

Thermodynamic extremization principles and their relevance to ecology

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Abstract Theories based on simple principles have provided much insight into the common processes that underpin complex ecological systems. Although such theories (e.g. neutral theory, metabolic theories) often neglect specific ecological details, they compensate for this with their generality and broad applicability. We review several simple principles based on ‘thermodynamic extremization’ (the minimization or maximization of a thermodynamic quantity) and explore their application and relevance to ecology. Thermodynamic extremization principles predict that certain energetic quantities (e.g. entropy production) will tend towards maxima or minima within ecological systems, subject to local constraints (e.g. resource availability). These principles have a long history in ecology, but existing applications have had a theoretical focus and have made few quantitative predictions. We show that the majority of existing theories can be unified conceptually and mathematically, a result that should facilitate ecological applications of thermodynamic extremization principles. Recent developments in broader ecological research (e.g. metabolic theories) have allowed quantitative predictions of ecological patterns from thermodynamic extremization principles, and initial predictions have been supported by empirical data. We discuss how the application of extremization principles could be extended and demonstrate one possible extension, using an extremization principle to predict individual size distributions. A key focus in the application of thermodynamic extremization principles to mainstream ecological questions should be the generation of quantitative predictions and subsequent empirical validation.

Key words: biodiversity, ecological thermodynamics, ecosystem ecology, entropy, maximum power.

INTRODUCTION

Theories based on simple principles have provided much insight into the common processes that underpin complex ecological systems. Examples include the metabolic theory of ecology (MTE; Brown *et al.* 2004), ecological neutral theory (Hubbell 2001) and the theory of island biogeography (MacArthur & Wilson 1967). Although the simple principles underlying these theories often neglect specific ecological details (e.g. see Clarke 2006; Clark 2012), such principles provide the basis for general and broadly applicable ecological theories (Alonso *et al.* 2006). The simplicity of these types of theories is often contentious, but the true test of an ecological theory is the predictions it generates (McGill & Nekola 2010). Despite their apparent simplicity, applications of many

of these principles produce complex predictions that are supported by theoretical and empirical research (e.g. West *et al.* 1997).

Thermodynamics has been used frequently in ecological studies, often because it provides the types of simple principles that lead to general ecological predictions (e.g. Gallucci 1973; Ernest *et al.* 2003; Brown *et al.* 2004). For example, the classical laws of thermodynamics are a core component of many metabolic theories, even if only through straightforward assumptions (e.g. mass is conserved; van der Meer 2006). Many ideas relating to the trophic structure of ecological communities also draw heavily on thermodynamic ideas (e.g. Trebilco *et al.* 2013). Similarly, extensions of classical thermodynamic laws to non-energetic contexts have led to several powerful, predictive ecological theories, such as the maximum entropy theory of ecology and related approaches (Shipley *et al.* 2006; Harte 2011).

Several simple principles, which we call ‘thermodynamic extremization principles’ (i.e. the minimization or maximization of a thermodynamic quantity), emerge when thermodynamic concepts are extended to dynamic, far-from-equilibrium systems

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(Kleidon 2010). Ecological systems, including organisms, populations, communities, and ecosystems, are far-from-equilibrium thermodynamic systems and should be governed by these thermodynamic principles (Kleidon *et al.* 2010). Thermodynamic extremization principles have been used sparingly in ecology, but sporadic applications have appeared for almost a century (Lotka 1922; Schrödinger 1945; Odum & Pinkerton 1955; Jorgensen & Fath 2004; Kleidon *et al.* 2010; del Jesus *et al.* 2012). These principles hypothesize that certain energetic quantities (e.g. entropy production) will be maximized or minimized in far-from-equilibrium systems, which can constrain the dynamics and structure of these systems (Martyushev & Seleznev 2006; Kleidon 2010). In an ecological context, these extremization principles can be used to predict the structures and dynamics we might observe, but also how these features might respond to external biotic or abiotic pressures (Kleidon *et al.* 2010; del Jesus *et al.* 2012). Although thermodynamic extremization is a simple concept, its basis in physical laws and capacity to be linked to other ecological theories (e.g. metabolic theories) make it a potentially fruitful avenue for many areas in ecology.

We review thermodynamic extremization principles and their application to ecology. We begin with a brief introduction to general thermodynamic principles, followed by a more specific introduction to thermodynamic extremization principles and their use in ecology. Existing studies of these principles often have been viewed as contentious and we explore the theoretical and empirical support for such approaches. We show that the majority of existing thermodynamic extremization principles can be unified theoretically and we discuss how the resulting unified principle could be used to generate quantitative predictions. We outline how recent developments in metabolic ecology (e.g. the MTE and dynamic energy budget (DEB) theory; Brown *et al.* 2004; Kooijman 2010) can be coupled with thermodynamic extremization principles and we provide a worked example of this approach, using a thermodynamic extremization principle to generate predictions for individual size distributions. Last, we highlight several details that should be considered when applying thermodynamic extremization principles to ecological questions.

THERMODYNAMICS FOR ECOLOGISTS

Equilibrium and non-equilibrium thermodynamics

Thermodynamic studies consider 'systems' embedded within an 'environment'. In ecology, the 'system' is the ecological system of interest and the 'environment' is

everything outside of that ecological system. Thermodynamic systems may be: (i) isolated, where no energy or matter is transferred between the system and the environment; (ii) closed, where energy but not matter is transferred between the system and the environment; or (iii) open, where energy and matter may be transferred between the system and the environment (Kondepudi 2008). Ecological systems are open systems, transferring matter and energy to and from their environment (Jorgensen *et al.* 1999).

Classical thermodynamics assumes that systems are in 'thermodynamic equilibrium', which is a state of maximum entropy (entropy = a standardized measure of the thermal energy unavailable to perform useful work). Without the influence of an external agent, a system in thermodynamic equilibrium has no capacity to change or to perform work (Kondepudi & Prigogine 1999). A system in this state has limited internal structure and would be lifeless and of little interest to ecologists (Kondepudi 2008).

