

Emerging Opportunities for Landscape Ecological Modelling

Nicholas W. Synes^{1,2} · Calum Brown³ · Kevin Watts⁴ · Steven M. White^{5,6} ·
Mark A. Gilbert^{6,5} · Justin M. J. Travis¹

© The Author(s) 2016. This article is published with open access at Springerlink.com

Abstract Landscape ecological modelling provides a vital means for understanding the interactions between geographical, climatic, and socio-economic drivers of land-use and the dynamics of ecological systems. This growing field is playing an increasing role in informing landscape spatial planning and management. Here, we review the key modelling approaches that are used in landscape modelling and in ecological modelling. We identify an emerging theme of increasingly detailed representation of process in both landscape and ecological modelling, with complementary suites of modelling approaches ranging from correlative, through aggregated process based approaches to models with much greater structural realism that often represent behaviours at the level of agents or individuals. We provide examples of the considerable

progress that has been made at the intersection of landscape modelling and ecological modelling, while also highlighting that the majority of this work has to date exploited a relatively small number of the possible combinations of model types from each discipline. We use this review to identify key gaps in existing landscape ecological modelling effort and highlight emerging opportunities, in particular for future work to progress in novel directions by combining classes of landscape models and ecological models that have rarely been used together.

Keywords Landscape ecology · Pattern · Process · Simulation modelling · Socio-ecological systems

This article is part of the Topical Collection on *Methodological Development*

✉ Nicholas W. Synes
nsynes@gmail.com

- ¹ Institute of Biological and Environmental Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ, UK
- ² School of Geographical Sciences & Urban Planning, Arizona State University, P.O. Box 875302, Tempe, AZ 85287-5302, USA
- ³ School of Geosciences, University of Edinburgh, Edinburgh EH8 9XP, UK
- ⁴ Forest Research, Alice Holt Lodge, Farnham, Surrey GU10 4LH, UK
- ⁵ Centre for Ecology & Hydrology, Benson Lane, Wallingford, Oxfordshire OX10 8BB, UK
- ⁶ Wolfson Centre for Mathematical Biology, Mathematical Institute, Radcliffe Observatory Quarter, Woodstock Road, Oxford, Oxfordshire OX2 6GG, UK

Introduction

Landscapes are the result of numerous processes that operate and interact across different spatial and temporal scales. Physical, biogeochemical, and anthropogenic factors are major determinants of landscape structure, and one of the primary goals in landscape ecology is to illuminate the relationships between this structure (or pattern) and ecological processes occurring on the land surface [1–3]. However, clear causal relationships between process and pattern are rare, not least because the two are interlinked, with patterns being formed by processes in the landscape and these patterns then influencing those processes in turn. For example, low-level disturbance patterns in conifer forests may be propagated by bark beetle populations; the interaction between pattern and process can lead to large scale population outbreaks and the acceleration of forest successional trajectories [4].

This complex dynamism between process and pattern presents significant difficulties for many aspects of landscape science, and modelling can provide a useful tool for meeting

these challenges. It can be prohibitively challenging and expensive to mount field experiments at appropriately large spatial and temporal scales, or to establish experimental controls and replications. These difficulties are compounded where mobile organisms are studied, with data collection on processes being especially time-consuming and difficult if species need to be tracked, captured, or monitored. Furthermore, substantial portions of studied populations will generally be undetectable, and bias in sampling methods or results make it difficult to translate findings up to population level patterns [5]. As a result, field experiments often produce highly case-specific and non-generalisable results. For example, many studies have identified that habitat corridors promote the key ecological processes of movement and dispersal of particular species between habitat patches, but few have shown an increase in the patterns in which we are most interested, such as population size and species diversity [6]. For these reasons, modelling—and especially simulation modelling—has become an important research tool in landscape ecology [7]. This approach allows "virtual" experiments to be run repeatedly, generating many data and exploring effects that would be impossible to investigate empirically. Findings can be compared to observations to validate or extend inference and further studies targeted at processes or factors that appear especially important (e.g. [8–11]).

Simulation modelling has already proved extremely valuable in landscape ecology. Notable advances have been made across landscape ecology and wider land systems science, and methods and findings continue to improve in sophistication and insight [12–14]. One of the greatest contributions of landscape ecological modelling has been informing spatial planning for conservation, where it has offered an important complementary approach to classical metapopulation theory by explicitly incorporating the contribution of the matrix (the environment between the habitat patches) [15–19]. However, this computational approach is not free of challenges. As is always the case in modelling, it can be easy to misapply or misinterpret models, and hard to ground them in reality [20]. Uncertainties and errors can go unrecognised, interact and propagate, and produce biased or erroneous results [21, 22]. In addition, assumptions must still be made in order to define a bounded and tractable system, and these assumptions can have important effects on model outcomes—for instance where they cause an influential process to be neglected or impose inappropriate spatial resolutions, scales, or structures [23, 24]. For example, the use of regular geometries to represent landscapes can introduce directional bias [23], and the use of an inappropriate spatial resolution can substantially bias estimates of the rate at which species expand their biogeographic ranges [25]. Nevertheless, the role of simulation methods is likely to continue to grow as it becomes increasingly necessary to understand the integrated dynamics of land systems and their responses to global change, an objective that is clearly beyond the scope of empirical studies alone.

The diversity of applications for landscape simulation has driven rapid methodological development, and it is important periodically to take stock and assess whether simulation techniques are achieving their potential in contributing to our understanding and management of landscape ecological dynamics, or whether opportunities to exploit emerging methodologies are, in some areas, being neglected [26]. Earlier reviews have focused on the use of neutral landscape models (NLMs) in landscape ecology [27], modelling methods in relation to environmental change [28], and the shared methodologies between complex systems science and landscape ecology [20]. However, we know of no existing reviews that span the partially divergent fields of modelling landscapes and their development (including human land-use) and modelling the dynamics of ecological systems in those landscapes. We undertake a review of this kind here, with the intention not only of promoting a more integrated approach to landscape ecological modelling but also of identifying the most valuable existing and potential links between models that focus on distinct landscape components. We first give a broad context by providing background across a diverse range of approaches used in landscape and ecological simulation modelling, discussing how the fields have developed, providing our thoughts on where there exist significant gaps, and thus important opportunities for future work, and highlighting likely future trends within the landscape ecological modelling field.

Background to Landscape, Ecological, and Landscape Ecological Modelling

The overall objective of our paper is to provide some future perspectives for landscape ecological modelling. To arrive at this point we first provide key background. Some of this is of work that has been at the intersect between landscape modelling and ecological modelling (i.e. landscape ecological modelling), but some is focussed on progress in one field that has not yet been applied in the other (of which there is a substantial amount, despite the somewhat artificial nature of the distinction) (see Table 1). Modelling methods (landscape modelling, ecological modelling, and landscape ecological modelling) can be broadly categorised into either pattern- or process-based approaches [30, 74]. Pattern-based approaches identify existing patterns in the landscape or ecological system (for example, species distribution), and aim to replicate or extrapolate those patterns without considering the generative processes. On the other hand, process-based approaches focus on representing the underlying processes that formed observed landscape or ecological patterns (see Fig. 1 for an illustration of some of the deployment of pattern and process based models in these fields; see Table 2 for some common applications of different modelling approaches). We will first discuss models of landscape and land-use dynamics before moving on to spatial ecological models.

Table 1 Broad categorisation of landscape simulation modelling methods. Grouped into separate landscape and ecology methods, with references to examples and review or comparison papers where available

Type	Example(s)	Review(s)
Landscape		
Neutral landscape models	QRULE [29]	[27]
Process-based anthropogenic disturbance models	G-Raffe [30]	
Biogeochemical models	RHESSys [31]	[32]
Process-based land-use models	CRAFTY [33] LUCITA [34] SWISSland [35]	[36, 37]
Ecology		
Species distribution models	MaxEnt [38] DOMAIN [39] BIOCLIM [40] Other statistical approaches not originally created for SDMs: Random Forests [41] GAMs [42]	[43, 44]
Forest landscape dynamics, succession and disturbance	iLand [45] LANDIS [46] SORTIE [47]	[48]
Dynamic global vegetation model (integrated biogeochemical and vegetation models)	CESM [49] ORCHIDEE [50] LPJ-GUESS [51]	[52]
Hybrid species distribution models	[53–55]	[56]
Meta-population (patch occupancy) or meta-community models	RAMAS Metapop [57] M-SET [58] [59, 60]	[61]
Cellular automata	[62]	[63]
Population abundance models	MIGRATE [64] Integrodifference equation models [65, 66]	
Individual-based models	RangeShifter [67] HexSim [68]	[69]
Integrated models		
Integrated human decision making and biophysical models	PALM [70] IMSHED [71]	[36]
Integrated socio-ecological models	[60, 72, 73]	

Pattern-Based and Process-Based Models of Landscapes and Land-Use Dynamics

Pattern-Based Models

Neutral Landscape Models Neutral landscape models (NLMs) are a set of approaches intended to create partially realistic landscape patterns, whilst remaining neutral with respect to the processes that formed them. The motivation for

using NLMs is that they provide a framework for landscape replication whilst controlling certain features of landscape configuration [75]; this allows for robust statistical analyses in relation to spatial structure [76, 77]. The first NLMs generated entirely random patterns using percolation theory [78]. Since then, hierarchical and fractal NLMs have been developed to improve the representation of patterns that are found in real landscapes—in particular, spatial autocorrelation, and repeated patterns across scales [79, 80]. Neutral landscapes have been shown to be statistically similar to real landscapes, but are unable to reproduce all landscape features [76, 81]. Thus, there are continuing developments to NLM methods to improve the representation of real landscape features such as patterns of land-ownership [82] and agricultural fields [83]. In addition to extensions of NLM models to incorporate increasing numbers of features, progress has also been made on developing the algorithms such that they are more efficient and free of some undesirable artefacts present in earlier versions [77].

NLMs are the landscape modelling approach that has been used the most in an ecological context. They have been used to investigate the ability of landscape indices and metrics to measure habitat fragmentation, spatial structure, and ecological processes [84–86] and to analyse methods for rescaling landscape data [87]. NLMs have also frequently been combined with population and movement models, for example to study how best to measure functional connectivity under varying levels of habitat fragmentation [88], to study the consequences of representing habitat as a binary as opposed to a continuous surface [89], to study the influence of habitat fragmentation on species persistence [90] and population size [91], and to study the importance of spatial scale when projecting species' range expansion dynamics [25]. They have also been used in the emerging field of eco-evolutionary dynamics, for example to demonstrate the potential for short and long distance dispersal strategies to evolve separately according to landscape configuration [92]. NLMs can also be used as null models when testing the ability of process-based models to recreate observed patterns (such as predictions of old-growth woodland distribution from a model of fire and land-form influences [93], or comparisons of fire spread algorithms [94]). NLMs are even used to guide the spatial planning of real-world experiments, as in the planting of experimental garden plots to study the importance of plant community spatial patterning for invasion resistance [95].

Statistical Landscape Models Aside from NLMs, there are a number of other approaches available from the field of landscape modelling that aim to generate anthropogenic landscape or land-use patterns without direct representation of the underlying processes. This class of model is typically termed either top-down (e.g. [96]) or pattern-based (e.g. [97]), due to the reductionist encapsulation of

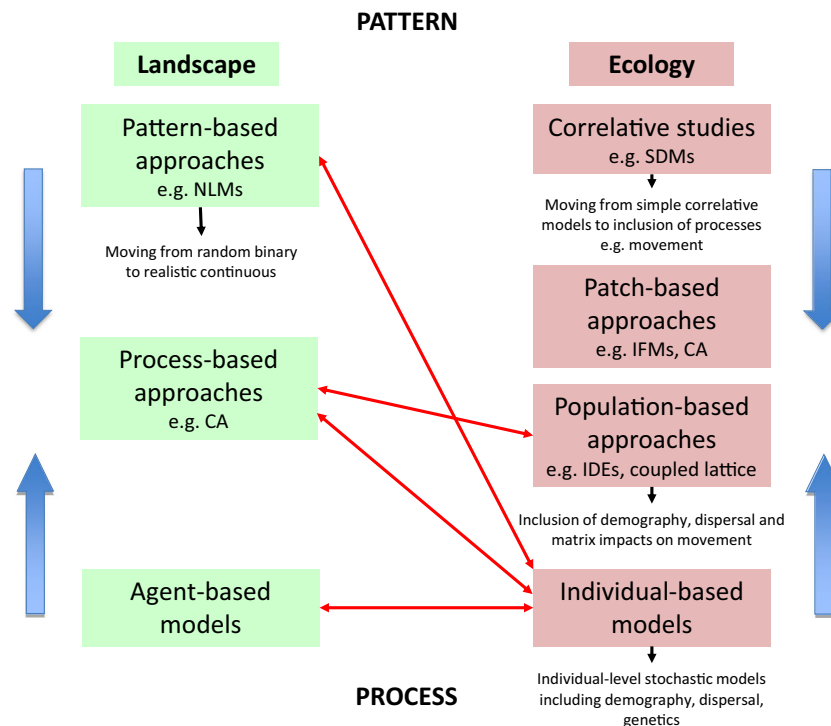


Fig. 1 The suite of approaches available for landscape and ecological modelling. Both fields have developed a range of approaches from relatively simple correlative and neutral modelling approaches through to complex agent or individual-based approaches. In both disciplines, there is increasing complementary use of approaches from different points along the complexity spectrum to address common problems (indicated by *blue arrows*). The *red arrows* highlight particular combinations of landscape and ecological model types that we believe offer major novel opportunities for landscape ecology. For instance, using emerging evolutionary, genetic, and epigenetic individual-based models together with NLMs may allow development of new theories of eco-evolutionary dynamics. There are great opportunities for providing

large spatial extent forecasts of how sets of species will respond to environmental changes (including land-use change) by using process-based land-use models together with population level ecological models such as IDEs, while combining process-based land-use models with IBMs has substantial promise for spatial planning questions in conservation at local and regional scales. Finally, we identify dynamic coupling of agent-based land-use models and individual based ecological models as a key future area where there is enormous scope to develop understanding of the dynamic of interacting socio-economic and ecological systems. (*NLM* neutral landscape model; *CA* cellular automata; *SDM* species distribution model; *IFM* incidence function model; *IDE* integrodifference equation)

observed system dynamics in general equations or algorithms based on statistically derived relationships. Here we refer to this group of landscape models as pattern-based. To date, these modelling approaches have been little used in an ecological context. Amongst the first landscape models was a highly influential application in urban studies (e.g. [98]) that used differential equations to model population growth. Subsequently, similar approaches were adopted in agricultural land-use change (e.g. [99–101]). Such models have become more and more sophisticated, incorporating a wide range of factors (e.g. [102]). Regression models and transition probability models are often used to project historical patterns of land-use and land-cover change into the future (e.g. [103–105]), and to study related effects such as patterns of air pollution (e.g. [106–108]). Such models have been developed to include demands for different land uses, allowing alternative future scenarios to be investigated [109]. There now exist very sophisticated and widely used models of land-use change that project future development of the land system on the

basis of systemic equations describing relationships between specific drivers and observed changes [96, 110–113]. These form the basis of the scenario-based climate change projections of the Intergovernmental Panel on Climate Change [114]. These types of models have rarely been coupled with ecological models, but see for example [96] in which land-use dynamics are represented by a large-scale pattern-based model and coupled with a process-based model of vegetation dynamics.

