

Gauging the impact of meta-analysis on ecology

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Abstract Meta-analyses are an increasingly used set of statistical tools that allow for data from multiple studies to be drawn together allowing broader, more generalizable conclusions. The extent to which the increase in the number of meta-analyses in ecology, relative to other types of papers, has influenced how questions are asked and the current state of knowledge has not been assessed before. Here, we gauge the impact of meta-analyses in ecology quantitatively and qualitatively. For the quantitative assessment, we conducted an analysis of 240 published meta-analyses to examine trends in ecological meta-analyses. Our examination shows that publication rates of meta-analyses in ecology have increased through time, and that more recent meta-analyses have been more comprehensive, including more studies and a greater temporal range of studies. Meta-analyses in ecology are the result of larger collaborations with meta-analyses being authored by larger teams than other studies, and those funded by collaborative centers have even larger collaborations. These larger collaborations result in a larger scope and scale of the analyses—by using more papers, datasets, species and years of data. Qualitatively, we discuss three examples: the strength of competition, the nature of how biodiversity affects ecosystem function, and the response of species to global climate change, where meta-analyses

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supplied the critical evaluation of accepted ecological explanations. As scientific criticism and controversy mount, the true power of meta-analyses is to serve as the capstone evidence supporting the validity of an explanation and to possibly herald the shift to other potential explanations.

Keywords Biodiversity · Collaboration · Competition · Debate · Ecosystem function · Hypothesis testing

Introduction

Traditionally, field observations and experiments served as the primary avenues to uncover empirical patterns and attribute mechanisms in ecology and ecosystem science (e.g., Connell 1961; Paine 1966). Globally, the results from thousands of observational and experimental studies have been published. To some, these types of studies have reinforced the perception that ecology is a science of idiosyncratic, provincial case studies, with limited support for broad generalities (Peters 1991; Lawton 1999). This pessimistic view of ecology has largely given way to a more optimistic search for the general mechanisms structuring communities (e.g., Hubbell 2001; Leibold et al. 2004; McGill 2006; Loreau 2010; Massol et al. 2011). Part of this renewed excitement has been catalyzed by the development or expansion of theoretical models, but it also stems from the burgeoning number of synthetic treatments that combine multiple studies into meta-analyses (Lindenmayer and Likens 2011).

Meta-analytic methods to combine experimental data and test general hypotheses in ecology emerged in the early 1990s (Gurevitch et al. 1992; Arnqvist and Wooster 1995; Gurevitch et al. 2001; Gurevitch and Hedges 2001). This quantitative data synthesis has the benefit of presenting the “bigger picture”, that is, meta-analyses allow data to be collected from a large number of publications, sites, taxa, etc., and permit the presentation of analysis in a standardized metric (Osenberg et al. 1999; Gurevitch et al. 2001; Gurevitch and Hedges 2001). In this sense, meta-analyses may provide a method for processing multi-scale spatial and temporal patterns of dynamic populations, communities, and ecosystems (Levin 1992).

Meta-analyses are a powerful approach for statistically testing hypotheses. Non-meta-analytic reviews that evaluate hypothesis support by enumerating the studies reporting positive results (i.e., vote-counting) have substantial drawbacks (Arnqvist and Wooster 1995; Gurevitch et al. 2001; Gurevitch and Hedges 2001). Statistical power is a product of the magnitude of the measured effect, observation variance and sample size. Small studies are less likely to find significant effects and thus vote-counting underestimates empirical support for hypotheses (Gurevitch and Hedges 2001). Conversely, meta-analyses explicitly account for sample error and sample size when comparing effect sizes and thus have the power to detect significant differences in the pooled data even when individual datasets fail to detect significant effects (Olkin 1996; Hedges et al. 1999; Gurevitch and Hedges 2001). Of course there are limitations with meta-analyses. Heterogeneity among sample sites or specific experimental treatments may be an important component of understanding the mechanisms producing patterns (Olkin 1996). In ecology, to understand and manage communities, the idiosyncratic forces generating community patterns may need to be accounted for (Simberloff 2006). Further, there may be a bias towards authors publishing positive results (Murtaugh 2002), which may bias the data towards larger effect sizes than

would be produced in a true random sample, though this criticism equally applies to vote-counting.

Regardless of the specific criticisms, there are clear epistemological reasons for ecologists to use meta-analyses to test hypotheses. Indeed, ecologists have broadly adopted meta-analysis as an analytical tool, as shown by number of meta-analyses published, which has been increasing at a rate faster than the general increase in ecological publications (Fig. 1; ecological papers have been increasing at an annual increase of $9\% \pm 0.05\%$, while meta-analyses have been increasing at a rate of $25\% \pm 1.1\%$). Perhaps more important than the epistemological reasons, there may be cultural and technological reasons why ecologists increasingly use meta-analyses. There have been cultural shifts in ecology that may reinforce meta-analyses as a normative activity for ecologists, for example, students are trained to do meta-analyses and there are special issues of journals dedicated to meta-analyses. Further, large meta-analyses may be easier to publish in high impact journals and receive more citations (Lindenmayer and Likens 2011), though most high impact journals do primarily publish empirical papers (Tucker and Cadotte 2011). Funding and cultural norms see meta-analysis as the pinnacle of collaborative data synthesis; therefore we should expect that meta-analytic publications are more collaborative than researcher-collected data analyses. The increasing quantity of data over time and the development of methods and infrastructure to archive and share data (Jones et al. 2006; Michener 2006) increase data accessibility, further reinforcing the push to do meta-analyses. These recent technological advances also mean that meta-analyses should increase in the number of datasets used, corresponding to increased number of sites, species and years included. Put another way, the scope and scale of meta-analyses should increase over time. To understand how meta-analyses have changed in the amount and type of data and whether they are more collaborative, we examine publication trends in 240 ecological meta-analyses. We also provide insights into the nature of collaborative meta-analyses.

