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ECOSYSTEMS

Foundations and Frontiers of Ecosystem Science: Legacy of a Classic Paper (Odum 1969)

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Abstract

Ecosystem ecology, like all scientific disciplines, is often propelled forward by ''classic'' papers that identify key concepts within the field and define the core questions for generations of scientists. Here, we examine the legacy and sustained impact of a paper long considered a classic in ecology, E.P. (Gene) Odum's 1969 ''The strategy of ecosystem development.'' Odum's paper presented testable predictions about species diversity, energy flow, and biogeochemical dynamics during ecosystem succession and provided guiding principles for environmental conservation and management. Odum's 24 predictions on ''ecosystem development'' were a key component of this paper's legacy: The framework was referenced in 62.0% and tested in 28.7% of 1598 citing papers we examined. Although we found that support for Odum's framework grew over time, support for any particular prediction was inconsistent, highlighting the unresolved nature of some of the framework's principles. Odum's conceptual framework for ecosystem studies—as well as his forward-thinking attempts to connect ecosystem ecology with humans and society—continues to be pertinent to current and future research frontiers. Simplicity of the framework was its strength, and major limitation, painting ecosystem functioning in broad strokes, with no acknowledgement about interactions among the predictions. Newer generations have their work cut out for them by bridging evolutionary biology and ecosystem science or metabolic theory and ecological stoichiometry. Similarly, newer generations are using Odum's multidisciplinary approach to address the most pressing global change issues and designing solutions that make the Earth life sustaining system compatible with growing human demands.

Key words: Odum; ecological systems; ecosystem science; classic papers; bibliographic analysis; human dimensions; succession; research frontiers.

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Introduction

In any field of science, a body of literature exists that is considered ''classic.'' In ecology, that literature would include Lindeman's ''Trophic-dynamic aspect of ecology'' and Hutchinson's ''Homage to Santa Rosalia,'' among many others (Lindeman 1942; Hutchinson 1959; Real and Brown 1991). In this paper, we ask why ''The strategy of ecosystem development,'' published in *Science* in 1969 by Eugene (Gene) P. Odum constitutes a ''classic paper'' in the field of ecology, and specifically, in the field of ecosystem ecology. First, we develop our definition of a ''classic paper.'' Then, we take a retrospective approach to investigate how the paper influenced the field of ecosystem ecology. Finally, we prospectively evaluate how Odum's ideas can continue to illuminate the future path of the discipline.

What makes a paper a classic? Analyses in various fields suggest that aspects such as magnitude of impact, how well ideas are expressed or articulated, the generality of the topics covered, and how interesting and credible a paper is (so-called MAGIC criteria; Abelson 1995) contribute to classic status. A crowd-sourced psychology survey suggested the following criteria: quality of presentation, theoretical significance, practical significance, substantive interest, methodological interest, and value for future research (Sternberg and Gordeeva 1996). Real and Brown amassed a compendium of classic ecology papers in their book, *Foundations of Ecology* (1991). Real and Brown defined a classic as ''a paper that has made a substantial contribution to our thinking about ecological processes.'' Invited commentaries in each group of their selected papers gave some insight into why the selected papers were seen as classics, but as Slobodkin (1992) noted in his review of their book, ''… 'classic' in a scientific context means that this is a statement about how one group of current ecologists view the documents that gave rise to the current state of ecology as they see it.'' Slobodkin goes on to say, ''Each generation sees as important the things that they imagine have led to themselves.'' Whether this is true or not, the judgment that a paper is a ''classic'' is clearly subjective. Drawing from these previous definitions, we suggest that for a paper to be a classic in ecology, it must meet several of the following criteria (Table 1). The paper must (1) have a lasting influence (permanence and persistence), (2) contain a strong central framework (conceptual framework), (3) present or lead to testable hypotheses (content/hypotheses), and (4) be valuable (relevance and utility).

We chose to evaluate ''The strategy of ecosystem development'' because we recognize E.P. Odum as one of the most influential ecologists of the twentieth century and this paper is his most cited work. Odum, along with his brother, Howard T. Odum, researched the structure and functioning of ecosystems and developed a holistic view of ecology based on thermodynamic principles. Elected to the National Academy of Sciences in 1970 and recipient of the 1977 Tyler prize and the 1987 Crafoord Prize from the Royal Swedish Academy of Science (co-awarded with H.T. Odum), E.P. Odum is recognized as a pioneer of ecosystem ecology. His textbook, *Fundamentals of Ecology*, co-written with H.T. Odum, has been widely used and updated since first published in 1953. ''The strategy of ecosystem development,'' with over 1700 citations since its publication as of 2010 (Figure 1), was intended to bridge the gap between evolutionary biology and ecosystem ecology, which were at the time opposing views. In his paper, Odum also proposed the view that people are an integral part of ecosystems, a vision that has become a central paradigm of more recent ecological research, conservation, and management at scales ranging from local to global (for example, Palmer and others 2004; Walker and others 2004; Hobbs and others 2006; Chapin and others 2010; Pickett and others 2011).