Cellular Automata Cellular automata (CA) models represent a middle ground between process- and pattern-based approaches. They have also been used to study land-use transitions [115] and residential dynamics [116] among other applications. CAs consist of a grid of cells which each exist in one of a finite set of states, with the future state of each cell determined by its previous state and that of its neighbours [117]. These models do not generally model the underlying processes directly, but rather the outcome of those processes. CA models can be suitable for systems in which neighbourhood

Table 2 Some common applications of landscape simulation modelling methods and potential data requirements when using such models

Type	Common applications	Basic data requirements
Landscape		
Neutral landscape models	<ul style="list-style-type: none"> • To generate artificial landscape patterns with predefined characteristics. • To verify other models, i.e. to investigate effects of landscape structure on model results. • To study effects of landscape structure on processes – social, ecological, biogeochemical, biophysical. 	<ul style="list-style-type: none"> • None
Process-based anthropogenic disturbance models	<ul style="list-style-type: none"> • To explore the potential effects of specific processes. • To generate artificial landscape patterns with predefined characteristics. • To identify whether modelled processes can generate observed landscape patterns. 	<ul style="list-style-type: none"> • None
Biogeochemical models	<ul style="list-style-type: none"> • To study hydrological and nutrient flows. 	<ul style="list-style-type: none"> • Soil, vegetation and climate data.
Process-based land-use models	<ul style="list-style-type: none"> • To study the role of individual behaviours in determining land-use patterns and dynamics. • To explore alternative behaviours under different economic, policy or environmental pressures. 	<ul style="list-style-type: none"> • Data to parameterise land-use decision-making. • Economic, policy or environmental data to drive the decision making.
Ecology		
Species distribution models	<ul style="list-style-type: none"> • To spatially or temporally extrapolate a known pattern of species habitat or climate associations. 	<ul style="list-style-type: none"> • Species observation data (presence-absence or abundance data). • Associated habitat and/or climate data.
Forest landscape dynamics, succession and disturbance	<ul style="list-style-type: none"> • To study processes and dynamics of vegetation at local to landscape scales. 	<ul style="list-style-type: none"> • Plant life-history data. • Disturbance data e.g. fire, pest-species.
Dynamic global vegetation model (integrated biogeochemical and vegetation models)	<ul style="list-style-type: none"> • To study vegetation cover at continental to global scales, incorporating biogeochemical and hydrological processes. 	<ul style="list-style-type: none"> • Plant life-history data. • Climate data.
Hybrid species distribution models	<ul style="list-style-type: none"> • To study species' habitat suitability whilst incorporating a representation of population dynamics, i.e. to move the patterns from pure "fundamental niche" towards the "realised niche". 	<ul style="list-style-type: none"> • Species observation data (presence-absence or abundance data). • Associated habitat and/or climate data. • Population demographics data.
Meta-population (patch occupancy) or meta-community models	<ul style="list-style-type: none"> • To study the viability of species populations. • To review potential habitat or population management options. 	<ul style="list-style-type: none"> • Population demographics data.
Cellular automata	<ul style="list-style-type: none"> • For studies in which each location can be represented by one of a number of states, and where state transitions are determined by neighbourhood interactions. 	<ul style="list-style-type: none"> • Data on potential system states. • Data on how neighbourhood interactions drive transitions.
Population abundance models	<ul style="list-style-type: none"> • To study population spread rates. 	<ul style="list-style-type: none"> • Population demographics data. • Dispersal or spread rate data.
Individual-based models	<ul style="list-style-type: none"> • To study the influence of individual behaviours and inter-individual variability on population dynamics. • To study the viability of species populations. • To review potential habitat or population management options. 	<ul style="list-style-type: none"> • Species life-history data.
Integrated models		
Integrated human decision making and biophysical models	<ul style="list-style-type: none"> • To study the interaction between humans and finite (often dynamic) environmental resources. 	<ul style="list-style-type: none"> • Dependent on the component models (as above).
Integrated socio-ecological models	<ul style="list-style-type: none"> • To study interactions between humans and species populations. 	<ul style="list-style-type: none"> • Dependent on the component models (as above).

association is important, but can struggle to incorporate more complex behaviour such as human decision making, at least without deviating substantially from the typical CA approach [118]. CAs have generally been applied with either a landscape or an ecological focus, however they have also been applied in landscape ecology studies, for example to evaluate conservation interventions in a human-dominated tropical landscape [119].

Overall, landscape modelling approaches that focus on the replication of observed patterns may help to identify the probabilities of different landscape or land-use transitions and to make conditional predictions, but they leave the identities of the underlying causative mechanisms open to interpretation [120]. Links between spatial patterns and ecological or socio-economic conditions have frequently been shown to be informative in some circumstances, but potentially

misleading in others (e.g. [85, 121, 122]), especially where spatial or temporal dynamics are neglected (e.g. [123, 124]). Furthermore, in encoding previously observed relationships into algorithms or equations, models of this kind become unsuitable for projecting changes in systems in which underlying mechanisms are not constant (as in socio-ecological systems subject to the varied and unpredictable forces of human behaviour; see e.g. [125]). Therefore, while neutral and pattern-based models have substantial roles to play, deeper understanding or exploration of system dynamics requires additional models that explicitly account for underlying processes and prioritise accurate description of the processes over pattern replication [126].

Process-Based Models Process-based landscape models are becoming increasingly used, with inclusion of progressively more detailed representations of the key behaviours and dynamics that drive landscape patterns. The application of such models inevitably involves a choice of processes to represent, as well as a choice of technical modelling approach to make the given processes tractable. A wide array of approaches exist for many different purposes and at different scales of detail and application. A number of highly focussed artificial landscape generators have been developed, which simulate a specific process to replicate real-world patterns. Many of these are concerned with human impacts on landscape, for example models of road development [127], and of the conversion of forests to arable land by the processes of road and field creation [30]. A substantial focus of modelling of this kind has been on urban growth [128–130]. Equivalent approaches are taken to discrete processes in natural systems. For instance, watershed models (e.g. [131]), which have been applied to study wetlands and riparian systems [132]. Hydrological models have also been integrated with nitrogen dynamics models to study the effect of the spatial distribution of agricultural practices [133].

Agent-Based Models Process-based models are also increasingly being applied in circumstances where the processes themselves are unclear or incompletely understood. In these cases, models are more exploratory than predictive in purpose (initially, at least), being used as “virtual laboratories” in which the effects of particular processes can be investigated and related to real-world observations [134, 135]. In landscape science, this is especially true of models of land-use change, where process-based approaches such as agent-based modelling (ABM) are used to increase model accuracy but also to explore alternative accounts of human decision-making under socio-economic or environmental pressures [136]. Process-based models are both relevant and problematic in this context because of the crucial role of complex individual, social, and institutional behaviours in determining the nature of land-use change. Such explorations are not possible without incorporating additional processes and interactions into our models,

even though appropriate limits on model complexity may be hard to identify.

Because of the complexity of the modelled system, land-use ABMs initially focused on carefully constrained systems and behaviours, covering small geographical extents, and specific land-uses (e.g. [137–140]). While these models generally retain a relatively narrow focus, they have expanded in scope in a number of ways over recent years. For instance, considerable attention has been paid to “upscaling” methodologies to allow model application at regional to global scales (e.g. [33, 35, 141, 142]). Thematic extension has also occurred, particularly through linkages between models of land-use and natural systems, with behavioural responses to environmental change often being prioritised [143, 144]. Additional detail has also been incorporated within the land-use system, with several recent models investigating the interactions of individual and institutional entities [33, 145, 146] (Fig. 2). This latter development is particularly notable because it makes such models ideal for testing the (potentially unexpected) outcomes of policy interventions [148–150]. Incorporating some of the complexity of these interactions into models can lead to the identification of unexpected non-linear behaviours and regime shifts [60, 151].

Notwithstanding their increasing contribution to knowledge about the land-use system and its links with other systems, process-based models of land-use change face several substantial difficulties. They require very many specific data on the characteristics and decision-making of individual actors when applied to the real world, and these data are not widely available. They are also difficult to validate robustly or to use predictively [152]. Perhaps most fundamentally, true (cognitive) process accuracy is hard to achieve [153, 154]. While process-based landscape models cannot yet achieve the same generality, efficiency or transparency as pattern-based models (and have, therefore, largely been used in a more targeted and complementary role), further refinement of the process-based approach does represent the best means of projecting land-use into future socio-economic conditions that are very different to those experienced to date. Although there are currently few examples of process-based landscape models being used in an ecological context (but see [60, 73]), these process-based landscape modelling approaches are now maturing sufficiently that they provide excellent opportunities to be used in conjunction with ecological models to address key questions in landscape ecology.

Pattern-Based and Process Based Models in Spatial Ecology

Pattern-Based Models

As in landscape modelling, pattern-based modelling approaches have been and continue to be widely used in

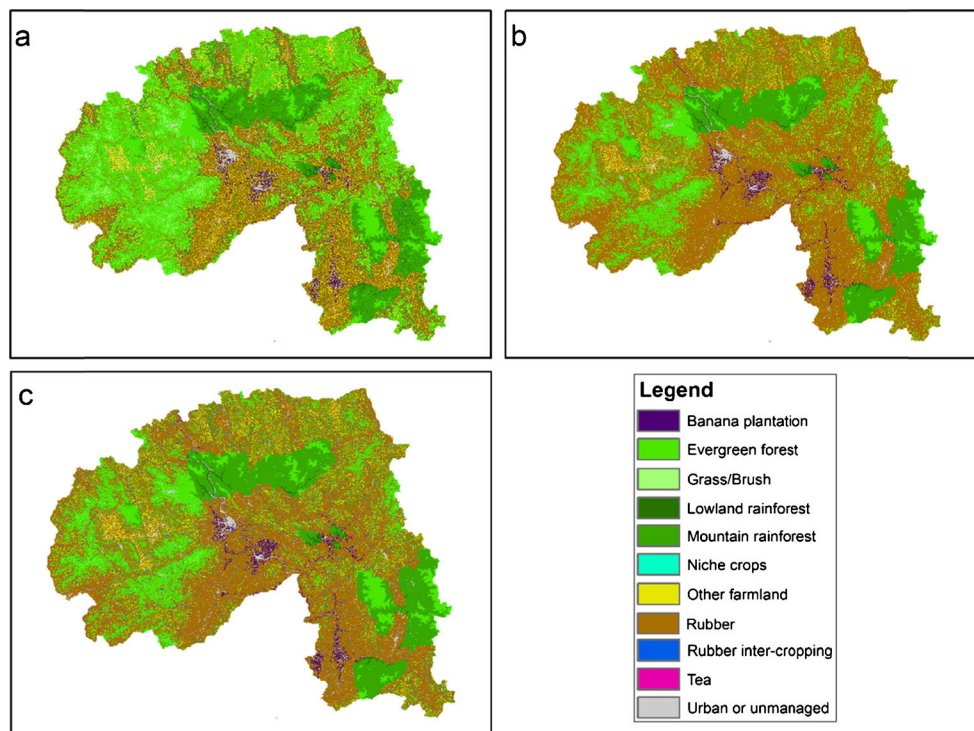


Fig. 2 Process-based land-use models are being developed rapidly and offer considerable promise for projecting land-use into the future. There is considerable potential to link these emerging models with ecological models, including integrodifference and individual-based models, to project biodiversity and ecosystem service futures. This example shows output from the agent-based model CRAFTY [33] of land-use scenarios in Xishuangbanna, China. Note: these are just a few of many scenarios, and should not be considered as predictive. **a** Model of land-use in 2010;

b projection for 2030 with increasing demand for rubber; **c** projection for 2030 with increasing demand for rubber, and institutional support for new niche crops and rubber inter-cropping. An ecological model, such as RangeShifter [67], could be used to assess population viability or potential for species range shifting on these future landscapes, while ecosystem modelling tools, such as InVest [147], could be used to project future ecosystem service provision under alternative future land-use scenarios

ecological studies. A key class of these pattern-based models includes species distribution models (SDM) or environmental niche models. These models use statistical methods to correlate patterns of species presence or occurrence with environmental factors [155, 156]. Many different approaches exist, all of which have underlying uncertainties related to the algorithm, variable selection, and biotic factors [157–161]. However, a fundamental assumption of these approaches is that the environmental factors can be measured throughout the landscape and that their relationship with species presence/occurrence remains constant in space and time [162]. This can be particularly problematic when studying invasive species [163]. Despite the limitations, SDM approaches have been used for species delimitation [164], to study the past distributions of species [165], to identify potential new areas of occurrence [166], and to project environmental niches into future conditions [167]. Whilst SDMs can predict areas where environmental conditions are broadly suitable there is now broad recognition that their application is limited, especially for making projections under rapidly changing conditions, by the lack of incorporation of ecological processes including intraspecific competition, dispersal, and interactions with other species [56, 168–170]. Further, under rapidly

changing conditions and especially at the physiological limits of a species' tolerance, we may expect to see evolution occurring on an ecological timescale. Thus, to improve our ability to project biodiversity futures, it will be important that we develop process based distribution models [170–172].

Process-Based Models

Metapopulation Models A shift of interest from pattern to process, and the need for spatial context in ecological models, led to the development of Levins-style metapopulation models [173, 174]. These models are also referred to as patch-occupancy models since they typically represent populations as either present or absent in each habitat patch, and do not model the number of individuals in different elements of the landscape. Metapopulation models are widely used for population viability analysis, to identify threatened populations and potential management options [175–177]. One such example is the incidence function model (IFM), which is derived from a first-order linear Markov chain of the presence or absence of a species in a habitat patch [178] and assumes constant, but patch-specific probabilities of colonisation and extinction. In the IFM, the probability of extinction is dependent on

population size (which is in turn dependent on patch area), and probability of colonisation is dependent on the distance to existing populations, and the areas of those patches and the patch being colonised. The IFM has been applied extensively, demonstrating that such models can be used to assess the potential of networks of habitat patches to support viable metapopulations of given species [178, 179]. While these metapopulation approaches are spatially explicit in that they incorporate the distances between patches they are not, in this standard form at least, landscape ecological models, as they do not account for what is between the patches, i.e. the matrix. However, extensions to the classical approach do now account for the matrix, most often by assuming that different matrix environments are more or less readily moved through by a dispersing organisms, and then calculating the least cost paths between patches and using these in place of the Euclidean distances [180–182].

Coupled Map Lattices To incorporate population dynamical realism that cannot be captured in classical metapopulation models, researchers have made use of a range of approaches that model population densities or abundances across either continuous or discretized, patchy modelled environments. A coupled map lattice is the technical name for a broad group of models that represent the environment as a grid of cells, each of which potentially supports a population. In these models, local dynamics in each patch are simulated and the patches are linked by dispersal. The local dynamics are modelled using one of a range of well-used population dynamic models that can incorporate differing degrees of complexity (for example they assume non-overlapping generations using the Ricker model [183] or similar, or they may include stage structure using a matrix-based formulation). Similarly dispersal can be incorporated in differing degrees of complexity/realism, most often being based on either nearest neighbour movements or a dispersal kernel approach [184, 185]. Coupled map lattices have been used to address a broad range of ecological, and eco-evolutionary questions. For example, they have been used to simulate the range expansion of species responding to climate change over a complex landscape [64].

Integrodifference Equations Another important class of spatial population models are integrodifference equations (IDEs), which are often used to predict species spread over landscapes [66, 186, 187]. As with coupled map lattices, these models explicitly represent local demography and dispersal. However, they typically assume space to be continuous (but see [188]). This means that estimates of population spread in homogeneous landscapes are possible via analytical techniques [65, 189], rather than based on costly simulation techniques, thus making parameter sensitivity analysis straightforward. Notable recent progress has been made on extending these approaches to work on heterogeneous landscapes,

although analytical expressions for spreading speeds have only been found for landscapes where the structure is a regular repeating pattern [190–192]. Because of the challenges involved in developing these analytical techniques and a lack of computational resources, few mechanistic IDE models have used large complex mapped heterogeneous landscapes to model spreading species. However, with increasing computing capacity and efficient algorithms (e.g. [193, 194]) it is now possible to predict species spread over realistic 2D landscapes. In Fig. 3, we plot the spread of spruce (*Picea*) trees in Glacier Bay, Alaska, using an IDE model. This area underwent a period of deglaciation which left fertile soil behind in the thawed terrain. Using land cover data [196], we created a landscape suitability map, which we relate to tree fecundity in the IDE model. The resulting model predicts the spread of spruce trees over the landscape, giving a spread rate that is commensurate with empirical estimates [197].