However, examining publication trends offers but a cursory overview of the meaningful impact that meta-analyses have had on ecology. There are many different types of ecological questions that have been subjected to meta-analyses, and perhaps many of these simply confirm previous well-supported hypotheses. Regardless of the novelty of the hypotheses, meta-analyses offer an opportunity to assess the strength or importance of ecological relationships and in this sense can have a major impact on our understanding, especially for controversial hypotheses. This is a difficult aspect to quantify, and we here review three case studies, where meta-analyses served to synthesize data to address lingering debates. The first is on the strength and importance of competitive interactions in shaping communities. The second is on the importance of species diversity effects on ecosystem function. The final example is on how global warming is affecting species within communities.

Survey of meta-analyses

On 2 September, 2008, we searched the literature database ISI Web of Science with the keywords (“meta-anal*” or “metaanal*” or “meta anal*”) in 28 ecological journals and four more general scientific journals with the added keywords (“ecol*” or “ecos*”) (see Appendix 1 for journal list). These searches resulted in a list of 457 publications. No unpublished studies were solicited. Publications were included in our meta-analysis only if they a) included a statistical analysis of more than two other publications and b) included

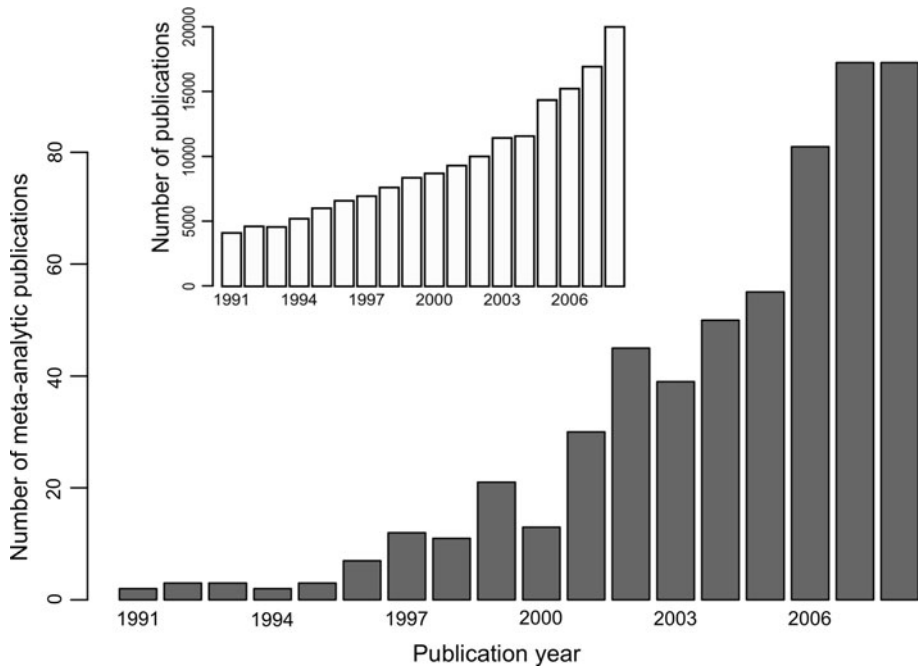


Fig. 1 Meta-analytic studies in ecology and ecosystem science first appeared in the early 1990s. The number of papers using meta-analysis methods has increased exponentially (*grey bars*) at a rate of 28 % per year ($SE = 1.44\%$), which is significantly higher than the general increase in ecology and ecosystem publications (*white bars*: 9 % per year, $SE = 0.05\%$)

ecological data. These filters resulted in a total of 240 publications being included in our study (see Appendix 2 for full list of publications used).

From these publications we extracted 17 variables (full list available in Appendix 1). Not all categories of variable could be obtained from each study. For example, if a study did not distinguish between publications used for meta-analysis and those used as references, “number of papers in meta-analysis” was left blank. We determined the number of unique years represented by the publications used in the dataset of each meta-analysis. For our analysis here, we were interested in how the scope and scale of meta-analyses have changed over time and thus examined how the number of species, datasets, publications and years used in the meta-analyses changed over time. We used linear regressions, modeling the log-transformed dependent variable as a function of publication year. However, the dependent variables exhibited increasing variance with time (inset Fig. 2), and so we also performed quantile regressions. When the quantile regression performed at the mode gave qualitatively similar results to the least-squares regressions, we present the results of the least-squares regression. However, we show the results for higher quantile (e.g., 75th or 90th quantiles) results when the least-squares regression was not significant. The linear regression on log-transformed data was used in lieu of Poisson regressions for count data, so that the results could be compared to quantile regressions.

We were further interested in how the scope and scale of meta-analyses affected the number of times they were cited by other papers. We examined how the number of species, publications, datasets and years affect citation accumulation, with each in a model that included the publication year of the meta-analysis and their interaction.

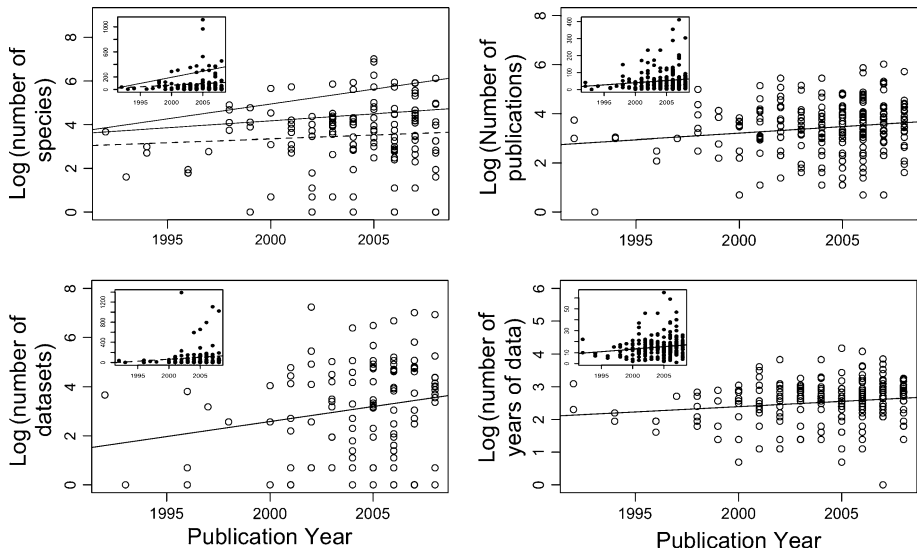


Fig. 2 Regressions of the number of species, publications, data sets and number years used in meta-analyses compared to year of publication. *Solid regression lines* indicate a significant relationship. In the first panel, the least-squares regression was not significant (*dashed line*) but quantile lines were (for 75th and 90th quantiles). *Insets* show the distribution of the untransformed data showing large increases in variance over time