'Non-equilibrium' thermodynamics relaxes the thermal equilibrium assumption, focusing on systems in which irreversible processes occur, that is, processes that produce entropy (Kondepudi 2008). Non-equilibrium thermodynamics typically proceeds by assuming local thermal equilibria, which allow thermodynamic quantities, such as entropy, to be defined and calculated (Prigogine 1955). Studies of non-equilibrium systems distinguish 'near-equilibrium' systems, which respond linearly to perturbations, from 'far-from-equilibrium' systems, which may respond non-linearly to perturbations. The linear nature of near-equilibrium systems facilitates formal analysis and, therefore, near-equilibrium systems generally are well understood (Kondepudi & Prigogine 1999). Much less is understood about far-from-equilibrium systems, but it is these systems that display the most interesting behaviours, such as self-organization and dissipative structures (complex thermodynamic structures in 'steady states', such as convection cells or cyclones) (Prigogine 1978). The term 'equilibrium' sometimes is used to describe ecological systems when populations are static over several generations and nutrient and energy fluxes are stable. However, such systems are in an ecological rather than a thermodynamic equilibrium and, from a thermodynamic viewpoint, are steady-state, non-equilibrium systems (Kleidon *et al.* 2010).

The laws of thermodynamics

Classical thermodynamics has four fundamental laws, which, when taken as axioms, are used to derive all of the relationships of classical thermodynamics. The First Law of Thermodynamics states that energy is conserved (within an isolated system) and

is fundamental to all processes. The Second Law of Thermodynamics states that the entropy of an isolated system does not decrease with increasing time. Non-isolated systems, such as ecological systems, have the potential to export entropy to their environment so that entropy may decrease locally. The Second Law applies in non-isolated systems because entropy cannot be destroyed and the total entropy of a non-isolated system (ecological system) plus its environment (everything outside of the ecological system) does not decrease with increasing time. The Third Law of Thermodynamics states that entropy approaches a constant value in highly dispersed systems, very cold systems (Nernst's Theorem), and in systems where very similar substances are mixed, allowing entropy to be calculated for these systems (Brostow 1972). This law is important for defining absolute values of the entropy, but is unlikely to have direct application to ecology. Last, the Zeroth Law of Thermodynamics states that two systems that are each in equilibrium with a third system must be in equilibrium with each other. This law is essential to the definition of temperature, but would not be expected to provide new insights into ecological questions.

The laws of thermodynamics in far-from-equilibrium systems

The laws of thermodynamics are universal; they apply to all physical systems. However, predictions from these laws are restricted largely to systems in or near thermodynamic equilibrium (Prigogine 1978). Brostow (1972) suggested that 'real' thermodynamic problems (i.e. far-from-equilibrium problems) require additional laws, but the existence of such laws remains uncertain. Ecological systems are far-from-thermodynamic-equilibrium, open systems, for which there are few established thermodynamic principles (Pross 2003).

Based on observations in fluids (e.g. Bénard cells; Schneider & Kay 1994) and climate systems (e.g. atmospheric transport; Kleidon 2004), a special case of the Second Law of Thermodynamics has been proposed for far-from-equilibrium systems: the rate of entropy production is extremized (maximized or minimized) subject to energy and mass-balance constraints and restrictions on microscopic dynamics (Kleidon 2010). This has been developed further into a range of quantities to be extremized (Table 1). The underlying principle is the same: far-from-equilibrium systems import high-quality energy (high free energy, e.g. sunlight) and export low-quality energy (e.g. heat) according to an extremization principle. These extremization principles play the role of 'laws' in non-equilibrium systems, similar to the second law of thermodynamics in equilibrium systems (Martyushev & Seleznev

2006). Such principles have strong theoretical support in certain physical systems (Kleidon 2010) and there is empirical support for extremization principles in many far-from-equilibrium systems, including ecological systems (Kleidon *et al.* 2010; del Jesus *et al.* 2012).

Related theoretical frameworks: thermodynamics, statistical mechanics and information theory

Thermodynamics is connected closely to statistical mechanics and information theory (Jaynes 1957; Kondepudi & Prigogine 1999). Thermodynamics considers transformations of energy in systems (particularly thermal systems), statistical mechanics considers the statistical properties of large aggregates of interacting particles, and information theory considers the transmission of information (Sethna 2006). These three fields arguably form a nested subset, with thermodynamics being a special case of statistical mechanics, which itself can be derived from information theory (Jaynes 1957). These concepts are related, and often are mathematically identical in their application to particular systems, but their underlying assumptions and quantities of interest can differ (Landauer 1996).

We focus on thermodynamics, restricting our discussion to the transfer and transformation of energy within and among ecological systems. Information and energy are closely related quantities, but the nature of this relationship is not yet fully understood (Smith 2008a,b,c; Frank 2009; Berut *et al.* 2012). We focus only on energetic approaches, and explore the potential applicability of thermodynamic extremization principles to ecological questions.

AN INTRODUCTION TO THERMODYNAMIC EXTREMIZATION PRINCIPLES IN ECOLOGY

Thermodynamic extremization principles were introduced to ecology by Lotka (1922) and cover some contentious ideas, such as H. T. Odum and Pinkerton's (1955) laws of energy. The fundamental basis of thermodynamic extremization principles is an energetic criterion (an example being the rate of energy use), which is predicted to be extremized (maximized or minimized) in ecological systems. The extremized energetic criterion has been related to the rate of energy use ('power'; Lotka 1922) and to the ability to gain free energy (energy available to perform work; Schrödinger 1945). Recent studies have shifted focus to entropy production (Kleidon 2010; Meysman & Bruers 2010) and to storage of exergy (= available energy; Jorgensen & Svirezhev 2004b).

