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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 ≈ 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 such as pattern-oriented modelling have been developed and advocated (Wiegand et al., 2003; Grimm et al., 2005).

Two contrasting perspectives

We have chosen to classify models **not** on methodological grounds but on the basis of the purpose for which they are employed; we consider two broad approaches to model implementation and analysis:

1. models designed and implemented with the primary purpose of effective prediction of the future dynamics of a system, rather than exploring its underlying causality; we term this 'predictive' modelling
2. models designed and implemented to gain insight about how and why the system of interest behaves as it does, rather than making explicit predictions; we term this 'exploratory' or 'heuristic' modelling.[1]

While this division represents a somewhat artificial dichotomy (Table 1), considering models and modelling along these lines helps to elucidate some of the similarities and differences in the ways that broad-scale vegetation change has been modelled. Furthermore, there are obvious synergies between the approaches; for example: (i) successful prediction can improve understanding and vice versa, (ii) process-based predictive modelling is often preceded by exploratory modelling and (iii) exploratory modelling can help to ascertain where predictive modelling may not even be appropriate or possible (Bankes, 1993; Brown et al., 2006). Similar classifications are discussed elsewhere in the ecological modelling literature; Loehle (1983) discriminates between predictive and theoretical models, Bankes (1993) between confirmatory and exploratory modelling, Gross and Strand (2000) between predictive, explanatory and heuristic models, and Oreskes (1998) between question- and answer-driven approaches. Pielke Jr. (2003) argues that clear statement of the *motivation* of a modelling exercise (exploration or prediction) is fundamental to the effective use of models. In terms of the data-understanding space (Fig. 1) in which ecological models are often placed, although exploratory modelling tends to occur where the availability of data describing the system and understanding of the system are both low (i.e. epistemic uncertainty is high), predictive modelling, while requiring descriptive data, does not assume causal understanding (i.e. epistemic uncertainty may or may not be high).

While our primary focus is the spatial facet of modelling vegetation dynamics, it would be remiss to completely ignore the *temporal* nature of successional change! In empirical–statistical models the focus is more usually on the endpoint of succession or the nature of the system at some point in the future, and the trajectory that the system has taken to reach that point is of less concern. Conversely, in dynamic spatial simulation models time *is* a primary concern, and a given model's outputs will typically consist of a time series of maps (spatial) or of vegetation abundance (non-spatial). Adding a temporal dimension to the analysis of spatial outputs is difficult; there are few tools for evaluating time-series of categorical maps, for instance. Nevertheless, in conceptualising the long-term dynamics of (forest) ecosystems the path taken to reach some system state may be as important to elucidate as the endpoint itself – this is especially the case if we taken the view that such systems are likely to be non-linear and show contingency-type behaviours.

Table 1. Some hallmarks of the predictive vs. exploratory approaches to ecological modelling

Predictive	Exploratory
• Reasonable system understanding and/or data	• Limited system understanding and/or data
• May or may not explicitly include mechanism	• Focus on elucidating mechanism
• Primary focus *usually* prediction	• Primary focus *usually* heuristic
• Model vs. data 'confrontation' approach to model analysis	• 'Experimental' approach to model analysis
• Answer-driven/focussed	• Question-driven/focussed

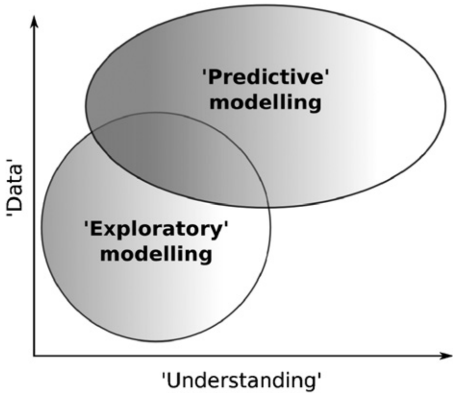

Fig. 1. Position of exploratory and predictive modelling in a hypothetical data-understanding space (after Starfield and Beloch, 1986); by data we mean the *amount* of information available to describe the system and its dynamics and by understanding we mean the level of process (causal) comprehension of the system and its dynamics that we possess.

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[1] According to the OED (2nd edition), heuristic means "serving to find or discover", a definition which we believe perfectly captures the essence of this approach to modelling.

Finally, we do not intend that this paper be seen as an exhaustive review of the state-of-the-art in modelling succession-disturbance dynamics.[2] Recent reviews of spatial models of vegetation dynamics have considered, in some depth, the conceptual and methodological underpinnings of frameworks including species distribution models (e.g. Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005; Heikkinen et al., 2006), individual-based 'gap' models (e.g. Bugmann, 2001; Shugart, 2002; Busing and Mailly, 2004), spatially explicit models of plant population and community dynamics (e.g. Czárán, 1997; Jeltsch and Moloney, 2002; Herben and Hara, 2003), large-scale spatial landscape models (e.g. Keane et al., 2004; Mladenoff, 2004; Perry and Enright, 2006; Scheller and Mladenoff, 2007) and applications of spatial models for management and monitoring (Turner et al., 1995, 2002; Hobbs and Lambeck, 2002). Together these contributions provide the interested reader with a thorough overview of this large and growing literature as well as numerous examples of model applications. The examples we consider here are intended as *illustrative*, rather than exhaustive, examples (see Table 2) and span a range of (primarily) forest ecosystems.

'Predictive' modelling

Modelling with the explicit goal of predicting the (specific) dynamics of a (specific) system is, arguably, closest to what most non-modellers envisage modelling as an intellectual activity to be; indeed, in many of the 'hard' sciences prediction *is* the primary purpose of modelling. While the usual view of prediction may imply possession of both data and understanding, this is not necessarily the case – predictive modelling can successfully proceed without causal understanding. Indeed in ecology this is often the case, especially as technologies such as remote-sensing provide ever increasing amounts of multi-temporal spatial data (Kerr and Ostrovsky, 2003). As Fig. 1 shows 'predictive modelling' spans the entirety of the understanding-axis (the x-axis); this emphasises how persuasive accurate predictions are when forwarding a theory to explain a phenomenon, although it is important to bear in mind that accurate predictions can be made for the 'wrong' reasons. There are many approaches to developing predictive ecological models; here we will focus on three that have been widely applied in the prediction of vegetation dynamics: (i) empirical–statistical (e.g. regression) models, (ii) transition matrix models and (iii) forest gap models.

