

A DYNAMICAL APPROACH TO ECOSYSTEM IDENTITY

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INTRODUCTION

Although various kinds of systems thinking have been present in ecology for many years (*e.g.*, [Tansley, 1935; Clements, 1936; Odum, 1983]), systems approaches in ecology have gained increasing prominence in recent times as a tool for the interdisciplinary exploration of complex human interactions with nature (*e.g.*, [Gunder-son and Holling, 2002; Norberg and Cumming, 2008; Waltner-Toews *et al.*, 2008]). Complex systems that are capable of adaptation and learning, such as human societies, are of particular interest. For example, complex adaptive systems with high current relevance for human well-being include such diverse entities as the global climate system; rainforest ecosystems; the economic systems that underlie the banking and housing sectors of the economy; the social dynamics that lead to terrorism; and social-ecological systems that range from local harvesting networks through to global oceanic fisheries.

Despite their diversity, complex adaptive systems are considered to have a number of common properties. They are assembled from diverse components that interact with one another. Complexity evidences itself through system dynamics, which include non-linear relationships between key variables, the presence of local equilibria and thresholds, feedback loops, and the ability to self-organize, learn, and respond actively to environmental change.

Ecosystems are a particular kind of complex adaptive system. They are commonly understood to consist of organisms, an abiotic environment, and a set of interactions that occur between organisms and between organisms and their environment [Tansley, 1935]. Although we focus here on ecosystems, many of the same ideas are more generally relevant to other complex adaptive systems.

The concept of an ecosystem, as summarised above and by Tansley [1935], is deceptively simple. On closer inspection, various practical problems arise with applying this definition. Such problems include questions like (1) ‘Who decides what constitutes an ecosystem, and how does their definition influence the outcome of an ecological or social-ecological analysis?’ (2) ‘What is inside the ecosystem and what is external to it? Where are its boundaries in space and time?’ and (3) ‘How do I know when the ecosystem that I have been observing is in fact a different ecosystem?’

In this chapter we consider these issues from a philosophical perspective, focusing on the need for ecosystem definitions to have a dynamical nature—that is, for our conceptual and empirical models of ecosystems to confront the processes of self-organization and adaptation that allow ecosystems to respond to change. After a brief discussion of the practical implications of ecosystem individuation, we describe the logic of dynamical system individuation and offer some specific observations of how this logic applies to ecosystems in particular. This section is followed by a description of various ecosystem meta-models and strategies for their use. Finally, we draw some general conclusions about how the apparatus we develop can be applied in practice.

1 THE PRACTICAL SIGNIFICANCE OF ECOSYSTEM INDIVIDUATION

Individuation refers to our ability to characterize an individual ecosystem. Before delving deeper into ecosystem individuation, however, we need to address the question, “Why bother?”

The determination of ecosystem identity has various practical consequences that bear on ecosystem sustainability and management, and ultimately (through ecosystem services and livelihoods) to human well-being [Millennium Assessment, 2005]. From a scientific perspective, clear definitions of ecosystems are necessary for comparisons in space and time. This need for comparability extends to both the science of ecology and its practical management applications. On the scientific side, generalities about pattern-process linkages in ecosystems can only be developed if potentially important similarities and differences between individual case studies are clear. For example, the tight relationship between rainfall and tree canopy cover in savanna ecosystems falls away in areas that experience over 700mm of rainfall per annum, creating a threshold beyond which interactions between soil type, herbivores, and fire can be expected to dominate ecosystem dynamics [Sankaran *et al.*, 2008].

On the practical side, spatial and temporal transferability of management models and approaches is contingent on system identity. If systems change in significant ways in space or time, there is no reason to expect that management approaches that have been successful in one place or time will be successful in other places or times. For example, a considerable amount of research on deforestation has been undertaken in the southern and eastern Amazon (*e.g.*, [Nepstad *et al.*, 2006]). As development marches along the TransAmazon highway towards the west, it is unclear whether existing models of deforestation and ecological impacts can simply be transferred from other study contexts, or whether there are aspects of the western Amazonian ecosystems (and social-ecological systems) that differ from those in other regions and could have significant impacts on outcomes. There is also the potential that the mechanisms underlying deforestation have changed in time, for instance through the development of new logging technologies or the implementation and enforcement of new laws, such that principles and data derived from research in the 1990s are no longer relevant to understanding deforestation in the

2010s. These kinds of question cannot be addressed without a clear definition of what constitutes the system and whether, or how, it has changed.

A further implication of ecosystem individuation concerns scale and hierarchies. Cumming *et al.* [2006] have argued that mismatches between the spatial, temporal and functional scales of ecological processes and management can lead to various management problems. Similarly, misunderstandings of the boundaries of an ecosystem or a social-ecological system can result in a narrow focus on optimising the management of a subset of a larger system, potentially leading to various pathologies in natural resource management [Holling and Meffe, 1996]. A dynamical account of ecosystem identity implies a dynamical account of its scale, which can potentially be matched with management processes. If there is a scale mismatch, then the scale-related nature of management problems will be easier to diagnose if a clear definition of system identity has been developed.