Consistent with Slobodkin's comments, Odum (1969) was not embraced by all ecologists upon its publication (Hagen 1992). The paper appeared at a time when ecological theory and community theory, in particular, were shifting away from the Clementsian paradigm of the superorganism (Clements 1936) popular in the first half of the twentieth century toward concepts of the individualistic distribution of species, a gene-centric view of evolution, and the continuum concept of communities (Gleason 1926; Williams 1966; McIntosh 1987). Many viewed Odum's holistic approach to succession as a throwback to Clementsian times (McIntosh 1985; p. 227). Along with this perception, others started to criticize the ecosystem approach for its descriptive nature and lack of theory (for example, Murdoch 1966). It fell on E.P. Odum, the leading proponent of the more holistic ecosystem approach, to defend against such criticisms. Surprisingly, there is barely a mention of Odum (1969) and its impact on ecology in Frank Golley's *A History of the Ecosystem Concept in Ecology* (Golley 1993). Yet, Odum's paper laid out explicit hypotheses based on ecological theory about how components

Table 1. Attributes of a Classic Paper in Ecology

Attribute	Explanation
1. Permanence and persistence	The paper continues to be influential since its publication, is still cited, is mentioned in textbooks, etc.
• Legacy	Spurred new research and research directions
• Breadth	Cited and used by diverse research communities
2. Conceptual framework	The paper features a strong, well-articulated central framework that links to well-developed theory and supports numerous concepts and hypotheses
• Completeness	Covers a wide range of phenomena and key questions in the field
• Appeal based on values	Is consistent with values, such as conservation goals, nature appreciation, pollution abatement, preventing extinction, etc.
3. Content/hypotheses	The paper presents strong ideas and/or hypotheses that are consistent with the conceptual framework and provide rich fodder for further research
• Testability	Hypotheses are testable in a wide range of situations
• Correctness	Hypotheses withstand tests and remain plausible explanations of observed phenomena
4. Relevance and utility	The paper continues to be valuable in its scientific field and to broader applications
• Relevant to new ideas	Conceptual or empirical advances in ecology are consistent with the main findings or message of the paper
• Useful to management	Ideas, data, or metrics and techniques from the paper have found their way into management and policy

Our group suggests that a classic paper must meet several, but not necessary all, of the criteria in this schema.

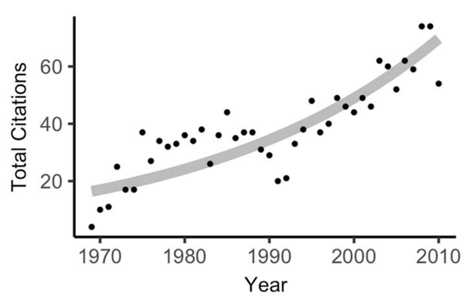

Figure 1. Yearly citations of Odum (1969) from 1969 to 2010. *Gray line* represents 3.5% increase through time.

of ecosystems change during succession, something that could be considered a direct response to critics claiming a lack of theory in ecosystem ecology.

To some extent, arguments about holism versus reductionism have faded over time. Holism had several influential proponents, including Margalef (1968) and Ulanowitz (1997), but resistance to holism and even ecosystem ecology, in general, persisted. For example, the first edition of the *Ecology* text by Begon and others (1986) did not have a chapter on ecosystem ecology, in fact, did not even use the word ''ecosystem,'' whereas the 4th edition is subtitled ''from individuals to ecosystems'' (Begon and others 2005). Today, despite broad acceptance of the ecosystem concept and its relevance to conservation and management, most texts have abandoned the systems-oriented, machine analogy of ecosystems promoted by E.P and H.T. Odum, R. Margalef and others, for more detailed, mechanistic, and process-based approaches (for example, Chapin and others 2012). The rise of landscape ecology contributed to the aversion to ''black box'' approaches, as ecologists turned to questions of heterogeneity and scale in ecosystems (Turner 1989; Levin 1992; Pickett and Cadenasso 1995), and advances in molecular methods allowed microbial ecologists to open the black box even further (Olsen and others 1986).

