

The Method of Synthesis in Ecology

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Abstract

Synthesis of results from different investigations is an important activity for ecologists but when compared with analysis the method of synthesis has received little attention. We usually proceed intuitively and this can lead to a problem in defining differences between the synthesis made by different scientists. It also leads to criticism from scientists favoring analytical approaches that the construction of general theory is an activity that does not follow the scientific method.

We outline a method for scientific inference about integrative concepts and illustrate how this can be applied in the development of general theory from investigations into particular ecological systems. The method requires a *causal scientific explanation* to be constructed and its *coherence* assessed. It uses approaches developed in the philosophy of science.

A causal scientific explanation has four characteristics. (1) It defines causal and/or organizational processes that describe how systems function. (2) These are consistent – under the same conditions the causal and/or organizational processes will produce the same effect. (3) A causal scientific explanation provides general information about events of a similar kind. (4) When experiments are possible then a designed manipulation will produce a predictable response.

An essential characteristic of synthesis to produce ecological theory is that it is progressive. We illustrate development of a causal scientific explanation for the concept of *long-lived pioneer* tree species. We show how the coherence of this explanation can be assessed and could be improved.

Introduction

Recent articles in *Oikos* have made calls for synthesis in ecology and advanced this as essential for progress in the subject. Turchin (1999) argues that to build mechanistic explanations in animal population ecology it is essential to use a synthetic approach linking statistical analysis of observational data, mathematical modeling of mechanisms, and experiments. Pickett (1999), considering the complete scope of ecology focuses on synthesis as integration between different scientific domains of the subject. He stresses potential cultural barriers to synthesis including what he considered the dominance of the subject by narrow reductive methods.

An important way that ecologists make a synthesis is to construct or develop *integrative concepts* about the organization or properties of ecological systems. *Ecosystem, population, community, or continuum* and *niche* describe or imply organization. *Ecosystem health, resilience, and stability* describe properties or features of these organizations. These integrative concepts cannot be measured directly, and both their definition and detailed description must be synthesized from studies of a number of systems (Ford 2000 p283). This type of concept may be first proposed early in the development of investigation into a topic,

provide a general heuristic for the science, but remain conjectural for considerable time.

Turchin (1999) calls for a synthetic approach, focussed on the integrative concept of population *regulation*. He does not say what methods should be used to synthesize information collected using the three techniques he discusses. Pickett (1999) considers there may be many opportunities for synthesis but "there is little ecologically accessible discussion of how this process might be facilitated." Austin (1999) describes community ecology as fragmented with no effective communication between groups espousing different theories such as those associated with the integrative concepts of *continuum* and *niche*. He illustrates how this has led to inconsistencies and lack of progress and states: "(f)ailure by different research groups to consider and test a range of already stated paradigms is reducing the possibility of achieving a synthesis for plant community ecology." He calls for evaluation that is more critical. Undoubtedly that is needed. However, comparative evaluation of theories requires a recognized and accepted method.

Our purpose is to define the process of synthesis for integrative concepts, identify, and illustrate its methods using a practical example. An important missing component of these recent debates is lack of definition of the methods of synthesis for developing integrative concepts.

Integrative Concepts and their Domains

We use three types of concept in ecology (Fig. 1). *Natural concepts* define and/or classify measurable or observable entities or events in the ecological world. *Functional concepts* define properties of natural concepts or express relationships between two or more natural concepts. Individual *plants* and *animals* are natural concepts. *Photosynthesis* and *herbivory* are functional concepts. As we learn more about functional concepts then we change classifications in the natural world (Ford 2000 p 291-293). For example, animals can now be classified as herbivores, carnivores, omnivores, or detritivores.

