
THE IMPORTANCE OF CONTROVERSIES IN THE EPISTEMIC PROGRESS OF ECOLOGY

PAULA G. NUÑEZ
and MARTÍN A. NUÑEZ

SUMMARY

Ecology, as a scientific discipline, has scarcely been studied relative to other fields of science. In general its epistemic changes were described as a cumulative trajectory of scientific progress, such as the one proposed by classical philosophers of science, or as a model of successive ruptures, as in Kuhn's interpretation of scientific change. In this paper we attempt to show that, like in other scientific disciplines, the trajectory of change in ecology can be different from these dynamics. Focus is placed on the analysis of controversies in ecology, one of the main sources of self-criticism in the discipline. In some cases, persistent controversies are seen as evidence of the immaturity

and/or weakness of this field. In this study controversies are not assumed to be detrimental. Even when controversies do not achieve a synthesis, as many in ecology do not, they can be progressive from an epistemic perspective. In this study two of the most prominent debates in the history of ecology are analyzed: the debate about plant succession and the debate on the role of competition as the principal force structuring natural communities. It is found that, contrary to the common perception of controversies as problems to be avoided, they can produce epistemic progress by means of the incorporation of new questions and the increase in rigor in hypothesis-testing.

The dynamics of change in science is one of the most debated topics in philosophy of science (Popper, 1963; Kuhn, 1999; Laudan, 1977). There have been profound analyses of several scientific disciplines such as physics (Nudler, 1999). However, analyses of other disciplines are less frequent. This is the case for ecology, which is the branch of biology interested in the relationships between organisms and their environment (Haila and Taylor, 2001).

Ecology does not adequately fit within the parameters of classic epistemology which entails the ideas elaborated in the first half of the 20th century by philosophers, mainly logical empiricists and critical rationalists, who defined the basis of the field. Neither does ad-

equately fit the parameters of more modern versions of classical epistemology, that critically revised the early work of Kuhn, Popper and other epistemologists, such as the work of Feyerabend (1970) or the last work of Kuhn (1962). However, ecology is still evaluated by these parameters (Mahner and Bunge, 1997; Peters, 1991).

Ecology does not have clear general rules that govern the systems it studies, even though most ecologists try to find regularities (Lawton, 1999). Also, the dynamics of ecology is difficult to describe in terms of continuous and cumulative progress, or successive ruptures. For classical philosophy of science those two aspects, the arrival of a set of general rules and the dynamics of change, are necessarily connected and progress is conceived as unique, cumulative and

continuous. In this study, a way in which change can be conceived in ecology is presented by analyzing two of the most prominent controversies in the history of ecology: the debate about plant succession and the debate on the role of competition as the principal force structuring natural communities.

Change in Science and its Implications to Ecology

Classical epistemology conceives change as cumulative progress, but this cumulative trajectory can be understood in two different ways. One view, the positive, sees change as growing knowledge about how the world is (Hempel, 1966). The other view, the negative, sees progress in science as growing

KEYWORDS / Competition / Controversies / Ecology / Epistemic Advance / Plant Succession /

Received: 12/14/2006. Modified: 10/15/2007. Accepted: 10/17/2007.

Paula G. Nuñez. Professor of Mathematics and History. Master Student in Philosophy and History of Science, Universidad Nacional del Comahue (UNCOMA), Argentina. Doctoral Student in Philosophy, Universidad Nacional de la Plata, Argentina. Address: Carrera de Historia, Centro Regional Universitario Bariloche, UNCOMA, Quintral s/n, Barrio Jardín Botánico. (8400) San Carlos de Bariloche. Río Negro, Argentina. e-mail: paulagabrielanu@yahoo.com.ar

Martín A. Nuñez. Licentiate in Biological Sciences, UNCOMA, Argentina. Ph.D. Candidate, University of Tennessee, USA.

knowledge about how the world is not. This last postulate corresponds to Popper (1963), who contended that scientists cannot be sure about their hypotheses but can be sure about their refutations.

Kuhn (1962) challenged the perspective that progress is cumulative and continuous in *The Structure of Scientific Revolutions*. In this book, the author maintained that the dynamics of science, far from being cumulative, corresponds to a model of successive ruptures. Kuhn compared each rupture with a revolution, and the end of the revolution is marked by acceptance of a new paradigm. He argued that the criterion to recognize advance in science is reaching agreement. He described "mature sciences" as disciplines that have paradigms, while "immature sciences" are those disciplines that still have not achieved a paradigm and contain different schools in dispute. This idea of paradigm has been used to revise the status of ecology. Studies by Simberloff (1980), Wiens (1989) and most recently Graham and Dayton (2002) try to understand ecology from Kuhn's perspective. However, the recognition of a paradigm with the levels of agreement imagined in Kuhn's conception is difficult in a discipline with continuous disputes. This does not mean that agreement is absent in ecology, but it implies that agreement is not as general as Kuhn's model expects. Because of the persistence of controversies in ecology, according to a strict Kuhnian classification of science, ecology would be cataloged as immature or pre-paradigmatic. In fact the permanence of debates has been considered a problem for progress in the discipline and a clear sign of immaturity (Mahner and Bunge, 1997; Jaksic, 2001).

We suggest that the pattern of advance in ecology may differ from the positive cumulative trajectory proposed by classical epistemology, the negative cumulative (or refutation) trajectory (Popper, 1963) or from Kuhn's successive ruptures model. Thus, it is not assumed that ecology is an immature science, and an attempt is made to study its characteristics without assuming that they are problematic. We believe that it can be useful to analyze the dynamics of change in ecology by considering the role of controversies (Nuñez and Nuñez, 2005).

The Role of Controversies

Historically, controversies and conflicts have been seen as an obstacle to scientific progress. However, in recent years the potential positive role of conflicts has been recognized. This change of view has generated reflections about science in which controversies have

begun to be recognized as necessities to produce scientific change (Dascal, 1998; Machamer *et al.*, 2000; Nudler, 2004). These analyses show that controversies may be progressive in an epistemic sense, even if the scientific community does not achieve general agreement. Controversy can develop only in the context of a set of previous agreements, because if the parties have nothing in common, dialogue is impossible, even in terms of a dispute (Nudler, 2004).