Finally, a dynamical account of ecosystem identity is helpful in understanding the nature and limits of ecosystem change. If we know the dynamical identity conditions, which are typically abstract organizational criteria, then we can more readily predict which sort of changes will be within the limits of the dynamical identity conditions and which will not. This allows a better understanding of how human interventions and natural changes like climate change will affect the stability and resilience of ecosystems, allowing better management and possible ameliorative actions, or in the worst case, better predictions of the impacts of human and natural factors. An example of the application of identity criteria to a real-world problem (the impacts of the TransAmazon highway on rainforest social-ecological systems) is presented in Cumming *et al.* [2005].

2 IDENTITY AND INDIVIDUATION OF DYNAMICAL SYSTEMS

Ecosystems are complex adaptive systems [Holland, 1995; Collier and Hooker, 1999] for which complete empirical descriptions are impossible [Rosen, 1991]. Although less systematic approaches exist, the incompleteness of empirical descriptions suggests that a systematic approach to ecosystem individuation is important for delineating analytical problems and strategies.

The difficulty of defining an ecosystem is complicated by the fact that any description of an ecosystem is from the perspective of an observer, and the focus of their description will be on the issues in which they are most interested [Weinberg, 1975; Kay, 2008]. In an era of postmodern science [Funtowicz and Ravetz, 1993], there are good theoretical and practical reasons for questioning whether there are general or specific kinds of models (either in terms of components or processes) that adequately cover all ecosystems, and for thinking that we need model all but the simplest ecosystems with a variety of kinds of models, or meta-models, simultaneously in order to obtain a reliable perspective on ecosystem dynamics and identity [Cumming and Collier, 2005]. Kay [2008] terms this approach “polyocular”, in the sense that our understanding is more complete if we look through a number of different lenses.

Despite the need to entertain multiple perspectives and working models, there are a number of characteristics common to all satisfactory ecosystem meta-models that allow them to be coordinated to give a more complete picture of ecosystem identity in general and of the identity of particular ecosystems. In particular, system identity in general, and ecosystem identity in particular, is most usefully represented in dynamical terms [Collier and Hooker, 1999]. This is because both measurements and interactions with any system are dynamical processes, so a dynamical account of identity allows the account to be applied directly to empirical and practical interactions with the system. The need for a dynamic character is also reflected in the fact that some of the most powerful frameworks for the analysis of complex adaptive systems are process-oriented rather than merely descriptive or structure-oriented (*e.g.*, [Darwin, 1859; MacArthur and Wilson, 1967; Holland, 1995]).

The analysis of ecosystem individuation turns on three primary issues: identity, unity, and cohesion. We next discuss these concepts in detail.

1. Identity

We start with the logical notion of identity [Collier, 2004a; 2004b], since the logical form is required of all satisfactory accounts of identity. It is straightforward, though there is some debate about condition (c), which we will address shortly.

Identity, $A = B$:

- (a) Is a logical condition, same for all things.
- (b) Is an equivalence relation: symmetric, transitive, reflexive.
- (c) $A = B$ implies that B has every property that A has, and vice versa.

This tells us virtually nothing, since it is a purely logical relation, but it does put some logical constraints on any concept of dynamical identity. Condition (a) rules out so-called relative identity, according to which things can be identical in different ways. This notion is awkward, and neither simplifies things nor adds clarity. Condition (b) just says that identity is an equivalence relation. Equivalence relations divide classes of entities into disjoint classes that all share the equivalence relation to each other. Identity is the strongest equivalence relation; its classes all have one member, and every member holds that relation to itself, so $(x)(x = x)$. Condition (c) is the one that distinguishes identity from all other equivalence relations. It says that $(x)(y)(P) (x = y \text{ if and only if } (Px \text{ if and only if } Py))$. Sufficiency, $(x)(y)(P)(x = y \text{ only if } (Px \text{ if and only if } Py))$ is uncontroversial, and is often called Leibniz' Law. Leibniz in fact preferred the stronger version, since he thought there must be some sufficient reason for two objects to differ, and that this could only be in their properties. However his reasoning is controversial. But for dynamical identity if two objects do not differ in their dynamical properties there is no dynamical difference, so they cannot be

distinguished dynamically. Barring nondynamical properties like *haecceity*, or bare otherness, there cannot be two particular distinct dynamical entities that do not differ dynamically. So even if the converse of Leibniz' Law is not true for everything that can be imagined (whatever the limits of that process are), that is irrelevant for dynamical purposes. If there are two objects with the same dynamical properties, then they cannot be distinguished by any interactions we might have with them.

