



The maximum power principle predicts the outcomes of two-species competition experiments

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The maximum power principle (MPP) states that biological systems organize to increase power whenever the system constraints allow. The MPP has the potential to explain a variety of ecological patterns because biological power (metabolism) is a component of all ecological interactions. I empirically tested the MPP by reanalyzing three two-species competition experiments by Gause, Vandermeer, and Fox and Morin. These experiments investigated competitive outcomes in microcosms of heterotrophic protists. I introduce metabolic state-space graphs to portray the metabolic trajectories of the communities and show that the steady-state outcomes of these experiments are consistent with the MPP. Winning species were successfully predicted a priori from their status as the species with the highest power when alone. In addition, periods of coexistence, although not predictable a priori, were consistent with the MPP because coexistence states had community-level power that was higher than either species could achieve alone. Thus, the outcomes of all ten trials were the maximum power states, given the options. The results suggest that the maximum power principle may represent a useful energetic organizing principle for communities.

Ecologists have long sought a general principle that explains both the directional change in non-equilibrium systems and the characteristics of steady-state systems. To this end, several thermodynamic goal functions have been offered that cast organization in biological systems as a maximization or minimization process for energetic quantities (see review of the topic and comparison of goal functions in Fath et al. 2001). The maximum power principle (MPP) is one of these principles. Originally formulated by Lotka (1922a) and further developed by Odum and Pinkerton (1955), the MPP states that biological systems capture and use energy to build and maintain structures and gradients that allow additional capture and utilization of energy. Non-biological systems such as the Atwood machine and Bernard cells have been used to explain the principle, but these analogies can make it hard to visualize what power maximization really looks like, or how to find it, in nature (Hall 1995, Odum 1995). The MPP was formulated more than 80 years ago, but to date very few ecological studies have sought to empirically evaluate the MPP concept (Hall 2004; but see Cai et al. 2006). Despite this, the MPP has been hotly debated in the ecological literature (Månsson and McGlade 1993, Patten 1993). In this paper, I strive to bring the MPP back to its biological roots and show that we can generate testable predictions about real biological phenomenon through the lens of the MPP.

Power has units of energy per time. Metabolic rate, usually expressed in watts (J s^{-1} ; i.e. energy per time), can be thought of as biological power and can be used as the quantity of interest for studies of MPP in ecology. One of

the great strengths of the MPP is that it directly relates energetics to fitness; organisms maximize fitness by maximizing power. With greater power, there is greater opportunity to allocate energy to reproduction and survival, and therefore an organism that captures and utilizes more energy than another organism in a population will have a fitness advantage (Lotka 1922a, Brown et al. 1993).

Interestingly, Lotka (1922b) proposed that the MPP was a fourth law of thermodynamics, and Odum (1995) viewed the MPP as a general principle for system self-organization. Thus, Lotka and Odum hypothesized that all levels of biological organization should show dynamics consistent with the MPP, not just individuals that maximize fitness. Such a possibility has been hard to test and is no doubt one of the reasons for the lack of empirical assessments of the MPP. Even with an appropriate measure of biological power such as metabolism, many states in ecological systems will be hard to assess in terms of the MPP because it is difficult to know whether a particular state is the maximum given what it could otherwise be, especially for systems that are temporally dynamic. Competitive exclusion, however, provides a fairly discrete ecological phenomenon that can be investigated in terms of the MPP.

Competition is an interaction among individuals in which the struggle for limited resources has negative consequences for all the organisms involved. The competitive exclusion principle states that species that compete for the same resources cannot coexist indefinitely (Gause 1934). Thus, under competition, one species will eventually go extinct and one species will persist. The winning species

clearly has some ability to maintain production that the losing species does not. One possible MPP interpretation is that in the aggregate, the individuals of the winning population are acquiring and utilizing more energy (i.e. have higher power) than the individuals in the losing population, and they therefore survive and reproduce at higher rates and win the competition. This leads to a prediction: the outcome of competition will be in favor of the species with the highest power. The power of the possible outcomes can be found by examining the total population-level metabolism of each competitor when alone. If the power of one species exceeds that of another, then that species should out-compete the other. If we see this outcome, then we can say that the community has organized to a maximum power state. (It is important to stress here that the 'maximum' in the MPP is not a fixed level of power. Rather, it is the highest level attainable given the constraints of the system. Thus, the maximum power of a system may change with the evolution of new traits or the introduction of a new species or new resources.)

Competitive interactions do not always lead to exclusion. Some species may coexist with little interaction, and others may actually facilitate the species with which they coexist. These two alternative outcomes are much harder to predict a priori from the power states of each species when alone. However, if coexistence occurs, the MPP suggests that the resulting communities should have higher power than either species could have alone. Similarly, if a species is facilitated by another, then that species should attain a level of power greater than what it could attain alone.

