



Energy and Evolution: The Systems Approach

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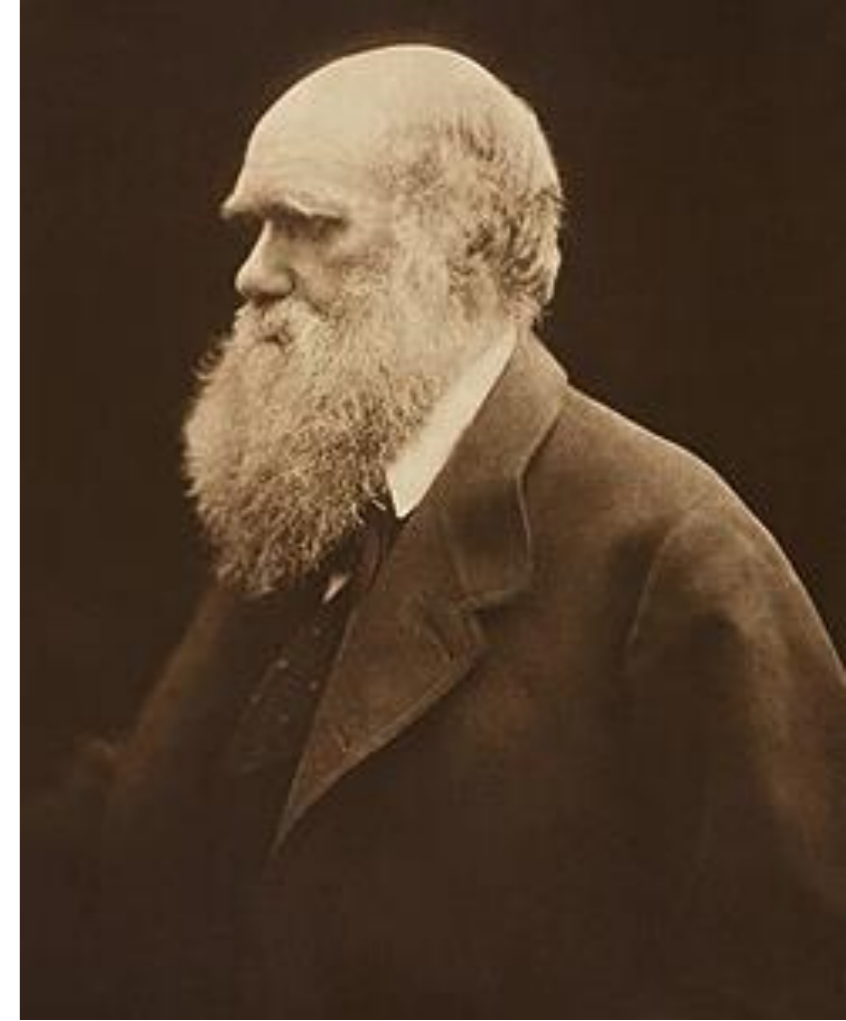
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Evolution by Natural Selection

- Darwin developed the concept of evolution by natural selection from the perspective of individual organisms and populations.
- But later investigators sought to understand evolution and natural selection in terms of energy.



What guides thermodynamic evolution?

Optimality Principles or **Goal Functions**

The Principle of Maximum Energy Flux (Lotka 1922a)

The Minimum Entropy Production Principle (Prigogine & Wiame 1946)

The Maximum Power Principle (Odum & Pinkerton 1955)

The Maximum Entropy Production Principle (Paltridge 1975)

Energy Return on Investment (Hall et al. 1986)

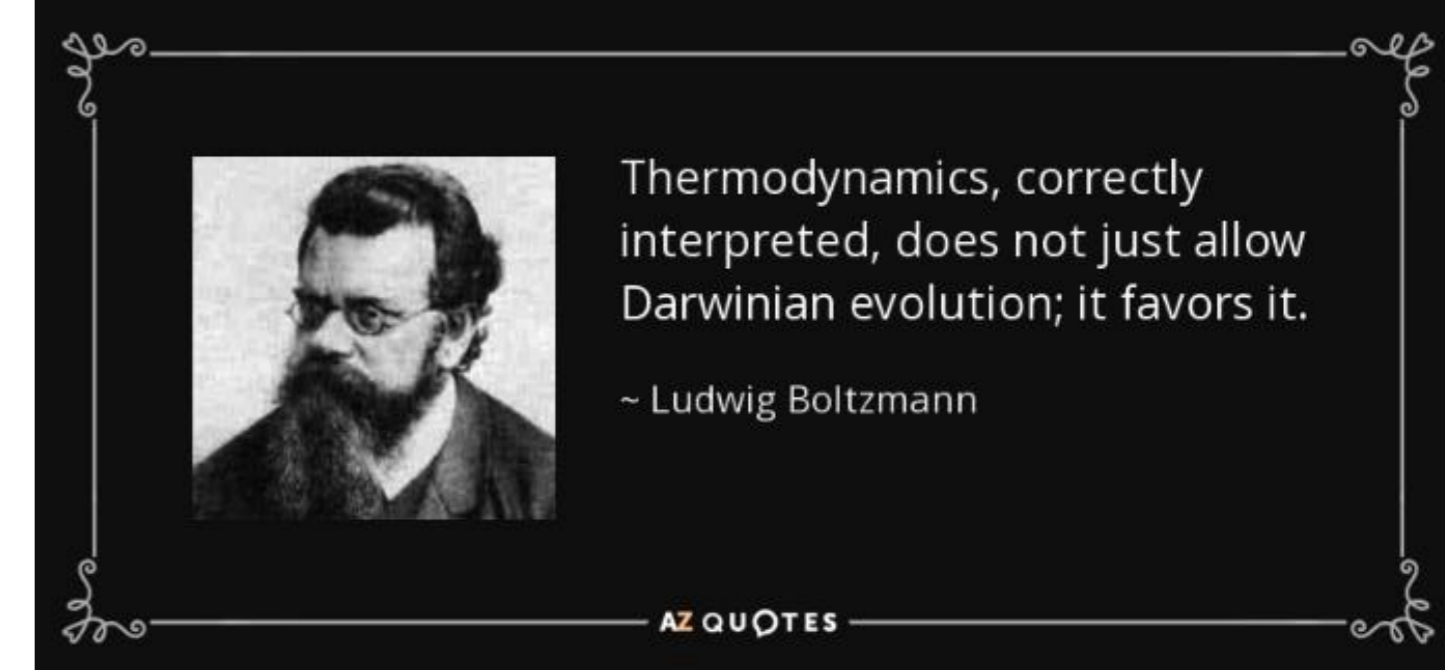
The Constructal Law (Bejan & Zane 1996)

The Equal Fitness Paradigm (Brown et al. 2018)

The Maximum Efficiency Principle (Glazier 2024)

And others: maximum dissipation, maximum reproduction, maximum biomass, maximum diversity, maximum profit, minimum heat, maximum stability, maximal energy dispersal, maximum ascendancy, ratio of direct and indirect effects, maximum storage, and maximum cycling.

- Collectively these principles have been described as being “**contradictory**,” referring to “**apples and oranges**” (Bejan & Lorente 2010), and “**local, and disunited**” (Bejan & Lorente 2011).



The Discussion of These Optimality Principles

- Many scientists have **championed their principle of choice** and argued that it is more “accurate” or more “general” than the other principles (Glazier 2024; Salthe 2010; Bejan & Lorente 2010; Brown & Burger 2024).
- In many cases, they have used **strawman arguments**, which undermine our ability to accurately understand the relation between these principles. There are two reasons for this problem:
 - 1. Complexity** -- Many of these principles are deceptively complex (e.g., Sciubba 2011).
 - 2. Fragmentation** -- The exponential growth of scientific research described by these optimality principles has made it increasingly difficult for scientists to keep up with relevant developments.
 - Chapman et al. write we “found evidence of a **highly fragmented** and disjointed historical development of the maximum entropy production principle (MEPP) and therefore of its impact on MEPP studies in ecosystem ecology and ecology in general” (2016).
 - Martyushev, L.M., Seleznev, V.D. wrote publications on the MEPP “were **fragmented** and different research teams ... were unaware of studies performed by other scientists” (2006).
 - In 2023, A Paleoecologist named Vermeij wrote a book entitled *The Evolution of Power: A New Understanding of the History of Life* and does not mention Odum’s maximum power principle or Lotka’s principle of maximum energy flux. The **Vermeij discipline** of the **maximum power principle department** of the **natural selection division** of the **thermodynamic school** of evolution.

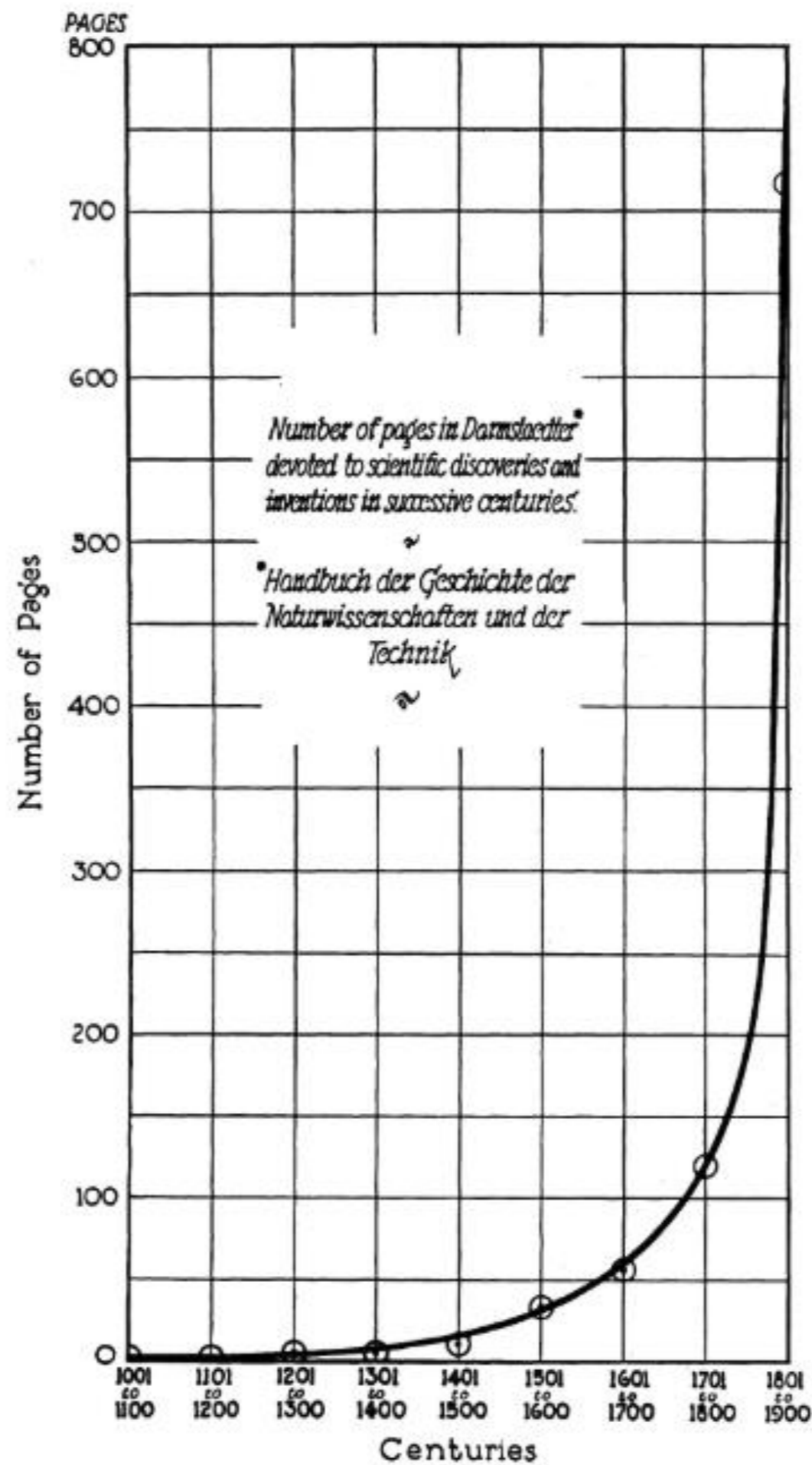
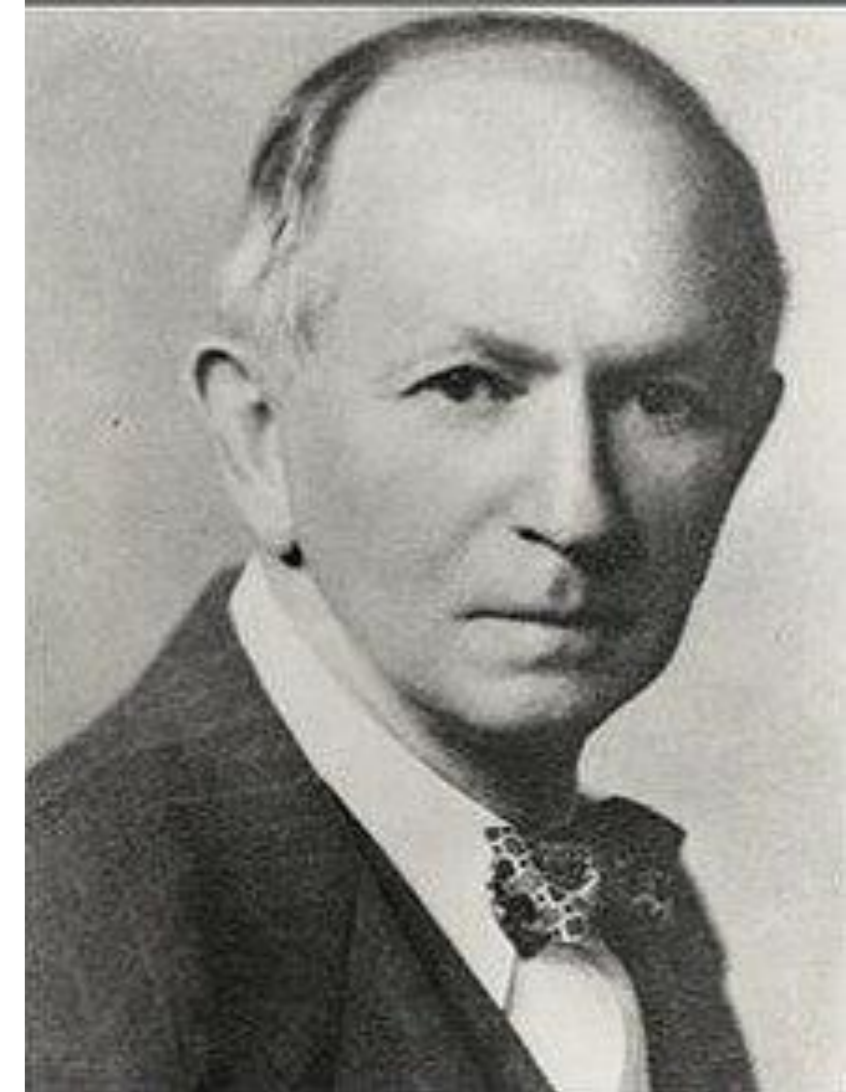