As noted above, a focal point of the 1969 paper is a general framework for understanding ecosystem succession with testable predictions about basic energy flow, community structure, and biogeochemical dynamics. The predictions are outlined in Table 1 of Odum (1969) (and rewritten in Table 2 here). Most studies have addressed only a few of the predictions, whereas comprehensive assessments are rare (but see Odum and Barrett 2005; Mitsch and Gosselink 2015). For example, Mitsch and Gosselink (2015) found that most of Odum's (1969) predictions applied to wetland restoration. The authors cite evidence that management practices that rely on ''self-design'' principles are more sustainable than the ''designer wetland'' approaches which are based on successful establishment of introduced or planted species (Mitsch and Gosselink 2015). Such ''self-design'' approaches are analogous to the model of ecosystem succession in Odum (1969), stressing that the self-organization

Table 2. Predictions of Trends to be Expected During Ecosystem Succession

Category	Pred. No.	Ecosystem attribute	Developmental stage	Mature stage
Community energetics	1	Production/respiration ratio	Greater or less than 1	Approaches 1
	2	Production/biomass ratio	High	Low
	3	Biomass supported/unit energy flow	Low	High
	4	New community production	High	Low
	5	Food chains	Linear, predominantly grazing	Weblike, predominantly detritus
Community structure	6	Total organic matter	Small	Large
	7	Inorganic nutrients	Extrabiotic	Intrabiotic
	8	Species diversity (variety)	Low	High
	9	Species diversity (equitability)	Low	High
	10	Biochemical diversity	Low	High
	11	Stratification and spatial heterogeneity	Poorly organized	Well organized
	12	Niche specialization	Broad	Narrow
	13	Organism size	Small	Large
	14	Life cycles	Short, simple	Long, complex
Nutrient cycling	15	Mineral cycles	Open	Closed
	16	Nutrient exchange rate, between organism and environment	Rapid	Slow
	17	Role of detritus in nutrient regeneration	Unimportant	Important
Selection pressure	18	Growth form	r-selection	K-selection
	19	Production	Quantity	Quality
Overall homeostasis	20	Internal symbiosis	Undeveloped	Developed
	21	Nutrient conservation	Poor	Good
	22	Stability	Poor	Good
	23	Entropy	High	Low
	24	Information	Low	High

Recreated from Odum (1969).

of ecosystems via natural colonization of species and survival of those species best adapted to current environmental conditions leads to sustained and stable ecosystem functioning. More comprehensive attempts to link the independent hypotheses, as in the aforementioned textbooks, may continue to provide advances in ecology.

Here, we have adopted a quantitative bibliographic approach, reviewing all papers citing Odum (1969), to provide a broader prospective of the general acceptance of Odum's model for ecosystem "development" (hereafter "succession") and the influence of the paper in the field of ecology. In this analysis, we consider the characteristics of the papers that cite Odum (1969) and assess whether and how his predictions of ecosystem succession were tested. We also compare insights from Odum (1969) as they relate to current research themes and frontiers in ecosystem ecology, particularly as identified by ethnographic analysis and insight from many ecosystem scientists summarized by Weathers and others (2016).

Methods for the Bibliographic Analysis

We compiled papers citing Odum (1969) published between 1969 and 2010. The citation list was downloaded from the Web of Science (©Thomson Reuters) in October 2010 (n = 1730). We used this complete list of papers to investigate the "permanence" and "relevance" of Odum (1969) (Table 1) by describing the subject area and type of papers in the citation list. The subject area classification was derived from the category classification data downloaded from the Web of Science. Because category classification data from the Web of Science are not jointly linked to the article data, this subject area analysis was performed on the complete citation list. We described the general subject areas of the citing articles by binning each category from the Web of Science analysis into the most relevant scientific discipline (Appendix S1, Table S1). We determined the type of articles that cited Odum (1969) by classifying each article used in the bibliographic analysis as a ''review'' (primarily a literature review), ''modeling'' (theoretical or computer modeling), ''meta-analysis'' (meta-analysis), or ''data'' (empirical or experimental) paper.

Next, we reviewed the citation list and removed unqualified papers before conducting our bibliographic analysis. Papers that cited Odum (1969) only in the bibliography but not within the text were removed from the citation list. The other criteria for inclusion in our bibliographic analysis included: (1) written in a language in which at least one person in our co-author group has fluency (English, Spanish, or Chinese), (2) published in the peer-reviewed literature, and (3) attainable through either the Arizona State University library system or Inter-Library Loan. To classify the ''hypotheses'' attribute in Table 1 (Attribute 3), we developed a schema to examine how each article cited Odum (1969) (n = 1598; Appendix S1, Figure S1). Specifically, we divided the articles randomly among the co-authors of this publication. Each co-author read approximately 150 assigned articles (50 of which were also reviewed by a second co-author to check for parity in interpretation), following a flowchart to categorize how the article addressed Odum 1969 (Appendix S1, Figure S1). First, we determined if the paper mentioned any of the 24 predictions in Odum (1969; Table 2). If the paper did not mention a prediction, we noted whether or not the paper had the data to test any of the predictions. Then, for each prediction mentioned, the prediction was marked as being either mentioned, but not tested; stated as fact; or tested. If a prediction was tested, we marked the outcome of test as being either (1) in support of, (2) against, or (3) ambiguous toward Odum's hypothesis of ecosystem succession. ''Ambiguous'' was used to classify outcomes that did not clearly support nor refute the prediction or provided evidence both for and against the prediction. If the co-author reading the article was unsure how to categorize the article, one or more other co-authors read the article and a categorical decision was made by consensus.