I tested the MPP with data from studies examining competitive outcomes in two-species microcosm communities of heterotrophic protists. Using reported steady-state densities of each species and allometric predictions of individual metabolic rates, I estimated the alternative power outcomes of all the competitors and compared the outcomes with predictions generated from the MPP. Specifically, I predicted that 1) a winning species uses more power at its steady-state density than the losing species uses at its steady-state density, 2) if coexistence occurs, it will be characterized by community-level power that exceeds the highest-power competitor's when grown in isolation, and 3) if facilitation occurs, it will be characterized by

population-level power that is higher for the facilitated species in the presence of the other species than when it is not. The results provide support for all three predictions, providing the first empirical demonstration that observable ecological dynamics are consistent with the MPP.

Methods

There is a large literature on competitive interactions, but few studies met the criteria for inclusion here. Studies must have focused on two species, been conducted in microcosms, reported steady-state densities of each competitor when alone, and showed time-series of the competitive trials. Several potential experiments of this sort were excluded because densities did not achieve convincing steady states, because microcosms were not maintained with a constant resource flow (i.e. carrying capacity decreased with time, precluding a steady-state outcome), or because more than two species were competing. Also, given uncertainties about how to identify the appropriate metric for metabolism in photosynthetic organisms, and the inadequacies of current metabolic allometries for photosynthetic unicells, studies on algae were excluded. Three studies had the requisite data: Gause (1934), Vandermeer (1969) and Fox and Morin (2001).

Culture conditions were not identical across experiments. However, in each study all populations were initiated with small numbers of individuals and allowed to grow. Each species was grown alone and in paired competition with each of the other species in the study. The competitive outcome for each species pairing was determined by the original authors (Table 1). Gause did not run all experiments until complete extinction of the losing species, but he stated, for example, that *Paramecium caudatum* always was displaced completely by *P. aurelia*. Similarly, Vandermeer ceased some experiments prior to the complete extinction of one species. In all cases, trials were run long enough to determine which species was the dominant competitor.

Details of the three experiments are as follows. Gause (1934) grew populations of *P. caudatum*, *P. aurelia* and

Table 1. Summary of competitive predictions and outcomes for the competition experiments of Gause (1934), Vandermeer (1969), and Fox and Morin (2001). Two sets of predictions for the winning species are shown. The MPP predicted that the winning species would be the one with the highest population-level metabolism at K-alone, and an alternative prediction was that the species with the highest K-alone would win. Incorrect predictions are shown in bold. Species are *Paramecium aurelia*, *P. caudatum*, *P. bursaria*, *Blepharisma* sp., *Stylonichia pustulata*, *Tetrahymena thermophila* and *Colpidium striatum*. *P. bursaria* was cultivated without symbiotic algae (Vandermeer 1969).

Species pair	Winning species	Winner predicted by MPP	Winner predicted by K-alone
Gause (1934)			
<i>P. aurelia</i> vs <i>P. caudatum</i>	<i>P. aurelia</i>	<i>P. aurelia</i>	<i>P. aurelia</i>
<i>P. aurelia</i> vs <i>S. pustulata</i>	<i>P. aurelia</i>	<i>P. aurelia</i>	<i>P. aurelia</i>
<i>P. caudatum</i> vs <i>S. pustulata</i>	<i>P. caudatum</i>	<i>P. caudatum</i>	<i>P. caudatum</i>
Vandermeer (1969)			
<i>P. bursaria</i> vs <i>P. caudatum</i>	<i>P. caudatum</i>	<i>P. caudatum</i>	<i>P. caudatum</i>
<i>Blepharisma</i> vs <i>P. aurelia</i>	<i>P. aurelia</i>	<i>P. aurelia</i>	<i>P. aurelia</i>
<i>P. bursaria</i> vs <i>Blepharisma</i>	<i>Blepharisma</i>	<i>Blepharisma</i>	<i>P. bursaria</i>
<i>Blepharisma</i> vs <i>P. caudatum</i>	<i>P. caudatum</i>	<i>P. caudatum</i>	<i>P. caudatum</i>
<i>P. bursaria</i> vs <i>P. aurelia</i>	<i>P. aurelia</i>	<i>P. aurelia</i>	<i>P. aurelia</i>
<i>P. aurelia</i> vs <i>P. caudatum</i>	<i>P. caudatum</i>	<i>P. caudatum</i>	<i>P. aurelia</i>
Fox and Morin (2001)			
<i>T. thermophila</i> vs <i>C. striatum</i>	Coexistence but <i>C. striatum</i> dominant	<i>C. striatum</i>	<i>C. striatum</i>

