

# The theoretical motivation for ecological comparisons

La motivación teórica de las comparaciones ecológicas

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## ABSTRACT

This article discusses how theory can provide the stimulus and the conceptual framework for the correct use of ecological comparisons. We show how comparative studies provide critical tests for various components of theory, including assumptions, concepts and hypotheses. Comparison intersects with theory more often through generalization. Abstraction, idealization and summarization of complex ecological processes are all aspects of generalization. The use of comparison in building generalizations must be based on a non-arbitrary selection of cases or situations. An appropriate "taxonomy" of cases for legitimate comparison should have a sound theoretical basis. Examples are given of theory-based comparative analyses. These pertain to the role of disturbance and succession, and new axes are suggested to guide future comparative studies in ecology.

**Key words:** Disturbance, succession, theory, hypothesis, generalization.

## RESUMEN

Este artículo discute cómo la teoría puede proveer el estímulo y el marco conceptual para el uso correcto de las comparaciones ecológicas. Nosotros mostramos cómo los estudios comparativos proveen una prueba crítica para varios componentes de una teoría ecológica, incluyendo suposiciones, conceptos e hipótesis. Las comparaciones se relacionan con la teoría a través de la generalización. La abstracción, idealización y síntesis de procesos ecológicos complejos son todos aspectos de la generalización. El uso de la comparación en la construcción de generalizaciones debe estar basado en la selección no arbitraria de casos o situaciones de estudio. Una "taxonomía" apropiada de casos para comparaciones legítimas debe basarse en un buen sustento teórico. Se presentan ejemplos de análisis comparativos basados en teorías. Estos análisis consideran el rol de las perturbaciones y de la sucesión, y se sugieren nuevos ejes que podrían guiar futuros estudios comparativos en ecología.

**Palabras claves:** Teoría, sucesión, hipótesis, generalización.

## INTRODUCTION

Ecology seeks to unravel natural patterns and to understand their underlying mechanisms at various temporal and spatial scales (e.g., Watt 1947, MacArthur 1972). A simple description of a site or an ecosystem is not sufficient for understanding. Comparison is necessary to advance our understanding of natural phenomena. Manipulative studies complement the understanding generated by comparisons. In this article we highlight the importance of comparison in building and testing ecological theory.

Comparison involves planned observation and data collection in contrasting or similar ecological situations. Yet, com-

parison has profound theoretical significance and implications. Data collection has been described by T.H.F. Allen (pers. comm.) as "the most abstract thing you can do." Theory is the tool that puts the abstractions underlying observation and data collection in a form in which they can be evaluated and used. Comparison is as much an empirical as a theoretical activity. However, its theoretical function and its dependence on theory are often overlooked or misunderstood. The purpose of this paper is to outline the theoretical basis for comparisons in ecology and to illustrate its significance for ecological studies. In doing this we will show several ways in which theory can intersect with comparison. This will set the stage for identifying theories that might guide existing and new comparisons.

We will use as an example the case of comparative studies of North and South American temperate ecosystems.

#### WHAT GOOD IS THEORY?

Many patterns in nature can be explained as the result of specific ecological processes. But, because both pattern and process in natural systems ultimately rely on observation, there is a third component of the complete understanding that ecology seeks. Theory supplies the link between pattern and process, and is thus the keystone of ecological understanding. Theory and comparison interact in a two-way form, as comparison can be a source of new conceptual schemes or theories and, at the same time, it provides critical evidence for testing existing theory.

The ecological discipline of vegetation dynamics, or succession in short, provides an example of how theory is required for comparison and understanding. Succession is the pattern of temporal change in plant communities and ecosystems. In order to understand succession, the pattern can be broken down into its component processes. Three processes are required: 1) provision of an open site; 2) differential availability of species at the site; and 3) dif-

ferential performance of species once they have reached the site. This hierarchical decomposition of the phenomenon of succession into three major processes must in turn be decomposed to identify the lower level processes determining the primary causes (Table 1). Such lower level causes are used to establish specific models, predictions, and hypotheses appropriate to various sites and conditions (Pickett *et al.* 1987). However, the first hierarchical decomposition suffices to introduce the need for theory, or how theory can guide our observations and data collection.