As an analogy to Lakatos' (1970, 1974) idea on the way science changes, controversies can be described as progressive or regressive. As a general proposition, it can be said that controversies are progressive if they relate to other controversies and enrich the discipline by incorporating new questions and hypotheses. On the other hand, if controversies do not produce new ideas or hypotheses, and all new ideas are *ad hoc* hypotheses developed to maintain the theoretical base, the controversies are considered regressive, because they do not produce an epistemic advance.

It is important to note that all scientific controversies are founded on a group of basic agreements. Progress, following this approach, is shown by the expansion of the discussion and not only by the agreement. In other words, synthesis or accord is fundamental to scientific progress but the existence of controversies can also be important. Controversies have been seen as necessary to arrive at agreements (Cosser, 1957; Dascal, 1998, 2003), but herein it is proposed that controversies can be important by themselves. Progress in science owing to controversies is possible because epistemic change is possible even with minimal agreement.

Controversies in Ecology

One characteristic of ecology is the persistence of many controversies. In order to review these aspects two principal controversies in the history of ecology will be studied: the debate about how to study plant successions and the debate about the role of competition. The dynamics of change in each case is investigated by analyzing the controversies in detail and the set of agreements tied to them. The difference in these two processes will help to understand the complexity of progress in ecology and facilitate the comprehension of the complex arena of discussions where the discipline is. In both controversies, arguments are found from opposite perspectives about how nature can be explained, but in one controversy the dialogue between the two opposing parties almost did not exist and in the other

case the discussion was so significant that it surpassed the disciplinary limits.

The Debate about Plant Succession

Plant succession was one focus of early ecology. Some ecologists, educated in a botanical tradition, began their studies assuming that the plant association governed all other organic relationships. One of the principal concepts defined by this group was the "climax" community. This term was introduced by R. Hult in 1885 (Clements, 1936) and formalized by Clements (1916), who proposed the climax as the final stable stage of plant associations.

The climax as a research program

Clements (1916) proposed that the climax, the mature stage of plant association, could form the basis of a natural classification of plant communities. The key idea in this research program was the metaphor of a plant community as a "complex organism". Shimwell (1971) indicated that in the first decades of the twentieth century most Anglo-American plant ecologists subscribed to this holistic perspective, which considered communities as an organism. An example of the application of this conception is

"... plant association may be regarded in its entirety as an organic entity, and as such it occupies a position in the field of ecological plant sociology which is homologous in a general way to that occupied by an individual plant or specimen in such fields of botany as plant morphology or plant taxonomy. As integral parts of the larger community, plant societies bear a relation to the association which is somewhat analogous to that borne by the various organs of an individual plant to the plant as a whole" (Nichols, 1923: 14).

The climax theory supposes that stability is reached owing to a universal vegetation tendency under a dominant climate. The force of change produces plant succession, which is unidirectional towards a climax, but only if anthropogenic effects are absent. In Clements' view, factors in the land (such as soil characteristics) were not as important as the climate. In other words, he believed in an absolute hierarchy of factors that operate similarly everywhere.

The diversity of biotic organizations and the diffuse limits between one vegetation type and another can also be explained from this perspective. The levels of different stages that researchers observe are understood as particular peri-

ods of "life" of these complex organisms. The climax is the adult organism, and all the less distinct stages are either initial (juvenile) or terminal (senile) stages, because plant association was conceived as an organism which is born and dies, as any other living being (Kingsland, 1991). In this context the climaxes were the basis for the natural classification of plant communities because they were visualized as the major unit of vegetation (Clements, 1936). The main characteristic of the climax, from this perspective, was permanence:

"Climaxes have evolved, migrated and disappeared under the compulsion of great climatic changes from the Paleozoic onward, but... they persist through millions of years in the absence of such changes and of destructive disturbance by man" (Clements, 1936: 256).

This organic metaphor has a teleological component. If someone accepts that a specific plant association is in juvenile stage, this implies that this association will necessarily converge to specific mature and senescent stages. The plant association has a fixed destiny.

The critics

Criticism started early and focused on two aspects of Clements' theory. An opposite perspective, the individualistic perspective, was developed by Gleason (1926, 1939), who opposed this holistic and teleological vision. The alternative perspective was also adopted by Tansley (1935), who rejected only the teleological aspect of Clements' idea.

Gleason felt that the plant communities defined by Clements were human-contrived abstractions for purposes of description, classification and management of vegetation. In this line of thought, the main criticism to the idea of plant communities as superorganisms was based on the fact that there were no natural boundaries between communities, temporally or spatially. This individualistic perspective was directed against holism. From a different perspective, Tansley criticized the idea of "complex organism" but not the holistic spirit of the hypothesis. This author indicated that well-integrated plant communities identified with plant associations had sufficient organismal characteristics to be considered as quasi-organisms. He noted that a plant community and an organism have characteristics in common, but he disagreed with the argument that biotic communities are organisms in a realistic sense. Tansley was a holist, but he rejected the teleological implications of the idea of a climax. He proposed the notion of "ecosystem" as an alternative based on understanding the plant association as a

physical system, which could have several "stable points", but not a deterministic development. From this perspective, a climax was redefined as a stability point.

The controversy

Neither Gleason's proposal nor Tansley's were considered by Clements and his many followers when they were first proposed. Clements' idea of climax continued in the theoretical framework of ecology up to the 1950s. According to Kingsland,

"These criticisms did not persuade Clements to drop the organism metaphor or to change his classification system in any way. The only major change in Clements' ideas in later years was to recognize the existence of animal populations as an integral part of the community. However, by the 1950s plant ecologists had abandoned many of the central principles of Clementsian dogma" Kingsland (1991: 6).

