

A Critical Review of Twenty Years' Use of the Resource-Ratio Theory

Thomas E. Miller,^{1,*} Jean H. Burns,^{1,†} Pablo Munguia,^{1,‡} Eric L. Walters,^{1,§} Jamie M. Kneitel,^{1,||} Paul M. Richards,^{1,#} Nicolas Mouquet,^{2,**} and Hannah L. Buckley^{1,††}

1. Department of Biological Science, Florida State University, Tallahassee, Florida 32306-1100;

2. Unité Mixte de Recherche 5554, Institut des Sciences de l'Évolution de Montpellier, Université Montpellier II, Place Eugène Bataillon, CC 065, 34095 Montpellier Cedex 5, France

Submitted August 19, 2004; Accepted December 20, 2004;
Electronically published February 11, 2005

Online enhancements: appendix, figures.

ABSTRACT: A model of species interactions based on their use of shared resources was proposed in 1972 by Robert MacArthur and later expanded in an article (1980) and a book (1982) by David Tilman. This "resource-ratio theory" has been used to make a number of testable predictions about competition and community patterns. We reviewed 1,333 papers that cite Tilman's two publications to determine whether predictions of the resource-ratio theory have been adequately tested and to summarize their general conclusions. Most of the citations do not directly test the theory: only 26 studies provide well-designed tests of one or more predictions, resulting in 42 individual tests of predictions. Most of these tests were conducted in the laboratory or experimental microcosms and used primary producers in freshwater systems. Overall, the predictions of the resource-ratio theory were supported 75% of the time. One of the primary predictions of the model, that species dominance varies with

the ratio of resource availabilities, was supported by 13 of 16 tests, but most other predictions have been insufficiently tested. We suggest that more experimental work in a variety of natural systems is seriously needed, especially studies designed to test predictions related to resource supply and consumption rates.

Keywords: competition, species interactions, literature survey, consumer-resource theory, R^* .

In 1980, David Tilman published "A Graphical-Mechanistic Approach to Competition and Predation" in the *American Naturalist*, which he followed in 1982 with a book entitled *Resource Competition and Community Structure*. At the time of their publication, ecologists were vigorously debating the importance of competition and the experimental rigor needed to demonstrate competition (Strong et al. 1984). In these two publications, Tilman (1980, 1982) presented a very logical vision of resource competition and a theory from which clear predictions were possible.

Up until the publication of these works, most ecologists' understanding of species interactions was phenomenological: per capita effects of one species on the growth rate of another species were quantified without consideration of mechanism of the interaction. In particular, the Lotka-Volterra models had been (and continue to be) used and extended to describe competition between two or more species. Predictions from these models directly inspired a large number of experiments, beginning with Gause's (1932) early studies on *Paramecium*. However, such models are generally recognized to be limited in application because they do not directly incorporate a mechanism (however, see Winsor 1934; Grover 1997).

The model presented by Tilman (1980, 1982) describes the interactions of competing species through their use of and effect on shared resources. The model is based on earlier work by MacArthur and others and describes a dynamic relationship between consumer species and limiting resources: individual species' growth rates are functions of resource availability, while resource availability is a function of resource supply rate in the environment and

* Corresponding author; e-mail: miller@bio.fsu.edu.

† E-mail: burns@bio.fsu.edu.

‡ E-mail: munguia@bio.fsu.edu.

§ Present address: Environmental Studies Program, Dartmouth College, Hanover, New Hampshire 03755-3755; e-mail: ewalters@dartmouth.edu.

|| Present address: Department of Biological Sciences, California State University, Sacramento, California 95819-6077; e-mail: kneitel@csus.edu.

Present address: National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, Florida 33149; e-mail: paul.richards@noaa.gov.

** E-mail: mouquet@isem.univ-montp2.fr.

†† Present address: Bio-Protection and Ecology Division, Lincoln University, P.O. Box 84, Canterbury, New Zealand; e-mail: buckleyh@lincoln.ac.nz.

Am. Nat. 2005. Vol. 165, pp. 000-000. © 2005 by The University of Chicago. 0003-0147/2005/16504-4058\$15.00. All rights reserved.

species consumption. Individual populations can increase in size, consuming more and more resources, until resources become limiting and constrain the population size to the level that can be supported by the resource supply rate in that environment. A simple prediction of this model is that species that can decrease resource levels to low values and survive at these lower resource levels should outcompete other species when that resource is limiting. When two or more resources are limiting, then trade-offs in the ability to use different resources may allow coexistence between competitors. Several names have been given to this theory and its descendants, including the resource-ratio theory, consumer-resource theory, and R^* theory: we will use the term “resource-ratio theory” (Tilman 1986).

Tilman’s two works (1980, 1982) had an immediate effect on the scientific community. The eminent plant ecologist John Harper, reviewing Tilman’s 1982 book, stated, “Plant ecology is desperately short of theory that can be tested. Tilman’s monograph gives us a theory that might account for much of the puzzling diversity of plant communities, and he presents much circumstantial evidence in its favour. There is now a golden opportunity for the plant ecologist to go back to the field with some real hypotheses that have been framed in a testable form. I suspect that this monograph may prove a major step in the development of plant ecology as a theoretical and experimental science” (Harper 1983, p. 664).