Individual-Based Models When researchers make use of models that aggregate individuals into populations they are, at least implicitly, making the strong assumption that individuals behave identically [198, 199]. Individual-based models (IBMs) (the ecological equivalent of land-use ABMs) are now widely used to study ecological processes, with their major strength being that they account for inter-individual, as well as spatio-temporal variation in individual behaviour. IBMs also make it more straightforward to relax assumptions that are frequently made in density-based models related to the omniscience of organisms, and their perfect adherence to optimal strategies [69]. In reality, organisms only have bounded rationality, and make mistakes in strategy selection—models that aggregate up to groups of populations will miss the stochasticity that arises from this effect. IBMs are particularly useful for constructing plausible hypotheses about how aggregate-level patterns emerge from individual behaviour, the impact of heterogeneity on system outcomes and for identifying the consequences of management decisions [120].

Individual-based models have seen substantial use in landscape ecology. They have been used to address questions at a range of spatial and temporal scales varying from models of home range dynamics and daily movements [200, 201] to multi-decadal models of species range shifting [19]. IBMs have also been used extensively to study landscape connectivity: identifying threats to populations [202] and testing the impacts of future scenarios [203, 204]. Notably a stochastic IBM approach has recently been demonstrated to provide better estimates of inter-patch connectivity (in terms of correlation with genetic estimates) than least-cost path and circuit theory approaches [205]. Most applications of IBMs for landscape connectivity have focussed on the process of dispersal, while the ability of the focal organism to form home ranges is rarely explicitly modelled. Recent work suggests that a focus on dispersal (to the point of ignoring home range movements)

Spread of spruce trees



Fig. 3 Emerging mathematical approaches for simulating population spread across heterogeneous landscapes offer substantial potential for landscape ecology, making possible highly computationally efficient projection of species range dynamics over large spatial scales. This is an example where the spread of spruce (*Picea*) trees at Glacier Bay, Alaska, is simulated. We simulate a 2D IDE using the adaptive mesh refinement algorithm from [193]. We assume a piecewise-linear growth function where the landscape-dependent population growth rate, $r_0(x)$, is constant below the carrying capacity, K (assumed, without loss of generality, to be 1). That is $f(N_t(x)) = \min(r_0(x)N_t(x), K)$, where $N_t(x)$ is

the population density at generation t and location x , and $r_0(x)$ is 15 years^{-1} on fertile land [195] and zero elsewhere. We also assume a 2D exponential kernel with a mean dispersal distance of 85 m. The landscape suitability map was calculated from the National Land Cover Database 2011 [196]. The figure shows areas of water, hostile, and fertile land. The contours depict predicted annual maximal spread of the spruce trees from the initial location. For the given parameters, the IDE gives a spread rate of 367 m year^{-1} , which closely matches empirical estimates [197]

may lead to an overestimation of functional connectivity [206]. However, it remains a challenge to identify the mechanisms by which stable home ranges can emerge from unbounded movement paths, with a number of alternative modelling approaches in use [207]. In many of the existing IBMs of movement processes across complex landscapes the key questions being addressed have related to connectivity [208–210], emergent dispersal mortality [211, 212], and home range formation [206, 213, 214], but in many cases these individual-based movement models have not been linked to models of population dynamics. When such links are made, it is possible to gain important new insights into the dynamics of species living on complex landscapes and into potential consequences of alternative management interventions [215]. In one recent example, [216] used RangeShifter to combine a stochastic IBM for movement with a spatially explicit population model to explore alternative plausible management scenarios for birds in the Taita Hills in Kenya, a biodiversity hotspot. The results demonstrated that while adding new habitat patches boosted overall population abundance, potential

risks exist of placing them in certain locations that may represent “disperser sinks”, effectively halting dispersers that would otherwise have immigrated into other existing patches and, therefore, reducing abundance in those existing patches.

Integrated Models With a growing recognition of the importance of ecosystem services, there is increased understanding of the need to understand the interactions between human decision making, our environment and ecological processes. A number of modelling approaches now integrate human behaviour with biogeochemical processes, for example linking human decision making to hydrological processes [217–220] and soil nutrient flow [70, 221–223]. There have also been studies on interactions between human decision making and ecology (habitat/land cover), for example in timber harvesting [224], and the impact of human activities on habitat metrics [225, 226]. Interactions between farmer decision making and ecological processes have perhaps received the greatest focus, with farm-based ABMs integrated with CA [72] and spatial stochastic simulation [73] to model pest species, and with

metacommunity models to study the impact of agri-environmental incentive schemes on biodiversity [60].

Model Verification and Validation

The choice of modelling approach is complicated by the difficulties and implications of verifying, validating, or otherwise evaluating model performance. Verification and validation can be conducted in a number of ways dependent on the type of model being used. A number of previous studies have highlighted confusion in the literature about the meaning of validation for simulation models [227, 228]. “Validation” is often used as a catch-all term incorporating concepts of verification, evaluation, analysis, and validation [228]. For pattern-based approaches, the approaches to verification and validation are relatively clear: if there is a pattern that the model aims to match, then the model is verified and calibrated to a subset of this pattern/data, and once the model has been verified as suitable, it is validated against the remaining pattern/data (i.e. to test the model’s predictive accuracy on independent data). This approach of course assumes that the purpose of the study is to match an existing pattern, but many studies aim to predict patterns in new geographic or climatic space. For such studies validation of final predictions is clearly not possible; instead the model must be verified and validated for current patterns. Predictions can then only be accepted if the relationship between the independent and dependent variables is expected to remain constant. Methods for assessing accuracy include the area under the curve of the receiver operating characteristic (AUC) for binary data (e.g. species presence-absence), and the Pearson correlation coefficient (r^2) for count data (e.g. species abundance). In land-use studies, a number of methods are commonly used to compare categorical maps [229, 230], although recent work has exposed potential weaknesses in some of these methods (Kappa indices) [231, 232]. Across fields, the practice of model verification and validation varies widely, often to the detriment of interpretability [228, 233–235].

Process-based models face particular difficulties because they are often required to incorporate processes that are not fully understood, or at least difficult to validate; the quest for process accuracy makes errors of omission harder to justify, but errors of commission more likely to occur. In ecological applications it may be reasonable to validate process representations on the basis of the patterns they produce, assuming that those processes are stable through time (e.g. breeding rates, dispersal characteristics). However, models involving more dynamic processes, especially those related to human behaviour, may only be able to achieve reasonable, as opposed to fully “valid”, representations [236]. In such cases, model transparency becomes crucial, along with verification of intermediate simulation outputs through modular testing [237],

and rigorous exploration of model behaviour through experiments or sensitivity and uncertainty analyses [238].

Nevertheless, models of complex natural and human systems can never be entirely accurate. The simplification inherent in the modelling process inevitably reduces accuracy, especially in its requirement for artificial systems boundaries [239]. Furthermore, the parallel testing of processes and resulting patterns is likely to require unsafe assumptions about unique causal relationships. Fundamentally, model verification and validation requires the same careful judgement as model design and use, with various analytical techniques useful for increasing understanding of model performance, but unable to demonstrate complete validity.

Current Opportunities

It is apparent from our brief review that there are many examples of links between land-use models and ecological models successfully providing increased understanding of how landscape ecological systems operate, making predictions or informing management. Our view is that developing greater linkages between land-use models and ecological models will be vital in meeting the current challenge of developing improved forecasts for biodiversity under environmental change [240]. Some combinations of land-use modelling and ecological modelling are particularly well represented. NLMs are the best represented class of landscape model in an ecological context, often being used in combination with metapopulation models to provide generic theory on how well populations persist in fragmented landscapes. NLMs are also increasingly used in conjunction with density based models and IBMs. It is clear that NLMs will continue to be an important part of landscape ecological modelling because of these combined applications.

We do not suggest that model integration should be used in all situations: many questions can and should be tackled with simpler stand-alone models (as discussed above), and model combinations may create as many problems as they solve. However, there are also some major gaps where combinations of landscape and ecological models have not been exploited to their potential. This is particularly true for the landscape models and ecological models that have only recently been developed in their respective fields. Here, we highlight five opportunities for combining landscape and ecological models in new ways to address what we believe to be a set of interesting and important questions. By no means is this intended to be an exhaustive list, and it certainly reflects our particular set of interests. We would encourage the reader to consider how their own particular field may benefit from new combinations of landscape and ecological model as we are certain there are great opportunities to be gained by looking beyond the approaches that we are each most accustomed to taking.

While NLMs have already been much used in landscape ecology, they certainly remain an important component in the landscape ecologist's toolbox and the first opportunity in our list is for NLMs to be coupled with emerging eco-evolutionary modelling approaches to tackle new questions. Our second also makes use of NLMs, in this case to systematically assess how model choices related to the spatial and temporal resolution of representing processes and/or patterns influences model outcomes—and to use these insights to guide best use of pattern-based and ABM land-use models. Our third opportunity provides one example of many that we believe exist for making use of pattern-based landscape models together with intermediate-complexity ecological models to make broad scale projections for how ecological systems will respond to environmental changes, including land-use change and climate change. Our fourth opportunity again includes pattern-based land-use models, but this time together with IBMs in order to inform future-proof spatial planning taken for conservation at more local scales. The final opportunity that we highlight is the dynamic coupling of complex, process-based land-use (i.e. agent-based) and ecological (i.e. individual-based) models to begin to develop theoretical insights into the dynamic interplay and non-linear feedbacks that are a key feature of socio-ecological systems.

Eco-Evolutionary Simulations on NLMs

There has been substantial recent interest in rapid evolutionary dynamics that occur fast enough to be important for ecological processes. These eco-evolutionary dynamics include, for example, evolutionary rescue, whereby a population facing a change in the environment would become extinct if not for evolutionary change [241, 242] and the rapid evolution of dispersal in fragmented landscapes [243–245] or during range expansions [246–248] or range shifts. While an increasing number of researchers are developing models to explore eco-evolutionary dynamics, they have yet to be linked to standard methods in landscape ecology in order to answer questions such as “How does the likelihood of evolutionary rescue depend upon the spatial configuration of different habitat and matrix elements” or “How do the movement rules adopted by individuals during dispersal depend upon the amount and arrangement of habitat” (but see [245] for one example). We also note that there are opportunities for novel work that takes a landscape perspective for major emerging themes in evolutionary biology. As two examples, we could begin to address questions related to the role of epigenetics in conferring adaptation across spatially heterogeneous landscapes by extending recent models that have focused on single populations [249, 250]. We could also ask how landscape properties influence the role of sexual selection in driving trait evolution and how this evolution then shapes the dynamics of species ranges by extending individual-based models from evolutionary biology

[251, 252], or how different landscape structures may drive the evolution of different mating systems, again by exploiting the new and flexible IBMs [251, 253] that are now being developed in the evolutionary field.

Use of NLMs for Systematic Assessment of Modelling Decisions

NLMs can be (and are) used to determine optimal resolutions and scales at which to provide landscape model output and/or to model processes, and novel opportunities of this kind can be expected as new models are introduced and tested. NLMs provide an ideal method for addressing key issues that we have discussed above, for example by investigating the effects of model representation of scale and temporal dynamics on model outputs [25, 254]. A major strength of the NLM approach is that it allows studies to focus on specific features of landscape structure [27], often systematically varying one or a few features while holding others constant. NLMs can provide an important tool to determine the optimum design of pattern-based and ABM landscape models such that they provide unbiased projections when used in an ecological context.

Modelling Organism Spread Rates by Integrating Population Density Ecological Models and Pattern-Based Landscape Models

A critical current ecological question relates to the rate at which species will be able shift their ranges in order to track climate change. Currently, large scale projections for the rates of spread of large numbers of organisms make extremely simplifying assumptions regarding the ecology and the landscape. For example, dispersal may be modelled as a negative exponential function derived from average dispersal distance [255], neglecting the influence of the intervening habitat matrix. In recent work, [256] used both IDEs and RangeShifter (an IBM) to estimate the potential spread rates of terrestrial mammal species, making the prediction that almost 30 % of terrestrial mammal species have spread rates slower than the velocity of climate change. This approach was interesting as it used a trait-based model to overcome data limitations. However, it only estimated rates of spread across homogenous landscapes. A major future challenge for landscape ecological modelling is predicting how well species will track climate change across complex, and temporally varying landscapes. Using IDEs, refined as in Fig. 3 to work over complex landscapes, offers a great opportunity for rapid progress.

Study Population Viability under Future Scenarios Using IBMs with Output from Pattern-Based Landscape Models

For large spatial extent modelling, targeting projections across many species, combining IDEs with pattern-based landscape

modelling is likely to offer the greatest rewards for researchers. However, when our focus is on a smaller number or focal species and at a smaller spatial extent, IBMs can be coupled with pattern-based landscape models to make projections for informing management decisions. The advantage of the IBM approach is that it allows for greater behavioural complexity, for example in critical dispersal behaviour, to be incorporated and can also allow for inter-individual heterogeneity in behaviours. For smaller numbers of species we can reasonably expect to be able to acquire the data to parameterise this extra complexity. Recent work has used IBMs that incorporate current landscapes to inform the choice between alternative options for landscape management targeting birds in fragmented forests [216] to inform the design of reintroduction or assisted colonisation strategies [257] and to determine how alternative possible management options for UK forests will facilitate the range shifting of species [19]. However, there are a lack of studies that consider how these conservation strategies will fare in the context of dynamically changing landscapes and thus using the IBMs with pattern-based models that provide spatio-temporal projections of landscapes would be a particularly valuable direction to pursue.

Dynamic Coupling of ABMs of Land-Use with IBMs for Ecological Systems

There is potential to gain generic understanding of the potentially complex interplay that human-environment or socio-ecological systems are likely to exhibit, through dynamic coupling of ABMs of land-use with IBMs for ecological systems. For example, while we often model the impacts of land-use on the distribution and abundance patterns of a species, we might also expect that the local abundances of either pest species or species of conservation concern may impact on the decisions that a landowner makes on their use of their land. This decision may be driven by straightforward economics (e.g. not planting a particular crop when a disease or pest is known to be present) or may be driven by regulation (e.g. not being allowed to damage habitat of a protected species). There can, therefore, be a dynamic interaction between land-use and ecological variables. While there is an expectation for such coupled systems to possess nonlinear dynamics, feedback mechanisms, time lags, and surprising behaviours [258, 259], the vast majority of existing work has focused either on the social or on the environmental issues, potentially neglecting crucial system interactions [37, 260]. Some studies have considered dynamic system interactions and shown promising results (e.g. [71–73]), including non-linear responses to agri-environmental biodiversity incentive schemes [60]. However, in these existing efforts to link the approaches, there have been fundamental differences between the representation of social and ecological elements. In particular, whilst moderately complex ABMs have been used to

represent the social system, the ecological system has, in these coupled modelling exercises, been represented through either habitat metrics, CA, or metacommunity modelling. We agree with [150] who suggested that an important future direction for socio-ecological modelling is to represent both systems at an individual level. Such an approach can be extremely valuable in future landscape ecological modelling and should further aid the identification of critical feedback mechanisms, and the ex-ante assessment of potential environmental and land-use policies.

Conclusions

We envisage that our research aims will increasingly require the modelling of interacting social and ecological systems. This will inevitably make model design and development more challenging. Integrated models may be substantially more complex than discrete models, not least because effects that would previously have been isolated within subsystems may propagate throughout the integrated system [261]. The development of models to represent systems from multiple fields of study can be a significant technical challenge, a task likely to require multi-disciplinary collaborative work [150, 262].

