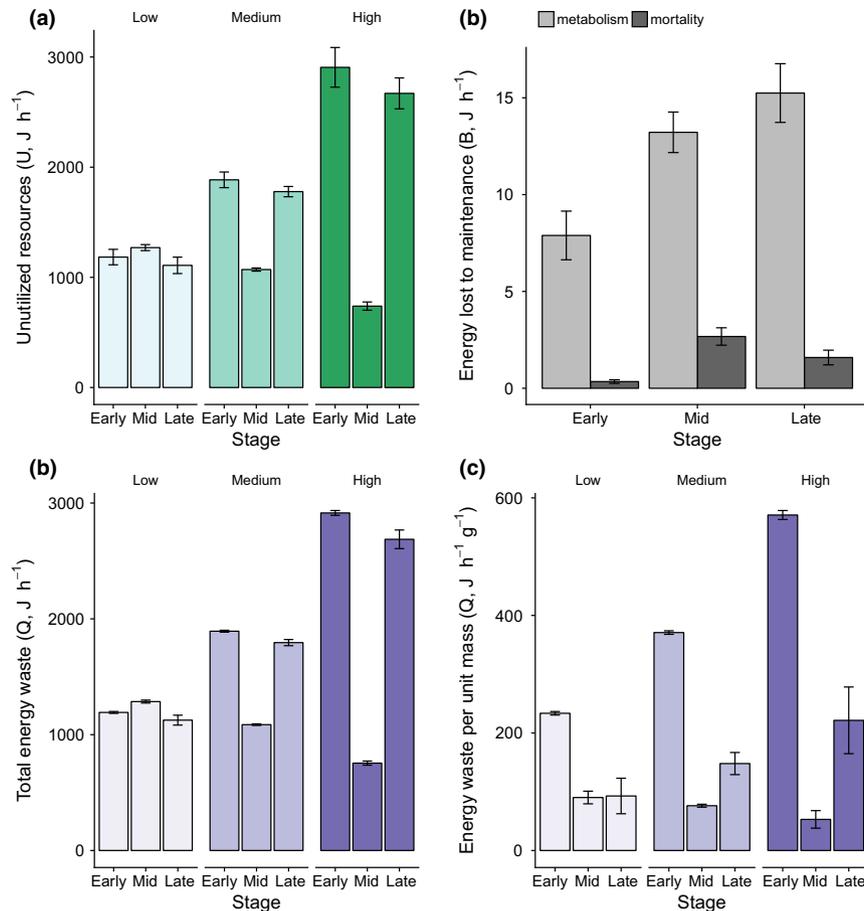


Figure 5 (a) Unutilised food resources (U) depends on both successional stage and food concentration, with mid-stage communities performing best at medium and high food concentrations. (b) Energy lost to metabolism and mortality (B) increases during succession as predicted by MacArthur. (c) U is driving patterns of overall energy wastage Q which varies across successional stages depending upon the concentration of food available, with mid-stage communities being the most efficient overall. (d) Energy waste per unit mass declines in later successional stages compared to early-stages under all food conditions. Nonetheless, mid-stages have lower energy wastage than late-stages, particularly under higher food concentrations.

successional trajectory and functioning of communities. Such species identity effects could have mediated transitions from competitive to facilitative interactions that are known to occur in this system when planktonic food resources increase (Svensson & Marshall 2015; Svanfeldt *et al.* 2017).

Other than species identity effects, there are other possible explanations for the poor performance of late-stage communities. One possibility is that the late-stage we sampled was a transitional stage. The decline in biomass observed in the late-stage might, indeed, suggest that previously established species suffered mortality (i.e. leading to a loss of biomass), whereas newly settled species were not yet grown to adults (thereby reducing food capture capacity). Nonetheless, the communities we sampled during succession were discernibly different in structure and followed typical patterns of succession, such as increases in average size of organisms, species richness, metabolism and mortality (Odum 1969; Connell & Slatyer 1977). These conditions should have been sufficient to satisfy MacArthur's predictions. Indeed, MacArthur minimisation principle does not rely on specific time frames of community development, but rather predicts that community efficiency should increase in a continuous fashion over any

temporal scale. Our results suggest that, perhaps, efficiency increases in a more discontinuous way. Community efficiency might increase from immature to mature communities overall, but with intermediate steps during which efficiency fluctuates following changes in species abundances and replacements.

