

The road to integrate climate change effects on land-use change in regional biodiversity models

Juliano Sarmiento Cabral¹, Alma Mendoza-Ponce^{2,3}, André Pinto da Silva^{4,5}, Johannes Oberpriller⁶, Anne Mimet⁷, Julia Kieslinger⁸, Thomas Berger⁹, Jana Blechschmidt¹, Maximilian Brönnner⁸, Alice Classen¹⁰, Stefan Fallert¹, Florian Hartig⁶, Christian Hof⁷, Markus Hoffmann¹¹, Thomas Knoke¹², Andreas Krause¹³, Anne Lewerentz¹, Perdita Pohle⁸, Uta Raeder¹¹, Anja Rammig¹³, Sarah Redlich¹⁰, Sven Rubanschki⁷, Christian Stetter¹⁴, Wolfgang Weisser⁷, Daniel Vedder^{1,15,16,17}, Peter H. Verburg¹⁸, and Damaris Zurell¹⁹

¹Ecosystem Modelling, Center for Computational and Theoretical Biology (CCTB), University of Würzburg

²Research Program on Climate Change, Universidad Nacional Autónoma de México

³International Institute for Applied Systems Analysis, Laxenburg, Austria

⁴Department of Ecology and Genetics, Animal Ecology, Evolutionary Biology Centre, Uppsala University

⁵Centre for Ecology, Evolution and Environmental Changes (cE3c), Faculdade de Ciências, Universidade de Lisboa

⁶Theoretical Ecology Lab, University of Regensburg

⁷Technical University of Munich, Terrestrial Ecology Research Group, Department of Life Science Systems, School of Life Sciences

⁸Chair of Human Geography and Development Studies, Institute of Geography, Friedrich-Alexander University Erlangen-Nuernberg

⁹Land-Use Economics in the Tropics and Subtropics, Hans-Ruthenberg Institute, Hohenheim University

¹⁰Department of Animal Ecology and Tropical Biology, Biocentre, University of Würzburg

¹¹Technical University of Munich, Limnologische Station Iffeldorf, Chair of Aquatic Systems Biology, Department of Life Science Systems, School of Life Science

¹²Technical University of Munich, Institute of Forest Management, Department of Life Science Systems, School of Life Sciences

¹³Technical University of Munich, Land Surface-Atmosphere Interactions, Department of Life Science Systems, School of Life Sciences

¹⁴Technical University of Munich, Agricultural Production and Resource Economics, School of Life Sciences

¹⁵Helmholtz Center for Environmental Research - UFZ, Department of Ecosystem Services

¹⁶Institute of Biodiversity, Friedrich Schiller University Jena

¹⁷German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig

¹⁸Institute for Environmental Studies, VU University Amsterdam

¹⁹Inst. for Biochemistry and Biology, University of Potsdam

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Juliano Sarmiento Cabral¹, Alma Mendoza-Ponce^{2,3}, André Pinto da Silva^{4,5}, Johannes Oberpriller⁶, Anne Mimet⁷, Julia Kieslinger⁸, Thomas Berger⁹, Jana Blechschmidt¹, Maximilian Brönnner⁸, Alice Classen¹⁰, Stefan Fallert¹, Florian Hartig⁶, Christian Hof⁷, Markus Hoffmann¹¹, Thomas Knoke¹², Andreas Krause¹³, Anne Lewerentz¹, Perdita Pohle⁸, Uta Raeder¹¹, Anja Rammig¹³, Sarah Redlich¹⁰, Sven Rubanschki⁷, Christian Stetter¹⁴, Wolfgang Weisser⁷, Daniel Vedder^{1,15,16,17}, Peter H. Verburg¹⁸, Damaris Zurell¹⁹

¹ Ecosystem Modelling, Center for Computational and Theoretical Biology (CCTB), University of Würzburg, Klara-Oppenheimer-Weg 32, 37074, Würzburg, Germany

² Research Program on Climate Change, Universidad Nacional Autónoma de México, Mexico City, Mexico

³ International Institute for Applied Systems Analysis, Laxenburg, Austria

⁴ Department of Ecology and Genetics, Animal Ecology, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden

⁵ Centre for Ecology, Evolution and Environmental Changes (cE3c), Faculdade de Ciências, Universidade de Lisboa, Lisbon, Portugal

⁶ Theoretical Ecology Lab, University of Regensburg, Universitätsstraße 31, 93053 Regensburg, Germany

⁷ Technical University of Munich, Terrestrial Ecology Research Group, Department of Life Science Systems, School of Life Sciences, 84354 Freising, Germany

⁸ Institute of Geography, Friedrich-Alexander University Erlangen-Nuernberg, Wetterkreuz 15, 91058 Erlangen, Germany

⁹ Land-Use Economics in the Tropics and Subtropics, Hans-Ruthenberg Institute, Hohenheim University, Hohenheim, Germany

¹⁰ Department of Animal Ecology and Tropical Biology, Biocentre, University of Würzburg, Am Hubland, 97074 Würzburg, Germany