Harper was prophetic; more than 20 years later, these two publications of Tilman (1980, 1982) are very widely read and have been cited in more than 1,300 peer-reviewed articles since 1982, and the rate of citation shows no sign of declining (fig. 1 in the online edition of the *American Naturalist*). Further, the general theory is now described in most introductory ecology textbooks along with the traditional Lotka-Volterra competition equations (e.g., Begon et al. 2000; Bush 2000; Ricklefs and Miller 2000; Krebs 2001; Stiling 2002). The original theory has also been modified and extended to address a variety of questions and ecological scenarios (see, e.g., Tilman 1984, 1986, 1988; Abrams 1988; Holt et al. 1994; Leibold 1998; Chase and Leibold 2003).

Here we present the results of a survey of the primary scientific literature that cited the two focal Tilman articles (1980, 1982) between 1980 and the summer of 2003. This article aims to determine whether the predictions of the original resource-ratio theory have been adequately tested, to summarize the general conclusions of studies that have tested or applied the resource-ratio theory, to suggest where further experimental work is needed, and to discuss briefly how general theories such as the resource-ratio theory are used in ecology. We briefly describe the history of the resource-ratio theory and major predictions (a more

complete history of resource competition theory can be found in Grover 1997), but this review is not intended to be an evaluation of the theory itself, which we believe to be a simple but logical view of species interactions through their resources.

Reviewing a general theory in science is like trying to hit a moving target: theories constantly evolve and adapt, often leading in multiple new directions and making the delineation and evaluation of any single “theory” difficult. We have restricted our review to articles that cite the focal Tilman articles rather than earlier presentations of the same theory (e.g., MacArthur 1972; Maguire 1973; O’Brien 1974) because Tilman’s works are so widely cited. Earlier articles that explored the same theory have generally not been recognized; for example, at the time of our survey, Maguire’s (1973) and Phillips’s (1973) resource-based models of competition had been cited only 45 and 27 times, respectively, and O’Brien’s (1974) further exploration of the theory and its application to phytoplankton growth had been cited 78 times, whereas the 1,300 citations of Tilman (1982) accumulated over a shorter time period. Further, many of these citations to earlier work also include citations to Tilman (1980) or Tilman (1982). Later articles presented either narrower interpretations of the model, like Tilman’s (1985) article entitled “The Resource-Ratio Hypothesis of Plant Succession,” or significant extensions of the model to phenomena other than competition, like the works of Tilman (1988), Holt et al. (1994), and Leibold (1996), and are not further discussed here.

Resource-Ratio Theory

History

Although his contribution is seldom acknowledged, the resource-ratio theory should probably be attributed to Robert MacArthur, on the basis of his 1972 book *Geographical Ecology*. In the appendix to chapter 2, MacArthur first describes the traditional Volterra competition equations and then presents an alternative graphical model in which species growth rates are a function of resource availability rather than of the abundance of other species. In turn, the abundances of the resources are determined as a function of the supply rate of the environment minus the resources used by competing species. MacArthur provided explicit equations describing the growth rates of the competing populations as well as the dynamics of their resources. Further, MacArthur presented a simple graphic visualization of the two-species, two-resource interaction by mapping the growth rate of each species onto the phase space defined by the abundance of the two resources (fig. 2 in the online edition of the *American Naturalist*; MacArthur 1972). He used a zero-net-growth isocline to sep-

arate the resource space into zones where the individual species had positive and negative population growth, demonstrating how resource conditions affected population growth and, ultimately, competitive outcomes. Further, he briefly discussed how the graphs could demonstrate competitive exclusion, invasibility, and even evolutionary convergence and divergence. Although MacArthur did not discuss the nature of different types of resources extensively, he recognized that the zero-net-growth isocline would be curvilinear if the two resources contributed non-additively to growth. Finally, he noted the necessary conditions for coexistence, especially that coexistence would occur only in the presence of a particular combination of species resource use and resource supply rates in the environment (a_{ij} and R values, respectively, in fig. 2).

Other very similar approaches were developed at about the same time. Maguire (1973) used a related model to describe effect and response components of the niche, as well as interactions between resource needs that lead to different zero-net-growth isoclines. Phillips (1973) used linked equations of resource and consumer dynamics to demonstrate that coexistence requires an equal or greater number of resources than consumer species and some combination of resources for each species at which all other species die out (see also Stewart and Levin 1973). O'Brien (1974) also used a similar mathematical model of nutrient competition, building on an earlier model of Dugdale (1967) and proposing that the model could be applied to phytoplankton dynamics. Dugdale himself appears to have been one of the first to suggest that rate of growth of competing species can be modeled as a Monod-type function of resource availability. Leon and Tumpson (1975) expanded on MacArthur's original resource-based model by determining how the criteria for coexistence varied with the substitutability of the resources. At around the same time, Taylor and Williams (1975) independently developed a similar theoretical approach to competition using Monod-type growth kinetics, demonstrating the criteria for stable and unstable coexistence under continuous-flow conditions.