Empirical–statistical models

Empirical–statistical models (such as regression-type approaches) epitomise the predictive modelling approach. A typical regression modelling framework involves collecting data, dividing those data into training and testing sets, parameterising the model (i.e. estimation of model coefficients) and then testing its predictive power via a variety of well-established statistical methods such as measures of explained variance or deviance, log-likelihood ratios, ROC curves, etc. (e.g. Mac Nally, 2000) In the context of succession and disturbance, regression models are often non-spatial,[3] temporally static (i.e. they assume stationarity) and focus on final outcomes rather than trajectories of change. One issue with any empirical model is the extent to which it can be successfully extrapolated to spatial or temporal settings or scales outside those for which it was parameterised – it is common for empirical models with high predictive power at a calibration site to show poor performance when applied elsewhere.

Predicting vegetation change with regression-type models

Empirical–statistical models have frequently been used to predict vegetation dynamics, especially in the context of land-use/cover change (LUCC). For example, Carmel et al. (2001) used linear and logistic regression models to predict vegetation change in the Galilee Mountains, northern Israel, over the period 1964–1992. They build and parameterise regression models including terms describing initial vegetation condition, local neighbourhood conditions in the initial vegetation map, topography and disturbance regime (grazing of stock) derived from a series of GIS-based maps interpreted from aerial photography. The regression models were calibrated using a subset of the total available data, and are then tested on the complete data set; using the estimated co-efficients and the parameter values in each grid cell in the landscape, the model outcomes can be 'mapped' across the landscape and then compared with observed conditions. The model was analysed by comparing the predicted and observed vegetation composition and spatial pattern, and by pixel-by-pixel comparison (aggregate vs. spatial similarity, *sensu* Brown et al., 2005). Carmel et al. (2001) also predicted vegetation change to the year 2020 based on (i) maintenance of the *status quo* and (ii) the removal of grazing from the site. Other regression-based models have considered the influence of human activity on transitions between forest and non-forest land-covers by directly considering anthropogenic variables related to human population and economic markets (e.g. Wear and Bolstad, 1998; Millington et al., 2007). While the

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[2] Indeed, the field has grown so rapidly that this is probably impossible for a single review in any case.

[3] Although there is no reason that space could not be included in such models, e.g. via spatial autoregressive models (Miller et al., 2007).

Table 2. Some illustrative examples of the range of approaches taken, questions addressed and systems studied by succession-disturbance models (* denotes an example considered in more depth in the body of the text); other codes are explained at the end of the table

Model type	Author	Method	Species/system	Key question	Spatial extent and grain	Spatially explicit?	Dynamic?	Humans?	Evaluation
Regression models	Carmel et al. (2001)*	Linear/logistic regression	Mediterranean vegetation, Galilee Mts, northern Israel	Are empirical models useful for understanding, planning and managing vegetation change?	10^2+ ha; $15 \times 15\,m^2$	N	N	I	SS, ST
	Cawsey et al. (2002)	GRASP	Various vegetation types, Central NSW, Australia	Can regression models provide reasonable predictions of pre-European vegetation conditions?	10^5+ km^2; $\approx 50 \times 20\,m^2$	Y	N	N	PL
	Millington et al. (2007)	Multinomial logistic regression and hierarchical partitioning	Range of land-uses (dehesa, pine forest, agricultural, urban), SPA 56, central Spain	What are the relative role of human and biophysical drivers of LUCC in the SPA 56?	10^5+ ha; $30 \times 30\,m$	Y	N	I	SS, ST, IT
	Wear and Bolstad (1998)	Negative binomial and logit regression models	Range of land-uses (urban, agricultural, forest), Southern Appalachians, USA	What is the role of human disturbance in driving LUCC in this system?	10^4+ km^2; 1 ha	Y	N	I	MS, QC
SDMs	Carey (1996)	Coupled regression and CA model	*Himantoglossum hircinum* in Britain	How will the distribution of *H. hircinum* be affected by climate change?	Britain; 10-km grid	Y	Y	I	ST, PL
	Iverson et al. (1999)*	Coupled regression tree and CA model	*Pinus virginiana* in south-eastern USA	How might *P. virgiana* fare under climate change and ongoing landscape fragmentation?	10^5+ km^2; 3 km	Y	Y	I	PL
	Lehmann et al. (2002)	GRASP	Various vegetation types, New Zealand; focus on fern species	What variables best predict fern species distributions in NZ? Are they species-specific?	NZ; 1-km grid	Y	N	N	ST
	Beerling et al. (1995)	Climate response surface via local	*Fallopia japonica* in Europe and SE Asia	What is the relationship between climate and *F. japonica* in Europe? How might this change?	Europe; 50-km grid	Y	N	I	ST

Table 2. (*continued*)

Model type	Author	Method	Species/system	Key question	Spatial extent and grain	Spatially explicit?	Dynamic?	Humans?	Evaluation
		regression models							
	Guisan et al. (1998)	Binomal and logistic GLMs	*Carex curvula*, Valais region alpine Switzerland	Can GLMs predict the potential distribution of this species?	$10^1+\mathrm{km}^2$; 250 m-grid	Y	N	N	ST
Disturbance regime	Cardille et al. (2001)	GLMs	Forested landscapes of the upper Midwest, USA	What are the roles of biotic, abiotic and human factors in determining origin of fires in the area?	$2.5\times10^5\,\mathrm{km}^2+$; 5–10-km cells	Y	N	I	ST, WC
	Malamud et al. (2005)*	Non-linear regression (power-law) models	18 ‘ecoregions’ spanning the conterminous USA	How does the frequency–area component of the fire regime vary with broad-scale patterns in environmental conditions?	Conterminous USA; ecoregion	Y	N	I	QI
	Moritz (1997)	Extremal event statistics	Chaparral and scrub, Los Padres National Forest, CA, USA	How have fire management and climatic forcing affected the fire regime (size vs. frequency)?	$7\times10^6+\mathrm{ha}$	N	N	I	ST, QI
	Schoenberg et al. (2003)	Non-linear regression models	Los Angeles Country	What is the frequency–area distribution of fires? Which statistical model best describes it?	Los Angeles County	N	N	N	ST
Transition matrix (TM) models	Hall et al. (1991)	TM model	Forested landscapes, northern Minnesota, USA	What are the key trends of forest change in this system? Does human action (logging, management) affect them?	$9.4\times10^2\,\mathrm{km}^2$; $3600\,\mathrm{km}^2$	?Y	Y	I	ST
	Li and Reynolds (1997)	Hybrid grid-based/TM model	Rangeland, New Mexico, USA	What is the relative role of allogenic and autogenic factors in desertification?	Unstated	Y	Y	I	QC, PL
	Romero-Calcerrada and Perry (2004)	TM model	Range of land-uses (dehesa, pine forest, agricultural, urban), SPA 56, central Spain	How will LUCC change the composition/structure of the landscape? And what are the implications for the fire regime?	$1\times10^5+\mathrm{ha}$; 30 m cells	N	N	I	SS, ST, PL
	Scanlan and Archer (1991)	TM model	Grass- and shrub-dominated rangeland, Texas, USA	What is the potential nature of vegetation change under different climatic and grazing regimes?	$\approx 1\times1\,\mathrm{km}$; 20 m grid	N	Y	I	ST, QI
	Yemshanov and Perera (2002)*	Time-dependent Markov model	North American boreal forest (Canada)	What are the long-term dynamics of these types of forest? What role does disturbance play in them?	$3\times10^7+\mathrm{ha}$; 1 ha-grid	Y	Y	N	QC, PL