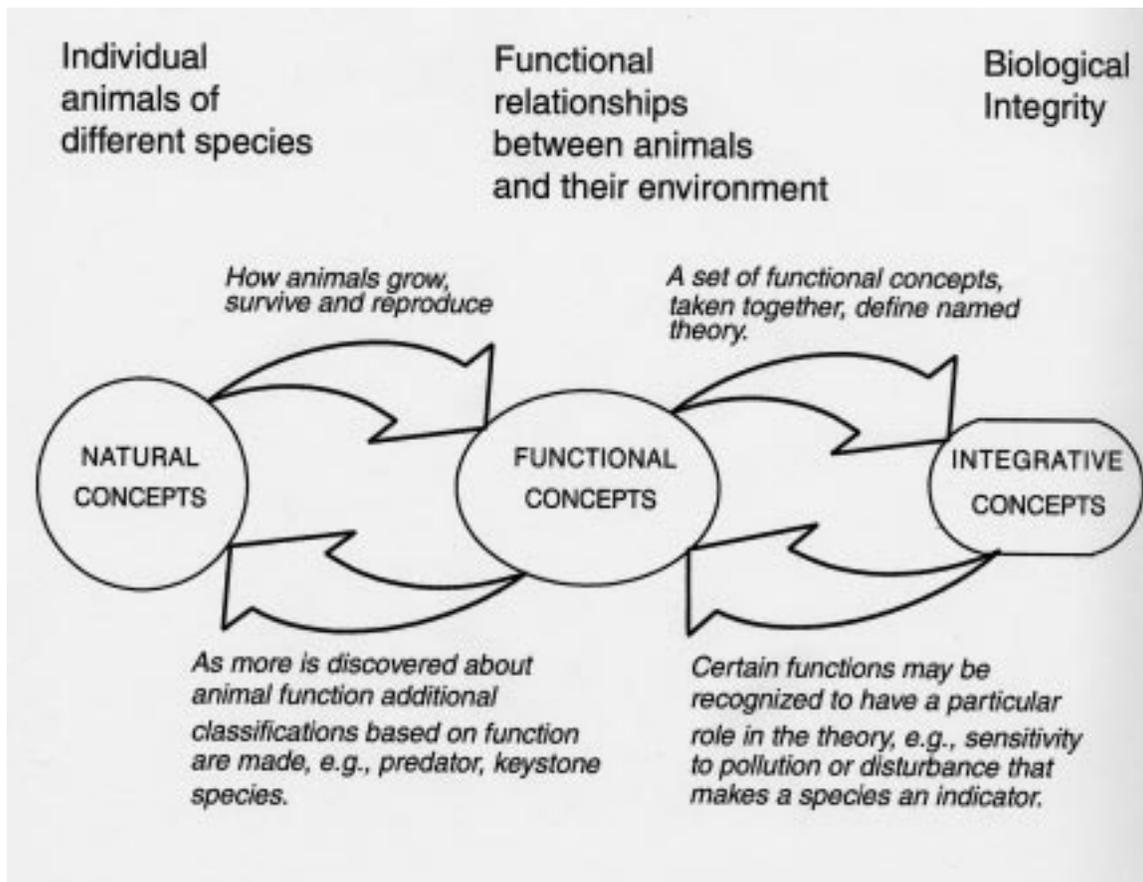


Figure 1. The integrative concept *biological integrity* depends upon the functional concepts of individual species interactions. An ecosystem has complete *biological integrity* when none of those interactions are sufficiently disrupted by disturbance and/or pollution to cause species to disappear. The relative absence of species is used as an *index of biological integrity*.

Biological integrity (Karr 1981, 1991) is an integrative concept applied to freshwater streams. It is based on the theory that human influence through various types of pollution and/or disturbance reduces the number of species present. Natural concepts are the species. The functional concepts are how individual animals find habitat and perpetuate life cycles.

Biological integrity was researched in streams in the Midwest of the United States using fish species. In polluted/disturbed streams there are fewer species, i.e., disrupted biological integrity. An Index of Biological Integrity (IBI) for a stream calculates species present relative to that expected (see. The functional concepts are not used by the IBI but their disruption is inferred if species numbers are reduced.