¹¹ Technical University of Munich, Limnologische Station Iffeldorf, Chair of Aquatic Systems Biology, Department of Life Science Systems, School of Life Science, Hofmark 1-3, 82393 Iffeldorf, Germany

¹² Technical University of Munich, Institute of Forest Management, Department of Life Science Systems, School of Life Sciences, 58354 Freising, Germany

¹³ Technical University of Munich, Land Surface-Atmosphere Interactions, Department of Life Science Systems, School of Life Sciences, 85354 Freising, Germany

¹⁴ Agricultural Production and Resource Economics, School of Life Sciences, Technical University of Munich, 84354 Freising, Germany

¹⁵ Helmholtz Center for Environmental Research - UFZ, Department of Ecosystem Services, Permoserstr. 15, 04318 Leipzig, Germany

¹⁶ Institute of Biodiversity, Friedrich Schiller University Jena, Dornburger Straße 159, 07743 Jena, Germany

¹⁷ German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstr. 4, 04103 Leipzig, Germany

¹⁸ Institute for Environmental Studies, VU University Amsterdam, De Boelelaan 1111, 1081 HV Amsterdam, The Netherlands

Abstract

1. Current modelling approaches to predict spatially explicit biodiversity responses to climate change mainly focus on the direct effects of climate on species. Integration of spatiotemporal land-cover scenarios is still limited. Current approaches either regard land cover as constant boundary conditions, or rely on general, typically globally defined land-use scenarios. This is problematic as it disregards the complex synergistic effects of climate and land use on biodiversity at the regional scale, as biophysical, economic, and social issues important for regional land-use decisions are also affected by climate change. To realistically predict climate impacts on biodiversity, it is therefore necessary to consider both, the direct effect of climate change on biodiversity, and its indirect effect on biodiversity via land-use change.
2. In this review and perspective paper, we outline how biodiversity models could be better integrated with regional, climate-driven land-use models. We provide an overview of empirical and modelling approaches to both land-use (LU) and biodiversity (BD) change, focusing on how integration has been attempted. We then analyse how LU and BD model properties, such as scales, inputs, and outputs, can be matched and identify potential integration challenges and opportunities.
3. We found LU integration in BD models has been frequently attempted. By contrast, integrating the role of BD in models of LU decisions is largely lacking. As a result, bi-directional effects remain largely understudied. Only few integrated LU-BD socio-ecological models have assessed climate change effects on LU and no study has yet investigated the relative contribution of direct vs. indirect effects of climate change on BD.
4. There is a large potential for model integration given the overlap on spatial scales, although challenges remain with respect to spatial scale, temporal dynamics, investigation of indirect effects, and bi-directionality, including feeding back to climate models. Efforts to better understand human decisions, eco-evolutionary dynamics, connection between terrestrial and aquatic systems, and format standardization of modelling outputs and empirical data should improve future models. Integrating biodiversity feedbacks into land-use and climate models requires modelling innovations, but should be feasible.

Keywords: agent-based models, biodiversity response, environmental change, indirect effects, integrative approaches, mechanistic models, socio-ecological systems, species richness

1 | INTRODUCTION

Biodiversity is under multiple threats, with land use being a key current stressor (Bühne et al., 2021; IPBES, 2019) and climate change effects likely to intensify in the future (Pereira et al., 2020). A challenge to disentangling the effect of these two stressor groups is that while climate is a key determinant of biodiversity patterns in general (Kreft et al., 2007), it is also a key driver of human land use (Yamaura et al., 2011). Consequently, changes in climate can be expected to exert multifold effects on biodiversity (Arneth et al., 2020; Leclère et al., 2020). These effects can follow direct and indirect pathways, with indirect pathways happening via climate-driven changes in land use (Fig. 1).

Most biodiversity and ecosystem assessments focus on the direct effects of climate change. Indeed, following the development of climate models and climate change projections at the global scale (e.g. Hijmans et al., 2005; with more recent projections by Fick & Hijmans, 2017; Karger et al., 2020), there has been a large production of biodiversity assessments under climate change. These assessments have mostly kept land use/cover and other global change drivers constant (e.g. Anderson et al., 2013; Sarmiento Cabral et al., 2013; Titeux et al., 2016). Even when climate change is combined with land cover change, the latter is not

modelled as a consequence of the former (e.g. Travis, 2003) and land-atmosphere feedbacks have been ignored (Wulfmeyer et al., 2018). Therefore, the indirect effects of climate change on biodiversity via its effects on land-use change (Fig. 1) remain underexplored.