Stylonichia pustulata in 5 ml microcosms in 10 ml test tubes with bacteria supplied as food at regular intervals. He centrifuged tubes daily and almost completely changed out the food medium, thereby removing most metabolic wastes. Temperature was maintained at 26°C, and samples were taken for density measurements daily. Vandermeer (1969) grew populations of *P. caudatum*, *P. aurelia*, *P. bursaria* and *Blepharisma* sp. in 5 ml microcosms in 10 ml test tubes with bacteria supplied as food at regular intervals. Temperature was maintained at 25°C, and microcosms were kept in darkness. He extracted and replaced 0.5 ml of medium daily, removing some of the metabolic wastes. Samples were taken for density measurements daily. Fox and Morin (2001) grew populations of *Tetrahymena thermophila* and *Colpidium striatum* in 100 ml microcosms in 240 ml glass bottles with populations of bacteria maintained with nutrient medium and wheat seeds. They replaced 10% of the medium and added a new wheat seed weekly. Samples were taken for density measurements every 2–3 days.

I used population counts from Gause (1934) as reported in his appendices; I used digital imaging software to recover the Vandermeer (1969) data from his figures; and I used original raw data supplied by JWF for the Fox and Morin (2001) study. Vandermeer presented log-transformed abundances, which I retransformed to abundance values. The steady state density of each population when alone (hereafter referred to as K-alone) was estimated in each of the original studies (Table 2), and I used the authors' original estimates of K-alone. Although replicated experiments were conducted, here I used the average population size per time step for each species-pair combination for consistency because it was impossible to separate Vandermeer's replicates. All replicates reached similar outcomes, alleviating any concerns of inconsistencies among replicates.

I obtained body mass estimates for each species from Foissner and Berger (1996) and Long and Morin (2005). For many protist species, body size is highly variable, and average individual mass may have been higher or lower in the original experiments than the estimates provided in the literature. I estimated the individual metabolic rate, B (W), of each species with an allometric relation, corrected for the exponential effect of temperature on metabolism, with:

$$B = b_0 M^\Theta e^{\frac{E}{k_b T} + c} \quad (1)$$

where M is the average body mass of the organism (g), E is the activation energy set at 0.61 eV, T is temperature (Kelvin), and k_b is the Boltzmann constant (eV Kelvin⁻¹). This equation can be used to estimate the average metabolic rates of many organisms, given taxon-specific constants. For unicellular organisms, the normalization constant, b_0 , = 0.0179, the scaling parameter, Θ , = 0.751, and the correction for the intercept of the relationship describing the temperature-dependence of metabolic rate, c , = 19.21 (Hemmingsen 1960, Gillooly et al. 2001, Brown et al. 2004). See Gillooly et al. (2001) and Brown et al. (2004) for further explanation of the body mass- and temperature-dependence of metabolism. I converted each measurement of population size at each time step and at K-alone into a measurement of population metabolism by multiplying the population size by the individual metabolic rate for that species (Table 2).

Metabolic state-space

The predictions I derived from the MPP are for the competitive outcomes, but all the studies analyzed here went through various temporal dynamics to get to those outcomes. To see these dynamics and the outcomes more clearly, I plotted the metabolic trajectories of competing species in a metabolic state-space (Fig. 1). Unlike a classic state-space that shows the abundance of each competing species at a point in time, this approach normalizes the competitors by the amount of energy they use. Each axis represents the population-level metabolic rate for a competitor, and each point in the space shows the population-level metabolism of both species at a given time. Distance from the origin increases with increasing community-level metabolic rate (the sum of both species' metabolisms). The steady-state abundance of each competitor when alone (K-alone) is indicated on its axis with a solid, black circle, and the system is expected to follow some path to the K-alone of the winning species, which is farther from the origin than the K-alone of the losing species (meaning it is the highest power alternative). Although I am not predicting the temporal dynamics of the competition trials in this study, the metabolic state-space graphs show us what these dynamics are like and should help with future development of theory about the dynamics of these systems.

Table 2. Estimated individual metabolic rates for each species in each study, corrected for the temperature of the study. See Table 1 legend for species names. Masses for Gause (1934) and Vandermeer (1969) are from Foissner and Berger (1996), and masses for Fox and Morin (2001) are from Long and Morin (2005). Per capita metabolic rates are calculated using Eq. 1. K-alone values are taken from the original studies.