In order to fully appreciate the role of theory in comparative ecology, we must agree on a modern definition of theory. Theory can be viewed as a conceptual system, or a linked family of models (Pickett & Kolasa 1989). The models may be verbal, mathematical, graphical, or physical (e.g., microcosms) emulations of nature. Other components of the conceptual system or theory are as important as the models, and include assumptions, concepts, facts, generalizations, laws, hypotheses, and predictions. Finally, there must be a framework connecting these elements in the body of the theory (Table 2).

TABLE 1

A nested hierarchy of general and specific causes of vegetation dynamics (after Pickett *et al.* (1987).

For simplicity, possible interactions among lower level causes that contribute primarily to different upper level causes are not indicated. Although the contributing causes can be further divided, such additional component causes are omitted here

Una jerarquía anidada de las causas generales y específicas de la dinámica de la vegetación (según Pickett *et al.* 1987). Por simplicidad, las interacciones entre niveles inferiores que contribuyen primariamente como causa a los niveles superiores no están indicadas. Aunque las causas pueden ser divididas de manera aún más fina, tales componentes han sido omitidos del esquema

General causes	Site availability	Differential species availability	Differential species performance
Contributing causes	Coarse-scale disturbance	Dispersal propagule pool	Resource pool Ecophysiology Life history strategy Environmental stress Competition Allelopathy Plant-consumer interactions

TABLE 2  
Some important components of theory  
(Pickett *et al.* 1992)  
Algunos de los componentes de una teoría

Assumptions
Concepts
Domain
Generalizations
Laws
Models
Hypotheses
Framework

Comparison intersects with theory through its various empirical and conceptual components (Table 2). However, some theories derive principally from a strong empirical foundation, whereas others are primarily deduced from a conceptual basis. Empirically derived theories rely heavily on an inductive strategy, i.e., finding commonality through many observations. Sound generalizations from a broad empirical base are central to inductive or concrete theories. Examples will emphasize the value of comparison for generalization and its links with theory.

#### COMPARISON AND GENERALIZATION

Comparative studies provide a way to generalize. Generalization involves three things: summarization, abstraction and idealization. Some generalizations tend to reduce a large body of empirical information to a manageable summary. For instance, a mean summarizes a series of values. But generalizations do *more* than simply summarize. Generalization also involves abstraction. In order to generalize, the complexity of the real world must be reduced. That is, only some of the potentially large amount of information derived from observations and data collection is incorporated into the generalization. In such abstraction, only key aspects of the system at hand are considered as important for the analysis. An example of an abstraction is the identification of

a few trophic guilds from the entire biota of an area. The third aspect of generalization is idealization. Often the factor(s) of interest in a system will be obscured by complicating phenomena. In order to construct a useful generalization, it may therefore be necessary to isolate the phenomenon of interest from other aspects of the system or the environment. Such isolation, for instance the "frictionless pendulum", is idealization. Certain highly idealized generalizations are central in theories, and provide points of reference about how systems should behave under specified ideal conditions. Understanding of the system can be advanced by learning how other forces influence the system and change the ideal behavior.

The three aspects of generalization—summarization, abstraction and idealization—can all be brought to bear in comparative studies. What parameters to summarize or to extract from the complex system, and what aspects of the ecosystem are likely to constitute "noise" to be expunged as far from ideal, are important theoretical decisions required for comparisons. The theory must be clearly stated in order for the generalizations to be evaluated by other workers and to be used, if appropriate, in comparative studies. We can modify Allen's statement about the abstractness of data collection, by saying that theory exposes the abstraction, idealization and summarization behind data collection. Theory also organizes these three basic activities.