Considering that land use is arguably the strongest driver of biodiversity change to date (IPBES, 2019), understanding the potential effects of climate change on land use is of high importance (Titeux et al., 2017). In this sense, global land-use models and integrated assessment models (IAMs – see Weyant 2017 for a review) allow assessing the impacts of climate on land-use changes, as well as quantifying potential climate feedbacks through greenhouse gas emissions. These models may consider economic rules of production and demand for commodities that utilize land, like agriculture, pasture and forestry (Havlík et al., 2011; Lotze-Campen et al., 2008). However, the typically coarse spatial resolutions and economic focus of these global models do not account for the diversity of farmer behaviours, decision-making strategies, and governance structures at the local to regional scale (Arneth et al., 2014; Rounsevell et al., 2014), and thus produce less precise rates of land conversion at the regional scales (Bayer et al., 2020). In addition, profit maximization, as it is assumed in many of the models, does not capture the complex socio-ecological systems that involve organized sustainable behaviour at the local and regional scales (Ostrom, 2009; see also Ceddia et al., 2015 for the specific consideration of forest rights). The standard models also ignore time lags arising from knowledge diffusion until informed decision-taking (Brown et al., 2018). Moreover, market-integrated landowners can consider fluctuations in market prices, costs, and yields in their decisions on local land allocation, although there can be other motivations, attitudes, and even contract obligations complicating land-use change processes (Debonne et al., 2021; Malek et al., 2019). As persons who are generally averse to risks and uncertainties (Pichon, 1997), landowners may decide to diversify their land-use types to buffer against risk and ambiguity such as that arising from climate change (Eisele et al., 2021; Knoke et al., 2011). Importantly, these decisions may depend on the regional context, be it traditional or cultural. Challenges for modelling land-use changes and their impacts on biodiversity at the regional scale thus lie in plausible climate-integrated, socio-economic models to simulate regional land allocation.

It is important to acknowledge that focusing on regional scales can be key to tackle the above-mentioned challenges. Indeed, climate change is spatially heterogeneous (Bowler et al., 2020), and species, ecosystems, political jurisdiction, and land users' responses and decisions tend to be region-specific. Additionally, empirical biodiversity assessments and conservation policies are mostly designed to address adaptation and mitigation options at regional scales (see Glossary for definitions). Only the regional scale enables working with fine-scale (spatial and thematic resolution) and land-use description (e.g. potentially integrating small landscape elements), while offering the possibility to explore biodiversity responses from the local (populations, communities) to the regional scale (species pool, homogenization). Therefore, besides the direct effects of climate and land use on regional biodiversity, integrating land-use change induced by climate change on biodiversity assessments seems paramount to support forward-looking conservation policies.

In this perspective paper, we argue for an integration of indirect pathways of climate change effects on regional biodiversity via connection between biodiversity and land-use models. To this end, we first review empirical and modelling studies of the effects of climate and climate change on regional land use, followed by studies of the effects of land use on regional biodiversity. The empirical overview provides insights on aspects not yet modelled, whereas the modelling overview highlights possible routes of how land-use and biodiversity models can be integrated by matching the resolution and input/output of the various modelling approaches. Finally, we discuss potential challenges and opportunities of feeding biodiversity effects back into land-use and climate models. This would effectively mean integrating all three modelling approaches at the regional scale, with three key (bi-directional) links between climate change, land-use change and biodiversity change models (Fig. 1). Our empirical and modelling overview as well as proposed integration links ultimately foster the dialogue between the research communities focusing on land-use and biodiversity modelling to achieve truly integrated assessments at regional scales.

1.1 | Glossary

Local scales/models : focused on single or small mosaics of populations, communities, stakeholders or habitats (i.e. from a few meters to several kilometers). Local models include population viability analysis (PVA) models, metapopulation models, reserve prioritization approaches (several small or single large debate), all of which typically focus on particular habitats or habitat networks or on particular local populations or communities.

Regional scales/models : anything from landscape to continental spatial extents, including pronounced and multiple environmental gradients (i.e. tens to thousands km). Approaches that calculate local variables but can be projected at any scale (e.g. dynamic vegetation models, species distribution models), including regional grid extents, are treated as regional. Most biodiversity models already fall within this category and typically focus on metapopulation dynamics across environmental gradients, on species ranges, on diversity distributions or on distribution of ecosystem functions.

Global scales/models : anything at global spatial extents (e.g. global circulation models). Biodiversity models at global scale often use coarse resolution and might focus on entire taxonomic groups or ecological guilds. Similarly, global land-use models often distinguish a number of world regions.

Biodiversity measures : any component or aspect defining variability of ecological entities (individuals, populations, communities, ecosystems), which may happen over space, time or within/across entities (i.e. intraspecific variability, population structure). Important ways to quantify aspects of biodiversity involve abundances, species richness, composition and function metrics. At the regional scales, components such as alpha (local), beta (internal turnover) and gamma (regional total) diversity are relevant for the different aspects.

Biodiversity models : models defining dynamics of any biodiversity component or aspect. These models should normally integrate information on spatial and temporal variation of environmental conditions and of model agents, which drive the variability of ecological entities (i.e. biodiversity).

Phenomenological models : models in which a variable state is correlated to other variables, which can be done by machine-learning, econometric, and statistical relationships.

Land use: economic and social functions of a land (Haines-Young, 2009). For simplicity, water use is excluded, but land use can affect adjacent water bodies.

Management: diversity of practices applied to a land to reach the targeted purpose of the land, e.g. cutting, fertilizing, removing deadwood. Management practices can be classified into input and output categories.