Species	Mass (g)	Per capita metabolic rate (Watt)	K-alone	Metabolic rate at K (Watt)
Gause (1934)				
<i>P. aurelia</i>	1.5×10^{-7}	1.56×10^{-9}	560	8.74×10^{-7}
<i>P. caudatum</i>	5.0×10^{-7}	3.85×10^{-9}	202	7.78×10^{-7}
<i>S. pustulata</i>	8.0×10^{-8}	9.71×10^{-10}	90	8.74×10^{-8}
Vandermeer (1969)				
<i>P. aurelia</i>	1.5×10^{-7}	1.44×10^{-9}	671	9.66×10^{-7}
<i>P. bursaria</i>	1.2×10^{-7}	1.22×10^{-9}	234	2.85×10^{-7}
<i>P. caudatum</i>	5.0×10^{-7}	3.55×10^{-9}	366	1.30×10^{-6}
<i>Blepharisma</i> sp.	2.5×10^{-7}	2.11×10^{-9}	194	4.09×10^{-7}
Fox and Morin (2001)				
<i>T. thermophila</i>	3.0×10^{-8}	2.86×10^{-10}	247	7.06×10^{-8}
<i>C. striatum</i>	6.5×10^{-8}	5.12×10^{-10}	719	3.68×10^{-7}

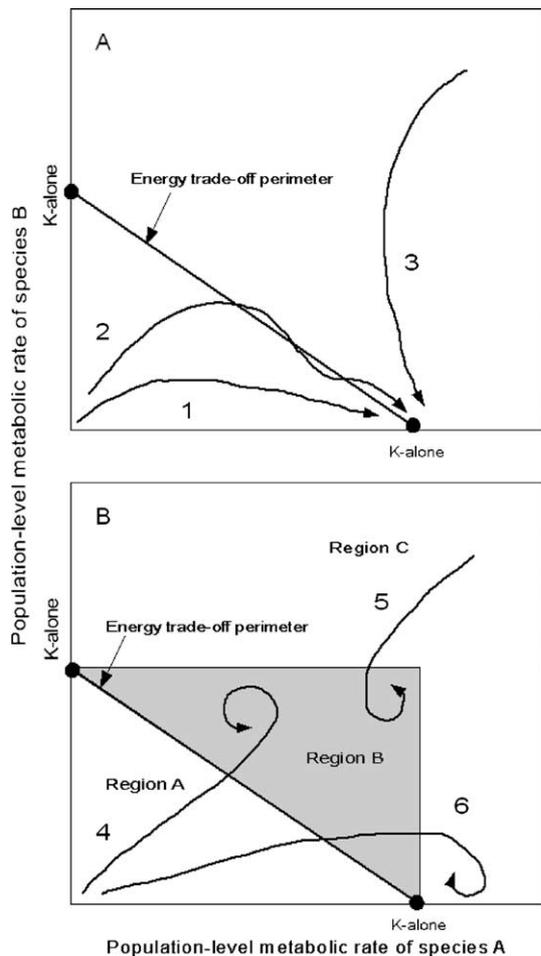


Figure 1. Metabolic state-space, showing generally the features necessary to investigate the community-level dynamics of two-species competition. (A) the population-level metabolic rate of the competing species are on the axes, and the metabolic rate of each population at its steady-state density when alone (K-alone) is shown as a heavy black dot, and the line connecting these two values is termed the energy tradeoff perimeter (ETP). The MPP predicts that populations initiated at low densities will grow and the species with the higher power (species A in this case) will exclude the other species (trajectory 1). Species may share resources equitably for some time, and then move along the ETP toward the winning species (trajectory 2). If populations are initiated at sizes above K-alone, community power will decrease rapidly toward the winning species (trajectory 3). (B) as in (A), but in this case we see that if two competing species can coexist, they should have steady states that occur beyond the ETP. Species that compete perfectly for resources can exist only in region A or along the ETP, and any community that occurs in region A should increase in power. If resource partitioning occurs, the metabolic trajectory should move past the ETP and reside in region B, where the total amount of community power is greater than the higher-power competitor could achieve when alone (trajectory 4). Likewise, species that can only partition resources but are initiated at locations in region C will decrease back to region B (trajectory 5). In region C, at least one species has power higher than it could achieve when alone, indicating facilitation (trajectory 6).

All of the experiments reanalyzed here were set up with fixed resource supply rates. Given that the resource is metabolism-supporting, competitors must divide up a limited amount of metabolism. A community of two

perfectly competing species should be able to flux no more energy than the superior competitor could when alone. Thus, the community power is traded off between the two species given this metabolic constraint. The tradeoff boundary is drawn by connecting the K-alone metabolic rates of the competing species with a line (Fig. 1A). Along this line, which I call the energy tradeoff perimeter (ETP), the community is dividing up metabolism between the two competitors, and all points along the ETP are intermediate in total community metabolism between the K-alone metabolisms of the two competing species. If the community metabolism falls on the ETP, it can achieve a higher power state by moving along the ETP toward the higher-power competitor. Thus, the ETP not only marks the metabolic constraint, but it acts as a directional for higher power.

