

SPECIAL FEATURE – EDITORIAL

META-ANALYSIS IN PLANT ECOLOGY

Advancing plant ecology through meta-analyses

Lorena Gómez-Aparicio^{1*} and Christopher J. Lortie²¹*Instituto de Recursos Naturales y Agrobiología (IRNAS), CSIC, PO Box 1052, Sevilla 41080, Spain; and* ²*Department of Biology, York University, Toronto, ON M3J 1P3, Canada*

Summary

1. The inherent complexity of nature produces a diverse and varied set of outcomes for any given ecological process. However, the advance of ecology requires making generalizations that synthesize current knowledge and guide new basic research and practical applications. Among the synthesis tools available for this specific purpose, meta-analysis is one of the most accurate and powerful methods.

2. This Special Feature examines the use that meta-analysis has received in plant ecology over the last two decades and provides examples of synthesis applied to contemporary topics in different areas of plant ecology from populations to ecosystems.

3. The number of meta-analyses in plant ecology has been increasing rapidly in the last two decades. However, this increase has not been accompanied by a parallel increase in quality. The opening review paper in this Special Feature provides a checklist of quality criteria specific to ecological meta-analysis that will largely contribute to improvement of the methodological and reporting standards of meta-analyses.

4. The following five papers in the Special Feature demonstrate the advantages of application of meta-analysis compared with other techniques of research synthesis. Meta-analysis is applied here to demonstrate the consistency of ecological hypotheses across large spatial scales (e.g. Janzen-Connell hypothesis), understand sources of variation in the magnitude of ecological processes (e.g. herbivory effects on leaf life span, effects of intraspecific genetic diversity on communities and ecosystems), measure synergistic impacts of environmental change drivers (e.g. CO₂, drought, land use) or assess research gaps within a certain sub-discipline of plant ecology (e.g. landscape fragmentation).

5. *Synthesis.* Meta-analysis can contribute to the advance of ecological theory by synthesizing the available evidence on specific topics and informing the scope of generalizations. However, plant ecologists can only take full advantage of this capacity if we improve our knowledge on how and when to conduct a proper meta-analysis, and by avoiding the frequent misuses that have characterized the use of this statistical tool in the ecological literature thus far.

Key-words: data synthesis, effect sizes, global change drivers, grassland function, intraspecific genetic diversity, Janzen-Connell hypothesis, landscape fragmentation, plant population and community dynamics, plant–herbivore interactions, strength of evidence

Introduction

Probably all scientists have at one time felt overwhelmed by the abundance of literature on any particular research topic, the finding of contradictory results and the prevalence of apparently idiosyncratic patterns. Because of the inherent complexity of nature, it is probably true that, for any given ecological process, a wide set of outcomes can be found under particular combinations of species and environmental

factors. However, the science of ecology can only advance if we are able to discern the exception from the rule, making generalizations that synthesize current knowledge and guide new basic research and practical applications. This fact is particularly true under a global change scenario, where ecologists are pressured to provide accurate quantitative assessments for the effects of major environmental drivers and facilitate evidence-based decision-making. The field of research synthesis is devoted to the integration of findings of primary research. Research synthesis will provide the means to evaluate the evidence for alternative hypotheses and examine generalizations in any discipline including ecology if transparently described

*Correspondence author: E-mail: lorenag@irnase.csic.es

(Lortie *et al.* 2014). Meta-analysis is one of the many tools available but also likely the most direct technique in many respects in summarizing evidence for a particular topic (Arnqvist & Wooster 1995; Nakagawa & Poulin 2012; Koricheva & Gurevitch 2013). Meta-analysis is a set of statistical methods for combining the magnitude of the outcomes (effect sizes) across different data sets addressing the same research question (*sensu* Koricheva & Gurevitch). Meta-analyses therefore provide an assessment of the strength of evidence of the respective primary research, and this is critical for decision-makers. Moreover, derived data sets and replicable syntheses will advance the state of knowledge for plant ecologists and will provide the capacity to identify limitations and research gaps in the literature.