The ''permanence'' and ''testability of content and hypotheses'' criteria for a classic paper were evaluated by examining the ontogeny of tests on Odum's predictions. We did this both across all predictions and for each individual prediction. As not all predictions were necessarily tested each year, we used a time interval of approximately 5 years to determine proportion of test outcomes for the individual prediction ontogeny. We binned 1969 and 1970 with the 1971–1975 interval to account for the lower number of articles published in these years immediately following the 1969 release of the Odum (1969) paper. All analyses were performed in R (ver 3.3.0) (R Core Team 2017). Detailed results of the bibliographic analysis are reported in the supplementary materials (Appendix S1).

Results and Discussion

Odum (1969) as a Classic Paper

In our somewhat subjective view, Odum (1969) meets multiple criteria for being considered as a classic paper in ecology (for example, Table 1). In terms of permanence, citation rates continue to grow (Figure 1). It is broadly relevant, having been cited in diverse fields, stimulated new ideas, and used in management. And, it features a testable, conceptual framework that, although now largely replaced by non-equilibrium theories of ecosystem change, retains heuristic value.

Permanence and Relevance: Characteristics of Papers Citing Odum (1969)

Since its publication, Odum (1969) has remained influential in the literature. Still, 40 years after publication, Odum (1969) continues to be widely cited (Figure 1). Many of the papers citing Odum (1969) have also been well cited, indicating the broad influence of the paper on the field of ecology. In ranking the papers citing Odum (1969) by their respective number of citations, the top three papers had more than 700 citations each, the top ten had more than 440 citations each, and the top twenty had more than 375 citations each (Appendix S1, Table S2). If a paper could have an H-index (hence, the number of papers citing a paper with at least that many citations), the H-index of Odum (1969) would be 154. The top three most cited papers themselves are often considered classic papers in different subfields within ecology: community ecology (Connell and Slatyer 1977; 1659 citations), macroecology (Brown and others 2004; 780 citations), and ecosystem ecology (Fisher and Likens 1973; 702 citations), reflecting the legacy of Odum (1969) in spurring new research directions.

Odum (1969) also has been cited and used by diverse research communities. Although a majority of the articles citing Odum (1969) are classified in the fields of ecology (34.2%) or biology (21.7%) (Appendix S1, Table S1 and Figure S2), a number of other disciplines are well represented. These other disciplines include the earth sciences, with oceanography and geology representing 4.2 and 2.6% of the papers, and the social sciences, representing 4.1% of the papers. Natural resources, representing publications with a more applied focus, represented a substantial portion of the papers, 15.9%, suggesting the utility of Odum (1969) for management and policy. The remaining 14.5% of articles fell into a broad categorization of disciplines that included chemistry, computer science, education, math, medicine, physics, and technology.

Content and Hypotheses: Tests of Odum's Model of Ecosystem Succession

When cataloging reasons for citing Odum (1969), the majority of citations refer to the conceptual framework. Of the 1598 articles used in the bibliographic analysis (Appendix S2), 62.0% (990) cited Odum (1969) in reference to one or more of the predictions related to ecosystem succession (Appendix S1, Figure S3). The majority of these papers, 86%, were data papers, suggesting that the conceptual framework in Odum (1969) spurred new research. Across the 990 publications referencing Odum's conceptual framework, there were a total of 3169 distinct mentions of the predictions and 960 tests of the predictions.

Although the conceptual framework in Odum (1969) clearly supported new research, the individual components of the framework (Table 2) were not equally explored in the literature in terms of mentions or citations. Predictions related to ''community energetics'' or ''community structure'' were mentioned most often (Figure 2). Predictions related to ''overall homeostasis'' were the least tested compared to total mentions, despite Odum's emphasis on thermodynamics and systems approaches, and the predictions related to species diversity (Predictions 8 and 9), often a focus in community ecology, were both most frequently mentioned and most often tested in proportion to their mentions.

Of the tests of Odum's predictions related to ecosystem succession, outcomes were generally in modest support of his hypothetical framework (Figure 2). Indeed, even though predictions related to species diversity (Predictions 8 and 9) were tested most frequently, the proportion of the tests supporting or refuting the predictions did not differ greatly from the proportion of the tests supporting or refuting other predictions. Within the 458 papers that actually tested the predictions, nearly 60% of the test outcomes were in support of Odum (1969), while only 23.7% of the tests found evidence contrary to his predictions. The results of the remaining tests (16.9%) were ambiguous.