Table 1. A summary of thermodynamic extremization principles, including interpretations and key authorities

Classification	Theory	Interpretation	Reference
Energy storage	Maximum exergy storage	Ecological systems maximize their storage of 'useful' energy, measured by the amount and organization of biomass	Jorgensen and Svirezhev (2004a)
	Maximum energy storage	Ecological systems maximize their energy storage. Emergy (= embodied energy) is the amount of solar energy required to build a given structure. This principle is consistent with maximum exergy storage	Odum (1983); Jorgensen and Svirezhev (2004a)
	Maximum residence time	Ecological systems maximize the residence time of energy. This is consistent with maximum exergy storage	Fath <i>et al.</i> (2001)
Energy dissipation	Maximum entropy production	Ecological systems maximize the rate of heat dissipation, more generally interpreted as a maximum rate of degradation of energy	Dewar (2010); Kleidon (2010)
	Minimum entropy production	Ecological systems minimize the rate of energy degradation. Theoretical proof exists for near-equilibrium systems under particular boundary conditions. This principle is uncommon in ecological applications	Prigogine (1955); Martyushev and Seleznev (2006)
	Min-Max principle of entropy production	Ecological systems first increase entropy production and then decrease entropy production as they mature. This principle implies maximum efficiency in mature ecological systems, with lower rates of efficiency in immature ecological systems. Consideration of system maturity is unusual in ecological thermodynamics, but the mature-ecological-system version of this principle is consistent with minimum specific energy dissipation (see below)	Aoki (2006)
	Maximum rate of gradient degradation	Ecological systems maximize dissipation of gradients in free energy or exergy. This principle is consistent with maximum entropy production	Schneider and Kay (1994)
	Maximum power	Ecological systems maximize their energy dissipation (power). Power has been related to metabolic rate, reproductive rate, or rate of 'useful' work. This principle is consistent with maximum entropy production	Lotka (1922); Brown <i>et al.</i> (1993); DeLong (2008)
	Maximum empower	This principle is identical to the maximum power principle, but defined for 'emergy' rather than energy. Emergy is the solar energy required to build a given structure. Emergy accounts for differences in energy quality	Odum and Pinkerton (1955)
	Increasing/maximum ascendancy	Ecological systems increase their 'ascendancy' to a maximum. Ascendancy is an information-theoretic measure of the size and complexity of an ecological system and is dominated by energy throughflow (power). This principle is consistent with maximum entropy production	Ulanowicz (1980); Ulanowicz (2003)
	Minimum specific energy dissipation	Ecological systems minimize energy dissipation per unit mass. This principle is based on observations of increased complexity and lower energy use per unit biomass (i.e., higher efficiency) as ecological systems mature. Low specific energy dissipation can co-occur with maximum total energy dissipation if energy storage is high. This principle therefore is consistent with maximum entropy production under an assumption of maximum energy storage	Margalef (1963)
	Maximum 'E intensity'	Ecological systems maximize their average rate of kinetic energy use (excluding heating) per unit area ('E intensity'). This principle considers optimal ratios of catalytic elements to be a key ecological requirement. Maximum E intensity is a form of the maximum power principle, but considers non-thermal energy. All other principles consider thermal energy, so this principle is not directly comparable with other approaches. It is likely that maximum E intensity is consistent with maximum rate of cycling, because nutrient cycling will improve availability of catalytic elements	Milewski and Mills (2010)
	Constructal law of evolution	Ecological (and non-ecological) systems develop such that energy becomes more accessible through time. This principle states that energy flow should become easier as time increases, allowing energy dissipation to increase. This principle is consistent with maximum entropy production.	Bejan and Lorente (2010)
Energy dissipation and energy storage	Maximum rate of cycling	Ecological systems maximize the rate of cycling of matter. Matter cycling is driven by energy flows, but the rate of cycling depends also on total matter availability. This principle is consistent with maximum energy dissipation under an assumption of maximum energy storage	Morowitz (1968)

Early studies did not yield quantitative predictions, with most supporting evidence based on qualitative predictions (e.g. 'ecosystem complexity will increase through time' or 'the number of trophic levels will be constrained'; Odum 1983). Further development of these ideas saw the introduction of several 'unified' theories based extremization principles (Wicken 1987; Brooks & Wiley 1988; Brooks *et al.* 1989; Weber *et al.* 1989; Schneider & Kay 1994). However, these theories often were based on information theory (i.e. they were not energetic) and retained the qualitative predictions common to earlier approaches (e.g. Brooks & Wiley 1988). Much of the discussion in these studies was focused on evolutionary (c.f. ecological) questions, such as the origin of life and the links between natural selection and thermodynamics or information theory (Wicken 1987; Brooks & Wiley 1988; Weber *et al.* 1989). Schneider and Kay (1994) introduced a broad ecological theory encompassing many earlier ideas, but they acknowledged the confusion created by thermodynamic versus information-theoretic concepts and the multitude of proposed extremization principles. Their approach highlighted the importance of ecological predictions, but they too were restricted to largely qualitative predictions.

More recent studies can be divided into theoretical and empirical categories, with most research taking a theoretical approach. Despite the issues highlighted by Schneider and Kay (1994), the increasingly quantified theoretical studies have focused largely on distinguishing among alternative extremization principles, with little emphasis being given to measurable predictions and empirical validation (e.g. Jorgensen & Svirezhev 2004b; Bejan & Lorente 2010; Niven 2010). Several unified theories have been developed during this period (e.g. Jorgensen & Svirezhev 2004b; Avery 2012) but, although these approaches build on a strong theoretical basis, they have been clouded by their inclusion of information-theoretic arguments and an absence of quantitative predictions and empirical evidence.

A small body of recent empirical work has focused on clear, quantitative predictions and on confronting these predictions with empirical data (Allen *et al.* 2003; Cai *et al.* 2006; DeLong 2008, 2012; Dewar *et al.* 2009; Dewar 2010; Holdaway *et al.* 2010; del Jesus *et al.* 2012). For example, DeLong (2008) used an extremization principle to predict correctly the outcomes of two-species competitive interactions in microcosms, while del Jesus *et al.* (2012) showed that an extremization principle predicted the spatial distribution of functional vegetation types at the scale of a river basin.