Integrative concepts can carry knowledge, defined by a theory, built in another (or many other) systems. For *biological integrity*, the theory is that pollution and/or disturbance may influence the functioning of species. The concept is extended by applying it to other systems. In some situations benthic organisms have been used rather than fish species (Karr 1994, 1999, Weisberg et al. 1997), i.e., the integrative concept remains but different natural and functional concepts are used in defining it. Difficulties arise in defining an index of biological integrity (IBI). Which species should be chosen; what natural background variation occurs in species composition; do species respond in the same way to different types of pollution/disturbance; how can species presence or absence be sampled effectively?

The exchange between Murray (1999a), Turchin (1999) and Murray (1999b) again, illustrates why some ecologists consider integrative concepts essential for ecology and others reject them as having little or no value. Turchin (1999) lists *r*, the realized per capita rate of population change as the central quality of interest in the analysis of animal population regulation. Regulation is an integrative concept. *r* is a functional concept. *r* has elements of theory in how it is calculated, i.e., use of the logarithmic scale so that $r = \ln N_t - \ln N_{t-1}$ where $\ln N_t$ is the natural logarithm of population density at time *t*, but it is calculated by counting (usually estimating) animal numbers at specified time intervals.

Two types of difficulty arise in constructing a theory for regulation. First, there are different possible influences on *r*. So, if a comprehensive theory is to be developed, there are likely multiple functional concepts to consider in defining regulation. Second, these various factors may have a different domain that is where, when, and on which species they operate. Turchin (1999) notes: "... we need to determine which of the alternative ecological mechanisms explains population regulation in any particular case study, or perhaps what are the relative contributions of several ecological factors to regulation." The domain of an integrative concept has two components: (i) specification of the extent of what the concept seeks to explain; (ii) specification of the set of functional concepts that an integrative concept uses (Ford 2000 p289). Specification of the domain is a component of the theory for the concept. Turchin (1999) wishes to build a theory for the integrative concepts of population regulation and density dependence. This would be a synthesis of the different processes observed, and when and where they apply.

In contrast, (Murray 1999a) proposes population limitation hypotheses. He gives examples of why populations stop growing. These include: competition for food as numbers increase when food is limited; that a population may attract predators as it grows larger; or where animals are territorial that habitat can only sustain a maximum number of breeders with territories. Turchin (1999) wishes to synthesize possible mechanisms into a theory for the integrative concepts of regulation and density dependence – to reason from many different

results toward a theory for regulation. Murray (1999b) not only does not see the need for this process but also argues strenuously against it on the grounds of methodology insisting that science must use testable hypotheses. Murray seeks empirical consistency. When that is found he will attempt to explain it. He argues that the type of verification that might be applied to *density dependence* is insufficient, and that a research program of the type proposed by Turchin lacks necessary rigor. Murray's (1999b) interest "is in discovering insights into biological processes by inventing universal laws, deducing predictions, and testing the predictions by comparing them with empirical fact."

Murray raises important questions. If we wish to proceed by synthesis how can we judge its effectiveness? Murray suggests Turchin's approach lacks rigor, that "the rules of epistemology, logic, and evidence transcend subject matter. They are as applicable to ecology as they are to physics." (Murray 1999b.) He quotes Feynman (1965); "*The test of all knowledge is experiment*. Experiment is the *sole* judge of scientific 'truth'" (Feynman's italics). Direct experiments cannot be made on integrative concepts, only on the functional concepts that we use to define them. So can Murray's criticism be met? Or is ecology doomed to be a subject lacking in rigor unless it abandons its integrative concepts?

We argue that integrative concepts are an essential part of ecology because they enable scientists to organize and reorganize ecological knowledge as the science progresses. Two things hinder this development: lack of definition of what constitutes an effective scientific inference about an integrative concept (the objective) and lack of a recognized procedure for synthesis (the means).