Through time, cumulative support and refutation of Odum's predictions have both grown linearly, but this rate is 2.6 times faster for support than

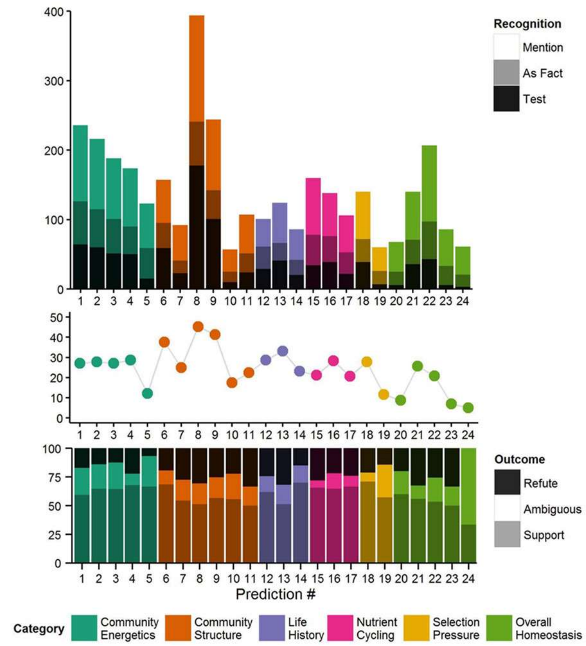

Figure 2. (*Top*) Analysis of how each prediction in Odum (1969) was addressed ($n = 3169$) when mentioned in a paper; a shading overlay is used to denote the different categories (for example, *black* is tested, *medium shade* is recognized as fact, or no shading is just mentioned). (*Middle*) Relative number of times a prediction was tested compared to being mentioned or recognized as fact. Note the scale: tests always accounted for less than 50% of total mentions. (*Bottom*) Relative outcome of tests with Odum's predictions either supported, refuted, or had an unclear assessment (''ambiguous''); a shading overlay is used to denote the different outcomes.

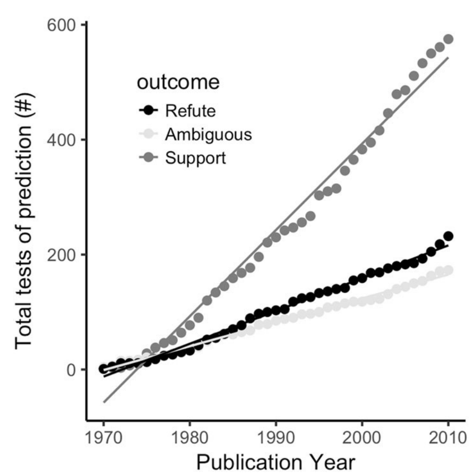

Figure 3. Cumulative outcomes of tests of predictions from Odum's framework of ecosystem succession.

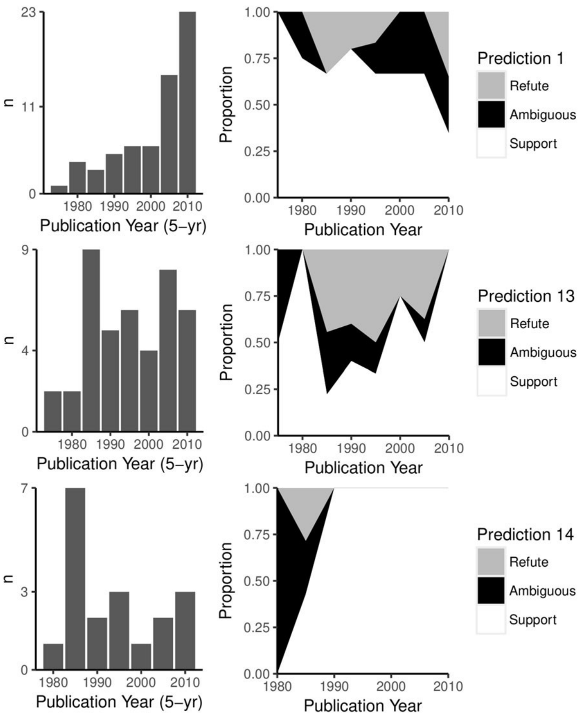

Figure 4. Ontogeny of the number of publications testing Odum's predictions of ecosystem development and the outcome of those tests for three of those predictions in five-year intervals (all ontogenies can be found in the supplementary material). Note differences in scale for number of publications (*n*) on *left panels*.

refutation (Figure 3). However, support for any particular prediction has changed through time (Figure 4; Appendix S1: Figure S4). Some predictions have been consistently supported in the literature, whereas others have not. For instance, although initial support for Odum's prediction of life cycles shifting from short and simple to long and complex with ecosystem maturation (Prediction 14) was low, it has been well supported in the literature since the 1990s. Conversely, although initial support for the prediction that the ratio of ecosystem production to respiration approaches one at a mature ecosystem state (Prediction 1) was mostly high, current support for this prediction has decreased. Furthermore, unlike overall support for Odum's framework, which has grown linearly, support for many of the predictions has shifted erratically through time (for example, Prediction 13).