Mechanistic models : models in which the state of a variable is explicitly influenced by factors via causal relationships, often dynamic ones. Rule-, equation-, and agent-based models as well as cellular automata are typical examples with such relationships.

Integrative models : models that integrate models from different fields of research, such as land use, biodiversity and/or climate.

Hybrid models : models that combine different modelling methods, such as agent-based and correlative components.

Land-use type : large category of land use such as agriculture, forestry, or urban settlements and infrastructures, characterized by certain types of input and output types and intensity of use.

Land cover: physical surface characteristics of land (Haines-Young, 2009).

Model input : any data read in from files during initialization and during model iterations.

Model output : data generated by the model and saved to file.

2 | LAND USE AT REGIONAL SCALE

2.1 | Climate change effects on land use

Regional land use, such as agriculture, forestry, and hunting practices, strongly depends on climate conditions. This is because different plants and animals, including both target product and potential pests, have different environmental preferences for optimal productivity. Consequently, environmental change strongly influences productivity and the stakeholder's decision on land use, both of which in turn affect regional economies. For instance, field experiments show that maize yields decline more (39%) under water stress than wheat yields (21%) (Daryanto et al., 2016). In addition, multiple lines of evidence suggest that the four major crops wheat, maize, rice, and soybean all respond negatively to temperature increases (Zhao et al., 2017), while irrigation represents an effective adaptation option if irrigation costs remain covered by the profit (Agnolucci et al., 2020). Globally, inter-annual climate variability accounts for around one third of the observed yield variability (Ray et al., 2015), whereas historical climate change (1974-2008) reduced consumable calories of the ten most important crops by 1% (Ray et al., 2019). The effects seem more drastic when looking on productivity, with indications that anthropogenic climate change has reduced global agricultural productivity by around 21% since 1961, with more severe consequences for warmer regions such as Africa and Latin America (Ortiz-Bobea et al. 2021). For Europe, climate trends since 1989 have slightly increased continent-wide maize and sugar beet yields, but significantly reduced, albeit with large spatial variability, wheat and barley yields (Moore & Lobell, 2015). Such climate-driven changes in crop yields directly affect regional land-use patterns. According to Zaveri et al. (2020), repeated dry anomalies have been responsible for around 9% of the rate of cropland expansion in developing countries over the last two decades. Furthermore, land-use patterns are likely to be affected by extreme weather events, with the little current evidence indicating that farmers temporarily and dynamically shift land use after weather shocks - e.g. away from cash and permanent crops one year after a drought, and away from horticulture and permanent crop after a flood (He & Chen, 2022; Olesen & Bindu, 2002; Ramsey et al., 2021; Salazar-Espinoza et al., 2015).

Climate change will continue over the next decades, thereby affecting agricultural productivity and triggering additional shifts in land-use patterns and crop choice (Alexander et al., 2018; Pugh et al., 2016). Strong shifts are likely to be caused by changes in precipitation patterns (Malek et al., 2018). Whereas irrigation may partially mitigate land-use changes, land-use change also depends on soil conditions as well as national or regional policies, agricultural prices, subsidies, consumer behaviour, and the structure of agricultural and silvicultural actors (the so-called Shared Socio-economic Pathways - SSPs, O'Neil et al., 2014). Unlike climate, economic or agricultural systems are very adaptive and strongly driven by human expectations and decisions. As a consequence, changes in these systems are even more difficult to project into the future than in natural systems due to the large uncertainties involved (Troost & Berger, 2015). For example, Ramsey et al. (2021) found that land-use responses to changing weather patterns vary across time and space. Indeed, it is crucial to determine the temporal scale at which these systems are satisfactorily predictable ('forecasting horizon'). Considering all these aspects, it seems mandatory that adequate modelling approaches should decide on what type of model is required for which problem and on which scale (Levin, 1992). Processes involving water supply at the regional (watershed) scale, impacts of yield change at the policy relevant scales, and adaptation measures at farm holding level are all necessary at the regional scale. Thus, responses of regional land use to climate change are complex and are driven not only by the natural conditions, but also by the socio-economic context.

2.2 | Modelling regional land-use change

Regional land-use models reflect the local or regional contexts more accurately than the global approaches. Current models include a continuum from mechanistic to phenomenological approaches (Table 1; see also the Summary for definitions). Phenomenological models statistically relate a set of explanatory socio-economic or biophysical variables to transitions in local land use (e.g. Verburg & Overmars, 2009). In these approaches, the quantity of change is given by transition matrices of two historical land-use maps and the allocation of changes

vary depending on the model. In other approaches, global economic or integrated assessment models are used to determine the region-level demands. Some of these models have applied neural networks approaches to produce a probability map of land-use changes (Dai et al., 2005; Qiang & Lam, 2015). Mechanistic models emulate processes in which drivers of change (e.g. sequence of land uses) interact, sometimes based on rules (Stéphenne & Lambin, 2001; Rouget et al., 2003), sometimes based on cellular automata (Liu et al., 2017; Clarke, 2008; Diogo et al., 2015). Agent-based models appear to be best suited to mechanistically integrate the individual farmer behaviour, policies, and biophysical tags (Murray-Rust et al., 2014a,b). Such models can be modified to include regional trade-offs among a large variety of socioeconomic input variables, to identify the main drivers of land-use change. However, they usually do not consider the impacts of climate change because their future projections are at short- to medium-term (i.e. few years or decades – Table 1), much shorter than the projection horizon of the climate models. Moreover, climate change projections are more global-based in nature with substantially less accuracy at regional scales, which is why such projections may have little relevance to individual land-users (e.g. farmers) and their decision making process (Morton et al., 2015, 2017). Nevertheless, there are few regional land-use change models that have projected long-term land-use trajectories integrating climate change (e.g. Mendoza-Ponce et al., 2018, 2019).