Construction of an ETP allows us to see the community power state relative to the system constraints. We can use the ETP to break the state-space into regions where qualitatively different interactions are occurring. Points closer to the origin than the ETP indicate the community is using less power than the constraint would allow, and further growth of one or both of the competing populations is expected. Whenever the community occurs above the ETP, i.e. in regions B or C in Fig. 1B, it is using more energy than either species could use at their K-alone. There are three ways that this could happen. First, perfect competitors could over-harvest the resource and temporarily increase the community-level metabolic rate above what either species can sustain. Second, resource-partitioning may occur, allowing each species to use a different part of the resource and therefore maintain metabolism that cannot be maintained by their competitor. This outcome should allow at least temporary coexistence, as the competitively inferior species should be able to maintain power using resources unused by the dominant competitor. Finally, facilitation between species may enhance population-level metabolic rates above what they could be when alone (region C in Fig. 1B), indicating that one competitor is altering the resource flow in some way as to increase its availability to the other competitor, such as by producing usable wastes.

Results

The outcome of all ten competitive trials supported the three predictions. First, where competitive exclusion occurred or had nearly occurred at the end of the experiment, the winner was the species with the highest metabolism at K-alone, as expected by the MPP (Table 1, 2; Fig. 2A–C, 3A–B, 3D–E). Even when coexistence occurred, the higher-power competitor was the dominant species in the system. This uniformity of outcomes in favor of the higher-power competitor is unlikely to occur by chance alone ($p < 0.01$, one-tailed test of equal proportions, $n = 10$). Second, there were three cases of coexistence, two of which showed community-level metabolism that exceeded the ETP. Vandermeer's pairing of *P. aurelia* versus *P. caudatum* (Fig. 3C) showed some fluctuations of metabolism and a slowed movement toward complete extinction of the losing species. The period of coexistence was centered along the

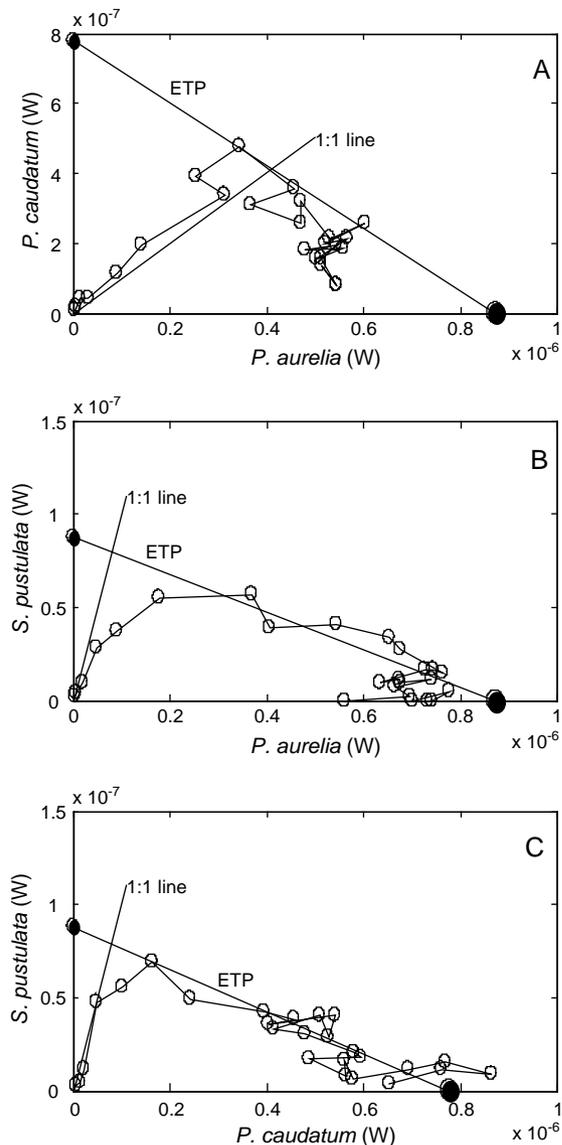


Figure 2. Metabolic state-space graphs depicting the community-level trajectories and outcomes of competition in Gause's (1934) experiment. Panels show competition between (A) *Paramecium aurelia* and *P. caudatum*, (B) *P. aurelia* and *Stylonichia pustulata*, and (C) *P. caudatum* and *S. pustulata*. Open circles represent the population power of species *x* and species *y* at any given sampling point, and the connecting line shows the trajectory of the population power through time. The thicker negative-sloping line connecting the population power for each species at carrying capacity when grown alone (K-alone, represented by solid circles along the respective species' axis, small for the lower-power species and large for the higher-power species) is the energy tradeoff perimeter (ETP). This line is intermediate in metabolism between each species at K-alone for all points along the line and serves as both a constraint marker and a directional for a higher-power trajectory. In all three panels, the outcomes were all highest-power states, given the options.