A Methodology for Synthesis

We practice synthesis whenever we make scientific inference. We do not take the results of a statistical inference at face value. We weigh them with our answers to such questions as: did the investigation penetrate to the heart of the matter or is it of little consequence; were the measurements effective (as well as accurate and precise) or are they a poor guide of what really must be measured; and, was the study comprehensive in design or did it lack some essential components? This type of synthesis focuses on the data of the study and is complementary to the analysis made before attempting any investigation, i.e., deciding what investigation to do, when and where to do it, and what measurements to make. The method of analysis and synthesis is little documented by present day scientists, but in the past was sometimes more explicit (see Falkenburg 1998 p105-108).

To make scientific inference about integrative concepts we must compare and weigh different investigations and decide what the different types of data they produced tell us. To do this we need to be explicit about the process of synthesis. There are three components (Ford 2000 p269-278). A synthesis must:

1. Be made of new results with existing theory.

2. Provide a *scientific explanation* of why something exists or occurs.
3. Explain both new and previously obtained information together in a *coherent* way.

Scientific inference about an integrative concept is distinguished by the definition of what makes an explanation and how we judge its coherence. We illustrate this by constructing a scientific explanation for the integrative concept *long-lived pioneer* as applied to tree species. Ishii (2000) used and developed this concept for *Pseudotsuga menziesii* (Douglas-fir) a dominant species in the old-growth *Pseudotsuga-Tsuga* forest of the Pacific Northwest of the United States (Franklin and Dyrness 1973).

Webb et al. (1972) introduced the concept of *long-lived pioneer* for *Diploglottis australis* in 12-year-old regrowth from an experimental clearing of moist sub-tropical rainforest in South Queensland. They did not specify the functional characteristics of the species in detail but called it a *long-lived pioneer* because it existed early in forest succession but did not die as other pioneer species did. Introduction of an integrative concept to describe the occurrence of something without defining how it functions is typical in ecology, but the names given usually imply something about functions. Swaine and Hall (1983) first discussed that *long-lived pioneer* tree species did not fit into the general classification of tropical tree species (Richards 1952) as either early seral stages (pioneer) species or mature forest (late successional) species. They worked in Ghana and noted that Keay (1957) used the concept *persistent seral* species in Nigerian tropical forest, i.e., the phenomenon was observed in different situations and different names given to it. *Long-lived pioneer* implies that a different theory for forest succession should be used where they occur from where they do not.

P. menziesii regenerates on disturbed ground but not the forest floor of established forests. It is certainly a pioneer species that invades following stand replacing fires. The important question is how it is so long-lived. Franklin and Hemstrom (1981) give typical maximum ages for *P. menziesii* as 750+ years, considerably longer than the late-successional species in the *Pseudotsuga-Tsuga* forest (*Tsuga heterophylla* 300+, *Abies amabilis* 400+, *Abies grandis* 300+) except for *Thuja plicata* at 1000+.

What we aim for is a *causal scientific explanation*. This has four characteristics:

1. *It is based on causal and/or associated organizational processes.* To construct a causal scientific explanation for this longevity we must specify why-type questions that can be answered using functional concepts. We constructed two why-type questions:

Why does *P. menziesii* live to a greater age than late successional species? That is, what intrinsically different causal process enables longevity in this species?

Why is *P. menziesii* not out-competed by late successional species? No matter what its potential longevity the species will not survive into the late successional stage of the stand unless it withstands or avoids competition.

These why-type questions constrain the scope of the answer needed by using a contrast. To construct a causal scientific explanation it is essential not to ask an open question such as "What causes longevity?" but to build information through a series of contrasts.

A number of reasons may contribute to differences in longevity between species (Loehle 1988) and the outcome of competition. The Wind River Canopy Crane Research Facility gives access to the old-growth forest canopy providing opportunity to investigate foliage growth and regeneration. We assumed that foliage production is important both for continued existence of an individual tree and in any competition with neighbors. This need (and opportunity) to focus an investigation means that we cannot be certain that the explanation produced is comprehensive.