To examine how meta-analyses have influenced the number of authors participating in a study, we compared the number of authors on meta-analyses to 240 randomly drawn papers from the same set of journals and time frame for the meta-analysis search above, repeated 500 times. We compared the observed mean number of authors of meta-analyses to the mean and 95 % confidence interval of the randomly chosen papers.

We were also interested in determining how these patterns of collaboration influence the scope and scale of meta-analyses. To do this, we used Poisson regressions to examine the relationships between number of authors and the number of species, datasets, years and publications.

All analyses were done using statistical program R (2.8) (R Development Core Team 2009).

Has the scope and scale of meta-analyses changed?

Comparing how the logged-transformed measures of meta-analysis scope and scale changed over time, we found that recent meta-analyses included a marginally significantly greater number of species (75th and 90th quantiles; $\beta_1 = 0.064$, $P = 0.063$ and $\beta_1 = 0.136$, $P = 0.055$, respectively), and significantly greater number of publications ($\beta_1 = 0.053$, $P = 0.015$) and datasets ($\beta_1 = 0.123$, $P = 0.031$), across more years ($\beta_1 = 0.032$, $P = 0.015$) than older meta-analyses (Fig. 2). Moreover using Pearson correlations, meta-analyses that used a greater number of publications represent more phyla ($r = 0.23$, $P < 0.05$) and species ($r = 0.35$, $P < 0.05$), and those whose data spanned a greater number of years also contained more phyla ($r = 0.25$, $P < 0.05$), species ($r = 0.39$, $P < 0.05$) and datasets ($r = 0.33$, $P < 0.05$). Since 2000 there has been an explosion in the number of meta-analyses published (Fig. 1) and during this period

extremely expansive meta-analyses have been published that combine data from hundreds of papers and datasets representing hundreds of species across multiple decades (Fig. 2 insets). While the mean number of publications, datasets, species and years used have all increased through time, the variance has dramatically increased because of the emergence of these large meta-analyses [examples of some of the largest meta-analyses include: Gross 2005 (1,113 species); Micheli and Halpern 2005 (525 species); Suding et al. 2005 (967 species); Karst et al. 2008 (1,023 datasets)].

Using Poisson models that account for publication year, the number of times a meta-analysis has been cited was significantly positively related to the number of publications used in the analysis ($\beta_1 = 2.770$, $P < 0.001$), to the number of species included ($\beta_1 = 1.544$, $P < 0.001$), and to the number of years included ($\beta_1 = 4.446$, $P < 0.001$), but unrelated to the number of datasets used in the analysis ($\beta_1 = 0.074$, $P = 0.102$). The discrepancy between number of publications and number of data sets reflects the fact that only half as many meta-analyses reported the number of datasets used compared to those that report the number of publications used ($n = 111$ vs. 220). The differing number of data points for each variable highlights the reality that many published meta-analyses do not report important details about the data used. With many not reporting summaries of the number of datasets used or the number of years represented in their data it is difficult to assess the potential influence of potentially confounding variables.

Our results also demonstrate notable changes in meta-analytical trends over the last two decades. Recent meta-analyses are more likely to include a greater number of publications in their databases, which in turn represent a greater number of unique publication years. This trend may reflect the ever-widening pool of ecological studies from which to draw every year and the relative ease with which papers and data can be electronically accessed. Older papers are increasingly accessible online and are thus more easily included in newer meta-analyses. Whatever the reason, these results demonstrate that authors of meta-analyses are gravitating towards more expansive datasets, that represent more ecosystems.

Meta-analyses and the nature of collaboration

Meta-analyses are the result of larger collaborations (Fig. 3). Papers published in the same journals and timeframe as the meta-analyses tend to have fewer authors (3.17 vs. 3.64 for meta-analyses). Using Poisson regressions, we found that papers with more authors result in meta-analyses that use significantly more species ($\beta_1 = 0.0127$, $P < 0.001$), more datasets ($\beta_1 = 0.0231$, $P < 0.001$), marginally more publications ($\beta_1 = 0.0054$, $P = 0.070$), but there was no effect on the number of years used ($\beta_1 = 0.0020$, $P = 0.727$). Further, using a Poisson regression accounting for publication year, meta-analyses with more authors were cited substantially more ($\beta_1 = 2.23$, $P < 0.001$), with each increase in author number resulting in 9.30 more citations. Research suggests that scientists are more likely to cite within their own area of expertise (Menge et al. 2009), so incorporating a large number of authors from a wide variety of fields could increase the readership and number of citations of a given meta-analysis.

The role of collaboration in science is critical, and is likely to continue to grow in importance. Scientific research itself has been described as an act of imagination and innovation (Hackett and Parker 2010), and the flow of ideas and the synthesis of methods, results, and expertise across a variety of spatial and temporal scales is compounded by multiple, independently-thinking contributors. Scientific synthesis increases “the generality, parsimony, applicability, or empirical soundness of scientific explanations and science-based innovations” (Carpenter et al. 2009). Ostensibly, the more experts examining the data and evaluating the methodology and results, the more sound the conclusions.