Why did it take 30 years for mainstream ecology to incorporate criticisms on Clements' views? Many factors may have contributed to this lag, and we suspect that it was simpler to conceive of an ordered nature with one initial stage, one mature stable stage and one final stage. In his seminal work from 1790, the philosopher I. Kant proposed that there was a need for a teleological judgment to understand the natural world, since this natural world was not clearly explained following the logic used in mathematics or physics (Kant, 1978; Copleston, 2002). Teleology, as a strategy, has a long tradition in the studies of nature and has been an efficient starting point for important contributions (Makinistian, 2004). This is why to assume a nature without destiny did not appear promising as a research field.

Another element to explain the resistance to change in the study of plant communities is the lack of dialogue between the parties involved in the controversy. Each group of investigators knew the ideas of the others and they even make short references to the existence of different points of view, but they did not start a systematic debate. When scientists adopted either metaphor (the organic or the physical one) they could find ways to avoid confrontations with researchers from the opposing school. So the limitations of each perspective were probably considered by each side on their own, and this isolation may have limited the possibilities to modify their perspectives during several years.

Climax has been proposed as the first paradigm in ecology

(Simberloff, 1980). However, it is difficult to define Clements' premises as a paradigm in a strict Kuhnian sense. This is because, from the first appearance of Clements' ideas, an important group of well-known scientists opposed his perspective on plant succession. Even though the postulates of Clements guided the work of many ecologists until the 1950s, alternative perspectives had been introduced in the ecological literature many decades earlier, based mostly on the difficulties of distinguishing climax stages. During this time, one can think of Clements' school as undergoing a regressive process. From Lakatos' (1970) perspective it can be mentioned that the problems in the use of the climax concept were solved by *ad hoc* hypotheses to explain systems that do not behave as climax theory predicted (Kingsland, 1991).

The ideas of Gleason and Tansley had a secondary, but still important place in the theoretical background of ecology during the first half of the 20th century. There is no clear moment when the scientific community abandoned the Clementsian research program and adopted a different one. The existence of alternative ideas enabled a gradual incorporation of other perspectives in the ecological theoretic framework. For example, in the 1960s studies on the flux of energy through ecosystems according to Tansley's ecosystem concept clearly became important. Nowadays, the complex synthesis of ideas can be perceived as follows:

"The present American concept of the community is a synthesis of Clements' association unit hypothesis with Gleason's continuum-individualistic hypothesis, together with a recognition that there may be several different kinds of associations, each explainable according to a different model. We have come to understand that the classical theories are inadequate for completely explaining and predicting vegetation patterns, and we have come to appreciate that the scale of complexity in nature makes the existence of a single model highly unlikely". (Barbour *et al.*, 1999: 185-186)

The abandonment of the Clementsian hypothesis and the end of the controversy to explain plant succession were progressive. The confidence in the climax as a real entity changed to a vision that sees it simply as a heuristic guide, because it turns out to be just a way of pointing to the stability of plant association. This change of status may be understood as progress in the discipline, because the "ecosystem research program" opens questions that the "climax" did not permit. However, this solution did not imply that

the controversy on plant succession was closed. In recent years new questions were introduced from new perspectives. Works like those by Lortie *et al.* (2004) or Davis *et al.* (2005) illustrate that this concept has different interpretations and that the strict individualistic conception (the inheritance of Gleason's perspective) needs a revision.

The difference between the debates from the beginning of the 20th century and those of nowadays consists in that, in the former, discrepancies revolved around the way nature was understood. Each idea, the organic metaphor adopted by Clements and the physicalist one adopted by Tansley or Gleason's proposal that followed, had methodological consequences, so that the adoption of any one of them excludes the others. In these early debates there was not a common ground of agreements and, probably because of this, progress was slow. Nowadays, debates do not involve antagonistic metaphors. Instead, differences in commitment sustained by different analytical perspectives seem to build new communicative barriers (see Simberloff, 2004; Lortie *et al.*, 2004).

The Debate about Competition

Competition as a force structuring communities deeply influenced ecology in its origins and in the development of its main theories. Gause (1934) proposed the concept of competitive exclusion, which maintained that if two species use resources in exactly the same way they cannot coexist indefinitely. This idea was molded by different early studies and it was finally formalized by Hutchinson (1957) who defined an ecological niche as the *n*-dimensional hypervolume in which a species can survive, a concept closely related to Gause's competitive exclusion principle. Kingsolver and Paine (1991) indicated that Hutchinson's proposal helped clarify the relationship between ecological partitions and coexistence or evolution within communities.

The impact of these theories and other influential studies made of Hutchinson one of the founding fathers of ecology. The definition of Hutchinson implies the hypothesis that interspecific competition was the principal force structuring biotic communities. This conception was incorporated into the established theoretical knowledge of ecology. Even when hypotheses are never accepted as definitively true, there is a group of them that investigators accept as a base for research and do not question. This group of basic hypotheses was labeled the "hard core" of a research program by Lakatos (1974), and the "paradigm" by Kuhn (1962). An example of an idea tied to the theoretic-

cal structure of ecology is Hutchinson's (1959) "1.3" rule. This rule indicated that coexistence between two similar species would be possible only if the difference in the sizes of their trophic apparatus was at least 30 percent. In other words, a size ratio of at least 1.3 assures that the two species use different resources or similar resources but in a sufficiently different way to permit coexistence.

The debates until the 1970s

The role of competition and other related ideas were not put in doubt until the 1970s, and it was an idea assumed to be fundamental by many influential ecologists in those times. For instance, MacArthur (1958) studied the coexistence of similar bird species in a tree. In this case, the similarities of the birds made it difficult to doubt the existence of competition between different species. MacArthur found that some species used mainly the upper parts of the tree, others the middle, and others the bottom parts of the trees. He assumed *a priori* the importance of competition and concluded that the birds were segregated to permit coexistence, following the well accepted ideas ruling ecology at this time that similar species cannot coexist without strongly competing with each other. This approach omitted other factors, such as the natural history or morphology of the birds, that might explain the situation from a different perspective without reference to competition.