This *Journal of Ecology* Special Feature aims to examine the use that meta-analysis has received in plant ecology over the last two decades and provide examples of synthesis successfully applied to provide new insights into contemporary topics in plant ecology. The Special Issue consists of six papers. The opening paper by Koricheva & Gurevitch (2014) offers the first review of the applications and contribution of meta-analysis to plant ecology and assesses the methodological and reporting quality of meta-analysis in this field. Koricheva & Gurevitch (2014) show that the number of meta-analyses in plant ecology has increased substantially during the last 20 years. This increase has been fostered by the accumulation of a sufficient number of individual studies to make scientists consider that the time was ripe for meta-analysis as well as by the popularization of meta-analytical statistical techniques. Whereas in the past, a large majority of the meta-analyses published in ecological journals used the software MetaWin (Rosenberg, Adams & Gurevitch 2000), today there is a much wider variety of options due to the development of new and complete open-access software such as R packages METAHDEP (Stevens & Taylor 2009), METAFOR (Viechtbauer 2010), MCMCGLMM (Hadfield 2010) and PHYLOMETA (Lajeunesse 2011) or the more recent OPENMEE (Dietz *et al.* 2013). This availability opens a whole world of possibilities for conducting meta-analyses of very different degrees of sophistication from the classic meta-analysis with a frequentist approach (e.g. Thébault *et al.* 2014; Zvereva & Kozlov 2014) to the most novel Bayesian meta-analysis (e.g. Kulmatiski *et al.* 2008; Ibáñez *et al.* 2014; Whitlock 2014). The diversity of options is reflected in the five studies that accompany the review by Koricheva & Gurevitch in this Special Feature.

Despite the increase in the number of papers, a worrisome conclusion of the Koricheva & Gurevitch review is the fact that we have not gained enough in quality over time. These authors highlighted the surprisingly high number of studies where the term 'meta-analysis' was used, but accepted meta-analysis methodology was not present in the synthesis (see Coté & Reynolds 2012 and Vetter, Rucker & Storch 2013 for similar conclusions in related sub-disciplines). For example, meta-analysis is still confounded with vote-counting or used anytime data from several studies are extracted and analysed in some way. The original definition of meta-analysis, coined by Glass (1976) in the field of educational science, was 'the

statistical analysis of a large collection of results from individual studies for the purpose of integrating findings'. This was probably too general and could have led to the current misuse of the term. At present, however, ecological meta-analysis has a much more precise definition (e.g. it must include effect sizes (Koricheva & Gurevitch 2013; Lortie *et al.* 2014). Conducting a meta-analysis therefore involves a well-defined number of steps and associated methods that have been summarized in the first handbook of meta-analysis written specifically for ecologists and evolutionary biologists (Koricheva, Gurevitch & Mengersen 2013). In an additional effort to raise the standards of meta-analysis in plant ecology, Koricheva & Gurevitch (2014) provide for the first time a checklist of quality criteria specifically for ecological meta-analysis that compile and improve previous lists proposed for assessing the quality of meta-analysis in ecology and related areas (Philibert, Loyce & Makowski 2012; Vetter, Rucker & Storch 2013). We are confident that this checklist will contribute to a consistent and well-defined usage of the term 'meta-analysis' by plant ecologists, to improve the reporting standards of future meta-analyses, and to help reviewers and editors identify meta-analyses that do not meet basic quality pre-requisites.

Meta-analysis has clear advantages over other qualitative and quantitative techniques of research synthesis. First, meta-analysis allows for an estimate of the magnitude (not only the existence) of an effect across studies, thereby taking into account the sample size and statistical accuracy of the individual studies combined. Second, meta-analysis can be applied to compare the magnitude of an effect on different related response variables (e.g. different components of landscape fragmentation, Ibáñez *et al.* 2014) offering a comprehensive assessment of the effects of complex processes on plants. Third, because it allows using covariates (i.e. explanatory factors) to understand sources of variation in the magnitude of the effect, it contributes to the clarification of the circumstances associated with increased likelihoods of positive effects. In fact, it is not uncommon to find meta-analyses wherein the overall effect size is small or non-significant, but comparisons of aggregated sets of effect sizes are significant such as groups of species, sites or ecological conditions (e.g. Knorr, Frey & Curtis 2005; Gómez-Aparicio 2009). The studies included in this Special Feature have been selected to illustrate these advantages for very different areas of plant ecology from populations to ecosystems.

