Agroforestry Systems **45**: 43–55, 1999.

Moving from descriptive to predictive ecology

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Key words: design of agricultural mimics, ecosystem function, non-equilibrium, prediction

Abstract. The science of ecology is undergoing many important shifts in emphasis and perspective which have important implications for its role in designing sustainable farming systems. In particular, a shift has occurred from the equilibrium paradigm to one which recognises the dynamic, non-equilibrium nature of ecosystems. Allied to this is the recognition that ecosystems can occur in any one of a number of alternative stable states, depending on the disturbance and management history. An increased emphasis on spatial patchiness in ecosystems has also emerged as appropriate tools have emerged to analyse spatial mosaics. These features have led to a recognition that considerable uncertainty is associated with the outcome of any particular ecosystem modification; hence predictive capacity is also low. Recent considerations of the interrelation between biodiversity and ecosystem function have also explored the questions of how many species need to be in a system to fulfil certain functions and confer resilience. We identify a set of steps that are required for the development of an agricultural system based on mimicking natural ecosystems. Central to this is identifying (1) the functions which are currently suboptimal in the agricultural system, and (2) the species which have key functional roles in the natural system, and then reaching decisions as to the array of species needed to confer system function and resilience.

1. Introduction: ecology at the crossroads

In this article we examine the ability of ecology to contribute to the design of sustainable farming systems. We examine the current state of ecology in the light of recent debate, and then highlight some of the radical changes in fundamental paradigms that have been occurring recently. We then discuss the study of the relationship between biotic diversity and ecosystem function, an area currently receiving considerable attention in ecology, and finally place these discussions in the context of developing agricultural systems.

The science of ecology has come under fire from numerous sources recently, and is currently undergoing a radical shift in emphasis. Many aspects of the science are undergoing revision. Botkin (1990) has provided a lucid and in-depth analysis of the gulf between ecological theory and empirical observations, and suggested that theory developed from mechanical and physical analogies does not fit natural systems very well. Further, natural resource management based on these theories is bound to fail since it does not take the changing nature of the environment into account. Keddy (1989) further criticised ecology for its inability to focus on important questions, rather than interesting or easily-answerable ones, and pointed out that the thrust of much ecological research is decided by a relatively small number of influential ecologists. Ecology also focuses disproportionately on certain types of organisms (particularly attractive vertebrates), and concentrates on the northern hemisphere temperate regions, which house the majority of ecologists but which have only a small proportion of the world's biota and ecological problems.

Shrader-Frechette and McCoy (1993) went further in pointing out that ecologists frequently use ambiguous, inconsistent or unclear terms, and spend a lot of time arguing over terminology and the importance of particular processes. They commented that:

> On the whole, general ecological theory has, so far, been able to provide neither the largely descriptive, scientific conclusions often necessary for conservation decisions, nor the normative basis for policy, both of which environmentalists have sought.

Peters (1991) provided further in-depth criticism of ecology and ecological methodology. The summary of his book on its cover stated that:

> Ecology suffers because it has ignored or minimised the important criterion of predictive power in assessing scientific quality. Instead, ecologists offer logical rationalisation, historical explanation and mechanistic understanding, so that the predictive failure of the science goes almost unnoticed. Given this context, ecologists fall prey to a number of minor failings that complicate and confound any assessment of the science. Even when predictions are possible, they are often vague, inaccurate, qualitative, subjective and inconsequential. Some of ecology has become scholastic problem-solving that directs concern away from the serious problems facing humanity.

Ecology, as with any science, is an evolving entity, and because it is a relatively young science dealing with a vast and complex subject matter, there is still a lot of disagreement about even the most basic of premises. The subject matter of ecology is complex and often inherently unpredictable, and results obtained in one type of system are not necessarily transferable to another. Generality and 'hard facts' are, thus, hard to come by. Matched against this, however, is the need to come up with answers to pressing environmental problems which cannot wait for theoretical arguments to be worked out. Among these is the vital task of ensuring the sustainability of agro-ecosystems, a task that all humans agree is fundamental to our survival. However, given the turbulence in ecology, how successfully can its practitioners contribute to this objective?

2. New paradigms in ecology

In line with the debate about the role of ecology described above, the science has undergone something of a quiet revolution during the past 20 years (Pickett et al., 1992; Pickett and Ostfield, 1995). Concepts that were considered firmly established in previous decades have undergone considerable revision, even reversal. Some of these re-interpretations are perhaps well known to those working in agro-ecosystems, but others are relatively recent and are still actively developing in the ecological literature. In this section, recent developments that we believe are of greatest importance to ecosystem ecology are briefly mentioned.