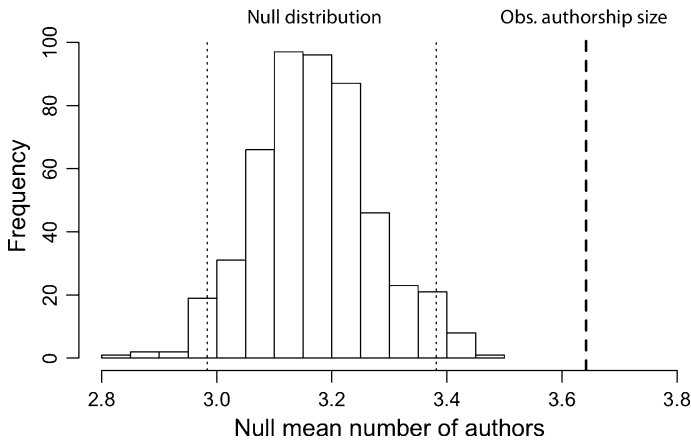


Fig. 3 A histogram of the mean number of authors for 500 randomly selected sets of 238 papers from the same journals and timeframe as the meta-analyses examined. The dotted lines are the 95 % CI for the means and the dark dashed line is the observed mean number of authors on meta-analyses

We assessed the affiliations of meta-analysis authors and their funding sources and over 15 percent ($n = 37$) of meta-analyses were affiliated with synthetic research centers, with the majority ($n = 31$) of these papers originating from the National Center for Ecological Analysis and Synthesis (NCEAS). The other centers include: National Evolutionary Synthesis Center, National Institute for Mathematical and Biological Synthesis, Center for Population Biology, Silverwood, Santa Fe Institute, Max Planck Institute. Some institutions have been around for a longer time while others are quite recent, but their prominence seemed to gain momentum in the mid 1990's and has had important impacts on the state of knowledge in ecology and how ecology is done (Hampton and Parker 2011). Using Poisson regressions, we found that significant differences existed between meta-analyses from synthetic centers and those from independently-affiliated researchers in a number of the variables examined. Meta-analyses from centers had nearly twice as many authors ($P < 0.05$), were published in journals with $1.6\times$ higher impact factor ($P < 0.05$), included $1.6\times$ as many species ($P < 0.05$), incorporated $1.4\times$ as many publications ($P < 0.05$) and had $1.3\times$ as many datasets in their analyses ($P < 0.05$) compared to meta-analyses from other papers. Such centers have funding designated for promoting international collaborations at themed workshops, assembling larger groups of researchers, and archiving and disseminating data, all of which would appear to be fertile ground for producing meta-analyses (Hampton and Parker 2011). Given the increasing incidence and impact of meta-analyses, we can expect synthesis centers to gain importance within the discipline of ecology.

The changing nature of collaboration has had a direct effect on meta-analyses. As researchers pursue larger collaborations to tackle larger, more complex problems, they bring with them knowledge from subdisciplines and more disparate data sets, making meta-analyses more probable and extending the scope and scale of meta-analyses. This changing cultural norm about collaboration has been reinforced by specific funding mechanisms and the creation of synthesis centers geared towards collaborative ventures.

Examples of meta-analyses that changed ecological understanding

The quantitative review above reveals that meta-analyses have increased in terms of their scale and scope over time, and are the results of larger collaborations. But the question remains, have they uniquely changed our understanding of ecological phenomena? Strictly speaking, a meta-analysis is the compilation of disparate studies that manipulate or observe the same factors. Thus, the opportunity for meta-analyses to make novel contributions is rather limited. Instead, the true power of meta-analyses is their ability to make robust conclusions about controversial ideas. While we cannot review the qualitative impact of all the meta-analyses included in this review, we will examine three examples where meta-analyses have supplied critical evidence to on-going debates.

Competition

Competition has a special place at the center of ecology. Charles Darwin posited that the competition between organisms is a fundamental mechanism determining patterns of diversity on Earth. Important mathematical work in the early twentieth century formalized how competitive interactions determine the coexistence or exclusion of species as well as population dynamics (Lotka 1925; Volterra 1931). Yet even as the central dogma of competition was becoming established (Gause 1934; Brown and Wilson 1956), there were dissenting voices questioning the actual importance of competition for species diversity (Ross 1957; Udvardy 1959; Hutchinson 1967), which reached a critical moment in the late 1970's-early 1980's (Schoener 1982). This crisis in the supremacy of competition occurred due to an accumulation of observational, theoretical and conceptual challenges to predictions based on competition. The tenor of this crisis is best captured by the debate between Jared Diamond and the tandem of Edward Connor and Daniel Simberloff (Diamond 1975; Connor and Simberloff 1979, 1983, 1984; Gilpin and Diamond 1984). Diamond concluded that patterns of bird species co-occurrence were the product of competitive interactions (Diamond 1975). Connor and Simberloff responded with a multipronged attack questioning the empirical and logical validity of that conclusion (Connor and Simberloff 1979). This debate was ultimately about the validity of drawing inferences from observational data without appropriate statistical tests, but it also questioned whether competition was the central force determining patterns of species diversity. In their papers, Connor and Simberloff explicitly asked whether community membership is simply the product of stochastic processes (Connor and Simberloff 1979, 1984).

While this debate about observational studies raged, manipulative experiments testing the strength of competition amassed in the 1970's (Connell 1983; Schoener 1983). Either because of the preceding crisis or the availability of a sufficient number of studies, or both, Connell (1983) and Schoener (1983), in an amazing coincidence, simultaneously reviewed the evidence for competition in manipulative field experiments. Through vote counting, they both concluded that experimental evidence revealed that competition was important in the majority of the interactions examined. For example Schoener (1983) concluded that "competition was found in 90 % of the studies and 76 % of their species, indicating its pervasive importance in ecological systems" (p. 276). However, doubt was cast on these reviews, especially concerning the use of vote counting to infer actual importance (Gurevitch et al. 1992). Gurevitch et al. (1992) used the newly formalized tools of meta-analysis to examine the magnitude of competitive interactions in manipulative experiments. One of the major reasons for their paper, they said, was the uncertainty in the frequency and magnitude of competition, which were not addressed in Connell's and

Schoener's reviews. In talking about these papers, Gurevitch et al. state: "We believe that one of the major reasons for the uncertainty surrounding the effects of competition in nature is the lack of adequate means for synthesizing the wealth of experimental results that have been gathered".