Issues of scale and aggregation become particularly important when linking landscape, land-use, biogeochemical, ecological, and evolutionary processes. Whilst the issue of spatial and temporal scale in landscape ecology has been widely discussed [2, 24, 263–266], it is of particular importance when integrating multiple system models [261, 267]. Across the wide range of topics that encompass landscape ecology, different processes and systems operate at different spatial and temporal scales and resolutions [268]. The level of aggregation of actors and processes can also be important for shaping interactions. For example, land-use decision-making may occur quite differently under a global and regional economy [269]. In both ecological IBMs and land-use ABMs, individuals may be aggregated into cohorts or groups, or directed by constraints and rules at a group level [270]. For example, households may be modelled as single land-use agents [271], and groups or nests may be modelled as an ecological “super-individual” [272]. When the processes being studied occur at group level, such aggregations are an important aspect of model design, maximising model simplicity while still generating the patterns or behaviours of interest [273].

Whilst the issues of scale are well recognised (e.g. systematic bias when modelling animal movement [25], influence of neighbourhood size on models forest fires [274]), few studies have used quantitative methods to determine the most appropriate scale (but see [275–277]). The geometry of the landscape is another important, but rarely considered issue. Use of regular grids introduces bias when studying connectivity and animal movement, since patterns are formed based on the

shape and orientation of the underlying grid structure [278]. The vast majority of landscape simulation studies use regular square geometry. Some studies have used hexagonal geometry because it gives equal weight to neighbourhood interactions [279–281]. Nevertheless, this does not remove the grid-induced bias [278], but only changes the pattern of the bias [282]. Irregular grids have been suggested as a solution [278, 283, 284], and have been used (for example in a CA of land-use change [285]), but their wider application is still rare. In light of this, [23] suggest the use of multiple landscape geometries to account for this potential source of modelling bias.

Another important consideration for future landscape ecological modelling is the temporal dynamics of the study system. Whilst some landscape ecological studies have incorporated the effect of temporal environmental dynamics (e.g. [286–289]), such studies are rare and have generally focussed on environmental variability over short time periods. Where the longer term impacts of environmental or landscape change on animal populations are considered, studies rarely treat the landscape as a temporally dynamic system [262, 290], instead running separate simulations with and without a prescribed landscape change (e.g. [19, 204, 291]). We believe that the future of landscape ecological modelling is in moving beyond models of human-environment systems which commonly consider only a unidirectional interaction, (i.e. humans are either drivers or users of the environment, but rarely both [267, 292]) towards representing human-environment interactions as bi-directional, with dynamic feedbacks from the human managed landscape to the ecological system and vice versa. Fully dynamically coupled models will provide the ideal environment to gain improved understanding and thus a capability to manage dynamic landscape ecological systems.

Acknowledgments This work was supported by the award of the Natural Environment Research Council grant NE/J008001/1 to J.M.J.T. and N.W.S. was additionally supported by the Science and Technology Facilities Council.

Compliance with Ethical Standards

Conflict of Interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

Open Access This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

References

1. Turner MG. Landscape ecology: the effect of pattern on process. *Annu Rev Ecol Syst.* 1989;20:171–97. Available from: <http://www.jstor.org/stable/2097089>.
2. Wiens JA. Spatial scaling in ecology. *Funct Ecol.* 1989;3:385–97. Available from: <http://www.jstor.org/stable/10.2307/2389612>.
3. Wiens JA, Stenseth NC, Van Horne B, Ims RA. Ecological mechanisms and landscape ecology. *Oikos.* 1993;66:369–80.
4. Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, et al. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience.* Oxford University Press; 2008 [cited 2016 Feb 11];58:501. Available from: <http://bioscience.oxfordjournals.org/content/58/6/501.full>.
5. Elphick CS. How you count counts: the importance of methods research in applied ecology. *J Appl Ecol.* 2008;45:1313–20.
6. Gilbert-Norton L, Wilson R, Stevens JR, Beard KH. A meta-analytic review of corridor effectiveness. *Conserv Biol.* 2010;24:660–8.
7. Peck SL. Simulation as experiment: a philosophical reassessment for biological modeling. *Trends Ecol Evol.* 2004;19:530–4. Available from: <http://www.sciencedirect.com/science/article/pii/S0169534704002162>.
8. Sui DZ, Zeng H. Modeling the dynamics of landscape structure in Asia's emerging desakota regions: a case study in Shenzhen. *Landsc Urban Plan.* 2001 [cited 2016 Jan 26];53:37–52. Available from: <http://www.sciencedirect.com/science/article/pii/S0169204600001365>.
9. Weng Q. Land use change analysis in the Zhujiang Delta of China using satellite remote sensing, GIS and stochastic modelling. *J Environ Manag.* 2002 [cited 2016 Feb 16];64:273–84. Available from: <http://www.sciencedirect.com/science/article/pii/S0301479701905092>.
10. Turner DP, Ollinger SV, Kimball JS. Integrating remote sensing and ecosystem process models for landscape- to regional-scale analysis of the carbon cycle. *Bioscience.* Oxford University Press; 2004 [cited 2016 Mar 15];54:573. Available from: <http://bioscience.oxfordjournals.org/content/54/6/573.full>.
11. Zurell D, Berger U, Cabral JS, Jeltsch F, Meynard CN, Münkemüller T, et al. The virtual ecologist approach: simulating data and observers. *Oikos.* 2010;119:622–35. Available from: <http://doi.wiley.com/10.1111/j.1600-0706.2009.18284.x>.
12. Turner BL, Lambin EF, Reenberg A. The emergence of land change science for global environmental change and sustainability. *Proc Natl Acad Sci U S A.* 2007 [cited 2015 Oct 27];104:20666–71. Available from: <http://www.pnas.org/content/104/52/20666.short>.
13. Drew CA, Wiersma YF, Huettmann F. Predictive species and habitat modeling in landscape ecology. In: Drew CA, Wiersma YF, Huettmann F, editors. *New York: Springer New York*; 2011 [cited 2016 Feb 22]. Available from: <https://ncsu.pure.elsevier.com/en/publications/predictive-species-and-habitat-modeling-in-landscape-ecology-conc>.
14. Epperson BK, McRae BH, Scribner K, Cushman SA, Rosenberg MS, Fortin M-J, et al. Utility of computer simulations in landscape genetics. *Mol Ecol.* 2010 [cited 2016 Jan 26];19:3549–64. Available from: <http://doi.wiley.com/10.1111/j.1365-294X.2010.04678.x>.
15. Millspaugh JJ, Thompson FR, editors. *Models for planning wild-life conservation in large landscapes.* Academic Press; 2011.
16. Gimona A, Poggio L, Brown I, Castellazzi M. Woodland networks in a changing climate: threats from land use change. *Biol Conserv.* 2012;149:93–102. Available from: <http://www.sciencedirect.com/science/article/pii/S0006320712000730>.
17. McRae BH, Hall SA, Beier P, Theobald DM. Where to restore ecological connectivity? Detecting barriers and quantifying

- restoration benefits. *PLoS One*. Public Library of Science; 2012 [cited 2016 Mar 14];7:e52604. Available from: <http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0052604>.
18. Dickson BG, Roemer GW, McRae BH, Rundall JM. Models of regional habitat quality and connectivity for pumas (*Puma concolor*) in the southwestern United States. *PLoS One*. Public Library of Science; 2013 [cited 2016 Mar 14];8:e81898. Available from: <http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0081898>.
 19. Synes NW, Watts K, Palmer SCF, Bocedi G, Bartoń KA, Osborne PE, et al. A multi-species modelling approach to examine the impact of alternative climate change adaptation strategies on range shifting ability in a fragmented landscape. *Ecol Inform*. 2015;30:222–9. Available from: <http://www.sciencedirect.com/science/article/pii/S1574954115000941>.
 20. Green DG, Sadedin S. Interactions matter—complexity in landscapes and ecosystems. *Ecol Complex*. 2005;2:117–30. Available from: <http://linkinghub.elsevier.com/retrieve/pii/S1476945X0500022X>.
 21. Canters F, Genst W De, Dufourmont H. Assessing effects of input uncertainty in structural landscape classification. *Int J Geogr Inf Sci*. Taylor & Francis Group; 2002 [cited 2016 Jan 27];16:129–49. Available from: <http://www.tandfonline.com/doi/abs/10.1080/13658810110099143>.
 22. Xu C, Gertner GZ, Scheller RM. Uncertainties in the response of a forest landscape to global climatic change. *Glob Chang Biol*. 2009 [cited 2016 Jan 22];15:116–31. Available from: <http://doi.wiley.com/10.1111/j.1365-2486.2008.01705.x>.
 23. Holland EP, Aegerter JN, Dytham C, Smith GC. Landscape as a model: the importance of geometry. *PLoS Comput Biol*. 2007;3:1979–92. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/17967050>.
 24. Wu J. Effects of changing scale on landscape pattern analysis: scaling relations. *Landsc Ecol*. 2004 [cited 2016 Jan 27];19:125–38. Available from: <http://link.springer.com/10.1023/B:LAND.0000021711.40074.ae>.
 25. Bocedi G, Pe'er G, Heikkinen RK, Matsinos Y, Travis JMJ. Projecting species' range expansion dynamics: sources of systematic biases when scaling up patterns and processes. *Methods Ecol Evol*. 2012;3:1008–18. Available from: doi:10.1111/j.2041-210X.2012.00235.x.
 26. Hobbs R. Future landscapes and the future of landscape ecology. *Landsc Urban Plan*. 1997 [cited 2015 Oct 30];37:1–9. Available from: <http://www.sciencedirect.com/science/article/pii/S0169204696003647>.
 27. Wang Q, Malanson GP. Neutral landscapes: bases for exploration in landscape ecology. *Geogr Compass*. 2008;2:319–39. Available from: doi:10.1111/j.1749-8198.2008.00090.x.
 28. Rounsevell MDA, Pedrolí B, Erb K-H, Gramberger M, Busck AG, Haberl H, et al. Challenges for land system science. *Land Use Policy*. Elsevier Ltd; 2012;29:899–910. Available from: <http://linkinghub.elsevier.com/retrieve/pii/S0264837712000099>.
 29. Gardner RH, Urban DL. Neutral models for testing landscape hypotheses. *Landsc Ecol*. 2007;22:15–29. Available from: <http://link.springer.com/10.1007/s10980-006-9011-4>.
 30. Pe'er G, Zurita GA, Schober L, Bellocq MI, Strer M, Müller M, et al. Simple process-based simulators for generating spatial patterns of habitat loss and fragmentation: a review and introduction to the G-RaFFe Model. *PLoS One*. 2013;8: e64968. Available from: <http://dx.plos.org/10.1371/journal.pone.0064968>.
 31. Tague CL, Band LE. RHESys: Regional Hydro-Ecologic Simulation System—an object-oriented approach to spatially distributed modeling of carbon, water, and nutrient cycling. *Earth Interact*. 2004 [cited 2016 Feb 10];8:1–42. Available from: [http://journals.ametsoc.org/doi/abs/10.1175/1087-3562\(2004\)8%3C1:RRHSSO%3E2.0.CO;2](http://journals.ametsoc.org/doi/abs/10.1175/1087-3562(2004)8%3C1:RRHSSO%3E2.0.CO;2).
 32. Krysanova V, Arnold JG. Advances in ecohydrological modelling with SWAT—a review. *Hydrol Sci J*. Taylor & Francis Group; 2008 [cited 2016 Mar 16];53:939–47. Available from: <http://www.tandfonline.com/doi/abs/10.1623/hysj.53.5.939>.
 33. Murray-Rust D, Brown C, van Vliet J, Alam SJ, Robinson DT, Verburg PH, et al. Combining agent functional types, capitals and services to model land use dynamics. *Environ Model Softw*. 2014;59:187–201. Available from: <http://www.sciencedirect.com/science/article/pii/S1364815214001583>.
 34. Deadman P, Robinson D, Moran E, Brondizio E. Colonist household decisionmaking and land-use change in the amazon rainforest: an agent-based simulation. *Environ Plan B Plan Des*. SAGE Publications; 2004 [cited 2016 Feb 10];31:693–709. Available from: <http://epb.sagepub.com/content/31/5/693.abstract>.
 35. Zimmermann A, Möhring A, Mack G, Ferjani A, Mann S. Pathways to truth: comparing different upscaling options for an agent-based sector model. *JASSS*; 2015 [cited 2016 Mar 15]. Available from: <http://jasss.soc.surrey.ac.uk/18/4/11.html>.
 36. Matthews RB, Gilbert NG, Roach A, Polhill JG, Gotts NM. Agent-based land-use models: a review of applications. *Landsc Ecol*. 2007;22:1447–59. Available from: <http://link.springer.com/10.1007/s10980-007-9135-1>.
 37. An L. Modeling human decisions in coupled human and natural systems: Review of agent-based models. *Ecol Model*. 2012 [cited 2014 Jul 15];229:25–36. Available from: <http://www.sciencedirect.com/science/article/pii/S0304380011003802>.
 38. Phillips SJ, Dudík M. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography (Cop)*. 2008;31:161–75.
 39. Carpenter G, Gillison AN, Winter J. DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodivers Conserv*. 1993 [cited 2016 Jan 9];2:667–80. Available from: <http://link.springer.com/10.1007/BF00051966>.
 40. Busby JR. BIOCLIM - a bioclimate analysis and prediction system. *Plant Prot Q*. 1991 [cited 2016 Feb 10]; Available from: <http://agris.fao.org/agris-search/search.do?recordID=AU9103158>.
 41. Breiman L. Random forests. *Mach Learn*. Kluwer Academic Publishers; 2001 [cited 2016 Jan 28];45:5–32. Available from: <http://link.springer.com/article/10.1023/A%3A1010933404324>.
 42. Hastie TJ, Tibshirani RJ. Generalized additive models. *Stat Sci*. CRC Press; 1990. Available from: <http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Generalized+additive+models#0>.
 43. Hernandez PA, Graham CH, Master LL, Albert DL. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography (Cop)*. 2006 [cited 2016 Feb 11];29:773–85. Available from: <http://doi.wiley.com/10.1111/j.0906-7590.2006.04700.x>.
 44. Matthews RB, Gilbert NG, Roach A, Polhill JG, Gotts NM. Agent-based land-use models: a review of applications. *Landsc Ecol*. 2007;22:1447–59. Available from: <http://doi.wiley.com/10.1111/j.1365-2699.2004.01076.x>.
 45. Seidl R, Rammer W, Scheller RM, Spies TA. An individual-based process model to simulate landscape-scale forest ecosystem dynamics. *Ecol Modell*. Elsevier B.V. 2012;231:87–100. Available from: <http://dx.doi.org/10.1016/j.ecolmodel.2012.02.015>.
 46. Mladenoff DJ. LANDIS and forest landscape models. *Ecol Model*. 2004 [cited 2016 Feb 10];180:7–19. Available from: <http://www.sciencedirect.com/science/article/pii/S0304380004003461>.
 47. Pacala SW, Canham CD, Silander Jr. JA. Forest models defined by field measurements: I. The design of a northeastern forest simulator. *Can J For Res*. NRC Research Press Ottawa, Canada; 1993 [cited 2016 Feb 10];23:1980–8. Available from: <http://www.nrcresearchpress.com/doi/abs/10.1139/x93-249#.VrszXlji8eE>.
 48. Seidl R, Fernandes PM, Fonseca TF, Gillet F, Jönsson AM, Merganičová K, et al. Modelling natural disturbances in forest ecosystems: a review. *Ecol Model*. 2011 [cited 2016

