



The “Biodiversity–Ecosystem function debate”: An interdisciplinary dialogue between Ecology, Agricultural Science, and Agroecology

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ABSTRACT

The “biodiversity–ecosystem function debate” is considered one of the most heated recent scientific issues within the discipline of Ecology. However, it can be better understood as an interdisciplinary dialogue between Ecology, Agricultural Science, and Agroecology. In this article, I review the interplay of these disciplines on the conflict, the resolution, and the implications of this debate. Agricultural Science and Agroecology challenged the relevance of nontransgressive overyielding and random assembly experiments, provided statistical and empirical methods for re-analyzing the results, and developed important recommendations for agroecosystems. This exemplifies how interdisciplinary approaches to science can contribute to improve research quality and relevance.

KEYWORDS

Agroecology; Ecology; Agronomy; interdisciplinary science; intercropping

Introduction

One of the most heated scientific issues in the last two decades was the “biodiversity–ecosystem function debate,” which concerned the role of biodiversity on the productivity, stability, and other functions of ecosystems and its implications for the future of the ecosphere (Tilman, Isbell, and Cowles 2014). This debate is widely viewed as evolving within the scientific discipline of Ecology, mainly a discussion between Community versus Ecosystem Ecology (Naeem 2002), which became entangled with issues over how ecological science should properly inform public policy (DeLaplante and Picasso 2011). However, this view may give an incomplete picture of the nature of the debate. The biodiversity–ecosystem function debate can be better understood as an interdisciplinary dialogue between the disciplines of Ecology, Agricultural Science, and Agroecology. The goal of this article is to identify the interplay of these contrasting disciplines in key aspects of the debate, so that we can draw lessons about how interdisciplinary science can contribute to improve scientific research quality and relevance.

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The biodiversity–ecosystem function debate

The early history of this issue (Figure 1) goes back to the “diversity increases stability” hypotheses from Odum and Elton in the 1950s, contradicted later by the modeling works of May and Pimm in the 1970s and 1980s (McCann 2000). In the early 1990s, large biodiversity experiments were established, where species diversity was manipulated by randomly assembling multispecies communities and the effects of these communities on ecosystem function (like total biomass productivity) were measured. The three main experiments were the Cedar Creek grasslands in Minnesota, USA (Tilman and Downing 1994), ECOTRON multitrophic aquatic systems (Naeem et al. 1994) in UK, and BIODEPTH grasslands (Hector, Schmid, and Beierkuhnlein et al. 1999) in various sites across Europe. These experiments provided empirical evidence of a positive relationship between diversity and productivity or stability. These results were criticized because of two main arguments. First, they contradicted observational studies where environmental conditions determined species diversity (Wardle, Zackrisson, and Ho et al. 1997). Second, the design of the experiments made their interpretation difficult or invalid, in particular because of the “sampling effect” (Huston 1997), i.e., the increase in productivity in diverse communities may be due to the higher probability of including a highly productive species in the mix. The biodiversity–ecosystem function was a research program with an explicit aim to inform public policy on biodiversity conservation (Naeem, Chapin, and Costanza et al. 1999). Probably because of this context, generalizations were too quickly made, and the debate turned into a public “full-blown war” in the media (Kaiser 2000).

After a conference in Paris in December 2000 (Figure 1), a synthesis framework emerged, reanalyses of experiments were carried out, concepts were redefined, and conciliation was reached: a large number of species are required to maintain ecosystem function, but whether this is because more

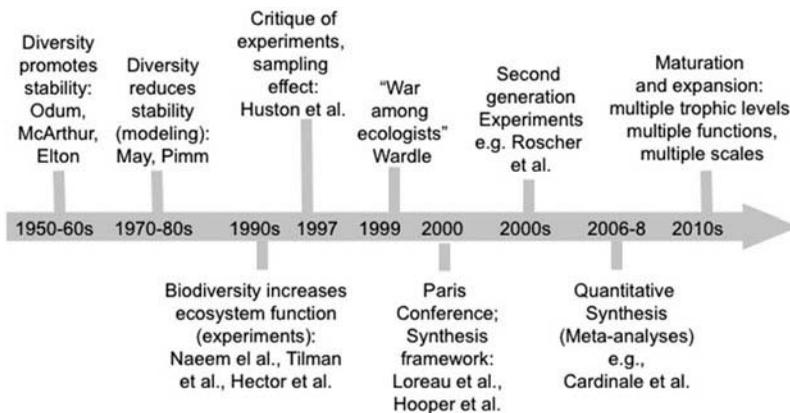


Figure 1. Timeline of the history of the biodiversity–ecosystem function debate.

