How the Second Law of Thermodynamics Has Informed Ecosystem Ecology through Its History

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Many attempts have been made to develop a general principle governing how systems develop and organize in ecology. We reviewed the historical developments that led to the conceptualization of several goal-oriented principles in ecosystem ecology. We focused on two prominent principles—the maximum power principle (MPP) and the maximum entropy production principle (MEPP)—and the literature that applies to both. Although these principles have conceptual overlap, we found considerable differences in their historical development, the disciplines that apply these principles, and their adoption in the literature. These principles were more similar than dissimilar, and the maximization of power in ecosystems occurs with maximum entropy production. These principles have great potential to explain how systems develop, organize, and function, but there are no widely agreed-on theoretical derivations for the MEPP and MPP, hindering their broader use in ecological research. We end with recommendations for how ecosystems-level studies may better use these principles.

Keywords: MPP, MEPP, second law of thermodynamics, ecosystem ecology, Howard T. Odum

Many theoretical frameworks have been proposed to unify the fundamental concepts of systems organization and development. For example, there are hypotheses that systems organization involves maximizing power (Lotka 1922), maximizing entropy production (Paltridge 1975), and maximizing embodied energy, or emergy (Odum HT 1988). There have been many frameworks grounded in nonequilibrium thermodynamics that seek to explain how systems develop, but a consensus remains elusive. Martyushev and Seleznev (2006) noted that many of these principles have been independently proposed. They argue that various researchers, unaware of the other studies in different subjects, have proposed these principles under different names, leading to considerable delays in theoretical advancements. Because these principles aim to provide a mechanism for why systems develop, these principles are sometimes referred to as *goal functions*. To add more complexity, Fath and colleagues (2001) argued that there is considerable overlap and that many of these approaches are complementary. Here, we focused on two of these goal-function principles that have received considerable attention in the ecosystem ecology literature: the maximum power principle (MPP) and the maximum entropy production principle (MEPP). We explored the links between these principles, as well as the possible reasons that they have gained surprisingly little traction with ecosystem ecologists writ large and how that can be changed.

Originally presented by Lotka (1922a) in the 1920s, the MPP states that systems develop to increase the total flow of energy or power through the system. Lotka (1922a) framed the MPP in the context of natural selection, arguing that the organisms that most efficiently harness available energy would be preserved. Lotka (1922a) even proposed that the MPP should be considered the fourth law of thermodynamics. H. T. Odum and Pinkerton (1955) reformulated the original principle and argued that systems develop to an efficiency level that maximizes power production. The reformulation of the MPP by H. T. Odum and Pinkerton (1955) explicitly addressed ecosystems-level thinking, whereas Lotka (1922a) focused on organisms as systems. Although the MPP was formulated nearly 100 years ago, there is still considerable interest in applying the principle to ecological studies (e.g., Cai et al. 2006, DeLong 2008), but surprisingly few ecosystem ecologists use the construct in their research (see Schneider and Kay 1994).

The MEPP is an extension of the Second Law of Thermodynamics in nonequilibrium systems. It is argued

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that an open, steady-state system far from equilibrium will maximize the production of entropy via internal system organization in an attempt to restore equilibrium. Similar to the use of the MPP in many fields, the MEPP has been applied to a variety of studies, including physics, astronomy, mathematics, and computer science. Several researchers throughout the twentieth century have independently proposed the MEPP. For example, Ziegler (1963) is credited with a derivation of the MEPP from a statistical mechanics framework, whereas Dewar (2003, 2005) derived the MEPP from the Bayesian inference of maximum uncertainty concept, derived from information theory, presented by Jaynes (1957)—and that was unfortunately called maximum entropy or MaxEnt (also see Martyushev and Seleznev 2006). The MPP and the MEPP are relatively young, and their importance and applicability in ecosystem ecology remain contested and unresolved (Månsson and McGlade 1993, Sciubba 2011).

As with these nonequilibrium thermodynamic principles, the concepts of ecosystem development and succession have their roots in the early twentieth century. Clements (1916) and Gleason (1926) laid the foundation for ecological succession and development. E. P. Odum (1969) argued that ecosystems in different states of system development share particular traits. His seminal work inspired many of these so-called contemporary goal-function principles as researchers sought to provide a theoretical basis for the traits that E. P. Odum (1969) described. For example, one of the traits of a maturing ecosystem was the ecosystem production to respiration (P:R) ratio. As systems age, E. P. Odum (1969) argued, P:R approaches 1. One of the goal functions that was developed to address this was the principle of maximum energy dissipation (Fath et al. 2001). The idea behind the principle of maximum dissipation is that through the creation of complex but ordered structure, at least in biological systems far from equilibrium, the rate of entropy production or energy dissipation is actually accelerated relative to that in simpler, nonordered systems. The MPP and the MEPP are principles that provide a mechanistic explanation for how systems develop and organize in the context of energy uptake (e.g., power) and energy use for system maintenance and biomass turnover (e.g., entropy).

Although there has been some advance and evolution in the theoretical aspects of these principles, fewer empirical ecosystem studies have actually tested the MPP and, to a lesser extent, the MEPP. The reason for the latter is that the MEPP appeared in the literature considerably more recently than the MPP. In this article, we asked, “Has the MEPP theoretically evolved from the MPP, and if so, how?” By examining the theoretical underpinnings and the applied empirical studies of both of these principles, we explored the similarities and differences between the MPP and the MEPP. Our objectives of this review were to (a) characterize the development of these principles in ecosystem ecology in the historical context of the Second Law of Thermodynamics, (b) examine the current state of the MEPP and the MPP literature, (c) elucidate the common themes and challenges of applying of these principles, and (d) explore possible reasons that neither has received more traction in ecosystem science.

Methods

To explore the links, similarities, and differences between these principles, we conducted targeted keyword searches using the Web of Science. We started by analyzing articles that were important in the theoretical development of the MEPP and the MPP. To examine the disciplines that have drawn from these principles, we reviewed a total of 520 papers that cited either one of the two papers that first proposed the MPP, albeit at different levels of ecological organization: (1) Lotka’s (1922a) paper, titled *Contribution to the energetics of evolution*, or (2) H. T. Odum and Pinkerton’s (1955) ecosystems-level paper. Our exploration of the theoretical development of the MEPP involved searches for papers citing either Jaynes (1957) or Ziegler (1963), which produced a total of 5324 records.

For a closer examination of how these principles have been used in the literature, we performed additional keyword searches using *maximum power principle* and *maximum entropy production*. From the 520 papers that cited Lotka (1922a) and H. T. Odum and Pinkerton (1955) and the 246 papers that cited *maximum entropy production*, we limited our meta-analysis to 32 papers by focusing on articles with a strong emphasis on ecological research, although not all were at the ecosystems scale. For the sake of simplicity, papers that used concepts such as *empower* and *exergy* were considered to be complementary with maximum power and were included in our analysis.