- Jan 18];222:903–24. Available from: <http://www.sciencedirect.com/science/article/pii/S0304380010005272>.
49. Hurrell JW, Holland MM, Gent PR, Ghan S, Kay JE, Kushner PJ, et al. The community earth system model: a framework for collaborative research. *Bull Am Meteorol Soc. American Meteorological Society*; 2013 [cited 2016 Jan 19];94:1339–60. Available from: <http://journals.ametsoc.org/doi/abs/10.1175/BAMS-D-12-00121.1>
 50. Krinner G, Viovy N, de Noblet-Ducoudré N, Ogée J, Polcher J, Friedlingstein P, et al. A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. *Glob Biogeochem Cycles*. 2005 [cited 2016 Feb 10];19. Available from: <http://doi.wiley.com/10.1029/2003GB002199>.
 51. Smith B, Prentice IC, Sykes MT. Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. *Glob Ecol Biogeogr*. 2001 [cited 2016 Feb 10];10:621–37. Available from: <http://doi.wiley.com/10.1046/j.1466-822X.2001.t01-1-00256.x>.
 52. Quillet A, Peng C, Gameau M. Toward dynamic global vegetation models for simulating vegetation–climate interactions and feedbacks: recent developments, limitations, and future challenges. *Environ Rev*. 2010 [cited 2016 Jan 11];18:333–53. Available from: <http://www.nrcresearchpress.com/doi/abs/10.1139/a10-016#VrxFbJi8eE>.
 53. Engler R, Guisan A. MigClim: predicting plant distribution and dispersal in a changing climate. *Divers Distrib*. 2009;15:590–601.
 54. Cabral JS, Schurr FM. Estimating demographic models for the range dynamics of plant species. *Glob Ecol Biogeogr*. 2010 [cited 2016 Mar 16];19:85–97. Available from: <http://doi.wiley.com/10.1111/j.1466-8238.2009.00492.x>.
 55. Dullinger S, Gatttringer A, Thuiller W, Moser D, Zimmermann NE, Guisan A, et al. Extinction debt of high-mountain plants under twenty-first-century climate change. *Nat Clim Chang. Nature Publishing Group*; 2012 [cited 2015 Dec 14];2:619–22. Available from: doi:10.1038/nclimate1514.
 56. Franklin J. Moving beyond static species distribution models in support of conservation biogeography. *Divers Distrib*. 2010;16:321–30. Available from: <http://doi.wiley.com/10.1111/j.1472-4642.2010.00641.x>.
 57. Akçakaya HR, Root W. RAMAS Metapop: viability analysis for stage-structured metapopulations. *Appl. Biomath. Setauket, NY*; 2002.
 58. Mokany K, Harwood TD, Williams KJ, Ferrier S. Dynamic macroecology and the future for biodiversity. *Glob Chang Biol*. 2012 [cited 2015 Oct 17];18:3149–59. Available from: <http://doi.wiley.com/10.1111/j.1365-2486.2012.02760.x>.
 59. Filotas E, Grant M, Parrott L, Rikvold PA. The effect of positive interactions on community structure in a multi-species metacommunity model along an environmental gradient. *Ecol Model*. 2010 [cited 2016 Feb 12];221:885–94. Available from: <http://www.sciencedirect.com/science/article/pii/S0304380009008357>.
 60. Polhill JG, Gimona A, Gotts NM. Nonlinearities in biodiversity incentive schemes: a study using an integrated agent-based and metacommunity model. *Environ Model Softw*. 2013;45:74–91.
 61. Lindenmayer DB, Burgman MA, Ak HR, Lacy RC, Possingham HP. A review of the generic computer programs ALEX, RAMAS-space and VORTEX for modeling the viability of wildlife metapopulations. *Lindenmayer, Burgman, Akcakaya, Lacy, Possingham. Ecol Model*. 1995;82:161–74.
 62. Hill MF, Caswell H. Habitat fragmentation and extinction thresholds on fractal landscapes. *Ecol Lett* 1999 [cited 2016 Feb 15];2:121–7. Available from: <http://doi.wiley.com/10.1046/j.1461-0248.1999.22061.x>.
 63. Hogeweg P. Cellular automata as a paradigm for ecological modeling. *Appl Math Comput*. 1988 [cited 2016 Mar 16];27:81–100. Available from: <http://www.sciencedirect.com/science/article/pii/0096300388901002>.
 64. Willis SG, Thomas CD, Hill JK, Collingham YC, Telfer MG, Fox R, et al. Dynamic distribution modelling: predicting the present from the past. *Ecography (Cop)*. 2009;32:5–12.
 65. Neubert MG, Caswell H. Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology. Ecological Society of America*; 2000 [cited 2016 Mar 16];81:1613–28. Available from: <http://cat.inist.fr/?aModele=afficheN&cpsid=1393825>.
 66. Bullock JM, White SM, Prudhomme C, Tansey C, Perea R, Hooftman DAP. Modelling spread of British wind-dispersed plants under future wind speeds in a changing climate. *J Ecol*. 2012 [cited 2016 Mar 16];100:104–15. Available from: <http://doi.wiley.com/10.1111/j.1365-2745.2011.01910.x>.
 67. Bocedi G, Palmer SCF, Pe'er G, Heikkinen RK, Matsinos YG, Watts K, et al. RangeShifter: a platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. *Methods Ecol Evol*. 2014;5:388–96.
 68. Schumaker N. HexSim. US Environmental Protection Agency. Environ Res Lab. Available <http://www.epa.gov/hexsim>. Accessed 2012.
 69. Grimm V, Railsback SF. Individual-based modeling and ecology. Princeton university press; 2013.
 70. Matthews R. The People and Landscape Model (PALM): towards full integration of human decision-making and biophysical simulation models. *Ecol Model*. 2006;194:329–43.
 71. An L, Linderman M, Qi J, Shortridge A, Liu J. Exploring complexity in a human–environment system: an agent-based spatial model for multidisciplinary and multiscale integration. *Ann Assoc Am Geogr*. 2005;95:54–79.
 72. Rebaudo F, Crespo-Pérez V, Silvain J-F, Dangles O. Agent-based modeling of human-induced spread of invasive species in agricultural landscapes: insights from the potato moth in Ecuador. *J Artif Soc Soc Simul*. 2011;14:7.
 73. Carrasco LR, Cook D, Baker R, MacLeod A, Knight JD, Mumford JD. Towards the integration of spread and economic impacts of biological invasions in a landscape of learning and imitating agents. *Ecol Econ*. 2012;76:95–103. Available from: <http://www.sciencedirect.com/science/article/pii/S0921800912000730>.
 74. Schröder B, Seppelt R. Analysis of pattern-process interactions based on landscape models—Overview, general concepts, and methodological issues. *Ecol Model*. 2006;199:505–16.
 75. Turner MG. Landscape ecology: what is the state of the science? *Annu Rev Ecol Evol Syst*. 2005;36:319–44.
 76. Li X, He HS, Wang X, Bu R, Hu Y, Chang Y. Evaluating the effectiveness of neutral landscape models to represent a real landscape. *Landsc Urban Plan*. 2004;69:137–48. Available from: <http://www.sciencedirect.com/science/article/pii/S0169204603002494>.
 77. Chipperfield JD, Dytham C, Hovestadt T. An updated algorithm for the generation of neutral landscapes by spectral synthesis. *PLoS One*. 2011;6, e17040.
 78. Gardner RH, Milne BT, Turnei MG, O'Neill RV. Neutral models for the analysis of broad-scale landscape pattern. *Landsc Ecol*. 1987;1:19–28.
 79. O'Neill RV, Gardner R, Turner MG. A hierarchical neutral model for landscape analysis. *Landsc Ecol*. 1992;7:55–61.
 80. With KA. The application of neutral landscape models in conservation biology. *Conserv Biol*. 1997;11:1069–80.
 81. Halley JM, Hartley S, Kallimanis AS, Kunin WE, Lennon JJ, Sgardelis SP. Uses and abuses of fractal methodology in ecology. *Ecol Lett*. 2004;7:254–71.
 82. Ko DW, He HS, Larsen DR. Simulating private land ownership fragmentation in the Missouri Ozarks, USA. *Landsc Ecol*. 2006;21:671–86. Available from: <http://www.scopus.com/inward/record.url?eid=2-s2.0-33746146970&partnerID=40&md5=2fb536ad672f7ed30b9d099bb902b16>.

83. Engel J, Huth A, Frank K. Bioenergy production and Skylark (*Alauda arvensis*) population abundance—a modelling approach for the analysis of land-use change impacts and conservation options. *GCB Bioenergy*. 2012;4:713–27.
84. Lustig A, Stouffer DB, Roigé M, Worner SP. Towards more predictable and consistent landscape metrics across spatial scales. *Ecol Indic*. 2015;57:11–21.
85. Tischendorf L. Can landscape indices predict ecological processes consistently? *Landscape Ecol*. Kluwer Academic Publishers; 2001 [cited 2016 Feb 13];16:235–54. Available from: <http://link.springer.com/article/10.1023/A%3A1011112719782>.
86. Neel MC, McGarigal K, Cushman SA. Behavior of class-level landscape metrics across gradients of class aggregation and area. *Landscape Ecol*. 2004;19:435–55. Available from: <http://www.scopus.com/inward/record.url?eid=2-s2.0-3042803269&partnerID=40&md5=249b89c35e65752963a84d17b1911841>.
87. Gardner RH, Lookingbill TR, Townsend PA, Ferrari J. A new approach for rescaling land cover data. *Landscape Ecol*. 2008;23:513–26.
88. Tischendorf L, Fahrig L. How should we measure landscape connectivity? *Landscape Ecol*. 2000;15:633–41.
89. Malanson GP. Dispersal across continuous and binary representations of landscapes. *Ecol Model*. 2003;169:17–24.
90. Roques L, Stoica RS. Species persistence decreases with habitat fragmentation: an analysis in periodic stochastic environments. *J Math Biol*. 2007;55:189–205. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/17294236>.
91. Roques L, Chekroun MD. Does reaction–diffusion support the duality of fragmentation effect? *Ecol Complex Elsevier BV*. 2010;7:100–6. Available from: doi:10.1016/j.ecocom.2009.07.003.
92. Bonte D, Hovestadt T, Poethke H-J. Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes. *Oikos*. 2010;119:560–6. Available from: doi:10.1111/j.1600-0706.2009.17943.x.
93. Weisberg PJ, Ko D, Py C, Bauer JM. Modeling fire and landform influences on the distribution of old-growth pinyon-juniper woodland. *Landscape Ecol*. 2008;23:931–43. Available from: //000259481900005.
94. Miranda BR, Sturtevant BR, Yang J, Gustafson EJ. Comparing fire spread algorithms using equivalence testing and neutral landscape models. *Landscape Ecol*. 2009 [cited 2015 Dec 1];24:587–98. Available from: doi:10.1007/s10980-009-9343-y.
95. Yurkonis KA, Wilsey BJ, Moloney KA. Initial species pattern affects invasion resistance in experimental grassland plots. *J Veg Sci*. 2012;23:4–12.
96. Verburg PH, Overmars KP. Combining top-down and bottom-up dynamics in land use modeling: exploring the future of abandoned farmlands in Europe with the Dyna-CLUE model. *Landscape Ecol*. 2009 [cited 2015 Dec 29];24:1167–81. Available from: <http://link.springer.com/10.1007/s10980-009-9355-7>.
97. Mas J-F, Kolb M, Paegelow M, Camacho Olmedo MT, Houet T. Inductive pattern-based land use/cover change models: a comparison of four software packages. *Environ Model Softw*. 2014 [cited 2016 Mar 15];51:94–111. Available from: <http://www.sciencedirect.com/science/article/pii/S1364815213002016>.
98. Tobler WR. A computer movie simulating urban growth in the Detroit Region. *Econ Geogr*. 1970 [cited 2016 Feb 12];46:234. Available from: <http://www.jstor.org/stable/143141?origin=crossref>.
99. Muller MR, Middleton J. A Markov model of land-use change dynamics in the Niagara Region, Ontario, Canada. *Landscape Ecol*. 1994;9:151–7.
100. Hall CAS, Tian H, Qi Y, Pontius G, Cornell J. Modelling spatial and temporal patterns of tropical land use change. *J Biogeogr (United Kingdom)*. 1995 [cited 2016 Feb 13]; Available from: <http://agris.fao.org/agris-search/search.do?recordID=GB9628564>.
101. Chomitz KM, Gray DA. Roads, land use, and deforestation: a spatial model applied to Belize. *World Bank Econ Rev*. 1996 [cited 2016 Feb 23];10:487–512. Available from: <http://wber.oxfordjournals.org/content/10/3/487.abstract>.
102. Verburg PH, de Koning GHJ, Kok K, Veldkamp A, Bouma J. A spatial explicit allocation procedure for modelling the pattern of land use change based upon actual land use. *Ecol Model*. 1999 [cited 2016 Feb 13];116:45–61. Available from: <http://www.sciencedirect.com/science/article/pii/S0304380098001562>.
103. Lambin EF. Modelling and monitoring land-cover change processes in tropical regions. *Prog Phys Geogr*. 1997 [cited 2016 Feb 13];21:375–93. Available from: <http://ppg.sagepub.com/content/21/3/375.short>.
104. Brown D., Pijanowski B., Duh J. Modeling the relationships between land use and land cover on private lands in the Upper Midwest, USA. *J Environ Manag*. 2000 [cited 2016 Feb 13];59:247–63. Available from: <http://www.sciencedirect.com/science/article/pii/S0301479700903694>.
105. Pijanowski BC, Brown DG, Shellito BA, Manik GA. Using neural networks and GIS to forecast land use changes: a Land Transformation Model. *Comput Environ Urban Syst*. 2002 [cited 2016 Feb 13];26:553–75. Available from: <http://www.sciencedirect.com/science/article/pii/S0198971501000151>.
106. Hoek G, Beelen R, de Hoogh K, Vienneau D, Gulliver J, Fischer P, et al. A review of land-use regression models to assess spatial variation of outdoor air pollution. *Atmos Environ*. 2008 [cited 2014 Nov 6];42:7561–78. Available from: <http://www.sciencedirect.com/science/article/pii/S1352231008005748>.
107. Arain MA, Blair R, Finkelstein N, Brook JR, Sahsuvaroglu T, Beckerman B, et al. The use of wind fields in a land use regression model to predict air pollution concentrations for health exposure studies. *Atmos Environ*. 2007 [cited 2016 Feb 13];41:3453–64. Available from: <http://www.sciencedirect.com/science/article/pii/S1352231006013008>.
108. Sahsuvaroglu T, Arain A, Kanaroglou P, Finkelstein N, Newbold B, Jerrett M, et al. A land use regression model for predicting ambient concentrations of nitrogen dioxide in Hamilton, Ontario, Canada. *J Air Waste Manag Assoc*. Taylor & Francis Group; 2006 [cited 2016 Feb 13];56:1059–69. Available from: <http://www.tandfonline.com/doi/abs/10.1080/10473289.2006.10464542>.
109. Verburg PH, Soepboer W, Veldkamp A, Limpiada R, Espaldon V, Mastura SSA. Modeling the spatial dynamics of regional land use: the CLUE-S model. *Environ Manag*. 2002 [cited 2016 Feb 13];30:391–405. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/12148073>.
110. Heistermann M, Müller C, Ronneberger K. Land in sight? Achievements, deficits and potentials of continental to global scale land-use modeling. *Agric Ecosyst Environ*. 2006 [cited 2016 Feb 13];114:141–58. Available from: <http://www.sciencedirect.com/science/article/pii/S0167880905005475>.
111. van Meijl H, van Rheenen T, Tabeau A, Eickhout B. The impact of different policy environments on agricultural land use in Europe. *Agric Ecosyst Environ*. 2006 [cited 2015 Nov 25];114:21–38. Available from: <http://www.sciencedirect.com/science/article/pii/S0167880905005323>.
112. Verburg PH, Eickhout B, van Meijl H. A multi-scale, multi-model approach for analyzing the future dynamics of European land use. *Ann Reg Sci*. 2008 [cited 2016 Feb 13];42:57–77. Available from: <http://link.springer.com/10.1007/s00168-007-0136-4>.
113. Meiyappan P, Dalton M, O'Neill BC, Jain AK. Spatial modeling of agricultural land use change at global scale. *Ecol Model*. 2014;291:152–74. Available from: <http://www.sciencedirect.com/science/article/pii/S0304380014003640>.
114. Strengers B, Leemans R, Eickhout B, Vries B de, Bouwman L. The land-use projections and resulting emissions in the IPCC SRES scenarios as simulated by the IMAGE 2.2 model. *GeoJournal*.