Despite this earlier work, Tilman's (1980, 1982) publications are those recognized by most ecologists as the origins of the resource-ratio theory. Many articles actually refer to "Tilman's resource-ratio theory," but this is through no fault of Tilman's because he has always fully acknowledged that his work was an application of earlier models. Instead, the attribution is probably due to his particularly clear presentation of the model as well as his demonstration that this theory could be applied to a broad variety of questions in ecology. He was one of the first scientists to apply this theory, predicting the outcome of competition among diatoms from growth of individual species in monocultures (Titman 1976; Tilman 1977; see

also Hansen and Hubbell 1980). Tilman's (1980, 1982) publications present a complete and comprehensive presentation of the basic resource-ratio hypothesis along with an exploration of applying the theory to a broad variety of ecology questions. We chose these articles as the basis for our survey on the assumption that they are landmarks that virtually must be cited by later publications that use the resource-ratio hypothesis.

Predictions

Tilman (1980, 1982) used the resource-ratio theory to make a number of predictions, although not all were clearly or explicitly stated. From these articles and other scientists' interpretations of them (in the form of articles citing Tilman 1980, 1982), we have compiled a list of predictions attributed to the basic theory (table 1). We will briefly review the predictions here; more detailed explanations can of course be found in Tilman's articles (1980, 1982).

The resource-ratio theory is based on the assumption of a dynamic relationship between resources and consumers. If resource levels are sufficient, then consumers will have positive population growth, which in turn will eventually drive down resource levels and lead to reduced population growth. If two species consume the same resource, then the resource-ratio theory predicts that the species that can maintain a positive growth rate at the lower resource

Table 1: Predictions from the resource-ratio theory, based on studies that cite Tilman (1980, 1982)

Prediction
1. The species that can survive at the lowest levels of a limiting resource will be the best competitor for that resource
2. Species dominance varies with the ratio of the availabilities of two resources
3. The number of coexisting species is less than or equal to the number of limiting resources
4. The vector describing the resource supply rate to an environment will affect whether competing species coexist and, if not, which species will competitively exclude the other
5. The vectors describing the consumption rates of resources for two species will determine whether competing species coexist or, if not, which species will dominate competitively
6. Trade-offs in resource use must occur for species to coexist along a gradient of ratios of the availabilities of two resources
7. The highest diversity of competing species will occur at an intermediate ratio of the availabilities of two resources

level will be the better competitor for that resource. This relationship is frequently expressed in terms of R^* , the minimum resource level that can support a consumer population. The best competitor for a single resource is predicted to be the species with the lowest R^* for that resource (prediction 1, table 1). To adequately test this prediction, the investigator should maintain each species in monoculture to determine growth isoclines or similar measures of the minimum resource levels that will sustain a population. Then, pairwise competition experiments must be conducted to determine whether the competitive dominant is the species with the lowest resource requirements. These experiments must be conducted when no other resources are limiting and over a sufficient time period to reach equilibrium or near-equilibrium values.

When two resources are limiting, then either one species can dominate by having a lower R^* for both resources or a trade-off can result if each species has a lower R^* for a different resource. When such trade-offs occur, the resource-ratio theory predicts that species dominance will depend on the ratio of the availabilities of the two resources (prediction 2, table 1). The two species may be able to coexist at intermediate ratios of the two resources, depending on the resource supply vectors for the two resources. An appropriate experimental test would be to vary the ratio of the supply rates of two resources while appropriately controlling for the absolute values of each. If the two species exhibit trade-offs in resource use and appropriate ranges of resources are used, then the competitive outcome should change predictably as the resource-ratio changes.

The resource-ratio theory predicts, however, that, if only two resources are limiting, two species at most can occur at equilibrium. That is, in the absence of spatial or temporal resource heterogeneity, the theory predicts that the number of coexisting species will be less than or equal to the number of limiting resources (prediction 3, table 1). Testing this prediction requires varying the number of limiting resources in relation to the number of competing species. Care must be taken to determine all limiting resources and to follow competitive outcomes to equilibrium.

Trade-offs in R^* 's do not always lead to coexistence in the resource-ratio theory. As in Lotka-Volterra formulations, each species must restrict its own growth more than it restricts the growth of the other species. In resource-ratio theory, this restriction is controlled by the relative values of the vectors describing the resource supply rates and the resource consumption rates. The result is two separate predictions, that the resource supply rates (prediction 4, table 1) and the consumption rates (prediction 5, table 1) will determine whether species can coexist or whether one will dominate the resources and competitively

eliminate others. Tests of this prediction require quantifying or controlling the supply or consumption rates of limiting resources: methods can be quite idiosyncratic and difficult for some systems.

Finally, the resource-ratio theory makes other specific predictions about conditions for coexistence. First, trade-offs in resource use must occur for two species to coexist; each species must consume more of the resource that limits its growth than does the other species (prediction 6, table 1). In the graphical two-species model (fig. 2), the zero-growth isoclines must therefore cross, and each species will be the dominant competitor at a different resource ratio. Also, because very low or very high resource ratios are likely to either exclude all species or allow a single species to persist, the highest diversity of competing species will occur at an intermediate ratio of the availabilities of two resources (prediction 7, table 1).