Completeness and Appeal of the Conceptual Framework: Analysis of How Odum (1969) Was Cited

Of all the papers citing Odum (1969) in our bibliographic analysis, less than a third (28.7%) of the total (458 out of 1598) and less than half (42%) of the data papers (394 out of 941) actually tested the predictions of ecosystem succession. Hence, more than two-thirds of the papers that mentioned the framework actually cited the predictions as facts (Figure 2). We found this result particularly striking as the model of ecosystem succession Odum described in his paper is hypothetical. One reason for acceptance of Odum's model of ecosystem succession may have been the growing support for Odum's predictions found in the literature (Figure 3) and authors no longer testing a prediction that has been supported elsewhere. However, our results show that support for any particular prediction was not absolute (Figure 2) and that support did not necessarily increase linearly through time, or, for that matter, increase at all (Figure 4, Appendix S1: Figure S4). Therefore, it would seem that acceptance of Odum's ideas on ecosystem development may have permeated the scientific literature before, as well as during and after, rigorous testing. We suggest the acceptance of Odum's ideas may have been more likely in fields outside of ecology—hence, among scientists less likely to be aware of the breadth of ecological literature—but further research is needed to test this hypothesis.

As references to the conceptual framework in Odum (1969) did not necessarily align with tests of that framework, we suggest a simple accounting of citations should not be used as justification for a paper being considered ''classic.'' A paper in which ideas are accepted as ''truth'' does not necessarily advance science in the same way as one that motivates new research. By delving into a bibliographic analysis of the citations, we were able to better answer whether or not Odum (1969) was able to ''spur new research'' (Table 1): Although Odum's predictions were often accepted as fact in the literature, Odum's predictions are still controversial and being tested with confounding results (Figure 4).

Relevance of Odum (1969) Beyond the Conceptual Framework

In our analysis, we also discovered a substantial number of citations that were unrelated to the 24 predictions in Odum (1969). Of the papers citing Odum (1969) that did not mention one of the 24 predictions (38% of total), many were ''data papers,'' suggesting that other concepts in Odum (1969) have provided the context or impetus for research endeavors. Indeed, a cursory survey of the papers that did not mention one of the 24 predictions reflects the breadth of topics covered in Odum

(1969): the role of ecology in agriculture and land-use planning (for example, Gross and others 1984; Wardle and others 1995), sustainability (for example, Slocombe 1993), the pulse stability concept (LaMontagne and others 1986; Stottlemeyer 1987; Holland and others 2000), ecological restoration (Zweig and Kitchens 2009), and disturbance theory (for example, Halford and others 2004; La Peyre and others 2003). A more in-depth analysis of the citations could better reveal which concepts from Odum (1969) have led to new fields, areas of inquiry, or morphed into other concepts. Although such an extensive analysis was beyond the scope of this paper, the breadth of the legacy of Odum (1969) both within and beyond the field of ecosystem ecology is supported by (a) the large proportion of citations not relating to the framework of ecosystem succession ($n = 608$), (b) the number of concepts found in those citations, and (c) the numerous disciplines outside of the field of ecology that cited the paper (Appendix S1: Table S1).

One major topic not covered in Odum's framework of ecosystem succession is the conservation of ecosystems. As many of the papers citing Odum (1969) are categorized under "natural resources," issues related to ecosystem management and conservation likely account for a substantial proportion of the citations to Odum (1969) and highlight the "relevance" of this paper (Table 1). In the second half of "The strategy of ecosystem development," Odum discusses a number of issues that are still relevant to conservation concerns today: monoculture cropping systems, trade-offs in land management, integrating urban centers into environmental considerations, alternative sources of food, and environmental education (Table 3). Therefore, while the table of predictions brought attention to and criticisms of Odum (1969), other insights that were likely ahead of their time, particularly with regard to ecosystem conservation, also remain broadly relevant today, as we consider further below.

Thinking Forward

To be a classic, we believe a paper ought to offer insight and relevance toward envisioning the future of the field. That is, will Slobodkin's context regarding contemporary times hold in the future? Recently, Weathers and others (2016) identified four frontiers in ecosystem science based on input and surveys of ecosystem ecologists. These frontiers are (1) rethinking the drivers of ecosystem change, (2) new insights into ecosystem processes, (3) new angles on problem-solving/applied research, and (4) evaluating human dimensions of ecosystem ecology. Here, we discuss how Odum (1969) relates to these frontiers with specific emphasis on Odum (1969)'s future relevance in the field. We chose Weathers and others (2016) as the focus of comparison because their paper relied on community meetings, town halls, and workshops with over 600 participants to identify research frontiers. Thereby, Weathers and others (2016) provided an inclusive outlook of the field. In addition, Weathers and others (2016) focused primarily on ecosystem ecology, rather than ecology as a whole (for example, Sutherland and others 2013). In comparing Odum (1969) with Weathers and others (2016), we directed more attention to the last half of his paper than the table of 24 strategies that drove much basic ecosystem research in the past. Overall, we found many parallels between insights from Odum (1969) and the frontiers identified by Weathers and others (2016).