A criticism of thermodynamic extremization principles is that they can be interpreted as being teleological (i.e. they imply a purpose or design in nature) (Jorgensen & Fath 2004). Teleological arguments often

are used implicitly to justify extremization principles (e.g. Odum & Pinkerton 1955) and, in some cases, this teleology is assumed explicitly (e.g. Lovelock 1972). However, teleology is not central to thermodynamic extremization principles, and an inevitable 'final state' is not part of many recent approaches (Hoelzer *et al.* 2006; see also *Emergence of patterns at community and ecosystem scales*, below). Extremization principles, interpreted correctly, are emergent patterns and do not require any coordination among components or an overall guiding agent (Hoelzer *et al.* 2006).

Mansson and McGlade (1993) levelled some broader criticisms at the thermodynamic extremization principles championed by H. T. Odum (e.g. Odum 1983). They claimed that energy is too diverse a concept to be a common ecological currency and that many of H. T. Odum's proposed energetic rules were either unverifiable or not supported by empirical data (Mansson & McGlade 1993). Other authors have noted that energy is a vague currency and have suggested that thermodynamic extremization principles should be grounded in core ecological processes, such as metabolic and demographic rates (Brown *et al.* 1993; Kozlowski 1996; Loreau 1998). These criticisms apply predominantly to H. T. Odum's approach, which forms only one of many possible thermodynamic extremization principles (Mansson & McGlade 1993). Many recent studies focus on more refined principles, with clearer theoretical and empirical justification (Bejan & Lorente 2010; Kleidon *et al.* 2010; Niven 2010).

The maximum entropy (MaxEnt) formalism (Shipley *et al.* 2006; Harte 2011) is being used increasingly in ecology, but is not equivalent to an energetic extremization principle. MaxEnt is based on an equilibrium thermodynamic concept with mathematical counterparts in statistical mechanics and information theory (Jaynes 1957). There is confusion about MaxEnt in ecological applications, which arises from unclear definitions and the conflation of thermodynamic, statistical mechanical and information-theoretic interpretations (see, e.g. Haegeman & Loreau 2008; Petchey 2010). The misunderstandings about MaxEnt have been compounded by its use as a tool for species-distribution modelling (Elith *et al.* 2011). To avoid adding to this confusion, we distinguish energetic extremization principles from MaxEnt.

Similarly, thermodynamic extremization principles do not necessarily encompass all metabolic and energetic approaches to ecology (e.g. Brown *et al.* 2004; Kooijman 2010). Although such studies often draw on thermodynamic laws, most make no assumptions or claims regarding the extremization of energetic quantities. We discuss possible links between metabolic theories and extremization principles below (see *Quantitative approaches to thermodynamic extremization principles*).

Emergence of patterns at community and ecosystem scales

The emergence of extremization principles at macroscopic scales might be viewed as contentious, but is common in many physical, chemical and biological systems (Martyushev & Seleznev 2006; Kleidon 2010). Indeed, the emergence of consistent patterns in ecological communities and ecosystems is the basis of many ecological studies (e.g. Levin 1998, 2005; Loeuille & Loreau 2005; Sole & Bascompte 2006). Thermodynamic extremization principles are predicted to emerge at all ecological scales (e.g. organisms, populations, communities) regardless of microscopic dynamics (e.g. organism-scale interactions).

Ecological systems might belong to the broader class of self-organizing systems or complex adaptive systems (Levin 1998; Hoelzer *et al.* 2006), in which case an extremization principle could be viewed as a self-organizing process. Self-organization is a spontaneous process that results from local interactions and does not imply the presence of an organizing agent (Levin 2005). Self-organization occurs in many physical and biological systems, with complex, non-linear interactions at the scale of particles (or organisms) generating consistent patterns at the system scale (Levin 2005; Hoelzer *et al.* 2006; Sole & Bascompte 2006). The Second Law of Thermodynamics has been used to explain why complex dynamical systems might self-organize, with the extremizing property of the Second Law thought to favour the persistence of particular system trajectories (Prigogine 1955; Dewar 2005). In ecological systems, natural selection would enhance self-organization by reinforcing the persistence of particular system trajectories (Hoelzer *et al.* 2006).

An analogy can be drawn between ecological thermodynamics and quantum physics. Quantum-physical systems differ from classical physical systems in their microscopic dynamics, but thermodynamic laws emerge in both classical and quantum systems (Gemmer *et al.* 2009). Similar to quantum-physical systems, ecological systems are distinguished from corresponding non-living systems by their microscopic dynamics, namely, the presence of organism-scale evolutionary processes. However, differences in microscopic dynamics do not preclude a thermodynamic principle applying at the macroscopic scale (Gemmer *et al.* 2009). Any system typified by complex microscopic interactions and dynamics has the potential to generate consistent macroscopic patterns irrespective of the microscopic details (Levin 1998).

A SURFEIT OF THERMODYNAMIC EXTREMIZATION PRINCIPLES

Many thermodynamic extremization principles have been proposed and applied to ecological questions

(Table 1). These principles are distinguished by the energetic quantity to be extremized, resulting in several seemingly distinct principles (Table 1). Many of the energetic quantities can be related to ecological quantities such as biomass, food-web complexity (e.g. link density), growth rates, life-cycle length and community stability, which have been proposed to follow predictable trajectories during ecosystem development (Odum 1969; Loreau 1998). The relevant literature is fragmented, and much attention has been given to distinguishing among alternative extremization principles. However, despite their apparent diversity, different thermodynamic extremization principles can be reduced to two themes: energy storage and energy dissipation (Table 1; see also Fath *et al.* 2001). We review several energy-storage and energy-dissipation principles.