2. Unity

Dynamical objects are typically made of parts held together over space and time by dynamical processes. So the next move is to look at what makes parts of something parts of that thing. This is provided by the unity relation [Perry, 2002]:

Unity is the relation among the parts of a thing A such that:

- (a) If a and b are parts of A , then aUb , and bUa (symmetric).
- (b) If a , b and c are parts of A , then aUb and bUc implies aUc (transitive).
- (c) If a is a part of A , then aUa (reflexive).
- (d) By (a), (b), and (c), U is an equivalence relation.
- (e) $U(A)$ is the closure of U , given any initial part.
- (f) By (a) to (d), $U(A)$ contains all and only the parts of A .

It is an empirical question what satisfies $U(A)$ for a given A . Typically the type of unity relation will depend on the kind of thing A is.

3. Cohesion

For dynamical objects, the parts and their relations must all be dynamical. In previous writing, Collier has called "dynamical unity" cohesion [Collier, 1986; 1988; 2003; 2004a; 2008; in press]:

Cohesion $C(A)$ is the unity relation for dynamical objects, such that:

- (a) All parts aCb are dynamical
- (b) C is dynamical

Cohesion both holds dynamical things together, and also individuates them from other dynamical things. For this reason it can be called it *the dividing glue* [Collier, 2004a]. Any dynamical account of individuation and diversity will be grounded in the formation and disruption of cohesion.

However, there is a lot more to cohesion than its formal definition. Details are spelled out at some length in Collier [2003], much of which derives from as yet unpublished work with C. A. Hooker. We will summarize the main points. First of all, a *dynamical system* is a set of interacting components that is characterized and individuated from other systems by its cohesion. It is therefore a natural object.

Its properties must be discovered, and its models must be tested. We need to have some basic idea of what the object is to begin with, and then we can use the properties of cohesion to sharpen our understanding. There are three ways that have been recognised in the literature on explanation (following [Salmon, 1984]) to explain natural unity. These are:

1. essential properties (natural kinds, archetypes)
2. stable properties (resistance to internal or external perturbations)
3. cohesion (causal relations that make physical wholes out of parts, or create *sine qua non* dependencies).

We can use the first two, or at least intuitions about the first two, to make a preliminary identification, and then use the cohesion concept and empirical investigation to home in on the appropriate properties. Then we can use cohesion to explain the individual essence of the system, and its stability. In a strict part-whole (nested) hierarchy, parts are integrated into wholes, and these wholes are further integrated into larger wholes, and so on. Cohesion increases as we go up to higher hierarchical levels. Things are somewhat more complicated if we have a non-nested hierarchy (such as a food chain, in which cohesion is provided by trophic relationships) or a hierarchy in which lower level members may belong to more than one cohesive higher level. Such systems are sometimes called *heterarchies*. For example, an individual actor in a natural resource management situation may belong simultaneously to a governmental agency, a political party, and a community action group. At higher hierarchical levels, these different memberships may serve to reinforce system cohesion in some circumstances and undermine it in others.

There are other pitfalls with the cohesion concept that must be minded. These can be divided into basic and derived properties (see [Collier, 2003] for more explicit detail). The basic properties derive from the nature of dynamical interactions and the concept of cohesion. B1: *The first basic property of cohesion is that it comes in degrees*. This is a direct consequence of its being grounded in forces and flows, which come in varying kinds, dimensions and strengths. Secondly, and following on from the first property together with the individuating role of cohesion, B2: *cohesion must involve a balance of the intensities of centrifugal and centripetal forces and flows¹ that favours the inward, or centripetal*. This balance is not absolute, but is probabilistic over the dimensions and boundaries of the cohesive entity. Just as there are intensities of forces and flows that must be balanced, there are, due to fluctuations, propensities of forces and flows that show some statistical distribution in space and time (or other relevant dynamical dimensions). B3: *Cohesion must involve a balance of propensities of centrifugal and centripetal forces and flows that favours the inward, or centripetal*. The asymmetry of this balance of tendencies implies a distinction between inner and outer, consistent with the

¹We get the term *centripetal* from [Ulanowicz, 1997, pp. 47–50, 94]. Collier suggested the addition of the converse centrifugal flows and forces; it is implicit in [Ulanowicz, 1997].

role of cohesion in individuating something from its surroundings, but it also plays down rare events and emphasizes more common events (for specific application to ecosystems, see [Ulanowicz, 1997, pp. 47–50 and 94]).