ETP. In Vandermeer's pairing of *Blepharisma* versus *P. bursaria* (Fig. 3F), a period of coexistence occurred in region B, with dominance shown by the higher-power competitor *Blepharisma*. Finally, Fox and Morin's pairing of *C. striatum* and *T. thermophila* (Fig. 4) showed an

extended period of coexistence that occurred in region C, far above the metabolic rate shown by *C. striatum* when alone, but with the higher-power competitor *C. striatum* clearly dominant. However, this trajectory later declined back toward the ETP, whereupon *T. thermophila* had a brief but large increase in power, followed by a crash to below the ETP, and finally some movement back toward the K-alone of *C. striatum* by the end of the experiment.

The temporal dynamics of the ten communities were variable but showed some general patterns (Fig. 2–4). Upon initiation of all experiments, community metabolism generally increased from the initial low-power state toward the end state, yet with many fluctuations and short-term drops in power evident. Many of the fluctuations in the trajectories were centered on the ETP. Gause's trajectories followed the ETP fairly closely (Fig. 2). Vandermeer's trajectories were more variable, but they still were centered on the ETP (except in the *Blepharisma* – *P. bursaria* pairing, Fig. 4F). In some cases, the community-level metabolic rate exceeded the ETP, but then retracted back down below it. Some competitors appeared to quickly dominate the power of the community (Fig. 3B–F, 4), with the winning or dominant competitor controlling the community power early on and rapidly moving the metabolic trajectory away from the 1:1 line. In other cases (Fig. 2A–C, 3A), there was some 'sharing' of the power for a few time steps, as evidenced by metabolic trajectories following along the 1:1 line of equal metabolism. In all cases, when the winning competitor pulled the metabolic trajectory away from the losing competitor and toward the final outcome, the trajectory did not travel back across the 1:1 line.

Discussion

The general idea of the MPP is that change in ecological systems is toward higher power, when the opportunity exists. One of the lingering difficulties of empirically demonstrating the MPP is that one must be able to estimate the power of the alternative states toward which a system may move. Since we can usually observe a system only in one place at one time, it becomes difficult to know if the current state has a higher power than the other possible states. This was the clear advantage of investigating two-species competition in view of the MPP: the alternative states were known and thus predictions were possible a priori. In the case of coexistence, the power outcome or even the opportunity for coexistence could not be predicted in advance, but the MPP allows us to at least predict that the community power would be greater under coexistence than with a single-species outcome.

The MPP invokes the fitness advantage of attaining higher power (Lotka 1922a, Brown et al. 1993). This is because higher power states reflect higher resource processing rates that allow greater reproduction or reduced death. Analogously, species that can reach higher power states presumably can maintain higher population growth rates than species that reach lower power states, making it clear that the stable attractor of the system should be the state of highest power. The ten competition trials reviewed here all showed outcomes that were the highest power state, given the possible outcomes. Winning species were those that had