Now that we have described the bases of generalization, we can discuss how this descriptive tool is used. There are two principal uses of generalization.

(1) Comparison-based generalization can be used to beget pattern. In this mode, generalization is a primary source of the raw material of empirically-derived theories. For instance, the generalizations, especially those regarding the variation and geographical distribution of organisms and communities, constructed by the great 18th and 19th century naturalists on their voyages, were key stimuli for the Darwinian Revolution, and for the birth of modern ecology.

(2) A second way to use generalization is as a test of the universality of patterns or of mechanisms underlying those patterns. Here, the generalization is used in conjunction with a hypothesis that a regularity observed in a limited set of cases is the regularity that holds in other appropriate cases. Testing for universality of pattern is of course important because those patterns that are more common may be more important or more fundamental, at least at the scale of the comparison. An example is the emerging, tentative generalization that mesic, broadleaved forests, experience the same recurrence interval for treefall gap formation, regardless of their latitude (Runkle 1989). Testing for universality of underlying mechanisms may be even more important because superficially different patterns may in fact have a common mechanistic basis. For instance, the emerging pattern of a common treefall rate in mesic broadleaved forest prompts a search for a common cause operating on a broad spatial scale. The stand development models of Oliver (1981, Oliver & Larson 1990) suggest that stand structure, tree species tolerance and life history, and external forcing of disturbance agents may interact in the same way in mesic broadleaved forests (Armesto *et al.* 1986). Both observational and experimental approaches may be employed in the search for universality of mechanism.

Generalization must be used exceedingly carefully. A critical aspect of such care is expressed in the need for a proper taxonomy of cases. Not all cases or ecological settings will be comparable, and attempting to compare among inappropriate situations is bound to fail, or worse, be misleading. After the failure of many major generalizations of the 1960s and 1970s, ecologists came to suspect generalization itself as the culprit. However, it may well be that the generalizations were constructed too broadly and without the benefit of proper systematization of cases. For instance, not all ecological assemblages increase in diversity toward the equator (e.g., Santelices *et al.* 1980). Dividing communities into various aquatic and terrestrial types was instrumental in

revitalizing the study of latitudinal diversity gradients (May 1981). Contemporary community ecology is poised to advance using a multidimensional universe in which to compare assemblages (Schoener 1986; Table 3).

A taxonomy or systematization of cases is not arbitrary. Rather it should itself have a sound theoretical basis. This realization is common among biosystematists, but rare among ecologists which often do not appreciate the need for a proper classification of ecological systems. Application of a taxonomy of cases can be valuable to test the theory on which it is based as well as to advance the theory to which it is applied. In building a theory for community ecology, the taxonomy of cases is based on other disciplines or models. Physiological ecology, population biology and biogeography are especially relevant bases for the taxonomy of ecological communities (Table 3).

The structure of theory, the use of generalization, and the necessity for effective taxonomy of cases together suggest an important point about comparison in ecology. Indeed, this is likely the most significant message of this consideration:

TABLE 3

An overview of the kinds of axes along which ecological communities may be ordinated for comparative or experimental studies (from Schoener 1986)

Una visión general de los tipos de ejes sobre los cuales las comunidades ecológicas pueden ser ordenadas para estudios comparativos o experimentales (según Schoener 1986)

<b>ORGANISMAL AXES</b>	
Body size	Small - Large
Source of new individuals	Closed - Open
Generation time	Short - Long
Mobility	Sessile - Mobile
Homeostatic ability	Low - High
Number of life stages	Few - Many
<b>ENVIRONMENTAL AXES</b>	
Severity of physical factors	High - Low
Trophic position	Low - High
Resource input	Open - Closed
Spatial fragmentation	Broken - Continuous
Long-term climatic variation	High - Low
Partitionability of resources	Low - High

Comparison is not mere observation. Comparative ecology does not aim, even when building theory from an empirical foundation, to innocently collect cases. Rather, comparison has a rich theoretical foundation and high theoretical aspirations (Cole *et al.* 1991).