Advancing plant population ecology through meta-analysis

Meta-analysis has a very real capacity to contribute to theory development in plant ecology. In the second paper of this Special Feature, Comita *et al.* (2014) present an excellent example of this opportunity by providing an updated, thorough synthesis of one of the most influential hypotheses in plant ecology, the Janzen-Connell hypothesis (Janzen 1970; Connell 1971). In contrast to the only meta-analysis conducted on the topic to date (Hyatt *et al.* 2003), Comita *et al.*

(2014) found significant support for both the distance- and density-dependent predictions of the Janzen-Connell hypothesis. Differences among both meta-analyses are explained on the basis of differences in the number of studies included (higher in Comita *et al.* 2014) as well as on a suite of fundamental decisions regarding study selection and integration into the meta-analysis. The work by Comita *et al.* nicely illustrates the advantages offered by meta-analysis to explore the consistency of an ecological hypothesis across large spatial scales difficult to cover in single studies. They compared the weight of evidence for the predictions of the Janzen-Connell hypothesis across latitudinal and precipitation gradients and by ecosystem types (temperate versus tropical) and continents. There was a trend for stronger distance dependence and density dependence in wetter sites compared with sites with lower annual precipitation. Comita *et al.* concluded that their synthesis supports the existence of significant overall effects of conspecific density dependence and distance dependence on survival in plant communities world-wide, but that further studies are needed in order to attribute these patterns to natural enemies as suggested by Janzen and Connell.

In the third study of this Special Feature, Whitlock (2014) synthesizes the research evidence around a hot topic, the role of intraspecific genetic diversity for communities and ecosystems. Whereas extensive efforts have focused on understanding and synthesizing species diversity effects on ecosystem function (Balvanera *et al.* 2006; Cardinale *et al.* 2006), the role of the intraspecific variation in diversity has been underexplored, and it was also identified as one of the 100 fundamental questions that can guide ecological research in the future (Sutherland *et al.* 2012). Whitlock (2014) detected an overall positive effect of population-level adaptive genetic diversity (but not of neutral genetic diversity) on community- and ecosystem-level ecological responses demonstrating that these two measures of intraspecific variation should not be used as ecologically equivalent. Moreover, he found strong variation in the effect of adaptive genetic diversity depending on the community (e.g. richness, evenness) and ecosystem measure (e.g. stocks, fluxes) chosen, as well as on the particular characteristics of the individual studies (e.g. spatial extent of the sampling unit, types of genetic diversity recorded). This synthesis advances the debate about whether relationships between genetic diversity and ecological structure are either positive or negative by showing how the strength and direction of these relationships changes with the different measures of diversity and importantly in different ecological contexts.

Advancing community and ecosystem ecology through meta-analysis

Meta-analysis has also contributed extensively to explicate the organization and interaction among species in plant communities. In fact, the first paper that introduced the methods of meta-analysis in ecology in the early 1990s synthesized the findings at that time for field-competition experiments at different trophic levels (Gurevitch *et al.* 1992). Since then,

meta-analysis has been frequently applied to summarize the variability in the sign and magnitude of plant–plant interactions (Goldberg *et al.* 1999; Maestre, Valladares & Reynolds 2005; Lortie & Callaway 2006; Gómez-Aparicio 2009; He, Bertness & Altieri 2013; Liczner & Lortie 2014), as well as to synthesize research on the interaction among plants and other trophic levels including herbivores (Hawkes & Sullivan 2001; Stiling & Cornelissen 2007), animal mutualists (Vázquez *et al.* 2005) or mycorrhizal fungi (Karst *et al.* 2008; Hoeksema *et al.* 2010). In the fourth paper of this Special Feature, Zvereva & Kozlov (2014) provide a novel contribution to the understanding of plant–herbivore interactions by synthesizing for the first time knowledge on the effects of herbivores on leaf life span. They demonstrated an overall negative effect of herbivory on leaf life span suggesting that premature abscission of damaged leaves can be viewed as one of the general responses of woody plants to herbivory. But as for Whitlock (2014), probably the most interesting contribution of this paper was to explain the high variation in such effect as a function of particular characteristics of the independent studies. Specifically, they showed that the variability in plant responses to herbivory depend substantially on species-specific leaf traits, suggesting it might be linked with the leaf economics spectrum (Reich *et al.* 1999; Wright *et al.* 2004).

