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Review

How might we model an ecosystem?

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ABSTRACT

Predicting ecosystem effects is of crucial importance in a world at threat from natural and human-mediated change. Here we propose an ecologically defensible representation of an ecosystem that facilitates predictive modelling. The representation has its roots in the early trophic and energetic theory of ecosystem dynamics and more recent functional ecology and network theory. Using the arable ecosystem of the UK as an example, we show that the representation allows simplification from the many interacting plant and invertebrate species, typically present in arable fields, to a more tractable number of trophic-functional types. Our compound hypothesis is that "trophic-functional types of plants and invertebrates can be used to explain the structure, diversity and dynamics of arable ecosystems". The trophic-functional types act as containers for individuals, within an individual-based model, sharing similar trophic behaviour and traits of biomass transformation. Biomass, or energy, flows between the types and this allows the key ecological properties of individual abundance and body mass, at each trophic height, to be followed through simulations. Our preliminary simulation results suggest that the model shows great promise. The simulation output for simple ecosystems, populated with realistic parameter values, is consistent with current laboratory observations and provides exciting indications that it could reproduce field scale phenomena. The model also produces output that links the individual, population and community scales, and may be analysed and tested using community, network (food web) and population dynamic theory. We show that we can include management effects, as perturbations to parameter values, for modelling the effects of change and indicating management responses to change. This model will require robust analysis, testing and validation, and we discuss how we will achieve this in the future.

Contents

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1. Introduction

Predicting or forecasting the responses of ecosystems is of considerable interest in a world under threat of human-mediated change. Predictive models could guide the identification of strategies for the mitigation of, and adaptation to, the effects of change on ecosystems. Such models might also be used to suggest management that would yield ecosystems with desirable properties, such as high productivity, or that have particular beneficial functions, such as elevated pollination or natural enemy activity. Probably the most important use for predictive ecosystem models is the analysis of trade-offs with change. Questions such as, 'Is it possible to increase crop yield while maintaining biodiversity?' might be investigated by the model, particularly where there are concerns that increasing productivity has led to loss of biodiversity. Ecosystem models would necessarily incorporate the important biological processes that structure ecosystems and drive their diversity and dynamics, and thus also be of great scientific interest.

Our concept of an ecosystem is similar to that of Odum (1971), and builds on earlier theories of trophic–dynamics in ecosystem ecology (Lindeman, 1942). The *ecological system* consists of a unit of all organisms in a given area interacting with one another and the physical environment so that a flow of energy leads to biotic diversity and dynamic. In principle, ecosystems can be modelled using existing methods that explicitly model interactions between species. However, there may be many hundreds of species to model, in the ecosystem, and potentially many more interactions. Such complexity would likely be prohibitive for the construction of ecosystem models. The models would be mathematically and computationally intractable. Even if such a species model were produced it would take a period of analysis approaching that of the analysis of observed ecosystem data. Indeed, in the nearly 75 or so years since the term 'ecosystem' was conceived by Roy Clapham (Willis, 1997) and discussed by Tansley (1935), we are still trying to analyse and understand these complex systems of species.

Translating ecosystems into models is a problem of appropriate representation and simplification. The representation we adopt here is one frequently used in functional ecology (Loreau et al., 2001), and we hypothesise that it will achieve a scientifically valid, ecological representation of important ecosystem processes. Functional ecology focuses on 'process rather than property' (Calow, 1987). By concentrating on processes, one looks at what drives the ecosystem dynamics; whereas species models only look at specific parts of ecosystems. Following this approach, one can investigate the effect of human activities and environmental changes on the functions of the ecosystem (Dyer et al., 2001; Pakeman, 2004; Liira et al., 2008). Potentially, functional ecology provides a simplification that is mathematically and computationally tractable. Furthermore, a functional model would enable us to build and test theories about the processes that drive ecosystems.

Functional ecological approaches have successfully described and been used to analyse a wide range of ecosystems (McGill et al., 2006) such as grasslands (Pakeman, 2004; Schaffers et al., 2008; Lavorel et al., 2008), arable farmlands (Lavorel et al., 1999; Hawes et al., 2009; Liira et al., 2008) and tropical forests (Slade et al., 2007; Delcamp et al., 2008; Deng et al., 2008; Aguirre and Dirzo, 2008). The functional ecology approach can arguably give a better description of the ecosystem than the analysis of pairwise species interactions that is more commonly used in ecology (McGill et al., 2006). However, although the concept of functional ecology is transferable from one ecosystem to the next, functional traits are typically identified and defined for each ecosystem. For instance, it is unlikely that functional traits defined for an aquatic ecosystem would be applicable to a terrestrial ecosystem. The location of each system (McKie et al., 2008) and the methodology for defining functional traits are important (Lavorel et al., 2008).

In this paper we argue for a novel method of modelling an ecosystem using a functional trait approach, and outline a model based on this concept. We try to achieve the maximum level of simplification that captures the diversity and dynamics that have been measured in real systems and those discussed in the literature. We believe that the simplifications and methodology we follow to make a model of an ecosystem are ecologically defensible. We do not attempt to cover all the ecosystem literature or even the ecosystem modelling done to date. Rather, we limit our discussion of the literature to fields directly relevant to the components of our compound hypotheses. The functional ecology approach we advocate is based upon the feeding, or trophic, interactions (or 'processes' sensu Calow (1987)) that occur between organisms residing within an ecosystem, and we explicitly model the 'flow' of biomass (energy) between different feeding groups. Potentially, this 'flow' is generic and therefore could be applied to any ecosystem. Here, though, we describe the construction of a model parameterised for the arable farmland ecosystem of the UK in order to test our view that "trophic-functional typing can explain the structure, diversity and dynamics of arable ecosystems."