While most land-use models focus on biophysical and socioeconomic drivers, some models have integrated incipient connections to biodiversity. For example, vegetation recovery rates or dynamics can influence the use of fuelwood (Stéphenne & Lambin, 2001; Kiruki et al., 2019) or management strategies (Verburg & Overmars, 2009; Murray-Rust et al., 2014b). Other models integrated information on ecosystem threats, such as alien species, to model transformed rates and areas (Rouget et al., 2003). These connections of biodiversity elements to land use mostly focus on plant or vegetation patterns, but a few examples also consider animal diversity as a driver (Soares-Filho et al., 2013; Dai et al., 2015). To summarize, while there are a few approaches that consider some aspect of biodiversity as a factor influencing regional land-use change, most models do not.

3 | LAND-USE EFFECTS ON REGIONAL BIODIVERSITY

3.1 | Land use effects on biodiversity

Land use has been the main driver of biodiversity decline over the past 50 years (IPBES, 2019; Pereira et al., 2012). Whereas physical actions on land as direct drivers of ecosystem change (e.g. agriculture, forestry, or urbanization) operate at the local level (Lambin & Meyfroidt, 2010), impacts of land use also operate at larger spatial scales (Haines-Young, 2009). These impacts include also aquatic ecosystems, such as rivers, with sediment and nutrient discharges affecting entire catchment areas (Alin et al., 2002; Bussi et al., 2016). In addition, the complexity of land-use-biodiversity relationships arises from the multidimensionality of both land use (e.g. type, management, intensity Erb et al., 2013; Kuemmerle et al., 2013) and biodiversity (e.g. taxonomic, functional, and phylogenetic diversity Devictor et al., 2010), with various multidirectional impacts overlapping, reinforcing, or mitigating each other (Haines-Young, 2009). Ecologists developed two main types of approaches to deal with this complexity.

The “management-oriented” approaches link the management dimensions of land use to biodiversity at local scale (Paillet et al., 2010), sometimes integrating the landscape-scale effects of land use (Müller et al., 2007). The studies using such approaches usually focus on a single land-use type (e.g. agriculture or forestry), and rely on detailed evaluation of the management practices and their intensity (Herzog et al., 2006; Jeliakov et al., 2016). These approaches have addressed multiple biodiversity dimensions. For example, taxonomic diversity can show strongly decreasing or flat responses to management intensity (Allan et al., 2015; Simons & Weisser, 2017; Tsiafouli et al., 2015). These observed patterns result from the loss of ecological opportunities (i.e. resource depletion, habitat degradation, micro-habitat loss) linked to the changes in abiotic and biotic conditions and in the disturbance regime.

The “type-oriented” approaches look for general impacts of land use on biodiversity, usually focusing on spatial

intensification and limiting their description of land use to one (e.g. Clavero & Brotons, 2010) or several (e.g. Herrera et al., 2016; Mimet et al., 2014; Uhler et al., 2021) land-use types. These approaches often consider the landscape effects of land use on biodiversity through the description of landscape composition, configuration, and connectivity (e.g. Clavero & Brotons, 2010; Fahrig et al., 2011). They show how landscape-level land use influences the functional composition and structure of species communities. For example, the homogenization of the landscape through intensive land use is related to lower beta-diversity (Gossner et al., 2016; Jeliaskov et al., 2016), whereas land-use intensification simplifies food webs (Jeliaskov et al., 2016; Mendoza & Araújo, 2019; Pellissier et al., 2017; Tsiafouli et al., 2015). Through changes in pressures and connectivity, land-use intensification can also induce phenotypic adaptation, e.g. via changes in phenology (Barbaro & Halder, 2009; Mimet et al., 2009) and trait evolution (e.g. dispersal ability Martin et al., 2017). Moreover, the type-oriented approach is particularly prevalent in studying aquatic ecosystems, as aquatic biodiversity can change due to agricultural and urban land-use changes (Allan, 2004; Polasky et al., 2011). Finally, few studies assess simultaneously the roles of both land-use type and intensity, showing that land-use type mainly drives the functional and taxonomic composition, while land-use intensity rather drives the functional redundancy of species (Birkhofer et al., 2017; Laliberté et al., 2010).