Literature Survey

We used Web of Science (Thompson ISI) to identify articles in peer-reviewed journals that cited either of the focal Tilman articles and were published between the beginning of 1980 and the summer of 2003. We were unable to work with 13 of the articles, either because of translation difficulties or because we lacked access to the journal. Each of the remaining 1,333 articles was evaluated by an initial reader (all readers are authors of this study), who assigned the article to one of five categories based on the use of the Tilman citation: clear direct tests of predictions from the focal Tilman articles (table 1), possible direct tests of these predictions, theoretical extensions or exploration of the resource-ratio theory, review articles on topics associated with the resource-ratio theory, and background or incidental citations. We were particularly interested in direct tests, in which the authors stated or showed clear intent to test one or more predictions from the focal Tilman articles. If the reader was unsure on first reading whether the article described a direct test, it was assigned to the "possible direct test" category for later reevaluation. Theoretical extensions had to build on the resource-ratio models used by Tilman or intentionally build alternative models stimulated by the resource-ratio approach. Review articles presented compilations of previously published articles, without novel analyses of data from the original articles. Review articles that included a novel reanalysis of previously published data were evaluated as direct tests. Finally, by far the largest number of articles included only incidental citations of the focal articles, generally as background information about resources or competition theory or as a reference for an experimental technique. If an article included tests for more than one prediction, each prediction was tabulated separately, but if it included more

than one experimental test for a given prediction, the results of the various tests were summarized by the reader into a single “support” or “no support” based on the preponderance of the evidence.

Discrepancies associated with individual readers were minimized by assignment of each possible direct test article to two new, randomly assigned readers who discussed it and arrived at a decision about whether the article constituted a direct test and should be reassigned to the direct test category. All articles in the direct test category were then randomly assigned to a further two new readers who independently determined the predictions tested in each study, as well as information about the system and type of experiment conducted. Finally, the readers evaluated the tests for each prediction, asking whether the test was sufficient to evaluate the prediction clearly and whether the test was sufficient, regardless of whether the results supported the prediction. Tests were deemed sufficient if the experiments addressed specific predictions from resource-ratio theory, if they used an unbiased design with appropriate controls and adequate replication, and if they were conducted over an appropriate time period (common difficulties associated with testing each prediction are discussed in the results). The two readers then discussed their independently derived conclusions and came to a consensus about the overall evaluation of the article. The experimental habitat and trophic positions of the species investigated were also noted. We freely admit that this method can be subjective and apologize to the original authors for any misrepresentations of their work. Because of the subjective nature of the data and the often small samples sizes, no statistical comparisons were conducted.

Several other types of articles were noteworthy but could not be dealt with in our review. Many articles may test aspects of the resource-ratio theory but fail to cite Tilman (1980) or Tilman (1982). For example, studies in specialized fields such as microbiology or marine biology may cite a different seminal article from their subject area, rather than either Tilman article. We made no attempt to identify and include such articles, and we acknowledge that this can lead to an unknown bias in the results. Also, a very small number of articles cited only the focal articles for incidental reasons but then included a test of a prediction of the resource-ratio theory without explicitly acknowledging Tilman (1980, 1982). Because we were interested in how the model stimulated further research, we categorized these articles as “incidental citations.”

Results

The great majority (85%) of citations of the focal Tilman articles were not directly relevant to the resource-ratio theory. Such incidental citations generally supported state-

ments about basic competition theory or general concepts such as substitutable resources. A remarkable number of these were single citations in the opening paragraph or even sentence of the article (e.g., “Many mechanisms have been proposed whereby a large number of plant species can co-exist in a single community”; Holah and Alexander 1999, p. 598). Other citations were used to support the use of specific methodologies or experimental studies reviewed by Tilman (1982), such as the Rothamsted grass experiment. One of the rather unusual citations was from a study that fit a Michaelis-Menten model, similar to that used by Tilman (1982), to serum iodine measures taken from coyotes that were allowed to feed on goats injected with iophenoxic acid (Knowlton and Olmstead 2001). An even smaller group of articles (2.9%) used data evaluated by Tilman (1982) as part of a larger review. These incidental and review articles were not of interest for our evaluation.

A significant number of articles (7.2%) were theoretical extensions of the resource-ratio theory or presentations of alternative theories. These theoretical articles fell into two subject areas. First, a number of articles published in the last 20 years have proposed extending the resource-ratio theory to other factors such as predation that can affect population growth (e.g., Leibold 1995; Chase and Leibold 2003). In doing so, they extend the general theory to a greater variety of community patterns. It recently has been argued that the original graphical framework can be extended to provide a more rigorous definition of the niche (Chase and Leibold 2003), a definition that incorporates both the effect of a species on its environment (Elton 1927) and the control by the environment of population growth (Hutchinson 1957).

The second subject area includes theoretical articles that have developed concepts similar or parallel to the resource-ratio theory but cite the focal Tilman articles only peripherally. In particular, the works of Huisman (e.g., 1999) and McClanahan (e.g., 1995) develop and test theory that uses linked sets of equations to describe population growth, resource dynamics, and species interactions.