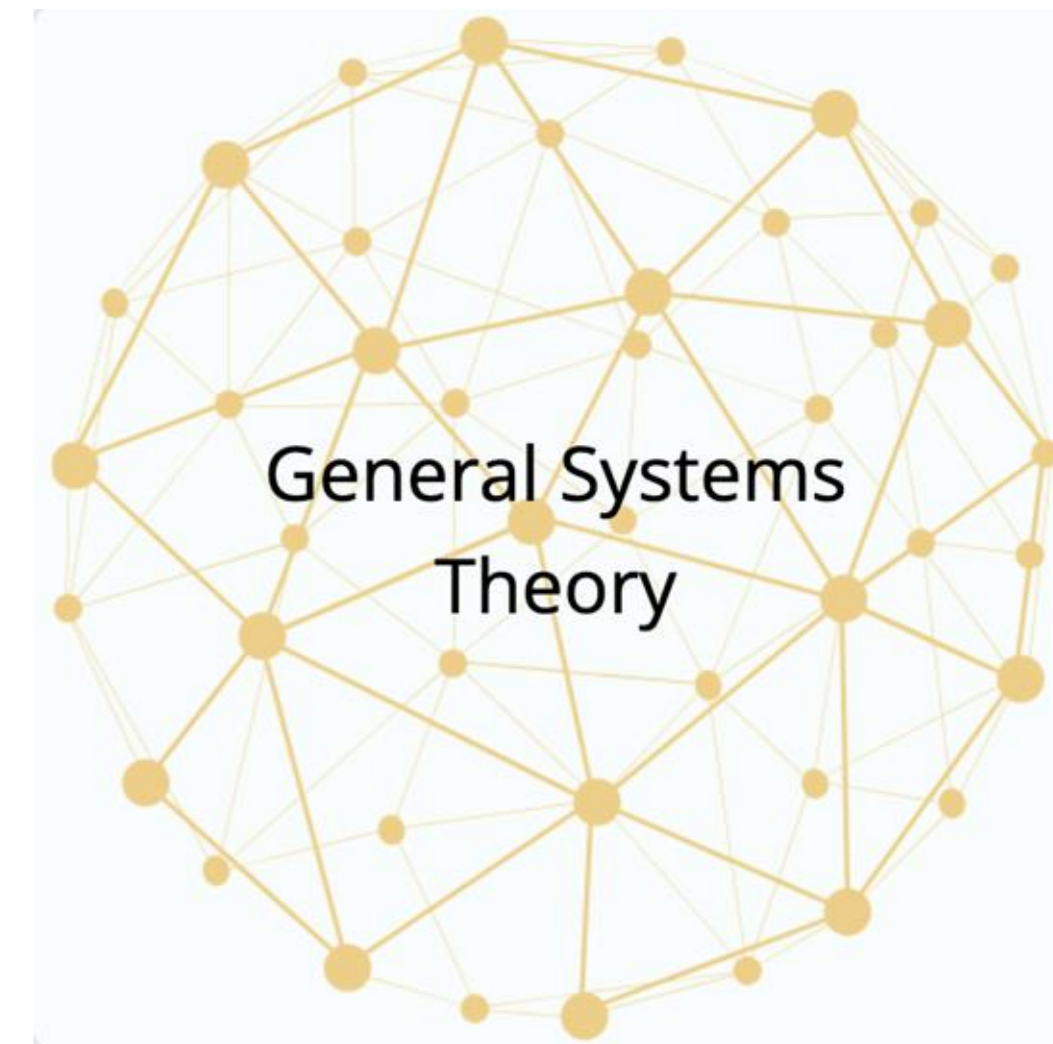
FIG. 4. Growth curve of human knowledge.



Lotka 1939, p. 625

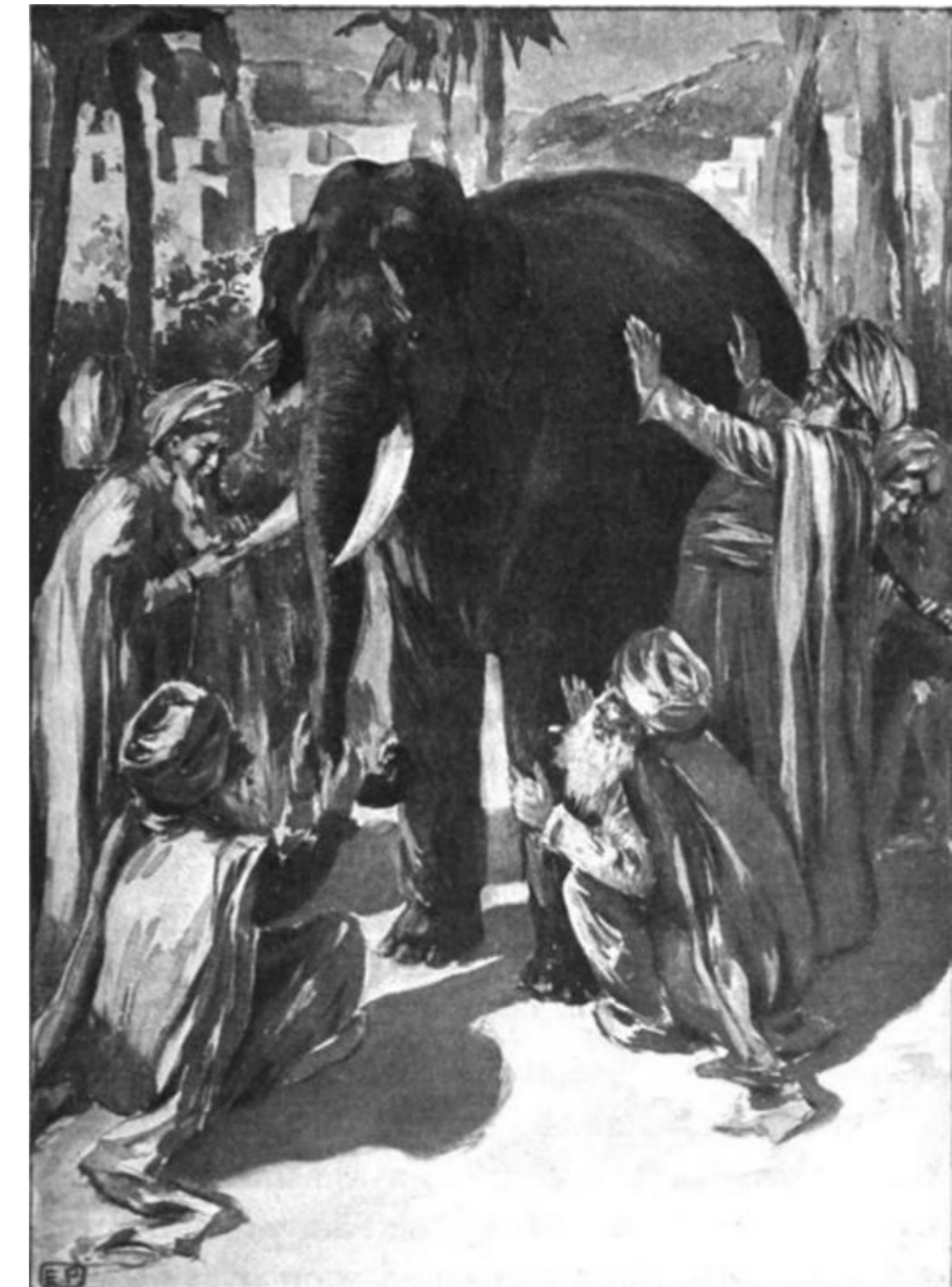
The Systems Approach

- A group of scientists has focused on illustrating how these optimality principles work together as a network or system. (Jorgensen 1992, 1994, 2001; Jorgensen et al. 1998, 2007, 2011, 2014, 2016, 2020; Patten 1995; Fath et al. 2001).
 - They view the evolutionary process as a complex system with many different parts that are **connected by a web of relationships** (Banathy 1997).
 - Jorgensen (1997) describes how the optimality principles work together in a way that forms a pattern, which he describes with his proposed 4th law of thermodynamics.
 - “If a system is moved away from thermodynamic equilibrium by the application of a flow of exergy, it will utilize all avenues available to build up as much dissipative structure (store as much exergy) as possible, to reduce the effects of the applied gradient.”
(1997, 339; cp. Schneider & Kay 1994, 29)



The Optimality Principles

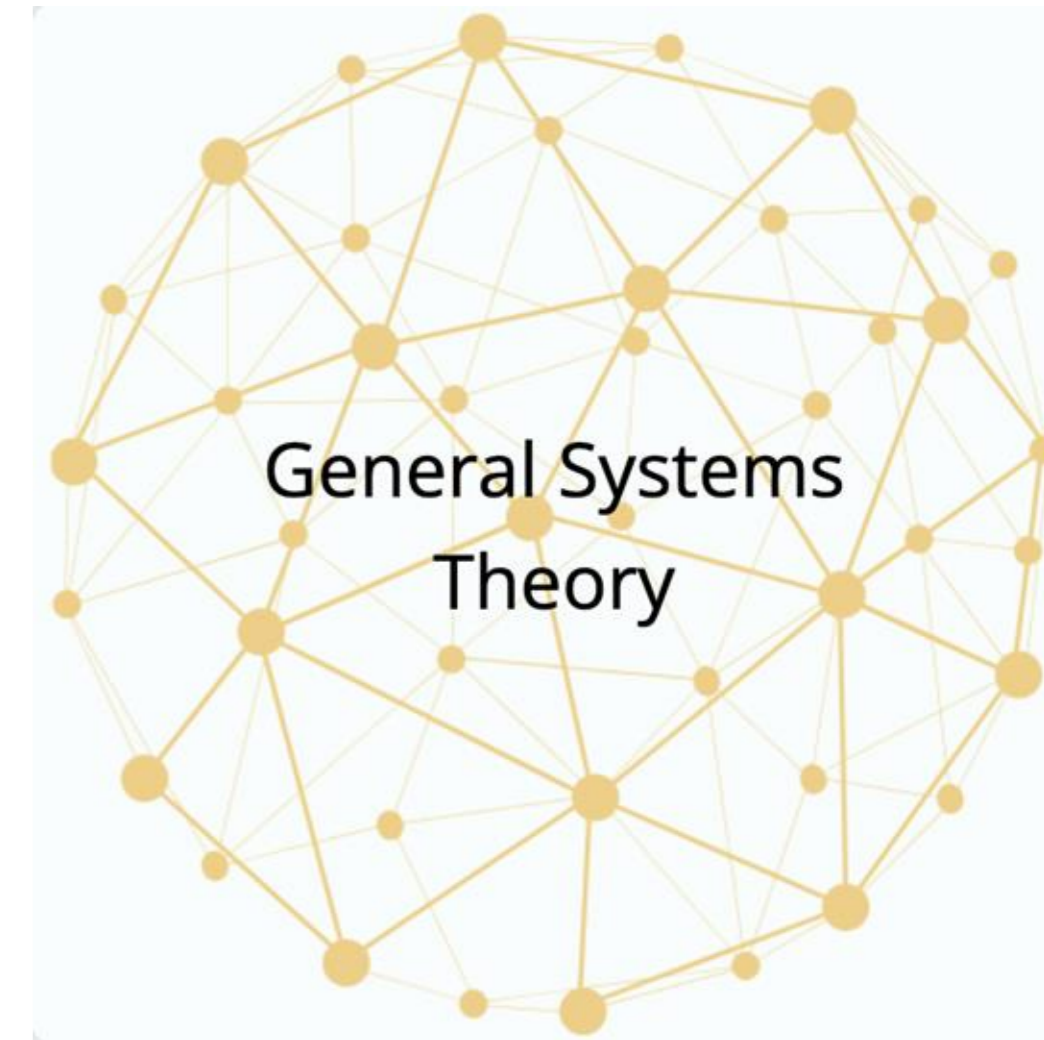
- Focus on ***different parts*** of the process of evolutionary development:
 - The maximization of power, the production of entropy, the persistence of biodiversity, the evolution of design...
- These principles provide an ability to predict, and in some cases, explain the phenomena in these parts of the process. But each principle only provides a partial picture of the evolutionary process.



The parable of the blind men and the elephant

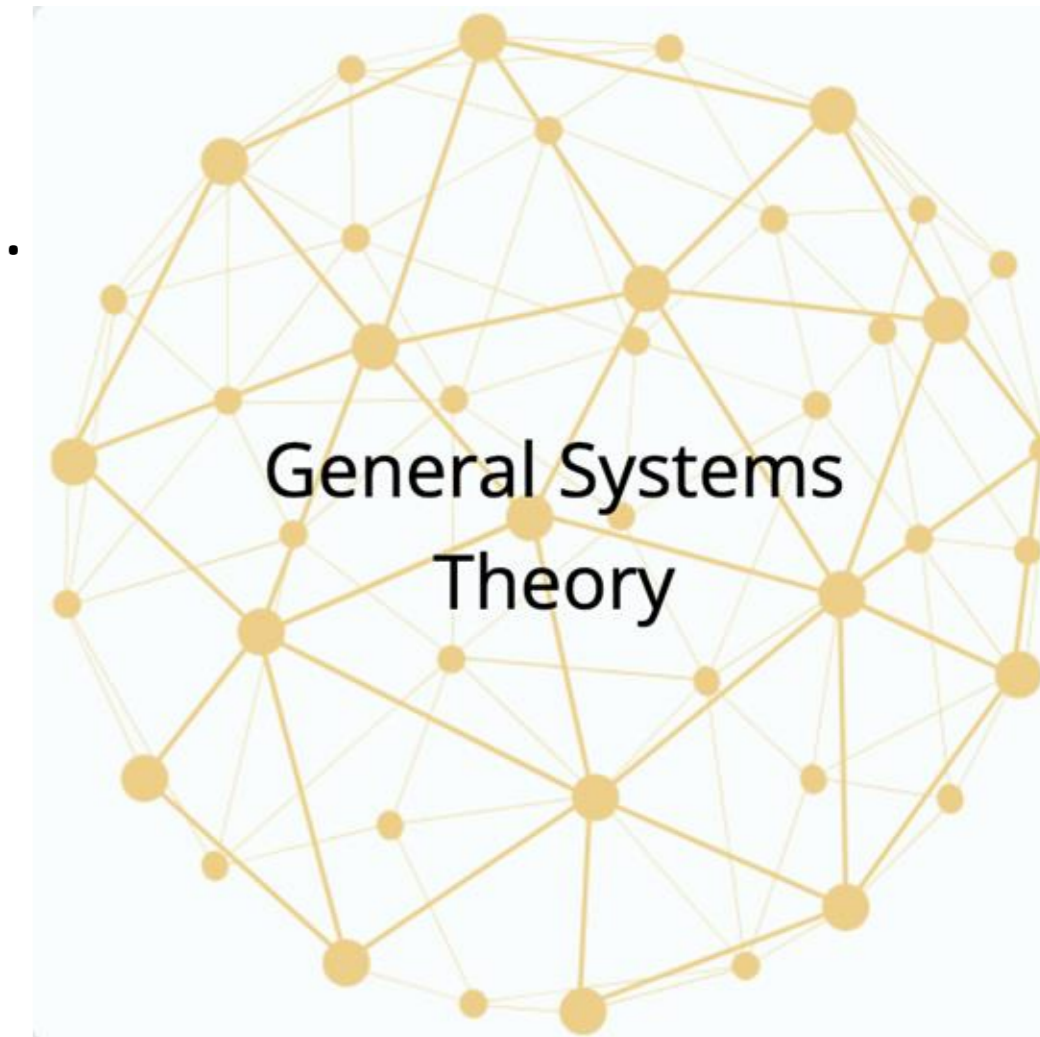
The Systems Approach

- Jorgensen describes H. T. Odum as a source for an optimality principle, but not as a source of a systems theory of optimality principles.
- However, Odum described optimality principles as “*special cases*” of the maximum power principle (1983a; 1983b): They align with the principle under certain conditions. They work together in a way that forms a pattern, which he describes using the maximum power principle.
 - He provides information throughout his work that supports this claim, which can be used to construct a systems theory of optimality principles.