- 2004 [cited 2016 Feb 23]; Available from: <http://agris.fao.org/agris-search/search.do?recordID=NL2012053845>.
115. Jenerette GD, Wu J. Analysis and simulation of land-use change in the central Arizona – Phoenix region, USA. *Landsc Ecol*. Kluwer Academic Publishers; 2001 [cited 2016 Feb 13];16:611–26. Available from: <http://link.springer.com/article/10.1023/A%3A1013170528551>.
 116. Benenson I. Multi-agent simulations of residential dynamics in the city. *Comput Environ Urban Syst*. 1998 [cited 2016 Feb 23];22: 25–42. Available from: <http://www.sciencedirect.com/science/article/pii/S0198971598000179>.
 117. Wolfram S. Cellular automata as models of complexity. *Nature*. 1984;311:419–24.
 118. Parker D. Multi-agent systems for the simulation of land-use and land-cover change: a review. *Ann Assoc Am Geogr*. 2003;93:314–37.
 119. Mondal P, Southworth J. Evaluation of conservation interventions using a cellular automata-Markov model. *For Ecol Manag*. 2010 [cited 2016 Mar 15];260:1716–25. Available from: <http://www.sciencedirect.com/science/article/pii/S037811271000472X>.
 120. Brown DG, Aspinall R, Bennett DA. Landscape models and explanation in landscape ecology—a space for generative landscape science? *Prof Geogr*. 2006;58:369–82.
 121. Collinge SK. Ecological consequences of habitat fragmentation: implications for landscape architecture and planning. *Landsc Urban Plan*. 1996 [cited 2016 Jan 31];36:59–77. Available from: <http://www.sciencedirect.com/science/article/pii/S0169204696003416>.
 122. Wrbka T, Erb K-H, Schulz NB, Peterseil J, Hahn C, Haberl H. Linking pattern and process in cultural landscapes. An empirical study based on spatially explicit indicators. *Land Use Policy*. 2004 [cited 2016 Jan 28];21:289–306. Available from: <http://www.sciencedirect.com/science/article/pii/S0264837703000929>.
 123. Kareiva P, Wennergren U. Connecting landscape patterns to ecosystem and population processes. *Nature*. 1995 [cited 2015 Dec 8];373: 299–302. Available from: <http://dx.doi.org/10.1038/373299a0>.
 124. Fridley JD, Stachowicz JJ, Naeem S, Sax DF, Seabloom EW, Smith MD, et al. The invasion paradox: reconciling pattern and process in species invasions. *Ecology*. Ecological Society of America; 2007 [cited 2015 Oct 22];88:3–17. Available from: [http://onlinelibrary.wiley.com/doi/10.1890/0012-9658\(2007\)88\[3:TIPRPA\]2.0.CO;2/full](http://onlinelibrary.wiley.com/doi/10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2/full).
 125. Aspinall R. Modelling land use change with generalized linear models—a multi-model analysis of change between 1860 and 2000 in Gallatin Valley, Montana. *J Environ Manag*. 2004 [cited 2016 Feb 23];72:91–103. Available from: <http://www.sciencedirect.com/science/article/pii/S0301479704000805>.
 126. Li X. Emergence of bottom-up models as a tool for landscape simulation and planning. *Landsc Urban Plan*. 2011 [cited 2016 Feb 23];100:393–5. Available from: <http://www.sciencedirect.com/science/article/pii/S0169204610003117>.
 127. Jiang Z. The road extension model in the land change modeler for ecological sustainability of IDRISI. *ACM*; 2007. p. 13.
 128. Silva E., Clarke K. Calibration of the SLEUTH urban growth model for Lisbon and Porto, Portugal. *Comput Environ Urban Syst*. 2002;26:525–52. Available from: <http://www.sciencedirect.com/science/article/pii/S019897150100014X>.
 129. Ward DP, Murray AT, Phinn SR. A stochastically constrained cellular model of urban growth. *Comput Environ Urban Syst*. 2000;24:539–58. Available from: <http://www.sciencedirect.com/science/article/pii/S0198971500000089>.
 130. Johnston R, Shabazian D, Gao S. Uplan: a versatile urban growth model for transportation planning. *Transp Res Rec J Transp Res Board*. 2003;202–9.
 131. Krysanova V, Müller-Wohlfeil D-I, Becker A. Development and test of a spatially distributed hydrological/water quality model for mesoscale watersheds. *Ecol Model*. 1998;106:261–89. Available from: <http://www.sciencedirect.com/science/article/pii/S0304380097002044>.
 132. Hattermann FF, Krysanova V, Habeck A, Bronstert A. Integrating wetlands and riparian zones in river basin modelling. *Pattern Process. Dyn. Mosaic landscapes – model. Simulation, Implic*. 2006;199:379–92. Available from: <http://www.sciencedirect.com/science/article/pii/S0304380006002833>.
 133. Beaujouan V, Durand P, Ruiz L. Modelling the effect of the spatial distribution of agricultural practices on nitrogen fluxes in rural catchments. *Ecol Model*. 2001;137:93–105. Available from: <http://www.sciencedirect.com/science/article/pii/S030438000000435X>.
 134. Magliocca NR, Brown DG, Ellis EC. Exploring agricultural livelihood transitions with an agent-based virtual laboratory: global forces to local decision-making. *PLoS One. Public Library of Science*; 2013 [cited 2016 Mar 15];8:e73241. Available from: <http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0073241>.
 135. Epstein JM. Why model?. *JASSS*; 2008 [cited 2016 Mar 15]. Available from: <http://jasss.soc.surrey.ac.uk/11/4/12.html>.
 136. Veldkamp A, Lambin E. Predicting land-use change. *Agric Ecosyst Environ*. 2001 [cited 2016 Mar 15];85:1–6. Available from: <http://www.sciencedirect.com/science/article/pii/S0167880901001992>.
 137. Lansing JS, Kremer JN. Emergent properties of balinese water temple networks: coadaptation on a rugged fitness landscape. *Am Anthropol*. 1993 [cited 2016 Mar 15];95:97–114. Available from: <http://doi.wiley.com/10.1525/aa.1993.95.1.02a00050>.
 138. Balmann A, Happe K, Kellermann K, Kleingam A. Adjustment costs of agri-environmental policy switchings: a multi-agent-approach. *Complexity Ecosyst Manag Theory Pract Multi-agent Syst*. 2002;127–57.
 139. Rouchier J, Bousquet F, Requier-Desjardins M, Antona M. A multi-agent model for describing transhumance in North Cameroon: comparison of different rationality to develop a routine. *J Econ Dyn Control*. 2001 [cited 2016 Mar 15];25:527–59. Available from: <http://www.sciencedirect.com/science/article/pii/S016518890000035X>.
 140. Torrens PM. Can geocomputation save urban simulation? Throw some agents into the mixture, simmer and wait... Centre for Advanced Spatial Analysis (UCL); 2001 [cited 2016 Mar 15]; Available from: <http://discovery.ucl.ac.uk/263/1/paper32.pdf>.
 141. van Delden H, van Vliet J, Rutledge DT, Kirkby MJ. Comparison of scale and scaling issues in integrated land-use models for policy support. *Agric Ecosyst Environ*. 2011 [cited 2016 Mar 15];142: 18–28. Available from: <http://www.sciencedirect.com/science/article/pii/S0167880911000892>.
 142. Armeth A, Brown C, Rounsevell MDA. Global models of human decision-making for land-based mitigation and adaptation assessment. *Nat Clim Chang*. Nature Publishing Group, a division of Macmillan Publishers Limited. All Rights Reserved; 2014 [cited 2016 Mar 15];4:550–7. Available from: doi:10.1038/nclimate2250.
 143. Veldkamp A, Verburg PH. Modelling land use change and environmental impact. *J Environ Manag*. 2004 [cited 2016 Mar 15];72:1–3. Available from: <http://www.sciencedirect.com/science/article/pii/S0301479704000684>.
 144. Milne E, Aspinall RJ, Veldkamp TA. Integrated modelling of natural and social systems in land change science. *Landsc Ecol*. 2009 [cited 2016 Mar 15];24:1145–7. Available from: <http://link.springer.com/10.1007/s10980-009-9392-2>.
 145. Manson SM. Agent-based modeling and genetic programming for modeling land change in the Southern Yucatán Peninsular Region of Mexico. *Agric Ecosyst Environ*. 2005 [cited 2016 Feb 25];111: 47–62. Available from: <http://www.sciencedirect.com/science/article/pii/S0167880905002422>.
 146. Barthel R, Janisch S, Schwarz N, Trifkovic A, Nickel D, Schulz C, et al. An integrated modelling framework for simulating regional-scale actor responses to global change in the water domain. *Environ Model Softw*. 2008 [cited 2015 Oct 7];23:1095–121. Available from: <http://www.sciencedirect.com/science/article/pii/S1364815208000224>.

147. Tallis H, Ricketts T, Guerry A, Nelson E, Ennaanay D, Wolny S. InVEST 2.1 beta User's guide: integrated valuation of ecosystem services and tradeoffs. Nat Cap Proj Stanford. 2011.
148. Van Berkel DB, Verburg PH. Combining exploratory scenarios and participatory backcasting: using an agent-based model in participatory policy design for a multi-functional landscape. *Landsc Ecol*. [cited 2016 Feb 11];27:641–58. Available from: <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4426888&tool=pmcentrez&rendertype=abstract>.
149. Lobianco A, Esposti R. The Regional Multi-Agent Simulator (RegMAS): an open-source spatially explicit model to assess the impact of agricultural policies. *Comput Electron Agric*. 2010 [cited 2016 Feb 22];72:14–26. Available from: <http://www.sciencedirect.com/science/article/pii/S0168169910000426>.
150. Malawska A, Topping CJ, Nielsen HØ. Why do we need to integrate farmer decision making and wildlife models for policy evaluation? *Land Use Policy*. 2014;38:732–40. Available from: <http://www.sciencedirect.com/science/article/pii/S0264837713002202>.
151. Filatova T, Polhill JG, van Ewijk S. Regime shifts in coupled socio-environmental systems: review of modelling challenges and approaches. *Environ Model Softw*. 2016;75:333–47.
152. Batty M, Torrens PM. Modelling and prediction in a complex world. *Futures*. 2005 [cited 2016 Jan 25];37:745–66. Available from: <http://www.sciencedirect.com/science/article/pii/S0016328704001788>.
153. Goldspink C. Modelling social systems as complex: towards a social simulation meta-model. *JASSS*; 2000 [cited 2016 Mar 15]. Available from: <http://jasss.soc.surrey.ac.uk/3/2/1.html>.
154. Conte R, Paolucci M. On agent-based modeling and computational social science. *Front Psychol*. *Frontiers*; 2014 [cited 2016 Mar 15];5:668. Available from: <http://journal.frontiersin.org/article/10.3389/fpsyg.2014.00668/abstract>.
155. Austin M. Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecol Model*. 2007 [cited 2014 Jul 10];200:1–19. Available from: <http://www.sciencedirect.com/science/article/pii/S0304380006003140>.
156. Elith J, Leathwick JR. Species distribution models: ecological explanation and prediction across space and time. *Annu Rev Ecol Syst*. 2009;40:677.
157. Araújo MB, Guisan A. Five (or so) challenges for species distribution modelling. *J Biogeogr*. 2006;33:1677–88. Available from: <http://dx.doi.org/10.1111/j.1365-2699.2006.01584.x>.
158. Heikkinen RK, Luoto M, Araujo MB, Virkkala R, Thuiller W, Sykes MT. Methods and uncertainties in bioclimatic envelope modelling under climate change. *Prog Phys Geogr*. 2006 [cited 2015 Dec 7];30:751–77. Available from: <http://ppg.sagepub.com/content/30/6/751>.
159. Pearson RG, Thuiller W, Araújo MB, Martinez-Meyer E, Brotons L, McClean C, et al. Model-based uncertainty in species range prediction. *J Biogeogr*. 2006 [cited 2016 Feb 13];33:1704–11. Available from: doi:10.1111/j.1365-2699.2006.01460.x.
160. Thuiller W, Albert C, Araújo MB, Berry PM, Cabeza M, Guisan A, et al. Predicting global change impacts on plant species' distributions: future challenges. *Perspect Plant Ecol Evol Syst*. 2008 [cited 2014 Jul 9];9:137–52. Available from: <http://www.sciencedirect.com/science/article/pii/S1433831907000376>.
161. Synes NW, Osborne PE. Choice of predictor variables as a source of uncertainty in continental-scale species distribution modelling under climate change. *Glob Ecol Biogeogr*. 2011;20:904–14.
162. Soberón J, Nakamura M. Niches and distributional areas: concepts, methods, and assumptions. *Proc Natl Acad Sci U S A*. 2009 [cited 2016 Feb 14];106(Suppl):19644–50. Available from: http://www.pnas.org/content/106/Supplement_2/19644.full.
163. Václavík T, Meentemeyer RK. Equilibrium or not? Modelling potential distribution of invasive species in different stages of invasion. *Divers Distrib*. 2012 [cited 2016 Jan 22];18:73–83. Available from: <http://doi.wiley.com/10.1111/j.1472-4642.2011.00854.x>.
164. Raxworthy CJ, Ingram CM, Rabibisoa N, Pearson RG. Applications of ecological niche modeling for species delimitation: a review and empirical evaluation using day geckos (*Phelsuma*) from Madagascar. *Syst Biol*. 2007 [cited 2016 Feb 14];56:907–23. Available from: <http://sysbio.oxfordjournals.org/content/56/6/907.short>.
165. Fløjgaard C, Normand S, Skov F, Svenning J-C. Ice age distributions of European small mammals: insights from species distribution modelling. *J Biogeogr*. 2009 [cited 2016 Jan 23];36:1152–63. Available from: <http://doi.wiley.com/10.1111/j.1365-2699.2009.02089.x>.
166. Williams JN, Seo C, Thorne J, Nelson JK, Erwin S, O'Brien JM, et al. Using species distribution models to predict new occurrences for rare plants. *Divers Distrib*. 2009 [cited 2016 Feb 14];15:565–76. Available from: <http://doi.wiley.com/10.1111/j.1472-4642.2009.00567.x>.
167. Berry PM, Dawson TP, Harrison PA, Pearson RG. Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Glob Ecol Biogeogr*. 2002 [cited 2016 Feb 14];11:453–62. Available from: <http://doi.wiley.com/10.1111/j.1466-8238.2002.00304.x>.
168. Schurr FM, Pagel J, Cabral JS, Groeneveld J, Bykova O, O'Hara RB, et al. How to understand species' niches and range dynamics: a demographic research agenda for biogeography. *J Biogeogr*. 2012;39:2146–62.
169. Thuiller W, Münkemüller T, Lavergne S, Mouillot D, Mouquet N, Schiffrers K, et al. A road map for integrating eco-evolutionary processes into biodiversity models. *Ecol Lett*. 2013 [cited 2016 Mar 15];16(Suppl 1):94–105. Available from: <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3790307&tool=pmcentrez&rendertype=abstract>.
170. Zurell D, Thuiller W, Pagel J, Cabral JS, Münkemüller T, Gravel D, et al. Benchmarking novel approaches for modelling species range dynamics. *Glob Chang Biol*. 2016 [cited 2016 Feb 15]; Available from: <http://www.ncbi.nlm.nih.gov/pubmed/26872305>.
171. Smolik MG, Dullinger S, Essl F, Kleinbauer I, Leitner M, Peterseil J, et al. Integrating species distribution models and interacting particle systems to predict the spread of an invasive alien plant. *J Biogeogr*. 2010;37:411–22. doi:10.1111/j.1365-2699.2009.02227.x.
172. Singer A, Johst K, Banitz T, Fowler MS, Groeneveld J, Gutiérrez AG, et al. Community dynamics under environmental change: how can next generation mechanistic models improve projections of species distributions? *Ecol Model*. 2015 [cited 2016 Jan 4]; Available from: <http://www.sciencedirect.com/science/article/pii/S0304380015005281>.
173. Levins R. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull Entomol Soc Am*. 1969;15.
174. Hanski I. Metapopulation dynamics: does it help to have more of the same? *Trends Ecol Evol*. 1989 [cited 2016 Feb 15];4:113–4. Available from: <http://www.sciencedirect.com/science/article/pii/016953478990061X>.
175. Boyce MS. Population viability analysis. *Annu Rev Ecol Syst*. *Annual Reviews* 4139 El Camino Way, P.O. Box 10139, Palo Alto, CA 94303–0139, USA; 1992 [cited 2016 Feb 11];23:481–506. Available from: <http://www.annualreviews.org/doi/abs/10.1146/annurev.es.23.110192.002405>.
176. Beissinger SR, Westphal MI. On the use of demographic models of population viability in endangered species management. *J Wildl Manag*. *Wildlife Society*; 1998 [cited 2016 Feb 11];62:821–41. Available from: <http://cat.inist.fr/?aModele=afficheN&cpsidt=2425383>.
177. Lacy R. VORTEX: a computer simulation model for population viability analysis. *Wildl Res*. *CSIRO PUBLISHING*; 1993 [cited 2016 Feb 11];20:45. Available from: http://www.publish.csiro.au/view/journals/dsp_journal_fulltext.cfm?nid=144&f=WR9930045.
178. Hanski I, Moilanen A, Pakkala T, Kuussaari M. The quantitative incidence function model and persistence of an endangered