Predictions of the Resource-Ratio Theory

Of the 1,333 articles evaluated, only 68 (5%) purported to test an assumption or prediction of the resource-ratio theory (appendix in the online edition of the *American Naturalist*). Several of these included tests of more than one prediction; overall, there were 101 tests of the predictions listed in table 1. After we eliminated studies that did not meet our criteria for experimental design, 26 acceptable articles remained, which included 42 acceptable tests of predictions. The majority (32) of these 42 tests were laboratory or artificial microcosm experiments, six

were field observational studies, and surprisingly, only four were field experiments.

Prediction 1 (table 1), that competitive dominance for any single resource is determined by the ability to grow at the lowest level of that resource, might be more correctly called an assumption of the resource-ratio theory. Twenty-two articles purported to test this prediction, but only 13 of them used an experimental design that met our criteria. In most of the other nine studies, we felt that the experiments did not last long enough for one species to be competitively eliminated or for the system to demonstrate that it was nearing an equilibrium state. Of the sufficient tests, eight supported the prediction, and five did not.

Prediction 2, that competitive outcome is determined by the ratio of resource availability, is a primary conclusion of the resource-ratio theory and its most tested prediction, but most (68%) of the 47 experimental studies that attempted to test it used flawed experimental designs. In particular, many studies failed to discriminate adequately between the effects of the ratio of the resources and the absolute magnitude of each. For example, Tilman (1984) simultaneously varied soil nitrogen and magnesium levels, achieving a range of resource ratios, and followed competitive outcomes in plant communities. He concluded both that nutrients were important and that magnesium became more limiting as nitrogen was added. The experiment used a substitutive design for the two nutrients; however, the two nutrient treatments were confounded, leaving unclear whether any response was due to either treatment individually or to their combination (ratio). Later articles on this system have never mentioned a role for magnesium (e.g., Tilman 1986, 1988; Tilman and Cowan 1989; Tilman and Olff 1991; Wilson and Tilman 1991), suggesting that the results of Tilman (1984) were primarily driven by nitrogen variation alone rather than by the ratio of nitrogen to magnesium.

Among studies that do correctly discriminate between the effects of the ratio and the absolute magnitudes of the resources, 13 of 16 support the second prediction. Sommer (1986) is a good example; species dominance in freshwater diatoms varied with silica and phosphorus levels as predicted by monoculture experiments and the resource-ratio theory.

Only three studies investigated prediction 3, that the number of limiting resources puts an upper boundary on the number of coexisting species. Two of these studies met our experimental standards; one supported the prediction. It is interesting that this prediction is so little tested because it is also a prediction of other models of competition. This is a difficult concept to test directly because the conditions for coexistence depend on much more than the number of limiting resources, and cases in which resources outnumber species are not informative. Significant knowledge

of the species and resources in a given system is probably essential for an adequate test of this prediction.

Predictions 4 and 5 are critical components for understanding coexistence and competitive outcome in the resource-ratio theory. The consumption and supply rates of each resource determine the conditions under which coexistence is possible. Only 11 studies tested hypotheses related to the effects of consumption vectors, and three investigated the effects of supply rates on competitive outcomes (table 2). Most of the eight studies that addressed one of these two predictions and met our design standards supported the resource-ratio theory. An excellent example is that of Rothhaupt (1988), in which growth isoclines for substitutable resources were estimated by the amount of each resource needed in monocultures of each of two rotifer consumers. Consumption vectors were estimated for each rotifer species so that the authors could make quantitative predictions about when each rotifer species would competitively eliminate the other and when they would coexist; these predictions generally held up under laboratory conditions.

Prediction 6, that coexistence of species will occur only in the presence of trade-offs in minimum requirements for different resources, was directly addressed by only five studies, three of which had experimental designs that met our criteria. Two studies supported the prediction, and that of Sommer (1986) was again a particularly good example. Sommer maintained mixtures of phytoplankton over a gradient of resource supply rates in the laboratory and followed competitive outcomes. He also followed the growth of each species in monoculture under phosphorus-limited conditions and determined the maximum growth

Table 2: Number of individual tests of the seven predictions of the resource-ratio theory listed in table 1

Prediction number	Test adequate?			Total
	Yes; prediction supported?		No	
	Yes	No		
1	8	5	9	22
2	13	3	31	47
3	1	1	1	3
4	5	1	5	11
5	2	0	1	3
6	2	1	2	5
7	0	0	10	10
Total	31	11	59	101

Note: The 101 overall tests were published in 68 different articles. Tests were classified as adequate if a clear and sufficient experimental design and appropriate replication were used. Studies were classified as supporting the prediction on the basis of our interpretation of the results presented in the corresponding article.

rate and half-saturation constants. The results revealed a trade-off between competitive ability at low resource-supply rates and growth rate at high resource-supply rates.

Finally, we found 10 studies that purported to test prediction 7, that a single species will persist at very high and very low resource ratios and therefore that the highest diversity of competing species will occur at an intermediate ratio. Unfortunately, methodological insufficiencies weakened the conclusions in all 10 articles. Perhaps the best test of this prediction comes from Leibold's (1999) observational study of freshwater plankton communities, in which a single resource, phosphorus, rather than any ratio of phosphorus and nitrogen, seemed to determine productivity and species composition. No maximum in diversity was observed at intermediate resource ratios.