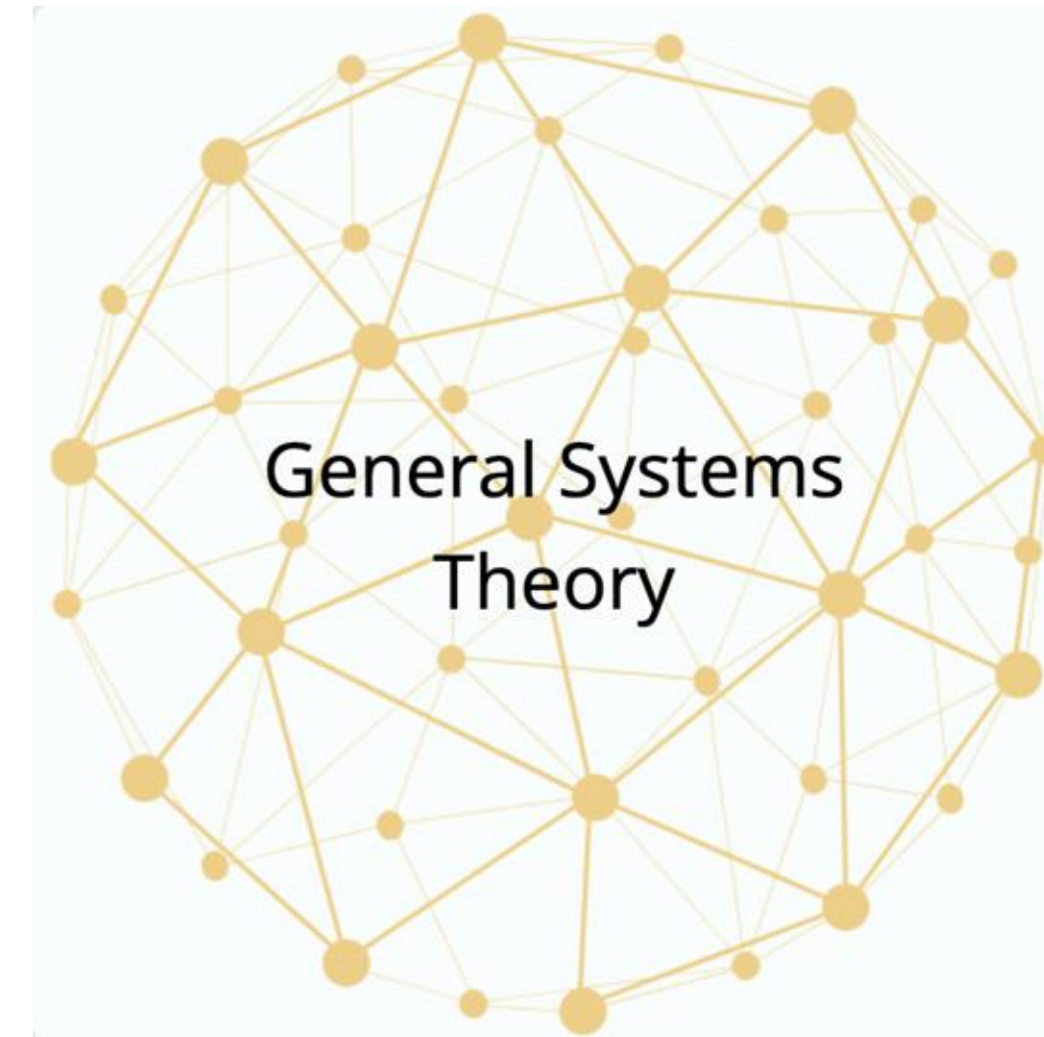
Our Book Project

1. Describes the systems theory of optimality principles H. T. Odum outlines in his work and compares it with those that have been developed since the 1990's.
2. Extends this systems approach to other principles that have not been considered.
 - The constructal law, the equal fitness paradigm, and the maximum efficiency principle, among others.
3. Clarifies the relation between the maximum power principle, the maximum entropy production principle and the principle of natural selection.
4. Addresses the strawman arguments that have been used against some of the optimality principles.



Our Presentation

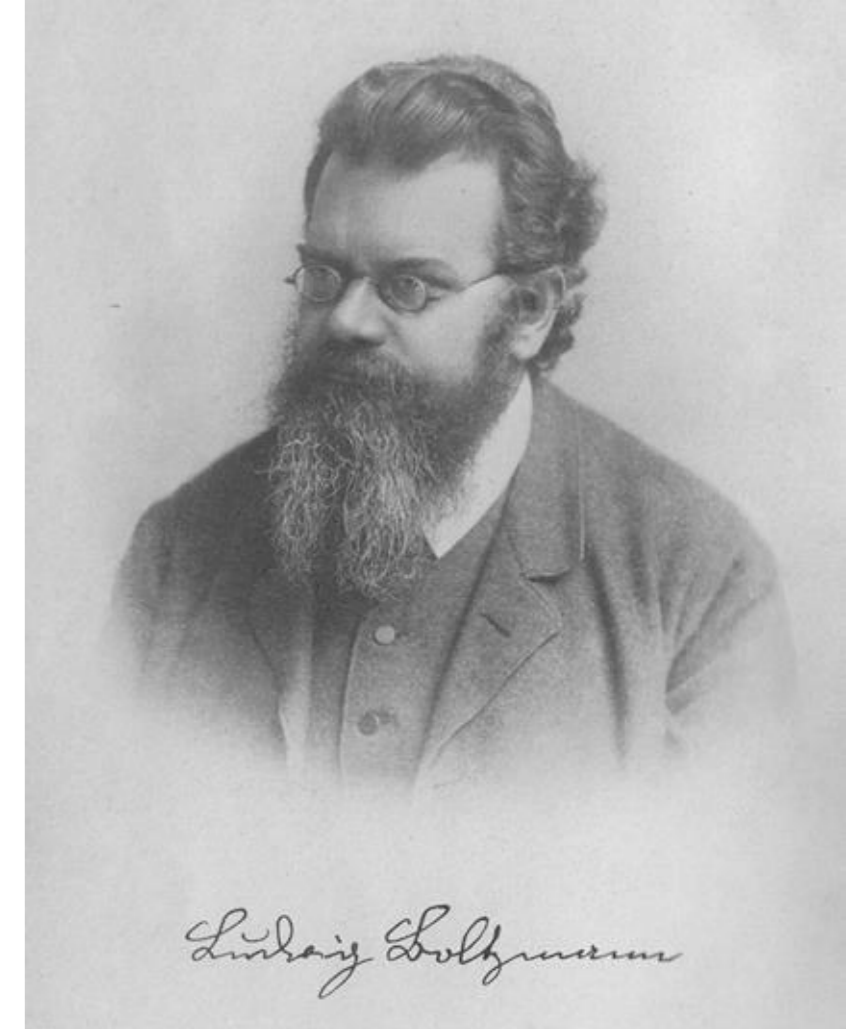
- This summary of the book project will focus primarily on explaining the relation between the two principles below, from Odum's perspective, and the perspective of the scientists that developed and use these principles.
 - the ***maximum power principle***
 - the ***maximum entropy production principle***
- In the course of this summary, we will also mention and discuss a number of the other optimality principles and how H. T. Odum believed they form a pattern that is described by the maximum power principle.



The "Thermodynamic School" of Evolutionary Theory (Fry 1995)

➤ Natural Selection in Thermodynamics

- Charles Darwin
 - The principle of natural selection.
- Ludwig Boltzmann
 - "The general struggle for existence of animal beings is therefore ... a struggle for [low] entropy, which becomes available through the transition of energy from the hot sun to the cold earth" (1886).



The Principle of Maximum Energy Flux (PMEF)

- Definition: “natural selection tends to make the energy flux through the system a maximum so far as compatible with the constraints to which the system is subject” (1922a).
- He noted that the reference to the “constraints to which the system is subject” “modifies” the meaning of the PMEF.
 - Organic systems that are more efficient have a selective advantage when the available energy is limited.
- PMEF applies to *all natural systems far from equilibrium*, both biotic and abiotic (1922b, cp. 1945).
- PMEF is discussed in terms of *available energy* (1922a).
 - Some contemporary scientists describe his work using the term **exergy** (Sciubba 2009, 2011), but Lotka did not distinguish between useful and unuseful forms of dissipation.



Alfred Lotka (1880-1949)

The Maximum Power Principle (MPP)

➤ Developed by H. T. Odum (and Richard Pinkerton) (1955), who attributed the principle to Alfred Lotka (1922).

- But Odum altered the MPP in substantive ways.

➤ ***Definition***

- “Lotka (1922) proposed a "law of maximum energy" for biological systems. He reasoned that what was most important to the survival of an organism was a large energetic output in the form of growth, reproduction, and maintenance ... Let us make the following postulate: Under the appropriate conditions, maximum power output is the criterion for the survival of many kinds of systems, both living and non-living” (1955).



H. T. Odum (1924-2002)

Similarities between the PMEF and the MPP

- Odum also believed the MPP applied “so far as compatible with the **constraints to which the system is subject**” (Lotka 1922a).
 - He argued that the optimum efficiency for maximizing power output increases as the available energy and resources decreases (1955, 2007).
 - Odum recognized that living systems have “special aspects” that affect the way the MPP applies to them (1983b).
- The MPP also applies to **all natural systems far from equilibrium**, both biotic and abiotic (Odum 2007; Lotka 1922b, cp. 1945).
- They both saw **Feedback Loops** contributing to evolutionary development (Lotka 1945; Odum & Odum 1976).



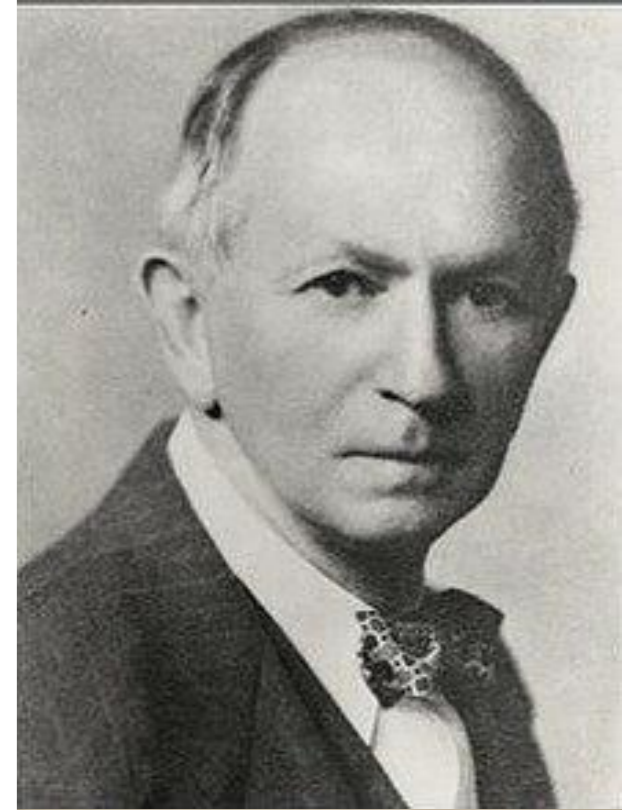
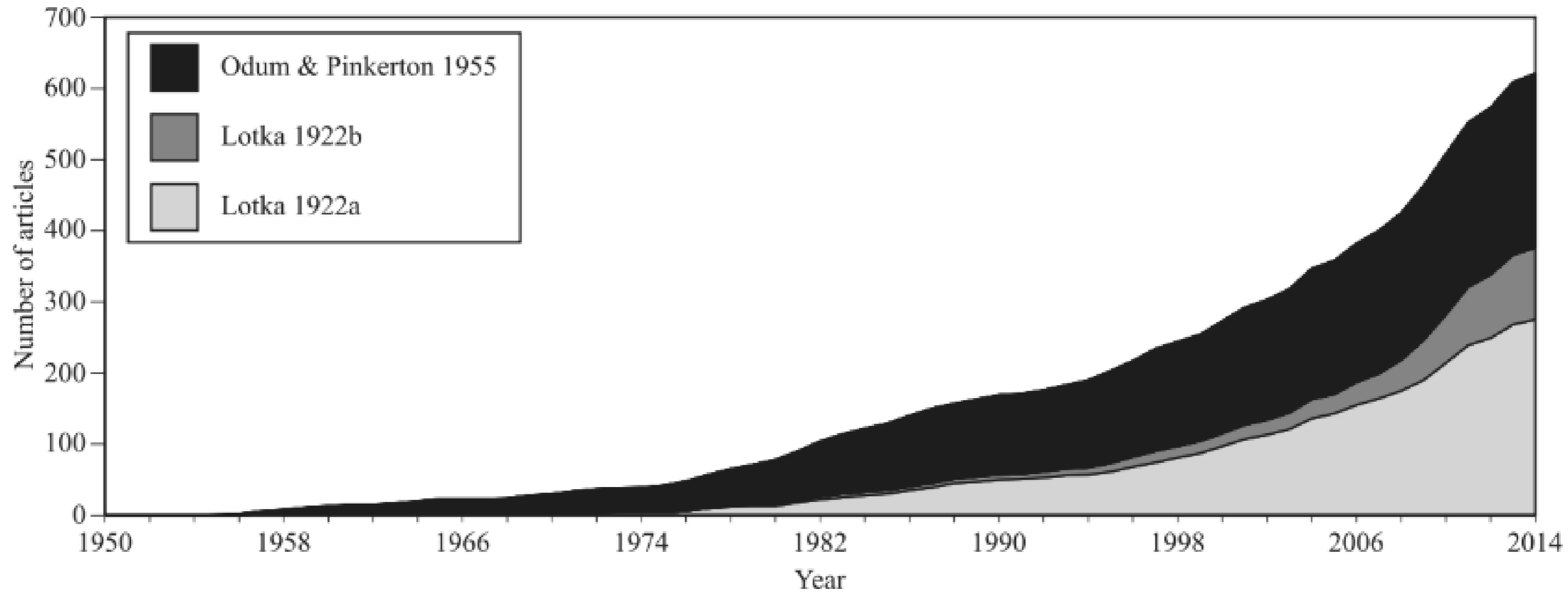
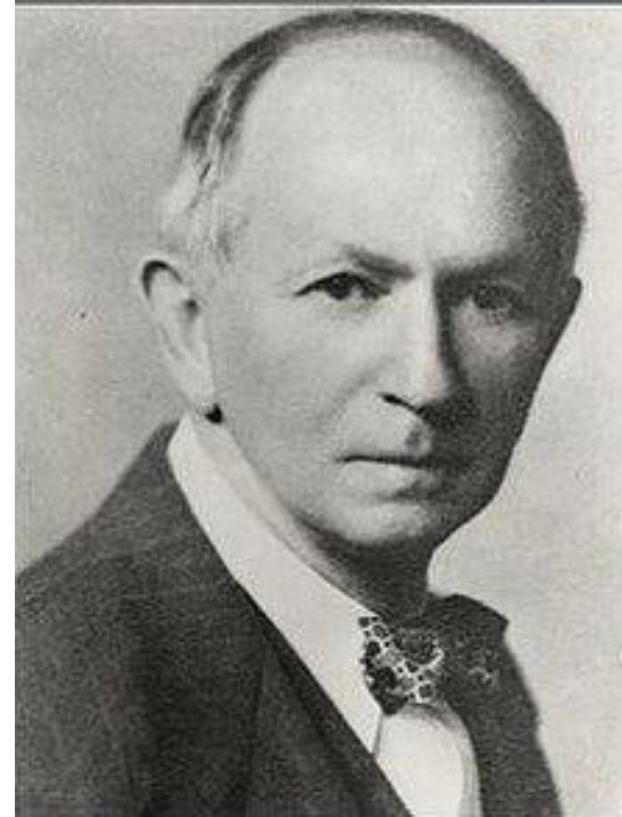


Figure 4. The cumulative number of publications that cite foundational maximum power production publications. From the 1950s to the 1970s, these papers were largely ignored; however, since the mid-1980s, all three of these papers have become increasingly recognized. These papers all follow similar temporal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

The Differences between the PMEF and the MPP

- Lotka focused on **available energy**; Odum describes the MPP in terms of energy that can be used in a **useful** manner.
- The PMEF focuses on the **flow of energy** through the system; the MPP focuses on useful **power output**.
- Odum and Pinkerton described how maximizing power entails a trade-off between the **Efficiency** and **Speed** of energy transformations (1955).



