Ecology after 100 years: Progress and pseudo-progress

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Abstract: Has the science of ecology fulfilled the promises made by the originators of ecological science at the start of the last century? What should ecology achieve? Have good policies for environmental management flowed out of ecological science? These important questions are rarely discussed by ecologists working on detailed studies of individual systems. Until we decide what we wish to achieve as ecologists we cannot define progress toward those goals. Ecologists desire to achieve an understanding of how the natural world operates, how humans have modified the natural world, and how to alleviate problems arising from human actions. Ecologists have made impressive gains over the past century in achieving these goals, but this progress has been uneven. Some sub-disciplines of ecology are well developed empirically and theoretically, while others languish for reasons that are not always clear. Fundamental problems can be lost to view as ecologists fiddle with unimportant pseudo-problems. Bandwagons develop and disappear with limited success in addressing problems. The public demands progress from all the sciences, and as time moves along and problems get worse, more rapid progress is demanded. The result for ecology has too often been poor, short-term science and poor management decisions. But since the science is rarely repeated and the management results may be a generation or two down the line, it is difficult for the public or for scientists to decide how good or bad the scientific advice has been. In ecology over the past 100 years we have made solid achievements in behavioural ecology, population dynamics, and ecological methods, we have made some progress in understanding community and ecosystem dynamics, but we have made less useful progress in developing theoretical ecology, landscape ecology, and natural resource management. The key to increasing progress is to adopt a systems approach with explicit hypotheses, theoretical models, and field experiments on a scale defined by the problem. With continuous feedback between problems, possible solutions, relevant theory and experimental data we can achieve our scientific goals.

Keywords: ecology; progress; resource management

Introduction

Science and progress have become synonyms during the last century, and for the most part the public appreciates and funds science because it is believed to lead to progress and to improvements in the quality of life for the people of the world. Many books and articles have discussed the relationships between science and progress (Kuhn, 1970; Losee, 2004) and many authors have evaluated how ecology and its subdisciplines in particular can best improve progress (Thompson *et al*., 2001; Graham and Dayton, 2002; Osmond *et al*., 2004; Salafsky *et al*., 2002). In this paper I revisit the issue of progress in ecology from an historical perspective. In particular I ask, given the scope and promise of ecology, what have we achieved, and how much have these achievements helped to address the ecological problems of the planet?

What did the ecologists of the early 20th century promise for the fledgling science of ecology? Charles Elton (1927), in one of the earliest textbooks of animal ecology, outlined the elements of the science—communities, habitats, limiting factors, the regulation of numbers, succession, and dispersal. He pointed out clearly in 1933 that progress in solving economic problems was an essential task of the new science. After mentioning sleeping sickness, malaria, the biological control of plant and animal pests, and conservation in Africa, Elton goes on to say:

> "…these practical problems undoubtedly provide one of the strongest and most urgent reasons for developing principles in animal ecology…" (Elton, 1933, p. 5)
>
> "Animal ecology is building up from basic surveys a science whose aim is the complete analysis of animal behaviour, numbers, and distribution. It has only recently progressed far enough to make close contact with the economic problems. It still has a long way to go." (Elton, 1933, p. 87).

This economic concern in ecology arose from important human problems, and I suggest that the promise early ecologists made relied in the end on providing solutions for these practical problems in disease management, agriculture, forestry, fisheries and conservation. But if this is the ultimate goal, how can we measure progress in ecology?

Philosophers of science have discussed in detail how science progresses, and there are two rather diametrically opposite models of scientific progress (Losee, 2004). William Whewell in 1837 suggested a "tributary river" model of scientific progress with facts and ideas forming the small rivulets that flow into larger theories and laws. Karl Popper in the last century proposed an "evolutionary tree" model of scientific progress in which natural selection operates on ideas and theories, and progress is defined by falsification of ideas that do not fit observations and experiments. The evolutionary model of progress was used by Graham and Dayton (2002) in their analysis of paradigms in ecology, but it is far from clear which of these two models is more appropriate for ecological science.