3.2 | Modelling regional biodiversity change

Several approaches have been proposed to model biodiversity at regional scales, varying from phenomenological (e.g. macroecological analyses, species distributions models) to mechanistic or process-based models (see Dormann et al., 2012; Zurell et al., 2016 for comparisons in the field of niche models). Whereas both types of models can assess potential effects of land-use and climate change, the mechanistic models can further account for transient, non-equilibrium, and novel conditions by explicitly simulating eco-evolutionary processes (Cabral et al., 2017; Dormann et al., 2012). For instance, ecophysiological models integrate processes on the basis of metabolic theories describing life-history of species, such as energy uptake, growth, respiration, and thermoregulation (e.g. Cabral et al., 2019; Kearney, 2012; Leidinger et al., 2021), and of ecosystem-level processes, such as carbon assimilation and metabolic costs (the so-called general ecosystem models GEMs for both autotrophic and heterotrophic biodiversity e.g. Harfoot et al., 2014; and the dynamic vegetation models DVMs e.g. Sakschewski et al., 2015). The ecosystem-level GEMs and DVMs that are agent-based and trait-based can account for functional diversity by defining functional types (e.g. SEIB-DGVM Sato et al., 2007; JeDi Pavlick et al., 2013; LPJml-FIT – Sakschewski et al., 2015) and have been applied to regional extents (e.g. Lautenbach et al., 2017; Sato & Ise, 2012; Thonicke et al., 2020) despite being also largely used in global studies. These ecosystem-level ecophysiological models often lack cross-region, spatial processes (e.g. disturbances, dispersal). To this end, models further based on metapopulation and metacommunity theories can also integrate demographic processes, such as reproduction, mortality, density-dependence, and dispersal, as well as biotic interaction processes, such as resource competition and trophic interactions (Cabral & Kreft, 2012; Hagen et al., 2021; Harfoot et al., 2014; Urban et al., 2016). Some models focus entirely on region-wide spatial processes, such as connectivity, which can be based for example on graph (e.g. Foltête et al., 2012) or circuit (e.g. McRae et al., 2008) theories and focus on particular species or group of species. These mechanistic models thus predict abundances, demographic rates, and connectivity, all of which have a higher information value than just presence probabilities (Ehrlén & Morris, 2015).

Mechanistic models jointly addressing climate change and land-use effects on biodiversity have been proposed almost two decades ago (Travis, 2003), but their application to real-world systems has so been limited, partly due to low species-specific data availability and computational runtimes which are unfeasible for automatic optimization (Cabral et al. 2017, Dormann et al. 2012). Still, several models can already use real-world environmental data as input (e.g. Hagen et al., 2021; Higgins et al., 2020; Malchow et al., 2021; McIntyre & Lavorel, 2007; Sarmiento Cabral et al., 2013), which should promote their application for addressing land-use effects. Indeed, biodiversity models including land use vary from hypothetical virtual experiments to real-world applications across regional scales (Table 2). These models address e.g. temporal dynamics and coexistence of functional groups under land-use management in complex landscapes (Boulangeat et al., 2014; Lautenbach et al., 2017; Quétier et al., 2007), or the geographical range of focal species (e.g. Bocedi et al.,

2014, 2021; Faleiro et al., 2013; Sales et al., 2020; Zamora-Gutierrez et al., 2021). The partial effect of land use on biodiversity (i.e disentangling its effect from other disturbances such as climate change) has been considered in few studies. For instance, Travis (2003) showed the proportion of habitat loss influences the threshold of response to climate change. Sarmento Cabral et al. (2013) compared simulations with and without habitat loss, revealing that land use negatively influences local abundances while not strongly affecting range size of shrubs. Synes et al. (2019) went further and compared uni- and bidirectional effects of crop yields on pollinator populations, demonstrating that the inclusion of bidirectional feedbacks revealed much stronger loss in crop yields. Considering high resolution can also improve performance of biodiversity predictions (Marshall et al., 2021). To summarize, there are a few approaches integrating both climate change and land-use effects on biodiversity, but the incorporation of land use in biodiversity dynamics under climate change has not always modified results (Dullinger et al., 2020), possibly due to the fact that climate change-driven changes in land use are not considered.