The derived aspects of cohesion now follow from the basic properties as they apply to specific systems with many properties. From B1, only some properties are relevant to cohesion. Thus, A1: *In general, a dynamical system will display a mix of cohesive and non-cohesive properties.* Next, from B2 and B3, A2: *Cohesion is not just the presence of interaction.* Whence, A3: *A property is cohesive only where there is appropriate and sufficient restorative interaction to stabilize it.* From A1 and A4: *Cohesiveness is perturbation-context dependent with system properties varying in their cohesiveness as perturbation kinds and strengths are varied.*

Furthermore, A5: *The cohesive support of nominal system properties may extend across within-system, system-environment and within-environment interactions.* There is no reason to think that a cohesive system must be closed. Rather, A6: *cohesion characterizes all properties, including higher order process properties that are dynamically stabilized against relevant perturbations.* Living systems are primarily characterized in terms of their process organization. Their structures may change, and must change somewhat whenever their adaptability is manifested; the more organized their adaptability, the higher order the cohesive processes that characterize them. Properties A1–A6 are relevant to the discussion of the application of cohesion to ecosystems in the next section.

3 ECOSYSTEM INDIVIDUATION AND CHANGE

There are several definitions of ecosystems that take into consideration their parts and/or their flows. These are the beginnings of dynamical definitions, but are too limited in certain respects. Tansley [1935] defined the ecosystem as ‘the fundamental concept appropriate to the biome considered together with all the effective inorganic factors of its environment’. In a more recent discussion of ecosystem definitions, Pickett and Cadenasso [2002] argue that ‘the main components of the [ecosystem] concept are its abiotic and biotic features and the interactions between them’. They add that although the definition of ecosystems is scale independent, ‘all instances of ecosystems have an explicit spatial extent’. So, Pickett and Cadenasso [2002] effectively argue that an ecosystem is defined by its materials, the relationships among them, and its location.

There are circumstances under which this definition is inappropriate or ambiguous. These problems are of particular importance when developing dynamic models of ecosystems. For example, as the global climate warms, we can expect to see a shifting of the spatial boundaries of ecosystems. If the boundaries of a deciduous forest gradually change until they lie 50 km to the north of its original location, does it remain the same ecosystem? Many ecologists would say that it does, but the ‘explicit spatial extent’ has changed. Or imagine a situation in which a large disturbance hits a particular sub-catchment and the entire flora and fauna of the area is destroyed. Recolonization from neighbouring areas occurs, and a

community develops that has exactly the same species composition and ecological functions as the previous one. Is the new ecosystem the same, or different? Although it might be the same kind in all important respects (*e.g.*, structure, location, components, interactions, functions), we would argue that the new ecosystem is different as an individual because its cohesion has been disrupted. In practice, of course, exact reconstitution of an ecological community would be so unlikely as to be impossible; but the thought experiment nonetheless raises an important point.

These two examples illustrate a particular kind of idea that our current definition of ecosystems fails to capture; that of continuity through space and time as a central component of identity.² In evolutionary biology, a close parallel to ecosystems lies in species concepts. The old definition of immutable species having some essential property or set of properties that could be determined from a single type specimen was gradually transformed as systematists thought through the full implications of Darwin's ideas. Species change over time, making the identification of a species on the basis of a single individual problematic at best (B1 above). The key distinction that led to the formulation of the evolutionary and phylogenetic species concepts was that made by the biologist Michael Ghiselin [1966; 1974; 1987] and the philosopher David Hull [1976; 1978]: species are natural individuals, not natural kinds. They are not like gold or lead, which remain gold and lead and would do so even were it possible to transform one into the other. Species, like ecosystems, are mutable, dynamic things. However, unlike species, which are scattered as both individuals and separate populations, ecosystems are typically localized and spatio-temporally contiguous. The lesson from the Ghiselin-Hull approach to species is that mutable, dynamical entities need not have essential properties that are present in all of their parts, but their identity is a relational property. The problem is to find suitable dynamical relations that determine ecosystem identity by binding the system into one (A3 above). These are the sort of natural properties that we should look for, not localized properties that are found in every part of the ecosystem (A1 above).

Our aim in raising these issues is not to provide a new ecosystem definition, because the appropriate definition in each case is context-dependent (A4 above). The point that we wish to highlight is the lack of temporal competence in most current definitions. We need some guidelines that enable us to say whether or not the same ecosystem exists under a wider range of conditions and possible events than our current definition can cope with. We propose that a reasonable addition would be that ecosystem identity abides in the continued presence, in both space and time, of key components and key relationships, though these may be rather abstract compared to individual organism or even species and their local interactions (A6 above). This perspective on identity permits gradual (and not

²David Wiggins [1967] uses spatio-temporal contiguity as the defining characteristic of identity. This works well for many cases, but it requires many subtle qualifications to deal with things like spatially discontinuous nation states, and spatiotemporally overlapping natural objects that interact with each other only minimally, such as hybridisation zones between sister species.

necessarily linear) change from one kind of system to another, through a series of intermediate stages; but saltationary change will always result in a new system. Just as species can change gradually from one into another, however, ecosystems can also transform and split (and merge, unlike most species).