Given the lack of a clear model, we are tempted to measure scientific progress empirically by the number of papers published or the size of the membership in an ecological society. The journal *Ecology*, for example, published about 200 pages per year in the 1920s, and now exceeds 2200 pages annually. The New Zealand Ecological Society began in 1952 with 150 members and in 2004 has 535 members, a three- to four-fold increase. By these measures ecology has progressed greatly but these measures still do not clearly define progress. "Bigger is better" can be a convenient substitute for a more careful analysis of how many problems have been solved by ecological research, and we need to develop a better metric of progress if we are to convince politicians that ecological research should receive higher levels of funding.

If we restrict the science of ecology to the analysis of the interactions that determine the distribution and abundance of organisms, we can ask what ecology should achieve. I suggest three broad goals that are consistent with the promises made by Charles Elton and many early ecologists: (1) to understand how the natural world operates; (2) to understand how humans modify the natural world; and (3) to find methods to alleviate the problems arising both from nature and from human actions. Progress in science can be identified most easily with effectiveness in problem solving (Losee, 2004), and the first two goals should have the ultimate aim of facilitating the third goal of alleviating problems. The background model for achieving all of these goals is illustrated in Figure 1, the application of the scientific method to ecological problems.

Understanding the natural world

Populations, communities, and ecosystems have a long evolutionary history, and as a starting point ecologists need to analyse and understand how these systems work in the relative absence of human interference. This goal is in many ways incompatible with the current state of the planet, where humans have appropriated much of the primary production (Pauly and Christensen, 1995; Vitousek *et al*., 1997) and resources such as water (Postel *et al*., 1996; Jackson *et al*., 2001). It is legitimate to ask whether or not this goal of studying the natural world is worth pursuing at the present time. The argument is that all of the earth is so affected by human actions that there is no natural world remaining to be studied, and moreover what is left in a natural state is so little as to be irrelevant to our current ecological problems. For example, less than 5% of the area of the European Union countries can be classified as natural landscape (Piorr, 2003). The contrary argument for the relevance of natural landscape studies has been well summarised by Sinclair (1998), who argued that natural systems found in national parks and other protected areas form the baselines against which we can measure human-affected ecosystems. The key point here can be illustrated by an analogy with medicine — unless we understand the workings of healthy human beings, we cannot begin to diagnose, understand, and alleviate diseases and other disorders.

Palaeoecology should be the starting point for placing our understanding of current ecological conditions into an historical framework. The key point is that our current ecological theories must be consistent

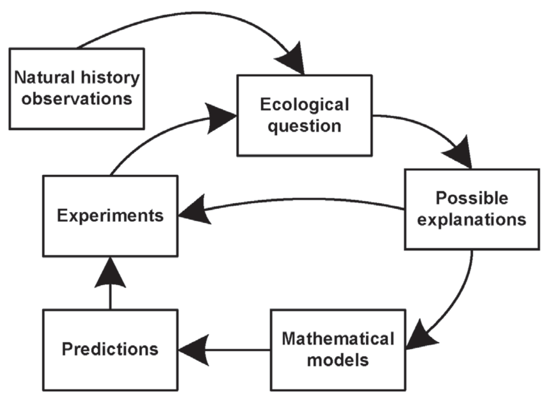

Figure 1. Key feedback loops that are necessary for ecological progress. All these elements are needed to achieve successful understanding, and one way to judge the utility of a hypothesis or a model is to see how many high-quality, useful, testable predictions and potential experiments flow from it.

with the information we can gain from palaeoenvironments. A classic example of the value of palaeoecological work has been the rejection of Clement's monoclimax hypothesis of succession and the idea that plant communities are integrated equilibrial systems (Giller and Gee, 1987). There are many examples now described in which past plant and animal communities have no modern analogue (Collinson and Scott, 1987; McGlone *et al.*, 2000; Brook and Bowman, 2004). The important message that palaeoecologists give to modern ecologists is to place their findings within a long-term framework that does not assume equilibrial dynamics. The current focus on the impacts of global change strongly underlines this message.