Another case is the analysis by Hairston *et al.* (1960) of the relationship between trophic levels. These authors argued that predation is an important interaction for the regulation of natural populations. Despite their belief that other types of interactions could also be important, they argued that interspecific competition exists and is important at all levels but that it is not possible to study it at every level. At the producer level (vegetation) competition is easy to study, for example, by seeking the difference in size or color of the leaves that permits coexistence when two plants compete for light. However, for predators, competition takes the form of diversification of niches and therefore is not directly observed. The authors assumed that competition is omnipresent and of fundamental importance even though it is difficult to document.

These cases illustrate how widely accepted the assumption of the fundamental importance of interspecific competition were. The main research programs were still adopting this view of competition, even after the publication of important articles as that by Andrewartha and Birch (1954), which introduces the importance

of density-dependence vs density-independent processes in community dynamics; or works discussing the interpretation of the quotient species/genera sustained in the role of competition (see Williams, 1947; Simberloff, 1970). In addition, during these years, some ecologists studied specific cases where competition theory was unable to explain community structure (Holling 1959; Paine 1966). Both Holling and Paine examined the importance of predation. Despite these seminal papers, ecology did not modify its theories relating to competition probably because these critics studied specific situations and did not challenge the role of competition as the main force organizing communities. These researchers tried to determine the role of predation in ecological communities but did not attempt to refute competition as the main force structuring these communities.

Controversy about competition

The species-to-genus ratio in island versus continental biota inspired some ecologists to reconsider the role of competition as the main force structuring communities. As Gotelli (2001) remarked, this and other taxonomic ratios were the starting point for the use of null models in ecology. Null models are pattern-generating models, based on randomization of ecological data that excludes a particular mechanism. This allows comparison of patterns observed in nature with patterns produced by stochastic processes (no mechanism involved) to quantify the importance of a specific mechanism (Gotelli and Graves, 1996). If the patterns produced by random processes can not be distinguished from the pattern observed in nature, it can be the case that the proposed mechanism to explain the observed patterns is not operating.

If it is assumed that species of the same genus are in general more similar than species of different genera, and because of their similarities are more likely to compete than species from different genera, one would expect lower species to genus ratios when competition is stronger. Lower species to genus ratios on islands were interpreted as direct evidence for the importance of competition. The belief was that competition is more intense on islands owing to the restriction in area and resources.

Revision of the view on the species-to-genus ratio and reconsideration of the overall role of competition started together. Simberloff (1970) examined differences between island and continental species-to-genus ratios. Simberloff applied null models and demonstrated that lower ratios on islands could be ex-

plained as a mathematical artifact that results from islands having fewer species than continents. Simberloff concluded that there was no need to invoke competition to explain lower species to genus ratios on islands. Williams (1947) mentioned similar results, but his publications did not have a large impact. Simberloff (1970) mentioned the inexplicable lack of attention to Williams' work, but his own paper did not attract a huge amount of attention, probably because not many researchers were passionate about this area of ecology and the use of null models in ecology was not yet widely accepted.

The assumption of competition as the most important force regulating natural communities continued to guide ecologists for many years after Simberloff's (1970) seminal paper. This lag may be an example of the usual resistance to starting debates about topics perceived as well understood, an aspect described by Kuhn (1962), Lakatos (1974) and many other influential philosophers such as Whitley (1972) and Torres Alberó (1994).

Gotelli (2001) stated that the most influential paper supporting the competition hypothesis was that of Diamond (1975), where "assembly rules" for biotic communities were formulated based wholly on the role of interspecific competition. In 1978 Simberloff criticized Diamond's (1975) study on the grounds that it lacked alternative hypotheses and appropriate ways of testing assembly rules. This opinion provoked little or no response. Connor and Simberloff (1979) wrote a more direct criticism of Diamond's ideas that had major repercussions in the field. It was entitled: "The assembly of species communities: chance or competition?" The abstract shows the direct criticism of Diamond's ideas:

"We challenge Diamond's (1975) idea that island species distributions are determined predominantly by competition as canonized by his "assembly rules". We show that every assembly rule is either tautological, trivial, or a pattern expected where species distributed at random. In order to demonstrate that competition is responsible for the joint distributions of species, one would have to falsify a null hypothesis stating that the distributions are generated by the species randomly and individually colonizing an archipelago." (Connor and Simberloff, 1979: 1132)

To recognize that chance had, in many instances, the same explicative power as competition led to a question: How can ecologists consider competition as the main force in nature

when explanations based on such hypothesis cannot be empirically distinguished from hypothesis based on stochastic effects? This question touched the theoretical framework of ecology and could not be ignored. The confidence in the possibility of erecting a set of rules that governs all natural systems was challenged because the main assumption that competition structures community was now in question. For some scientists, the use of null models implied an abandonment of biological principles. For instance, Levins and Lewontin (1982) observed that the null model approach did not add any biological hypothesis, so they saw this approach as unproductive for the advancement of the discipline.

The view of null models as negative for ecological progress allows to inquire about what definition of scientific progress permits that accusation. The concept of scientific progress goes hand in hand with Kuhnian concepts. In this view, progressive change arises inside biological theories, those that form the paradigm. The claims of the critics of null models state that competition was not discussed with arguments of the same kind. In Kuhnian terms, a paradigm must be discussed with another paradigm. And the proponents of null models (nullists) cast doubt on the universality of competition (or even the paradigm). The contribution of nullists was a new perspective that allows to think about new alternatives, generate new questions and cast doubt on the old assumptions.