Gap models	Chen and Twilley (1998)	Gap model (FORMAN based on FORET)	Mangrove forests in southern Florida, USA	What are the temporal patterns of long-term Mangrove forest dynamics?	500 m^2; IBM	N	Y	N	QI
	Hall and Hollinger (2000)*	Gap model (LINKNZ derived from LINKAGES)	Various indigenous forest types in New Zealand	How will a generalised gap model (developed in the US) perform for NZ forests?	0.083 ha; IBM	N	Y	N	ST, TO
	Lafon (2004)	Gap model (LINKADIR derived from LINKAGES)	*Tsuga canadensis*-northern hardwoods forests, Adirondack Mts, New York	How do occasional ice-storms affect long-term forest structure and change?	0.083 ha; IBM	N	Y	N	QL, QI
	Miller and Urban (1999)	Gap model (based on ZELIG)	Range of vegetation including grassland, chaparral and forest, Sequoia and Kings Canyon NP, California	How do surface fire and climate interact to drive forest dynamics in these systems?	9 ha; IBM	Y	Y	I	SS, QL
	Seagle and Liang (2001)	Gap model (derived from ZELIG)	Riparian forest, Maryland, eastern USA	How are riparian forest (seedling) dynamics affected by white-taileddeer browse?	800 m^2; IBM	N	Y	N	ST, QL
Metaphor models	Green (1989)	Grid-based model	Abstract	How do dispersal and fire interact to drive spatial pattern formation in the vegetation?	50 × 50 grid; IBM	Y	Y	N	MS
	Pausas (2006)*	Grid-based model (FATELAND)	Abstract: Mediterranean-type heathland	What are the implications of fire regime and landscape pattern for community structure?	10^2 + ha; 10 × 10 m^2	Y	Y	N	MS
	Roy et al. (2004)	CA model of succession and disturbance.	Abstract: Disturbance-structured system	How does landscape dynamism affect coexistence?	Not specified; grid-based IBM	Y	Y	N	MS
	Solé and Manrubia (1995)*	CA model (Forest game)	Abstract: Tropical rain forest	Do tropical rain forests approach a self-organised critical state?	Up to 256 × 256 grid; grid-based IBM	Y	Y	N	ST, QL
	Savage et al. (2000)	Grid-based model	Abstract: Mixed fire-adapted forest	How are important are contingency effects in long-term ecosystem change?	100 × 100 grid; IBM	Y	Y	N	MS, QI
Detailed exploratory models	An et al. (2005)	Coupled grid- and agent-based model	Wolong Panda Reserve, China	How are growing human populations and associated pressures affecting panda habitat?	10^4 + km^2; 90–360 m grid	Y	Y	Y	MS, PL, QI, QL
	Baxter and Getz (2005)	Grid-based model	Elephant-savanna dynamics, southern African savanna	How do high elephant densities effect savanna vegetation dynamics (fire regime and tree–grass coexistence) and biodiversity?	1 km^2; 1ha-grid	Y	Y	I	PL, QC, QC, MS

Table 2. (*continued*)

Model type	Author	Method	Species/system	Key question	Spatial extent and grain	Spatially explicit?	Dynamic?	Humans?	Evaluation
	Hall and McGlone (2001)*	Gap model (LINKNZ derived from LINKAGES)	Forest vegetation in southern NZ	Can reconstructions of palæoclimate be used to simulate palæolandscape vegetation dynamics?	10^5 + km^2 (see text); IBM	Y	Y	N	ST, PL
	Jeltsch et al. (1996)	Grid-based model	Savanna systems, Kalahari, southern Africa.	How do grass and trees coexist in savanna systems?	50 ha; IBM (5×5 m^2)	Y	Y	N	POM, TO, MS
	Matthews (2006)	Coupled grid- and agent-based model (PALM)	Mid-hills of Nepal	How do resources become available and move through a subsistence agricultural community in this setting?	10^2 + ha; ABM (variable grain)	Y	Y	Y	ST, PL, QI, QL
	Perry and Enright (2002)	Grid-based model	Heathland-forest mosaic, Mont Do Botanical Reserve, New Caledonia	How have fire and human activity interacted to shape present-day landscape pattern?	≈ 1 km^2; 10×10 m^2	Y	Y	I	QL, TO, MS

Validation: ST = statistical confrontation, IT = use of information theoretic approaches, PL = assessment of plausibility of model outcomes (qualitative), SS = evaluation of spatial pattern; e.g. via spatial statistics (pixel-by-pixel, pattern metrics), MS = sensitivity of model structure and parameters, POM = use of pattern-oriented modelling, QC = qualitative comparison with field observations, TO = ability to reproduce 'target outcomes', QI = qualitative interpretation of model outcomes.

Human inclusion: N = no, I = indirect (not directly represented but included in parameter estimates, etc.), E = explicit (directly represented as in agent-based models).

regression models in these examples reproduce landscape dynamics with some accuracy at the site they considered, the question remains of how transferable such site- and scale-specific results really are. Furthermore, the frequent inability of such models to achieve land-cover predictions with accuracies greater than the 'null model' of no change (i.e. the original land cover map) has been documented (Pontius Jr. et al., 2004).