Repeatedly surveyed *in situ* branch maps (Stoll and Schmidt 1998) of different species provided contrasting alternatives to *P. menziesii* both with species that do not live as long and between different positions in the crown. These showed (Ishii and Ford *submitted a*) that *P. menziesii* regularly produces epicormic shoots along its existing branch structure whereas three other species, *Abies amabilis*, *A. grandis*, and *Tsuga heterophylla*, do not or rarely do. There was very little damage and loss of foliage bearing shoots and branches that could be responsible for stimulating epicormic growth – in this situation it is an intrinsic rather than externally stimulated process. A detailed study of epicormic growth on old-growth *P. menziesii* (Ishii and Ford *submitted a*) showed extensive regeneration of foliage through epicormic shoot production: (i) within clusters of foliage bearing shoots; (ii) along branches to produce completely new sub-branches; and, (iii) along the tree trunk producing completely new branches that form within, and somewhat lower than, the crown of foliage formed by the original branch structure. On 400 year-old trees epicormic shoot production is the major process producing foliage. More the 90% of foliage is of epicormic origin in one or other of these processes.

Spatial analysis (Freeman and Ford *submitted*) provided evidence for competition between trees. Large, upper canopy trees were spatially evenly distributed, which is taken to be the end result of competition, while all trees taken together were clumped, which is taken to be an indication of patterns of natural regeneration. Branch extension was greatest on small and medium trees of *Abies amabilis* and *Tsuga heterophylla* (Ishii and Ford *submitted b*). Other than for these trees shoot extension was not positively related to light level. There seems very slow horizontal crown expansion of all species in the upper part of the canopy. The crowns of *P. menziesii* hold foliage above that of other trees and in this forest *P. menziesii* seems isolated above the zone of active crown competition. Measurements and projections of height growth (Ishii et al. 2000) suggest this situation likely to continue for another 100 years. The foliage of *P. menziesii* in the lower part of the crowns had morphological features indicative of acclimation to shade.

These investigations establish potential causal reasons for *P. menziesii* as a *long-lived*

pioneer enabling it to persist in this type of forest. This persistence is essential because the return period of stand replacing fires can be 500 years or more and the species requires disturbance for successful regeneration (Franklin and Hemstrom 1981, Agee 1993). As typical of many ecological investigations the information is a partial definition of cause. There has been no anatomical and/or physiological investigation into the intrinsic (non-damage related) process of epicormic shoot production. In addition, the investigation has not been repeated at another site. However, establishment of a potential cause raises the status of *long-lived pioneer* from simply a classification for observations made in a number of forests. It requires that further analysis of long-lived pioneers must explain similarities and differences of causal processes and their effects.

2. *Causal scientific explanations are consistent. Under the same conditions, the causal process will produce the same effect.* The question we must ask is whether there is a consistent causal basis for the essential characteristic of the integrative concepts. For *long-lived pioneer* essential requirements may be regeneration of foliage without increasing size and ability to withstand competition from late successional species – but different causal processes may achieve this. If different causal processes are found, or the same causal processes do not have the same effects, then concepts and theories have to be elaborated. The first requirement is investigation of old-growth *P. menziesii* in different forests to see if the same causal processes enable longevity and survival in the canopy.
3. *Causal scientific explanations are general. To explain a kind of event causally is to provide some general explanatory information about events of that kind.* This is undetermined for temperate coniferous forests. Other species in temperate coniferous forests may be classified as *long-lived pioneers*, e.g., the Sierra redwood, *Sequoiadendron gigantea*. Garden specimens have extensive, non-damage induced, epicormic shoots (Unpublished observations E. D. Ford and H. Ishii). However, scientific investigation in forests must analyze its importance for foliage regeneration and the process by which trees of this species are not replaced by successional species. The full set of characteristics that may make a species a *long-lived pioneer* has not been defined.