Trophic Levels and Habitats Used to Test the Resource-Ratio Theory

The earliest applications of the resource-ratio theory were to primary producers in aquatic systems (O'Brien 1974; Tilman 1977), but the major proponent of later application of the theory, David Tilman, specifically proposed its use in terrestrial plant communities (Tilman 1982, 1984, 1988). It is of interest after more than 20 years to see where the theory has been applied and supported.

Examination of all studies of predictions of the resource-ratio theory reveals that aquatic producers are still the system used most often to test its predictions (fig. 3). Producers were investigated in more than 70% of the articles; most were from freshwater or terrestrial habitats. Primary consumers were the second-most-tested trophic level; the majority were freshwater zooplankton. As is probably generally true in ecological studies, detritivores appear to have been seldom investigated.

Perhaps a more interesting question is where the

Table 3: The habitat type used for each of the 42 adequate tests shown in table 2

Prediction supported?	Freshwater	Marine	Terrestrial
Yes	23	5	3
No	8	1	2

Note: The majority of adequate tests were performed in freshwater habitats.

resource-ratio theory seems best supported. Of the individual tests within studies that met our design criteria, grouped by habitat, 31 tests supported the resource-ratio theory, and 11 did not; most of the tests were conducted in freshwater systems (table 3). The aquatic systems seemed generally to support the resource-ratio theory. Although the sample size was very small (only five tests), terrestrial studies did not consistently support the resource-ratio theory. When the adequate tests were grouped by trophic level (table 4), tests from all trophic levels generally supported the theory. Small sample sizes make it difficult to draw conclusions for detritivores and consumers.

Discussion

Has the Resource-Ratio Theory Been Adequately Tested?

About one in every 18 articles that cite the focal articles provides some experimental test of predictions of the resource-ratio theory. It is difficult to know whether this proportion is higher or lower than the "average" for any given theory. These publications provide 101 tests of the seven predictions we propose, and 42 of those tests meet our design criteria. Another significant group (96) of the cited articles are theoretical extensions of the original resource-ratio theory.

Overall, the predictions of the resource-ratio theory

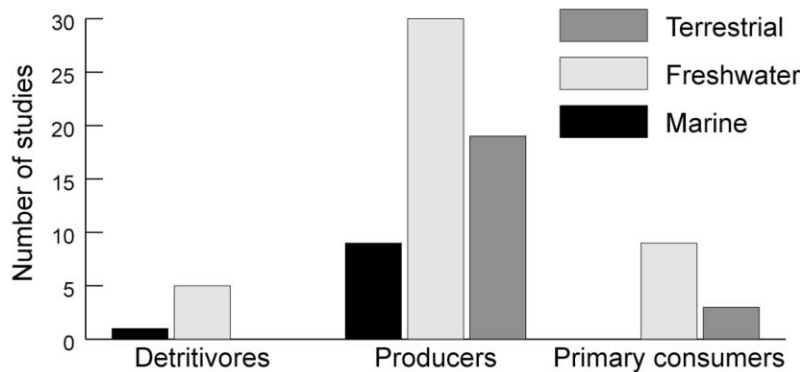


Figure 3: Numbers of proposed tests (from 68 published articles) of the resource-ratio theory by trophic level and habitat. Some studies included more than one trophic level and are represented in more than a single category.

Table 4: Trophic groups used in each of the 42 adequate tests shown in table 2

Prediction supported?	Producer	Primary consumer	Detritivore
Yes	22.5	5.5	3
No	8.5	1.5	1

Note: If more than one trophic group was involved in a single test, then contributions were weighted by the number of trophic groups. The majority of adequate tests involved primary producers.

were supported 75% of the time by adequate experimental studies. This number is not especially meaningful, as the theory is not expected to hold true in all environments at all times. It is much more interesting to ask which predictions are supported and where.

What Can We Conclude from Tests of the Resource-Ratio Theory?

Unfortunately, many of the predictions of the resource-ratio theory have simply not been tested often enough. Only three of the seven predictions have been experimentally addressed more than 10 times (table 2), and many of these tests were deemed insufficient by our standards. Only prediction 1 (that species with lower resource needs for a given resource are better competitors for that resource) and prediction 2 (that species dominance varies with the ratio of the availabilities of the two resources) have been adequately tested in more than 10 studies. Both can be tested by manipulation of resource levels and observation of species abundances at or near equilibrium. Some of the other predictions can be very difficult to test. For example, predictions 4 and 5 are critical to the theory for determining when species should coexist. Yet testing either prediction requires quantifying resource flux rates, which is very difficult in many systems.

We can also draw conclusions about what types of habitats or species have been used to test the resource-ratio theory, although we acknowledge that some research areas may be more likely to cite Tilman than others. Most tests to date have involved freshwater systems, where predictions of the theory have drawn broad support (table 3). These studies usually involve either phytoplankton or zooplankton, which can be ideal for experimental studies and are very amenable to growth in chemostats, where resources can be highly controlled. On the other hand, only five adequate tests, all on plants, have been conducted in terrestrial systems. Only half of these studies support the resource-ratio theory, but the small number of studies precludes drawing any conclusions. When the studies are divided by trophic level, strong support for the theory emerges from experiments conducted with producers, pri-

marily with aquatic phytoplankton (table 4). No other trophic groups have been well investigated.