Late-stage communities also suffered the highest mortality rate per unit mass which, if due to predation, could account for their higher overall energy wastage. Food web theory predicts that the addition of higher trophic levels (i.e. predators of sessile invertebrates in this case) can reduce community functioning to intermediate values of efficiency and biomass (Loreau 2010). To an extreme, top-down control can overexploit resources (i.e. sessile invertebrate consumers), reducing standing stock and ecosystem functioning (Silliman *et al.* 2013). Marine sessile communities are open systems and, as such, subject to varying levels of predation (Sutherland 1974; Keough & Downes 1986). Sessile organisms typically respond to increased predation by investing more energy in chemical or structural defences (Pawlik 1993). Hence, higher predation rates in late-stage communities might not only explain their lower biomass and low food consumption, but also their higher metabolic rate.

Considerations of how energy waste varies during succession could be clarified by accounting for changes in biomass – a greater community biomass (such as in mid-stages) would most likely lead to higher consumption rates and maintenance costs. Once we accounted for changes in biomass, we found that energy waste (Q) per unit biomass declined from early to mid and late successional stages. This is an important result which suggests that succession promoted combinations of species that minimised mass-specific energy wastage. For instance, late-stages had similar consumption rates to early-stages, but supported a much higher biomass and metabolic rate. This result finds support in biodiversity theory, which has shown that species interactions can promote species coexistence by minimising differences among species fitness, such that lower performing species perform better in more diverse communities (Vandermeer 1981; Chesson 2000; Loreau 2004; Isbell *et al.* 2009). These positive effects of diversity among species performance can stabilise community functioning to environmental fluctuations (Ives *et al.* 2000; Isbell *et al.* 2015).

Finally, can MacArthur's principle explain the inconsistent effects of diversity on invasibility? More diverse communities are usually more resistant to invasion and one reason for this could be that diversity improves resource use within a trophic level (Hector *et al.* 2001; Stachowicz *et al.* 2002; Levine *et al.* 2004). Indeed, whether an invader successfully establishes often depends upon conditions of resource availability (Davis *et al.* 2000) and whether they match with the arrival and resource requirements of the invader itself (Hart & Marshall 2012). However, our results suggest that diversity is a poor proxy for the ability of communities of competitors to exploit food sources. This result may help explain why species richness is sometimes positively associated with invasion, at least in situations where the invader's success is determined by food availability.

In conclusion, we found mixed support for MacArthur's minimisation principle. We observed that energy wastage per unit mass decreased during succession, but this was not true for overall energy wastage and diversity did not explain this pattern. Our study is the first to experimentally test MacArthur's minimisation principle, hence we cannot draw parallels with other tests of this theory. We can, however, make two final considerations. First, MacArthur principle might be correct, but only on longer temporal scales that account for fluctuations in the energy wasted as unutilised food resources during succession. Second, MacArthur's minimisation principle might be incorrect if competition is not the strongest driver of energy use in a community. MacArthur's theory is centred on the idea that competitive effects are dominant in shaping the course of succession. However, others have challenged this view suggesting that other interaction types (e.g. trophic, facilitative, mutualistic) might be equally important (Connell & Slatyer 1977; Osman & Haugsness 1981; Stachowicz 2001; Bruno *et al.* 2003) and might therefore modify the way a community captures or spends energy. These other processes might provide a continuous source of variation in community resource capture that could prevent the minimisation of energy wastage, and we eagerly await further tests. This uncertainty highlights how nebulous our understanding of ecosystem functioning still is, yet resolving it will prove crucial to predict how ecosystem processes will change in future environments.

ACKNOWLEDGEMENTS

ML was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41). DJM, ML and CRW were supported by the Australian Research Council.

AUTHORSHIP

DJM, ML and CRW conceived the experiment, DJM oversaw the experiment, DJM and GG analysed the data and GG wrote the first draft of the manuscript. All authors contributed substantially to revisions.

DATA ACCESSIBILITY STATEMENT

The datasets supporting this article are deposited in the Figshare repository: <https://doi.org/10.4225/03/5ae78ffdb9c74>.