Species distribution models (SDMs)

SDMs are another much applied predictive ecological modelling framework (Franklin, 1995; Guisan and Zimmermann, 2000; Pearson and Dawson, 2003; Heikkinen et al., 2006; Rodríquex et al., 2007). SDMs are "empirical models relating field observations to environmental predictor variables, based on statistically or theoretically derived response surfaces" (Guisan and Thuiller, 2005, p. 994). The approach relies heavily on the concept of the Hutchinsonian (realised) niche in linking species' distributions to their environments (Guisan and Zimmermann, 2000). Despite the success and widespread use of SDMs (see examples in Table 2) they have been criticised on the basis of (some of) their assumptions, in particular the view that species' (or higher taxa's) distributions are in equilibrium with the environment and the limited consideration of biotic processes and interactions such as competition and dispersal (Pearson and Dawson, 2003). While SDMs serve a variety of applied purposes, including the prediction of range expansion under climate change or by invasive species and aiding in the design of reserve networks, they are also used to explore fundamental biogeographic and ecological questions. Those building SDMs have adopted many statistical methodologies including those based on climatic envelopes, regression-methods (classification and regression trees, generalised linear and generalised additive models), artificial neural networks and genetic algorithms, among others (Guisan and Thuiller, 2005; Heikkinen et al., 2006).

Recently, SDMs have been integrated with cellular-automata (CA) models to increase their spatial dynamism. For example, Iverson et al. (1999) integrated the DISTRIB and SHIFT models to predict possible range shifts of *Pinus virginiana* (Virginia Pine) under climate change. DISTRIB is a regression-tree model designed to isolate the suite of environmental predictors that best explain a species' current distribution. By changing input values (e.g. altered temperatures), DISTRIB can be used to statically assess *potential* range changes. SHIFT is a stochastic CA model that predicts migration rates of tree species under altered environmental conditions. Based on habitat availability in 'donor' and 'recipient' cells (H_j and H_i, respectively), the abundance of the species of interest in the donor cell (F_j), and the distance between the cells (D_{ij}^a), SHIFT produces a dynamic description of the probability that unoccupied cells will become occupied (C_i):

$$C_i = H_i \times S(H_j \times F_j \times D_{ij}^a), \tag{1}$$

where a is a power function exponent describing the distance-decay curve for colonisation probability.

Iverson et al. found that while the range of *P. virginiana* may be markedly reduced under various climate change scenarios, the species does not seem threatened. More generally, they suggest that the specific spatial pattern of migration that a species exhibits will be influenced by its abundance in specific parts of the landscape, landscape heterogeneity, and potential migration lags. The broad advantage of this coupled approach is that it surmounts some of the criticisms of static SDMs regarding their treatment of landscape-level heterogeneity such as: (i) the interplay between fragmentation and rate of migration and (ii) the possibility that environmental change may produce low habitat-quality 'barriers' that inhibit species movement (Hansen et al., 2001; Iverson et al., 1999).

Predicting disturbance with empirical models

Finally, empirical–statistical models have been developed with a focus on characterising the frequency–size component of the disturbance regime. The disturbance that has received the most attention in this regard is fire – both 'natural' and anthropogenic in origin (e.g. Malamud et al., 2005, Table 2). Malamud et al. (2005) analysed spatial variation in the frequency–area structure of the wildfire regime over the period 1970–2000 across the conterminous USA. They described the fire regime in each of 18 ecoregions based on the parameters of a power function relating fire frequency $\dot{f}(A_F)$ to size A_F ($\dot{f}(A_F) = \alpha A_F^{-\beta}$); $\log \alpha$ provides an indication of the number of fires per unit area and the power-law exponent β measures the ratio of large to small fires in a given area ($\beta = 0$ suggests the same number of fires of all sizes). They found that wildfire regimes systematically changed east to west across the USA, possibly due to different human land-uses and patterns of fragmentation, and that there were differences in the frequency–area statistics for fires ignited by lightning versus anthropogenic sources. Malamud et al. developed a quantitative method for predicting wildfire recurrence intervals using their estimates of α and β. Studies such as these in some ways bridge the gap between predictive and exploratory modelling; while prediction is often their main focus, they are also concerned with attempting to isolate the drivers of spatio-temporal variability in the wildfire regime, with the (tacit) recognition that better causal understanding should lead to improved predictive ability.

Transition (Markov) models

The transition matrix (Markov) approach is often used to project vegetation change (see Table 2). Central to such models is a matrix, $\boldsymbol{P}$, whose elements contain the probability of a discrete vegetation class making the transition from type i to type j in some time-step (t):

$$\boldsymbol{P} = \begin{bmatrix} p_{11} & p_{12} & \cdots & p_{1n} \\ p_{21} & p_{22} & \cdots & p_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ p_{n1} & p_{n2} & \cdots & p_{nn} \end{bmatrix} \tag{2}$$

Repeatedly multiplying $\boldsymbol{P}$ by a $1 \times n$ state vector (x_t), which contains the abundance of each vegetation type (1 to n) at time t, projects the composition of the system into the future (Eq. (3)). This state-vector ultimately stabilises to reach what might be interpreted as the Clementsian 'climax' condition. Thus, and assuming that the transition probabilities are stationary:

$$x_{t+1} = x_t \cdot P, \quad x_{t+2} = x_{t+1} \cdot P = x_t \cdot P^2 \ \ldots \ x_{t+k} = x_t \cdot P^k. \tag{3}$$

The key assumptions of the transition matrix approach are that:

1. transitions within the system are temporally stationary; in reality this is unlikely due to endogenous processes such as density-dependence and exogenous drivers such as disturbance or anthropogenic forcing
2. local neighbourhood processes are not deemed important (spatial stationarity); thus the vegetation at a given site does not affect transition rates at nearby sites (e.g. via seed dispersal), nor does landscape position, although a stratified approach in which different matrices are derived for different site conditions may be used
3. the state of the system at time $t+1$ is predictable from (and determined by) the state of the system at time t; in other words, history and legacy effects are not considered (although this can be relaxed, at the expense of tractability, if nth-order Markov models are used).

Yemshanov and Perera (2002) use a modified transition matrix approach to explore patterns of forest succession over large spatial extents in the North American boreal forest. They use a time-dependent Markov model (see Acevedo et al., 1995) in which p_{ij} is dependent on the length of time spent in i. In Yemshanov and Perera's model time-dependence is considered via the probability of discrete-state persistence (p_{ii}):

$$p_{ii}(t) = \xi(t)p_{ii}, \tag{4}$$

where $\xi(t)$ is a probability distribution function based on time constraints.

Yemshanov and Perera (2002) parameterise their transition matrix model using data from a range of disparate sources (the model as 'synthesis tool'), including previously published data, raw multi-temporal data (permanent plot chronosequences and remotely sensed imagery), and fine(r)-scale forest gap models. These data sources enabled Yemshanov and Perera (2002) to stratify vegetation transition probabilities by climatic zone, moisture regime and soil nutrient status. Model projections showed vegetation trajectories in broad accordance with previously published case studies (i.e. shifts toward late-successional forest species assuming no disturbance).