Energy storage

Energy-storage principles propose that ecological systems maximize the amount of energy they contain (e.g. in biomass). Minimum energy storage is unlikely to occur; minimum energy storage suggests that ecological systems should be as small and simple as possible, which is not generally seen in ecological systems. The form of energy differs among proposed applications, but all approaches suggest that an organism's survival depends on its ability to gather and to retain energy through processes such as growth (Table 1).

The maximum exergy-storage approach of Jorgensen and Svirezhev (2004b) is an example of an energy-storage principle. Exergy is a form of free energy that is defined relative to a reference environment and measures the amount of useful work (i.e. changes to the environment) that can be performed when bringing a system into equilibrium with the reference environment (Zhou *et al.* 1996). Jorgensen and his colleagues suggested that several ecological and biological observations are explained by the principle of maximum exergy storage (e.g. resource allocation in plants, nutrient cycling in lakes, genome size in animals) (reviewed in Jorgensen & Fath 2004; Jorgensen & Svirezhev 2004b). Exergy storage (= available energy) is related to the amount and organization of biomass and to the amount of genetic information (Jorgensen & Svirezhev 2004a; but see Gaudreau *et al.* 2009). The methods used by Jorgensen and Svirezhev (2004b) to quantify genetic information relied on information-theoretic ideas and, as such, do not have an energetic basis (i.e. they do not explain genetic information from an energetic viewpoint).

Energy dissipation

Energy-dissipation principles propose that ecological systems extremize rates of energy use.

Energy-dissipation principles suggest that an organism's survival depends on its ability to gather and to use energy (Table 1). The majority of energy-dissipation principles are maximization principles; few consider minimum energy dissipation (Table 1). Minimum energy dissipation suggests efficient energy use, whereas maximum energy dissipation implies high throughput (i.e. organisms use energy as fast as possible). Maximum energy dissipation does not necessarily imply inefficient use of other resources (e.g. water or nutrients) because efficient use of these resources may be essential to high energy dissipation. We outline two examples here: maximum entropy production and maximum power.

The maximum entropy-production (MEP) principle states that all non-equilibrium thermodynamic systems produce entropy as fast as possible, returning the system to the equilibrium state of maximum entropy as quickly as possible (Martyushev & Seleznev 2006). Early examples of MEP considered near-equilibrium systems (i.e. non-ecological systems), but the search for a general principle resulted in MEP being applied to complex, far-from-equilibrium systems, such as the global climate system and the global biosphere (Paltridge 1975; Kleidon 2004, 2010). Maximum entropy production has been used to explain optimal plant function, with optimal plant traits (e.g. those relating to shoot or canopy photosynthesis) related to entropy production (Dewar *et al.* 2009; Dewar 2010). Ecological studies of MEP have focused predominantly on finding evidence of MEP in ecological systems with little attention to prediction or to application (Kleidon *et al.* 2010).

Despite theoretical and empirical evidence for MEP in several near-equilibrium physical systems (e.g. the velocity distribution function for non-equilibrium gas systems follows the MEP principle), there has been little evidence for MEP in far-from-equilibrium ecological systems (Martyushev & Seleznev 2006). There have been several attempts to derive a general proof for far-from-equilibrium systems (Dewar 2003, 2005), but these attempts have not yet been successful (Grinstein & Linsker 2007). Despite this, the many successful applications of MEP to hydrodynamic, material and chemical systems suggest that the MEP approach may be useful for ecology (Martyushev & Seleznev 2006).

Maximum entropy production includes several explicit principles, each with different domains of applicability (Martyushev & Seleznev 2006; Bruers 2007). These principles distinguish between near-equilibrium and far-from-equilibrium systems and the method by which entropy production is maximized (e.g. mechanisms that select among alternative states versus mechanisms that drive systems towards one state). *Ad hoc* definitions typically are used, capitalizing on the intuitive appeal of MEP concepts, and possibly

stemming from the difficulty of defining and measuring entropy production (Corning & Kline 1998; Grandy 2008). Some approaches implicitly assume that systems are near-equilibrium, negating the application to far-from-equilibrium systems. Dewar (2003, 2005) suggested that MEP is a physical principle resulting from MaxEnt, but he later noted that MEP may be an information-theoretic principle representing our state of knowledge of system trajectories rather than a physical mechanism *per se* (Dewar 2009).

The maximum power principle (MPP) states that individual organisms maximize the rate at which they perform work (power = work/time = energy/time) and has been used to predict the outcomes of experiments on interspecific competition (DeLong 2008) and the optimal body mass of mammals (Brown *et al.* 1993; but see Kozłowski 1996) and to explain the observed negative relationship between adult body size and temperature (DeLong 2012). H. T. Odum (2002) advocated a maximum 'empower' principle, where empower is power defined for embodied energy ('energy' = the amount of solar energy required to build a given structure; Odum 1996). Odum (2002) used the maximum empower principle to explain 12 ecological phenomena, including biomass allocation to early growth, productivity-evenness relationships and richness-latitude-area relationships (but see Mansson & McGlade 1993).

The definition of power differs among studies, which probably explains some of the contention among different approaches. Power has been related to metabolic rate (DeLong 2008), rate of 'useful' energy use (e.g. conversion to biomass or reproduction; Jorgensen & Svirezhev 2004b), rate of 'energy' use (Odum 1996; Hall 2004; Tilley 2004) and 'fitness' or rate of reproduction (Brown *et al.* 1993). Loreau (1998) noted that each of these definitions of power encompasses only one aspect of energy use, and suggested that appropriate definitions of power should be based on ecological processes (e.g. demography, resource use).

UNIFYING EXISTING THERMODYNAMIC EXTREMIZATION PRINCIPLES: A SYNTHESIS OF ENERGY STORAGE AND ENERGY DISSIPATION

Recent studies of thermodynamic extremization principles have been dominated by theoretical approaches and have focused on finding evidence for, and distinguishing among, alternative extremization principles. The classification of extremization principles into two categories (Table 1) suggests that similarities among different principles may simplify discussions of these seemingly competing principles. The relationship between the two categories (energy storage and

energy dissipation) is important because consistencies between energy storage and energy dissipation would suggest that existing thermodynamic extremization principles might be unified.