The Maximum Power Principle (MPP)



➤ Efficiency

- Odum writes, “Silvert said we used mechanical analogies to infer things about living systems. Incorrect; we used energetic formulations as the general case for which mechanical and living examples are special cases, each with special aspects” (1983b).
- See Silvert 1982, Sciubba 2011, and Glazier 2024.

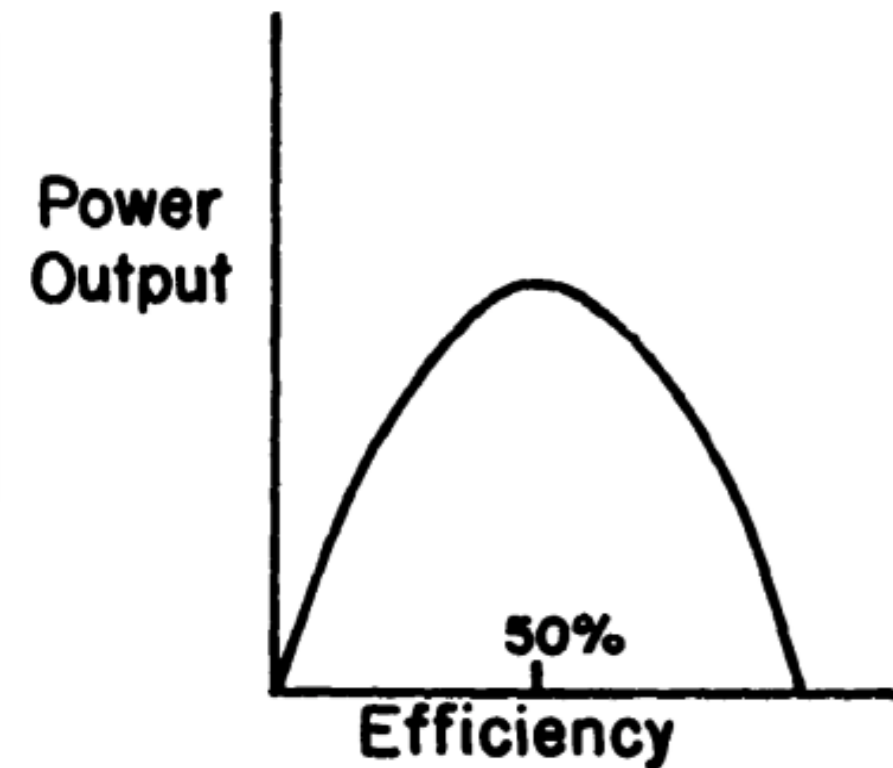


Fig. 2. Power output [of *Atwood's Machine*] is given as a function of efficiency for systems where there is no leakage (I) and the efficiency (E) is thus equal to the force ratio (R). (1955, p. 333)

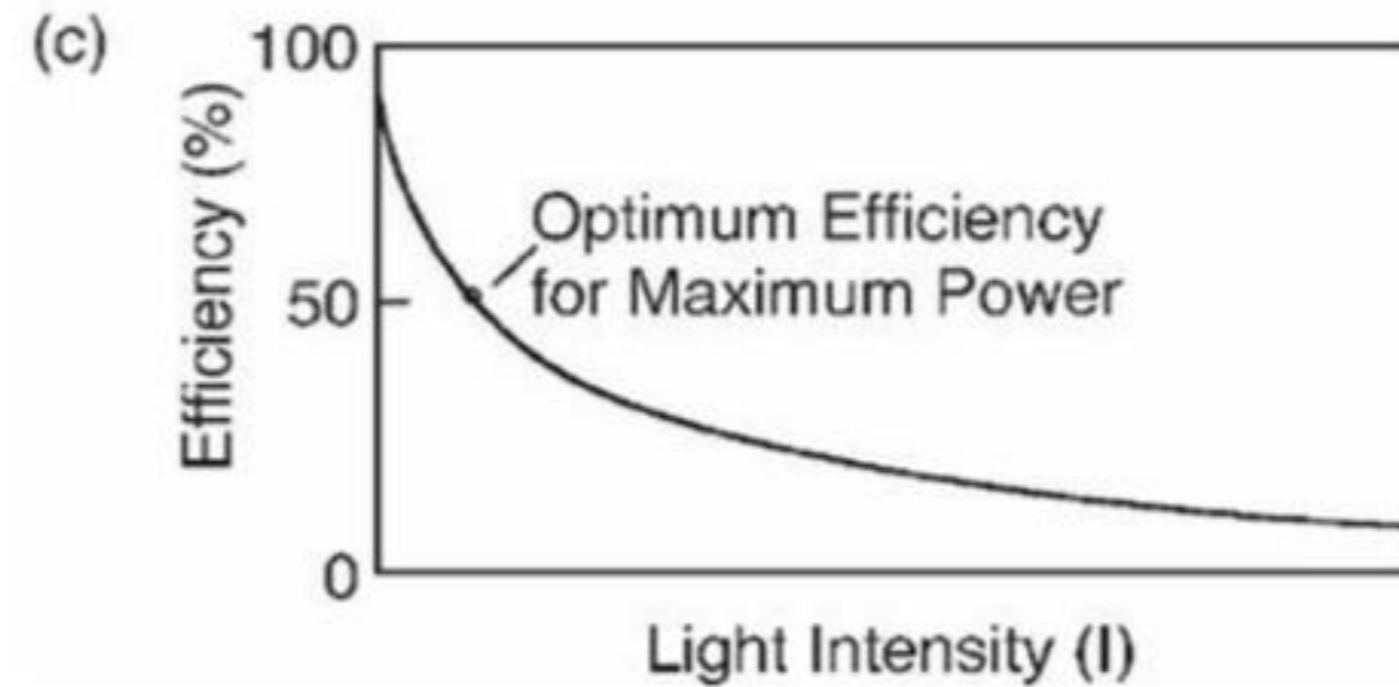


FIGURE 3.3(c) photosynthetic efficiency as a function of varying light intensity using equations in appendix fig. A4. (Odum, 2007, p. 40, Fig. 3.3(c))

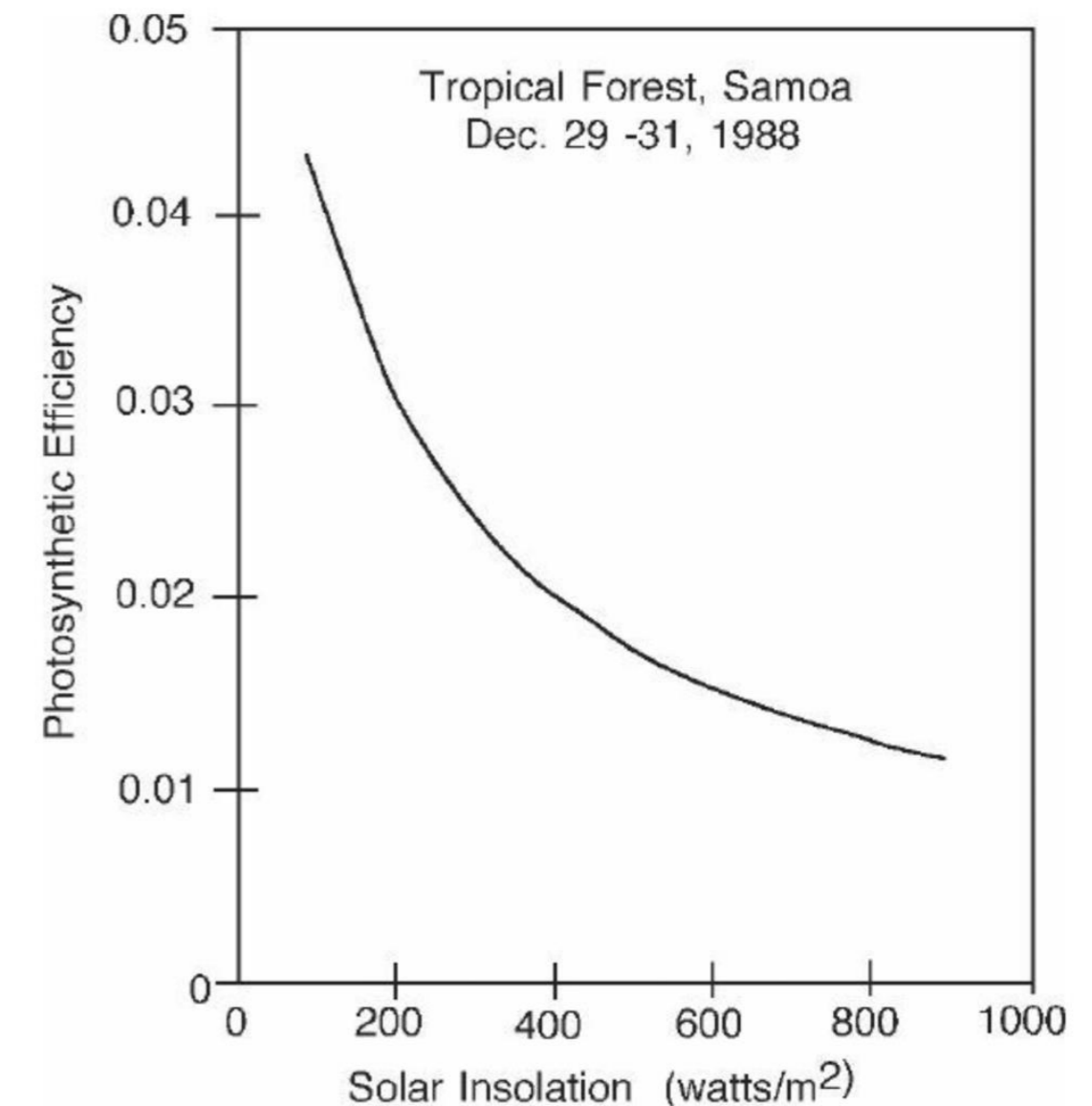


FIGURE 3.5 Efficiency of forest photosynthesis as a function of light intensity in a tropical forest in Samoa (Ryan 1990) (Odum 2007, p. 41).