One of the most popular uses of ecological meta-analysis in the last two decades has been the synthesis of independent studies assessing the effects of different global change drivers on plants (Koricheva & Gurevitch 2014). The last two papers of this Special Feature represent well-executed examples of this application. Ibáñez *et al.* (2014) presented the most comprehensive analysis to date of the integrated effects of landscape fragmentation on plant species and communities. Interestingly, whereas fragmentation is usually perceived to negatively affect plant communities, they found that both positive and negative responses to fragmentation are common, but neither is dominant. None of the covariables used in their analyses (biomes, vegetation types, functional groups, life stages) satisfactorily explained the high heterogeneity of responses found. They conclude that broad generalizations about the effects of fragmentation on plant communities might not be possible due to the large variety of processes and responses associated with fragmentation. This is a significant conclusion from a synthesis perspective because it clearly identifies the need for additional, context specific research and management. Given this lack of consistent findings, Ibáñez *et al.* provide a suite of specific recommendations on possible avenues to overcome the difficulties inherent in the assessment of the effects of the different components of landscape fragmentation (isolation, edge effects, fragment size, time since fragmentation) on plants. This is also an excellent synthesis as it clearly illustrates the power and consistency of Bayesian statistics. Sensitivity analyses are critical in any set of analyses, and given the level of abstraction sometimes needed in meta-analyses, this work provides a useful example for ecological synthesists that tackle highly context-dependent topics or embrace powerful but sometimes challenging analytical tools.

Finally, Thébault *et al.* (2014) used meta-analysis to explore the relative importance of local management practices (fertilization, fire, abandonment, mowing) versus climate change drivers (increased CO₂, warming, drought, flooding) on plant productivity and soil processes. This synthesis provides an example of the use of absolute value contrasts of effect sizes, decoupled from the sign of respective and aggregated effects, as a means to assess the relative importance of drivers between different groups or levels. By contrasting the effect sizes of these different factors, they found that combinations of local management practices had a much larger effect on grassland functions than individual or even the interactive effects of climate change factors. This synthesis thus provides much needed insights into the potential projected responses of grassland ecosystems to climate change because it suggests that local-scale, land management practices must be included in global models. Moreover, this work emphasizes a frequently assumed, but rarely demonstrated ecological principle, that the synergistic impacts of several drivers of environmental change have greater effects on plant communities and ecosystems than any one factor acting in isolation.

Conclusions

The studies included in this Special Feature demonstrate that meta-analysis has the capacity to contribute to the advance of ecological theory by synthesizing the available evidence on specific topics and informing the scope of broad generalizations. Independently of whether the conclusion of the studies was the existence (e.g. Comita *et al.* 2014) or not (e.g. Ibáñez *et al.* 2014) of enough evidence in support of the specific hypothesis tested, all syntheses included here identified the gaps of knowledge needed to inform future research efforts by avoiding replicated studies and inspiring novel approaches. The significant benefits that the application of meta-analytical techniques can provide are, however, limited to some extent by their frequent misuse in plant ecology (Koricheva & Gurevitch 2014). We still lag behind other disciplines such as medicine or the social sciences in the correct or effective use of meta-analysis (Roberts, Stewart & Pullin 2006; Lau *et al.* 2013). Differences in decisions regarding the number and type of studies included in a meta-analysis or in the degree of conservatism of the statistical techniques applied can change the results of meta-analyses conducted on a same topic, as shown by two papers in this Special Feature (Comita *et al.* 2014; Whitlock 2014). To ensure that meta-ecological analyses illuminate and summarize effectively, we need to improve our knowledge on how and when to conduct a proper meta-analysis and also take advantage of available cutting-edge meta-analytical methods (e.g. Curtis & Queenborough 2012). We hope that this Special Feature serves as a useful starting point for these efforts.

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