It might be that whenever we find non-injury induced epicormic shoot production then trees live longer than they do otherwise. However, not all of those cases need to be in pioneer species (e.g., Remphrey and Davidson 1992, Ito 1996, Bégon and Fillion 1999). In addition, trees may maintain foliage without increasing in size in other ways, e.g., the short-shoot system of *Cedrus*. Similarly, long-lived pioneers might survive not by avoiding canopy competition but by being better competitors. It seems unlikely that both generality and complete consistency are achieved together and what must be sought are causal reasons why there are both similarities and differences.

1. *When experiments are possible, a designed manipulation or intervention of the causal process produces a predictable response.* Direct experimental analysis of

characteristics resulting in increased longevity and competitive ability and/or avoidance seems unlikely with old-growth trees. The difficulty, sometimes impossibility, of doing experiments is a drawback but it is important to recognize that there are three other characteristics of causal explanations.

Scientific Inference for Integrative Concepts

The objective is a coherent explanation, one that is consistent throughout its parts (Thagard 1992). However, a characteristic of ecology is that we do not achieve coherent causal explanations immediately but progress towards them by accepting, rejecting, and refining components. We make scientific inference by assessing the coherence of a causal scientific explanation. This can be judged using six criteria (Ford 2000 p275-276).

- i. *Acceptability of individual propositions, including that they have been tested with data.* The two main propositions are that longevity is achieved because foliage is maintained by non-injury induced epicormic regeneration and the crowns of large trees are vertically isolated, at least in part, from competitors. While it is not possible to test these propositions experimentally, at least for the long-term dynamics of tree crowns, confirmation in other forests would increase acceptability particularly if the same causal processes were found in other species. However, other characteristics need definition for *long-lived pioneer* for comparison with discovered and analyzed characteristics of early and late successional species (Bazzaz 1979). The existence of *long-live pioneers* has been confirmed but the complete causal processes that distinguish them have not.
- ii. *Concept definitions are consistent throughout the theory network.* For a concept such as *long-lived pioneer* the theory network should apply to all species classified in this way. It should include scientific explanation of differences between examples. We need to define concepts consistently. Repeated analyses have shown that ecologists are lax about consistency in concept definitions (McIntosh 1985, Peters 1991, Shrader-Frechette and McCoy 1993, Grimm and Wissel 1997). There are some genuine difficulties. For example, in applying the concept of *long-lived pioneer* to *P. menziesii* we are considering a species that lives for hundreds of years in a temperate coniferous forest following a stand replacing disturbance. Originally Swaine and Hall (1983) used the concept to classify trees that colonized gaps within a tropical forest stand and persisted to become part of the mature forest canopy, as opposed to species that colonized gaps but did not persist. Their study lasted for only 5 years although a maximum tree height of 17m was reached in that time. Webb et al. (1972) used the concept in study of 12 years regrowth of a tropical forest. The value of the concept is similar in all cases. It is evidence against universal classification of tree species into early and late successional – but the causal processes involved in each instance need to be specified.
- iii. *Part and kind relationships are consistent throughout the theory network. Parts*