By analyzing papers that cited these pioneers in the theoretical development of the MPP and the MEPP, we were able to account for studies that did not explicitly state an application of these principles. For example, Kemp and Boynton (2004) argued that H. T. Odum’s (1957) early work examining the trophic structure of Silver Springs was one of the first empirical studies of the MPP, but this was not explicitly stated in his 1957 paper. In the Web of Science, it is possible for papers to be listed across multiple research areas. Therefore, papers listed in more than one research area were counted more than one time in our examination of these principles and the research disciplines that use them.

Results and discussion

The following section is organized in the following subsections: “History,” “Current trends,” “Interdisciplinarity and the MEPP,” and “Interdisciplinarity and the MPP.” We start our examination of the MEPP, the MPP, and their role in ecosystem ecology within a historical context. We review the origin of the Second Law of Thermodynamics and how the Second Law of Thermodynamics gave rise to the MPP and the MEPP. Next, we focus on the current use of the MEPP and MPP within the broader literature, as well as within the

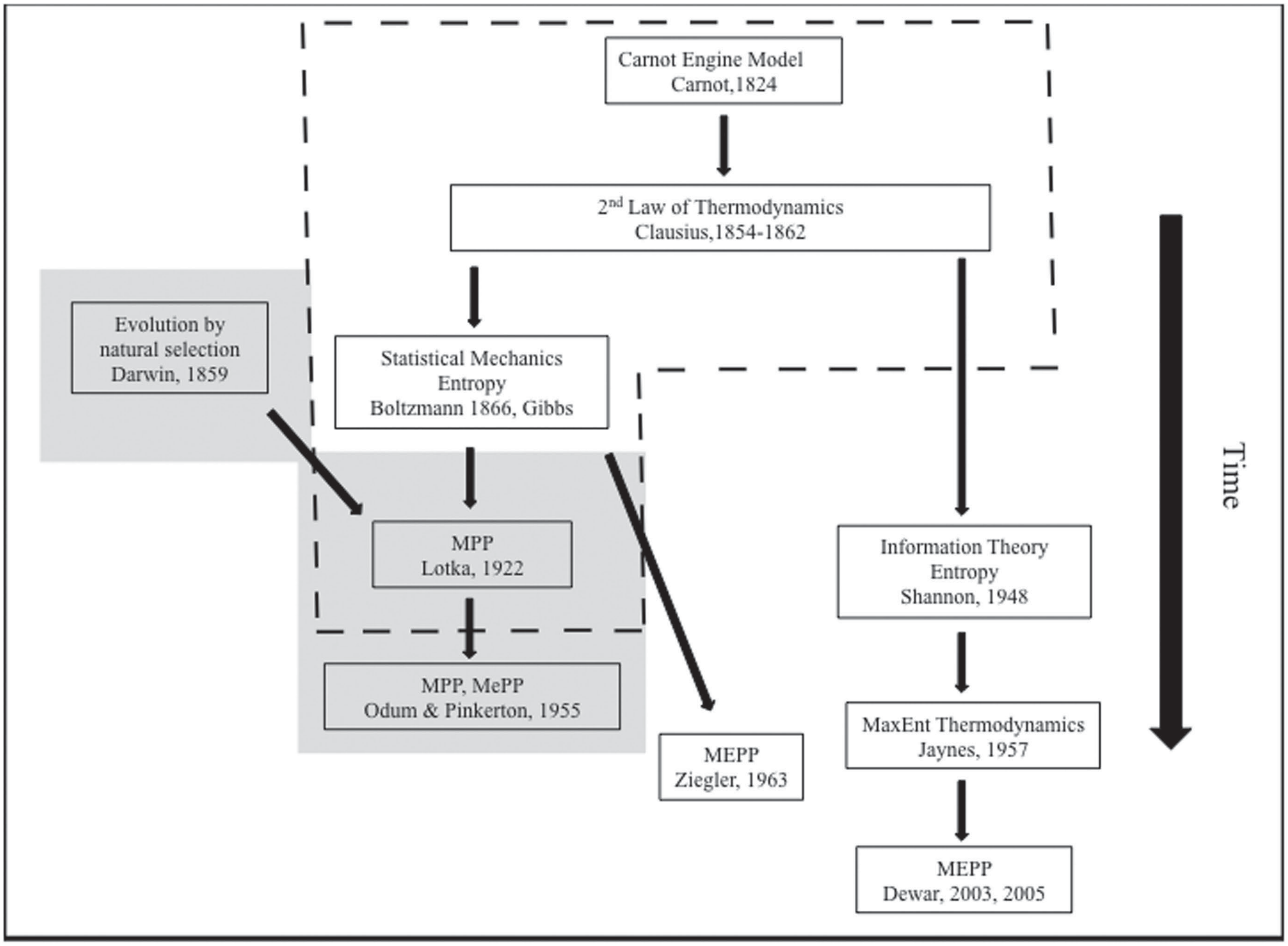

Figure 1. A conceptual map of the evolution and origin of several optimality priniciples in biology, physics, and chemistry. The MPP and the MEPP both evolved from the Second Law of Thermodynamics. The dashed line represents theoretical developments prior to the introduction of the nonequilibrium thermodynamics approach by Onsager (1931). The gray box represents explicit theoretical development in biological sciences. The reviewed studies did not widely cite derivations of MEPP from Swenson (1989) or Prigogine and Nicolis (1971) and were omitted from this map. Abbreviations: MaxEnt, maximum entropy; MEPP, maximum entropy production principle; MePP, maximum empower principle; MPP, maximum power principle.

ecological literature. We conclude with an exploration of the disciplines that use the MEPP and the MPP.

History. Nonequilibrium theoretical principles such as the MPP and the MEPP are grounded in the classical equilibrium laws of thermodynamics, specifically the Second Law of Thermodynamics. Here, we briefly discuss the history of the Second Law of Thermodynamics to put nonequilibrium thermodynamic principles into a historical context. We discuss the early importance of the Carnot engine, the Second Law of Thermodynamics, work by Boltzmann, and (most importantly) the development of the concept of entropy for the development of the MPP and the MEPP. For a more comprehensive review of the history of the Second Law of Thermodynamics, see Ozawa (2003).

The Second Law of Thermodynamics has its roots in the early part of the nineteenth century (figure 1). Carnot (1824) made large theoretical strides with his only published work, a book originally published in French, titled *Reflections on the Motive Power of Fire and on Machines Fitted to Develop that Power*. His work on heat engines would become the foundation and inspiration for the development of the Second Law of Thermodynamics.

German mathematician and physicist Rudolf Clausius first articulated the Second Law of Thermodynamics in the 1850s. In *The Mechanical Theory of Heat,* translated into English in 1879, Clausius (1879) refined Carnot's work to develop the Second Law of Thermodynamics and introduced the concept of entropy. From Clausius' (1879) definition, entropy is the energy that must be lost as heat to the surroundings at temperature T when thermal energy is converted to work. The Second Law of Thermodynamics states that in isolated systems, entropy can only increase or remain constant. His famous 1865 proclamation "the entropy of the universe tends to maximum" is still one of the most common ways to state and teach the Second Law of Thermodynamics.