In its simplest form the transition matrix framework "represents (forest) change as a null model" (Yemshanov and Perera, 2002, p. 203). Romero-Calcerrada and Perry (2004) use a transition matrix approach as a null model in their investigation of human-driven landscape change in SPA 56, 'Encinares del río Alberche y Cofio', Central Spain. They used the *failure* of transition matrix models to successfully predict vegetation change, to identify potential sources of non-stationarity in the landscape. Johst and Huth (2005), using a grid-based model, extended the transition matrix approach to encompass time-dependent transitions, neighbourhood influences on rates of change (transition times to some state i are reduced if a cell's neighbours are already in that state) and disturbance dynamics. Thus their framework, which they used to explore the shape of the relationship between disturbance and diversity, circumvents some of the assumptions listed above; other similar spatially implemented transition models have also been developed (e.g. Li and Reynolds, 1997). The cost, of course, is that the models are no longer analytically tractable. Although Markov models have proven very useful for efficiently predicting vegetation change over large spatio-temporal extents in a wide range of different systems, their empirical (site- and scale-specific) nature makes them difficult to transfer to other sites and/or scales.

Forest gap models

Since Botkin et al. (1972) described JABOWA, the gap model approach has become one of the most widely adopted frameworks for simulating small-scale forest change (Shugart, 2002, Table 2). Gap models simulate the establishment, growth and eventual demise of all individuals in a small plot ($\approx$ 0.01–0.1 ha); thus, they provide an example of an 'individual-based model' (IBM). Early gap models were typically non-spatial, with new recruits being drawn from a potential list of occupant species. Recent gap model variants (e.g. SORTIE – Pacala et al., 1996; Deutschmann et al., 1997) have been spatially explicit and represent spatial processes such as seed dispersal and recruitment in detail (see Busing and Mailly, 2004). Gap models have been successfully used to describe the effects of altered disturbance regimes on forest structure and composition (e.g. Miller and Urban, 1999; Lafon, 2004), climate change (e.g. Bugmann, 1997; He et al., 1999), herbivory/browsing dynamics (e.g. Dyer and Shugart, 1992; Seagle and Liang, 2001) and the basic nature of forest succession in various forest ecosystems (see examples in Shugart, 1998); they have also been adapted for other vegetation types such as mangrove fields and shrublands (e.g. Chen and Twilley, 1998; Peters, 2002). Using state-of-the-art computational tools, gap models can now consider larger areas and large numbers of individuals (e.g. TROLL can simulate up to 2×10^7 individuals over an area of $\approx 20\,\mathrm{km}^2$ Chave, 1999). Nevertheless, the computational limits inherent in tracking the fate of every individual means that gap models usually focus on relatively small areas (see Table 2).

In gap models, each individual is defined by its diameter (D) and various allometric relationships link diameter to other biometric descriptors such as height. Growth is modelled as change in diameter ΔD (Bugmann, 2001):

$$\frac{\Delta D}{\Delta t} = GD\left(1 - \frac{DH}{D_{\max}H_{\max}}\right)\frac{1}{b(D)}f(e), \qquad (5)$$

where H is the tree's height, $b(D)$ describes the allometric relationship between height and diameter, G is a growth rate parameter, $D_{\max}$ and $H_{\max}$ are the maximum dimensions of the tree, and t is time (usually years).

The effects of the abiotic and biotic environment on growth are given by a scalar $(f(e) : 0 \leqslant f(e) \leqslant 1)$ that reduces growth rate below the optimal; for example:

$$f(e) = g_1(\mathrm{AL}) \cdot g_2(\mathrm{SBAR}) \cdot g_3(\mathrm{DD}), \qquad (6)$$

where $g_1(\mathrm{AL})$ is a function of light availability, $g_2(\mathrm{SBAR})$ is a function of stand basal area and $g_3(\mathrm{DD})$ is a function of the annual-degree day sum.

Other models include other key limiting factors; for example, Chen and Twilley's, 1998 gap model of mangrove forest dynamics (FORMAN) includes the effects of salinity on tree growth.

Gap models occupy an interesting middle-ground between exploratory and predictive models. While they rely heavily on empirical information for their parameterisation and can be used predictively (e.g. to estimate changes in timber volumes per unit area Landsberg, 2003), they can also be used heuristically (e.g. to explore the conditions under which certain system dynamics occur). As an example, Hall and Hollinger (2000) describe the LINKNZ model, which is a non-spatial modification of the LINKAGES gap and nutrient dynamics model, for NZ forest systems. They evaluate LINKNZ by comparing its predictions to: (i) the observed structure or composition of stands of a given age and (ii) developmental trajectories in various NZ forest types. Fire and wind-throw events are included by way of a reduction in biomass (tree death) and the return of that biomass to the local biogeochemical cycle; individual disturbance events are *not* modelled mechanistically. LINKNZ model produces 'plausible' predictions of forest dynamics, although Hall and Hollinger (2000, p. 25) note that "detailed patterns may not be exactly reproduced, especially during the early-establishment phases". Having demonstrated the predictive adequacy of the model, Hall and Hollinger (2000) use it to explore some open issues in NZ forest ecology: (i) the 'regeneration gap' (the *apparent* widespread failure of gymnosperm recruitment), (ii) the 'beech gap' (absence of *Nothofagus* spp. from areas where they might be expected to grow) and (iii) the dynamics of natural monocultures (e.g. *Nothofagus solandri* var. *cliffortioides* and *N. menziesii*). Thus, the model is used both predictively and heuristically – in this case the model predictions are used to assess its adequacy *before* its heuristic use.

Analysis strategies for predictive models

Compared to exploratory models there are reasonably well-established tools for analysing predictive models; as Mayer and Butler (1993) outline these are typically quantitative, and include both graphical (e.g. plots of observed vs. predicted data) and statistical methods (e.g. analysis of residuals). While the emphasis lies heavily on the predictive accuracy of the model, rather than the structure of the model itself, recent information theoretic methods do emphasise trade-offs between predictive accuracy and model complexity (Johnson and Omland, 2004; Hobbs and Hilborn, 2006). However, evaluation of predictive models remains problematic. A now much-discussed problem for model evaluation, considered in some depth, by Oreskes et al. (1994) and Oreskes and Belitz (2001), is non-uniqueness or under-determination. In essence, the argument goes that because more than one model can produce the same observations, simply finding a match between a model's predictions and (empirical) observations to some predetermined acceptable goodness-of-fit, is not grounds to state that a model is either 'true' or 'correct'. Following Oreskes and Belitz (2001), this non-uniqueness can be numerical (multiple solutions to equations), parametrical (multiple input data produce the same outcomes – this is termed 'equifinality' by Beven (2002)) or even conceptual (multiple conceptual models equally well explain empirical observations). It is also important to distinguish between logical and temporal prediction (*sensu* Oreskes, 2000), that is predictions about phenomena that are independent of the location in time and space at which they occur as opposed to those that are not. Falsifying a logical prediction has much greater explanatory value than falsifying a prediction about a specific time (or place), yet most model evaluation (tools) focus on temporal prediction.