rich communities have some key species (selection) or complementary among various species was unknown (Hooper et al. 2005; Loreau, Naeem, and Inchausti et al. 2001). Research separating complementarity and selection effects followed (Loreau and Hector 2001). A second generation of biodiversity experiments was developed (e.g., Jena Project in Germany; Roscher et al. 2007), usually including all monocultures, a balanced treatment design to allow separating species effects (e.g., Picasso et al. 2008), and true replications and blocks (Figure 1). Later on, a series of meta-analysis of experiments showed that diversity effects were positive, due mainly to complementarity effect, and transgressive overyielding (i.e., the diverse mix produces more yield than the highest yielding monoculture) was found only in long-term experiments (Cardinale et al. 2007). Recently, this research program has matured and expanded (Figure 1) to provide empirical and theoretical evidence on the importance of biodiversity for ecosystem function for multiple trophic levels, multiple functions, and global scales (Maestre et al. 2012; Schuman et al. 2016; Tilman, Isbell, and Cowles 2014). A detailed review of the historical, philosophical, and political context of this debate is not the scope of this article, but it can be found elsewhere (DeLaplante and Picasso 2011).

Ecology versus Agricultural Science and Agroecology

In order to address whether this debate can be more usefully understood as an interdisciplinary dialogue between the disciplines of Ecology, Agricultural Science, and Agroecology, we first must briefly address the conceptual and methodological differences between these three disciplines. All scientific disciplines are dynamic conceptual abstractions, addressing the one and complex reality from different angles or viewpoints. Therefore, as with any other disciplines, the boundaries in terms of objects of study and methods are diffuse and change over time. However, the scientific traditions, the history and accumulation of scholarship, the existence of distinct research communities, and scientific journals are enough criteria to set these three disciplines apart, and identify their unique contributions. Figure 2 illustrates these three disciplines across the broader landscape of other sciences. This figure is not intended to be complete, and it leaves out many scientific disciplines, as well as other areas of academic pursuit, like Humanities, Medical sciences, and Engineering.

Ecology, Agricultural Science, and Agroecology are scientific disciplines with different traditions and approaches, although with some considerable overlapping. One main difference between Ecology and Agricultural Science is the object of study: the first one is mainly interested with natural ecosystems, while the second one studies human managed ecosystems with the purpose of food and fiber production (i.e., agroecosystems). Agroecology shares this object of study (agroecosystems), although it is expanded from the field and

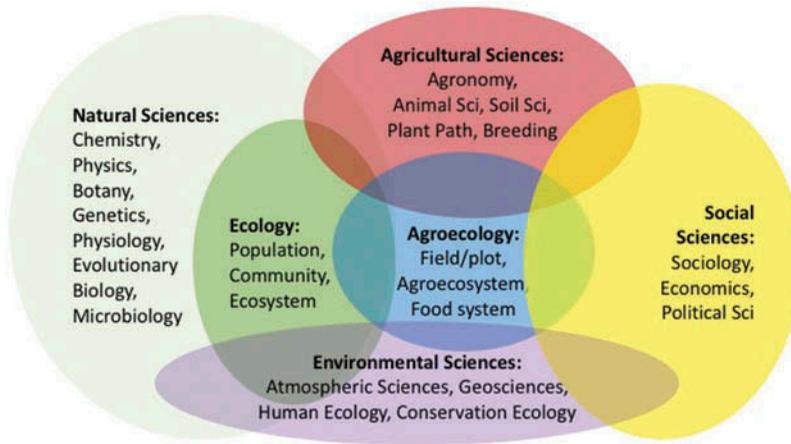


Figure 2. A graphical representation of Ecology, Agricultural Sciences, Agroecology, other related scientific disciplines, and some of their subdisciplines.

farm scale to the entire food system, including the environmental and socio-economic dimensions (Francis et al. 2003; Gliessman 2015; Gliessman, Rosado-May, and Guadarrama-Zugasti et al. 2007; Wezel et al. 2009).