Testing the Maximum Power Principle



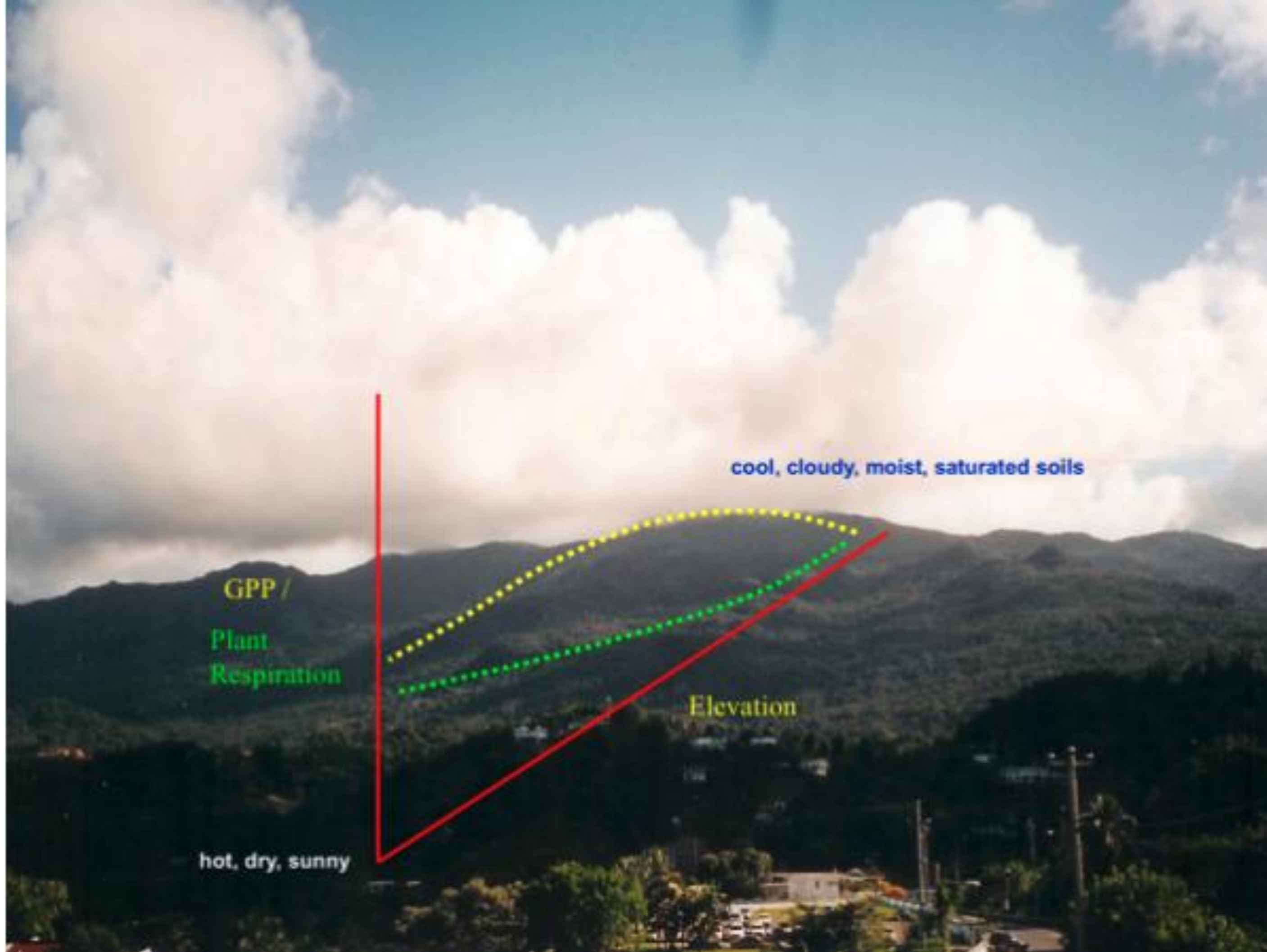




Fig. 7.15 How to access the upper leaves in a large tropical tree

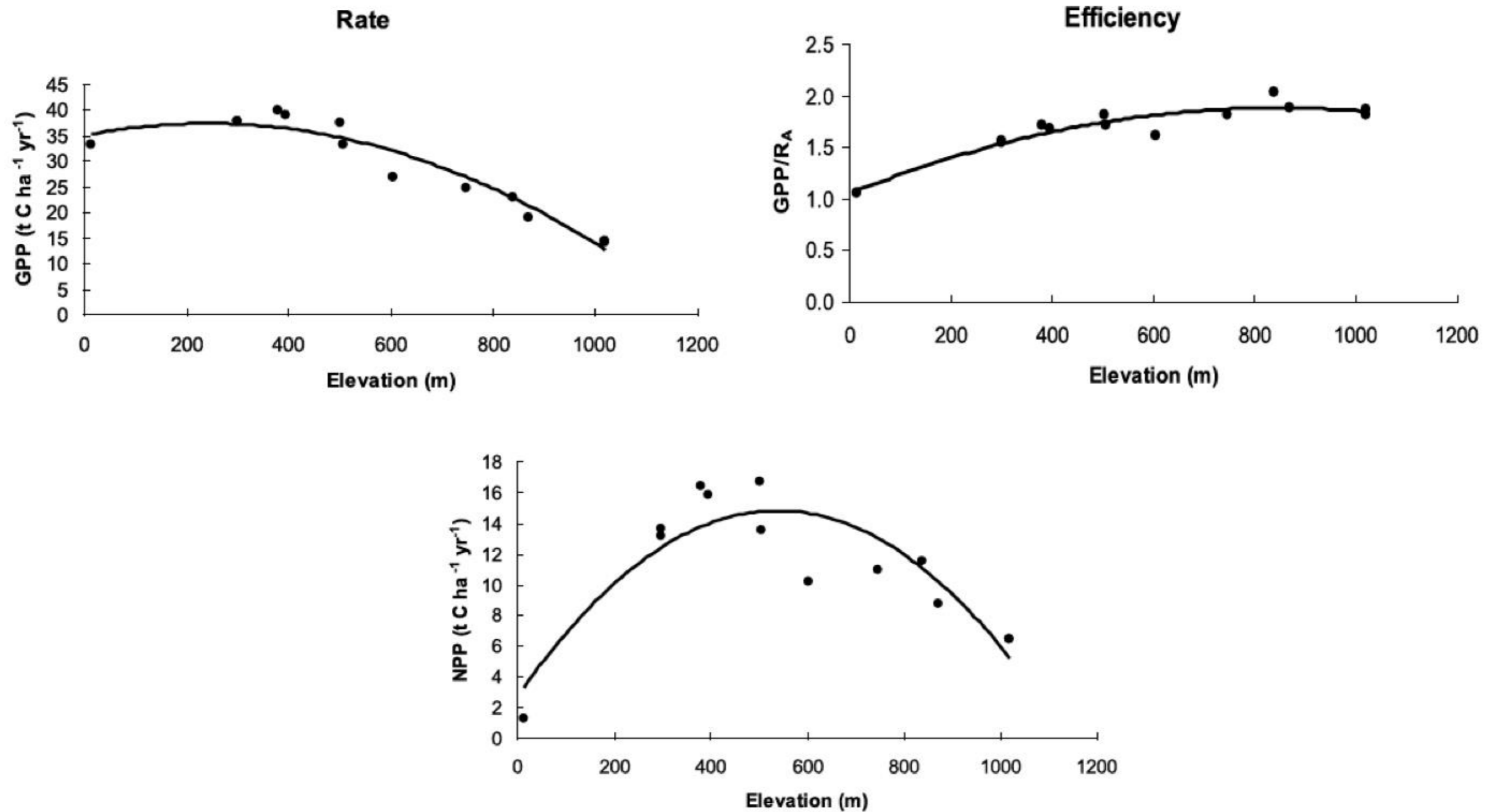
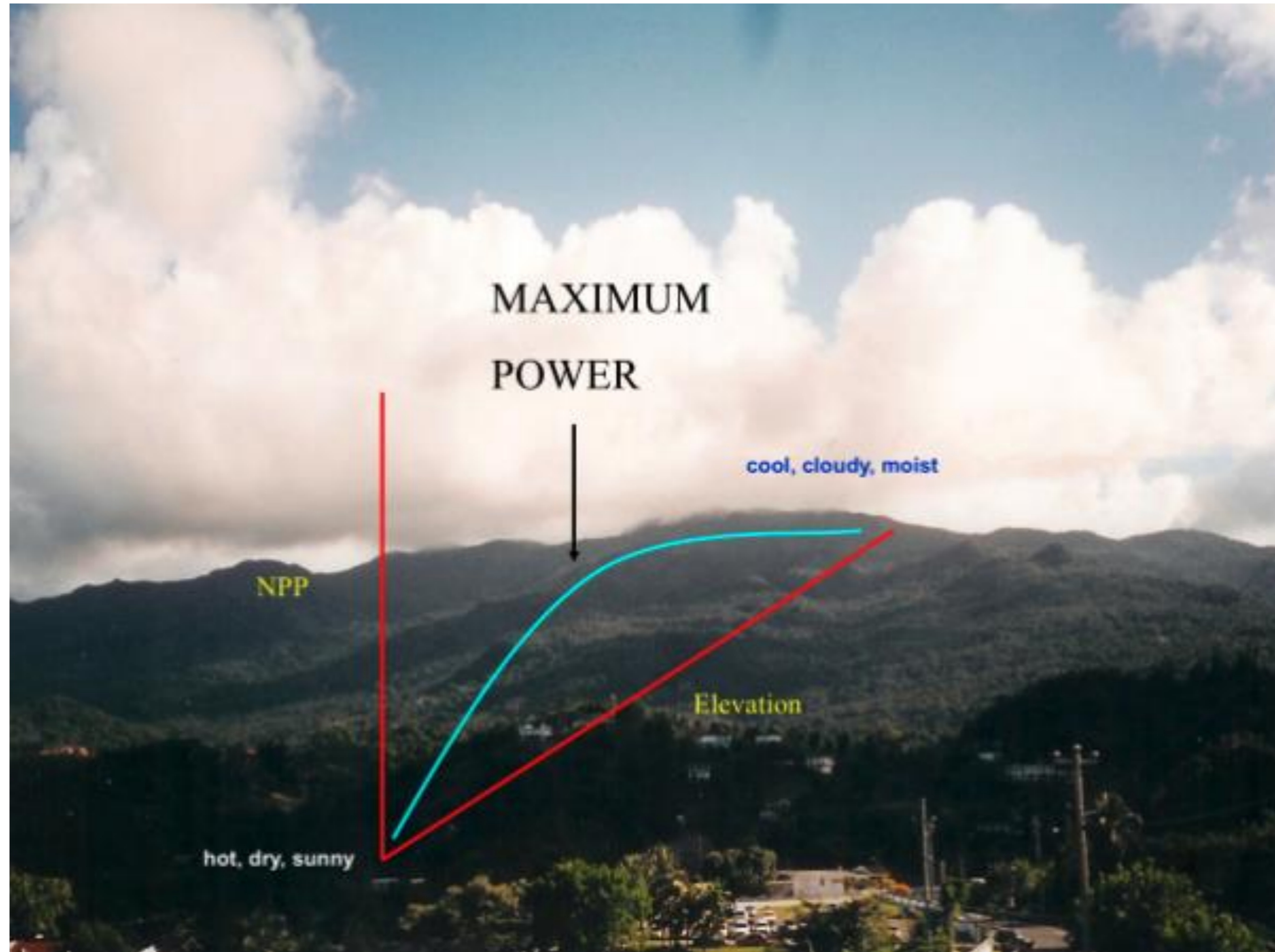


Fig. 5 Results of studies by Harris *et al.* that measured the gross photosynthesis and community respiration of a column of forest along a gradient of elevation in the Luquillo Forest, Puerto Rico. These data show a tradeoff of rate and efficiency of carbon capture, with the difference (net primary production) being maximum at an intermediate elevation, consistent with the maximum power hypothesis of Howard Odum. See [Hall and McWhirter \(2023\)](#).



The Maximum Power Principle (MPP)



➤ “Long Range Power”

- Odum describes the MPP maximizing “long range power” (1983b).
- “The maximum power principle explains why **early succession** minimizes diversity and **later succession** maximizes diversity” (2007, p. 56-57).
 - **Early succession** -- “The first priority of a system is to maximize energy intake, to cover the area with energy receivers quickly, with units adapted for most rapid growth.”
 - **Later succession** – “The second priority is to maximize efficiency in its energy processing. When there are no excess, unused resources to be found, a high diversity of cooperating units develops, with **better efficiency** and division of labor.” Maximizing diversity becomes more important than maximizing the production of biomass (1983b, 79).

Odum's Systems Theory of Thermodynamic Evolution: A Brief Summary



➤ **Early succession**

- The MPP will be more closely aligned with:
 - The maximum biomass principle (1983b, p. 79)
 - The maximum reproduction principle (2007, p. 56-57)
 - The maximum storage principle

➤ **Later succession**

- The MPP will be closely aligned with:
 - The maximum efficiency principle (2007, p. 56-57)
 - The maximum diversity principle (2007, p. 56-57)
 - The equal fitness paradigm

➤ **Near Equilibrium**

- The MPP will be closely aligned with:
 - The minimum entropy production principle (1983b, p. 79; 1982, p. 37)



Fig. 1 EROI in action. The trees along this forested road in Oregon keep their branches on the road side of trunks where there is enough light to support the metabolic requirements of the branches, but slough the branches off on the forested side. Photo by Hunter Tidwell-Prediletto.

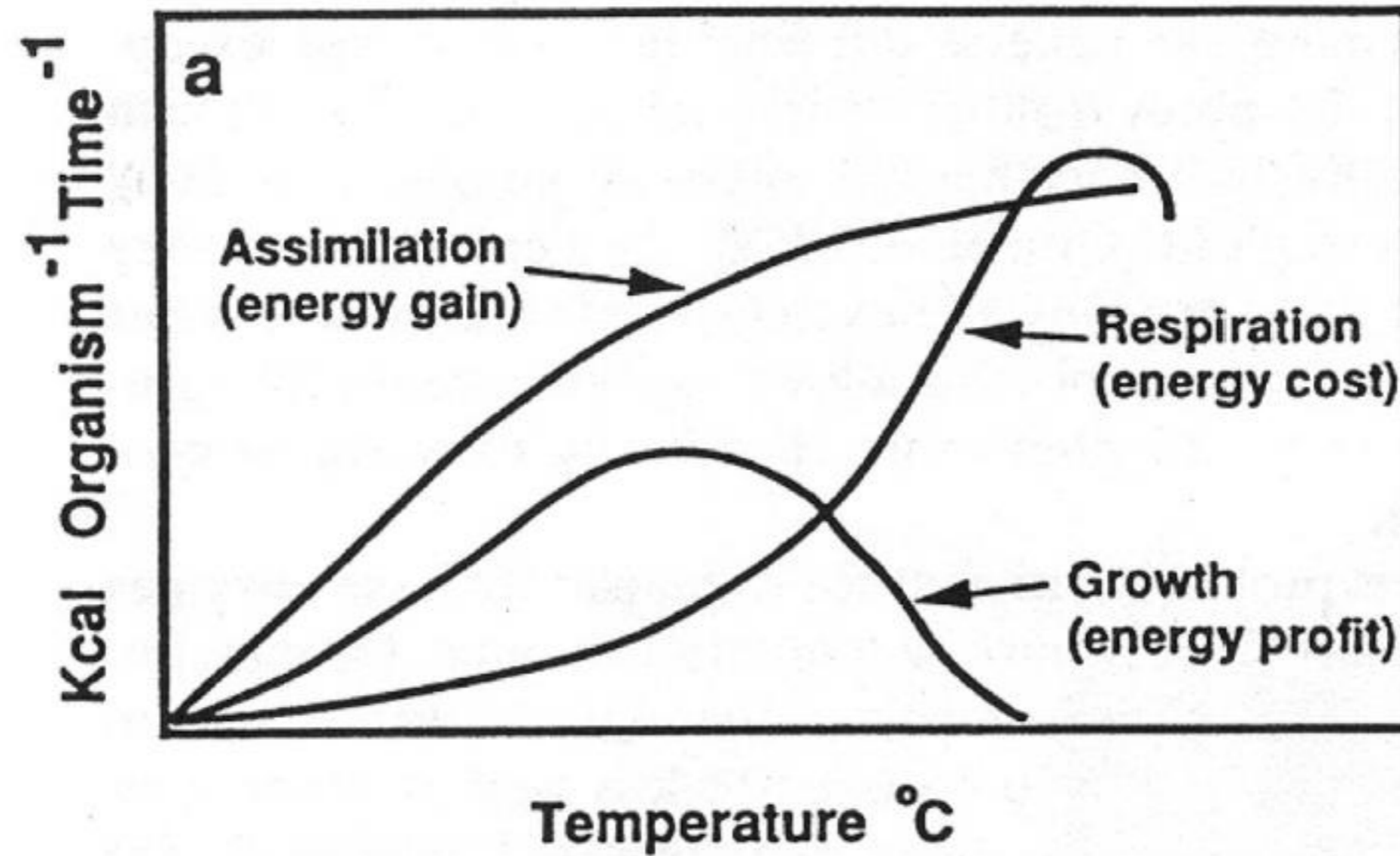


Fig. 2 Energy costs and gains, hence EROI, are often forced by physical conditions of the environment, organism size or other factors that are outside the control of an organism. In this depiction the growth of a cold-blooded organism, such as a tree or fish, is dependent upon the temperature of the environment. Optimal growth is normally found in average conditions where the fish is found. From [Hall *et al.* \(1992\)](#).