Many methods have been developed to compare observed and predicted maps on the basis of their overall composition and pixel-by-pixel matches (Pontius Jr. et al., 2004; Wealands et al., 2005). One key issue is finding appropriate comparisons for model evaluation. Pontius Jr. et al. (2004) note that many land-use and cover change models make predictions no better (if not worse) than a null model that simply retains the original map as a prediction of the future (e.g. see Millington et al., 2007). In general terms, despite the existence of many statistical frameworks for the evaluation of models and data, deciding on an appropriate null model is not necessarily easy. A large number of measures have been developed that aim to quantitatively describe aspects of landscape pattern (broken into landscape composition [what's there?] and landscape structure [where is it?]). All such metrics are derived from measures of the geometry of patches: patch perimeter, patch area and patch adjacency structure (Gustafson, 1998). These metrics are widely used, for example, to compare model simulations with observed patterns and/or to compare sets of model simulations under alternative parameterisations. While such metrics may be useful for comparison, finding links between metric values and specific ecological processes has proved difficult (Cale and Hobbs, 1994; Li and Wu, 2004).

'Exploratory' modelling

In disciplines such as, for example, engineering, modelling (stereo-)typically proceeds from a solid conceptual basis and is underpinned by substantial quantitative data. However, this is not often the case when models of ecological systems are being developed. Where data are scarce, hard to obtain, and/or uncertain, modelling is more likely to be exploratory than predictive. This does not, however, lessen the utility of modelling – as Bankes (1993, p. 441) states "for many problems partial information can provide partial answers". Exploratory modelling is an approach that (tacitly) emphasises the use of a model or models to reduce epistemic uncertainty; it usually adopts an experimental view of model analysis (Winsberg, 2003; Peck, 2004), with the qualitative nature of the model outcomes being more important than the quantitative details. Bankes (1993), Pielke Jr. (2003) and Turner (2003) provide reasons why the exploratory approach is valuable:

1. the use of models as 'existence proofs' (i.e. to demonstrate that certain system dynamics are plausible)
2. the development of models early in research as a guide/framework (i.e. hypothesis generation) for future endeavours (whether model-based or empirical)
3. the development of multiple and/or new ways of conceptualising a system via critical and/or creative thinking
4. risk assessment; for example, generation of worst conceivable outcomes
5. synthesis and integration of disparate/alternative sources of knowledge and understanding.

Abstract models as metaphors

To some extent *all* models are metaphors, but, in this context, we are referring to highly abstracted models that are not targeted at a specific system, but rather aim to capture the key traits of some general class of system. One much discussed and debated example is Per Bak's well-known forest-fire model (Bak and Chen, 1990), which is intended to represent open, dissipative systems, and uses 'real' forests and 'real' fires as a metaphor (see Millington et al., 2006). The hallmark of such models is their comparative simplicity and level of abstraction. Their 'simplicity', however, does not mean that they are not powerful and useful tools for exploring complex systems[4]; in particular such 'metaphor' models have proved useful for exploring where and how a system's macroscopic statistical properties arise from micro-level interactions and processes (so-called 'emergence').

An example of the use of metaphor models for the exploration of forest dynamics is the "forest game" model described by Solé and Manrubia (1995). This simple stochastic lattice-model attempts to mirror the nature of gap dynamics processes in species-rich tropical rainforest systems. The model comprises a two-dimensional $L \times L$ lattice, with, at each time step, each cell containing a tree of size S_t – the model assumes all trees are of the same species. The model contains four basic rules (with asynchronous updating):

1. *birth*: New trees appear at empty sites with p_b.
2. *death*: Trees die at rate p_d or when they exceed some maximum size.

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[4] By *complex* we mean systems in which the (possibly few) components interact to produce unexpected outcomes ('emergence'), whereas by *complicated* we mean systems comprising many elements interacting in a linear or otherwise predictable fashion.

3. *growth*: Tree size is updated as a function of the tree's size relative to that of its neighbours.
4. *gap formation*: On the death of a tree, some of that tree's neighbouring cells are cleared as a function of the tree's size.

The "forest game" provides a metaphor for the complexities of gap-phase dynamics in species-rich forests, and is clearly a gross simplification of the dynamics of such systems. Nevertheless, it does capture some of their macroscopic structure – in particular, it exhibits multi-fractal behaviour in the form of a power-law distribution of gaps similar to that observed in the 'real' system (Solé and Manrubia, 1995). Thus, a simple model containing minimal *specific* process detail appears to capture some of the key characteristics of a complex system – this observation, that complexity can emerge from simplicity has been made repeatedly using models such as this, and has lead to the rise of 'complexity science' (Bascompte and Solé, 1995).

Building on abstract models of: (i) the spread of contagious disturbances and (ii) the spatial structure of heterogeneous landscapes, Pausas (1999, 2006) has developed CA-type models of Mediterranean forest succession and disturbance that incorporate plant functional types and idealised disturbance regime characteristics. Pausas (2006) describes a spatially explicit model (FATELAND) in which species compete in grid cells as a function of their life-history characteristics and the fire regime. Using artificial landscapes following a gradient of coarse-to-fine spatial texture, Pausas explored the interplay between spatial pattern, life-history traits and the fire regime. The results are placed in the context of the management and restoration of fire-prone ecosystems in the Mediterranean Basin. FATELAND shows that not only do species respond differentially to alternate fire regimes, but that the nature of their response varies with landscape pattern. Although models such as FATELAND are not direct representations of specific systems they bridge the gap between highly abstract models, such as Bak and Chen's forest fire model (Bak and Chen, 1990; Millington et al., 2006), and detailed site-specific simulation models.