When an ecosystem definition is applied to a specific instance the temporal component of the system must be dealt with explicitly. If the preceding argument is sound, an adequate working specification of an ecosystem should encompass the following: (1) the ecosystem components, which may be defined in varying degrees of detail; (2) the relationships between ecosystem components; (3) the location and spatial scale at which the definition is applicable, and the importance (or lack of it) of spatial constancy; and (4) the temporal scale at which the definition is applicable, and the author's perspective on the question of identity through time. This final point is essential to the distinctions that we wish to make in the next section of the chapter. These four points are logically related and mutually constraining, so it is not enough to consider the fourth point alone. The relationships among the ecosystem components constrain the types of components that are suitable for maintaining identity. At the same time, the components determine the sort of relations that they can have with each other and still maintain a cohesive system. Unlike designed artefacts, an ecosystem is self-organized; it must emerge naturally from the interactions of its components and its environment, and its very possibility depends on both the nature and the existence of its components. Furthermore, the very notion of an ecosystem component itself depends on the mutual constraints of ecosystem relations and component nature. Although the atoms making up an ecosystem are constituents, they are not really components, since they can vary freely (and typically do) without changing the nature of the ecosystem (point A1). Being a component must be understood in terms of having a relevant role in overall functioning of the ecosystem, not just being there as a constituent of the system. Lastly, the scale and limits of the interactions will determine both the scale and limits of the ecosystem itself, both spatially and temporally, as well as determining the nature of the boundaries of the ecosystem, including how it is nested within larger ecosystems.

Given these points and their consequences, for the purposes of the next section we have adopted the view [Cumming and Collier, 2005] that ecosystems are determined by their main components (abiotic and biotic), the relationships of these components to one another, *and the maintenance of both spatial and temporal continuity* (ecosystems may move in space, and inevitably move in time, but saltation in either instance constitutes a loss of identity).

On this view, an ecosystem is a network of components connected by various relations. Given that the relations are dynamical, they constitute constraints and flows of various kinds, including inputs, outputs, feedbacks, and external constraints. The main problem of ecosystem identity, or unity, is to decide what is internal to the system and what is external. Collier [Collier, 1986; 1988; 2003; Collier and Hooker, 1999] has suggested in other contexts that the best way to decide dynamical unity is to compare the strength of internal relations among components

with those of external relations. This not always possible, since the relations come in degrees (B1), and vary in kind. Furthermore, only some of the relations are relevant to system unity. Which these are is an empirical issue, and varies for each type of dynamical system. Another approach to assessing dynamical unity is through the three different lenses of asymmetries, networks, and information processing [Norberg and Cumming, 2008]; relations between components in the same system may be easier to clarify if one explores whether they share membership in a hierarchy, whether they are connected via some kind of network, and whether they contribute to information processing and/or systemic responses. Individuation of different types of ecosystems may require focusing on different kinds of relations; however, as we suggested in the last paragraph, all relationships that are included in the definition should have a role in the overall functioning of the system. The closure of such relations determines the dynamical unity of the system.

This closure is typically going to be immensely complex, and simplifications will be needed. Ulanowicz [1986] developed a network account that relies on the strength of flows of carbon, reasoning that carbon flows are a good stand-in for species interactions, though they don't directly capture behavioural interactions that may be important to ecosystem unity. Nonetheless, he was able to create workable models of trophic relations for complex estuary ecosystems using this model, as well as to come up with a measure of connectedness and ecosystem health based on a mutual information that could calculate the degree of connectedness (at least by way of carbon flows). It should be noted, though, that the sort of closure required for ecosystem identity is not complete; there can be, and will be, flows into and out of the ecosystem, at the very least sunlight and water, but also typically organism migration both in and out, and the flushing of wastes (point A5). Ecosystems are not like organisms, since they are not actively self-regulatory, but they are not mere collections of interacting things either. They depend for their continued existence on predictable interactions both within the system and without, and the latter may depend on predictable supporting processes within larger ecosystems.