Few studies have considered consistencies among thermodynamic extremization principles (but see Patten 1995; Fath *et al.* 2001); here we synthesize maximum energy storage and maximum energy dissipation, which, together, encompass the majority of existing approaches (Table 1). This synthesis does not include minimum energy-dissipation principles explicitly, but Fath *et al.* (2001) noted that minimum specific energy-dissipation principles are consistent with maximum energy-dissipation principles under conditions of maximum energy storage (Table 1).

We define energy storage as the total biomass of a given system: $M = \int_{m_1}^{m_2} mN(m)dm$, where m is a positive

value representing organism mass, m_1 and m_2 are minimum and maximum body masses, respectively, and $N(m) dm$ is the number of organisms with body size between m and $m + dm$. Similarly, energy dissipation is the transformation of energy (energy use) in a system, which can be regarded as the metabolic rate of a given system. We define energy dissipation, $P(N(m))$,

as a functional of $N(m)$ satisfying $\frac{\delta P(N(m))}{\delta N(m)} \geq 0$ in

the interval (m_1, m_2) , where $\frac{\delta P(N(m))}{\delta N(m)}$ is the func-

tional derivative of $P(N(m))$ with respect to $N(m)$ (Giaquinta & Hildebrandt 1996). The constraint $\frac{\delta P(N(m))}{\delta N(m)} \geq 0$ implies that adding a positive incre-

ment to $N(m)$ either will increase energy dissipation or leave it unchanged, that is, adding individuals to any size-class does not decrease energy dissipation. These definitions assume that both energy storage and metabolic rate are functions only of organism size. This necessarily is a simplification, but such an assumption is supported both empirically and theoretically (West *et al.* 1997). We have made no assumption about the form of relationship between energy use and organism size, and the restriction on $\frac{\delta P(N(m))}{\delta N(m)}$ is weak and allows a range of functionals representing energy dissipation.

We propose the following theorem: maximum energy dissipation (metabolic rate) implies maximum energy storage. This statement can be justified informally: living organisms always dissipate energy, so an ecological system can increase its energy dissipation by increasing its energy storage (biomass) until energy storage reaches a maximum (i.e. the system becomes resource-limited). A formal proof of this theorem is provided in Appendix S1. By relating maximum energy dissipation and maximum energy storage, the

proof in Appendix S1 shows that almost all thermodynamic extremization principles are compatible with one another.

Few studies have considered the validity of a general thermodynamic extremization principle in ecology. Fewer still have considered the application of such a principle to ecologically relevant questions. Studies of thermodynamic extremization in ecology would benefit from the application of general extremization principles to ecological questions, rather than the continued study of competing extremization principles.

QUANTITATIVE APPROACHES TO THERMODYNAMIC EXTREMIZATION PRINCIPLES

Greater availability of data has allowed the quantitative assessment of thermodynamic extremization principles (e.g. Allen *et al.* 2003; Holdaway *et al.* 2010; Zupanovic *et al.* 2010; del Jesus *et al.* 2012). Although quantities related to ecosystem functioning (e.g. whole-system respiration or production) are rarely measurable directly, methods such as the eddy covariance technique are beginning to provide high-resolution estimates of these quantities (Baldocchi 2003). Similarly, the capacity to use remote-sensing data to estimate key quantities of interest is improving rapidly, with physical, chemical and biological factors all now able to be estimated using these data (Kerr & Ostrovsky 2003). Eddy covariance data already have been used to test extremization principles (e.g. Holdaway *et al.* 2010), but current approaches have been limited to single systems and qualitative predictions. Combined with more quantitative predictions (e.g. absolute values or explicit distributions rather than trends), improved data collection will allow better tests of extremization principles over large spatial scales.

Developments in metabolic theories have provided insights into thermodynamic extremization principles (e.g. DeLong 2008). The two most prominent developments in metabolic theory in recent decades have been the broad application of quarter-power scaling to ecology using the MTE (West *et al.* 1997; Brown *et al.* 2004) and the increased uptake of DEB theory, which partitions an organism into several key components (e.g. 'structure' and 'reserve') and makes predictions for individual metabolism based on the dynamics of energy and material among these components (Kooijman 2010; Sousa *et al.* 2010). These two developments are not necessarily compatible with one another (Kearney & White 2012), but both provide opportunities to test and to apply thermodynamic extremization principles.

Simulation approaches, particularly individual-based modelling (IBM) methods, have provided

substantial insight into ecological patterns (Grimm & Railsback 2005). However, a key challenge for these models is determining and quantifying relevant parameters, such as metabolic rate (Martin *et al.* 2012). These parameters are central to many applications, but often are difficult to measure directly (Martin *et al.* 2013). Martin *et al.* (2012) have developed an IBM framework based on DEB, and this framework has been used successfully to link organism-scale measurements and theory to population-scale patterns (Martin *et al.* 2013). However, these models are limited by the need for taxon-specific parameter estimates (Martin *et al.* 2013). Extremization principles could be used to facilitate the application of these models, with individual transitions and updates based on an extremization principle. This approach still allows stochastic dynamics (e.g. neutral dynamics), but avoids the need to parameterize models in detail. By combining predictions from IBMs with empirical data, the implications of extremization principles could be explored.

Alongside IBMs, many theoretical studies of extremization principles require estimates of organism-level physiological parameters. DeLong (2008) used MTE to quantify the metabolic rates of different size-structured populations and used these values to predict the outcomes of two-species competition experiments, highlighting one way in which metabolic theories could be used to test extremization principles. Such ideas can be extended readily to large-scale systems because MTE allows estimates of several community-scale quantities, such as metabolic rate, nutrient flux, resource use and production (Brown *et al.* 2004). Combining these estimates with the predictions of extremization principles (e.g. maximum energy dissipation) will generate predictions for many community-scale patterns (e.g. trait distributions).