4 | THE ROADMAP TO INTEGRATE CLIMATE CHANGE WITH SOCIO-ECOLOGICAL SYSTEMS

4.1 | Integrating climate-driven biodiversity change into land-use models

Differently from biodiversity models, which often integrate land use (Table 2 and previous section), land use models rarely consider biodiversity (Table 1). Hence, the integration of land-use models with biodiversity models is largely missing, although land users may not solely prioritize profits and may as well weigh biodiversity and ecosystem opportunity costs (foregoing an attractive alternative). In fact, it is unlikely that land users would only respond to prices and costs to maximize land rent – a key motivation for developing agent-based land-use models (Berger & Troost, 2014). While it is clear that landowners indeed respond to economic opportunities and risks, assuming pure profit-maximizing behaviour will not suffice to analyze land-use and associated human-driven biodiversity changes (Berger, 2001; Castro et al., 2018; Lambin et al., 2001). For example, subsistence farmers need to sustain their families and might thus not be profit maximizers, but risk minimizers, going for guaranteed results. They might even have ecological objectives (Knoke et al., 2014), but have to sustain their families. In contrast, industrial-style farmers are mostly profit maximizers, which explains the expansion of oil palms (Fisher et al., 2011), soy, or rubber (Warren-Thomas et al., 2018). The land-use change models currently focus on the relationships among farmers decisions and biophysical elements (Table 1). This reflects the fact that individual decisions, cultural practices, and regional policies on subsidies underlie the land-use change processes. In this regard, biodiversity is often not included in the land-use change models because it is not yet considered a key driver of the decision of farmers or even of human population size, dietary preferences, economy, climate change, and technology. However, regional models should start integrating biodiversity change beyond simply considering vegetation cover. The ability of biodiversity models to predict abundances, demographic rates, and connectivity may be important for land-use decisions. Indeed, biodiversity can lead to ecosystem modifications at the local level, like influencing the selective extraction of valuable species (Cazzolla Gatti et al., 2015; Poudyal et al., 2019) or modifying crop yields (Synes et al., 2019). Moreover, biodiversity loss may affect consumer behaviour if correctly communicated (Schaffner et al., 2015), which has been, for example, used for palm oil-free products and many dedicated product certifications. Biodiversity economic value may be also evoked and could become a driver in economic land allocation models (e.g. Bateman et al., 2013), while the resulting relationships between comprehensive economic ecosystem value and biodiversity are variable (Paul et al., 2020). All these aspects indicate multiple ways to integrate biodiversity into land-use models, from influencing the decisions of subsistence farmers to improving yields, product demand, and biodiversity-influenced regional policies. Some ways have been already tackled, although not in land-use models addressing climate change effects (and thus not featured in Table 1).

Regional or global land-use change models commonly integrate biodiversity in two ways: 1) as a restriction for

anthropogenic land-use expansion through limitation rules inside protected areas or intact forests (Alexander et al., 2018; Schmitz et al., 2014) or 2) a post hoc overlap analysis of model outputs over biodiversity-rich areas (Kobayashi et al., 2019; Powers & Jetz, 2019). As an alternative, land allocation approaches building on multiple criteria methods allow for integration of biodiversity as an own objective function, for example to represent the preferences of conservationists (e.g. Knoke, Gosling, et al., 2020; Knoke, Paul, et al., 2020). Moreover, mathematical models have been developed to assess forest enrichment with coarse woody debris to elevate biodiversity at minimum costs in forest enterprises (Härtl & Knoke, 2019). Further integration of biodiversity could be achieved through modelling the expansion of common plant species (e.g. via range models Sarmiento Cabral et al., 2013; Bocedi et al., 2014, 2021) that would directly impact the land cover. Another flexible and theoretically consistent framework to model land allocation decisions might be the use of household models (Singh et al., 1986), which account for departures from traditional profit-maximization. The household is assumed to maximize utility, which is a function of many aspects beyond profit and weather such as, e.g., cultural practices, subsistence, biodiversity, leisure, or environmental protection. This framework allows for integration of biodiversity aspects into land-use modelling from a behavioural point of view, which could have positive feedbacks to biodiversity. Indeed, focusing landscape management based both on legislation and traditional agriculture can have positive effects on biodiversity, especially on specialist species (Santos et al., 2016).

Some challenges to integrate biodiversity model output as land-use model input lies on the differences and incompatibilities of spatial and temporal scales. This demands particular attention across land-use models, which often apply and report different resolution formats and units (compare geographical resolutions across models in Table 1). Besides, a key epistemological issue is that many mechanistic biodiversity models run in hypothetical landscapes and ecological systems (e.g. Travis, 2003). Moreover, in many hypothetical and real-world biodiversity models, the spatial resolution is a grid cell and temporal resolution is a generation. To make the output of such biodiversity models useful for land-use models, the species parameters and landscape scales must be adequately calibrated. For example, explicitly calibrating a grid cell to 1 km² to match a given land-use model should be accompanied by adequate dispersal ability, carrying capacity, and local population dynamics of the target species, community, or functional group. Furthermore, to fully integrate the two modelling approaches, it is necessary to relate individual land users' actions and decisions, which may take place at local scales (e.g. the field level for farmers), to biodiversity outcomes (i.e. extirpation of local populations) that may vary in scale from local to regional.

4.2 | Integrating climate-driven land-use change into biodiversity models

We found four main approaches for the inclusion of land use in biodiversity modelling:

1. In the first approach, authors perform an overlay of the outputs of both land-use and biodiversity models to identify land-use change within important biodiversity areas or to identify suitable areas for biodiversity (e.g. Faleiro et al. 2013, Martinuzzi et al. 2014, Sales et al. 2020). Thus, in this approach only the modelling results are analysed together.
2. In the second approach, authors apply land-use field data or land-use model outputs from previously developed models as input for a biodiversity model (e.g. Struebig et al. 2015). This input may include time-series of land-use changes.
3. A third approach uses a land-use model where each land-use type is associated with biodiversity values calibrated on literature data (e.g. Santos et al. 2016, Koch et al 2019). In this approach, land use itself can be interpreted as specific calibration for biodiversity models.
4. Finally, we found simulations of land use and biodiversity in the same study through model coupling (e.g. Bastos et al. 2018, Marshall et al. 2020, Redhead et al. 2020). This latter type of approach constitutes the most integrative one, in which both models are simultaneously simulated. However, this integration remains largely uni-directional, with bi-directional feedbacks between land use and

biodiversity rarely attempted (but see Synes et al., 2019). In fact, uni-directionally coupled models may miss important dynamics, as bi-directional models revealed greater influence of land-use change (Synes et al., 2019).