A second difference is the theoretical versus applied nature of the disciplines. Ecology is more fundamental or theoretical in nature. Ecology also has many subdisciplines including population, Community, Ecosystem Ecology, among others. Although there are many applications of ecological science, e.g., in conservation biology, the bulk of the Ecology work is understanding nature. On the other hand, Agricultural Science is an applied field of science focused mainly on increasing crop and animal productivity, comprising Agronomy, Breeding, Soil Science, among other subdisciplines. Agroecology, again, shares this applied focus, expanding the goal toward the multiple dimensions of sustainability. Agroecology comprises the subdisciplines of field/plot Ecology, Agroecosystems Ecology, and Food Systems Ecology (Wezel and Soldat 2009). Theories come second after practice in these disciplines.

Probably the most important difference for understanding the contributions to this debate is related to the descriptive versus prescriptive criteria. Ecology is descriptive and predictive, i.e., it is interested in describing, modeling, and explaining natural variation in ecosystems. In contrast, Agricultural Science is normative and prescriptive: it has the goal of understanding how farming systems can perform in order to optimize certain functions like crop productivity (Vandermeer, Lawrence, and Symstad 2002). Agricultural scientists are interested in what management decisions can maximize crop yields and farm income. Considering this criteria, Agroecology shares with Agricultural Science its prescriptive nature. The main difference is that Agroecology has a more explicit broader goal of agroecosystems and food systems sustainability,

i.e., achieving productivity, stability, resilience, environmental quality conservation, social acceptability, equity, and economic profitability, through exploring the benefits of increased biodiversity in farming systems and increased fairness in the food system (Gliessman, Rosado-May, and Guadarrama-Zugasti et al. 2007).

Contributions of Agricultural Science and Agroecology to the debate

In the following section, we provide evidence of the contributions of Agricultural Science and Agroecology to three key aspects of the debate: the conflict, the resolution, and the implications.

First, the agriculture perspective played a relevant role in creating the conflict in the debate. Agricultural scientists and agroecologists confronted ecologists for initially neglecting the literature on intercropping and crop mixtures (Wardle, Huston, and Grime et al. 2000) which had shown that mixtures of few species usually are more productive than the average of the species grown in monoculture (i.e., mixtures show nontransgressive overyielding), but not greater than the most productive monoculture (i.e., mixtures do not show transgressive overyielding), with the exception of legume–grass mixtures (e.g., Anders, Potdar, and Francis 1995; Trenbath 1974). The focus of agricultural scientists was on transgressive overyielding to maximize crop production, and therefore ecological research results celebrating the novelty of nontransgressive overyielding were criticized (Garnier et al. 1997). Ecologists argued that agroecosystems fall in the low end of the biodiversity range, and usually operate at higher nutrient concentrations (e.g., soil nitrogen) than natural systems, therefore insisting that Agricultural Sciences and Agroecology literature was irrelevant for understanding natural ecosystems (Naeem 2000). This was a major contribution to articulating the conflict.

Furthermore, the hottest area of debate, i.e., the interpretation of the sampling effect as an artifact of the experimental design (Huston 1997) or as a valid biological assembly mechanism (Tilman, Lehman, and Thomson 1997), can be interpreted also as a debate between the agricultural and ecological perspectives. Farmers do not plant a random assortment of crops in their fields, so experiments with species assembled at random where the sampling effect was operating had little relevance for agricultural scientists and agroecologists. In contrast, extinctions in natural ecosystems could be more random, and therefore the biodiversity experiments were informative for natural ecosystems.

While much of the heat of the debate may have come from the contrasting views of Agriculture and Ecology, the interdisciplinary dialogue between the disciplines helped resolving the debate. Here, Agroecology played a key relevant mediation role. Indeed, the introduction of intercropping indices

like relative yield totals to separate transgressive versus nontransgressive overyielding, widely used previously in agroecology research (De Wit and Van Den Bergh 1965; Vandermeer 1989), played a central role in the development of the synthesis framework in 2000. Indeed, these indices are the basis for the partitioning between selection and complementarity effects that clarified the mechanisms behind the biodiversity–ecosystem function relationships (Loreau and Hector 2001).