2.1. *The flux of nature*

Previous generations of ecologists operated largely on the assumption that the natural world was fundamentally a stable place, a collection of communities in which each species had its ordered position and in which any disturbance would result in an ordered successional progression leading through subclimax phases back to the original climax (Christensen, 1988). Ecological communities were considered to be organised, patterned collections of co-evolved species, into which incompatible species could not penetrate (Simberloff, 1982). Ecologists now speak of this era as the period of the equilibrium paradigm. In recent years we have seen this notion of organisation and stability give way to a vision of flux. Most ecologists have come to the view that the natural world is characterised more by instability than permanence, by frequent disturbance that continually pushes ecosystems in alternative directions instead of causing them to return inevitably and regularly to their original condition; more by unique specific responses than co-ordinated, predictable, tightly constrained combinations of species, as individualistic responses outweigh tendencies towards regularly occurring communities. Awareness that the natural world is an uncertain place in which disturbances are constantly causing alterations in composition of assemblages and in spatial pattern of the environment has led now to the non-equilibrium paradigm (Pickett et al., 1992; Fiedler et al., 1997). This paradigm does not hold that ecological equilibria are non-existent, but rather that they are scale-dependent and embedded in non-equilibrial conditions. Nevertheless, the non-equilibrium paradigm does imply that predictable end-points to the successional process following disturbance are rare, that multiple stable states may exist, and that some quasi-stable states can persist for long periods.

2.2. *Multiple stable states*

Disturbance inevitably sets in train some form of succession. It is apparent now that the course of the succession is difficult to predict, because the direction which the ecosystem or assemblage takes is contingent upon the particular circumstances of the disturbance and the nature of the biophysical conditions that precede and follow it. The notion of contingency brings history to the fore: history very much matters in patterns and processes of community change. As a consequence, the end-point of many successional processes is not a predictably uniform outcome; instead, several states are possible, depending on the contingent circumstances (Noble and Slatyer, 1980; Hobbs, 1994). Depending on the frequency of the disturbances, these multiple states may be stable for long periods of time, and distinct thresholds may exist which limit the transition from one state to another. The differences among outcomes of successional events in seemingly similar assemblages or ecosystems may well follow broadly interpretable patterns, but the itineraries are not easily predictable at the outset of the journey.

2.3. *Patchiness and landscape ecology*

Recognition of the importance of spatial and temporal variability, together with the increased availability of suitable tools for analysing it, has galvanised landscape ecology. Its re-emergence springs from realisation that understanding and management of the natural world depends as much on the analysis of flows of resources across ecosystems as it does on the study of quadrats. But perhaps the principal issue underpinning landscape ecology is recognition of the vital importance of patchiness (Turner and Gardner, 1991). Patchiness does not yet possess a complete or unified theory, but is a rapidly developing conceptual tool (Levin, 1989; Ostfeld et al., 1997). Patchiness focuses on the spatial matrix of ecological processes, and emphasises the fluxes of materials and organisms within and between parts of the landscape. It is a form of spatial heterogeneity in which boundaries are discernible, and in which units appear as contrasting, discrete states of physical or ecological phenomena (Ostfeld et al., 1997). An array of patches constitutes a mosaic at whatever scale is appropriate for investigation (although it is important to note that multiple scales may be important). The study of patch dynamics promises to provide a valuable framework in which to understand and to manage the landscape mosaic, although there is still much work to be done in this area.

2.4. *Prediction*

The non-equilibrium paradigm sees ecosystems as probabilistic rather than deterministic; inherently, therefore, most ecologists believe that ecosystems are characterised by uncertainty rather than by predictability. Because of the overwhelming importance of this uncertainty, ecologists have invested considerable intellectual energy in trying to comprehend environmental stochasticity – correlated variability in chance events caused by patches in a landscape experiencing a similar environment, including both physical and biotic features – and catastrophes – correlated variability of large magnitudes that occur at a low frequency. We cannot avoid the lack of predictability; consequently, there is a need to identify the bounds or conditions under which decisions can be made in the face of uncertainty. Risk analysis and adaptive management through more detailed involvement of managers in research and development, are the principal routes by which ecologists are struggling to work with unpredictability. Although admission of the extreme difficulty of prediction has initially caused ecologists to be concerned that their science is fuzzy, a focus on uncertainty and risk analysis is common to many people in the social, political and economic spheres (Graham and Wiener, 1995), and quantitative risk assessment is widely used in engineering and technology. Hence, ecology is not necessarily difficult, in this sense, for decision-makers to comprehend.

