SPECIAL FEATURE

Meta-analysis in Ecology: Concepts, Statistics, and Applications[1]

One gauge of the maturity of a scientific discipline is the extent to which results are synthesized across studies to test and refine the conceptual foundation of the discipline. Over the past three to four decades, as field experiments have become entrenched as a primary ecological tool, experimental results have flooded the literature. This vast literature has been treated in three different ways by most authors trying to summarize the state of the field: (1) as a large pool from which a small number of exemplars are selected to illustrate particular ecological principles; (2) as a source for narrative qualitative reviews, as well as the discussions of most primary research papers; or (3) as a database from which to conduct semiquantitative reviews using vote-counting procedures. Reaction in other fields to the problems with all of these approaches has led to the development of formal statistical techniques for ''meta-analysis,'' i.e., the quantitative synthesis and analysis of a collection of experimental studies.

Although meta-analysis holds great promise for addressing ecological questions that cannot be resolved by single studies, its future role in ecology remains uncertain. As a result, we convened a working group at the National Center for Ecological Analysis and Synthesis (Santa Barbara, California, USA) to help evaluate and guide the application of meta-analysis to ecological questions. This Special Feature represents a summary of some of our findings and is intended to stimulate additional research into the development of meta-analytic approaches appropriate to resolving ecological questions and furthering the development and testing of ecological theory.

Many important issues relating to meta-analysis have been discussed in the literature of other disciplines (e.g., medicine, sociology, psychology). However, borrowing too heavily from other disciplines may mislead ecologists; we tend to study more-diverse systems, ask more-diverse questions, and use more-diverse experimental methods than do the human-focused disciplines in which meta-analytical techniques have been developed. Therefore, this Special Feature tackles issues that are ecological in nature and not illustrated, or necessarily available, in the existing literature on meta-analysis.

In the first paper, Osenberg et al. set the stage by discussing the first and most critical step in any meta-analysis: the specification of the question and therefore the definition of effect size. They argue that resolving ecological questions will demand approaches that move beyond null-hypothesis tests and statistically based metrics toward greater reliance on estimation of the magnitudes of ecological response. Defining appropriate measures of effect size will often require specification of a biological model. However, ecologists will not always have sufficient information to choose an appropriate model and therefore may need to rely on other considerations for choosing measures of effect size. Goldberg et al. describe a set of empirical criteria for making such choices and illustrate these issues by evaluating whether the intensity of competition among plants intensifies as primary production increases.

Once the problem and metric have been specified, data must be selected for analysis. By comparing the results of meta-analyses in which data were selected using different sets of criteria, Englund et al. illustrate that the conclusions of a meta-analysis can be seriously influenced by peripheral decisions used to select data or studies. They recommend that meta-analytic patterns be examined for their robustness to changes in selection criteria, and they caution against the use of criteria that relate to the perceived ''quality'' of studies because of the potential for unconscious bias.

With question, metric, and data in hand, the meta-analyst must consider statistical issues. One consideration arises because data used in meta-analysis have two sources of variation: variation among studies in the true effect, and variation arising from error in measuring the effect for any given study. The within-study error term may be more heterogeneous in meta-analyses than in

[1] Reprints of this 65-page Special Feature are available for $9.75 each. Prepayment is required. Order reprints from the Ecological Society of America, Attention: Reprint Department, 2010 Massachusetts Avenue, N.W., Suite 400, Washington, DC 20036.

primary studies due to differences in methodology and design. Thus, as Gurevitch and Hedges discuss, weighted analyses that rely on these estimates of variances are recommended. Separately estimating these sources of variance also can provide a means to test hypotheses about the consistency of the effect size among experiments.

Estimation of effect sizes and variance components, however, requires access to appropriately summarized data. Often, only statistical test results are given (e.g., reported as *P* values or ANOVA tables), or the data are summarized, but in ways that preclude calculation of effect sizes and within-study variances. Indeed, poor reporting of primary data is often the greatest impediment to conducting a meta-analysis. The Ecological Society of America has addressed this need by creating *Ecological Archives* (see *Bulletin of the Ecological Society of America* **79**:177–181), where primary data and meta-analysis data sets can be permanently archived. To facilitate future meta-analyses derived from the data used in this Special Feature, all authors have archived their data in ESA's Electronic Data Archive, *Ecological Archives* E080-005 through E080-009. We hope this becomes a common practice.

The statistical procedures that exist for meta-analysis assume that estimates of effect size are independent; an assumption that is likely to be violated in most ecological meta-analyses, e.g., when multiple estimates are taken from a single paper, particular investigators contribute many papers on a topic, or certain habitats or taxa are disproportionately represented in the literature (see Gurevitch and Hedges). It is also likely that nonindependence arising from phylogenetic history and publication bias will further affect the universe to which the results have relevance. Although these issues were discussed extensively by the working group and peripherally addressed in several of the papers, these topics demand further investigation and will certainly be a source of controversy in ecology, as they have been in other fields.

Aside from these general considerations of statistical inference, application of meta-analysis to any specific problem requires an understanding of the statistical properties of the chosen metric. Often, ecologists use metrics whose statistical properties are not well known. In such cases, the statistical properties must be specified so that efficient and unbiased estimators can be obtained, and the domain of their applicability specified. Hedges et al. illustrate these issues with response ratios, which underlie a family of metrics commonly used by ecologists.

Finally, Downing et al. provide an illuminating example of ecological meta-analysis using data on the effects of nutrients on production of marine phytoplankton. Their results illustrate the importance of time scale in interpreting ecological data and demonstrate that current understanding of nutrient limitation in the world's oceans is biased, in part, by nonrandom selection of study sites and by spatial variation in the magnitude by which algal production is limited by different nutrients.

This Special Feature is hardly an exhaustive or definitive treatment of the role and application of meta-analysis in ecology. It does, however, provide an initial foundation for ecologists seeking to apply meta-analysis to their questions and, more generally, should help to define the role of synthesis in ecology. Meta-analysis, in combination with ecological theory and a collection of well-executed primary studies, helps us describe patterns of variation in responses, test ideas designed to explain these patterns, and generate new hypotheses when existing theory fails. In this light, meta-analysis—and quantitative synthesis in general—is a central and indispensable part of the scientific method. We hope this Special Feature will stimulate the development of better tools for applying meta-analysis in ecology and thus improve quantitative syntheses as well as the primary studies whose quality ultimately constrains the insights gained from synthesis.

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