Rethinking the Drivers of Ecosystem Change

Odum (1969) is still guiding the future of ecology because it defined a very simple conceptual framework against which new experimentation will continue to be deployed and new theories

Table 3. Selected Quotes from Odum (1969) Emphasizing Relevance to Contemporary Conservation, Management, and Ecosystem Science Challenges and Frontiers

Concept	Quote (page number)
Monoculture	"…it would be suicidal to cover the whole land area of the biosphere with cornfields…" (267)
Trade-offs in land management	"Vast manmade lakes solve some problems, at least temporarily, but yield comparatively little food or fiber…" (267)
Urban ecology	"…the urban–rural landscape, where lie today's most serious problems" (267)
Sustainable food systems	"There is no reason why man cannot make greater use of detritus and thus obtain food…" (268)
Environmental Education	"Education, as always, must play a role in increasing man's awareness of his dependencies on the natural environment." (269)

developed. The value of the model is its simplicity, but its simplicity constrains the cases in which it can be successfully used. The model painted ecosystem functioning in broad strokes and left most of the detail work for generations to come. Moreover, each of the 24 hypotheses was presented as independent, whereas today most ecologists see interactions among the themes as a means to integrate different subdisciplines in ecology, such as diversity–productivity and diversity–stability relationships (Tilman and others 2014).

A reason Odum's paper is still relevant is because it calls attention to the differences between systems in early growth or exploitation phase that are experiencing rapid change, and those in a conservation phase, which are potentially more ''locked-in'' to a single configuration (''K'' in Holling's adaptive cycle; Holling 2001). Some of the predictions of the Odum (1969) hypotheses, in fact, are mirrored in the description of how systems undergo change to become more connected, with higher biomass, greater rigidity, and a potential to flip into an alternative state (Gunderson and Holling 2001; Scheffer and others 2001).

The systems approach laid out in Odum (1969) remains a fundamental framework for spurring ecological research and bridging the gap between evolutionary biology and ecology (Hagen 1992). The theory of ecosystem development proposed in Odum (1969) is a systems-based framework, where thermodynamics and information theory dictate ecosystem succession. This approach is unlike other major theories in ecology with similar goals of unification. For example, both the Metabolic Theory of Ecology (Brown and others 2004) and Ecological Stoichiometry (Sterner and Elser 2002) are based on processes at or below the organismal level. Indeed, Brown and others (2004) state explicitly that their metabolic framework could be used to address questions raised by Odum (1969), such as predicting how productivity or biogeochemical cycles change with plant size during succession. This clearly ties back to the energetics component of Odum's model. Further attempts to unify ecology exist; for example, the Gordon Research Conference on Unifying Ecology across Scales provides a biannual gathering to discuss connecting the aforementioned theories. Juxtaposing Odum (1969) with these or other ecological theories may better achieve the goal of bridging evolutionary biology and ecology or predicting ecosystem responses to change, or at least help guide the ecological community in defining research priorities.

New Insights into Ecosystem Process

The Odum (1969) framework still is the basis for the broadening of ecological scales, which is one of the research frontiers identified in Weathers and others (2016). Odum called for expanding the scale of ecosystem research, an idea on which he elaborated in later papers (Odum 1977, 1989). The current scale of ecosystem ecology research extends from micro- or mesocosms to regional or global scales, reflecting the multi-scale approaches for which Odum (1969) called. This broadening of the scale of ecosystem science is made necessary by the current large-scale questions dominating the field. For example, what are terrestrial or aquatic ecosystems' contributions to the global carbon budget? How does the alteration of the global nitrogen cycle impact ecosystem processes? How does biodiversity loss influence ecosystem function? By taking Odum's approach and linking smaller-scale studies with studies or observations at larger scales, ecosystem ecologists have been able to link mechanistic processes with global change, for example, scaling results of microcosm studies, linking composition and function to landscape processes based on insights from flux towers and, ultimately, to continental processes through FLUXNET (Baldocchi 2014; Eugster and others 2005). To address future global environmental challenges, a clear frontier of ecosystem ecology is continuing to expand on the call by Odum (and others) to understand ecosystem processes, function, and responses to change at multiple spatial and temporal scales.