In their meta-analysis of competition, Gurevitch et al. (1992) found that across studies and taxa, there was a strong effect of competition on the abundance of species. However, they also observed substantial heterogeneity in the size of the effect attributed to competitive interactions, something not possible with vote-counting. They found that one important source of this variation was that competition was very strong among herbivores, moderately so for primary producers and only weak for carnivores (Gurevitch et al. 1992). They also found that in studies that were run for a short duration and that utilized few replicates were more variable. Further, they provided evidence showing that experimental methodology affected the results. For example, experiments performed in enclosures recorded higher competition than those that were open (Gurevitch et al. 1992), ostensibly because organisms can move to find other resources and predators mediate competitive interactions (e.g., Holt 1977). In addition, they showed that few studies revealed very large competitive effects, and these tended to be experiments with few replicates. Taken together, these results reveal that competition is an important structuring mechanism, but unlike the reviews of Schoener and Connell, the Gurevitch et al. study revealed that competition was not universally important. Further, they revealed that the experiments themselves—their design and implementation—strongly affect the overall conclusions about the strength of competition.

Legacy

The previous reviews by Connell (1983) and Schoener (1983) concluded that competition was extremely pervasive and a ubiquitous interaction while the meta-analysis by Gurevitch et al. (1992) challenge this ubiquity. In an important follow-up study, Gurevitch et al. (2000) used a meta-analysis to assess the relative strengths of competition and predation and found that competition was weaker in the presence of predators, but both significantly contributed to the growth and survival of organisms. Again, these results, unlike vote-counting, quantified competitive effects and put conditions on when competition is important and set its context as one of several processes affecting species. These conclusions could have been achieved with a nuanced review of competition at the right time, but given the collective excitement about meta-analyses in ecology and their perceived epistemological rigor, a deserved greater authority accompanies such a meta-analysis. These meta-analyses changed the basis of the competition debate. Whereas ecologists originally wondered whether competition was important, the question subsequently morphed into one probing the strength of competition's effect and under what conditions it is important. Since these meta-analyses there have been other serious challenges to competition as the central paradigm (Bell 2001; Hubbell 2001). The other challenges do not negate the role of competition, but rather add other potential mechanisms for how communities are structured when competition among species is relatively weak.

Biodiversity and ecosystem function

Concern about reduced ecosystem function resulting from the loss of biodiversity was explicitly addressed in the first Global Biodiversity Assessment in 1995 (United Nations Environment Programme 1995). This global recognition of a potentially catastrophic

problem stimulated a plethora of experiments that manipulated species richness and assessed impacts on ecosystem function (Naeem et al. 1994; Naeem and Li 1997; Tilman et al. 1997, 2001; Hector et al. 1999; Loreau 2000; Spehn et al. 2005). The important claim from these studies was that a loss of species would reduce the level of functioning. This broad claim was quickly attacked (Aarssen 1997; Huston 1997; Wardle 1999; Huston et al. 2000). The main thrust of the attacks was methodological, including (1) a lack of an ability to account for the influence of including dominant or productive species that would increase polyculture productivity over the expectation from the monocultures if some species have low biomass monocultures; and (2) an inability to distinguish different mechanisms that would result in a similar relationship between species richness and productivity. These concerns lead to a prolonged period of developing new statistical methods (e.g., Loreau and Hector 2001; Fox and Harpole 2008) and assessing alternative mechanisms (e.g., Cardinale and Palmer 2002; Cardinale et al. 2004).

These criticisms changed the trajectory of research in this area (Hooper et al. 2005), with subsequent experiments likely avoiding including realism or complexity to instead focus on the experimental design issues. With 15 years of experimental results, a general consensus that richness was important for ecosystem function was emerging but residual concerns about the consistency or ubiquity of these relationships remained (Hooper et al. 2005), and thus in the mid 2000's the time was ripe for meta-analyses. In fact the timing was so right that two independent meta-analyses were published in the same year (Balvanera et al. 2006; Cardinale et al. 2006). These two meta-analyses differed in key aspects, but they both combined hundreds of experiments that spanned different trophic levels and systems and measured ecosystem function in multiple ways (e.g., biomass production, nutrient use, other trophic levels supported, etc.), and they both explicitly stated that the ongoing debate was the impetus for these analyses. For example, as Cardinale et al. (2006) state in their abstract: “the generality of patterns and processes observed in individual studies have been the subjects of considerable debate” (p. 989), and Balvanera et al. (2006) similarly state that the experimental designs and results have “not been consistent and the field has been contentious...” (p. 1146).

The meta-analysis by Balvanera et al. (2006) assesses the strength of the relationship between species richness and ecosystem function by combining the correlation coefficients from individual studies. Their primary goal was to see if: (1) there were consistent positive correlations and (2) if there were important differences among different functions, taxa, different scales or trophic levels. Overall, they concluded that biodiversity significantly affected ecosystem function. They found that the higher the trophic level from the manipulated level, the weaker the relationship. Overall, this meta-analysis strongly supported the positive relationship between richness and function.