Boltzmann (1886) developed the field of statistical mechanics and refined the Clausius (1879) definition of entropy using a statistical framework (figure 1). The formulation of nonequilibrium thermodynamics was equally important to the development of the MPP and the MEPP. It was not until the 1930s that considerable theoretical development in nonequilibrium thermodynamics occurred. Onsager (1931) provided the first deduction of nonequilibrium thermodynamics. Fundamentally, advancements in nonequilibrium thermodynamics provided a theoretical bridge that allowed H. T. Odum and Pinkerton (1955) to make their ecosystem-scale step from the evolutionary/organismal scale by Lotka (1922a). We suggest that one of the reasons that so little of ecosystem ecology touches on MPP and the MEPP is that few ecosystem ecologists know of Onsager's work or this bridge to nonequilibrium systems.

The early development of thermodynamics was entirely and explicitly using physical systems. Lotka (1922a, 1922b) linked the early thermodynamic concepts of statistical mechanics, pioneered by Boltzmann (1886) and Gibbs (1902) in physical systems, with evolution and natural selection to develop the MPP at the organismal level (figure 1). In fact, Lotka's (1922a) work preceded most of the empirical and theoretical work that led to the modern discipline of ecosystem ecology, including (a) early seminal work by Elton (1927) on food chains; (b) interactions among soil, minerals, and plants by Hutchinson (1957); (c) the introduction of the term "ecosystem" by Tansley (1935); and 4) the concept of energy flow through an ecosystem by Lindeman (1942). It was Lotka's (1922a) merging of evolution and natural selection with Boltzmann's (1886) approach to entropy, statistical mechanics, and the Second Law of Thermodynamics that first gave rise to the MPP.

The Second Law of Thermodynamics and the concept of entropy inspired many new disciplines. For example, using information theory, Shannon (1948) defined *information entropy* as a measure of unpredictability (figure 1). The Shannon entropy approach inspired Jaynes (1957) to explore the link between statistical mechanics and information theory. Jaynes (1957) is often credited as starting the maximum entropy (MaxEnt) approach to thermodynamics—not to be confused with the MEPP (figure 1). Martyushev and Seleznev (2006) noted that Dewar (2003) attempted to theoretically ground the MEPP using the Jaynes (1957) formalism. Although Martyushev and Seleznev (2006) were critical of Dewar (2003) and the usefulness of his approach is still debated, many of the papers we reviewed cited Dewar (2003) as the sole source of the theoretical foundations for the studies.

It is difficult to attribute the theoretical origin of the MEPP to a single researcher. This is in contrast to the MPP, which has a clear origin in Lotka (1922a) at the organismal level and H. T. Odum and Pinkerton (1955) at the ecosystem level. Martyushev and Seleznev (2006) credited Ziegler (1963) with the introduction of the MEPP. Martyushev and Seleznev (2006) also discussed the importance of the work done by Prigogine (1945, 1947) on his minimum entropy production. It is important to note that although the principle of minimum entropy may seem contradictory to the MEPP, several researchers have argued that this is not the case (Martyushev and Seleznev 2006). Different principles have been developed for different scales or domains of application. Although Martyushev and Seleznev (2006) acknowledged the importance of Prigogine's (1945, 1947) contributions to the development of the MEPP, they credited Ziegler (1963) with the derivation of the MEPP because of its wider applicability. They acknowledged that several researchers before and after Ziegler (1963) developed the idea of the MEPP independently, including a slightly different minimum entropy production principle by Prigogine (1945), but they also argued that Ziegler's (1963) formulation was the "most evident and simplest." Although the historical origin of the MEPP is convoluted, the derivation of the MEPP by Ziegler (1963) is favored for its grounding in nonequilibrium thermodynamic theory.

Current trends. Despite the fact that the MPP and the MEPP originated almost 100 and almost 70 years ago, respectively, we found fewer examples of these principles being applied in current ecosystem-ecological literature than we expected. That said, both of these principles are being tested more than they have been before. We argue that the MPP and the MEPP may be undergoing a renaissance within the general literature as well as within ecosystems research (figures 2 and 3). To visualize this current trend within the MEPP and the MPP literature, we analyzed the cumulative number of published articles from the general literature that used *maximum entropy production* and *maximum power principle* as keywords (figure 2). Not only were studies investigating either the MEPP or the MPP increasing at an increasing rate, but this acceleration also seems to have begun as recently as the early 2000s (figure 2). We found a similar increasing trend in ecological publications that cited either the MEPP or the MPP in the last 10–20 years (figure 3).

Interdisciplinarity and the MEPP. In the following two sections, we expand our historical foundational work of the MEPP and the MPP (figure 1) by explicitly tying them to a range of research disciplines. Since the introduction of the Second Law of Thermodynamics by Clausius (1879), countless studies from a range of research disciplines—from psychology to ecosystem ecology—have drawn on his formulation of the Second Law. We assessed to what extent disciplines that used the MPP or the MEPP overlapped with disciplines that frequently cite the Second Law of Thermodynamics.

A keyword search using *second law of thermodynamics* produced 1768 papers cross-listed among more than 50 Web of Science research areas, for a total number of 2704 records. Sixty-one percent of the papers we found were published in three disciplines: physics (29%), mechanics (11%), and engineering (10%; table 1). This finding was not surprising