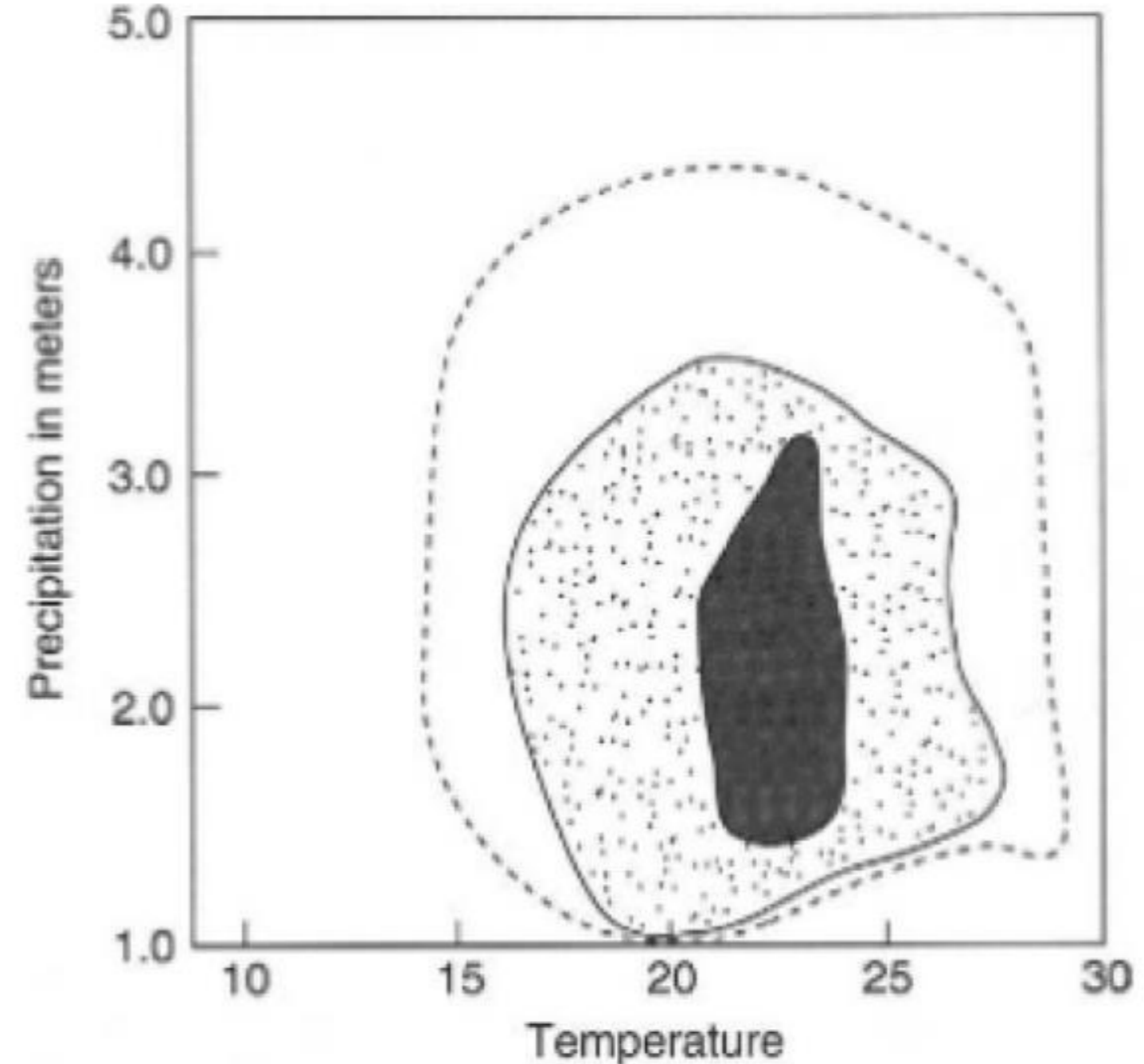
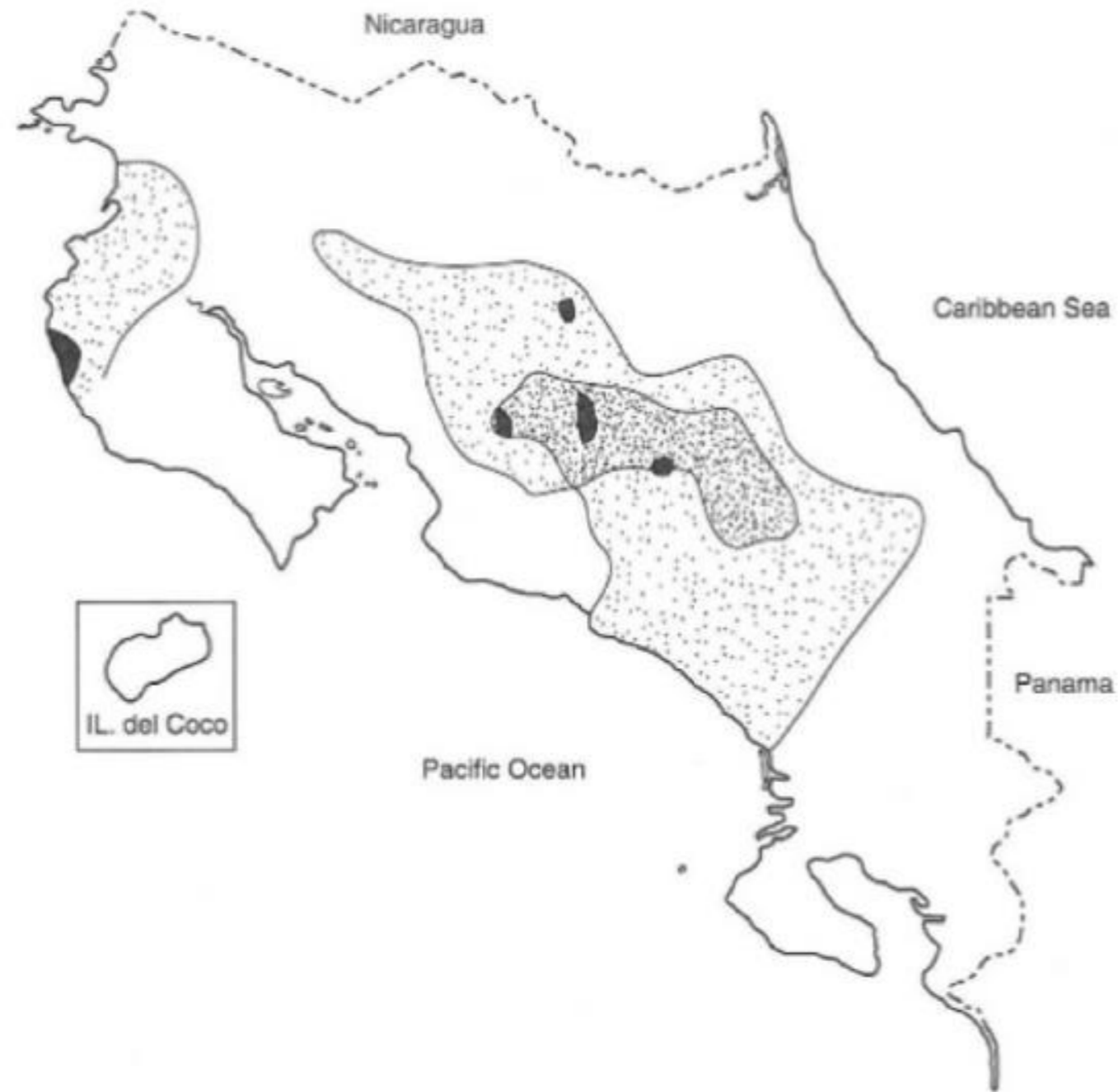


Fig. 4 Distribution of coffee productivity in Costa Rica as a function of (left) geographic space and (right) gradient space (mean annual temperatures and precipitation in meters). The dashed lines in the right figure are the limits of what conditions are available within Costa Rica. Black areas are where yields of at least 1.4 T/ha are found, stippled areas are where yields of 1–1.4 tons/ha are found, and blank areas yields are less than 1 ton per ha.

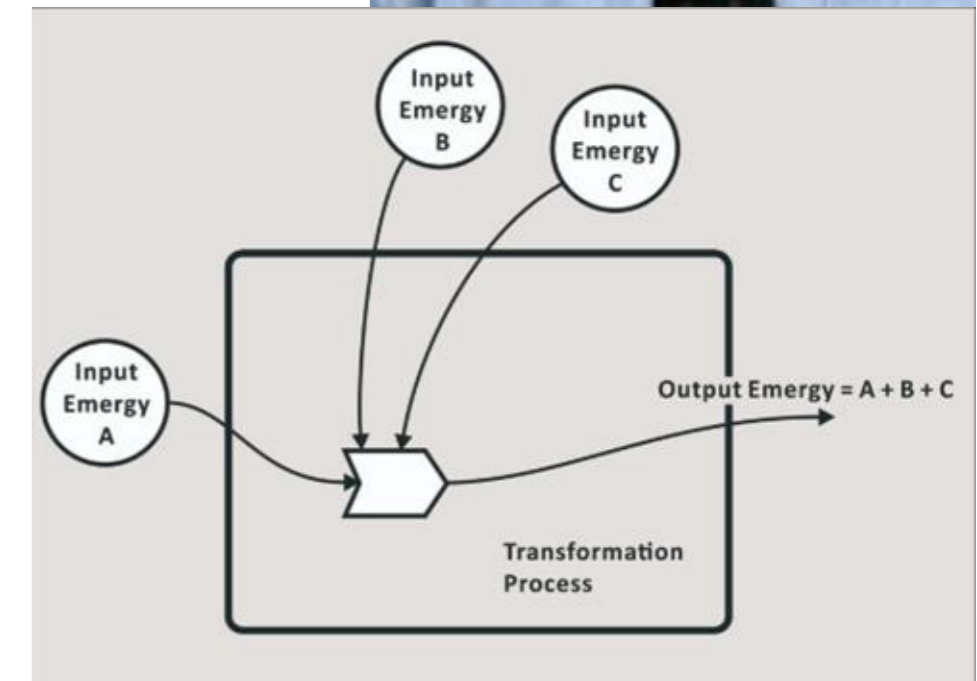
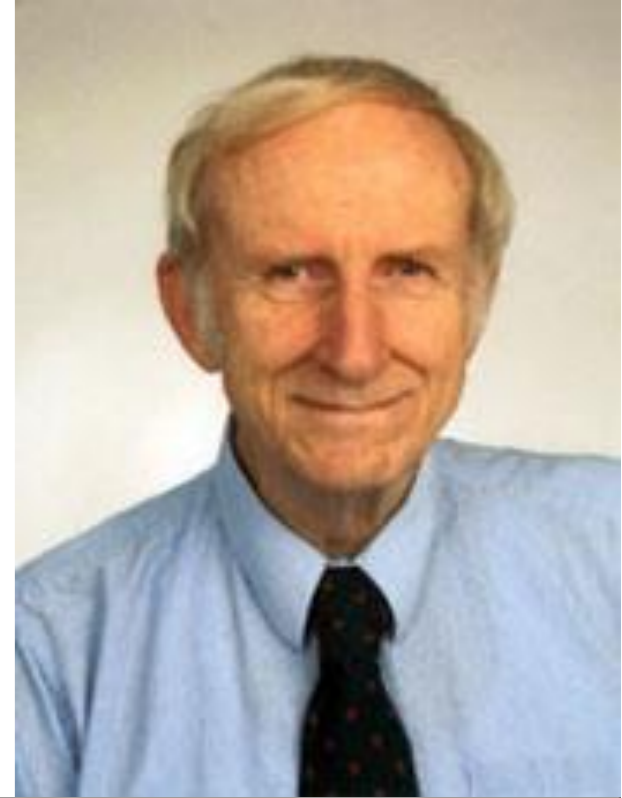
The Maximum Empower Principle (MEP)

➤ The Quality of Energy

- Forms of energy are not equal: solar energy is abundant but too dilute; fossil fuels are more efficient to use. Odum believed the quality of a form of energy could be measured by the amount of energy required to develop that form of energy.
- **Emergy** is the amount of energy used to develop a heat unit (Kcal or Joule) of a product or service.
- **Empower** is the flow rate of **emergy**.
- The **Maximum Empower Principle** holds that evolution maximizes empower.

➤ MEP and the MPP

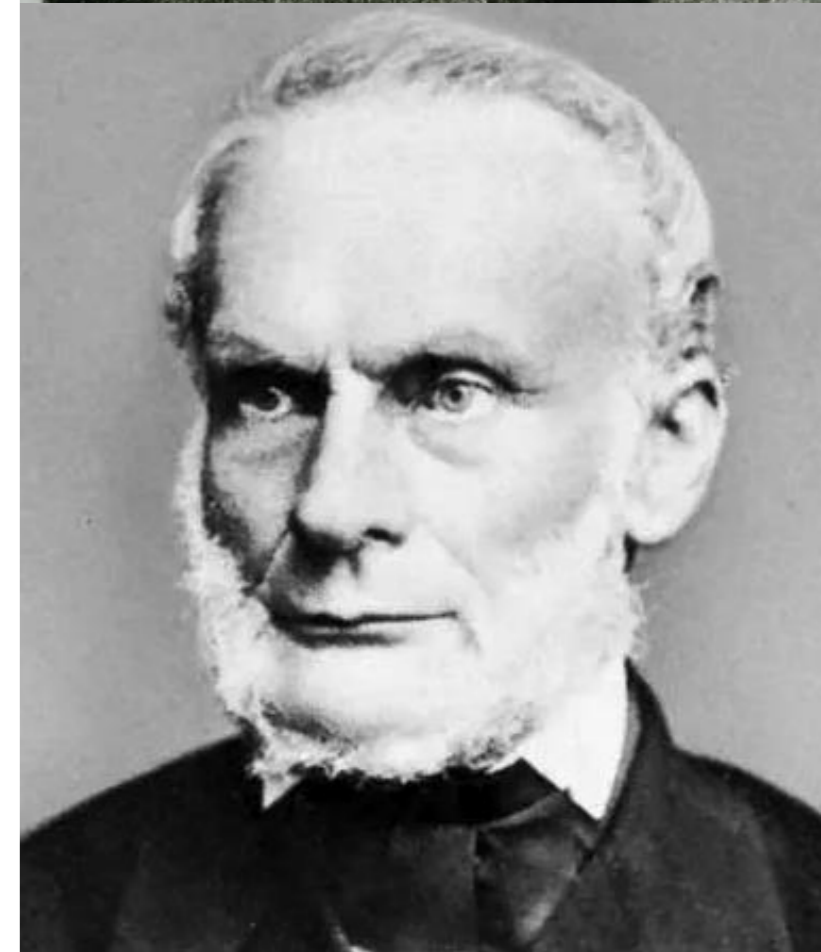
- Odum believed that “**maximizing empower also maximizes power**” because the use of higher quality sources of energy and reinforcing energy cycles increases the flux of energy through systems and the efficiency of their ability to transform lower-quality sources of energy (Odum 1995a).



The “*Thermodynamic School*” of Evolutionary Theory

➤ The “Second Law Division”

- Sadi Carnot (1796-1832)
 - Developed the first successful theory of the maximum efficiency of heat engines (1824).
- Rudolf Clausius (1822-1888)
 - Developed the second law of thermodynamics
“Heat can never pass from a colder to a warmer body without some other change, connected therewith, occurring at the same time.” (1856).
- The Maximum Entropy Production Principle
 - Hans Zielger, Garth Paltridge, Rod Swenson, Roderick Dewar, and Axel Kleidon.



The Maximum Entropy Production Principle (MEPP)

- Ziegler (1963), Paltridge (1975), Ulanowicz & Hannon (1987), Swenson (1989), Dewar (2003, 2005).
- “Systems increase entropy at the maximum rate available to them” (Morel & Fleck 2006).
- **Interdisciplinary**
 - Used in ecology, chemistry, biology (origin of life), sociology, earth systems science, and cosmology.
- **Entropy Near and Far from Equilibrium**
 - Dewar provides a proof of the MEPP for systems far from equilibrium (2003, 2005). Before 2003, entropy was only defined for systems near equilibrium.
- Entropy is **maximized as an average over time** (Vallino 2010), not instantaneously.



The Maximum Entropy Production Principle (MEPP) -- Published Papers (Chapman et al. 2016)

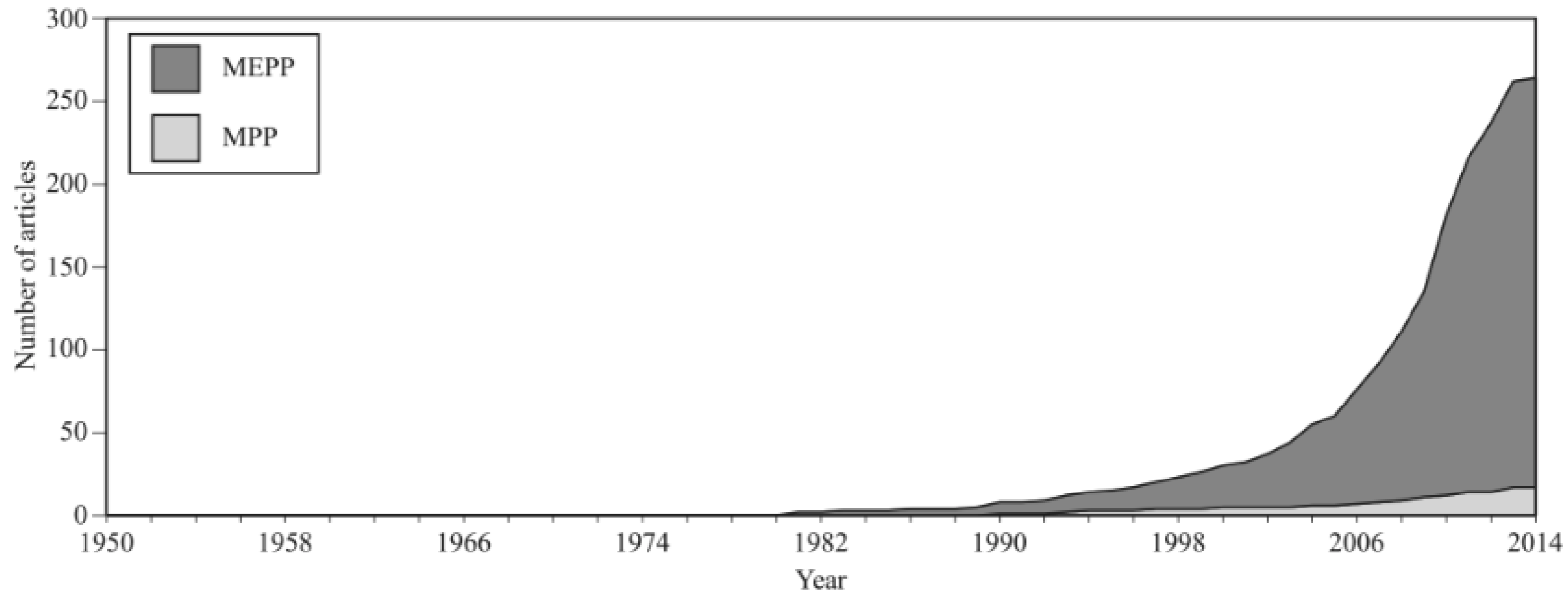
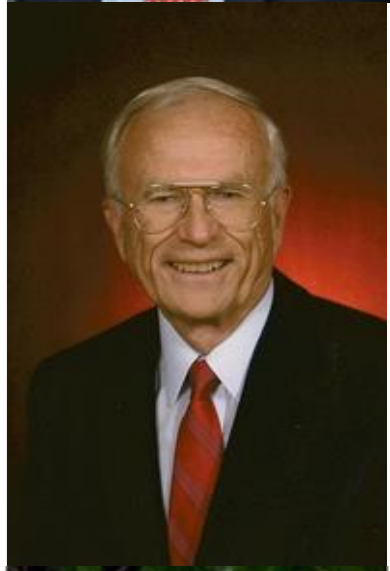


Figure 2. Maximum entropy production principle (MEPP) and maximum power production (MPP) cumulative number of published papers. Since the early 2000s, there has been an exponential increase in the number of articles that discuss the MEPP and to a lesser extent the MPP.