The Cardinale et al. (2006) meta-analysis had many of the same goals (strength of relationships, compare across systems and taxa, etc.). However, Cardinale et al. were able to assess the shape of the relationship between richness and function and how much more function was obtained in polycultures compared to monocultures, whereas Balvanera et al. looked for a linear correlation. Cardinale et al. also concluded that there was a strong average effect of species richness on ecosystem function, but their analyses allowed for a more subtle analysis of the mechanisms (Cardinale et al. 2006). They were able to test whether polycultures functioned at a higher level than either the average of the constituent monocultures or the highest performing monoculture. They found that while ecosystem functioning was higher than the monoculture average, it was not greater than the best performing species, consistent with a sampling effect (Cardinale et al. 2006).

Legacy

The meta-analyses (Balvanera et al. 2006; Cardinale et al. 2006) signaled a critical transition in biodiversity-ecosystem function research. The previous decade of research seemed to have focused on solving statistical issues and to account for the effects of individual species. The post-debate stage of this research has been expanding our understanding of how and when, and what kinds of diversity matter for ecosystem functions. Three areas of inquiry have greatly expanded recently. In the first, recent research has focused on how mechanisms of community assembly and niche differences result in diversity-function relationships (Cardinale 2011; Carroll et al. 2011). The second stream of research has been focused on accounting for ecological similarities and differences among species (Cadotte et al. 2009; Flynn et al. 2011). Finally, researchers have been asking how diversity relates to multiple functions simultaneously (Hector and Bagchi 2007; Zavaleta et al. 2010; Peter et al. 2011).

Species responses to global warming

Global climate change may have important implications for patterns of species diversity and the stability of ecosystem services (Sala et al. 2000; McCarthy et al. 2001). The first published accounts of increasing temperatures were over 30 years ago (Broecker 1975), and much of the early intellectual work focused on understanding and predicting climate change as a physical process (Houghton et al. 2001) with biological and societal implications remaining unresolved. As predictive models and computer simulations have clarified future climate change scenarios (e.g., Cox et al. 2000), one of the obvious next steps has been to ask what these climate predictions mean for the biosphere (Drake et al. 1997; Sala et al. 2000; McCarthy et al. 2001).

Ongoing ecological research has been collecting data to answer such questions. There has always been a priority placed on collecting long-term datasets because they have allowed researchers to observe ecological patterns and processes that change slowly (Franklin et al. 1990). Short-term projects that form the majority of ecological research simply cannot detect slow incremental change over background environmental and demographic stochasticity. However, even though long-term ecological monitoring may provide observations about the impacts of climate change, these are often restricted geographically or taxonomically and thus limit the ability to draw an inference about climate change that is generally applicable. Given the accumulation and availability of such studies, Root et al. (2003) assessed whether population responses to climate change were consistent.

To evaluate how populations were changing, Root et al. (2003), collected 143 long-term datasets that accumulated information on population or individual traits that have showed some local change (i.e., population size, phenology and timing, morphological or behavioural changes, and gene frequencies). They examined whether these traits showed consistent changes across taxa and regions. Using vote-counting, they show that over 80 % of 1473 species showed climate-associated changes over time (Root et al. 2003). Using a meta-analysis, they found that species were growing faster and reproducing 5.1 days earlier per decade (Root et al. 2003). Further, the individual datasets that were non-significant reinforced the meta-analysis results of earlier shifts—something that the vote-counting analysis discounts. These individual studies may have lacked the statistical power or methods necessary to provide strong inference, but in the meta-analysis, they provide valuable evidences for changes in timing.

The paper by Root et al. (2003) again reveals that the true power of a meta-analysis is not necessarily to test new hypotheses, but rather to definitively show that certain patterns are generalizable. This paper has been cited over 1200 times (as of April 2012) not because it made a novel claim about species showing changes in their density or phenology, but rather because they provided broadly supported estimates of the rates of change in natural populations. This meta-analysis has formed the basis for discussions about climate change impacts (e.g., Parmesan 2006).

Legacy

As noted earlier in this paper, the accumulation of ecological data along with technological (and cultural) advances in storing and sharing data, have facilitated the use of meta-analyses to develop broad, general conclusions about ecological phenomena. The meta-analysis by Root et al. (2003) reinforces how meta-analyses can utilize data that have a limited geographical extent to search for broader generalities. This tension between local data collection and searching for broad generalizations has been explicitly addressed in a number of large data collection initiatives. For example, the Long-Term Ecological Research (LTER) network (<http://www.lternet.edu/>) facilitates the collection and sharing of long-term ecological monitoring across 26 research reserves. More recently, the National Ecological Observatory Network (NEON—<http://www.neoninc.org/>), has the mandate to monitor ecological phenomena across 64 sites for 30 years to observe biological changes associated with climate change. These initiatives have the advantage of standardized sampling methodology and direct comparability among the different data sets, whereas meta-analyses necessarily include variation from among-study differences in methodology. Detecting broad scale patterns despite this large degree of variation reveals the power of meta-analyses to offer insights into important environmental issues.

Coda: gauging the impact and future of meta-analyses

Science is inherently defined by controversy and conflict. As new evidence or ideas emerge that question the validity of accepted theories, scientists must reevaluate existing paradigms and there are critical moments that herald a shift in the collective understanding (Lakatos 1976). Meta-analyses can act as this herald. As data analyses testing a particular theory accumulate, and questions about the generality or importance of a theory emerge, meta-analyses offer the opportunity to combine the results from multiple independent experiments and to quantify the importance of a particular process. The ecological world is messy, full of idiosyncrasies and variability. Because of this, Popperian critical tests (Popper 1963) should not be how ecologists change their belief in an explanation of a particular phenomenon. Instead, multiple lines of evidence need to consistently expose deficiencies in an explanation, and this coupled with the availability of a new, more robust explanation should be guiding theory acceptance (Lakatos 1976).