Understanding the natural world implies some generality of ideas rather than an assumption that every ecosystem is different, and it is this search for generality, or good paradigms, that is itself controversial. By generality of understanding I mean the development of some ecological principles or "laws" that are more specific than the exponential growth law (Berryman, 2003) but cover particular ecosystems or trophic compartments in such a way that predictions about future behaviour can be made and tested. For example, a generalisation that *community structure on rocky intertidal shores is determined by keystone predators* is useful because it predicts general patterns on all continents independent of the actual species involved. These kinds of generalisations will have exceptions and need testing, but they serve as paradigms or guideposts for further research (Paine, 2002). Developing good paradigms has been a major focus of basic ecological research over the last 50 years.

Population ecology and behavioural ecology have developed an extensive and reliable understanding of ecological processes at the individual and population level of abstraction, and are the most developed of the ecological disciplines. Community ecology and ecosystem ecology have also made progress in dealing with more difficult issues, and are hampered by the issue of scale and the difficulty of doing large-scale experiments (Osmond *et al.*, 2004). All of these subdisciplines have progressed because they have good mathematical theory supporting their claims – whether it be population mathematics, Mendelian population genetics, or energy flow. Without some form of mathematical theory, no subdiscipline is able to decide if its quantitative data are correctly balanced. The simplest examples come from population mathematics — if you know the birth, death and movement rates for a local population, you can calculate the population growth rate and compare this with measured changes in numbers. A second example would be the analysis of soil nutrient dynamics in ecosystems, in which, by the law of conservation of mass, what goes in must come out, unless storage changes.

Landscape ecology, by contrast, has not developed any mathematical theory. Landscape ecology asks how the spatial arrangements of habitats affect the distribution and abundance of species, and how landscape patterns affect ecosystem processes. These questions are not being answered at present, although many ecologists view them as critically important in human-dominated areas, and at present landscape ecology continues as a set of GIS-type technologies in search of a question. There are important issues that must be attacked at the landscape level, but so far landscape ecology has not articulated these or developed a paradigm that would define progress in this area (Wiens, 1999).

By all rights, theoretical ecology ought to be a key to ecological progress but to date its main contribution has been to push bandwagons that promise everything and deliver little. Theoretical ecology has made a disappointing contribution for two major reasons. First, many mathematical models score high in elegance and low in empirical relevance. Models with parameters that cannot be measured only rarely lead to scientific progress (*cf.* Ginzburg and Jensen, 2004). Second, without empirical feedback (Fig. 1), models become divorced from reality and become an end in themselves rather than part of the solution to a problem. Almost none of the material in the journal *Theoretical Population Biology*, for example, bears any relation to analysable problems in the real world. There is no harm in exploring hypothetical worlds, but the observation I make is that none of this has helped ecologists solve practical problems. Third, the arrogance many mathematical modellers have shown in the past toward empirical ecologists has hardly helped bring about the desired interactions (illustrated in Fig. 1) that are essential for progress. Fortunately this problem is now largely historical, and has been alleviated by a new generation of mathematical ecologists who think about reality in creative ways (e.g. McCallum *et al.*, 2001; Barlow *et al.*, 2002).

Understanding how humans modify the natural world

If ecologists have achieved some understanding about how the natural world operates, they can then apply these insights into an assessment of how human actions have affected ecosystems. Humans have four broad impacts on ecosystems. First, they simplify communities with crop or forest monocultures that replace complex natural communities. Second, they translocate exotic species to new areas. Third, they add new chemicals to the natural world or enhance nutrient cycling in unique ways. Such pollution problems are a major concern to humans. Fourth, they harvest renewable resources. The overarching mantra for all these problems is sustainability and the general goal of maintaining long-term system properties like biodiversity or soil fertility.