The Relation Between the MEPP and the MPP

- Power measures the rate at which work is done ($P = W/T$); when work is done, energy is expended; when energy is expended, entropy is produced.
 - **Power is therefore fundamentally related to the production of entropy.**
- The MEPP and the MPP do not describe two different processes of evolutionary development; they provide **descriptions of two different parts of the same process.**
 - Odum believed that the MEPP “is another way of referring” to the MPP when systems are **far from equilibrium** (1983b).
 - Kleidon et al. write, “the proposed principle of maximum entropy production (MEP), ... states that thermodynamic processes far from thermodynamic equilibrium will adapt to steady states at which they dissipate energy and produce entropy at the maximum possible rate” (2010).
 - The maximization of dissipation and entropy production are included together.



Axel Kleidon
Max Planck Institute

*They describe two different parts **of the same process***

- Both focus on “long range” maximization. (Vallino 2010; Odum 1983b)
 - This fact brings these two principles closer. The MEPP does not distinguish between useful and unuseful (e.g., low grade heat) entropy production, but it does distinguish between entropy production that maximizes future entropy production and entropy production that does not do this.
- Both involve the same trade-off between the speed and efficiency of energy transformations.
 - It is implied by Odum’s and Pinkerton’s work on the MPP and Odum’s description of the MEPP as being “another way of referring” to the MPP when systems are ***far from equilibrium*** (1983b).



Axel Kleidon
Max Planck Institute

They describe two different aspects of the same process (Chapman et al. 2016)

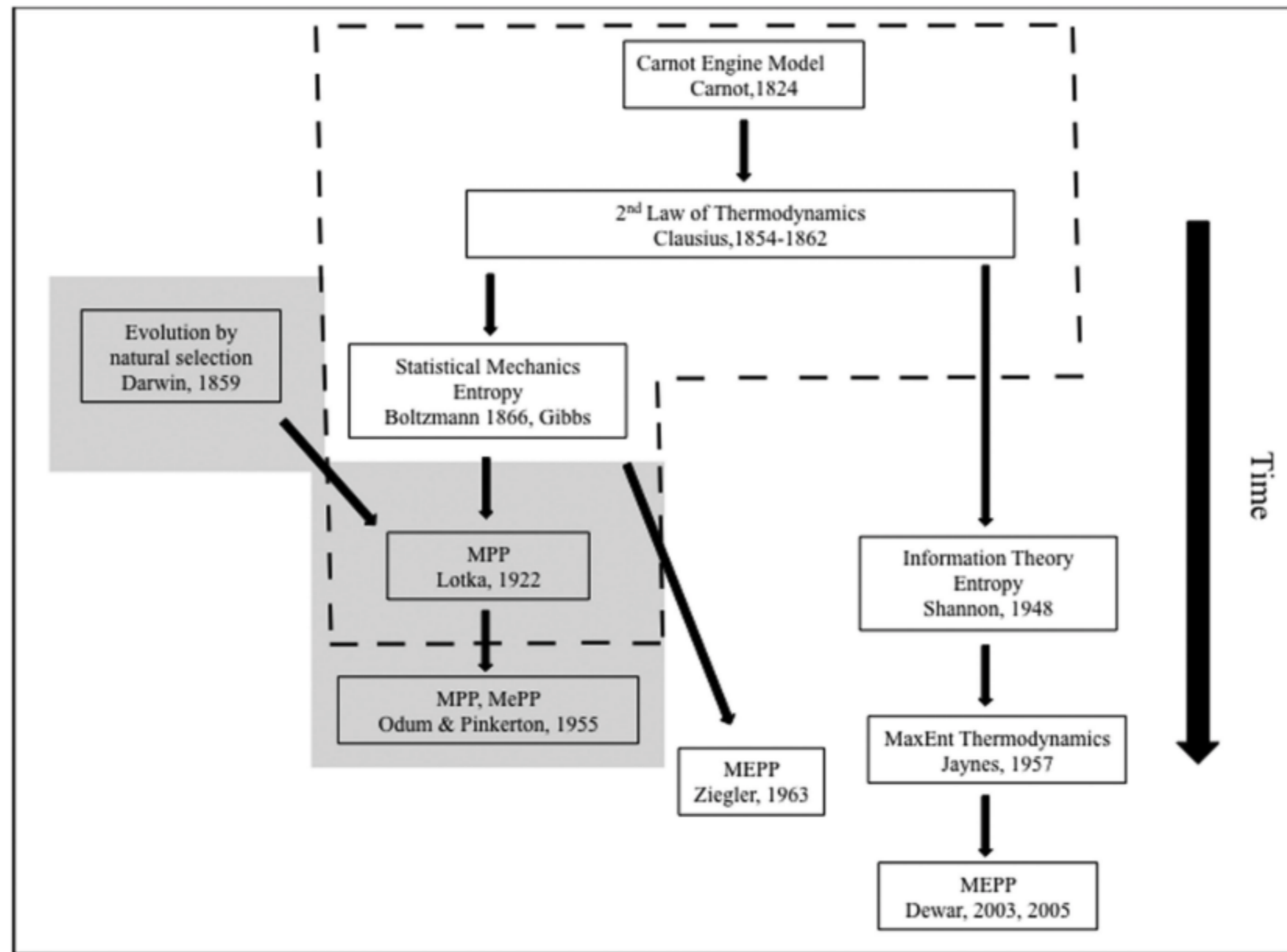
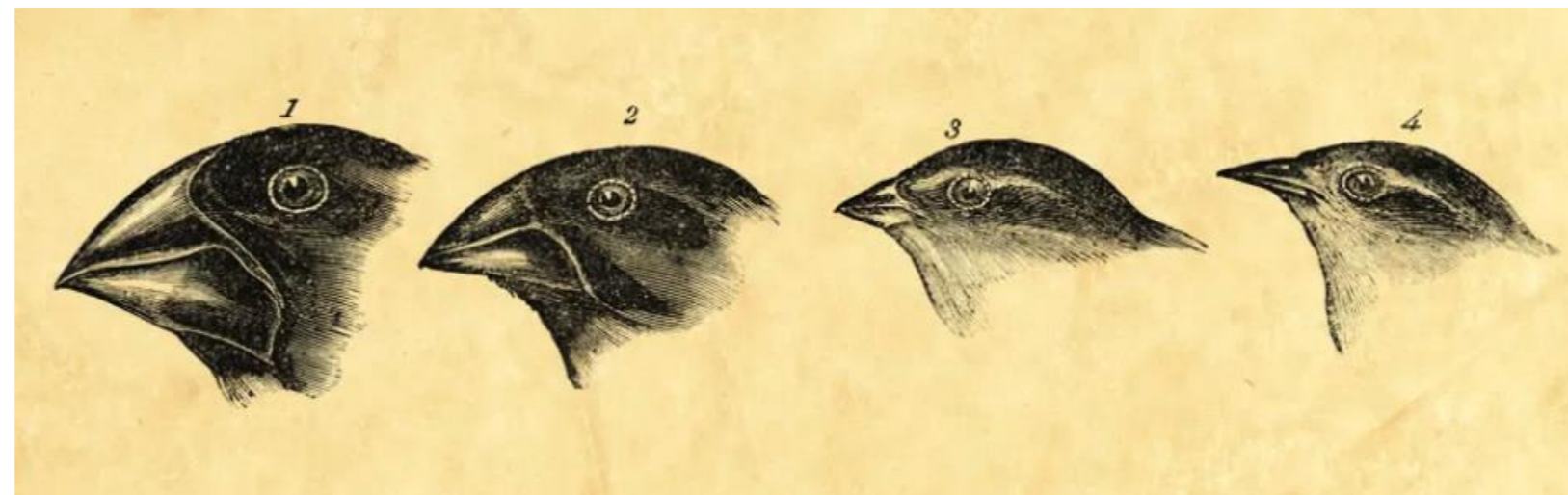


Figure 1. A conceptual map of the evolution and origin of several optimality principles in biology, physics, and chemistry. The MPP and the MEPP both evolved from the Second Law of Thermodynamics. The dashed line represents theoretical developments prior to the introduction of the nonequilibrium thermodynamics 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.

They describe two different aspects of the same process

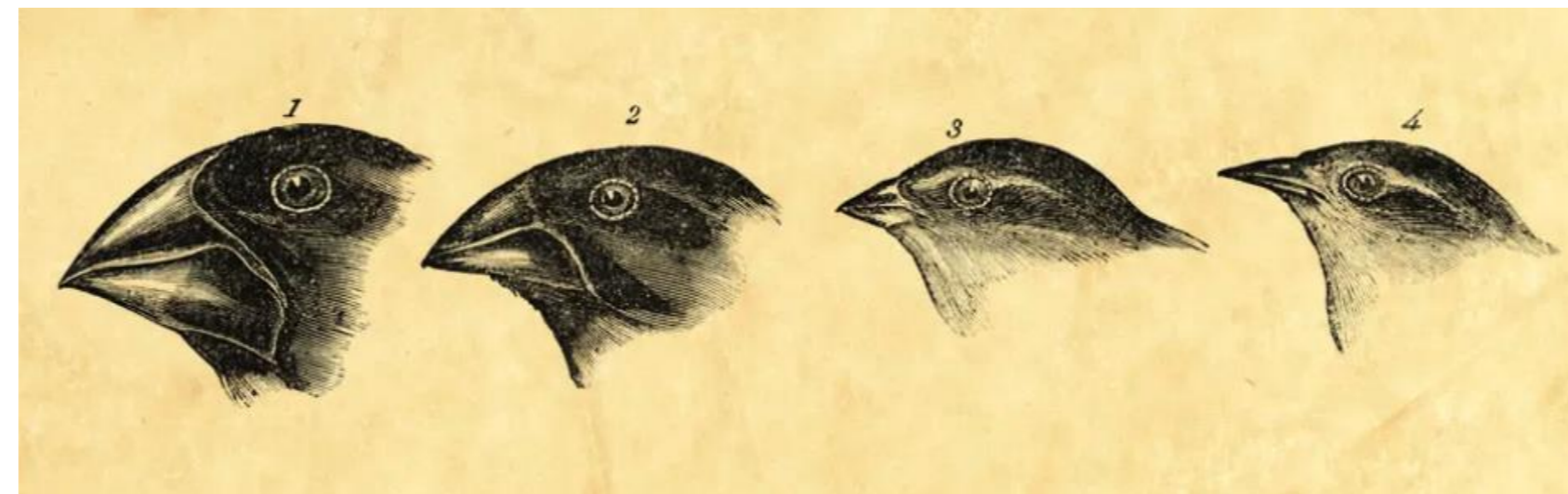
- The MPP describes the maximization of useful power output.
 - This output is defined as being in the form of “growth, reproduction, and maintenance.”
 - ***The MPP is selected directly by natural selection.***
 - Kleidon writes, “after all, it would seem indisputable that performing work is of central importance for driving dynamics” (2023).



They describe two different aspects of the same process

$$\Delta S \geq 0$$

- The MEPP is defined in terms of the maximization of the production of entropy.
 - The production of entropy does not have a direct impact on the processes that affect natural selection, like “growth, reproduction, and maintenance.”
 - MEPP is selected necessarily, but *indirectly*, because of its fundamental relation to power.
 - Some scientists from the “second law division” see this distinction as being arbitrary or unimportant.
 - Many scientists from the “natural selection division” insist that it is important.



They describe two different aspects of the same process

$$\Delta S \geq 0$$

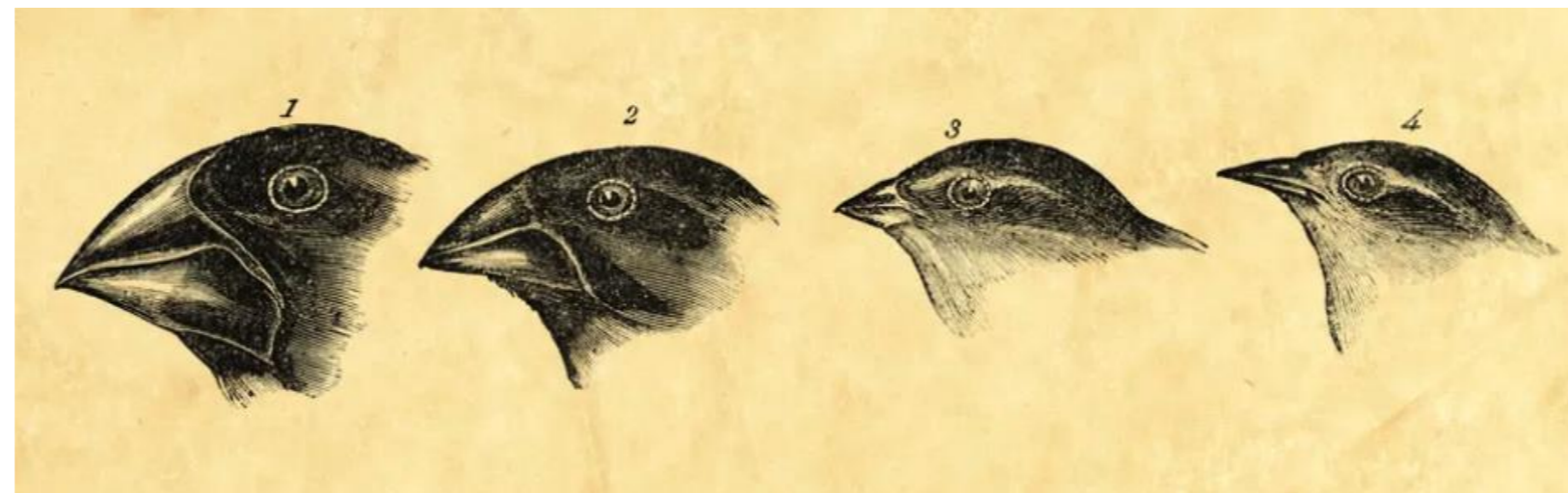
- Schneider and Kay (and *Jorgensen*) argued that natural systems develop in ways that “degrade gradients” to reach a “state of equilibrium” (Schneider and Kay 1994; Jorgensen 1997).
 - Their language is based on an analysis of systems near equilibrium (the Bernard cell) rather than systems far from equilibrium, like life.
 - ***Their view does not follow from the principle of natural selection.***
 - Here we see the tension between the ***natural selection*** and ***second law*** divisions of the thermodynamic school of evolution.
 - Jorgensen writes, “the open question is, however, whether life by Darwin’s theory gives survival...higher priority than reducing imposed gradients” (1997, 339).