Areas Where Further Research Is Needed

Our review shows that several aspects of the resource-ratio theory have not been adequately tested. Although some of the broadest predictions of the model have been tested (e.g., prediction 2), important components of the theory pertaining to resource supply and use have generally not been tested. Predictions from the resource-ratio theory involve more than zero-growth isoclines; the supply and use vectors are equally important for determining whether and when species can coexist. Although the value of the resource-ratio theory may be largely qualitative, we feel that quantitative predictions related to these components (predictions 3 and 4) must be experimentally tested in a variety of systems.

The dearth of adequate experimental field studies is also a problem, although other studies have replicated different types of habitats under artificial conditions. The types of conditions used to test the theory's predictions are also strongly biased. Most experiments to date used primary producers in aquatic systems, perhaps because of the original systems used (e.g., by O'Brien 1974; Taylor and Williams 1975; Tilman 1977), the experimental ease of working with aquatic systems, or scientists' expectations about where the theory will best apply. For example, few scientists have applied the resource-ratio theory to terrestrial plant communities, and three of the five acceptable studies were conducted at the same locality (Cedar Creek). Patchy resource availability and the relatively long generation times may make it difficult to evaluate the resource-ratio theory in these types of communities. More experiments testing predictions of the resource-ratio theory are needed to determine the breadth and limits of its application.

Finally, we found it disconcerting that so many studies intended to test predictions of the resource-ratio theory were inadequately designed to do so. By their very nature, reviews like this one include experiments conducted in different systems that have different biases, methods, and standards (see, e.g., Connell 1983; Schoener 1983; Sih et al. 1985). Further, such reviews often take experiments

somewhat out of context: the authors' goals may have been much more limited and cautiously interpreted than our use suggests. Still, 60% of the experiments reviewed here purported to test the resource-ratio theory but were deemed unacceptable because of flaws in the experimental design. It is also surprising that only four of the acceptable tests of predictions were from experimental field studies, with the rest being observational or conducted in artificial microcosms. More well-designed field studies of the resource-ratio theory are needed.

Evaluating Theory in Science

The role of theory in science has long been debated (Rouse 1987). Theory can range from a purely heuristic tool to a more detailed model that allows detailed predictions. Therefore, evaluation of theory, especially of general theory, can be highly problematic and is rare. Broad theories in ecology and evolution have, however, been evaluated by large reviews (e.g., Connell 1983; Schoener 1983; Sih et al. 1985; Kingsolver et al. 2001); arguably, these reviews help to define the applicability of a particular theory as well as to provide direction for further research.

If we view the resource-ratio theory as purely heuristic, then we can say that it has been incredibly successful. It has stimulated a great deal of experimental and theoretical work. More importantly, it helped to change how we think about competition; it allowed ecologists to visualize competition in a mechanistic fashion and species as interacting through shared resources.

On the other hand, if we evaluate the resource-ratio theory for its more explicit predictions, then we would have to say that, at best, the theory has been insufficiently tested. Its predictions are widely accepted and cited, and the concept is included in most major textbooks on ecology. However, it has been rigorously tested only a limited number of times in a small range of community types (table 2) and almost never in natural communities.

Here, our intent was not to evaluate the resource-ratio theory itself but to review its use and to begin a discourse on its application. We hope our review will lead to more rigorous experimental evaluation, evaluation of the role of resource supply and use vectors, and an application of the theory to a broader variety of habitats and trophic levels. Ultimately, we hope it leads to a shift from considering whether to considering where the resource-ratio theory applies.

Acknowledgments

We are grateful to J. Grover for providing helpful comments and spotting several important problems with earlier versions.