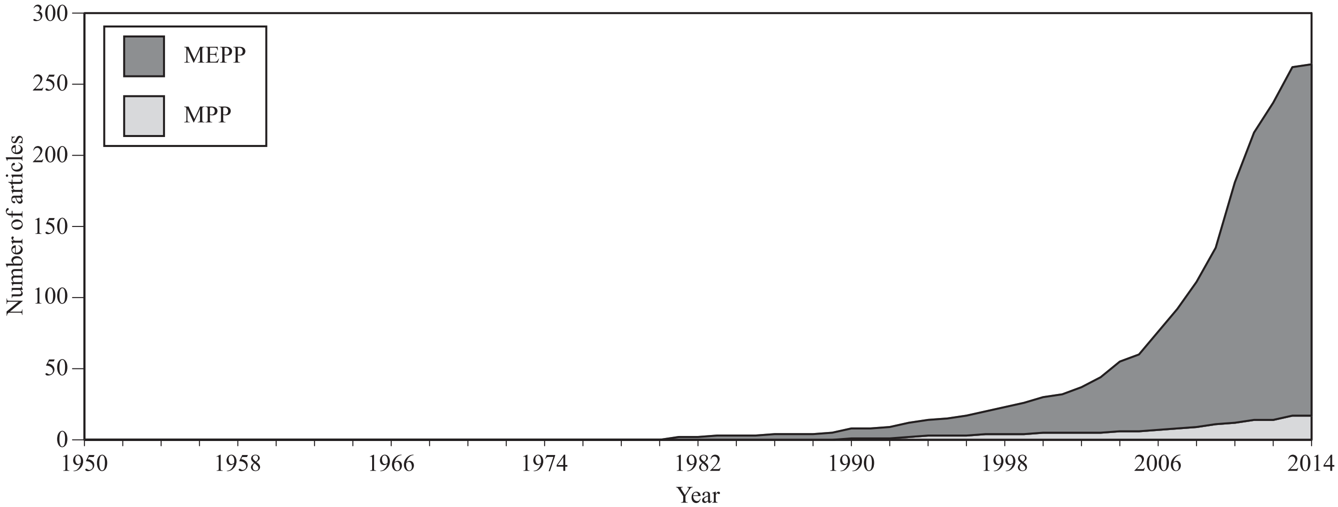

Figure 2. Maximum entropy production principle (MEPP) and maximum power production (MPP) cumulative number of published papers. Since the early 2000s, there has been an exponential increase in the number of articles that discuss the MEPP and to a lesser extent the MPP.

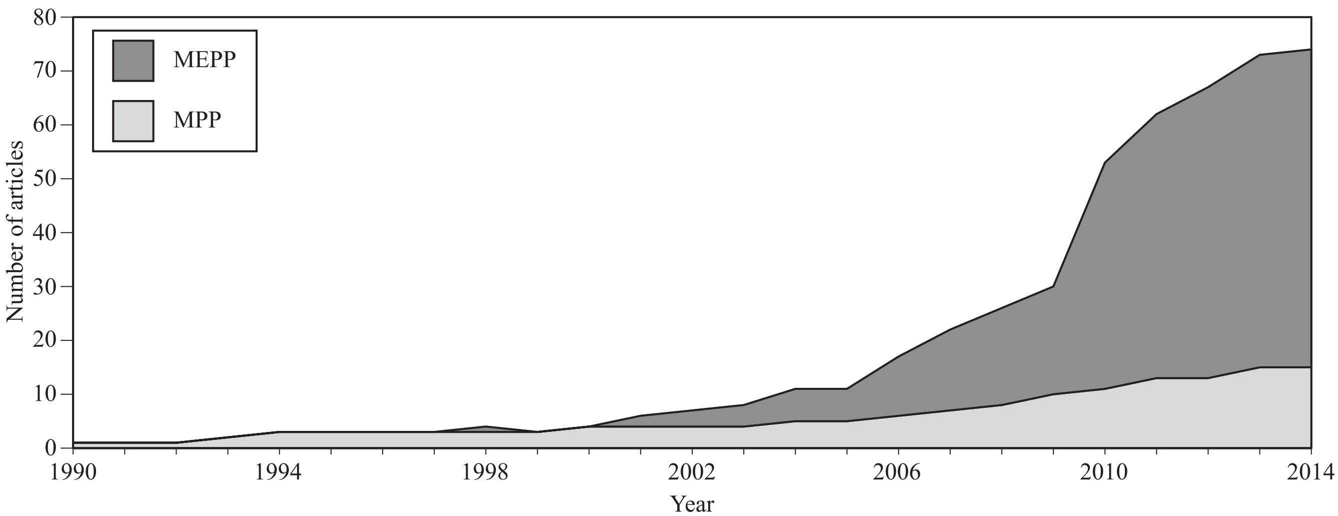

Figure 3. Maximum entropy production principle and maximum power production cumulative number of ecological studies published papers by year.

given that these are disciplines frequently associated with thermodynamic constructs. Despite its inextricable link to and foundation in the Second Law of Thermodynamics, ecologically related studies accounted for only 54 of the 2704 records, or 2% of the total studies. It was particularly surprising that ecosystem ecology was not well represented in this keyword search. We suggest that this may be because ecosystem-scale research either only implicitly considers the Second Law of Thermodynamics or that a sizable population of ecosystem ecologists feel no intrinsic connection to or importance of the Second Law.

To explore the extent of the disciplinary overlap between the Second Law of Thermodynamics and the MEPP, we focused on research areas that most often cited the MEPP, and we found considerable overlap. Papers that cited pioneers in the MEPP framework (Jaynes 1957, Ziegler 1963) showed a strong connection with disciplines that traditionally study the Second Law of Thermodynamics: physics, mechanics, engineering, mathematics, and materials science (table 1). Papers that cited Ziegler (1963) were also most likely to identify with disciplines that frequently refer to the Second Law of Thermodynamics: mechanics and engineering accounted for 11% and 10% of the papers referring to "the Second Law of Thermodynamics" and 27% and 18% of those citing Ziegler (1963), respectively. Given the importance of the physical disciplines to both the Second Law of Thermodynamics and the MEPP, the considerable disciplinary overlap was not surprising.

Our final keyword search relating to the MEPP was for papers that have referred to *maximum entropy production*

Table 1. Keyword searches by percentage of each discipline.

	"second law of thermodynamics"	Jaynes 1957	Ziegler 1963	"maximum entropy production"	Lotka 1922	Odum and Pinkerton 1955	"maximum power principle"
Physics and mechanics	51	40	45	26	4	0	0
Engineering	10	9	18	3	5	0	8
Thermodynamics	8	0	3	0	0	0	0
Mathematics	4	8	6	0	0	0	0
Materials science	4	0	14	0	0	0	0
Environmental science ecology	0	3	0	6	33	41	48
Biology miscellaneous	0	0	0	20	19	28	36
Geology	0	0	6	8	0	0	4
Other	23	40	9	37	39	31	4

Note: The Web of Science keyword searches are in columns and disciplines are in rows. Values are in percentages.

(table 1). This search generated 307 total records that spanned 28 different research areas. As with papers that cited Ziegler (1963) and Jaynes (1957), most of these were physics or atmospheric sciences papers. Studies from the ecological sciences were less common but much more prevalent than papers that cited Ziegler (1963) or Jaynes (1957). Although the environmental sciences ecology research area accounted for 6% of the total studies that referred to *maximum entropy production*, this proportion increased to 10% in papers published since 2010. This appears to be driven by 15 articles in a special issue in *Philosophical Transactions of the Royal Society Biological Sciences,* published in 2010, which focused on the MEPP in biological systems.

Interdisciplinarity and the MPP. Our focus on the MPP in the literature was based on papers that cited Lotka (1922a), H. T. Odum and Pinkerton (1955), or used the term *maximum power principle*. A total of 275 papers have cited Lotka (1922a), representing 55 different research areas, for a total number of 424 records. One-third of the papers that cited Lotka (1922a) were from the environmental sciences ecology research area (table 1). Given the strong influence that Darwin had on Lotka and the interest that Lotka had in biological systems, these results are not surprising from an organismal perspective.

