

Evaluating Support for the Resource-Ratio Hypothesis: A Reply to Wilson et al.

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We reviewed 1,333 papers that cite Tilman (1980, 1982) and test specific predictions of the resource-ratio hypothesis (RRH). The primary conclusions of our article (Miller et al. 2005) were (1) that relatively few articles that cite Tilman's publications (1980, 1982) provide well-designed tests of predictions of RRH; (2) that most of these tests were conducted in labs or experimental microcosms and involved primary producers in freshwater systems; (3) that overall, the majority of the well-conducted experiments do support RRH; and (4) that many of the predictions of RRH have been insufficiently tested to allow generalization, especially predictions related to resource supply and consumption rates. We encouraged further studies on RRH, especially in natural systems.

In their note, Wilson et al. (2007) appear to agree with all of these conclusions. Instead, their concern is that the magnitude of support for one prediction of RRH was

much greater than we stated in our article, and they feel we should have noted this strong support. In table 2 of our article, we list the number of articles that we felt support or do not support seven different predictions of RRH. Prediction 1 (competitive dominance is determined by the ability to grow at the lowest level of a given limiting resource) was addressed by 13 of the studies we reviewed. We felt that eight of these studies support this prediction and five do not, but we made no further evaluation of this specific result. Wilson et al. (2007) evaluate these articles differently, suggesting that 12 papers support prediction 1, and one paper (Grover 1991) was not applicable. They feel that this constitutes strong support and that we should have specifically noted such support for this one of the seven predictions we identified for RRH.

We have reevaluated the five articles in question and politely disagree with Wilson et al. However, this difference of opinion illustrates the difficulty of conducting a large subjective review in which many of the papers cannot easily be identified as either supporting or not supporting RRH. We would argue that some of the five papers in question would clearly not support prediction 1. In Tilman and Wedin (1991), for example, the authors themselves acknowledge that their results are not consistent with prediction 1, and in fact, they provide a thoughtful and important discussion on possible limits to the application of RRH. Others of the four papers can be quite difficult to place in simple "yes" or "no" categories. For Huisman et al. (1999), we felt that the actual resource levels from monocultures at equilibrium should be used to test prediction 1 rather than least square fits to time series data that included data from when the cultures were not at equilibrium. If so, then the competitive ranking predicted from monocultures does not match that observed from competition studies, and this study does not clearly support prediction 1. Finally, at least one study may have been miscategorized in our article; Spijkerman and Coesel's (1996) excellent study on algal competition (listed in the appendix to our article) does appear to support prediction 1.

We do wish to clarify that we enumerated results by article rather than by individual experiments within an

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article. For example, each study in table 2 was counted only once, whether it contained 10 experiments or only one. Because studies reflect the adherence of a particular system to RRH, if any experiment within a study failed to support a prediction, then we counted the entire study as a “no” in table 2. For example, Hu and Zhang (1993) present their results in their figures 1–5. We felt that their figures 2 and 3 clearly showed coexistence of species for significant periods of time, although the RRH would predict competitive exclusion. Because two of the five tests were not consistent with prediction 1 of RRH, we put this article in the “no” category, which differs from the evaluation of Wilson et al. 2007.

However, we do not wish to get into an unproductive argument about the subjective evaluation of specific articles, especially since Wilson et al. (2007) appear to be in general agreement about the overall conclusions of our review. They are in agreement with our evaluation that a majority of the articles that test prediction 1 were found to support this prediction of RRH. Further, Wilson et al. state that they agree with our original conclusion that further research is needed to test the resource-ratio hypothesis, especially in a variety of systems. We would suspect that Wilson et al. would also agree that there still is insufficient evidence to evaluate the majority of the predictions we identify from RRH (predictions 3–7 in table 2 in our article [Miller et al. 2005]).

We do wish to emphasize that knowledgeable readers can come to very different conclusions about the same article, especially when the experimental work was not specifically designed to test a given prediction of RRH. We recognized this problem while conducting our review and duly modified our methods. Each article in table 2 ultimately was read by five of the eight authors of Miller et al. (2005). The readers determined whether the article was sufficiently well designed to address at least one of the

seven identified predictions. They also interpreted the conclusions of any relevant experiment with regard to the predictions. It was somewhat frustrating that the multiple readers frequently differed in the interpretations of the results, and some discussion was often necessary to reach a consensus. Finally, as we noted (Miller et al. 2005, p. 443), “We freely admit that this method can be subjective and apologize to the original authors for any misrepresentations of their work.”

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