Simple models such as the "forest game" have benefited ecological theory, especially by contesting the (intuitive) view that understanding complicated systems requires complicated explanations. Furthermore, they play an important role in developing broad understanding of a class of systems, and in allowing the generation of hypotheses about the dynamics of those systems. Nevertheless, the key question is 'what have we *specifically* learned from these models?' Answering this question means we need to consider how far we can push the metaphor. The simplicity that such abstract models engender can be beguiling, and it is easy to fall into the trap of believing that since simple models appear to reproduce the dynamics of some complex system(s), those complex system(s) themselves must be simple. As Frigg (2003) points out, there is a risk of over-interpreting 'emergent' behaviours; it is important to ask whether a given 'emergent' phenomena is robust to different representations and parameterisations. Likewise, it is easy to forget that the models *are* (intended as) metaphors, and caution needs to be used if they are applied to specific dynamics in specific systems (Millington et al., 2006). If a given model *is* to be applied to specific dynamics in specific systems then there will be a minimum amount of empirical information such a model will need to contain. The amount of information that is required will depend upon the current state of knowledge about that system and the scale of representation at which the model is constructed.

Detailed models as heuristic tools

Models for learning are not limited to abstract, stripped-back models such as those described above; detailed models are also frequently used to explore specific facets of vegetation dynamics in specific systems. These models are usually informed by considerably more empirical information than are the 'metaphor models' described above, and might be best thought of as tools for integration and synthesis (*sensu* Turner, 2003).

Exploring palæolandscapes with models

Much use has been made of succession-disturbance models to try to reconstruct historical landscape dynamics (Anderson et al., 2006). This application straddles the division between models for learning and models for prediction – they are tools for learning, as they usually focus on trying to understand how a given landscape composition and structure was achieved, but they are often analysed in a predictive sense by: (i) comparing their predictions against other observed data (e.g. comparison of model outputs to palynological reconstructions) and (ii) seeking to use historical reconstructions to predict future change. A recent example of model-based landscape reconstruction is provided by Hall and McGlone (2001), who used the LINKNZ model (described above) to reconstruct forest composition and test estimated palæo-climatic conditions in south-eastern New Zealand. Hall and McGlone modelled forest composition in the recent past (700–800 yr BP) and in the early Holocene (7000–8000 yr BP). Various proxy climatic data suggest that in the early Holocene temperatures were approximately 1 °C warmer than present-day with rainfall approximately 60% lower; dominant forest taxa in the pollen record (at that time) include *Dacryidum cupressinum*, *Nothofagus menziesii*, *Dacrycarpus* spp., *Weinmannia* spp. and *Podocarpus* spp. Simulations were conducted on ≈2000 separate landscape patches representing the broad range of bioclimatic conditions across the region; thus, Hall and McGlone (2001) take a stratified 'sample' of the landscape (see Urban et al., 1999). Parameterising LINKNZ to mirror early Holocene climatic conditions resulted in successful reproductions of the palynological record, supporting previous climatic reconstructions. The model was then used to predict likely future vegetation trajectories under current climate conditions. In this example the modelling exercise is heuristic in the sense that: (i) it seeks to confirm the plausibility of various hypothesised system dynamics, (ii) it synthesises and integrates previous non-model studies and (iii) provides new hypotheses about the nature of the palæo-environment in this part of NZ.

Using models to explore human disturbance and management

Detailed models are also used to assist in decision-making in forests ecosystems by managers. While models can be used to explicitly predict the future states and dynamics of a system, they are more commonly used to explore the potential outcomes of different management strategies or scenarios. For example, LANDIS (Mladenoff, 2004; Scheller et al., 2007), a stochastic spatial simulation model that considers vegetation dynamics over large space–time extents (10^6+ ha and 1000s of years), has been used to explore the consequences of a number of landscape-level management options (e.g. patterns of harvesting or fuel management). Gustafson et al. (2000) describe a timber management model which they added to LANDIS. In their module management occurs in zones with specific objectives and associated harvest prescriptions; the prescriptions are described by a spatial component (where? how large?), a temporal component (single- vs. multi-stage harvest strategies) and cohort removal component (which age cohorts?). The module also includes 'ranking algorithms' that prioritise harvested stands based on criteria such as a stand's age, economic value or age–class distribution. Gustafson et al. (2000) used this model to compare the outcomes of three different harvest strategies (no harvest, even-aged, uneven aged) in south-eastern Missouri. They found that the different strategies produce landscapes with profoundly different spatial configurations. Gustafson et al. highlighted the ability to use the model experimentally, noting that "the model framework invites evaluation and comparison of management alternatives" (p. 40). He et al. (2004) discuss the use of LANDIS to provide information for wildfire regime management by allowing managers to explore the implications of different fuel management practices (e.g. prescribed burning, fuel reduction, fire suppression) for landscape structure. They demonstrate the use of the model by comparing the long-term outcomes of fire suppression either with or without reduction of coarse fuels via fuel treatment in the Missouri Ozarks. He et al. (2004) emphasised the trade-offs required to simulate fire regime management over broad spatio-temporal extents; for example, LANDIS is stochastic and so cannot be used to predict the outcomes of specific individual events, but it does enable consideration of longer-term spatial patterns and the outcomes of different management approaches. Indeed, the strength of using models in this way is their facilitation of *learning* via an experimental approach.

Analysis strategies for exploratory models

Specific analysis strategies for exploratory or heuristic models are less well-established than those for predictive models. Although, the statistical tools discussed above are frequently used to evaluate exploratory models, if the focus of the modelling exercise is heuristic, then predictive accuracy may become of reduced importance; this means that evaluation may focus on a model's structural realism to ensure than any (novel) outcomes it produces are plausible, but not 'hard-wired' into its assumptions. It is fair to state, however, that model analysis remains in practice dominated by technical and quantitative approaches. Recently, and in light of some important criticisms of this quantitative approach to model evaluation, strategies such as 'pattern-oriented modelling' (POM, Fig. 2) have been advocated for the evaluation of the complex simulation models often used in exploratory ecological analyses (Grimm and Berger, 2003; Grimm et al., 2005; Wiegand et al., 2003). As Grimm et al. (2005) emphasise, models that are too simple fail to capture the essence of the system being considered, but models that are too detailed become difficult to analyse and interpret. Thus, locating the optimal representational detail for the question of interest is of fundamental importance in model building and implementation; it is this optimum that POM helps

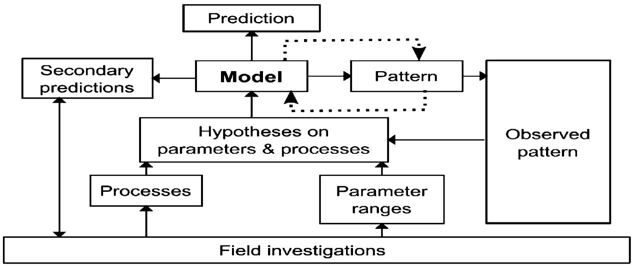

Fig. 2. Schematic overview of the pattern-oriented approach to model design and analysis (after Wiegand et al., 2003); reproduced with kind permission of Wiley-Blackwell Publishing.