They describe two different aspects of the same process

- Wicken is described by Schneider as arguing that the “**second law**” **provides the “go” of life**, “giving life its direction and reason for being” (2005, 105).
- However, Wicken actually writes that “thermodynamics is above all the science of spontaneous process, the ‘go’ of things” (1987, 5). “**Dissipation is the driving force** of the universe’s building up or integrative tendency. **Entropic dissipation propels evolutionary structuring**; nature’s forces give it form” (1987, 72). The **MPP** describes the **maximization** of this **entropic dissipation**.
- For scientists in the natural selection division, arguing the second law provides the “go” of life is like arguing that the vapor trails planes leave behind propel them forward.



Jeffrey S. Wicken, Professor of Chemistry, Penn State University 1942-2002



They describe two different aspects of the same process

$$\Delta S \geq 0$$

- The MEPP describes the maximization of the production of entropy.
 - Martyushev and Seleznev suggest the MEPP can be viewed as a ***corollary of the second law*** (2006).
 - Dewar develops a version of the MEPP that he considers to be ***an extension of the second law to non-equilibrium systems*** (2003).
 - Kleidon et al. describe the different versions of the MEPP as ***being “motivated” by the “second law”*** (2010).
- ***The MEPP illustrates how the evolution of natural systems is consistent with the second law.***

They describe two different aspects of the same process



➤ ***Information-based MEPP***

- Is an inference procedure based on Shannon information theory which holds that if predictions maximize the entropy of information, it reduces the risk of surprise (Kleidon & Dyke 2010).
- Using the MEPP, both thermodynamic and information-based, ***provides accurate predictions of the evolution of natural systems.***

The maximum power and entropy principle

- **Hans Ziegler initially proposed a link between a maximum entropy production principle and a maximum dissipation principle** (1963, 1968, 1970, 1972, 1983; Moroz 2008).
- This principle can be defined in the same way that Kleidon et al. define the MEPP: “thermodynamic processes far from thermodynamic equilibrium will adapt to steady states at which they dissipate energy and produce entropy at the maximum possible rate” (2010).
- **Dewar et al. established a “general link”** between the MEPP and Ziegler’s maximum dissipation principle that holds for “systems arbitrarily far from equilibrium” (2014).
- This combined principle has the ability to explain how the maximization of power directly impacts evolutionary processes, and how these processes are consistent with the second law.



Hans Ziegler
(1911-1999)

Studies of the MPP at the Ecosystem Scale (Chapman et al. 2016)

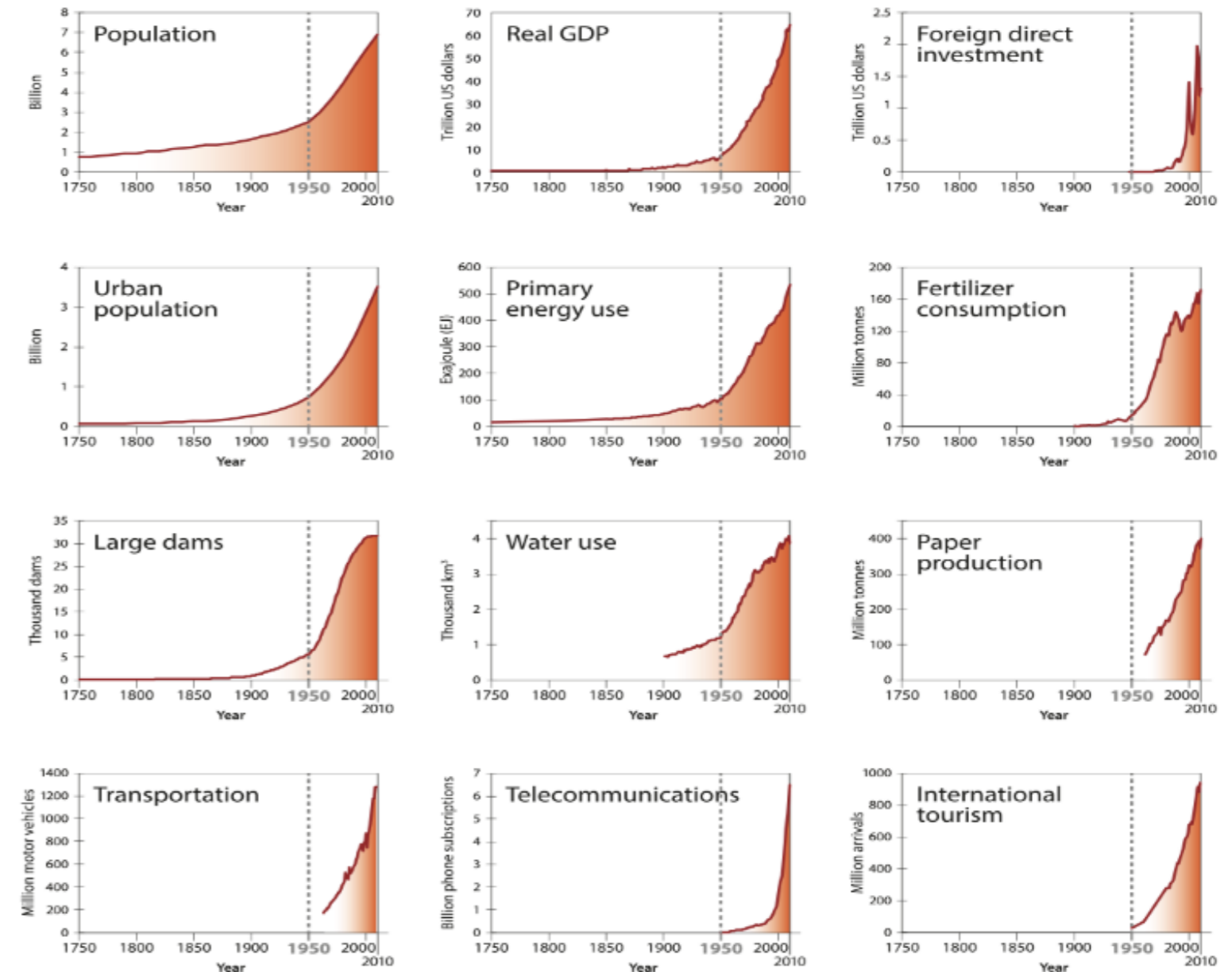
1. The MPP has been applied to studies that used models to optimize exergy relative to the effects on planktonic and zooplankton body size in aquatic ecosystems (Ray et al. 2001).
2. Used to constrain hydrological conceptual models (Westhoff and Zehe 2013).
3. Used to model the role of exotic species ecosystem self-organization (Campbell et al. 2009).
4. Applied to studies that simulated the role of the MPP in self-organizing forest plantation ecosystems (Li et al. 2013).
5. The MPP has been used to predict the outcomes of competitive exclusion experiments (DeLong 2008).
6. To indicate benthic ecosystem recovery following a disturbance (Libralato et al. 2006).
7. To examine microcosm ecosystem self-regulation using pH to control photoperiod (Cai et al. 2006).
8. To model the ecosystem organization of energy flows and storage (Fath et al. 2004).
9. It has been used in simulations of ecosystem responses to resource pulses (Lee 2014).
10. It has been used to predict the leaf area index in forests at different elevations (Hall et al. 2013).

Evidence that is consistent with the MPP and the MEPP

➤ Empirical evidence from other disciplines.

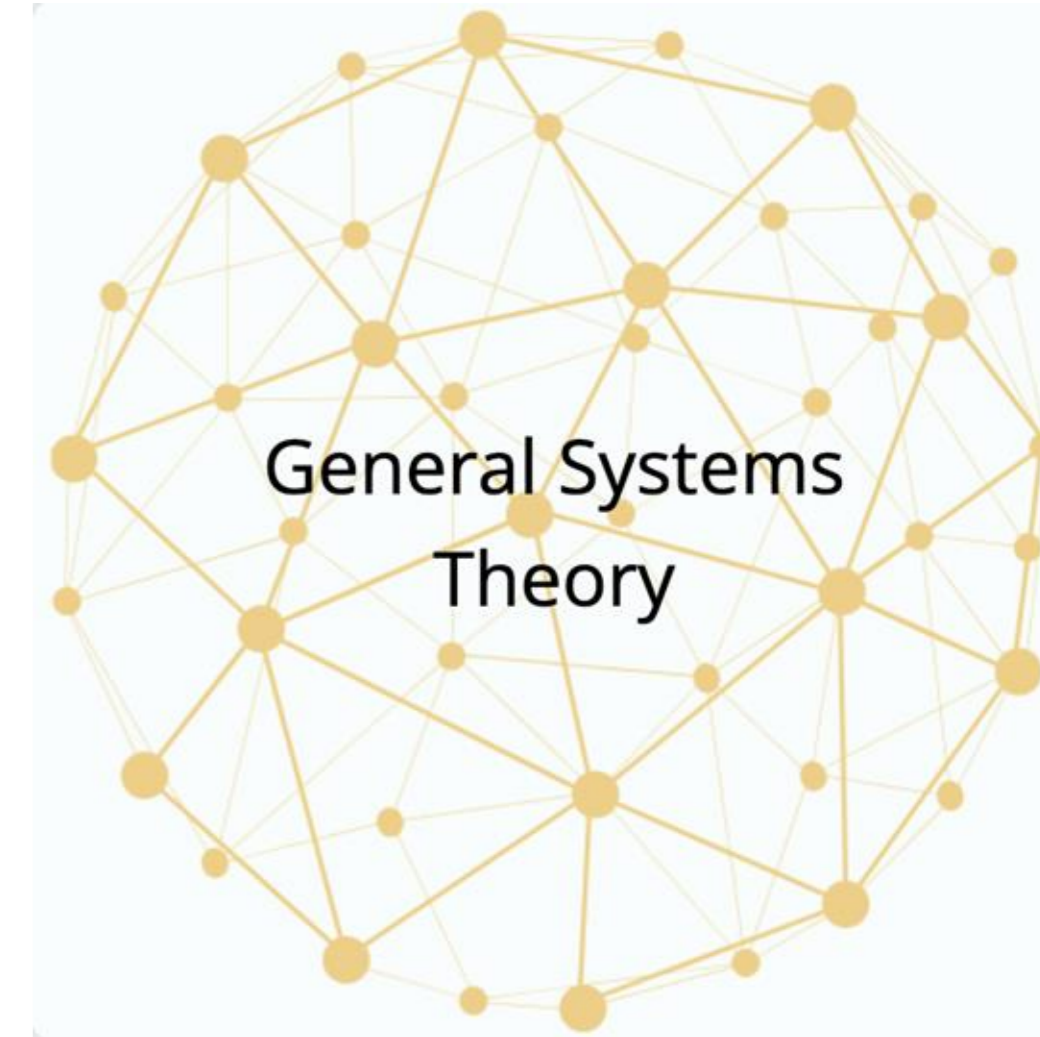
- The Great Acceleration – Climate Science (Steffen et al. 2015)
- Energy revolutions in earth and human history – Climate Science (Lenton et al. 2016)
- The earth and energy – Energy, Environmental & Chemical Engineering (Thimsen 2024)
- Evolution and the mind and consciousness – Philosophy (Nagel 2012)

Socio-economic trends



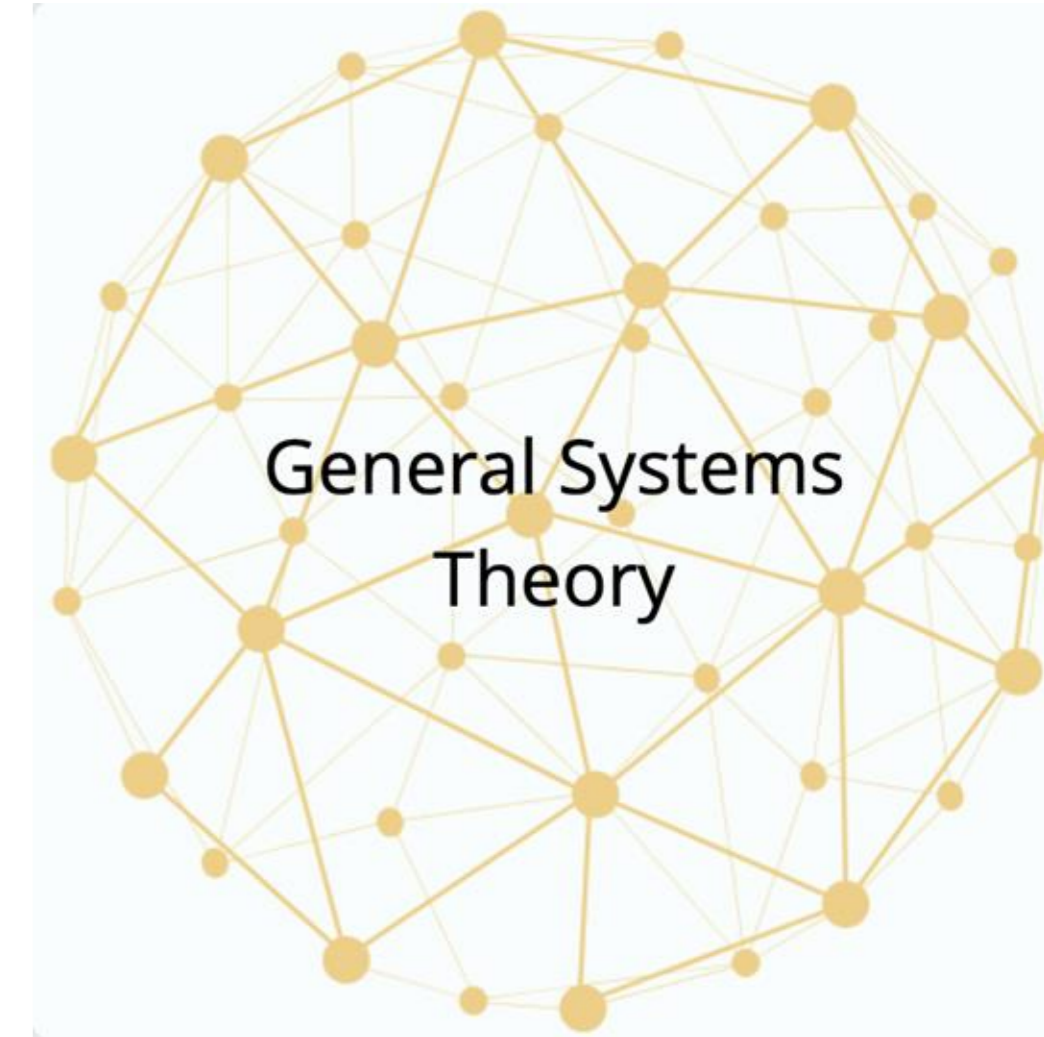
Conclusion

- The MPP and the MEPP emerged independently from different sources and they describe two different aspects of the ***same evolutionary process***.
 - ***Both are consistent with the evidence*** we have of evolutionary development.
 - There is ***some tension*** in the literature on these two principles concerning their relation to the principle of ***natural selection*** that is understandable given the differences in the history and focus of these two lines of research.
- Improving our understanding of the relations among all the optimality principles will improve our ***understanding*** of evolutionary development.



Conclusion

- **Odum's work provides a framework for this systems approach**, which has been overlooked.
- His approach **resolves the tension** in the literature regarding the role of the **principle of natural selection**.
- We plan to develop this framework into a systems theory of optimality principles,
 - extend it to optimality principles that have not yet been considered,
 - and critically examine its relation to the systems theories developed by Jorgensen and his colleagues.



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