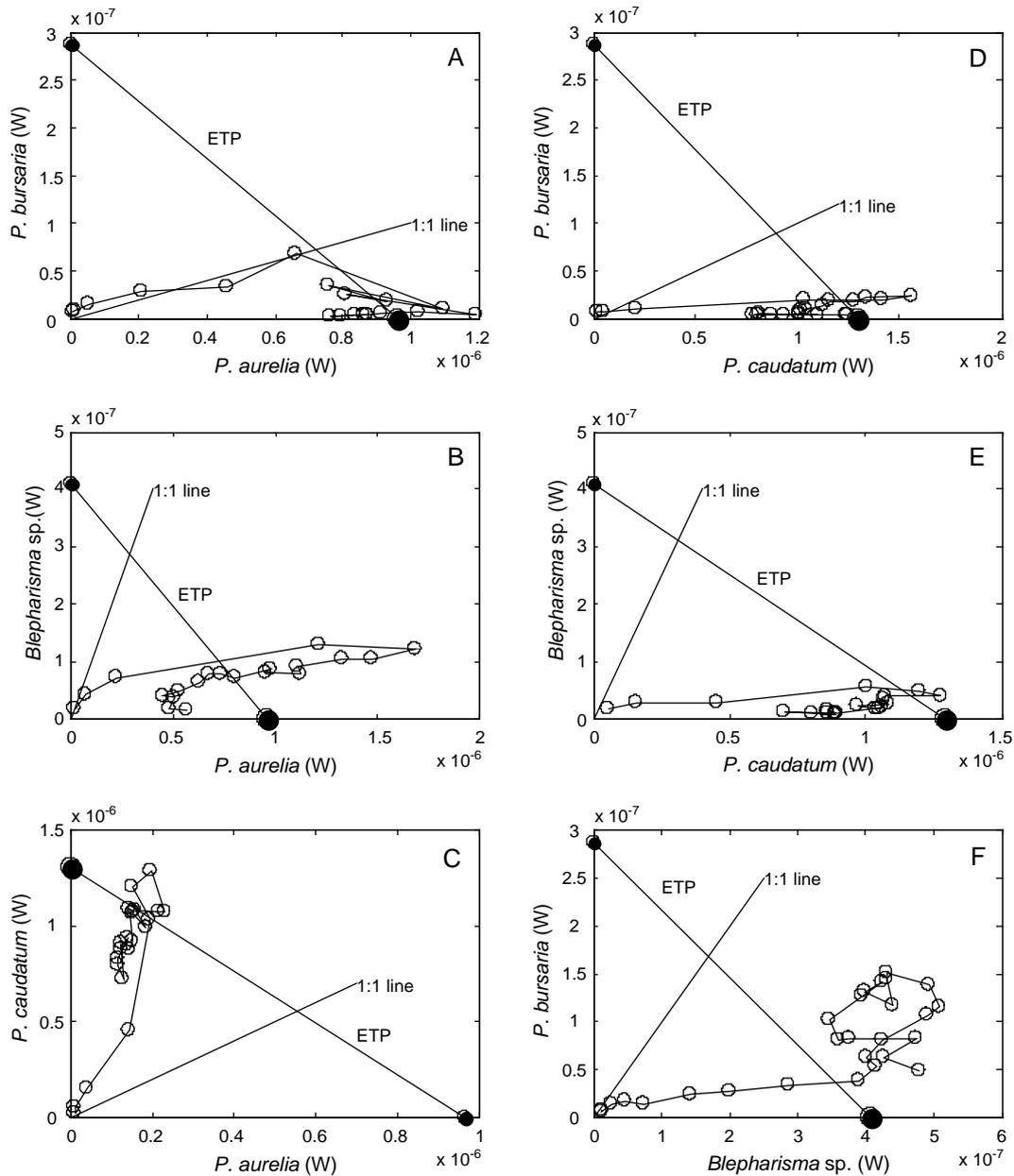


Figure 3. Metabolic state-space graphs depicting the community-level trajectories and outcomes of competition in Vandermeer's (1969) experiment. Panels show competition between (A) *Paramecium aurelia* and *P. bursaria*, (B) *P. aurelia* and *Blepharisma* sp., (C) *P. aurelia* and *P. caudatum*, (D) *P. caudatum* and *P. bursaria*, (E) *P. caudatum* and *Blepharisma* sp., and (F) *Blepharisma* sp. and *P. bursaria*. Plots as in Fig. 2. Outcomes were similar to those in Fig. 2, but with periods of coexistence in (C) and (F).

the highest power when alone. Coexisting species generally showed community-level power that exceeded that of the constituent species when alone. Although the instances of coexistence were not predicted a priori, the results showed that when coexistence was an option, it was the highest-power state.

The three cases of coexistence in these competitive trials offer insights into the mechanics of competitive interactions. Vandermeer's match-up of *Blepharisma* and *P. bursaria* (Fig. 3F) showed a period of coexistence where the community power was higher than that attainable by either species when alone (region B), suggesting niche separation of the two species. Fox and Morin's match-up of

C. striatum and *T. thermophila* (Fig. 4) showed rapid dominance by the higher-power competitor, *C. striatum*. The community-level metabolic rate occurred in region C, above the population-level power of *C. striatum* at K-alone but below that for *T. thermophila*. Hence, in the presence of *T. thermophila*, *C. striatum* sustained a higher population-level power than it could without *T. thermophila*, which suggests that either *T. thermophila* was facilitating *C. striatum*, or that the transient dynamics of *C. striatum* included an overshoot of their K-alone that took several time steps to resolve. The latter possibility seems a real possibility, because after the period of coexistence in region C, the community power crashed, leading to a brief increase

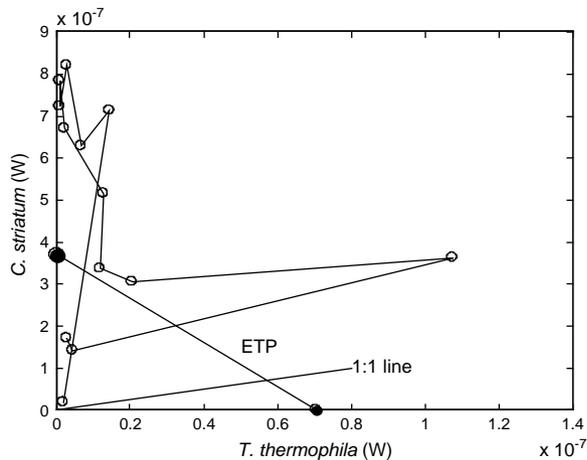


Figure 4. Metabolic state-space graph showing dominance by the higher-power competitor (*C. striatum*) over the low-power competitor *T. thermophila* and a period of coexistence in Fox and Morin's (2001) experiment. Plot as in Fig. 2.