Papers that cited H. T. Odum and Pinkerton (1955) showed a similar research area breakdown. Of the 364 papers we found, spread across 39 research areas, 211, or 58%, had research that at least overlapped with ecosystem science (table 1). This is not particularly surprising given that most of H. T. Odum's work was firmly entrenched in ecosystem ecology. We also found that the keyword *maximum power production* had substantial representation in the ecological literature (table 1). Our analyses of the MEPP and the MPP papers suggested that there were clear disciplinary distinctions in the use of these principles and that ecosystem ecologists and ecologists in general have, by and large, focused their work on the MPP from a percentage basis. In addition, many disciplines have used the MEPP over time, but the use of the MPP has mainly been by ecologists.

The pattern of an increasing rate of publications that apply the MEPP (figure 3) was also observed with the number of articles that cited the foundational MPP papers (figure 4). The number of articles published per year that cited either of Lotka's (1922a, 1922b) publications or H. T. Odum and Pinkerton (1955) increased substantially in the 2000s. We found close parallels in the pattern of citations of these three papers (figure 4), because authors commonly cited both in the same paper. This common co-citation of Lotka (1922a) and H. T. Odum and Pinkerton (1955) suggested broad recognition of the theoretical link between them but does not acknowledge that Lotka focused his MPP work mainly at the organismal level whereas H. T. Odum's focus was on ecosystems. Confusion about this distinction may be one reason that these Second-Law principles have not gained greater traction in ecosystem ecology.

Maximum power principle with a focus on ecology and ecosystems

As we noted above, Lotka (1922a) was the first formulation of the MPP. While referencing Boltzmann's contribution that energy is the basis of life struggle, Lotka (1922a) argued that systems—more specifically organisms—that best capture energy to ensure future survival would have an evolutionary advantage. He further stated that if there are untapped energy sources within the system and there are mechanisms to use that energy, the total energy flux through the system might be increased.

Although Lotka (1922a) pioneered the conceptual context for the MPP, H. T. Odum and Pinkerton (1955) provided a much stronger theoretical framework and applied it directly to ecosystems. For example, their paper framed system power output as a function of system efficiency and hypothesized a general power–efficiency relationship

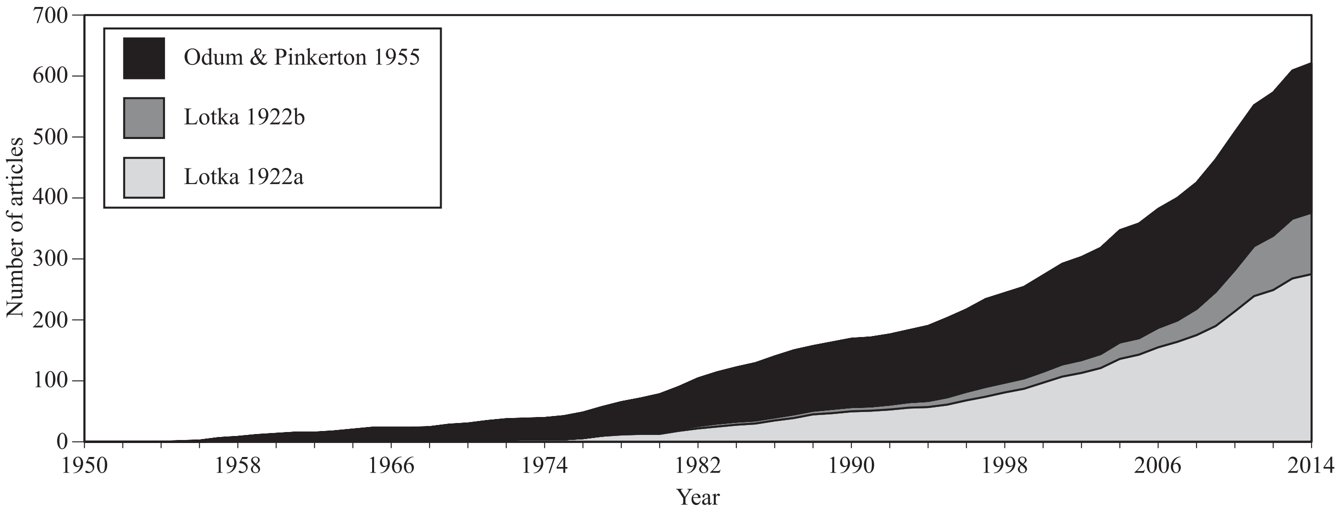

Figure 4. The cumulative number of publications that cite foundational maximum power production publications. From the 1950s to the 1970s, these papers were largely ignored; however, since the mid-1980s, all three of these papers have become increasingly recognized. These papers all follow similar temporal patterns, suggesting co-citations.

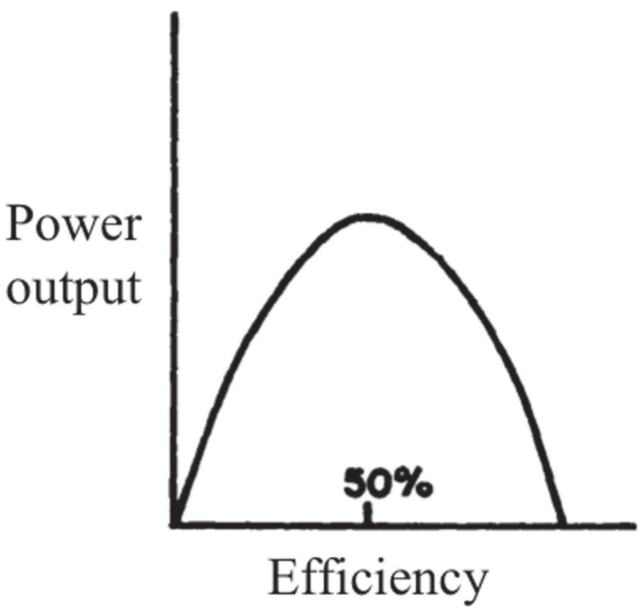

Figure 5. Power output as a function of efficiency. Maximum power output is observed at an intermediate frequency (from figure 2 in H. T. Odum and Pinkerton [1955]).

(figure 5). They also discussed several ecosystems that operate at maximum power. Since Lotka (1922a) and H. T. Odum and Pinkerton (1955), there have been about a dozen studies that have explicitly tested the MPP. H. T. Odum's early papers, from the 1950s, did not always explicitly state that testing the MPP was an objective; therefore, accounting for all of the early implicitly tested studies of the MPP by H. T. Odum or others was somewhat difficult. That is, studies that did not explicitly use the term *MPP* or cite key papers within the framework were difficult to interpret. For this reason, it is likely that the number of studies that have tested the MPP is underreported in the literature. One of the earliest applications of the MPP was H. T. Odum (1957; see Kemp and Boynton 2004). Even though H. T. Odum (1957) did not explicitly state that this study was a test of the MPP, because he studied the trophic structure and energy flow through Silver Springs, it seems reasonable to assume that this was his intent. By examining early MPP empirical studies and the theoretical underpinnings of the MPP, we can see a clearer picture emerge of what some of the early pioneers in MPP literature intended from these types of ecosystem studies.