Worked example: individual size distributions

As an example, consider predicting the individual size distribution (the probability that an organism is a particular size, irrespective of species identity; White *et al.* 2007) using a maximum energy-dissipation principle. Here, we are interested in the distribution of abundance against body size and we use the relationship between body size and energy use as an input. Combining this input relationship with equations for energy dissipation and an assumption of constrained biomass we can predict the individual size distribution that we might expect to observe (Fig. 1). One possible equation for (ensemble average) energy dissipation is

$$P = \int_{m_1}^{m_2} \epsilon(m)p(m) \left(\frac{1}{1 + f(m)(p(m))^2} \right) dm \quad (1)$$

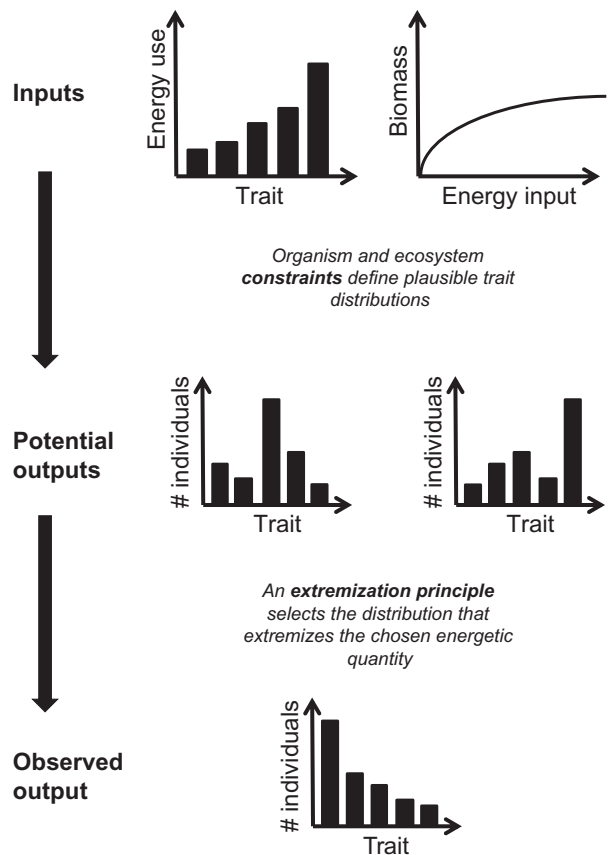


Fig. 1. Generating predictions using thermodynamic extremization principles. Resource constraints (represented here as a constraint on total biomass) and organismal properties (energy use as a function of traits) can be used to predict the observed community-scale distribution of traits. Observed trait distributions are selected from several potential distributions according to an extremization (maximization or minimization) principle (e.g. maximum energy dissipation).

where m_1 and m_2 are minimum and maximum body size, respectively, $\epsilon(m)$ is organism metabolic rate as a function of size, and $p(m)$ is the individual size distribution, that is, the probability that an individual has a body size between m and $m + dm$. The bracketed term introduces size-dependent density dependence within size-classes (DeLong *et al.* 2013; see also Appendix S2). The constraint $\int_{m_1}^{m_2} p(m)dm = 1$ is added to ensure that $p(m)$ is a valid probability distribution.

For moderate to high abundances, the ensemble average energy dissipation is equivalent to the total energy dissipation, so that maximizing average energy dissipation is equivalent to maximizing total energy dissipation. The predicted $p(m)$ is a probability distribution, so does not account for variations in total biomass (i.e. community energy use could always be increased by adding more biomass or individuals).

Assuming that biomass is constrained by environmental factors (e.g. resource availability) circumvents this issue because $p(m)$ then maximizes community energy use by distributing a fixed amount of biomass among size-classes (i.e. the community cannot support additional biomass or individuals).

Given an expression for energy dissipation or energy storage, variational calculus (Giaquinta & Hildebrandt 1996) can be used to find the distribution that maximizes this quantity subject to constraints (Fig. 1). The distribution $p(m)$ maximizing P is

$$p(m) = \sqrt{\frac{\varepsilon(m) - 2\lambda + \sqrt{\varepsilon(m)[\varepsilon(m) - 8\lambda]}}{2\lambda f(m)}}; m_1 \leq m \leq m_2,$$

which, for $\varepsilon(m) \gg \lambda$, can be approximated by

$$p(m) \approx \frac{1}{\sqrt{\lambda}} \left(\frac{\varepsilon(m)}{f(m)} \right)^{\frac{1}{2}},$$

where the constant λ is defined by the constraint

$$\int_{m_1}^{m_2} p(m) dm = 1.$$

This predicted $p(m)$ is dependent on the inputs $f(m)$ and $\varepsilon(m)$ and encompasses many alternative distributions, including those predicted by existing theories (e.g. power law, Weibull and exponential distributions; Coomes *et al.* 2003; Muller-Landau *et al.* 2006). For example, setting $\varepsilon(m) = m^\theta$ and defining $f(m)$ to be a power law in m generates a power law individual size distribution. Although the exponent of this distribution might differ from that predicted by Enquist and Niklas (2001), such differences have been noted elsewhere (Muller-Landau *et al.* 2006), and different assumptions would generate a range of exponents. This prediction for the individual size distribution is based on an explicit mechanistic principle and explicit energetic assumptions, which are amenable to testing and can be updated as new information arises. Although we have not made a unique prediction for the individual size distribution, our example highlights that extremization principles can be linked to key ecological details (e.g. competition, metabolic rate) and knowledge of these details (i.e. defining $f(m)$ and $\varepsilon(m)$) would generate explicit predictions for ecological patterns.

CONSIDERATIONS WHEN APPLYING THERMODYNAMIC EXTREMIZATION PRINCIPLES TO ECOLOGY

Several details should be considered when exploring thermodynamic approaches to ecology. Consideration of these details should increase the amount of evidence for or against thermodynamic extremization principles and should address many of the perceived shortcomings of thermodynamic extremization principles in ecology.