Monocultures of agricultural crop plants or fish in pens are possibly the most extreme examples of human-structured communities that exceed the boundaries of single-species dominance observed in species-diverse natural ecosystems. Monocultures have been the dominant model for Western, temperate-zone agriculture for the last century because of the belief that this type of farming created maximum crop production, maximum profit, with minimum labour. But monocultures cause problems in pest management and potential problems in soil fertility, so that in the medium to long term, profit may be reduced and in some cases eliminated by crop diseases and pests. Tropical agriculture by contrast has developed empirically with mixed crops (Vandermeer, 1989), and there are strong reasons why monocultures are both less productive and socially less desirable in tropical systems. The reassessment of the use of monocultures in agriculture has come from a social movement toward a desire to achieve sustainable agriculture. At the same time we need to develop standardised biotic indicators that will provide feedback on future trends in agricultural-land- use practices, whether they involve monocultures or mixed cropping systems (Osinski *et al*., 2003).

There are surprisingly few detailed data available on the ecological and economic advantages and disadvantages of monocultural agriculture and forestry (Reganold *et al*., 2001; Rothe and Binkley, 2001; Sanderson *et al*., 2004). For example, there is no clear indication that soil nitrogen is increased in mixed forest stands compared with monocultures (Rothe and Binkley, 2001). Nor is it clear that species-rich pastures translate into higher livestock production (Sanderson *et al*., 2004). The general recommendation that higher biodiversity is better in agricultural systems is an article of faith among ecologists, but this generalisation has a weak scientific foundation.

Species introductions are a global problem that has the potential to produce pest catastrophes. New Zealand is an interesting case in point because of the high level of species introductions and agricultural changes that have affected native species (Parkes and Murphy, 2003). Introduced species of both plants and animals have caused extinctions and range restrictions that are being reversed at great cost by intensive pest management. Australia suffers from many of the same problems with introduced species and a systematic failure to adopt sustainable agricultural practices (Short, 1998; Richards and Short, 2003). The interaction of conservation management with agricultural production in New Zealand is especially interesting because of the need to harmonise sustainability of human industries with the conservation of biodiversity.

Pollution of ecosystems with both natural compounds and human-produced chemicals is a third source of concern for the earth's ecosystems. These problems are multi-disciplinary involving chemistry, environmental science, and medicine as well as ecology. At present we make little progress in dealing with many forms of pollutants because the interdisciplinary groups have not yet formed to attack these complex problems. Until this happens, ecologists must rely on describing pollution catastrophes after the fact, the classic example being DDT (Grier, 1982; Lindell *et al*., 2001. The largest focus of ecologists has been on understanding the impacts of climate change on ecosystems, a critical and difficult task because of the variability of response of different species to changes in the physical environment (Mueter *et al*., 2002; Logan *et al*., 2003; Parmesan and Yohe, 2003). Predictions about the impacts of climate change have so far been very general, and rely on a simple postulate that all geographic ranges are limited by climatic variables. Specific predictions about the biological impacts of climate change are in high demand by the public, but are hazardous for ecologists because such long-term predictions must rely on models that are far too simple to capture the complexities of the interactions between climate change and species interactions.

Harvesting of renewable resources has been the fourth critical area that ecologists have studied in detail in order to manage fisheries and forestry resources sustainably. Ironically, fishery scientists were among the first to discuss sustainability, and yet fish are almost universally overharvested around the world (Ludwig *et al*., 1993; Pauly *et al*., 2002; Myers and Worm, 2003). Most of the problems of overharvesting are economic, social and political rather than biological, and the ecological principles of sustainable harvesting are now well worked out (Pauly *et al*., 2002). This is a case in which ecologists have been successful in their science (with many mistakes along the way), but their message has not transferred across to politicians and managers.