REFERENCES

- Brew, J.S. (1982). Niche shift and the minimization of competition. *Theor. Popul. Biol.*, 22, 367–381.
- Brey, T., Rumohr, H. & Ankar, S. (1988). Energy content of macrobenthic invertebrates: general conversion factors from weight to energy. *J. Exp. Mar. Biol. Ecol.*, 117, 271–278.
- Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003). Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.*, 18, 119–125.
- Chesson, P.L. (1990). Geometry, heterogeneity and competition in variable environments. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 330, 165–173.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.
- Clark, G.F. & Johnston, E.L. (2011). Temporal change in the diversity-invasibility relationship in the presence of a disturbance regime. *Ecol. Lett.*, 14, 52–57.
- Connell, J.H. & Slatyer, R.O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.*, 111, 1119–1144.
- Davis, M.A., Grime, J.P. & Thompson, K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.*, 88, 528–534.
- Dunstan, P.K. & Johnson, C.R. (2004). Invasion rates increase with species richness in a marine epibenthic community by two mechanisms. *Oecologia*, 138, 285–292.
- EPA (2010). Baywide water quality monitoring program. Milestone Report No 5. (March 2010). In: Environment Protection Authority Victoria, www.epa.vic.gov.au.
- Ferguson, N., White, C.R. & Marshall, D.J. (2013). Competition in benthic marine invertebrates: the unrecognized role of exploitative competition for oxygen. *Ecology*, 94, 126–135.
- Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D. *et al.* (2007). The invasion paradox: reconciling pattern and process in species invasions. *Ecology*, 88, 3–17.
- Gatto, M. (1990). A general minimum principle for competing populations – some ecological and evolutionary consequences. *Theor. Popul. Biol.*, 37, 369–388.
- Ghedini, G., White, C.R. & Marshall, D.J. (2017). Does energy flux predict density-dependence? An empirical field test. *Ecology*, 98, 3116–3126.
- Ghedini, G., White, C.R. & Marshall, D.J. (2018). Metabolic scaling across succession: do individual rates predict community-level energy use? *Funct. Ecol.*, in press (accepted). <https://doi.org/10.1111/1365-2435.13103>
- Hart, S.P. & Marshall, D.J. (2012). Advantages and disadvantages of interference-competitive ability and resource-use efficiency when invading established communities. *Oikos*, 121, 396–402.

