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METHODOLOGICAL DEVELOPMENT (A TYRE, SECTION EDITOR)

Emerging Opportunities for Landscape Ecological Modelling

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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*

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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 landform 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

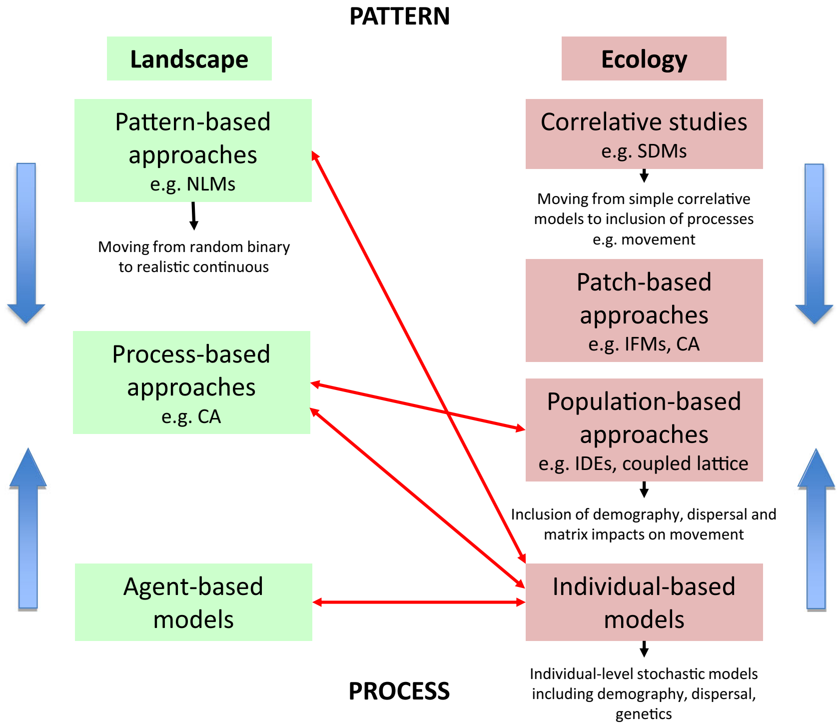

Fig. 1 The suite of approaches available for landscape and ecological modelling. Both fields have developed a range of approaches from relatively simple correlative and neutral modelling approaches through to complex agent or individual-based approaches. In both disciplines, there is increasing complementary 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	• 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.	• None
Process-based anthropogenic disturbance models	• 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.	• None
Biogeochemical models	• To study hydrological and nutrient flows.	• Soil, vegetation and climate data.
Process-based land-use models	• 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.	• Data to parameterise land-use decision-making. • Economic, policy or environmental data to drive the decision making.
Ecology		
Species distribution models	• To spatially or temporally extrapolate a known pattern of species habitat or climate associations.	• Species observation data (presence-absence or abundance data). • Associated habitat and/or climate data.
Forest landscape dynamics, succession and disturbance	• To study processes and dynamics of vegetation at local to landscape scales.	• Plant life-history data. • Disturbance data e.g. fire, pest-species.
Dynamic global vegetation model (integrated biogeochemical and vegetation models)	• To study vegetation cover at continental to global scales, incorporating biogeochemical and hydrological processes.	• Plant life-history data. • Climate data.
Hybrid species distribution models	• 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".	• 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	• To study the viability of species populations. • To review potential habitat or population management options.	• Population demographics data.
Cellular automata	• 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.	• Data on potential system states. • Data on how neighbourhood interactions drive transitions.
Population abundance models	• To study population spread rates.	• Population demographics data. • Dispersal or spread rate data.
Individual-based models	• 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.	• Species life-history data.
Integrated models		
Integrated human decision making and biophysical models	• To study the interaction between humans and finite (often dynamic) environmental resources.	• Dependent on the component models (as above).
Integrated socio-ecological models	• To study interactions between humans and species populations.	• 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