2.4.1. *Human beings and ecology*

Recognition of the inevitability of disturbance, and of its profound ecological consequences, leads inevitably to the inclusion of humans as primary agents of flux in ecosystems (Pickett et al., 1992; McDonnell and Pickett, 1993; Hobbs, 1997; Vitousek et al., 1997). Ecology is now beginning openly to extend its interest from supposedly ‘natural’ systems, in order to include human-dominated systems. Anthropogenic disturbance can now be incorporated into ecology in the same way as any natural disturbance, rather than being considered as distracting noise. The incorporation of human activities into ecological investigations is most obvious in the field of conservation biology, but one can predict that the ecology of agricultural systems will also undergo fresh growth in the coming years, as a result of hybrid vigour.

2.5. *Ecology and environmental management*

Pahl-Wostl (1995) has recently summarised the changing situation in ecology and its ability to provide input to environmental management (Table 1). While we do not agree entirely with all of the points raised in her original publication, we do agree with her contention that significant shifts are required in attitudes and expectations of what ecology can deliver, and how environmental risks should be assessed. Of particular note is her suggestion that risks should be measured in terms of the reduction of degrees of freedom for future action; in other words, the extent to which future options are foreclosed.

3. Biodiversity and ecosystem function

After a period of neglect, the question of how biotic diversity and ecosystem function are related is now considered one of the fundamental questions in ecology. The early neglect of this question can be traced to the fragmentation of ecology into distinct branches, most notably with a split between organism-centred population and community approaches and the material flux approach of ecosystem ecology (‘things’ *versus* ‘stuff’: Pickett et al., 1994;

Table 1. Contribution of ecological research to environmental management.

	Current attitude	Required attitude
Research	reduces uncertainties	uncovers uncertainties
	makes quantitative predictions	generates innovative, qualitative knowledge
	provides expert knowledge	engages as partner in a social dialogue
	views nature as a machine	views nature as partner
	is rigid, controlling	is flexible, adaptive
	aims at change towards preconceived goals	fosters evolution, innovative action
Risk assessment		
source	individual phenomenon or process	overall system structure and organisation
risk	undesirable events	restriction of evolutionary potential
measure	probability × damage	decrease in degrees of freedom

Source: Modified from Pahl-Wostl (1995).

Jones and Lawton, 1995). A large international program organised by SCOPE recently examined the question in detail, both from a theoretical point of view and in terms of what we know from examples from a variety of ecosystem types (Schulze and Mooney, 1993; Baskin, 1994; Mooney et al., 1996). The societal relevance of the question has also recently been explored in the context of ‘ecosystem services’ and ‘how the diversity of life sustains us’ (Baskin, 1997; Daily, 1997).

During the course of the SCOPE program, it became apparent how remarkably few data there were with which to assess the question of how biodiversity might affect ecosystem function. For instance, a review of information available for southwestern Australia provided only one study which addressed the question directly, and even then the interpretation was equivocal (Hobbs, 1992; Hobbs et al., 1995). Recently, experimental approaches to the problem have been employed, resulting in data which are widely quoted as indicating a clear link between biodiversity (equal to species number in this context) and elements of ecosystem function (Naeem et al., 1994; Tilman and Downing, 1994; Naeem et al., 1995, 1996; Tilman et al., 1996). However, the validity of the interpretation of results from these experiments has been questioned by Huston (1997), who argues that it is impossible to separate the effects of changing biodiversity from the effects of other ‘hidden treatments’ in the experiments. Tilman’s findings have also been questioned by Aarssen (1997) who suggested that observed differences in function were related more to differences in individual species characteristics than to diversity *per se*.

Ecologists are thus currently in the middle of a flurry of activity surrounding the question of the role of biodiversity in ecosystem function, but are also apparently in a bit of a muddle at the same time. Part of the problem has been a failure to define exactly what question is being asked.