This debate took on a complex rhetoric that even today generates mixed feelings among ecologists, because the theoretical framework of ecology seemed to be at risk as its foundation was in question (Gotelli, 2001). Ecologists perceived that the discipline was broken into two irreconcilable parts: those who wanted to challenge the role of competition and those who wanted to defend it (Lewin, 1983). As stated previously, controversies are only possible in the context of a set of basic agreements, and this case is no exception. Neither group opposed the existence of competition as an important interaction or doubted that the ecological scientific community (rather than other specialists communities such as philosophers of science) was the right place to discuss the different arguments on the subject. And both parties admitted the need to clarify positions regarding the use of null models. Hard criticism disappeared from the debate some years later. This change in the dispute over this topic can be interpreted as a decrease in personal passions but not as a final resolution. The process of debate is clearer if

the controversy is looked upon, not the agreement.

One element to review in this debate is the different levels of discussion described below. Connor and Simberloff (1979) used null models based on chance and independence of species, as well as the philosophical-methodological ideas in Popper's (1963) *Conjectures and Refutations*. Simberloff and colleagues designed their null models following the Popperian principle of putting in doubt their own beliefs (Vazquez and Collins, 1999). Popper maintained that all premises of an empirical investigation need to be tested rigorously. Connor and Simberloff charged that rigorous tests were not common in investigations of competition until the development of null models. The scientists who rejected the idea of abandoning competition as the main force attempted to weaken the argument of null model advocates by challenging their arguments and methods (see Diamond, 1986; Diamond and Case, 1986). We propose that the attack over many different arguments blurs the controversy, because the topics under debate became clouded.

The philosophical aspects of the debate need to be mentioned, as does the fact that none of the protagonists argued about the risks or benefits of adopting one or the other philosophical perspective. For both sides this was a dispute mainly about ecology, not about epistemology. The epistemological debate was never resolved, because the defenders of competition never clarified their own philosophical commitment (Sargent, 1986) and the nullist made few references to Popper's work. Those who criticized the Popperian commitment of null models did it by trying to refute the doubt about the role of competition and not from a deep reflection about epistemology or philosophy of science. Here, *a posteriori* reflection suggests that the problem in this controversy about competition was the introduction of philosophical notions into a scientific debate (Sloep, 1993). Sloep claimed that the philosophical problems introduce noise in science, but he overlooked the point that in this there was no philosophical debate, only some isolated references to the background of the nullist approach. We think that the complex dimension of the debate was caused by the effervescence of passion and the mixing of the main arguments, in an attempt to consolidate each position.

A different perspective of analysis was introduced by Looijen (1998), who argued that the debate on the use of null models confronted the holistic perspective of Diamond with the individualistic perspective of Simberloff. In an

evaluation of this debate, Looijen found that there was a loss in the logical sense and strategies of analyses by adopting the individualist proposal. In opposition with this perspective of the debate, we believe that the debate was focused on the acceptance or not of a process (competition) as a ubiquitous force structuring communities, and that it had a logical sense.

Another aspect, no less important to consider, is that the revision introduced by the use of null models was different from Holling's (1959) or Paine's (1966) argument. Both authors questioned the role of competition in one system. But here, it was the competition paradigm that was challenged. The nullists discussed the presumption of competition as part of the methods of investigation and claimed the need to review the assumptions of different studies. If the Connor and Simberloff (1979) proposal was just methodological (as a purely analytical revision), the reaction against these ideas was out of proportion. However, if their proposal was against one of the bases of the then accepted ecological wisdom, the reaction is more comprehensible.

The framework of theoretical commitments in which the nullists set the debate must be considered. This academic framework had been elaborated since the 1950s. In this period the descriptive goal of the early 20th century changed and the discipline took an experimental character (Kingsland, 1991). In this process, mathematical analyses became ever more important and scientific work was oriented to the search for common patterns. It can be thought that, in those times, investigations were guided by the presumptions of classical philosophy of science, because one of the objectives considered as possible in the 1950's was the search for general rules, with the concomitant abandonment of the study of particular circumstances (see MacArthur, 1972; Roughgarden *et al.*, 1989). This confidence in the possibility of finding general rules did not rest only in the mathematization but also in the widespread presence of a fundamental factor structuring ecological systems: competition. Null models provided evidence that competition could not be generalized as the most important factor structuring communities. Those models allowed questions to arise as to the genuine existence of general mechanisms in the organic world. The main difference between the Clements-Gleason debates and those initiated in the 1980s is that in the first case a metaphor is discussed, but in the second one a revision of the values of classic science was at stake and, with it, the existence of general

rules in the organization of nature at the ecological level of analysis.

Debates about the role of competition were not restricted to epistemological aspects. In the set of the works using null models reconsidered, the criticism of Hutchinson's "1.3 rule" took a special place. When Simberloff and Boecklen (1981) used null models to re-examine previous studies that had supported the 1.3 rule, they found that most of the results were not different from results expected solely from chance. Consequently, the 1.3 rule lost its explanatory capacity. Part of the ecological scientific community was moved by this strong criticism against the idea proposed by the "father" of ecology.

In general, the growing debate revolved around two matters: the biological significance of this result and the mathematical details of the tests. In both debates, participants revealed their assumptions and new perspectives were subsequently introduced. In the biological debate, the defenders of competition argued that null models assume that communities are organized by stochastic forces, an idea difficult to reconcile with observations and natural history (Levins and Lewontin, 1982). Along these lines, Grant and Abbott (1982) rejected the application of null models because they understood that the approach assumes non-evolutionary principles. Ecologists who use null models replied that chance was not an explanation; it was only a way of testing the importance of competition. In this debate, the rhetoric was notably belligerent. In general, it was difficult to find points of agreement. Ecologists who used null models were not a homogeneous group. Some of them understood null models as only a heuristic tool to examine presuppositions, which does not presuppose any particular mechanism (Simberloff, 1982). Others understood chance as part of concrete natural scenarios (Colwell and Winkler, 1984; Gotelli and Graves, 1996).