- define the divisions components, a branch is part of a tree crown. *Kinds* define the similarities and differences in function; all epicormic shoots should have the same function. This qualitative consistency is difficult to achieve in ecology. All species categorized as *long-lived pioneers* do not have the same type of foliage production. Foliage regeneration within the crown might be achieved in different ways (but see vi). If there are differences then these must be resolved, for example by defining a concept of foliage regeneration that could comprise different processes.
- iv. *There are not ad hoc propositions that include special circumstances.* Again, this is difficult in ecology. We build general knowledge through investigation of particular situations and explanation of what is similar and what is different has to be made. There can be a tendency to focus on similarities and not to explain differences but rather to use *ad hoc* propositions to exclude them from consideration.
 - v. *Generally, theories with fewer rather than more propositions are favored as explanations that are more coherent.* We might prefer it if all forest succession could be explained by using concepts of *pioneer*, *disturbance*, and *early-* and *late-successional species* particularly if all part and kind relationships between them were the same. This preference provides an important resistance to the haphazard propagation of new theories. If *long-lived pioneer* is to be accepted as an important concept then it should explain much (see vi).
 - vi. *The explanation applies to broad questions and circumstances.* Because of difficulties in achieving coherence using (i) through (v) ecologists often concentrate on this type of reasoning. The theory of *long-lived pioneer* would gain in coherence if another long-lived pioneer such as *Sequoiadendron gigantea* (Stephenson 1984) were confirmed as having similar characteristics to those of *P. menziesii*. There would be two reasons for this. First, in the forests where it is dominant, in size if not numbers, natural regeneration requires high-intensity low-frequency fires to create gaps (Bonnicksen and Stone 1982) so there is a similar requirement for longevity. Second, *Pseudotsuga menziesii* and *Sequoiadendron gigantea* are not closely related phylogenetically. Non-injury induced epicormic based foliage regeneration in both of these species could be considered as parallel evolution which some ecologists consider as evidence of important underlying ecological processes (e.g., Grubb 1992). Of course, this also implies that the environmental conditions that can result in high-intensity, low-frequency of return, fires have been persistent. Making a causal analysis of tropical forest *long-lived pioneers* is also a requirement.

Discussion

There are two important reasons why ecologists need an explicit definition of synthesis. First because both the quality and quantity of ecological knowledge has been questioned. What causes concern is the lack of general theory that has developed from particular investigations. Shrader-Frechette and McCoy (1993) suggest that ecology may turn out to be

a science of case studies and practical applications and may have to sacrifice generality for the precision gained in the case study approach. In a more optimistic review, Lawton (1999) identifies nine patterns of what he terms macroecology, mostly from population biology. He suggests; "To discover general patterns, laws and rules of nature, ecology may need to pay less attention to the 'middle ground' of community ecology relying less on reductionism and experimental manipulation, but increasing efforts into macroecology." However, general theory is built upon particular investigations. In ecology, we build theory over time, and through successive investigations – we make *progressive synthesis* (Ford 2000 p467). There can be reasoned and legitimate differences in the importance attached to the six criteria for judging explanatory coherence. If these differences are to be resolved, we need to analyze them to define what type of additional information is required.

Second because the scientific method used in ecology has been challenged (e.g., Peters 1991, Shrader-Frechette and McCoy 1993, Weiner 1995). Murray (1999a, b) makes a direct challenge on the basis that ecologists do not follow the methods of physics and the teachings of Popper (1963, 1968). However, the properties of physical law, as expounded by Feynman (1964), and extolled as exemplary by Murray, have been shown to be ideals that are simply not realized in practice (Cartwright 1983). Physics can be left to look after itself. What is germane is whether ecologists should follow the falsificationist method of Popper as interpreted by Murray (1999a, b). Among philosophers of science, Popper is recognized as having made substantial contributions – but the subject has progressed. Work that is more recent defines and illustrates how scientific theories develop through increasing the certainty with which component parts can be considered as acceptable or should be rejected. This can be seen in the work of Niiniluoto (1987 p196). He analyzes Popper's concept of verisimilitude, (which contains measures of truth and falsity content), shows where it is inadequate (that the proposed measure of falsity content does not reflect different distances that informative statements can be from a true one), and defines improvements (see also Kiesappä 1996). Thagard (1992) illustrates that some theory change can occur through the development and replacement of concepts and that major revisions can occur. Salmon (1990) provides discussion on the theory of explanations. These are examples of the diversity of approaches in the philosophy of science. The essential point is that the development of scientific theories is recognized to be a more complex and exhaustive process than some scientists attribute to Popper's ideas about it.

Ecologists pay much attention to the analytical part of research and the weight that should be given to data obtained in an investigation. However, the lack of attention paid to the process of synthesis for integrative concepts restricts rational debate on wider issues. Some scientists, involved with the details of a particular investigation, may feel that developing integrative concepts is not essential for their work. However, in addition to communicating with scientists in related but not identical fields, integrative concepts may be essential for communicating with general audiences.

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