Types of studies and ecological scales. We found 11 studies in the literature that tested the MPP at the ecosystem scale. Within these 11 papers, there is not one particular type of study or method that is more prevalent (table 1). We found many studies using models to apply or test the MPP and similar principles (exergy and maximum empower, MePP) in a variety of contexts. For example, the MPP has been applied to studies that (a) used models to optimize exergy relative to the effects on planktonic and zooplankton body size in aquatic ecosystems (Ray et al. 2001), (b) used the MPP to constrain hydrological conceptual models (Westhoff and Zehe 2013), (c) modeled the role of exotic species in ecosystem self-organization (Campbell et al. 2009), and (d) simulated the role of the MPP in self-organizing forest plantation ecosystems (Li et al. 2013). The MPP has also been used to predict the outcomes of competitive exclusion experiments (DeLong 2008), to indicate benthic ecosystem recovery following a disturbance (Libralato et al. 2006), and to examine microcosm ecosystem self-regulation using pH to control photoperiod (Cai et al. 2006). It has also been used to model the ecosystem organization of energy flows and storage (Fath et al. 2004) and in simulations of ecosystem responses to resource pulses (Lee 2014). It is clear that the MPP has guided systems–based ecological studies at all levels of organization—not just with ecosystems—for decades.

Common themes. We found that half of these 11 papers (n = 6) cited both of the well-recognized theoretical foundational MPP papers. All of them cited Lotka (1922a), except for one (i.e., Westhoff and Zehe 2013), and that study discussed the theoretical background of the MEPP, citing work by Dewar (2009, 2010), but designed their model to test the MPP. In the studies that did not cite Lotka (1922a) and H. T. Odum and Pinkerton (1955), we found that the authors typically cited other H. T. Odum papers (e.g., Ray et al. 2001, Campbell et al. 2009, Lee 2014). One paper cited foundational papers from both the MPP and the MEPP literature (Fath et al. 2004).

Although the MPP has guided organismal and community-scale ecological research, it has most often been tested at the ecosystem scale. The difficulty of designing experiments and models to test the MPP translated to a limited literature of empirical studies. Given this, we found it surprising that a large percentage of the studies attempted to draw results from large and relatively complex ecosystems. This may be a direct reflection of the legacy and influence of H. T. Odum and his ecosystem approach. In addition to testing the MPP at the ecosystem scale, a number of the studies we reviewed used the principle in the context of ecosystem development and system organization (per Odum EP 1969; e.g., Fath et al. 2004, Campbell et al. 2009, Li et al. 2013, Lee 2014).

Is the maximum entropy production principle an evolving theory?

Paltridge (1975) is commonly cited as the first known application of the MEPP in his attempt to model global atmospheric circulation patterns (see Ozawa 2003,Vallino 2010, Virgo 2010). If the global transport of heat is assumed to operate at maximum entropy, he argued, then meridional energy flux, cloud cover, and meridional temperature distributions should all be predictable. Interestingly, although Paltridge is widely credited as the first empirical application of the MEPP, he did not cite any of the theoretical foundational MEPP papers (figure 1, table 2). Paltridge originally framed the global atmospheric circulation patterns in the context of minimum entropy production; it was only later that others recognized his approach as the MEPP. This lack of an explicit link between his approach and the MEPP is surprising given the large impact that his study has had on the MEPP field. For example, the Paltridge (1975) approach has also been applied to the atmosphere of Titan and Mars (Lorenz et al. 2001).

Types of studies and ecological scales. Studies using the MEPP in an ecological context constituted a smaller percentage of the MEPP literature compared with the ecological fraction of the MPP literature, but overall, we found more ecological MEPP studies. We reviewed 22 MEPP articles, compared with the 11 we found for the MPP. We found a similar variety in the types of research and the scales of application, and again, a large fraction of them were modeling studies. The latter included models of ATP synthase enzyme design (Dewar et al. 2006), enzyme kinetics (Dobovišek et al. 2011), chemical replicators (Martin and Horvath 2013), systems with multiple equilibria (Herbvert et al. 2011b), detrital-based ecosystems (Meysman and Bruers 2007), ecosystem biogeochemistry (Vallino 2010), food webs (Meysman and Bruers 2010), watershed development (Kleidon et al. 2013), ecological succession (Skene 2013), and glacial maximum climates (Herbert et al. 2011b). Other studies include using eddy-flux data to calculate entropy in developing ecosystems (Holdaway et al. 2010), and several studies described community organization and physiology in the context of MEPP (Lin et al. 2009, Volkov et al. 2009, Dewar 2010, Schymanski et al. 2010, Jia et al. 2012). Among the studies applying the MEPP, we found a diverse range of scales being tested and a heavy emphasis on using modeling.

Common themes. To a larger extent than MPP studies, we found that a high prevalence of MEPP-related research relied on modeling approaches. This is not surprising given the difficulty and complexity of the types of systems that ecosystem scientists study. We also found evidence of a highly fragmented and disjointed historical development of the MEPP and therefore of its impact on MEPP studies in ecosystem ecology and ecology in general. For example, five of the 21 studies did not cite any of the recognized theoretical foundations of the MEPP approach. All of these independently proposed that variations of the MEPP have contributed to the strength of this approach. However, there seem to be two main disconnects within the theoretical development: (1) Some used entropy in the thermodynamic context, whereas others used it in an information-theory context, and (2) the appropriate scale to apply the MEPP is not clear. For instance, it is a strength of the principle that it has been developed many times independently, but this fragmented history hinders critical feedback and theoretical development. The theoretical disconnect across these studies suggests that although the MEPP is a general principle, some confusion remains about how it is currently being applied to ecological systems. This is in contrast to the MPP, which is less used but more uniformly accepted and cited.

Complementarity and challenges

By examining the historical theoretical development of the MPP and MEPP and the studies that have applied these principles, we concluded that the MPP and the MEPP actually guide complementary rather than discrete or competing approaches to studying ecosystems (Fath et al. 2001). Despite their parallel historical developments (figure 1) and the relatively few crossover citations in the literature between these two approaches (table 2, table 3), both MPP and MEPP studies have tested fundamental thermodynamic concepts that are deeply linked. One way to consider

Table 2. Reviewed papers that use the maximum entropy production principle (MEPP) and similar principles.