#### ILLUSTRATION OF THE INTERACTION OF THEORY AND COMPARISON

In describing the utility of theory and the nature of comparison in the context of theory we have given a few examples along the way. In this section, we wish to cement the insights about how theory and comparison interact by presenting several examples in more detail.

The study of disturbance indicates how comparison is advanced even by using an emerging theory. Because, at the community level, disturbance is the disruption of the structure and resource availability of an assemblage, predicting the impact of a disturbance must account for system structure (Pickett *et al.* 1989). Contrasting types of community structure have been deduced from first principles (Fig. 1). The first assumption underlying the deduction is that systems will differ in the degree of attachment to the substrate. The second assumption is that species will differ in the amount of biomass allocated to above and below substrate structures. Together, the assumptions lead to the recognition of four structural types of assemblage (Pickett & White 1985). If the disturbance agents of interest originate from above the substrate, e.g., wind or crown fire, then the impact of each type will differ depending on its intensity and on the structure of the system. A severe wind, such as a tornado, will obliterate much of a Type I system, but little of a Type II system. If recovery is dependent on remnants of the pre-disturbance system, then Type II systems should be more resilient, *ceteris paribus*. Of course, the mode(s) of regeneration present in the community, and the size and novelty of the disturbance are potential *ceteris differentibus*.

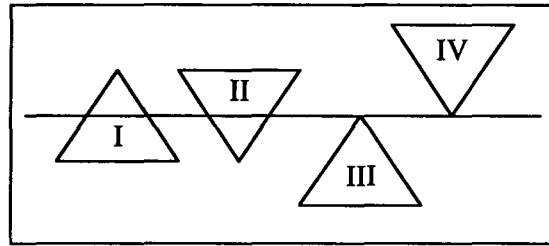


Fig. 1: An *a priori* classification of systems by structure to clarify predictions of the impact of disturbance. Type I communities have the majority of biomass above the substrate; Type II have most biomass below the substrate; Type III are anchored to the substrate but the biomass is above the substrate, and Type IV communities exist within the substrate (after Pickett & White 1985). Una clasificación *a priori* de los sistemas, de acuerdo a su estructura, puede clarificar la predicción del impacto de la perturbación. Comunidades Tipo I tienen la mayor parte de su biomasa sobre el sustrato; las Tipo II tienen más biomasa bajo el sustrato; las Tipo III están ancladas al sustrato, pero su biomasa está por encima de éste; y el Tipo IV existen dentro del sustrato (modificado de Pickett & White 1985).

Earlier, we introduced succession theory to indicate the difference between pattern and process and the hierarchical relationship of those ideas. This theory can be used to illustrate additional features of the relationship between comparison and theory. The theory has more than two hierarchical levels. Each of the three principal processes causing succession must itself be broken down into specific mechanisms (Table 1). In turn, the specific mechanisms are subject to modification by factors that appear on a still lower hierarchical level. This new framework and its embedded causes has proven to be useful in comparison. For example, the three logically exclusive, net effects proposed by Connell and Slatyer (1977) to organize the study of succession, led to confusion in actual application. The hierarchy of mechanisms (Table 1) being a more complete framework for succession permitted successful comparison and avoided the confusion in comparing facilitation, tolerance and inhibition. Armesto *et al.* (in press) compared the analogous vegetations of the California Chaparral and the Chilean Matorral examining the relative importance of various mechanisms from the successional framework (Table 1).

These were more useful than net effects in understanding the differences in vegetation dynamics and proposing hypotheses about succession in the two systems. The contrasting role of natural vs. human started fires, and the role of native vs. introduced herbivores are notable points for comparison.