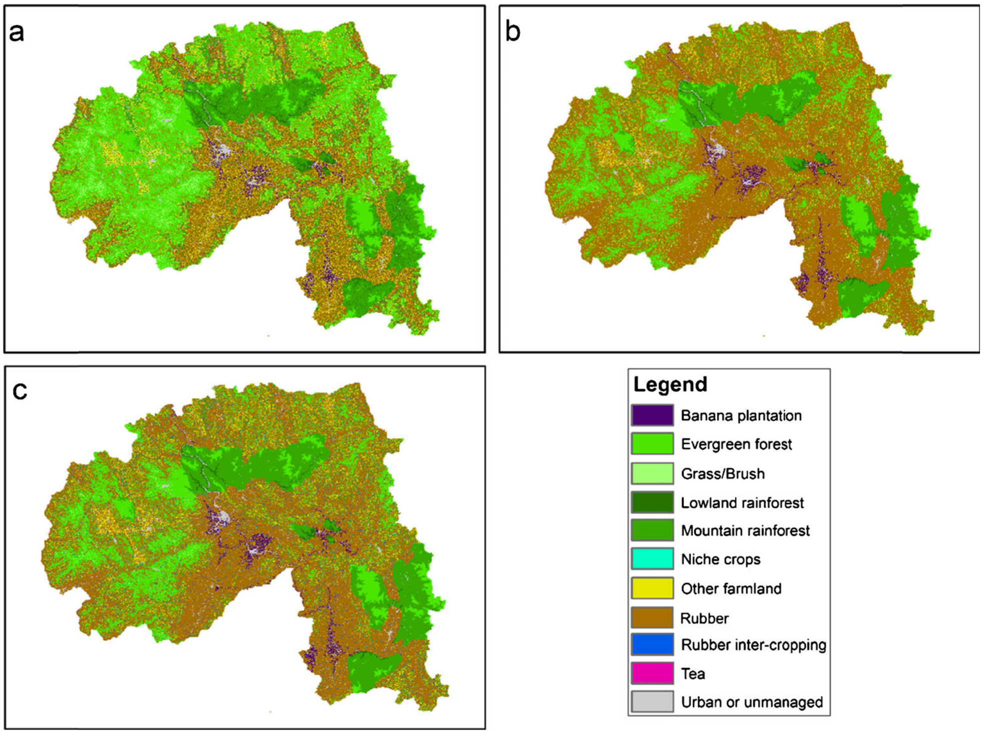

Fig. 2 Process-based land-use models are being developed rapidly and offer considerable promise for projecting land-use into the future. There is considerable potential to link these emerging models with ecological models, including integrodifference and individual-based models, to project biodiversity 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)

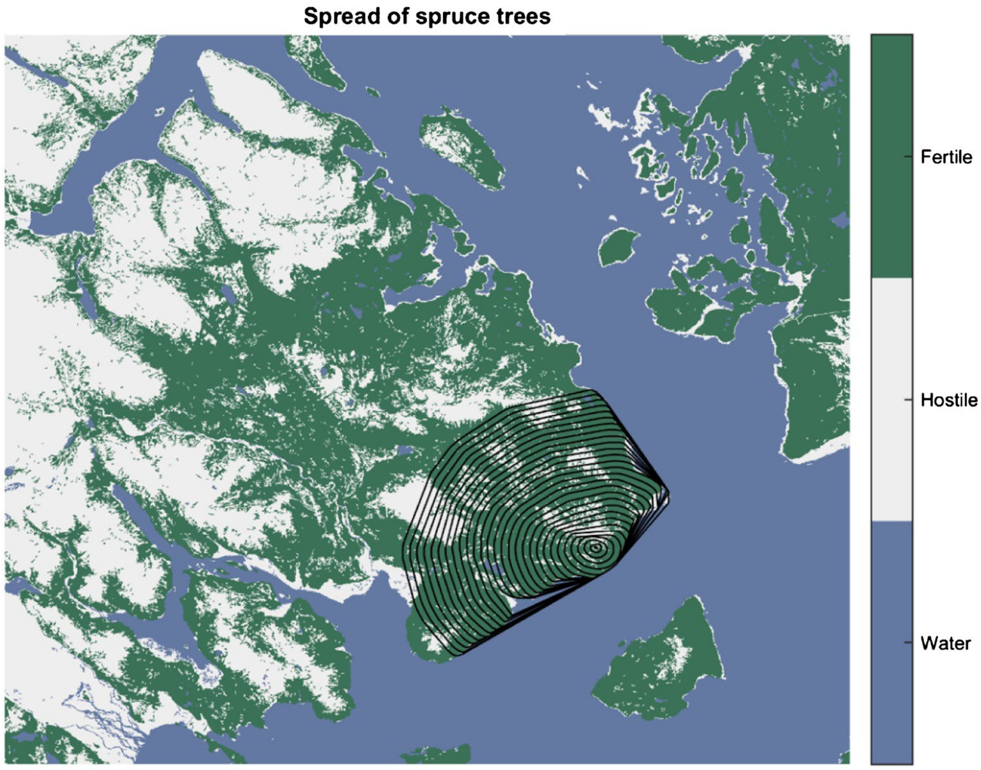

Fig. 3 Emerging mathematical approaches for simulating population spread across heterogeneous landscapes offer substantial potential for landscape ecology, making possible highly computationally efficient projection of species range dynamics over large spatial scales. This is an example where the spread 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.

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Compliance with Ethical Standards

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

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