Type	Scale	Principle	Theoretical foundations	Source
Plant physiology and maximum entropy	Organism	MaxEP	None	Jia et al. 2012
Self organization of plant communities	Community	Maximum dissipation	Lotka, H. T. Odum, Prigogine	Lin et al. 2009
Energetics of succession model	Ecosystem	MEPP	Boltzmann, Lotka, H. T. Odum and Pinkerton	Skene 2013
Species interaction models in tropical forest	Community	MEPP	Boltzmann, Shannon, Jaynes, Dewar	Volkov et al. 2009
Carbon assimilation and ecosystem spatial organization	Ecosystem	MEPP	Dewar	Jesus et al. 2012
Semiarid system heterogeneity models	Ecosystem	MEPP	Dewar	Schymanski et al. 2010
Chemical replicator model	Organism	MEPP	Dewar, Prigogine	Martin and Howarth 2013
Glacial maximum climates	Global	MEPP	Jaynes, Dewar	Herbert et al. 2011b
Multiple equilibria models	Global	MEPP	Jaynes, Dewar	Herbert et al. 2011a
Bacterial chemotaxis and maximum entropy	Bacterial	MEPP	Jaynes, Prigogine, Swenson, Dewar	Zupanovic et al. 2010
Amazon ecosystem development	Ecosystem	MEPP	Lotka, H. T. Odum and Pinkerton	Holdaway et al. 2010
Ecosystem biogeochemistry model	Ecosystem	MEPP	Lotka, H. T. Odum and Pinkerton, Prigogine, Dewar, Swenson	Vallino 2010
Organization of watersheds models	Watersheds	MEPP	Lotka, H. T. Odum, Dewar	Kleidon et al. 2013
Metabolic networks	Molecular, Bacterial	MEPP	None	Unrean and Srienc 2011
Soil hydrological processes model	Ecosystem	MEPP	None	Porada et al. 2011
Plant optimization theories and	Multiple	MEPP	Dewar	Dewar 2010
Climate system dynamics	Global	MEPP	None	Paltridge 1975
Detrital based ecosystems model	Ecosystem	MEPP	H. T. Odum	Meysman and Bruers 2007
Food web models	Ecosystem	MEPP	Prigogine	Meysman and Bruers 2010
Enzyme kinetics and maximum entropy	Molecular	MEPP	Swenson, Dewar, Prigogine, Ziegler	Doboviseik et al. 2011
ATP synthase enzyme design	Molecular	MEPP	Jaynes, Dewar	Dewar et al. 2006

Note: The MEPP was used for ecosystem succession models to bacterial chemotaxis studies. The scale of the study ranged from bacterial to the ecosystem and global levels. There were two studies within this literature that were considered complementary to the MEPP: maximum dissipation and maximum entropy production (MaxEP).

the complementarity of these approaches is through the concept of thermodynamic maximization in each principle under transient versus steady-state conditions. Consider an ecosystem in which energy throughput (i.e., power) is a function of standing biomass. During early succession and ecosystem development, when biomass is low, energy acquisition is used for net growth. During this period, the ecosystem operates under the MPP, because this objective function maximizes biomass accumulation rate; biomass increases exponentially (P:R >> 1). However, exponential growth cannot occur indefinitely, because either available energy or, more typically, elemental resources will eventually become limiting. As the ecosystem transitions into a mature, or climax, state (or pseudosteady state where P:R = 1), it follows the MEPP. Here, the ecosystem has organized either to consume all available energy (energy limited), or to consume as much energy as available resources allow (resource limited). In both cases, the energy consumed by the ecosystem is simply dissipated as heat by the actions of maintenance and predator–prey cycles. This is the very definition of thermodynamic entropy, the conversion of high-quality energy to low-quality heat. Consequently, the MPP and MEPP may simply describe different phases in an ecosystems development. Our review of the MPP and the MEPP literature also suggested some difficulties with these approaches. One of the challenges with the MPP, and to a lesser extent the MEPP, was a lack of empirical studies testing the principle(s). Although we found that interest in both has recently been increasing (figure 2, figure 3), there are still relatively few MPP or MEPP studies in the literature. Another difficulty is designing and implementing studies that explicitly test concepts in

Table 3. The reviewed studies that use the maximum power principle.

Type	Scale	Principle	Theoretical foundations	Source
Exergy as indicator of recovery	Ecosystem	(MPP)	Lotka	Libralato et al. 2006
Planktonic body size and exergy	Organism	(MPP)	Lotka, Odum	Ray et al. 2001
Exergy and ecosystem development model	Ecosystem	(MPP)	Lotka, H. T. Odum and Pinkerton, Prigogine	Fath et al. 2004
Constraining hydrological models	Watersheds	MPP	Dewar	Westhoff and Zehe 2013
Competition exclusion experiments	Community	MPP	Lotka, H. T. Odum and Pinkerton	DeLong 2008
Photoperiod and power acquisition microcosm	Ecosystem	MPP	Lotka, H. T. Odum and Pinkerton	Cai 2006
Review of Odum Silver Springs study (1957)	Ecosystem	MPP	Lotka, H. T. Odum and Pinkerton	Kemp and Boynton 2004
Behavioral thermal regulation in fish model	Organism	MPP	Lotka, H. T. Odum and Pinkerton	Bryan et al. 1990
Ecosystem based power model	Ecosystem	MePP	Lotka, Odum	Lee 2014
Invasion/ introduction of exotic species model	Ecosystem	MePP	Lotka, Odum	Campbell et al. 2009
Mechanistic model for plantation empower	Ecosystem	MePP	Lotka, H. T. Odum and Pinkerton	Li et al. 2013

Note: The types, scales, and theoretical foundations of these papers varied greatly. (MPP) refers to studies that use exergy as an indicator or principle. MePP refers to maximum empower principle studies. Studies that cited H. T. Odum but not H. T. Odum and Pinkerton (1955) have Odum listed as theoretical foundations.

the theoretical foundations of the principles. For example, many of the MPP papers that we reviewed cited Lotka (1922a) and H. T. Odum and Pinkerton (1955). However, there are also many MPP papers that only cited Lotka (1922a; table 1). Although Lotka (1922a) originally conceptualized the MPP for organismal systems, it was H. T. Odum and Pinkerton (1955) that added theoretical rigor and an ecosystems-level focus. In those papers that cited H. T. Odum and Pinkerton (1955), we found none that explicitly used power output, per H. T. Odum and Pinkerton (1955), as a function of system efficiency. We suggest that future studies strive to test the original concept demonstrated in figure 2 of H. T. Odum and Pinkerton (1955; figure 5). The strength of this revolutionary idea is framing system power output as a function of system efficiency.

One of the main challenges to the MEPP approach is the lack of agreement about the scale over which it applies, and, to a lesser extent, the confusion regarding entropy itself. Although Prigogine's (1945, 1947) minimum entropy production can be shown to be a special case of MEPP (Kleidon and Lorenz 2005), others have found that although subparts of a system operate at minimum entropy production, the system as a whole operates under MEPP. For instance, river networks organize to minimize drag (i.e., minimum entropy), but this maximizes the dissipation rate of gravitational potential (Kleidon et al. 2013). Likewise, do individual organisms follow the MEPP, or is it only ecosystems? As to entropy, there still seems to be some confusion between thermodynamic entropy and information, in which order is important for the latter but not for the former (Morrison 1964). These issues of the scale and definition of entropy must be resolved before a mature MEPP can effectively advance ecosystem science.