- Hart, S.P. & Marshall, D.J. (2013). Environmental stress, facilitation, competition, and coexistence. *Ecology*, 94, 2719–2731.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G. *et al.* (1999). Plant diversity and productivity experiments in European grasslands. *Science*, 286, 1123.
- Hector, A., Dobson, K., Minns, A., Bazeley-White, E. & Lawton, J.H. (2001). Community diversity and invasion resistance: an experimental test in a grassland ecosystem and a review of comparable studies. *Ecol. Res.*, 16, 819–831.
- Isbell, F.I., Polley, H.W. & Wilsey, B.J. (2009). Species interaction mechanisms maintain grassland plant species diversity. *Ecology*, 90, 1821–1830.
- Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C. *et al.* (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, 526, 574–577.
- Ives, A., Klug, J. & Gross, K. (2000). Stability and species richness in complex communities. *Ecol. Lett.*, 3, 399–411.
- Keough, M.J. & Downes, B.J. (1986). Effects of settlement and post-settlement mortality on the distribution of the ascidian *Trididemnum opacum*. *Mar. Ecol. Prog. Ser.*, 33, 279–285.
- Kooijman, S.A.L.M. (2013). Waste to hurry: dynamic energy budgets explain the need of wasting to fully exploit blooming resources. *Oikos*, 122, 348–357.
- Kozlovsky, D.G. (1968). A critical evaluation of trophic level concept. I. Ecological efficiencies. *Ecology*, 49, 48–60.
- Lagos, M.E., Barneche, D.R., White, C.R. & Marshall, D.J. (2017). Do low oxygen environments facilitate marine invasions? Relative tolerance of native and invasive species to low oxygen conditions. *Glob. Change Biol.*, 23, 2321–2330.
- Lindeman, R.L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, 23, 399–418.
- Levine, J.M. & D'Antonio, C.M. (1999). Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, 87, 15–26.
- Levine, J.M., Adler, P.B. & Yelenik, S.G. (2004). A meta-analysis of biotic resistance to exotic plant invasions. *Ecol. Lett.*, 7, 975–989.
- Loreau, M. (1998). Biodiversity and ecosystem functioning: a mechanistic model. *Proc Nat Acad Sci USA*, 95, 5632–5636.
- Loreau, M. (2004). Does functional redundancy exist? *Oikos*, 104, 606–611.
- Loreau, M. (2010). *From Populations to Ecosystems: Theoretical Foundations for a New Ecological Synthesis*. Princeton University Press, Princeton, NJ.
- MacArthur, R. (1969). Species packing, and what competition minimizes. *Proc. Natl Acad. Sci. USA*, 64, 1369–1371.
- MacArthur, R. (1970). Species packing and competitive equilibrium for many species. *Theor. Popul. Biol.*, 1, 1–11.
- MacArthur, R.H. (1972). *Geographical Ecology: Patterns in the Distribution of Species*. Princeton University Press, Princeton, NJ.
- Marshall, D.J. & Keough, M.J. (2009). Does interspecific competition affect offspring provisioning? *Ecology*, 90, 487–495.
- McNaughton, S.J., Oesterheld, M., Frank, D.A. & Williams, K.J. (1989). Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature*, 341, 142–144.
- Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature*, 368, 734–737.
- Norrbin, F. & Båmstedt, U. (1984). Energy contents in benthic and planktonic invertebrates of Kosterfjorden, Sweden: a comparison of energetic strategies in marine organism groups. *Ophelia*, 23, 47–64.
- Odum, H.T. (1956). Efficiencies, size of organisms, and community structure. *Ecology*, 37, 592–597.
- Odum, E.P. (1969). Strategy of ecosystem development. *Science*, 164, 262–270.
- Osman, R.W. & Haugsness, J.A. (1981). Mutualism among sessile invertebrates – a mediator of competition and predation. *Science*, 211, 846–848.
- Pawlik, J.R. (1993). Marine invertebrate chemical defenses. *Chem. Rev.*, 93, 1911–1922.
- Platt, T. & Irwin, B. (1973). Caloric content of phytoplankton. *Limnol. Oceanogr.*, 18, 306–310.
- Silliman, B.R., McCoy, M.W., Angelini, C., Holt, R.D., Griffin, J.N. & van de Koppel, J. (2013). Consumer fronts, global change, and runaway collapse in ecosystems. *Annu. Rev. Ecol. Evol. Syst.*, 44(44), 503–538.
- Stachowicz, J.J. (2001). Mutualism, facilitation, and the structure of ecological communities. *Bioscience*, 51, 235–246.
- Stachowicz, J.J., Fried, H., Osman, R.W. & Whitlatch, R.B. (2002). Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. *Ecology*, 83, 2575–2590.
- Sutherland, J.P. (1974). Multiple stable points in natural communities. *Am. Nat.*, 108, 859–873.
- Svanfeldt, K., Monro, K. & Marshall, D.J. (2017). Field manipulations of resources mediate the transition from intraspecific competition to facilitation. *J. Anim. Ecol.*, 86, 654–661.
- Svensson, J.R. & Marshall, D.J. (2015). Limiting resources in sessile systems: food enhances diversity and growth of suspension feeders despite available space. *Ecology*, 96, 819–827.
- Tikhonov, M. (2016). Community-level cohesion without cooperation. *eLife*, e15747: 1–15.
- Tilman, D., Wedin, D. & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, 379, 718–720.
- Vandermeer, J. (1981). The interference production principle – an ecological theory for agriculture. *Bioscience*, 31, 361–364.
- Veldhuis, M.J.W. & Kraay, G.W. (2000). Application of flow cytometry in marine phytoplankton research: current applications and future perspectives. *Sci. Mar.*, 64, 121–134.
- Wacasey, J.W. & Atkinson, E.G. (1987). Energy values of marine benthic invertebrates from the Canadian Arctic. *Mar. Ecol. Prog. Ser.*, 39, 243–250.
- Walsberg, G.E. & Hoffman, T.C.M. (2005). Direct calorimetry reveals large errors in respirometric estimates of energy expenditure. *Journal of Experimental Biology*, 208, 1035–1043.
- Whalen, M.A. & Stachowicz, J.J. (2017). Suspension feeder diversity enhances community filtration rates in different flow environments. *Mar. Ecol. Prog. Ser.*, 570, 1–13.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information section at the end of the article.

Editor, Jonathan Chase

Manuscript received 13 March 2018

First decision made 13 April 2018

Manuscript accepted 17 April 2018