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References

- Aarssen LW (1997) High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos* 80:183–184
- Arnqvist G, Wooster D (1995) Metaanalysis—synthesizing research findings in ecology and evolution. *Trends Ecol Evol* 10:236–240
- Balvanera P, Pfisterer AB, Buchmann N, He J-S, Nakashizuka T, Raffaelli D, Schmid B (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol Lett* 9:1146–1156
- Bell G (2001) Neutral macroecology. *Science* 293:2143–2148
- Broecker WS (1975) Climatic change: are we on the brink of a pronounced global warming? *Science* 189:460–463
- Brown WL Jr, Wilson EO (1956) Character displacement. *Syst Zool* 5:49–64
- Cadotte MW, Cavender-Bares J, Tilman D, Oakley TH (2009) Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS One* 4:e5695
- Cardinale BJ (2011) Biodiversity improves water quality through niche partitioning. *Nature* 472:86–89
- Cardinale BJ, Palmer MA (2002) Disturbance moderates biodiversity–ecosystem function relationships: experimental evidence from caddisflies in stream mesocosms. *Ecology* 83:1915–1927
- Cardinale BJ, Ives AR, Ichausti P (2004) Effects of species diversity on the primary productivity of ecosystems: extending our spatial and temporal scales of inference. *Oikos* 104:437–450
- Cardinale BJ, Srivastava DS, Duffy JE, Wright JP, Downing AL, Sankaran M, Jouseau C (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443:989–992
- Carpenter SR, Armbrust EV, Arzberger PW, Chapin FS, Elser JJ, Hackett EJ, Ives AR, Kareiva PM, Leibold MA, Lundberg P, Mangel M, Merchant N, Murdoch WW, Palmer MA, Peters DPC, Pickett STA, Smith KK, Wall DH, Zimmerman AS (2009) Accelerate synthesis in ecology and environmental sciences. *Bioscience* 59:699–701
- Carroll I, Cardinale B, Nisbet R (2011) Niche and fitness differences relate the maintenance of diversity to ecosystem function. *Ecology* 92:1157–1165
- Connell JH (1961) Influence of interspecific competition and other factors on distribution of barnacle *chthamalus stellatus*. *Ecology* 42:710
- Connell JH (1983) On the prevalence and relative importance of interspecific competition—evidence from field experiments. *Am Nat* 122:661–696
- Connor EF, Simberloff D (1979) The assembly of species communities: chance or competition? *Ecology* 60:1132–1140
- Connor EF, Simberloff D (1983) Interspecific competition and species co-occurrence patterns on islands: null models and the evaluation of evidence. *Oikos* 41:455–465
- Connor EF, Simberloff D (1984) Neutral models of species co-occurrence patterns. In: Strong DR, Simberloff D, Abele LG, Thistle A (eds) *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, pp 341–343
- Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408:184–187
- Diamond JM (1975) Assembly of species communities. In: Cody ML, Diamond JM (eds) *Ecology and evolution of communities*. Harvard University Press, Cambridge
- Drake BG, Gonzalez-Meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO₂? *Annu Rev Plant Physiol Plant Mol Biol* 48:609–639
- Flynn DFB, Mirotchnick N, Jain M, Palmer MI, Naeem S (2011) Functional and phylogenetic diversity as predictors of biodiversity–ecosystem function relationships. *Ecology* 1573–1581
- Fox JW, Harpole WS (2008) Revealing how species loss affects ecosystem function: the trait-based price equation partition. *Ecology* 89:269–279
- Franklin JF, Bledsoe CS, Callahan JT (1990) Contributions of the long-term ecological research-program - an expanded network of scientists, sites, and programs can provide crucial comparative analyses. *Bioscience* 40:509–523
- Gause GF (1934) *The struggle for existence*. Hafner Publishing Company, New York
- Gilpin ME, Diamond JM (1984) Are species co-occurrences on islands non-random, and are null hypotheses useful in community ecology? In: Strong DR, Simberloff D, Abele LG, Thistle A (eds) *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton
- Gross CL (2005) A comparison of the sexual systems in the trees from the Australian tropics with other tropical biomes—more monoecy but why? *Am J Bot* 92:907–919
- Gurevitch J, Hedges LV (2001) Meta-analysis: combining the results of independent experiments. In: Scheiner SM, Gurevitch J (eds) *Design and analysis of ecological experiments*. Oxford University Press, Oxford, pp 347–369