The importance of MEPP and MPP to ecosystem ecology

Although our review has compared and contrasted the development and application of the MEPP and MPP over time, here, we emphasize the importance and usefulness of these theories in ecosystem ecology. Our study has shown that there has been a steady increase in the number of publications associated with the MEPP and MPP over the last several decades (figures 2 and 3); however, the use of these principles for describing ecosystem organization and function has not gained wide acceptance by the larger community. We propose two reasons for this lack of enthusiasm: (1) confusion surrounding which of the competing theories is "correct" while missing the shared underlying premise and (2) an inherent desire to explain the mechanistic details of individual ecosystems at the expense of uncovering general theories. We address these two points below, as well as explain the usefulness of these principles.

As we discussed in the introduction, there exist several goal-oriented objective functions for describing ecosystem organization and function in addition to the MEPP and MPP. Indeed, all of the theories appear more similar than different (Fath et al. 2001). Some may be more appropriate under transient conditions, whereas others apply to steady-state conditions, so choosing one versus another can be confusing. Furthermore, the subtle differences between competing theories mask their common theoretical foundation. At the core of both the MEPP and MPP is the hypothesis that systems, whether animate or inanimate, internally organize to dissipate available energy (also known as free energy, Gibbs energy, exergy, or energy potential). This hypothesis is clear in the MEPP, because entropy production by definition is this reduction in usable energy. In the MPP, this core hypothesis may not be obvious, but at steady state, the flow of power through an ecosystem is ultimately dissipated as heat by the balanced actions of growth and decomposition, as was described above. This simple principle, first articulated by Lotka (1922a), is a powerful statement, because it describes a possible trajectory for Darwinian evolution. Ecosystems are often studied from the perspective of large multicellular organisms whose characteristic time scales are long; consequently, there is a tendency to describe organisms evolving in a static fitness landscape. Under this context, evolution is well posed. However, fitness landscapes are not static (Mustonen and Lässig 2009), which is most evident in microbial-based systems whose characteristic time scales are short. As microorganisms grow and evolve, they rapidly alter their environment, dynamically producing new niches in the process, such as through changes in nutrient concentration, redox state, pH, and transport characteristic (Esteban et al. 2015). The fitness landscape evolves as quickly as the microbes, rendering Darwinian evolution a tautology (Murray 2001).

The directionality provided by the MEPP and MPP is not law but rather a tendency based on probabilities. Hurricane organization may be disrupted by vertical wind shear, and food web hierarchy may be disrupted with sufficient environmental perturbation (Fernando et al. 2010), but given sufficient time, both will recover, because the organized systems increase entropy production and power throughput relative to their unorganized states. As with classical thermodynamics, the larger the number of particles (i.e., organisms), the more definitive their probability distributions become, and the more resilient they are to perturbations (Dewar 2009). Governing theories, such as the MEPP and MPP, are crucial for developing predictive models or theories, but they are not a panacea. Similarly, neither is the law of conservation of mass, but it is still a useful tool. Any proposed theory regarding ecosystem organization and function that contradicts mass conservation—or is at odds with the MEPP or MPP—is likely to be wrong over sufficiently long time scales, but this simple litmus test is seldom applied.

The second reason for the lack of acceptance of the MEPP or the MPP is the inherent propensity of ecosystem scientists—or all ecologists, for that matter—to focus on case studies. For instance, ecosystems, and associated specialists, are usually categorized by location—for example, tropical, temperate, and polar—and are further subdivided into terrestrial or aquatic. But these ecosystems are all the same from the perspective of the MEPP and MPP; only the drivers and the temporary inhabitants differ. The case-study approach is a reasonable endeavor. There is only one Earth, so understanding the details matters, but developing general theories that explain all of the details is likely not possible. A ball thrown in a vacuum follows a perfect Newtonian ballistic trajectory, but predicting its final location if it lands on a cobblestone road becomes challenging. The details of the cobblestone topography drive the solution, and general theories are less useful for such problems. As a consequence, general theories are often thought not to apply, but they can be useful if applied at the appropriate scale. For instance, the MEPP has been used as a basis for modeling methanotrophic communities (Vallino et al. 2014) and metabolic switching associated with nitrate reduction in anaerobic environments (Algar and Vallino 2014). To study the MPP, Cai and colleagues (2006) devised an experiment that allowed the organisms themselves to be in control of the power source. In these approaches, no attempt was made to describe or predict the details of microbial population dynamics. Rather, the goal was to predict how the system was likely to organize to dissipate energy given some knowledge of the metabolic functions that the community was capable of expressing. By not focusing on the details, some predictions can be made. Both the MEPP and MPP can be useful in this regard, but this requires us to appreciate the spatial and temporal scales over which these theories are likely to be valid. As with climate models that forego details needed to predict weather, the MEPP and MPP provide constraints on energy and mass flow through ecosystems at the expense of understanding the dynamic details of individuals and food webs that are difficult or impossible to predict over long time scales.

Conclusions

The MPP and the MEPP have been applied to ecosystem ecology in complementary ways and have often been focused on ecosystem development and organization. These are still young and developing principles, and their application is clearly not completely settled. However, both the MEPP and the MPP have strong potential to further inform our understanding of ecosystem dynamics. Our historical review of the Second Law of Thermodynamics literature revealed that although the MEPP is generating more interest among ecologists than the MPP, the MEPP did not evolve from the MPP. Instead, both of these approaches were developed independently and are complementary to one another. The MPP is more widely used by ecosystem ecologists, although there are more ecological studies that refer to the MEPP. Through our study of the historical development of the MPP and the MEPP from the Second Law of Thermodynamics, we sought to clarify theoretical developments and misconceptions within the principles. Despite their shortcomings, our examination of MPP- and MEPP-based studies clearly demonstrates the general applicability of the MEPP and the MPP across scales and their promise to better inform how ecosystems structure and function.

We were encouraged to see a wide variety in the ecological scales at which these principles are being applied. We need to test the MEPP at the ecosystem scale and across multiple systems to assess validity not at one particular scale. Because the MPP is clearly an ecosystem-scale construct, we suggest that the MPP has the most potential at the ecosystem scale. We end with suggestions for future studies using the MEPP and the MPP approaches: (a) We encourage broader collaboration across the multitude of disciplines that test these principles, (b) we should focus on theoretical development and an agreeable theoretical derivation of the MEPP, (c) we invite an increased number of experiments to test the MPP and the MEPP, and (d) those studies that test the MPP should strive to frame experimental designs in terms of the approach outlined by H. T. Odum and Pinkerton (1955).

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