At its core, Odum (1969) presents a generic ecosystem model, one that can be applicable to any ecosystem type; for example, lake, forest, laboratory microcosm. In his paper, he directly compares the latter two and uses this comparison as the foundation for his model of energetics in ecosystem succession. Yet, this approach of using ecosystem comparisons is likely underutilized in contemporary ecology; in a review of literature from terrestrial and aquatic ecosystems, citations were much less likely to come from papers done in different ecosystem types (Menge and others 2009). One promising approach in ecosystem science is the emergence of network science (Fraser and others 2013). Networks like the Global Lake Ecological Observatory Network (GLEON), International Long-Term Ecological Research (iLTER) Network, and US National Ecological Observatory Network (NEON), and distributed, coordinated efforts (for example, Nutrient Network, Borer and others 2014) have been instrumental in connecting researchers from different ecosystems. Indeed, a review of work based on long-term ecological research in the LTER network provides a novel expansion of the model of ecosystem succession presented in Odum (1969) and Kominoski and others (2018). Infusing ideas about ecosystem functioning from Odum (1969) into cross-ecosystem comparisons, as has already been done by Kominoski and others (2018), may continue to provide a useful guide to research frontiers in ecosystem ecology.

New Angles on Problem-Solving/Applied Research

Odum (1969) combined biology with geomorphology and ultimately social sciences as a precursor to the current interdisciplinary view of social–ecological systems, an approach called for in Weathers and others (2016). This foreshadowed the intellectual expansion of multidisciplinarity, an approach we expect to continue as it is useful to address both (1) applied problems, for example, sustainability of our planet under rapid change and (2) intellectual curiosity, for example, unexpected insights gained by juxtaposing multiple fields or disciplines.

Evaluating Human Dimensions of Ecosystem Ecology

Odum (1969) explicitly called for the incorporation of humans into ecosystem ecology leading into vibrant new programs. For example, social–ecological systems theory (Berkes and others 2008) and coupled human–natural systems work (Liu and others 2007, NSF program in coupled natural–human [CNH] systems) are guiding much research in ecosystem science of cities (McPhearson and others 2016; Groffman and others 2017) and of agricultural landscapes (Robertson and others 2008; Jordan and Warner 2010).

Odum's (1969) statement, ''Until recently mankind has more or less taken for granted the gas-exchange, water-purification, nutrient-cycling, and other protective functions of self-maintaining ecosystems…'' may represent one of the earliest recognitions of ecosystem services as an important bridge between ecosystems and society (Collins and others 2011). This concept of ecosystem services has become an important principle in ecosystem management worldwide (Carpenter and others 2009; Guerry and others 2016) and has been identified as a continued frontier of ecosystems research (Weathers and others 2016). Additionally, Odum's proposed compartment model (Figure 2 in Odum 1969) represents one of the first attempts to start evaluating and managing the environment and human-dominated landscapes at a large scale. By identifying with a systems analysis perspective, he proposed continually evaluating and adapting to the use and impact in real-world situations. We now consider this common and a best practice in ecosystem-based adaptation projects. Both ecosystem services and adaptive management of social–ecological systems are key to enhancing the future resilience of a system in the face of expanding local and global challenges (for example, Walker and others 2004; Ostrom 2009).

Conclusion

For reasons described in this paper, Odum (1969) was hugely influential to the field of ecology. His paper laid out a series of predictions about ecological attributes in an ecosystem based on succession following disturbance. Yet, the legacy of Odum (1969) for the future of ecology lies beyond his model of ecosystem development. While wading through the morass of large datasets or dispersed collaborations, it could be useful for ecologists to be exposed and re-exposed to the foundations of ecosystem ecology, to the philosophical foundations of our field, in other words, to read Odum (1969) and other classic papers, but do so within the context of present-day theory. Odum (1969) put forth expected trends for ecosystem development based on principles of energy flow, thermodynamics, and information theory. The trends span organismal to population to ecosystem ecology and could tractably be tested by comparing the ecological structure or processes within ecosystems at different stages of development. Indeed, many of the multiple, testable hypotheses put forth in Odum (1969) continue to be productive fodder for generations of ecologists, whereas others are currently out of vogue. One rather obvious deficiency is that Odum's predictions were presented independently of each other. Yet, conceptual advances, such as biodiversity and ecosystem function, explicitly link multiple predictions from Odum (1969). Future conceptual advances might best be based on integrating multiple themes from Odum (1969) rather than conducting further tests of individual hypotheses. For example, metabolic theory might be blended with ecological stoichiometry and patterns of species diversity to better understand how organisms or communities will respond to changes in resource availability and warming under global environmental change.

Currently, general goals in ecosystem ecology include doing excellent ecosystem science and connecting this science to human systems and

Earth stewardship (Chapin and others 2011). Odum (1969) laid out a framework that pushed forward the field of ecosystem ecology and implored the field to take on environmental challenges by integrating ecosystem science into human society (for example, Lubchenco 1998). This call is just as relevant today as it was in 1969. Given its legacy and continued relevance, we posit that Odum (1969) will remain a classic in ecology for the foreseeable future. We hope our paper will garner renewed interest in Odum (1969) among the next generation of ecologists, as this classic paper and its predictions are integrated into today's non-equilibrium conceptual frameworks for understanding ecosystem change. We also hope that our project encourages similar, objective assessments of how other classic papers have influenced progress in the field of ecology and will influence the future of this discipline.

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