- butterfly metapopulation. *Conserv Biol.* 1996 [cited 2016 Feb 11];10:578–90. Available from: <http://doi.wiley.com/10.1046/j.1523-1739.1996.10020578.x>.
179. Hanski I, Thomas CD. Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. *Biol. Conserv.* 1994 [cited 2016 Feb 15];68:167–80. Available from: <http://www.sciencedirect.com/science/article/pii/S0006320794903484>.
 180. Haines AM, Tewes ME, Laack LL, Horne JS, Young JH. A habitat-based population viability analysis for ocelots (*Leopardus pardalis*) in the United States. *Biol. Conserv.* 2006 [cited 2016 Jan 26];132:424–36. Available from: <http://www.sciencedirect.com/science/article/pii/S0006320706001923>.
 181. Urban DL, Minor ES, Treml EA, Schick RS. Graph models of habitat mosaics. *Ecol Lett.* 2009 [cited 2016 Mar 15];12:260–73. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/19161432>.
 182. Etherington TR. Least-cost modelling and landscape ecology: concepts, applications, and opportunities. *Curr Landsc Ecol Reports.* Springer International Publishing; 2016 [cited 2016 Sep 20];1:40–53. Available from: <http://link.springer.com/10.1007/s40823-016-0006-9>.
 183. Li J, Song B, Wang X. An extended discrete Ricker population model with Allee effects. *J Differ Equations Appl.* Taylor & Francis Group; 2007 [cited 2016 Mar 16];13:309–21. Available from: <http://www.tandfonline.com/doi/full/10.1080/10236190601079191>.
 184. Labra FA, Lagos NA, Marquet PA. Dispersal and transient dynamics in metapopulations. *Ecol Lett.* 2003 [cited 2016 Mar 16];6:197–204. Available from: <http://doi.wiley.com/10.1046/j.1461-0248.2003.00413.x>.
 185. de-Camino-Beck T, Lewis MA. Invasion with stage-structured coupled map lattices: Application to the spread of scentless chamomile. *Ecol Model.* 2009 [cited 2016 Mar 16];220:3394–403. Available from: <http://www.sciencedirect.com/science/article/pii/S0304380009006115>.
 186. Coutinho RM, Godoy WAC, Kraenkel RA. Integrodifference model for blowfly invasion. *Theor Ecol.* 2012 [cited 2016 Mar 16];5:363–71. Available from: <http://link.springer.com/10.1007/s12080-012-0157-1>.
 187. Skarpaas O, Shea K. Dispersal patterns, dispersal mechanisms, and invasion wave speeds for invasive thistles. *Am Nat.* 2007 [cited 2016 Mar 16];170:421–30. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/17879192>.
 188. White SM, White KAJ. Relating coupled map lattices to integrodifference equations: dispersal-driven instabilities in coupled map lattices. *J Theor Biol.* 2005 [cited 2016 Mar 16];235:463–75. Available from: <http://www.sciencedirect.com/science/article/pii/S0022519305000536>.
 189. Kot M, Schaffer WM. Discrete-time growth-dispersal models. *Math Biosci.* 1986 [cited 2016 Mar 16];80:109–36. Available from: <http://www.sciencedirect.com/science/article/pii/S002556486900696>.
 190. Gilbert MA, White SM, Bullock JM, Gaffney EA. Spreading speeds for stage structured plant populations in fragmented landscapes. *J Theor Biol.* 2014 [cited 2016 Mar 16];349:135–49. Available from: <http://www.sciencedirect.com/science/article/pii/S0022519314000411>.
 191. Gilbert MA, Gaffney EA, Bullock JM, White SM. Spreading speeds for plant populations in landscapes with low environmental variation. *J Theor Biol.* 2014 [cited 2016 Mar 16];363:436–52. Available from: <http://www.sciencedirect.com/science/article/pii/S0022519314004779>.
 192. Dewhurst S, Lutscher F. Dispersal in heterogeneous habitats: thresholds, spatial scales, and approximate rates of spread. *Ecology.* 2009 [cited 2016 Mar 16];90:1338–45. Available from: <http://doi.wiley.com/10.1890/08-0115.1>.
 193. Gilbert M, White S, Bullock J, Gaffney E. Speeding up the simulation of population spread models. *Methods Ecol Evol.* in press.
 194. Gilbert MA. AdaptiveIDE version 1. 2016 [cited 2016 Mar 16]. Available from: <http://zenodo.org/record/45509>.
 195. Clark JS, Lewis M, Horvath L. Invasion by extremes: population spread with variation in dispersal and reproduction. *Am Nat.* 2001 [cited 2016 Mar 16];157:537–54. Available from: <http://europepmc.org/abstract/med/18707261>.
 196. Homer CG, Dewitz JA, Yang L, Jin S, Danielson P, Xian G, et al. Completion of the 2011 National Land Cover Database for the conterminous United States—Representing a decade of land cover change information. *Photogramm Eng Remote Sens.* 2015;81:345–54.
 197. Fastie CL. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology.* Ecological Society of America; 1995 [cited 2016 Mar 16];76:1899–916. Available from: <http://cat.inist.fr/?aModele=afficheN&cpsidt=3689293>.
 198. Huston M, DeAngelis D, Post W. New computer models unify ecological theory. *Bioscience.* 1988;38:682–91.
 199. DeAngelis DL, Mooij WM. Individual-based modeling of ecological and evolutionary processes. *Annu Rev Ecol Evol Syst.* Annual Reviews; 2005 [cited 2015 Sep 21];36:147–68. Available from: <http://www.annualreviews.org/doi/abs/10.1146/annurev.ecolsys.36.102003.152644>.
 200. Wang M, Grimm V. Home range dynamics and population regulation: an individual-based model of the common shrew *Sorex araneus*. *Ecol Model.* 2007;205:397–409. Available from: <http://www.sciencedirect.com/science/article/pii/S0304380007001226>.
 201. Watkins A, Noble J, Foster RJ, Harmsen BJ, Doncaster CP. A spatially explicit agent-based model of the interactions between jaguar populations and their habitats. *Spec Issue Ecol Model Ecosyst Sustain Sel Pap. Present. 19th ISEM Conf.* 28–31 Oct. 2013, Toulouse, Fr. 2015;306:268–77. Available from: <http://www.sciencedirect.com/science/article/pii/S0304380014005560>.
 202. Wiegand T, Knauer F, Kaczensky P, Naves J. Expansion of brown bears (*Ursus arctos*) into the eastern Alps: a spatially explicit population model. *Biodivers Conserv.* 2004;13:79–114.
 203. Schumaker NH, Ernst T, White D, Baker J, Haggerty P. Projecting wildlife responses to alternative future landscapes in Oregon's Willamette Basin. *Ecol Appl.* 2004 [cited 2016 Feb 13];14:381–400. Available from: <http://doi.wiley.com/10.1890/02-5010>.
 204. Gimona A, Poggio L, Polhill JG, Castellazzi M. Habitat networks and food security: promoting species range shift under climate change depends on life history and the dynamics of land use choices. *Landsc Ecol* 2015;1–19.
 205. Coulon A, Aben J, Palmer SCF, Stevens VM, Callens T, Strubbe D, et al. A stochastic movement simulator improves estimates of landscape connectivity. *Ecology.* 2015 [cited 2016 Mar 16];96:2203–13. Available from: <http://doi.wiley.com/10.1890/14-1690.1>.
 206. Pe'er G, Henle K, Dislich C, Frank K. Breaking functional connectivity into components: a novel approach using an individual-based model, and first outcomes. *PLoS One.* 2011;6:e22355. Available from: http://www.researchgate.net/publication/51559930_Breaking_Functional_Connectivity_into_Components_A_Novel_Approach_Using_an_Individual-Based_Model_and_First_Outcomes.
 207. Börger L, Dalziel BD, Fryxell JM. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecol Lett.* 2008 [cited 2015 Nov 17];11:637–50. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/18400017>.
 208. Pe'er G, Saltz D, Münkemüller T, Matsinos YG, Thulke H-H. Simple rules for complex landscapes: the case of hilltopping movements and topography. *Oikos.* 2013 [cited 2016 Mar 16];no-no. Available from: <http://doi.wiley.com/10.1111/j.1600-0706.2013.00198.x>.
 209. Bartoń KA, Hovestadt T, Phillips BL, Travis MJJ. Risky movement increases the rate of range expansion. *Proc Biol Sci.* 2012 [cited 2016 Mar 16];279:1194–202. Available from: <http://rspb.royalsocietypublishing.org/content/279/1731/1194.short>.
 210. Lookingbill TR, Gardner RH, Ferrari JR, Keller CE. Combining a dispersal model with network theory to assess habitat connectivity. *Ecol Appl.* 2010 [cited 2016 Mar 16];20:427–41. Available from: <http://doi.wiley.com/10.1890/09-0073.1>.

211. Hovestadt T, Messner S, Poethke HJ. Evolution of reduced dispersal mortality and “fat-tailed” dispersal kernels in autocorrelated landscapes. *Proc Biol Sci.* 2001 [cited 2016 Mar 16];268:385–91. Available from: <http://rspb.royalsocietypublishing.org/content/268/1465/385>.
212. Poethke HJ, Hovestadt T, Mitesser O. Local extinction and the evolution of dispersal rates: Causes and correlations. *Am Nat.* University of Chicago Press; 2003 [cited 2016 Mar 16];161:631–40. Available from: <http://cat.inist.fr/?aModele=afficheN&cpsid=14752862>.
213. Kubisch A, Poethke H-J, Hovestadt T. Density-dependent dispersal and the formation of range borders. *Ecography (Cop.)*. 2011 [cited 2016 Mar 16];34:1002–8. Available from: <http://doi.wiley.com/10.1111/j.1600-0587.2010.06744.x>
214. Buchmann CM, Schurr FM, Nathan R, Jeltsch F. An allometric model of home range formation explains the structuring of animal communities exploiting heterogeneous resources. *Oikos*. 2011 [cited 2016 Mar 16];120:106–18. Available from: <http://doi.wiley.com/10.1111/j.1600-0706.2010.18556.x>.
215. McLane AJ, Semeniuk C, McDermid GJ, Marceau DJ. The role of agent-based models in wildlife ecology and management. *Ecol Model.* 2011 [cited 2016 Mar 16];222:1544–56. Available from: <http://www.sciencedirect.com/science/article/pii/S0304380011000524>.
216. Aben J, Bocedi G, Palmer SCF, Pellikka P, Strubbe D, Hallmann C, et al. The importance of realistic dispersal models in planning for conservation: application of a novel modelling platform to evaluate management scenarios in an Afrotropical biodiversity hotspot. *J Appl Ecol.* 2016 [cited 2016 Mar 14];n/a-n/a. Available from: <http://doi.wiley.com/10.1111/1365-2664.12643>.
217. Becu N, Perez P, Walker A, Barreteau O, Le Page C. Agent based simulation of a small catchment water management in northern Thailand: description of the CATCHSCAPE model. *Ecol Model.* 2003;170:319–31.
218. Yu C, MacEachren AM, Peuquet DJ, Yarnal B. Integrating scientific modeling and supporting dynamic hazard management with a GeoAgent-based representation of human–environment interactions: a drought example in Central Pennsylvania, USA. *Environ Model Softw.* 2009 [cited 2016 Jan 26];24:1501–12. Available from: <http://www.sciencedirect.com/science/article/pii/S1364815209000802>.
219. Schreinemachers P, Potchanasin C, Berger T, Roygrong S. Agent-based modeling for ex ante assessment of tree crop innovations: litchis in northern Thailand. *Agric Econ.* 2010;41:519–36.
220. Hu Y, Cai X, DuPont B. Design of a web-based application of the coupled multi-agent system model and environmental model for watershed management analysis using Hadoop. *Environ Model Softw.* 2015;70:149–62. Available from: <http://www.sciencedirect.com/science/article/pii/S1364815215001206>.
221. Gaube V, Kaiser C, Wildenberg M, Adensam H, Fleissner P, Kobler J, et al. Combining agent-based and stock-flow modelling approaches in a participative analysis of the integrated land system in Reichraming, Austria. *Landsc Ecol.* 2009;24:1149–65.
222. Schreinemachers P, Berger T. An agent-based simulation model of human–environment interactions in agricultural systems. *Environ Model Softw.* 2011;26:845–59. Available from: <http://www.sciencedirect.com/science/article/pii/S1364815211000314>.
223. Marohn C, Schreinemachers P, Quang DV, Siripalangkanont P, Hörhold S, Berger T, et al. Interpreting outputs of a landscape-scale coupled social-ecological system. 2012.
224. Evans TP, Kelley H. Assessing the transition from deforestation to forest regrowth with an agent-based model of land cover change for south-central Indiana (USA). *Geoforum.* 2008;39:819–32.
225. Linderman MA, An L, Bearer S, He G, Ouyang Z, Liu J. Modeling the spatio-temporal dynamics and interactions of households, landscapes, and giant panda habitat. *Ecol Model.* 2005;183:47–65.
226. Monticino M, Acevedo M, Callicott B, Cogdill T, Lindquist C. Coupled human and natural systems: a multi-agent-based approach. *Environ Model Softw.* 2007;22:656–63.
227. Rykiel EJ. Testing ecological models: the meaning of validation. *Ecol Model.* Elsevier; 1996 [cited 2016 Sep 6];90:229–44. Available from: <http://linkinghub.elsevier.com/retrieve/pii/0304380095001522>.
228. Augustiak J, Van den Brink PJ. Merging validation and evaluation of ecological models to “evaluation”: a review of terminology and a practical approach. *Ecol Model.* 2014;280:117–28.
229. Pontius RG. Quantification error versus location error in comparison of categorical maps. *Photogramm Eng Remote Sens.* 2000;66:1011–6.
230. Visser H, De Nijs T. The map comparison kit. *Environ Model Softw.* 2006;21:346–58. Available from: <http://linkinghub.elsevier.com/retrieve/pii/S1364815204003019>.
231. Pontius RG, Millones M. Death to Kappa: birth of quantity disagreement and allocation disagreement for accuracy assessment. *Int J Remote Sens.* Taylor & Francis; 2011 [cited 2016 Sep 6];32:4407–29. Available from: <http://www.tandfonline.com/doi/abs/10.1080/01431161.2011.552923>.
232. Olofsson P, Foody GM, Herold M, Stehman SV, Woodcock CE, Wulder MA. Good practices for estimating area and assessing accuracy of land change. *Remote Sens Environ.* 2014;148:42–57.
233. Araújo MB, Pearson RG, Thuiller W, Erhard M. Validation of species–climate impact models under climate change. *Glob Chang Biol.* 2005;11:1–10. Available from: <http://darchive.mblwhoilibrary.org:8080/handle/1912/2470>.
234. van Vliet J, Bregt AK, Brown DG, van Delden H, Heckbert S, Verburg PH. A review of current calibration and validation practices in land-change modeling. *Environ Model Softw.* 2016;82:174–82.
235. Rosa IMD, Ahmed SE, Ewers RM. The transparency, reliability and utility of tropical rainforest land-use and land-cover change models. *Glob Chang Biol.* 2014 [cited 2016 Sep 22];20:1707–22. Available from: <http://doi.wiley.com/10.1111/gcb.12523>.
236. Brown C, Brown K, Rounsevell M. A philosophical case for process-based modelling of land use change. *Model Earth Syst Environ.* Springer International Publishing; 2016 [cited 2016 Sep 23];2:50. Available from: <http://link.springer.com/10.1007/s40808-016-0102-1>.
237. Kleijnen JPC. Verification and validation of simulation models. *Eur J Oper Res.* North-Holland; 1995 [cited 2016 Sep 6];82:145–62. Available from: <http://linkinghub.elsevier.com/retrieve/pii/0377221794000166>.
238. Troost C, Berger T. Dealing with uncertainty in agent-based simulation: farm-level modeling of adaptation to climate change in Southwest Germany. *Am J Agric Econ.* Oxford University Press; 2015 [cited 2016 Sep 23];97:833–54. Available from: <http://ajae.oxfordjournals.org/cgi/doi/10.1093/ajae/aa076>.
239. Schindler DE, Hilborn R. Prediction, precaution, and policy under global change. *Science.* 2015;347.
240. Urban MC, Bocedi G, Hendry AP, Mihoub J-B, Pe’er G, Singer A, et al. Improving the forecast for biodiversity under climate change. *Science.* 2016;353.
241. Bourne EC, Bocedi G, Travis JMJ, Pakeman RJ, Brooker RW, Schiffrers K. Between migration load and evolutionary rescue: dispersal, adaptation and the response of spatially structured populations to environmental change. *Proc Biol Sci.* 2014 [cited 2016 Feb 16];281:20132795. Available from: <http://rspb.royalsocietypublishing.org/content/281/1778/20132795.short>.
242. Boeye J, Travis JMJ, Stoks R, Bonte D. More rapid climate change promotes evolutionary rescue through selection for increased dispersal distance. *Evol Appl.* 2013 [cited 2016 Mar 15];6:353–64. Available from: <http://doi.wiley.com/10.1111/eva.12004>.
243. Travis JMJ, Dytham C. Dispersal evolution during invasions. *Evol Ecol Res.* Evolutionary Ecology, Ltd.; 2002 [cited 2016 Mar