Progress in scientific knowledge is one result of this debate, with ecology evolving into a more complex and rigorous discipline. The increase in level of rigor can be seen in the wide use of tests that were not an integral part of the discipline before this debate. Ecology became a more complex discipline because the debate on the role of competition led to other questions and discussions. Negative interactions between organisms (i.e. predation, parasitism, competition) and positive ones, such as symbiosis or mutualism, are now recognized as having similar explanatory power. Even today, some aspects of null models are still contentious (Colwell *et al.*, 2005; Hawkins *et*

al., 2005; Zapata *et al.*, 2005), but null models are being used in many areas of ecology and provide new ways of testing ecological hypotheses (Gotelli, 2001).

By describing this debate and some of its consequences it is shown that epistemic advance in ecology does not necessarily follow a conceptual change. This controversy introduced modifications in the hierarchy of explanatory factors. Presently, competition, mutualism, and chance are not understood in a new way, but the natural world is studied from new perspectives. In the past, competition had a predominant role over other types of interactions; and because of this controversy the different explanatory factors now have similar status. Another modification inside the discipline is the abandonment of the notion that some factors are omnipresent, leading to questions about the characteristics of ecology as a natural science.

Conclusion

Recursive controversies in ecology have been traditionally seen as problems or difficulties; this study shows that they can contribute to the advancement of ecological knowledge. To perceive the history of advancement, it is needed first to accept that controversies are not necessarily a problem but a possible way of progress. We argue that progress through controversies can be an important mechanism in the advancement of ecology as a scientific discipline and that perhaps it is better to seek rather than to avoid controversies.

The controversy about the way to understand plant communities shows that the existence of alternative schools of thought does not foreclose the possibility of future agreements. On the other hand, limits in the dialogue between schools can limit possibilities of advance.

Finally, the controversy about competition shows the existence of a basis of agreement even in the strongest disputes. In this case, the entire scientific community understands ecology as an empirical discipline, but the abandonment of the supposed importance of competition opened questions about the sense of searching for general rules in a world that perhaps does not have them at the ecological level of analysis as compared with the physics level of analysis (Lawton, 1999). The debate about the role of competition remains open and all the new questions are expanding the perspectives of ecological analysis. This process enriches the discipline but can create uncertainty among researchers about the course of the discipline (Graham and Dayton, 2002). Nowadays, the status of ecology is

under debate because the possible absence of general rules is seen, by some investigators, as a weakness of ecology (Lawton, 1999). However, as we try to show in this work, the problem lies in sustaining the perspective of classical science. Simberloff (2004) discusses that the goal of finding exact and general laws may not be realistic. Labels such as “weak” or “immature” do not contribute to study ecology as a science, because they unnecessarily construe some characteristics of the discipline as problems. Ecology could be analyzed in a better way with models alternative to classical philosophy of science; that is, by abandoning physics as the model of science.

The present analysis of two controversies in ecology suggests that far from being products of scientific immaturity, disagreements should be seen as key elements in the development of scientific knowledge. Even when these controversies do not achieve a synthesis, as many in ecology do not, they can be progressive from an epistemic perspective because they open new questions and foster new avenues for research, given the intrinsic complexity of ecological systems (Boyce, 2004). It is more likely that ecology as a science is not immature but has its own set of characteristics, such as the permanence of some controversies associated to partial agreements.

ACKNOWLEDGMENTS

The authors thank Daniel Simberloff, Sandy Echternacht, Lara Sousa and Michael Collins for their comments on this manuscript. M.N. was supported by a summer research grant from the Department of Ecology and Evolutionary Biology, University of Tennessee, USA.