'The ecosystem function of biodiversity' is a ridiculously broad term, and both 'ecosystem function' and 'biodiversity' can be interpreted in numerous ways. Ecosystem function can refer to the primary functions of water, carbon, energy and nutrient cycling, or it can refer to the myriad of processes which go to make up these cycles, including biotic interactions. It can also be interpreted in more utilitarian way to mean 'ecosystem services' for particular human purposes, such as the supply of fresh water, disease prevention etc. Similarly, biodiversity incorporates all levels of biological organisation from genes to landscapes, although it is frequently interpreted simply as 'number of species'. Species can also be grouped in a number of different ways, and attempts are being made to define sensible groupings which have functional significance (Smith and Shugart, 1996; Woodward and Cramer, 1996). Without defining exactly what aspect of ecosystem function one is trying to relate to what element of biodiversity, it is unlikely that useful questions can be asked.

A further problem has been the lack of consideration of the impact of different kinds of species. Although it may seem slightly ridiculous to those participating in this workshop, experimental work has concentrated almost exclusively on the number of species rather than the mix of different types of species. For instance, Tilman's experimental work constructed grassland plant communities by randomly drawing species from a total species pool. Other ecological work on community assembly rules suggests that there may be readily-defined reasons why certain plant assemblages develop in response to particular environmental and biotic factors which act to 'filter' species from the regional species pool (Keddy, 1992; Weiher and Keddy, 1995). It is also clear that individual species vary greatly in terms of their functional importance (e.g. in their quantitative contribution to particular processes), and a variety of terms have been derived for species which strongly influence system structure or function: e.g. 'keystones' (Mills et al., 1993; Paine, 1995; Stone, 1995), 'drivers' (Walker, 1992), and 'ecosystem engineers' (Jones et al., 1994). Huston (1997) questions the assumption that species diversity can be divorced from the effects of species identity. Indeed, the debate needs to focus more on the importance of particular elements of biodiversity rather than the importance of biodiversity *per se*.

An allied question is the degree of functional redundancy inherent in natural communities (Walker, 1992). In practice, however, the perception of redundancy depends on the time scales and functions considered. Apparently functionally-similar species are likely to respond to environmental variation or disturbance differently and hence, may increase the resilience of the system (Main, 1992; Hobbs and Mooney, 1995; Walker, 1995). Functional redundancy thus provides 'fail safe' or 'back up' capacity.

Recent accounts of the relationship between biodiversity and ecosystem function take greater cognisance of these dual questions of the functional significance of particular biotic elements and the importance of functional redundancy in conferring system resilience (Chapin et al., 1997). Future research on these issues will not only provide a better understanding of how systems work, but will also allow assessment of which system components are functionally the most important to system integrity or persistence, and hence which components are essential both to retain in existing ecosystems and to introduce into constructed systems.

4. Relevance to designing agricultural systems

If we are to use natural ecosystems as potential models for agricultural systems, we now ask whether the above considerations have any relevance to the agricultural situation. This question has already been asked recently in a slightly different context by Jordan (1995), who noted that most resource management guidelines were to a large extent empirical and derived from the practical experience of the resource manager. Concomitant with that was the fact that ecological concepts and theory often did not translate into workable guidelines, a proposition also discussed elsewhere (Hobbs, 1998). Jordan (1995) therefore took a recent summary of important ecological ideas (Odum, 1992) and interpreted them in a resource management framework. He produced the following set of statements (slightly modified by us):

1. To develop a sustainable system, we must understand that we are part of the system.
2. To develop a sustainable system, we must analyse the system in which we are embedded. To analyse the system we need a common currency. Energy is one convenient currency with which to analyse a system. Energy flows through all ecosystems and the way it is used and stored determines the characteristics of each ecosystem. Material and information flows are also important.
3. Energy flow through natural ecosystems is not random but is controlled and self-regulated by internal feedback interactions between organisms, or between organisms and the environment.
4. Stability and sustainability of energy flow through ecosystems are enhanced by mutualistic functions. As ecosystems became large and complex, organisms within a natural community evolved towards mutually beneficial functions. Evolution has selected many mutualistic species because of the higher efficiency of the functions they perform.
5. In managed systems, the mutually beneficial functions and natural subsidies that lend stability and sustainability to natural systems are usually destroyed. For this reason, energy subsidies are usually required.
6. The stability and sustainability of a managed system can be maintained (or increased?) by replacing external energy subsidies with the mutually beneficial functions found in nature.
7. The stability and sustainability of all systems may be enhanced by maintaining species and landscape diversity.

