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Spatial modelling of succession-disturbance dynamics in forest ecosystems: Concepts and examples

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Abstract

Over the last few decades it has become increasingly obvious that disturbance, whether natural or anthropogenic in origin, is ubiquitous in ecosystems. Disturbance-related processes are now considered to be important determinants of the composition, structure and function of ecological systems. However, because disturbance and succession processes occur across a wide range of spatio-temporal scales their empirical investigation is difficult. To counter these difficulties much use has been made of spatial modelling to explore the response of ecological systems to disturbance(s) occurring at spatial scales from the individual to the landscape and above, and temporal scales from minutes to centuries. Here we consider such models by contrasting two alternative motivations for their development and use: prediction and exploration, with a focus on forested ecosystems. We consider the two approaches to be complementary rather than competing. Predictive modelling aims to combine knowledge (understanding and data) with the goal of predicting system dynamics; conversely, exploratory models focus on developing understanding in systems where uncertainty is high. Examples of exploratory modelling include model-based explorations of generic issues of criticality in ecological systems, whereas predictive models tend to be more heavily data-driven (e.g. species distribution models). By considering predictive and exploratory modelling alongside each other, we aim to illustrate the range of methods used to model succession and disturbance dynamics and the challenges involved in the model-building and evaluation processes in this arena.

Keywords: Succession; Disturbance; Vegetation dynamics; Spatial models; Model evaluation; Model analysis

Introduction

What and why?

Since Henry Chandler Cowles described vegetation change in the Indiana dune fields of Lake Michigan (Cowles, 1899), succession and disturbance have been dominant themes in ecology (McIntosh, 1999). In the first half of the twentieth-century ecology's focus on equilibrial conditions saw disturbance as atypical (building on the climax theory espoused by Clements and followers), before a shift to a more disequilibrial perspective, which emphasises the crucial role that disturbance plays in ecosystems, occurred (Wu and Loucks, 1995; Perry, 2002). Paralleling this shift was a move toward a spatially explicit view of ecological

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systems. On one hand, these changes in perspective have resulted in increased consideration of the interactions between ecological pattern and process in large spatially heterogeneous systems (the landscape ecology approach – Turner, 2005) while on the other it has led to increasing focus on fine-scale spatio-temporal interactions within plant populations and communities (the 'plant's-eye view' – Stoll and Weiner, 2000); our focus here is largely on the former.

Various model-based methodologies have been employed to unravel the ecological implications of spatial heterogeneity and disturbance, including: (i) 'classical' mathematical models, (ii) statistical–empirical models, and (iii) mechanistically rich simulation models. 'Classical' ecological models, such as the Lotka–Volterra system, adopt a mean-field approach in which all organisms are identical and interact with each other and the environment equally (i.e. they see a homogeneous average of the system); typically such models are also deterministic. While these 'classical' models remain important in theoretical ecology, recent simulation models of succession-disturbance dynamics are often spatially explicit and incorporate stochastic events (Perry and Enright, 2006; Scheller and Mladenoff, 2007). These simulation models operate at scales from small plots, typically $\approx$ 1–10 ha as in the 'gap models' derived from JABOWA and FORET (see Bugmann, 2001), to tens of thousands of hectares (or more) as in spatially explicit landscape models (SELMs) such as LANDIS (see Mladenoff, 2004). However, and irrespective of the spatial scale they consider, such representationally rich models usually lack tractability, and comparing them with analytical models highlights the 'realism-tractability' trade-off that plagues ecological modelling.

Challenging issues

The challenges involved in spatial modelling of ecological dynamics are many, but they can be distilled to those relating to *scaling*, *representation*, and *model evaluation* (Green et al., 2005; Perry and Enright, 2006; Scheller and Mladenoff, 2007). Understanding forest succession necessitates integrating processes operating from the instantaneous (e.g. photosynthesis) to the generational (e.g. tree longevity). Likewise the temporal grains of disturbance processes span seconds (e.g. the physico-chemical processes that explain fire behaviour) to centuries (e.g. soil changes, nutrient fluxes and decomposition). Representing all of these processes in a single model is difficult – it is possible to represent fine-grained patterns over small extents or, conversely, coarse(r) patterns over large extents, but not both. Given that incorporating all scales within a single model is problematic, and likely not desirable, trade-offs in the way in which processes are represented are inevitable – this 'dilemma of representation' is the key challenge for effective ecological model building. Trade-offs in representation often hinge on how much mechanism is included in a given model. For example, if we consider seed dispersal, is a mechanistic approach, in which every propagule and its subsequent dispersal as a function of meteorological processes is represented, required? Or is a phenomenological approach, in which the relationship between distance from parent and seed rain fraction received is described by some probability function, more appropriate? While implementing a mechanistic model may be feasible at fine grains and small extents, at larger extents phenomenological alternatives are more likely to be appropriate (and computationally feasible) (Nathan and Muller-Landau, 2000). The issues of scale and representation are inextricably intertwined and lie at the heart of adequate model conceptualisation.

Representing disturbance dynamics becomes even more challenging if we consider human activity. Humans can (i) rescale the disturbance regime by altering the frequency, size and severity of disturbance events (e.g. Hansen et al., 2005, discuss changes to fire and flood regimes in exurban landscapes) and/or (ii) introduce novel disturbances, such as pathogens, to ecosystems (e.g. Jules et al., 2002 discuss movement of pathogens by humans across and between watersheds). While ecology has traditionally focused on 'natural' or 'unmodified' systems (Liu, 2001), more and more research is focusing on human-driven change in ecosystems; this is especially important in places such as the Mediterranean basin where landscape patterns reflect long periods of human occupation and use, and are cultural as much as ecological (Blondel and Aronson, 1999).

Having implemented any model the next challenge lies in analysing and evaluating it (Gardner and Urban, 2003). While there are well-established tools for analysing deterministic 'classical' ecological models, a framework for analysing stochastic spatial models is comparatively much less developed. A first problem lies in the data requirements of such analyses (lack of empirical data is often a primary motivation for the development of ecological models – Urban et al., 1999). Second, stochastic models pose challenges for analysis that deterministic ones do not; they necessitate adopting a probabilistic approach and may require sophisticated strategies for their analysis (e.g. Monte Carlo and stochastic geostatistical methods). Finally, the tools available for model analysis tend to focus on time (e.g. comparison of observed and predicted time series – Mayer and Butler, 1993) rather than on space; there is a paucity of methods for direct comparison of spatial patterns or predictions. The lack of a comprehensive analytical framework for stochastic, spatially explicit simulation models has hampered their effective application – in response to this, 'new' evaluation frameworks