The complexity of ecosystems, with their openness and nonlinear dynamical interactions, shows complexly organized behaviour (*sensu* [Collier and Hooker, 1999]). This in itself is not a problem for studies in many cases, in which we can segment and focus on specific issues, but it becomes an issue if we are interested in whole ecosystem function. Even where specific issues like predator-prey relations are studied, it is well known that they can show highly unpredictable behaviour (*e.g.*, [Barkai and McQuaid, 1988]). It is well known now that complex dynamical systems are emergent from their components and their local relations. Specifically, they cannot be circumscribed by single closed models. Rosen [1991] explains this in detail, in full logical form, though he identifies such systems with living systems, which is probably not correct, since complexly organized systems are found in physics (*e.g.*, [Bénard cells; Chandrasekhar, 1961]), and ecosystems cannot be said to be alive in anything like the sense in which organisms are alive. His argument that complexly organized systems cannot be reduced to the local

interactions of their components or to input-output relations is sound, however. It is a direct consequence that no single model can mathematically capture all the possible behaviour of such a system. This means that more open models will be required, and typically more than one (and even then we can't get a fully circumscribed combination of models). The reasoning follows from the nature of complex dynamical systems, especially self-organizing ones, and issues in logic stemming from Gödel and Turing. It becomes somewhat of a pragmatic issue which models to use. For that reason it is useful to have a set of kinds of models available to use and guide empirical work.

4 ECOSYSTEM META-MODELS

The reason why there are so few truly general ecosystem models is undoubtedly the irreducible complexity of ecosystems.³ At the heart of cohesive models of ecosystems are a few extremely complex issues. Ecosystems are dynamic entities that span multiple spatial and temporal scales; the distinction between endogenous and exogenous dynamics is not always clear; and because of their many components, the outcome of manipulations on the system may differ depending on relatively small differences in starting conditions.

Despite these complexities, however, ecology has made some progress towards developing a more general framework for understanding ecosystems. The many specific models of ecosystems together with accumulating empirical evidence have begun to produce a few more general models that incorporate and summarize the findings of many specific models. Such models are a step back from the immediate process of prediction; they are simple, often tantalizing statements that hint at an underlying order to the workings of the world. Their value comes from the way in which they somehow capture the essential ingredients of many interrelated models in symbolic form. Consequently, we term them 'meta-models'.⁴

Meta-models are not hypotheses in the commonly-used sense. They are not necessarily rigorous quantitative statements, although they must be supported by rigorous quantitative studies. Indeed, they are more a kind of specific metaphor; a way of thinking about things that serves as a powerful tool for the generation of specific hypotheses in specific cases. In this respect they are more like Kuhnian paradigms, or Lakatosian research programmes. Their value is measured more in terms of their impacts and their usefulness than their immediate scientific testabil-

³However, general models that deal solely with complexity issues and their consequences can be very general. Robert Ulanowicz [1986; 1997] has used such models to explain very general features of ecosystems that can be applied powerfully to draw conclusions about the growth and development of ecosystems and the stability of specific ecosystems such as Chesapeake Bay and the Baltic Sea. These models, however, require a wealth of specific information about flows throughout the ecosystem, and cannot be constructed directly from individual trophic relations and resource and waste flows.

⁴There is a more detailed discussion of the meta-models in [Cumming and Collier, 2005], along with helpful animated diagrams and a comparative table in the .pdf version. The discussion here follows that discussion.

ity. However, although they have that certain vagueness that is bred of generality, meta-models must be clearly and unambiguously defined. They are not models of specific systems; but at the same time they are not as broad as the ‘world views’ or paradigms outlined by Holling and Gunderson [2002]. Again, although they are less explicit than the ‘ecosystem models’ discussed by Pickett and Cadenasso [2002], they are considerably less vague than their ‘ecosystem metaphors’. Recognition of the strengths and weaknesses of our own meta-models, and consideration of alternative meta-models, should serve a useful purpose in refining concepts and highlighting the key distinctions between them.

Holling’s *adaptive cycle* [Holling, 1986; 1987; 2001; Holling and Gunderson, 2002] is one of the few well-defined, well-supported interpretations of ecosystem dynamics. The behaviour of systems of a certain kind has been shown to closely match the adaptive cycle. Because it seems to fit many ecological and social systems, and few or no counter-examples have been described, the adaptive cycle has been criticized for being too broad. Few critics have appreciated that the adaptive cycle is really a meta-model; a broader class of model that encapsulates the key dynamics of numerous other models.⁵ We have argued firstly that there are other meta-models of ecosystem function; and secondly, that these meta-models should not be expected to pick out the same aspects of system dynamics as the adaptive cycle, because they are models of a fundamentally different kind. Evaluation of the adaptive cycle has yet to move beyond systems or models that have essentially the same dynamics as the models from which the meta-model was constructed; from this comes the illusion that the adaptive cycle explains everything. By defining rigorously the properties that are expected of systems that match different kinds of meta-model, we can move a step closer to understanding what the central ingredients of particular system behaviours are and develop an improved appreciation of their commonalities and differences. Furthermore, the various meta-models give us a set of tools to use when it is unlikely that one meta-model, even one as successful as the adaptive cycle, will be complete.