- 16];4:1119–29. Available from: <http://www.evolutionary-ecology.com/abstracts/v04/1413.html>.
244. Cheptou P-O, Carrue O, Rouifed S, Cantarel A. Rapid evolution of seed dispersal in an urban environment in the weed *Crepis sancta*. *Proc Natl Acad Sci U S A*. 2008 [cited 2016 Feb 11];105:3796–9. Available from: <http://www.pnas.org/content/105/10/3796.short>.
245. Martin AE, Fahrig L. Matrix quality and disturbance frequency drive evolution of species behavior at habitat boundaries. *Ecol Evol*. 2015 [cited 2016 Mar 16];5:5792–800. Available from: <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4717347&tool=pmcentrez&rendertype=abstract>.
246. Travis JMJ, Dytham C. Habitat persistence, habitat availability and the evolution of dispersal. *Proc R Soc B Biol Sci*. 1999 [cited 2015 Dec 7];266:723–8. Available from: <http://rspb.royalsocietypublishing.org/content/266/1420/723>.
247. Henry RC, Bocedi G, Travis JMJ. Eco-evolutionary dynamics of range shifts: elastic margins and critical thresholds. *J Theor Biol*. 2013 [cited 2016 Mar 16];321:1–7. Available from: <http://www.sciencedirect.com/science/article/pii/S0022519312006285>.
248. Kubisch A, Hovestadt T, Poethke H-J. On the elasticity of range limits during periods of expansion. *Ecology*. 2010 [cited 2016 Mar 16];91:3094–9. Available from: <http://doi.wiley.com/10.1890/09-2022.1>.
249. Klironomos FD, Berg J, Collins S. How epigenetic mutations can affect genetic evolution: model and mechanism. *Bioessays*. 2013 [cited 2016 Mar 16];35:571–8. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/23580343>.
250. Kronholm I, Collins S. Epigenetic mutations can both help and hinder adaptive evolution. *Mol Ecol*. 2015 [cited 2016 Mar 16]; Available from: <http://www.ncbi.nlm.nih.gov/pubmed/26139359>.
251. M’Gonigle LK, Mazzucco R, Otto SP, Dieckmann U. Sexual selection enables long-term coexistence despite ecological equivalence. *Nature*. Nature Publishing Group, a division of Macmillan Publishers Limited. All Rights Reserved.; 2012 [cited 2016 Mar 16];484:506–9. Available from: <http://dx.doi.org/10.1038/nature10971>.
252. Bocedi G, Reid JM. Evolution of female multiple mating: a quantitative model of the “sexually selected sperm” hypothesis. *Evolution*. 2015 [cited 2016 Mar 16];69:39–58. Available from: <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4312924&tool=pmcentrez&rendertype=abstract>.
253. Bocedi G, Reid JM. Coevolutionary feedbacks between female mating interval and male allocation to competing sperm traits can drive evolution of costly polyandry. *Am Nat*. 2016 [cited 2016 Mar 16];187:334–50. Available from: <http://europepmc.org/abstract/med/26913946>.
254. Cambui ECB, Nogueira de Vasconcelos R, Boscolo D, Bernardo da Rocha PL, Miranda JGV. GradientLand software: a landscape change gradient generator. *Ecol Inform*. Elsevier B.V.; 2015;25: 57–62. Available from: <http://www.sciencedirect.com/science/article/pii/S1574954114001617>.
255. Schloss CA, Nuñez TA, Lawler JJ. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proc Natl Acad Sci U S A*. 2012 [cited 2016 Mar 16];109:8606–11. Available from: <http://www.pnas.org/content/109/22/8606.abstract>.
256. Santini L, Cornulier T, Bullock JM, Palmer SCF, White SM, Hodgson JA, et al. A trait-based approach for predicting species responses to environmental change from sparse data: how well might terrestrial mammals track climate change? *Glob Chang Biol*. 2016.
257. Heikkinen RK, Pöyry J, Virkkala R, Bocedi G, Kuussaari M, Schweiger O, et al. Modelling potential success of conservation translocations of a specialist grassland butterfly. *Biol Conserv*. 2015 [cited 2016 Mar 16];192:200–6. Available from: <http://www.sciencedirect.com/science/article/pii/S0006320715301208>.
258. Liu J, Dietz T, Carpenter SR, Alberti M, Folke C, Moran E, et al. Complexity of coupled human and natural systems. *Science*. 2007;317:1513–6.
259. Filatova T, Polhill G. Shocks in coupled socio-ecological systems: what are they and how can we model them? *iEMSS*. 2012.
260. Liu J, Mooney H, Hull V, Davis SJ, Gaskell J, Hertel T, et al. Systems integration for global sustainability. *Science*. 2015;347: 1258832.
261. Voinov A, Shugart HH. “Integronsters”, integral and integrated modeling. *Environ Model Softw*. 2013;39:149–58.
262. Luus KA, Robinson DT, Deadman PJ. Representing ecological processes in agent-based models of land use and cover change. *J Land Use Sci*. 2011;8:1–24.
263. Levin S. The problem of pattern and scale in ecology. *Ecology*. 1992;73.
264. Schneider DC. The rise of the concept of scale in ecology. *Bioscience*. Oxford University Press; 2001 [cited 2016 Feb 15];51:545. Available from: <http://bioscience.oxfordjournals.org/content/51/7/545.full>.
265. Veldkamp A, Verburg PH, Kok K, de Koning GHJ, Priess J, Bergsma AR. The need for scale sensitive approaches in spatially explicit land use change modeling. *Environ Model Assess*. Kluwer Academic Publishers; 2001 [cited 2016 Feb 15];6:111–21. Available from: <http://link.springer.com/article/10.1023/A%3A1011572301150>.
266. Chave J. The problem of pattern and scale in ecology: what have we learned in 20 years? *Ecol. Lett*. 2013 [cited 2016 Jan 28];16(Suppl 1):4–16. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/23351093>.
267. Filatova T, Verburg PH, Parker DC, Stannard CA. Spatial agent-based models for socio-ecological systems: challenges and prospects. *Environ Model Softw*. 2013;45:1–7.
268. Schulp CJE, Nabuurs G-J, Verburg PH. Future carbon sequestration in Europe—effects of land use change. *Agric Ecosyst Environ*. 2008 [cited 2016 Feb 12];127:251–64. Available from: <http://www.sciencedirect.com/science/article/pii/S0167880908001321>.
269. Brown C, Murray-Rust D, van Vliet J, Alam SJ, Verburg PH, Rounsevell MD. Experiments in globalisation, food security and land use decision making. *PLoS One*. 2014;9.
270. Bousquet F, Le Page C. Multi-agent simulations and ecosystem management: a review. *Ecol. Model*. 2004 [cited 2014 Jul 11];176: 313–32. Available from: <http://www.sciencedirect.com/science/article/pii/S0304380004000948>.
271. Evans TP, Kelley H. Multi-scale analysis of a household level agent-based model of landcover change. *J Environ Manag*. 2004 [cited 2016 Feb 16];72:57–72. Available from: <http://www.sciencedirect.com/science/article/pii/S0301479704000787>.
272. Scheffer M, Baveco JM, DeAngelis DL, Rose KA, van Nes EH. Super-individuals a simple solution for modelling large populations on an individual basis. *Ecol Model*. 1995 [cited 2015 Dec 5];80:161–70. Available from: <http://www.sciencedirect.com/science/article/pii/030438009400055M>.
273. Grimm V, Revilla E, Berger U, Jeltsch F, Mooij WM, Railsback SF, et al. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science*. 2005;310:987–91.
274. Boer MM, Johnston P, Sadler RJ. Neighbourhood rules make or break spatial scale invariance in a classic model of contagious disturbance. *Ecol Complex*. 2011 [cited 2016 Feb 1];8:347–56. Available from: <http://www.sciencedirect.com/science/article/pii/S1476945X11000626>.
275. Orrock JL, Pagels JF, McShea WJ, Harper EK. Predicting presence and abundance of a small mammal species: the effect of scale and resolution. *Ecol Appl*. Ecological Society of America; 2000 [cited 2016 Feb 13];10:1356–66. Available from: [http://onlinelibrary.wiley.com/doi/10.1890/1051-0761\(2000\)010\[1356:PPAAOA\]2.0.CO;2/full](http://onlinelibrary.wiley.com/doi/10.1890/1051-0761(2000)010[1356:PPAAOA]2.0.CO;2/full).

276. Johnson CJ, Parker KL, Heard DC, Gillingham MP. Movement parameters of ungulates and scale-specific responses to the environment. *J Anim Ecol*. 2002 [cited 2016 Feb 13];71:225–35. Available from: <http://doi.wiley.com/10.1046/j.1365-2656.2002.00595.x>.
277. Holland EP, Aegerter JN, Smith GC. Spatial sensitivity of a generic population model, using wild boar (*Sus scrofa*) as a test case. *Ecol Model*. 2007 [cited 2016 Feb 13];205:146–58. Available from: <http://www.sciencedirect.com/science/article/pii/S0304380007000853>.
278. Dunn AG. Grid-induced biases in connectivity metric implementations that use regular grids. *Ecography (Cop.)*. 2009 [cited 2016 Feb 1]; Available from: <http://doi.wiley.com/10.1111/j.1600-0587.2009.05980.x>.
279. South AB, Kenward RE. Mate finding, dispersal distances and population growth in invading species: a spatially explicit model. *Oikos*. 2001 [cited 2016 Feb 13];95:53–8. Available from: <http://doi.wiley.com/10.1034/j.1600-0706.2001.950106.x>.
280. Trunfio GA. Predicting wildfire spreading through a hexagonal cellular automata model. Springer; 2004. p. 385–94.
281. Huber PR, Greco SE, Schumaker NH, Hobbs J. A priori assessment of reintroduction strategies for a native ungulate: using HexSim to guide release site selection. *Landsc Ecol*. 2014 [cited 2016 Feb 13];29:689–701. Available from: <http://link.springer.com/10.1007/s10980-014-0006-2>.
282. Schönfisch B. Anisotropy in cellular automata. *Biosystems*. 1997 [cited 2016 Feb 1];41:29–41. Available from: <http://www.sciencedirect.com/science/article/pii/S0303264796016644>.
283. Etherington TR. Least-cost modelling on irregular landscape graphs. *Landsc Ecol*. 2012 [cited 2016 Feb 1];27:957–68. Available from: <http://link.springer.com/10.1007/s10980-012-9747-y>.
284. Ortigoza GM. Unstructured triangular cellular automata for modeling geographic spread. *Appl Math Comput*. 2015 [cited 2016 Jan 5];258:520–36. Available from: <http://www.sciencedirect.com/science/article/pii/S0096300315001484>.
285. Stevens D, Dragičević S. A GIS-based irregular cellular automata model of land-use change. *Environ Plan B Plan Des*. SAGE Publications; 2007 [cited 2016 Feb 1];34:708–24. Available from: <http://epb.sagepub.com/content/34/4/708.abstract>.
286. Yamanaka T, Tatsuki S, Shimada M. An individual-based model for sex-pheromone-oriented flight patterns of male moths in a local area. *Ecol Model*. 2003;161:35–51.
287. Thorbek P, Topping CJ. The influence of landscape diversity and heterogeneity on spatial dynamics of agrobiont linyphiid spiders: an individual-based model. *Biocontrol*. 2005;50:1–33.
288. Bennett DA, Tang W. Modelling adaptive, spatially aware, and mobile agents: Elk migration in Yellowstone. *Int J Geogr Inf Sci*. 2006;20:1039–66. Available from: <http://www.tandfonline.com/doi/abs/10.1080/13658810600830806>.
289. Parry HR, Evans AJ, Morgan D. Aphid population response to agricultural landscape change: A spatially explicit, individual-based model. *Pattern Process Dyn Mosaic Landsc Model Simul Implic*. 2006;199:451–63. Available from: <http://www.sciencedirect.com/science/article/pii/S0304380006002894>.
290. Bithell M, Brasington J, Richards K. Discrete-element, individual-based and agent-based models: tools for interdisciplinary enquiry in geography? *Geoforum*. 2008;39:625–42.
291. Imron MA, Herzog S, Berger U. The influence of agroforestry and other land-use types on the persistence of a Sumatran Tiger (*Panthera tigris sumatrae*) population: an individual-based model approach. *Environ Manag*. 2011;48:276–88.
292. Matthews R, Selman P. Landscape as a focus for integrating human and environmental processes. *J Agric Econ*. 2006;57:199–212.