- Gurevitch J, Morrow LL, Wallace A, Walsh JS (1992) A metaanalysis of competition in field experiments. *Am Nat* 140:539–572
- Gurevitch J, Morrison JA, Hedges LV (2000) The interaction between competition and predation: a meta-analysis of field experiments. *Am Nat* 155:435–453
- Gurevitch J, Curtis PS, Jones MH (2001) Meta-analysis in ecology. *Adv Ecol Res* 32(32):199–247
- Hackett E, Parker J (2010) Leadership in scientific research groups. In: 4S Annual meeting, University of Tokyo, Tokyo
- Hampton SE, Parker JN (2011) Success in synthesis. *Bioscience* 61:900–910
- Hector A, Bagchi R (2007) Biodiversity and ecosystem multifunctionality. *Nature* 448:188–190
- Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, Hogberg P, Huss-Danell K, Joshi J, Jumpponen A, Korner C, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Pereira JS, Prinz A, Read DJ, Scherer-Lorenzen M, Schulze ED, Siamantziouras ASD, Spehn EM, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH (1999) Plant diversity and productivity experiments in European grasslands. *Science* 286:1123–1127
- Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. *Ecology* 80:1150–1156
- Holt RD (1977) Predation, apparent competition, and structure of prey communities. *Theor Popul Biol* 12:197–229
- Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–35
- Houghton JT, Ding Y, Gribbs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA (2001) Climate change 2001: the scientific basis. Cambridge University Press, Cambridge
- Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography, vol 32. Princeton University Press, Princeton
- Huston M (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110:449–460
- Huston M, Aarssen LW, Austin MP, Cade BS, Fridley JD, Garnier E, Grime JP, Hodgson JG, Lauenroth WK, Thompson K, Vandermeer J, Wardle DA (2000) No consistent effect of plant diversity on productivity. *Science* 289:1255
- Hutchinson GE (1967) A treatise on limnology, vol 2. Wiley, New York
- Jones MB, Schildhauer MP, Reichman OJ, Bowers S (2006) The new bioinformatics: integrating ecological data from the gene to the biosphere. *Annu Rev Ecol Evol Syst* 37:519–544
- Karst J, Marczak L, Jones MD, Turkington R (2008) The mutualism-parasitism continuum in ectomycorrhizas: a quantitative assessment using meta-analysis. *Ecology* 89:1032–1042
- Lakatos I (1976) Proofs and Refutations. Cambridge University Press, Cambridge
- Lawton JH (1999) Are there general laws in ecology? *Oikos* 84:177–192
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JD, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 7:601–613
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967
- Lindenmayer DB, Likens GE (2011) Losing the culture of ecology. *Bull Ecol Soc Am* 92:245–246
- Loreau M (2000) Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* 91:3–17
- Loreau M (2010) From populations to ecosystems: theoretical foundations for a new ecological synthesis. Princeton University Press, Princeton
- Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76
- Lotka AJ (1925) Elements of physical biology. Williams and Wilkins, Baltimore MD
- Massol F, Gravel D, Mouquet N, Cadotte MW, Fukami T, Leibold MA (2011) Linking community and ecosystem dynamics through spatial ecology. *Ecol Lett* 14:313–323
- McCarthy JJ, Canziani OF, Leary NA, Dokken DJ, White KS (2001) Climate change 2001: impacts, adaptation and vulnerability. Cambridge University Press, Cambridge
- McGill BJ (2006) A renaissance in the study of abundance. *Science* 314:770–772
- Menge BA, Chan F, Dudas S, Eerkes-Medrano D, Grorud-Colvert K, Heiman K, Hessing-Lewis M, Iles A, Milston-Clements R, Noble M, Page-Albino K, Richmond E, Rilov G, Rose J, Tyburczy J, Vinuela L, Zarnetske P (2009) Do terrestrial ecologists ignore aquatic literature? *Front Ecol Environ* 7:82–83
- Micheli F, Halpern BS (2005) Low functional redundancy in coastal marine assemblages. *Ecol Lett* 8:391–400
- Michener WK (2006) Meta-information concepts for ecological data management. *Ecol Inform* 1:3–7

- Murtaugh PA (2002) Journal quality, effect size, and publication bias in meta-analyses. *Ecology* 83:1162–1166
- Naeem S, Li SB (1997) Biodiversity enhances ecosystem reliability. *Nature* 390:507–509
- Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM (1994) Declining biodiversity can alter the performance of ecosystems. *Nature* 368:734–737
- Olkin I (1996) Meta-analysis: current issues in research synthesis. *Stat Med* 15:1253–1257
- Osenberg CW, Sarnelle O, Cooper SD, Holt RD (1999) Resolving ecological questions through meta-analysis: goals, metrics, and models. *Ecology* 80:1105–1117
- Paine RT (1966) Food web complexity and species diversity. *Am Nat* 100:65
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. In: *Annual review of ecology evolution and systematics*, vol 37. Annual reviews, Palo Alto, pp 637–669
- Peter H, Ylla I, Gudas C, Romani AM, Sabater S, Tranvik LJ (2011) Multifunctionality and diversity in bacterial biofilms. *PLoS One* 6:8
- Peters RH (1991) *A critique for ecology*. Cambridge University Press, Cambridge
- Popper K (1963) *Conjectures and refutations: the growth of scientific knowledge*. Routledge, New York
- R Development Core Team (2009) *R: a language and environment for statistical computing*. R foundation for statistical computing. ISBN 3-900051-07-0, URL: <http://www.R-project.org>. In, Vienna, Austria
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60
- Ross HH (1957) Principles of natural coexistence indicated by leafhopper populations. *Evolution* 11:113–129
- Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Biodiversity—global biodiversity scenarios for the year 2100. *Science* 287:1770–1774
- Schoener TW (1982) The controversy over interspecific competition. *Am Sci* 70:586–595
- Schoener TW (1983) Field experiments on interspecific competition. *Am Nat* 122:240–285
- Simberloff D (2006) Rejoinder to: don't calculate effect sizes; study ecological effects. *Ecol Lett* 9:921–922
- Spehn EM, Hector A, Joshi J, Scherer-Lorenzen M, Schmid B, Bazeley-White E, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, Hogberg P, Huss-Danell K, Jumpponen A, Koricheva J, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Palmberg C, Pereira JS, Pfisterer AB, Prinz A, Read DJ, Schulze ED, Siamantziouras ASD, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH (2005) Ecosystem effects of biodiversity manipulations in European grasslands. *Ecol Monogr* 75:37–63
- Suding KN, Collins SL, Gough L, Clark C, Cleland EE, Gross KL, Milchunas DG, Pennings S (2005) Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proc Nat Acad Sci USA* 102:4387–4392
- Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300–1302
- Tilman D, Reich PB, Knops J, Wedin D, Mielke T, Lehman C (2001) Diversity and productivity in a long-term grassland experiment. *Science* 294:843–845
- Tucker CM, Cadotte MW (2011) The empirical divide (<http://evol-eco.blogspot.ca/2011/07/empirical-divide.html>). In: *The EEB and Flow* vol 2011
- Udvardy MFD (1959) Notes on the ecological concepts of habitat, biotope and niche. *Ecology* 40:725–728
- United Nations Environment Programme (1995) *Global biodiversity assessment*. Cambridge University Press, Cambridge
- Volterra V (1931) Variations and fluctuations of the number of individuals in animal species living together. In: Chapman RN (ed) *Animal ecology*. McGraw-Hill, New York
- Wardle DA (1999) Is “sampling effect” a problem for experiments investigating biodiversity–ecosystem function relationships? *Oikos* 87:403–407
- Zavaleta ES, Pasari JR, Hulvey KB, Tilman GD (2010) Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proc Nat Acad Sci USA* 107:1443–1446