The adaptive cycle is defined by phases that follow one another sequentially. These can be summarized as resource accumulation; resource release followed immediately by system reorganization and reconfiguration; and re-entry into an accumulation trajectory. It is a meta-model of a continuous dynamic process, in which complex interactions between system components result in a long, slow build-up that contains the seeds of its own subsequent collapse. Other essential ingredients of the adaptive cycle meta-model include a focus on the role of endogenous dynamics; a view of systems as continuous entities in both space and time; and an emphasis on periodic reorganization, through endogenous or exogeneous drivers.

Although the adaptive cycle offers a persuasive approach to characterizing and understanding ecosystem dynamics, it is only one of a set of possible meta-models that might explain or clarify different aspects of ecosystem function. We propose that further attempts to develop, refine and examine alternative meta-models will

⁵See Ulanowicz [1997] for an explanation of Holling’s adaptive cycles that is compatible with the context of this chapter.

help us to make further progress in ecosystem ecology. To find exceptions, we must look for systems that are discontinuous; that exhibit few or no relevant internal dynamics or are continuously overwhelmed by external forces; and that have little or no self-organizational ability or 'adaptive capacity'. In the next section we consider some candidates for alternative meta-models that may explain different kinds of ecological phenomena. Some of the most interesting alternative meta-models for complex systems may be those that mirror many of the dynamics of the adaptive cycle but can be distinguished from it in one or more crucial ways.

Alternative meta-models will be relevant wherever a system is in clear violation of one of the central features of the adaptive cycle. We use a strict definition of the adaptive cycle, believing that it is only through making the details of each meta-model clear and explicit that we will be able to progress towards a consistent framework. Continuous modification of the adaptive cycle to encapsulate all possible ecosystem dynamics is neither useful nor desirable.

1. Random walk

The most obvious alternative meta-model is encapsulated in unpredictability. Under this model, ecosystems wander randomly through a multivariate space. Their dynamics and components would undergo continuous, stochastic changes at irregular intervals of time. There is no cycling, and no particular regularity in system properties. This model is primarily a null hypothesis that exists to be disproven, and has been disproven in many cases. Nonetheless, it is worth stating explicitly because it is a null model against which other models must be contrasted; alternative meta-models must encapsulate some form of order or repetition. A topical example of a largely stochastic ecological process is that of the location and timing of species invasions [May, 1976]. These can act as profound constraints on adaptive cycles, changing the dynamics beyond recognition.

2. Replacement

The adaptive cycle is not an appropriate meta-model for systems that lose their continuous identity in either space or time. Such systems may follow after one another, be similar to one another, and occur in the same location as one another; but they are not true examples of a single system that undergoes a periodic cycle of growth and reorganization. Replacement may occur with a predictable or semi-predictable frequency, and may be weakly reinforced by internal dynamics. These characteristics make it distinct from a purely stochastic meta-model. Nonetheless, cohesion criteria require that the old and new systems are not the same ecosystem.

An example of a biological system that fits a replacement meta-model better than it fits an adaptive cycle meta-model is that of a lotic (flowing water) ecosystem. The quantity of water flowing in a stream is largely an exogenous property of the system. Following a severe flood, sediments are rearranged and many organisms are swept away. The community that remains or is reconstituted after the disturbance is a combination of legacies ('ecological

memory') from the previous community, plus new colonizers. There may be profound changes in the components from which the system is constructed and their relationships to one another. According to the continuity criterion, what remains is a different system. There is no fundamental dynamic of reorganisation, no return to the previous trajectory, and no obvious accumulation of 'capital' (in the sense that forests accumulate wood or companies accumulate money) between disturbance events. The system is dynamic, but the adaptive cycle does not offer an adequate summary of it. Obviously, at smaller scales, alternative kinds of system dynamic (including the adaptive cycle) may be possible.

Systems in which substantial legacies are left after disturbances fall into a grey area between replacement and reorganization. The ends of the continuum (disturbances leave no legacy, or disturbances leave a legacy of the entire system) are easy to classify as instances of replacement or the adaptive cycle respectively. At locations mid-way between these two extremes, there is no simple answer. The solution will depend on the proportion of the subsequent biotic community that is endogenous, the extent to which the abiotic environment was altered by the disturbance, and the degree to which biotic interactions in the new ecosystem have changed. Of course the cohesion criterion of ecosystem identity implies that there will be intermediate cases, just as there are intermediate cases between species.

3. Succession

The adaptive cycle uses the older meta-model of succession as its fundamental dynamic. Holling's important insight was to recognize the process of reorganization that occurs between successional events as an integral part of ecosystems, and to make it explicit; a natural extension of successional theory. Any system that does not undergo both succession and a subsequent reorganization phase of some kind does not fit the adaptive cycle meta-model.