The nature of the site has been a major distinction in succession studies from the initiation of the concept. Secondary versus primary successions are differentiated on the basis of the novelty of the surface. However, new bases for contrast and comparison are emerging. Empirical experience has indicated that some secondary successions are quite slow and behave very much like primary successions. It appears therefore that a more appropriate basis for comparison of successions might be a two dimensional space defined by an axis of resource availability and propagule availability. Secondary successions on resource poor (or highly degraded) sites or those distant from appropriate seed sources are expected to be slow (Armesto, unpublished MS).

A prominent failure in community ecology has been the study of the relationship of diversity and stability. The initial role that theory might play in saving this situation is one of clarifying the basic discourse. The early concern was clearly with functional diversity. However, for reasons of operational simplicity, simple diversity of species was used instead. With the development of new computational tools to describe the complexity of networks, the discipline might be reinvigorated. There is simply no good reason to expect that the number of species, or evenness of species is necessarily a proper index for functional diversity in a system.

#### COMPARISON WITHOUT THEORY?

It is possible that successful and important ecological comparisons can be conducted without an explicit theoretical basis. Society may demand comparisons of polluted with less polluted or pristine sites. Or detecting and monitoring global change

might require a worldwide network of comparable sites. However, we suspect that even societally mandated comparisons can benefit from an explicit theoretical basis. Such a theory might 1) improve the location of sampling sites, 2) reduce the number of confounding input variables, 3) indicate which variables are substitutable or not, and 4) guide the incorporation of new or substitute variables over the long term. We will present a single example of how to, relate a practical comparison and a theoretical basis.

The pollution of air in England with the industrial revolution is a well known trend. This phenomenon manifested itself in many societally important ways. But one stands out for its scientific importance. The peppered moth, *Biston betularia*, experienced dramatic changes in phenotype and genetics as a result of air pollution. The utility of this (and other organisms) as indicators is largely accidental, and results from the cumulative efforts of amateur collectors. However, once the basic responsiveness of this moth had been discovered, it was used as a powerful indicator. Bishop (1972) measured the proportion of the melanic phenotype in the population along a transect from Liverpool. Besides demonstrating the indirect impact of air pollution on a common organism, the study also interacts with evolutionary theory. The observations are made comprehensible by an understanding of the predator prey relationships of the moth, the genetic response of the moth and the sensitivity of lichens to the pollution.

The example of the peppered moth also relates to a general theory of the ecological community. Ecological communities are very profitably abstracted as responding to complex ecological gradients. Such gradients represent continua of physical stressors, resource availability, and intensity of biotic interaction (Whittaker 1975, Stevens 1989). Ecologists have most often restricted their attention to gradients that have been little or only inconspicuously affected by humans. The peppered moth example exploits an urban-rural gradient that is driven by a conspi-

cuous anthropogenic stress. We expect such gradients to be common (McDonnell & Pickett 1990). In fact, the current extent and continuing spread of urbanization indicate that anthropogenic gradients, ordinated from cities and their surroundings, will become even more important in the future. Applying the community gradient theory to this underinvestigated case is a productive intersection of comparative ecology and a societally important situation.

#### CONCLUSION

Comparison is a major tool for constructing and evaluating theory. Especially in empirically based theories is comparison necessary to generate the patterns and generalizations that are central to the theory. The comparison of temperate forest ecosystems in North and South America has been relatively neglected. It may be that novel patterns remain to be discovered along that axis. Regardless of the fruitfulness of such comparison in revealing new patterns, the comparison can be used to test existing theory. Disturbance, and community organization have been mentioned in this chapter to suggest how theory and comparison might interact. These areas of inquiry, among others to be discussed throughout this volume, are areas in which hypotheses can be tested using North and South American temperate forest ecosystems.

We have outlined the structure of theory in order to indicate that comparison and theory can intersect at a variety of levels. For instance, assumptions can be tested, concepts refined, hypotheses tested, models elaborated and verified, generalizations applied and tested in comparative studies. Explicit statement of the theory that does, or might, motivate a particular comparison can do much to generate wide interest for comparison, and to guide the choice of parameters and structure of the comparison. Using or developing appropriate taxonomies of cases in which to couch generalizations or conduct tests is a critical need for comparative ecological studies.