Alignment with mainstream ecology

Thermodynamic extremization principles are uncommon in the ecological literature. Most studies are in the literature of theoretical ecology or philosophy, and many extremization principles are controversial to ecologists (e.g. Odum & Pinkerton 1955). Notable exceptions are the maximum power study of Brown *et al.* (1993) and the work of DeLong (2008) and del Jesus *et al.* (2012). The distinguishing feature of these studies is their focus on mainstream ecological questions (trait distributions, interspecific competition and vegetation distribution, respectively). Future applications of ecological thermodynamics must address questions of fundamental interest to ecologists.

Quantification of predictions and empirical validation

Studies of thermodynamic extremization principles predominantly have been theoretical, with very little empirical work. However, the empirical studies discussed above (Allen *et al.* 2003; Cai *et al.* 2006; DeLong 2008; Dewar *et al.* 2009; Dewar 2010; Holdaway *et al.* 2010; del Jesus *et al.* 2012) suggest that empirical validation of thermodynamic extremization principles is possible. Given our increasing capacity to quantify physiological and metabolic rates, quantitative predictions and empirical data should be central to the study of thermodynamic extremization principles.

The abstract nature of concepts such as entropy and exergy (a proxy for available energy) probably alienates empirical ecologists, and has led some researchers to rely on numerical modelling (e.g. Meysman & Bruers 2010; Marchi *et al.* 2011). Our synthesis of extremization principles suggests that their interpretation is not restricted to abstract quantities (e.g. entropy). Quantitative predictions could be based around measurable quantities (e.g. metabolic rate), which would remove the dependence on numerical modelling and would allow extremization principles to become accessible to empirical ecologists.

Both experimental and observational data could be used in this context. Micro- and mesocosms could be used to assess whether an extremization principle applies (e.g. DeLong 2008; Zupanovic *et al.* 2010), while patterns predicted by these principles could be compared with observational data and assessed for consistency (e.g. del Jesus *et al.* 2012). The use of multiple spatial and temporal scales is crucial to micro- and mesocosm approaches (Carpenter 1996), and inferences from observational data are not 'strong' (McGill 2003), but experimental and observational

data together would assess the relevance of thermodynamic extremization to ecology.

Explicit distinction between thermodynamics and information theory

Information-theoretic interpretations cloud existing studies of extremization principles, particularly those claiming to develop unified ecological theories (e.g. Brooks *et al.* 1989; Jorgensen & Svirezhev 2004b). Most of the confusion relates to the definition of entropy (Corning & Kline 1998). Thermodynamics defines entropy (in equilibrium systems) as a physical quantity related to thermal energy, statistical mechanics defines entropy based on microstate counting, while information (Shannon) entropy quantifies missing information in a probability distribution (Jaynes 1957). While these terms are mathematically equivalent in many cases, this does not mean that the underlying quantities are the same (Jaynes 1957). Confusion can be avoided through the explicit acknowledgement, at the outset, of whether an energetic or information-theoretic approach is being used. We note that this practice is becoming common in ecological applications of MaxEnt (e.g. Harte 2011).

The relationship between information theory and thermodynamics does not imply that all information-theoretic concepts can be applied directly to thermodynamic systems. Studies based on ‘maximizing uncertainty’ or ‘maximizing Shannon entropy’ probably apply an information-theoretic approach and should be interpreted accordingly. While information-theoretic approaches are valid when applied appropriately, they typically are used as an inferential technique and do not represent an underlying energetic principle (e.g. Harte 2011; but see Frank 2009 and Frank 2011 for a discussion of information theory as a unifying law).

Explicit distinction between analogy and mechanism

Thermodynamic concepts often are used by those adopting the view that ecological systems bear a superficial resemblance to equilibrium thermodynamic systems (e.g. Volkov *et al.* 2004). Under this view, ecological organisms may be viewed as particles and ecological species as energy levels and one can use standard tools of equilibrium thermodynamics to predict the distribution of organisms (particles) among species (energy levels). Although this approach makes a prediction for this distribution, it confounds analogy and mechanism. Ecological systems are far-from-equilibrium thermodynamic systems and so

are not amenable to analysis by standard equilibrium techniques.

CONCLUSION

Simple principles have provided insight into many ecological patterns and processes, and the generality and applicability of these approaches often compensates for their lack of specific ecological detail. Thermodynamic extremization principles are based on one such simple concept: an energetic criterion (e.g. energy dissipation) is maximized or minimized in ecological systems. This prediction emerges when the laws of thermodynamics are extended to far-from-equilibrium thermodynamic systems. Extremization principles have been used successfully to predict optimal body size in mammals, the outcomes of interspecific competition, variation in plant traits and the large-scale distribution of vegetation. These approaches do not encompass the maximum entropy formalism, which has been applied to ecology in several different contexts, or the metabolic theories of ecology, which are the most well-known examples of ‘energetic’ or ‘thermodynamic’ ecology.

Existing studies of extremization principles have focused mainly on distinguishing among competing theories, restricting their applicability to ecological systems. We showed that existing extremization principles can be categorized into two broad classes, energy storage and energy dissipation, and that these two classes are encompassed by one general principle. This unification of extremization principles should simplify their application, and facilitate a shift in focus towards empirical analyses.

Empirical studies of thermodynamic extremization principles are rare, but are essential to our understanding and application of these approaches. Recent advances in data collection technologies and metabolic theories have allowed some empirical tests, the results of which have been largely positive. We demonstrated how empirical approaches could be extended to generate predictions for ecological communities, using an extremization principle to predict the individual size distribution. Our approach could be adapted to predict a broader range of ecological patterns, which would further assess the relevance of thermodynamic principles to ecology. The generation of quantitative predictions and empirical validation of these predictions are exciting avenues of research, and should facilitate the application of thermodynamic principles to mainstream ecological questions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Synthesis of energy-dissipation and energy-storage principles.

Appendix S2. Mathematical details for predicting individual size distributions.