As a thought experiment, imagine that through careful management, a system could be kept in the ' r to k ' phase of the adaptive cycle indefinitely. Next, imagine that the manager could gradually remove his or her influence by developing the self-organizational capacity of the system. And finally, imagine that the manager could completely withdraw and leave the system perpetually stuck in the r to k phase. To argue that this situation is only possible by maintenance of adaptive cycles at a smaller scale is to miss the point. The point is that such a system, if it existed, would fit the successional meta-model better than it does the adaptive cycle. Decades of work have shown that few or no real-world systems fall into this category [Holling and Meffe, 1996]; but without these rigorous tests of real-world dynamics, we would not be able to dismiss the successional meta-model so readily. This sort of model implies a much higher degree of regulation than is typically found in natural ecologies, and is more typical of that found in organisms. The existence of self-regulating systems suggests that the succession model

is not impossible.

4. Dynamic limitation

Another potential meta-model is encapsulated in the idea that ecosystems are constrained by external drivers. This can be visualized as a case in which the ecological system dynamics leading to growth and expansion, for example, are constantly pushing against external limits. As the system boundaries change along any of the multiple axes that pertain (such as in space, substrate or temperature), components of the ecosystem either go extinct or expand to exploit the full plausible state space. In this meta-model there is no accumulation or reorganization, and cycling is not a necessary condition; limitation comprises a set of forward and backward movements as if between two dance partners, with an occasional 'explosion' or release when constraints are removed.

The process of dynamic limitation is also distinct from the replacement model. The internal dynamics of the system will depend heavily on ecological processes, and there is no reason why the endogenous or finer-grained exogenous dynamics should not follow the adaptive cycle meta-model, but the dynamic limitation model is applied at a broader scale than this. Dynamic limitation is primarily a boundary condition, not a system-wide driver. Changes in limitation do not produce an entirely new system; there is no obvious replacement event, except possibly through some kind of accumulation of small changes. In this meta-model, exogenous drivers 'tinker' with some of the pieces of the system, and endogenous variation occurs at such a fine scale that it is largely irrelevant.

5. System Evolution

The theory of evolution provides us with another example of a meta-model, and has been criticized in a similar fashion ('it's not falsifiable') to the adaptive cycle. Holling and Gunderson [2002] incorporate 'nature resilient' within a world view of 'nature evolving', suggesting perhaps that they see the adaptive cycle as one member of a subset of evolutionary meta-models.

In the strict sense, it is not obvious that ecosystems can be said to evolve. Darwinian evolution implies a mechanism by which variations are generated and selection removes individuals that are poorly suited to current conditions. Although there may be ecological parallels to anagenesis, cladogenesis at an ecosystem level would be difficult to demonstrate. Applying the assumptions of a rigid evolutionary meta-model of adaptation to entire ecosystems leads inevitably to the murky arena of group selection. Since many ecosystems are unique, and there is little opportunity for one ecosystem to displace another (anthropogenic impacts aside), it seems that the evolutionary meta-model is not relevant in this context. Rather than dilute the clear insights of Darwin's theory by applying it outside its original context, it seems wiser to capture change in ecosystems using other conceptual frameworks.

However, selection with cladogenesis is not the only way to get directed change. Ulanowicz [1997] argues that ecosystems have a tendency to increase *ascendency*, which he defines as the product of the total system throughput (analogous to the economic GDP) and the average mutual information of the trophic network. The limiting factor is the overhead, or manoeuvring room resulting from endogenous and exogenous factors. One limit is too much diversity, which leads to collapse of the system, but if this can be managed, gradual increases in ascendency are possible, leading to a version of the succession model.

We have focused here on the adaptive cycle and a set of meta-models of ecosystems that offer alternatives to the same kind of dynamic description. It is important to note that a wide variety of other kinds of dynamic meta-model (many of which are quite different from the adaptive cycle in their framing and intent) have been published for complex adaptive systems. For example, Kay and Boyle [2008] present a model that uses thermodynamic principles and ideas about dissipation and exergy to set the stage for self-organization in social-ecological systems; and Holland [1995] focused on agency and adaptation as central processes in the development of complexity from simpler building blocks. These different views lead to different kinds of insight into system individuation, and together with other examples, demonstrate how the consideration of multiple meta-models can be useful for understanding ecosystem processes.

5 CONCLUSIONS

The issue of ecosystem individuation is of both theoretical and practical importance. Ecosystems are dynamical systems, so a dynamical account of ecosystem is more appropriate than a static definition. Dynamical definitions are also more useful if we want to study ecosystem change and the possible limits of that change. A dynamical account is especially useful for ecosystem management and intervention, since, aside from the issue of matching management scale with ecosystem scale, these are dynamical interactions themselves, and their dynamics must be incorporated into the existing ecosystem dynamics. Because ecosystems are typically complexly organized, and thus not subject to one grand model, it is useful to develop a number of working models that can be applied in specific cases as appropriate. In many cases more than one model or meta-model will apply, and different models can be used to constrain each other, especially in cases where ecosystems skirt the borders of specific meta-models.

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