A second agricultural contribution to the resolution of the debate was the focus on the principles of statistical design of experiments, like using true replications of treatments and local control of variability (blocking), which has been central to Agricultural Science since the early 1900s (Fisher 1960). Because of the wide range of ecological variation, ecological studies not always have true replications, and use pseudo-replications instead (Huston 1997). Also, related to that, ecological analyses commonly use multiple regressions and other multivariate statistical techniques, which are less powerful for determining causation than analysis of variance of well-replicated agronomic (often randomized complete blocks) designs. Understanding and addressing these statistical issues was key to move forward in the debate.

Finally, Agricultural Science and Agroecology contributed to derive implications from the results of the debate. Sustainable agriculture systems must be productive and stable, control invasions of pests and diseases, and recycle nutrients efficiently among other ecosystem functions. Modern agriculture systems usually have low biodiversity (both planned and associated), and the annual grain monocultures are the extreme example of this. Increasing managed biodiversity in agroecosystems may increase productivity and ecosystem functions. In fact, several publications out of biodiversity–ecosystem function research suggested recommendations to agriculture systems, particularly for grasslands management (Minns et al. 2001), forage production and grazing systems (Sanderson et al. 2004; Tracy and Faulkner 2006), dual-purpose polyculture systems (Picasso et al. 2008), and cellulosic biofuel systems (Tilman, Hill, and Lehman 2006). Although the importance of increasing biodiversity in agricultural systems has long been proposed and it is one of the main tenants of Agroecology (Altieri 1989; Gliessman, Rosado-May, and Guadarrama-Zugasti et al. 2007; Jackson 2002), the conclusions and recommendations of this debate provided more evidence and strength to this argument.

Back to Charles Darwin's advice

In *The Origin of Species*, Charles Darwin (1859) refers to an English garden experiment from 1816 where “*it has been experimentally proved that if a plot of ground be sown with one species of grass, and a similar plot be sown with distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised.*” For this statement, Darwin has been named

the father of the biodiversity–ecosystem function debate (Hector and Hooper 2002). Interestingly enough, Darwin pointed to a “sown” plot rather than a natural grassland. Furthermore, in the next line, Darwin continues: “*The same has been found to hold good when first one variety and then several mixed varieties of wheat have been sown on equal spaces of ground.*” Darwin was referring to an agriculture situation, rather than a natural situation, more precisely, to an intercropping wheat field. As he did throughout his book starting with “variation under domestication” and then moving to “variation under nature,” Darwin drew many examples from familiar agriculture situations to help explain natural phenomena. In Darwin’s time, the disciplinary boundaries that may seem so thick today between Evolutionary Biology, Ecology, Agroecology, and Agronomy did not exist. Therefore, learning from both “nature” and “domestic productions” was not only allowed, but encouraged as a proper way to understand reality. “*As has always been my practice, let us seek light on this head from our domestic productions. We shall here find something analogous*” (Darwin, 1859). This interdisciplinary learning, going from ecosystems to agroecosystems and back, is one of the essential features of Agroecology, and for this, Charles Darwin should also be considered the great grandfather of Agroecology. Hopefully, Darwin’s advice will provide insight today in this much needed interdisciplinary dialogue between Ecology, Agricultural Science, and Agroecology.

Lessons for interdisciplinary science

Scientific progress can occur by focusing on clarifying definitions and assumptions, which is the first step in an interdisciplinary dialogue. Indeed, one of the benefits of interdisciplinary science is that it allows for explicitly acknowledging each individual discipline’s ignorance of what’s outside their own domain. Acknowledging ignorance is the first step for learning and understanding new phenomena. Explaining our definitions and assumptions to colleagues outside our own discipline is useful for revisiting these assumptions. A second step in the interdisciplinary dialogue is to acknowledge different methods and approaches, and realizing their usefulness and limitations. In rare successful occasions, the integration of different methods can be achieved, and a new understanding emerges. This was the case of the biodiversity–ecosystem function debate. And that is why this debate made substantial contributions both in the scientific understanding of the ecosystem and in suggesting management and policy decisions in biodiversity conservation and agricultural sustainability.

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