in power by *T. thermophila*, and ultimately a crash to below the ETP. Nonetheless, the sustained period of coexistence did occur in region C, with dominance by the higher-power competitor. Vandermeer's pairing of *P. aurelia* and *P. caudatum* (Fig. 3C) displayed a period of coexistence that centered on the ETP. It is possible that this period of coexistence occurred because the species are closely-matched competitors, and the higher-power competitor simply did not have the metabolic advantage required to drive the other competitor extinct very quickly (slow exclusion). Note that *P. aurelia* and *P. caudatum* switched competitive dominance between Gause's study (Fig. 2A) and Vandermeer's study (Fig. 3C). *P. aurelia* was the higher-power competitor in Gause's study and *P. caudatum* was the higher-power competitor in Vandermeer's study, but the MPP predicted the correct dominant competitor in both cases.

Generally, there were increases in power through time that were contemporary with the increases in population size. Although trivial on the face of it (more individuals = more power), the fitness incentive of the individuals in the population, according to the MPP, is to increase power whenever possible, even if it is unsustainable. Thus, one might expect that decreases in power through time could also occur if the metabolic trajectory crossed the ETP or if populations were initiated in areas above the ETP (Fig. 1). When species that cannot coexist show a metabolic trajectory that crosses the ETP, the trajectory is expected to travel back down below the ETP as the resource is depleted. Thus, the MPP does not necessarily predict that power will always go up through time. Indeed, the studies reviewed here showed considerable fluctuations of power that showed short-term ups and downs in power as well as evidence of resource depletion as trajectories moved above the ETP and then back down (Fig. 2–4). In addition, the trajectories themselves varied considerably. Some communities increased power along the 1:1 line prior to veering toward the winning species, suggesting that competing species may share metabolism equitably for at least some period of time while densities are low. In two cases,

competitors shared resources almost perfectly until the metabolism constraint was reached at the ETP (Fig. 1A, 1C). In other cases, the winning species dominated community power very quickly, and no 'sharing' was evident (Fig. 2D–E). The variation in the temporal dynamics of these systems indicates that there is more than one way for a higher-power competitor to dominate the power of a community. Future work should investigate the metabolic trajectories in more detail and should try to understand how such variation comes to be. For example, is the magnitude of the difference in power at K-alone related to whether a metabolic trajectory follows the 1:1 line or veers off quickly toward the winning species? Does the fitness incentive for individuals to increase power when possible lead to fluctuations or overshoots of the ETP, and why do some trajectories do this more than others?

A major goal of competition theories is to predict the outcomes of competition and the structure of communities from characteristics of the species when alone (Hansen and Hubbell 1980). One such characteristic is numerical advantage, i.e. a high K-alone, or a high growth rate. These traits suggest a strong competitive ability (Gause 1934, Gilpin et al. 1986). However, the competition studies reanalyzed here show that K-alone (numerical advantage) was not as good a predictor of competitive outcomes as power at K-alone (Table 1). Predictions of competitive outcomes based on the MPP – the species that has the greatest metabolic power at K-alone wins – were correct for each species-pairing, whereas predictions based on simple numerical dominance were incorrect some of the time.

Similarly, the R^* principle predicts that winning species will be those that can maintain a positive growth rate at the lowest resource levels (Tilman 1982). Many studies have found support for the R^* principle, including microcosm studies that investigated competitive outcomes with heterotrophic protists (Fox 2002). Given that resource consumption is the basis for metabolic power, the R^* principle and the MPP may be invoking essentially the same processes. However, the MPP is applicable to a broader range of phenomena than the R^* principle. The R^* principle predicts outcomes of competition, but it does not predict the properties of communities of coexisting species. In contrast, the MPP makes at least the qualitative prediction that, when supported by the same resources, power should be higher for a two-species community than a single-species population. Thus, the R^* principle could be viewed as a manifestation of the MPP, with resource levels as the metric of interest, rather than the biological power of the competitors.

In summary, these results show that given a biological measure of power, such as metabolism, the MPP may provide insight into ecological organization. Accurate predictions of competitive outcomes may flow from knowledge of species' metabolic power when alone. Many additional studies could be undertaken to test whether the MPP could be a useful organizing principle for ecology in general. Specific possibilities include 1) developing a defensible approach to estimating power in autotrophs and reexamining competition studies that focused on plants and algae for maximum power outcomes, 2) conducting new competition experiments where both R^* levels and metabolism can be measured simultaneously and

compared with outcomes, 3) identifying characteristics of competing species that make them similar or different in power at K-alone, such as body size, degree of relatedness, or morphology, and 4) looking for maximum power outcomes in other ecological situations where multiple states can be identified, such alternative stable states, biological invasions, and systems with and without predators.

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