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#### LITERATURE CITED

- ARMESTO JJ, JD MITCHELL & C VILLAGRAN (1986) A comparison of spatial patterns of trees in some tropical and temperate forests. *Biotropica* 18: 1-11.
- ARMESTO JJ, PE VIDIELLA & HE JIMENEZ (in press). A comparative analysis of causes and mechanisms of succession in mediterranean-type regions of Chile and California. In: MT Kalin, M Fox & P Zedler (eds.). *Ecology of convergent ecosystems: Mediterranean-climate ecosystems of Chile, California and Australia*. Springer, Berlin.
- BISHOP JA (1972) An experimental study of the clines of industrial melanism in *Biston betularia* (L.) (Lepidoptera) between urban Liverpool and rural North Wales. *Journal Animal Ecology* 41: 209-243.
- COLE J, G LOVETT & S FINDLAY, eds. (1991) *The comparative analysis of ecosystems: patterns mechanisms and theories*. Springer-Verlag, New York.
- CONNELL JH & RO SLATYER (1977) Mechanisms of succession in natural communities and their role in community organization. *American Naturalist* 111: 1119-1144.
- MACARTHUR, RH (1972) *Geographical ecology: patterns in the distribution of species*. Princeton University Press, Princeton, NJ.
- MAY, RM (1981) Patterns in multispecies communities. In: May RM (ed.) *Theoretical Ecology. Principles and Applications*: 197-227. Sinauer Associates, Sunderland, Massachusetts.
- McDONNELL MJ & STA PICKETT (1990) The study of ecosystem structure and function along gradients of urbanization: an unexploited opportunity for ecology. *Ecology* 71: 1232-1237.
- OLIVER CD (1981) Forest development in North America following major disturbances. *Forest Ecology and Management* 3: 153-168.
- OLIVER CD & BC LARSON (1990) *Forest stand dynamics*. McGraw-Hill, New York.
- PICKETT STA & J KOLASA (1989) Structure of theory in vegetation science. *Vegetatio* 83: 7-15.
- PICKETT STA & PS WHITE (1985) Patch dynamics: a synthesis. In: Pickett STA & PS White (eds.). *The ecology of natural disturbance and patch dynamics*: 371-383. Academic Press, New York.
- PICKETT STA, SL COLLINS & JJ ARMESTO (1987) Models, mechanisms and pathways of succession. *Botanical Review* 53: 335-371.
- PICKETT STA, J KOLASA & CG JONES (in press) *Ecological understanding: the nature of theory and theory in nature*. Academic Press, Orlando.
- PICKETT STA, J KOLASA, JJ ARMESTO & SL COLLINS (1989) The ecological concept of disturbance and its expression at different hierarchical levels. *Oikos* 54: 129-156.

- RUNKLE JR (1989) Synchrony of regeneration, gaps, and latitudinal differences in tree species diversity. *Ecology* 70: 546-547.
- SANTELICES B, JC CASTILLA, J CANCINO & P SCHMIEDE (1980) Comparative ecology of *Lessonia nigrescens* and *Durvillaea antarctica* (Phaeophyta) in central Chile. *Marine Biology* (Berlin) 59: 19-132.
- SCHOENER TW (1986) Overview: Kinds of ecological communities - Ecology becomes pluralistic. In: Diamond J & TJ Case (eds.) *Community Ecology*: 467-479. Harper and Row, New York.
- STEVENS GC (1989) The latitudinal gradient of species diversity: How so many species coexist in the tropics? *American Naturalist* 133: 240-256.
- WATT AS (1947) Pattern and process in the plant community. *Journal of Ecology* 35: 1-22.
- WHITTAKER RH (1975) *Communities and ecosystems*. Second edition, Macmillan, New York.