Finding methods of alleviating problems

The key contribution of ecology to human welfare will be to work out methods to reduce the problems caused both by nature (diseases like malaria and yellow fever) and by the human population. This is the bottom-line justification for supporting scientific ecological research, and the key performance indicator will be to score successes. Applied ecology has two major areas of success — the biological control of weeds and pests and the management of water quality. Conservation biology has also produced success stories at the level of individual species and (much more rarely) at the level of communities and ecosystems.

Applied ecology has achieved success by operating with the single-species paradigm, and yet ecologists in general argue that we need to consider problems at the community and ecosystem level of analysis (Forsyth *et al.*, 2000). The dialectical interplay of the reductionist, single-species approach with the more holistic, ecosystem approach has produced a schism in ecology that hinders our attempts to alleviate problems. At the simplest level, it has produced specialisation, resulting in ecosystem ecologists rarely talking to population ecologists, and new specialised journals that proliferate faster than anyone can read them (Graham and Dayton, 2002). How can we find the middle ground?

Ecological problems are often regarded as single-species problems, and we need to develop better ways of judging which single-species problems are in reality hidden, community dynamics problems that will lead to further difficulties (the Law of Unintended Consequences, e.g. Hickling *et al.*, 1999). One way to achieve this goal is to demand a food-web analysis for any particular ecological problem, whether it concerns an endangered species or a pest species. For example, if the rabbit is a pest species, we must ask what will be the results of reducing or eliminating rabbit populations. If the direct and indirect effects that propagate through the food web can be anticipated, the experimental designs needed to inform decision makers can be specified (Courchamp *et al.*, 2003). The call is for multi-species management, and this must be the future of pest control. The possum in New Zealand is an excellent example of the need for multi-species approaches, and we need to ask what would be the impact of reducing or eliminating these pests from New Zealand forests (Montague, 2000; Norton, 2000; Veltman, 2000). For some pest species, the results are clear-cut and reduction or eradication can proceed with few side effects. This is clearly the case with eradicating rats that have been introduced to islands (Myers *et al.*, 2000; Towns and Broome, 2003). But it will not be true for all pest species and there are already too many examples of pest control gone wrong by not anticipating unintended consequences (Secord, 2003).

There is now a rich literature of the unintended consequences of management actions, and every management proposal should start by reviewing the historical background of the intended actions in order to avoid repeating the same mistakes (Keedwell *et al.*, 2002). The use of adaptive management is the second general recommendation for agencies dealing with resource management, but at present it is used more in discussion than in practice (Salafsky *et al.*, 2002; Shea *et al.*, 2002). By adaptive management I mean experimental management, the application of standard scientific experimental protocols to management problems. There is no doubt that the use of the adaptive management approach would greatly improve our ability to manage renewable resources effectively.

The present tendency in both basic and applied ecology is to develop mathematical models to investigate system behaviour. Unfortunately, there is a complete disjoint between the time it takes to model a problem and the time it takes to test a hypothesis with a properly replicated field experiment or to measure the parameters of the model, so that ecological modelling has far outstripped ecological knowledge. Typically a modelling paper in journals like the *American Naturalist* now ends by stating that "unfortunately we do not have the data to test this model". This statement must not be construed as an argument against mathematical modelling — what is missing too often is the critical feedback loop Fig. 1. Nigel Barlow was one of a growing list of modellers who recognised this need very early (Barlow, 1995, 2000a, 2000b; Barlow *et al.*, 1997, 2002). If the feedback loops shown in Fig. 1 were implemented for every ecological problem, we would have a better chance of developing effective solutions more rapidly.