find. Compared to the confrontational approach discussed above, this type of model evaluation considers both the structure of the model itself (are the essential things included?) and its outcomes (does the model reproduce specific dynamics [patterns] of the system of interest?). This simultaneous consideration of structure and outcome is a strength of the approach. As a strategy pattern-oriented modelling:

- endeavours to make the choice of model structure less arbitrary, by focusing on the optimal complexity (in terms of the suite of processes/parameters included) required for specific questions to be addressed;
- hinges on identifying *multiple* spatial and temporal patterns and the minimal structure required for their 'emergence' from a model; Grimm and Berger (2003, p. 412) note that "usage of multiple 'weak' patterns is more fruitful than focusing on one single 'strong' pattern" and
- produces 'structurally realistic' models that contain the fundamental structures/processes necessary to capture the essence of the system; this is achieved by comparing *independent* model outcomes with known properties of the system.

Along similar lines, O'Sullivan (2004, p. 291) states that "It is clear that assessment of the accuracy of a model as a representation must rest on argument about how competing theories are represented in its workings, with calibration and fitting procedures acting as a check on reasoning". He argues that models should be rigorously assessed on the basis of the theories represented in the model and their adequacy – this type of evaluation cannot be achieved solely via technical or algorithmic means (Kleindorfer et al., 1998). In this context, models may best be seen as types of thought experiments where the implications of different conceptualisations can be explored. POM and other model evaluation frameworks (e.g. see Castella et al., 2005 for a discussion of 'social validation') can provide understanding different to that which more 'traditional' confrontational evaluation methods give.

Where to from here?

The place of humans

Few ecosystems remain unaffected by human activity, yet relatively few ecological models have explicitly considered humans as agents of change (Liu, 2001). This is rather surprising because: (i) the need for environmental management to integrate biophysical and social perspectives is widely discussed (Chave and Levin, 2003; Pickett et al., 2005) and (ii) numerous conceptual frameworks designed to encourage this integration have been developed (Vogt et al., 2002).

A key question in successful integration of biophysical and social and economic problems is at what spatial and temporal scale(s) the system(s) should be analysed (Bockstael et al., 1995; Vogt et al., 2002). For example, while ecologists often view spatial dynamics as being as important as temporal dynamics, economists generally ignore spatial dynamics and set the spatial extent of their model boundaries according to the extent of the market (Bockstael, 1996). Temporally, ecologists are more interested in dynamics over longer extents (often considering 100+ years), whereas economists have restricted themselves to shorter time-horizons (up to decades) as they are less confident about their ability to predict future perturbations to their systems (Bockstael et al. 1995). The 'landscape', on the scale of the human observer, seems a potential common-ground here as it represent a scale at which both the natural and social sciences have historically collected and analysed data (Vogt et al., 2002; Matthews and Selman, 2006).

In the past, human action has often been included in models in static and/or implicit (and arguably unsatisfactory) ways such as the manipulation of parameters describing disturbance frequency and/or size; of the 34 case-studies presented in Table 2, 18 consider humans but of these only two do so directly . As Wainwright (2006) discusses, such indirect, static and immutable 'scenarios' fail to capture the dynamic relationships and feedbacks that typify human–environment interactions, and at the worst can result in extremely unrealistic model dynamics (e.g. the ongoing acquisition of resources long after they have passed some usable lower threshold). Recently, however, models that represent environmental change and human activity and decision-making more 'realistically' have received increasing attention. Over recent years a number of models have been developed that represent human decision-making (e.g. via an agent-based approach) in spatially explicit and temporally dynamic landscapes (e.g. via a grid-based or CA model); Parker et al. (2003) review the use of such models in the context of LUCC. Matthews (2006) highlights two areas where such models need development are (i) between-agent communication and interaction in the decision-making process and (ii) representation of dynamics in the landscape (beyond simple cover change).

We anticipate that such integrated models will continue to be developed and refined; nevertheless, the development of integrated socio-ecological and ecological–economic models is clearly a complicated endeavour and such models have the potential to become extremely detailed. Furthermore, the collaboration between ecological modellers and modellers from other disciplines that such an integrated approach suggests may not be as straight-forward as might be hoped. For example, Drechsler et al. (2007) suggest that ecological modellers must be aware that analytical tractability is valued more highly in economics than is generally the case in ecology (but note equally that economists must be prepared for greater model complexity than they may be used to). Potential difficulties in inter-disciplinary modelling collaborations are likely to arise from differences in perception and understanding between experts from different disciplines – both regarding the systems being modelled themselves and the objectives and potential of the models being constructed.

Representation and scale

There is no single 'best' way of modelling succession and disturbance dynamics, rather there are more or less appropriate strategies depending on the questions of interest and the purpose of the modelling exercise. The modelling approaches described here range from data-driven empirical approaches (e.g. regression models) to representationally rich individual-based models (e.g. forest gap models). A primary concern over which approach will be taken will be the necessary trade-off between spatio-temporal grain and spatio-temporal extent. Individual-based models have been limited to small spatial scales; the earliest gap models operated on patches smaller than 1 ha and considered only a few hundred individuals, but more recent gap model variants (e.g TROLL – Chave, 1999) *can* consider up to 2×10^7 individuals over areas of $\approx 20\,\text{km}^2$. Nevertheless, for now, spatial extents of the order of tens of thousands of hectares remain the domain of more aggregated models. However, given the ever increasing availability of computational power, individual-based models, such as TROLL, will be able to consider more and more individuals on larger and larger landscapes. While this 'brute-force' approach might seem appealing, it is debatable whether more and more detailed representation over ever largening extents will prove useful; there are inevitable limits to the amount of model detail that can be supported in terms of either understanding (representation) or data (parameterisation). As Levin (1997, p. 334) points out, the risk of developing over-detailed simulations is that the "…models produce cartoons that may look like nature but represent no real systems." The essence of effective modelling, in any context, remains in isolating the 'details that matter' (Pacala and Deutschmann, 1995), and identifying the local components of the system that contribute to broad(er)-scale dynamics and those that are simply noise (Levin et al., 1997; Urban, 2005; Hastings et al., 2005). A broader view of model evaluation than the traditional confrontation between model and data (e.g. new frameworks such as pattern-oriented modelling), will help in this context.

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