8. The transition from non-sustainable to sustainable systems requires time and has a cost.
9. Despite the cost, there is an urgent need to make the transition.

While Jordan recognises that some of the ideas contained in these statements are still controversial and not proven in a strict scientific sense, they encapsulate most of what we wish to say in relation to agricultural systems. Statements 2–5 emphasise the importance of bridging the current gap between natural systems with internal feedbacks and mutualistic interactions, and managed systems that require heavy energy subsidies. Statement 6 implies that the way to do this is to replace lost mutualistic support functions. Important questions to be asked are: which are the most important functions, and which species or sets of species need to be replaced to achieve these? We tend to think mostly in terms of plant diversity (structural and compositional), but soil biota may be at least as important.

Statement 7 suggests that both species diversity and landscape diversity are likely to be important. From the agricultural perspective, the question develops into the vital decision as to whether species diversity must be increased (or better balanced) within individual blocks of land (i.e. increasing alpha diversity), or whether the same effect can be achieved by diversifying between blocks of land. We consider that this is one of the key issues to be addressed, and working out the necessary spatial relationships is vital if we are to make progress.

Statement 8 identifies the important question of the costs of achieving a transition to a sustainable system. An essential element of making the transition will be ensuring that these costs are met in a socially equitable manner.

5. Conclusions: has ecology anything to offer?

We have presented a picture of ecology as a science in transition, moving from one set of paradigms to another and grappling with new sets of questions. The move from description to prediction, although still problematic, is timely in relation to the theme of this book. The other major shift occurring in ecology is the recognition that classical ecologists are no longer simply concerned with the natural bits that are left in nature reserves, but have to consider areas managed for production purposes too. It is often forgotten that many of the major conceptual advances in ecology have come from simplified managed systems, and it is now clear that ecology can make a contribution to redesigning these systems to meet the new challenges they are facing. Having said that, however, it is also clear that ecology has no simple formulae or models available with which to do this. We still do not have a set of rules for the design of a system which will meet specified requirements in terms of its functioning. Nevertheless, the design of agroecosystems is a fertile area for the advancement of ecological understanding; by trying to construct something, we learn more about how it works (Jordan et al., 1987). Using natural systems as a reference point, we can start developing more effective assembly rules and design guidelines. The potential for natural ecosystems to occur in alternative states also allows for optimism that productive agricultural systems can be developed using certain elements or states of the natural system, and that we may be able to chose to mimic the state which best suits our purpose.

In the absence of clear predictive ability, we can still provide guidance which will focus efforts and maximise the likely benefits of these efforts. We suggest that the following steps are required for the development of an agricultural system which replaces external subsidies with mutualistic functions of nature:

1. Identify the system functions which are currently suboptimal in the managed system.
2. Identify the suite of species which carry out these functions in the natural ecosystem.
3. Within this suite of species, identify species with key functional roles.
4. Identify the likely range of environmental conditions and disturbances, and select an array of species needed to confer system resilience.
5. Consider how many of these species are required for the managed system, in the context of trading-off environmental risks *versus* long and short term costs and benefits. For instance, is it essential to install the full suite of species immediately, or can a phased approach be employed?
6. Consider the merits of developing mixtures of these species *versus* placing species in blocks across the landscape (i.e. increasing landscape diversity), or gradations between the two (such as alley cropping). Again, we consider this to be a fundamental issue which has important ramifications for how we frame the overall questions relating to developing mimics.
7. Provide socio-economic instruments which facilitate implementation.
8. Develop systems in an adaptive management framework, with adequate monitoring and the capacity to modify elements of the design.

Points 7 and 8 above are really central to the likely success of any attempts to develop natural systems agriculture. The task is complex and the methods by which to achieve desired outcomes will not always be obvious. Despite considerable rhetoric on the need for adaptive management of ecosystems, ecologists have only rarely attempted to work in an adaptive management framework. We now have the opportunity to do this in agroecosystems, and to put the idea into practice.

Given that natural systems are dynamic and often non-equilibrium, there is no reason to assume that sustainable agricultural systems will be static, or that there will be only one solution. Natural systems provide a multitude of examples of organisms coping with the same set of environmental and biotic constraints and stresses in vastly different ways. We rejoice in nature's diversity, and perhaps one of the best ways to mimic natural ecosystems in agriculture is to facilitate the development of a diversity of responses to today's problems.

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