Literature Cited

- Abrams, P. A. 1988. Resource productivity and consumer-species diversity: simple models of competition in spatially heterogeneous environments. *Ecology* 69:1418–1433.
- Begon, M., J. L. Harper, and C. R. Townsend. 2000. *Ecology: individuals, populations, and communities*. Blackwell Scientific, Oxford.
- Bush, M. B. 2000. *Ecology of a changing planet*. Prentice Hall, Upper Saddle River, NJ.
- Chase, J. M., and M. A. Leibold. 2003. *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press, Chicago.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* 122:661–696.
- Dugdale, R. C. 1967. Nutrient limitation in the sea: dynamics, identification and significance. *Limnology and Oceanography* 12:655–695.
- Elton, C. 1927. *Animal ecology*. Sidgwick & Jackson, London.
- Gause, G. F. 1932. Experimental studies on the struggle for existence. I. Mixed populations of two species of yeast. *Journal of Experimental Biology* 9:389–402.
- Grover, J. P. 1997. *Resource competition*. Chapman & Hall, London.
- Hansen, S. R., and S. P. Hubbell. 1980. Single-nutrient microbial competition: qualitative agreement between experimental and theoretically forecast outcomes. *Science* 207:1491–1493.
- Harper, J. 1983. Resource competition and community structure, by D. Tilman (book review). *Journal of Ecology* 71:663–664.
- Holah, J. C., and H. M. Alexander. 1999. Soil pathogenic fungi have the potential to affect the co-existence of two tallgrass prairie species. *Journal of Ecology* 87:598–608.
- Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitation and apparent competition. *American Naturalist* 144:741–771.
- Huisman, J., P. van Oostveen, and F. J. Weissing. 1999. Species dynamics in phytoplankton blooms: incomplete mixing and competition for light. *American Naturalist* 154:46–68.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Springs Harbor Symposium in Quantitative Biology* 22:415–427.
- Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, P. Gilbert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. *American Naturalist* 157:245–261.
- Knowlton, F. F., and S. R. Olmstead. 2001. Using iophenoxic acid injections of prey to identify mammals that feed on them. *Wildlife Society Bulletin* 29:495–500.
- Krebs, C. J. 2001. *Ecology: the experimental analysis of distribution and abundance*. Benjamin Cummings, San Francisco.
- Leibold, M. A. 1995. The niche concept revisited: mechanistic models and community context. *Ecology* 76:1371–1382.
- . 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence and diversity patterns in communities. *American Naturalist* 147:784–812.
- . 1998. Similarity and local co-existence of species in regional biotas. *Evolutionary Ecology* 12:95–110.
- . 1999. Biodiversity and nutrient enrichment in pond plankton communities. *Evolutionary Ecology Research* 1:73–95.
- Leon, J. A., and D. B. Tumpson. 1975. Competition between two

- species for two complementary or substitutable resources. *Journal of Theoretical Biology* 50:185–201.
- MacArthur, R. H. 1972. *Geographical ecology: patterns in the distribution of species*. Princeton University Press, Princeton, NJ.
- Maguire, B. 1973. Niche response structure and the analytical potentials of its relationship to the habitat. *American Naturalist* 107:213–246.
- McClanahan, T. R. 1995. Harvesting in an uncertain world: impact of resource competition on harvesting dynamics. *Ecological Modelling* 80:21–26.
- O'Brien, W. J. 1974. The dynamics of nutrient limitation of phytoplankton algae: a model reconsidered. *Ecology* 50:930–938.
- Phillips, O. M. 1973. The equilibrium and stability of simple marine biological systems. I. Primary nutrient consumers. *American Naturalist* 107:73–93.
- Ricklefs, R. E., and G. L. Miller. 2000. *Ecology*. 4th ed. W. H. Freeman, New York.
- Rothhaupt, K. O. 1988. Mechanistic resource competition theory applied to laboratory experiments with zooplankton. *Nature* 333:660–662.
- Rouse, J. 1987. *Knowledge and power: toward a political philosophy of science*. Cornell University Press, Ithaca, NY.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* 122:240–285.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* 16:269–311.
- Sommer, U. 1986. Phytoplankton competition along a gradient of dilution rates. *Oecologia (Berlin)* 68:503–506.
- Stewart, F. M., and B. R. Levin. 1973. Partitioning of resources and the outcome of interspecific competition: a model and some general considerations. *American Naturalist* 107:171–198.
- Stiling, P. D. 2002. *Ecology: theory and applications*. 4th ed. Prentice Hall, Upper Saddle River, NJ.
- Strong, D. R., D. Simberloff, L. G. Abele, and A. B. Thistle. 1984. *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, NJ.
- Taylor, P. A., and P. J. LeB. Williams. 1975. Theoretical studies on the coexistence of competing species under continuous-flow conditions. *Canadian Journal of Microbiology* 21:90–98.
- Tilman, D. 1977. Resource competition between planktonic algae: experimental and theoretical approach. *Ecology* 58:338–348.
- . 1980. A graphical-mechanistic approach to competition and predation. *American Naturalist* 116:362–393.
- . 1982. *Resource competition and community structure*. Princeton Monographs in Population Biology 17. Princeton University Press, Princeton, NJ.
- . 1984. Plant dominance along an experimental nutrient gradient. *Ecology* 65:1445–1453.
- . 1985. The resource-ratio hypothesis of plant succession. *American Naturalist* 125:827–852.
- . 1986. Nitrogen-limited growth in plants from different successional stages. *Ecology* 67:555–563.
- . 1988. Plant strategies and the dynamics and structure of plant communities. Princeton Monographs in Population Biology 26. Princeton University Press, Princeton, NJ.
- Tilman, D., and M. L. Cowan. 1989. Growth of old field herbs on a nitrogen gradient. *Functional Ecology* 3:425–438.
- Tilman, D., and H. Olff. 1991. An experimental study of the effects of pH and nitrogen on grassland vegetation. *Acta Oecologica* 12:427–441.
- Titman, D. 1976. Ecological competition between algae: experimental confirmation of resource-based competition theory. *Science* 192:463–465.
- Wilson, S. D., and D. Tilman. 1991. Components of plant competition along an experimental gradient of nitrogen availability. *Ecology* 72:1050–1065.
- Winsor, C. P. 1934. Mathematical analysis of growth of mixed populations. *Cold Spring Harbor Symposia on Quantitative Biology* 2:181–187.

Editor: Jonathan B. Losos
Associate Editor: James P. Grover