The greatest danger is with present-day ecological models that pretend to be able to predict community and ecosystem dynamics at long timescales. Many mathematical models are developed explicitly to address the long-term consequences of some management actions. Ecologists are on the horns of a dilemma over these requests. What will happen, for example, to the carbon balance of peatlands if global warming continues? These questions are real, immediate, and important, and ecologists have been easily seduced into trying to answer them with models that incorporate current knowledge, for example of peat decomposition and deposition rates in relation to climate. The serious issue is that all these long-timescale models are explicitly untestable during the lifetime of a typical scientist. If any prediction must require even a 20 to 30 year time span, confirmation of such a model must be forfeited (Oreskes *et al.*, 1994). Such models may be useful for exploring scenarios of what might happen, but they cannot be viewed as scientifically valid instruments of prediction and are little more than mathematical excursions with a potential for misleading the public as well as other scientists. A crucial comparison here is with the prediction of weather. In spite of well-defined physical models of the atmosphere, a large array of daily data, and vast resources (compared with ecology), detailed weather predictions are unreliable beyond a few days (Sarewitz *et al.*, 2000; Pielke and Carbone, 2002). Our ability to predict in ecology is at present more severely limited, particularly for communities and ecosystems, and we should focus only on models that apply over the short term in ways that can be tested empirically. Models that address

Table 1. Circumstances holding back scientific progress in ecology, and possible solutions.

Problem	Solutions
Shallow research questions	Frequent discussion and agreement on critical issues in ecology
Posing of unanswerable questions	Develop paradigms that work to solve problems
Lack of replication	Repeat experiments in space (preferably) or in time
Lack of suitable scale of study	Groups of researchers Additional funding
Time frame of studies too limited	Design interlocking studies Fund long-term ecological sites
Inadequate statistical analysis	Screen experimental designs before doing the research, using knowledgeable people
No alternative hypotheses or vague hypotheses	Require clear statements of hypotheses in publications
Making vague predictions from hypotheses	Require clarity of logic and specific predictions in research proposals and publications
Models with parameters that cannot be measured	Request models that have empirical parameters from modellers who understand natural systems
Additional funding	Develop clear lines of communication to people who allocate funding in government or privately
Bandwagon research funding	Multiple funding agencies with different priorities and different time frames

long-term issues may be useful as heuristic devices, but should not be presented as predictive statements. Making definite statements about long-term issues may gather political support in the present at the price of longer-term undermining of confidence in ecology when the predictions are found to be in error. Defining long-term predictions from complex models as "scenarios" is intellectually dishonest. Ecologists may take such predictions with a grain of salt but the public and politicians will not be so critical. If there is a message for the long term that ecologists need to amplify, it is that we must learn to live with scientific uncertainty and respond to it creatively with a worldview that includes the precautionary principle.

Disease ecology is an important area to which ecologists have much to contribute. Diseases are not simply a medical problem, and if we do not develop the understanding of how diseases like the West Nile virus and AIDS develop, propagate, and transmit from other animals to humans, we will be condemned to a reactive type of science that misses ecological causes. Disease ecology is an underdeveloped part of ecological science that needs much more investment (Mills and Childs, 1998; Mills, 1999).

Finally, ecologists ought to recognise that while we are able to develop solutions for current problems, these will often not be implemented for financial, social or political reasons (Table 1). In a world driven by dollars, sensible environmental policies on climate change, for example, may have little hope of passing. For some modern trends like climate change, ecologists may find themselves mapping in detail the angle of repose of the deckchairs on the *Titanic*, rather than solving problems. Education is the long-term solution to the lack of political determination on many environmental issues, but ecological ignorance still rules on even simple problems like the impact of domestic animals on wildlife (Lepczyk *et al.*, 2004). Nevertheless, ecologists must press forward to develop solutions to problems. We should be confident that in the long run we will prevail and will have made a substantial contribution to the development of a sustainable human society with the ecological values we hold to be self-evident.

Conclusion

There has been a great deal of soul-searching about progress in ecological science (Loehle, 1987; Peters, 1991; O'Connor, 2000). Much of the disagreement over the rate of progress has its origin in how to measure scientific progress. To many ecologists these issues are irrelevant, but to a larger public that supports science the issue of progress is critical for continued funding. I suggest that we should adopt as the metric of progress our ability to solve ecological problems. To achieve these goals we need to do better science (Anderson *et al.*, 2003) with better theories, better models, and better experiments. We can all profit by raising the bar in ecology for all these areas.

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