REFERENCES

- Andrewartha HG, Birch LC (1954) *The Distribution and Abundance of Animals*. University of Chicago Press. Chicago, IL, USA. 782 pp.
- Barbour MG, Burk JH, Pitts WD, Gilliam FS, Schwartz MW (1999) *Terrestrial plant ecology*. 3rd ed. Benjamin/Cummings. Menlo Park, Canada. 634 pp.
- Boyce MS (2004) Realities of nature. In Taper ML, Lele SR (Eds.) *The Nature of Scientific Evidence: Statistical, Philosophical, and Empirical Considerations*. University of Chicago Press, Chicago, IL, USA. pp. 217-220.
- Clements FE (1916) *Plant succession, an analysis of the development of vegetation*. Carnegie Institution. Washington, DC, USA. 512 pp.
- Clements FE (1936) Nature and structure of the climax. *J. Ecol.* 24: 252-284.
- Colwell RK, Winkler DW (1984) A null model for null models in biogeography. In Strong DR, Simberloff D, Abele LG, Thistle AB (Eds.) *Ecological communities: Conceptual issues and the evidence*. Princeton University Press. Princeton, NJ, USA. pp. 344-359.
- Colwell RK, Rahbek C, Gotelli NJ (2005) The mid-domain effect: There's a baby in the bathwater. *Am. Naturalist* 166: 149-154.
- Connor EF, Simberloff D (1979) The assembly of species communities: chance or competition? *Ecology* 60: 1132-1140.
- Copleston F (2002) *Historia de la filosofía 6: de Wolff a Kant*. Ariel. Barcelona, Spain. 347 pp.
- Coser L (1957) Social Conflict and the Theory of Social Change. *Br. J. Sociol.* 8: 197-207.
- Dascal M (1998) The study of controversies and the Theory and History of Science. *Sci. in context* 11: 147-154.
- Dascal M (2003) *Interpretation and understanding*. Benjamins. Amsterdam, Holland. 714 pp.
- Davis M, Perglb J, Truscott A, Kollmann J, Bakker J, Domenech R, Prach K, Prieur-Richard A, Veeneklaas A, Pysek P, del Moral R, Hobbs R, Collins S, Picket S, Reich P (2005) Vegetation change: a reunifying concept in plant ecology. *Persp. Plant Ecol. Evol. Systemat.* 7: 69-76.
- Diamond JM (1975) Assembly of Species Communities. In Cody ML, Diamond JM (Eds.) *Ecology and Evolution of Communities*. Belknap, Harvard, pp. 342-444.
- Diamond JM (1986) Overview: Laboratory experiments, field experiments and natural experiments. In Diamond JM, Case TJ (Eds.) *Community Ecology*. Harper and Row. NY, USA. pp 3-22.
- Diamond JM, Case TJ (Eds.) (1986) *Community Ecology*. Harper and Row. NY, USA. 165 pp.
- Feyerabend PK (1970) *Contra el método. Esquema de una teoría anarquista del conocimiento*. Ariel. Barcelona, Spain. 330 pp.
- Gause GF (1934) *The Struggle for existence*. Williams and Wilkins. Baltimore, MD, USA. 163 pp.
- Gleason HA (1926) The individualistic concept of the plant association. *Bull. Torrey Bot. Club* 53: 7-26.
- Gleason HA (1939) The individualistic concept of the plant association. *Am. Midl. Natur.* 21: 92-110.
- Gotelli N (2001) Research frontiers in null model analysis. *Global Ecol. Biogeogr.* 10: 337-343.
- Gotelli N, Graves G (1996) *Null models in ecology*. Smithsonian Institution. Washington, DC, USA. 368 pp.
- Graham MH, Dayton PK (2002) On the evolution of ecological ideas: paradigms and scientific progress. *Ecology* 83: 1481-1489.
- Grant PR, Abbott I (1982) Interspecific competition, island biogeography and null hypotheses. *Evolution* 34: 332-341.
- Haila Y, Taylor P (2001) The Philosophical Dullness of Classical Ecology, and a Levinsian Alternative. *Biol. Philos.* 16: 93-102.
- Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control and competition. *Am. Naturalist* 94: 421-425.
- Hawkins BA, Diniz JAF, Weis AE (2005) The mid-domain effect and diversity gradients: Is there anything to learn?. *Am. Naturalist* 166: 140-143.
- Hempel C (1966) On the structure of scientific Theories. In Suter R (Ed.) *Isemberg Memorial Lectures Series, 1965-1966*. Michigan State University Press. East Lansing, MI, USA. pp. 11-38.
- Holling CS (1959) The components of Predation as Revealed by Study of Small Mammal Predation on the European Pine Sawfly. *Can. Entomol.* 91: 293-320.
- Hutchinson GE (1957) Concluding Remarks. *Cold Spring Harbor Symp. Quant. Biol.* 22: 415-427.
- Hutchinson GE (1959) Homage to Santa Rosalia; or, Why Are There So Many Kinds of Animals?. *Am. Naturalist* 93: 145-159.
- Jaksic F (2001) *Ecología de comunidades*. Universidad Católica de Chile. Santiago, Chile. 233 pp.
- Kant I (1978) *Prolegómenos a toda metafísica del porvenir. Observaciones sobre el sentimiento de lo bello y lo sublime. Crítica del Juicio*. Porrúa. Buenos Aires, Argentina. 406 pp.
- Kingsland SE (1991) Defining Ecology as a Science. In Real L, Brown J (Eds.) *Foundations of Ecology. Classic Papers with Commentaries*. University of Chicago Press. Chicago, IL, USA. pp. 1-13.
- Kingsolver JG, Paine RT (1991) Theses, Antitheses and Syntheses. Conversational Biology and Ecological Debate. In Real L, Brown J (Eds.) *Foundations of Ecology. Classic Papers with Commentaries*. University of Chicago Press. Chicago, IL, USA. pp. 309-317.
- Kuhn T (1962) *The Structure of Scientific Revolutions*. University of Chicago Press. Chicago, IL, USA. 168 pp.
- Lakatos I (1970) The methodology of Scientific Research Programs. In *Philosophical Papers*. Vol 1, Cambridge University Press. Cambridge, UK. pp. 91-196.
- Lakatos I (1974) *Historia de la ciencia y sus reconstrucciones racionales*. Tecnos. Madrid, Spain. 160 pp.
- Laudan L (1977) *Progress and its problems: Towards a theory of scientific growth*. University of California Press. Berkeley, CA, USA. 257 pp.
- Lawton JH (1999) Are there general laws in ecology? *Oikos* 84: 177-192.
- Levins R, Lewontin R (1982) Dialectics and reductionism in ecology. In Saarinen E (Ed.) *Conceptual issues in ecology*. Reidel. Dordrecht, Holland. pp. 107-138.
- Lewin R (1983) Santa Rosalía was a goat. *Science* 221: 636-639.
- Looijen RC (1998) *Holism y reductionism in biology and ecology. The mutual dependence of higher and lower level research*. Kluwer. Dordrecht, Holland. 269 pp.
- Lortie CJ, Brooker RW, Choler P, Kikvidze Z, Michalet R, Pugnaire F, Callaway R (2004) Rethinking plant community theory. *Oikos* 107: 433-438
- MacArthur RH (1958) Population Ecology of some Warblers of Northeastern Coniferous Forests. *Ecology* 39: 599-619.
- MacArthur RH (1972) *Geographical Ecology: Patterns in the Distribution of Species*. Harper & Row. New York, USA. 269 pp.
- Machamer P, Pera M, Baltas A (Eds.) (2000) *Scientific Controversies. Philosophical and historical perspectives*. Oxford University Press. Oxford, UK. 278 pp.
- Mahner M, Bunge M (1997) *Foundations of Biophilosophy*. Springer. New York, USA. 423 pp.

- Nichols G (1923) A working basis for the ecological classification of plant community. *Ecology* 4: 11-23.
- Nudler O (1999) Filosofía de la ciencia ¿empresa descriptiva o prescriptiva? In Sota E, Urtubey L (Eds.) *Epistemología e Historia de las Ciencias*. Paidós. Buenos Aires, Argentina. 537 pp.
- Nudler O (2004) Hacia un modelo de cambio conceptual: espacios controversiales y refo-calización. *Rev. Filosofía* 29: 7-19.
- Núñez MA, Núñez PG (2005) Controversias en ecología: la competencia, de la certeza a la pregunta. *Ecol. Austr.* 15: 229-238.
- Makinistian AA (2004) *Desarrollo histórico de las ideas y teorías evolucionistas*. El Aleph. Madrid, Spain. 294 pp.
- Paine RT (1966) Food web complexity and species diversity. *Am. Naturalist* 100: 65-75.
- Peters RH (1991) *A critic for ecology*. Cambridge University Press. Cambridge, UK. 384 pp.
- Popper KR (1963) *Conjectures and Refutations*. Routledge & Keagan. London, UK. 583 pp.
- Roughgarden JR, May M, Levin S (1989) Introduction. In Roughgarden J, May RM, Levin S (Eds.) *Perspectives in Ecological Theory*. Princeton University Press. Princeton, NJ, USA. 408 pp.
- Sargent RC (1986) Book Review of Community Ecology by J. Diamond and T.J. Case (Eds.). *Quart. Rev. Biol.* 61: 569-570.
- Shimwell D (1971) *The description and classification of vegetation*. University of Washington Press. Seattle, WA, USA. 322 pp.
- Simberloff D (1970) Taxonomic diversity of island biotas. *Evolution* 24: 24-47.
- Simberloff D (1978) Using Island Biogeographic Distributions to Determine If Colonization Is Stochastic. *Am. Naturalist* 112: 713-726.
- Simberloff D (1980) A succession of paradigms in ecology: essentialism to materialism and probabilism. *Synthese* 42: 3-39.
- Simberloff D (1982) "Replay". In Saarinen E (Ed.) *Conceptual issues in ecology*. Reidel. Dordrecht, Holland. pp. 139-153.
- Simberloff D (2004) Community Ecology: Is It Time to Move On? *Am. Naturalist* 163: 787-799.
- Simberloff D, Boecklen W (1981) Santa Rosalía reconsidered: size, ratios and competition. *Evolution* 35: 1206-1228.
- Sloep P (1993) Methodology Revitalized? *Br. J. Philos. of Sci.* 44: 231-249.
- Tansley AG (1935) The use and abuse of vegetal concepts and terms. *Ecology* 16: 284-307.
- Torres Alberó C (1994) *Sociología Política de la Ciencia*. Siglo XXI. Madrid, Spain. 239 pp.
- Vazquez DF, Collins MD (1999) Entrevista con Daniel Simberloff. *Bol. Asoc. Argent. Ecol.* 8: 34-38.
- Whitley R (1972) Black-boxism and the sociology of science: A discussion of the major developments in the field. *Sociol. Rev. Monogr.* 18: 61-92.
- Wiens JA (1989) *The ecology of bird communities*. Cambridge University Press. Cambridge, UK. 557 pp.
- Williams CB (1947) The Generic Relations of Species in Small Ecological Communities. *J. Anim. Ecol.* 16: 11-18.
- Zapata FA, Gaston KJ, Chown SL (2005) The mid-domain effect revisited. *Am. Naturalist* 166: 144-148.

LA IMPORTANCIA DE LAS CONTROVERSIAS EN EL PROGRESO EPISTÉMICO DE LA ECOLOGÍA

Paula G. Núñez y Martín A. Núñez

RESUMEN

La ecología, como disciplina científica, ha sido analizada por la filosofía de la ciencia en menor medida que otros campos de la ciencia. En general sus cambios epistémicos han sido presentados de forma de progreso acumulativo, acorde a la propuesta de la filosofía clásica de la ciencia; o como rupturas sucesivas, siguiendo la interpretación kuhniana de cambio científico. En este trabajo se busca mostrar que, como en otros campos de la ciencia, la trayectoria de cambio de la ecología es diferente a estas dinámicas. Para ello se centra el análisis en las controversias con carácter permanente de la ecología, una de las principales fuentes de autocrítica disciplinar. La subsistencia de las controversias ha sido interpretada como signo de inmadurez o

debilidad de la ecología. En este trabajo no se supone que la persistencia de las controversias sea problemática. Aun cuando las controversias no arriben a una síntesis, pueden ser progresivas desde un punto de vista epistémico. En este estudio se analizan dos de los más prominentes debates en la historia de la ecología: el debate sobre la sucesión vegetal y el debate sobre el rol de la competencia en la estructuración de comunidades. En estos casos se encontró que, en oposición a la percepción usual de las controversias como problema a resolver, las mismas pueden producir crecimiento epistémico a través de la incorporación de nuevos interrogantes e incrementar la rigurosidad en la evaluación de hipótesis.

A IMPORTÂNCIA DAS CONTROVÉRSIAS NO PROGRESSO EPISTÊMICO DA ECOLOGIA

Paula G. Núñez e Martín A. Núñez

RESUMO

A ecologia, como disciplina científica, tem sido analisada pela filosofia da ciência em menor medida que outros campos da ciência. Em geral suas mudanças epistêmicas têm sido apresentadas como forma de progresso acumulativo, de acordo à proposta da filosofia clássica da ciência; ou como rupturas sucessivas, seguindo a interpretação kuhniana de mudança científica. Neste trabalho se busca mostrar que, como em outros campos da ciência, a trajetória de mudança da ecologia é diferente a estas dinâmicas. Para isso a análise é focada nas controvérsias com caráter permanente da ecologia, uma das principais fontes de autocrítica disciplinar. A subsistência das controvérsias tem sido interpretada como signo de imaturidade ou debilidade da

ecologia. Neste trabalho não se supõe que a persistência das controvérsias seja problemática. Mesmo quando as controvérsias não sejam uma síntese, podem ser progressivas desde um ponto de vista epistémico. Neste estudo se analisam dois dos mais proeminentes debates na história da ecologia: o debate sobre a sucessão vegetal e o debate sobre o rol da competência na estruturação de comunidades. Nestes casos se encontrou que, em oposição à percepção usual das controvérsias como problema a resolver, as mesmas podem produzir crescimento epistémico através da incorporação de novas interrogantes e incrementar a rigurosidade na avaliação de hipóteses.