Most of the identified studies only account for LU effects on habitat availability or suitability (e.g. Travis 2003). This has also been highlighted in recent reviews (Santos et al. 2021; Davidson et al. 2021). Land-use effects on demography have been considered by Quetier et al. (2007) through variation of fecundity rates, dispersal ability, and mortality (via disturbances) in plant functional groups, while Sarmiento Cabral et al. (2013) considered the loss of habitat to reduce local carrying capacity of studied species. Effects of land use on dispersal have been explored by Bocedi et al. (2014) when looking at how anthropogenic disturbance effects vary depending on individuals' settlement rules during dispersal. The inclusion of climate change effects was mainly done through assessment of direct effects on biodiversity (see Struebig et al., 2014; Zamora-Gutierrez et al. 2018). There was only one example of simultaneous inclusion of direct and indirect effects of climate change on biodiversity via climate-driven land-use change (Dullinger et al. 2020 - a study with type 4 approach). Nevertheless, there is still a large disconcert of modelling studies in integrating climate, climate change, and climate-change induced land-use change (Table 2, Fig. 2a), with explicit comparisons as well as relative quantification of direct vs. indirect effects of climate change has yet to be investigated.

How can the relative role of direct and indirect effects of climate change on biodiversity be quantified? For a start, we suggest increasing focus on **model coupling**, as this has been successfully done both with correlative (Dullinger et al. 2020) and process-based (Synes et al. 2019) biodiversity models. Agent-based models seem a straightforward way for this integration as the framework is used by both the land-use and biodiversity communities (Tables 1-2; Fig. 2a). We consider the following factors to be key to successful model integration:

Spatial resolution : A key direction for improving model integration is the harmonization of spatial scales (units and file formats), but this is not a limiting factor since land-use and biodiversity models considerably overlap in terms of spatial extents and resolutions (Fig. 2b-c). Most land-use models do generate outputs that could be used as input by biodiversity models to some extent (compare output variable in Table 1 with input variables in Table 2). Despite the improvement in relation to the coarse resolution used in global models, regional land-use models still vary considerably in the spatial resolution (Table 1), from polygon-based models (particularly useful when farmers are the agents) to raster-based. Considering that polygons and raster can be quickly converted back and forth, biodiversity models would require a raster conversion plugin to readily use different output and input formats of land-use models. This can be easily done, but most current biodiversity models do not have such plugins and thus any format synchronization needs to be done before simulation.

Temporal resolution : Moreover, temporal resolution and extent seem to require further attention. Most land-use change studies focus on relatively short temporal extents (e.g. 20 years), with few time steps. Whereas this reflects inherent uncertainty of the behaviour of human agents and of socioeconomic dynamics, it also limits its utility to biodiversity models, which often require yearly (and sometimes even coarser) resolution for longer time period (compare temporal extents in Table 1-2). For generational-based biodiversity models (e.g. Sarmiento Cabral et al., 2013), matching temporal resolution of biodiversity and land-use models require considering particular years or dates as references. The best direction here is that both models converge to generation- and agent-agnostic time steps, such as year.

Indirect effects of climate change : Disentangling direct and indirect effects of climate change on biodiversity revealed to be a largely understudied subject. Though we have not found studies to have tackled it through mechanistic approaches, this seems achievable as mechanistic land-use models that consider climate input have been already coupled with mechanistic biodiversity models (see Synes et al. 2019 combining RangeShifter, Bocedi et al., 2014, with CRAFTY, Murray-Rust et al., 2014a). Furthermore, an avenue to explore such indirect effects at regional level is becoming more feasible as mechanistic land-use models that incorporate climate scenarios are being applied to larger extents (Brown et al. 2021).

Bi-directional feedbacks : The simultaneous simulation of land use and biodiversity with process-based models should allow for the inclusion of bi-directional feedback between models (Fig. 3). This would account for emergent interactions between both systems, something that has been recently called for (Urban et al., 2021). Therefore, the current knowledge of land-use effects is in fact mostly based on the unidirectional effect from land use on biodiversity. In fact, all integrated approaches were primarily those mostly focusing on biodiversity. The land-use-focused paper that came closest to an integrated approach coupled an ecosystem model to simulate crop yield and natural vegetation, although number of species per se was not explicitly modelled (Murray-Rust et al. 2014a).

4.3 | The full integration: challenges to integrate socio-ecological change into climate models

The influence of land use and land-use change on climate is already well known (e.g. Deng et al., 2013), but the integration of biodiversity and per extension also of socio-ecological models into climate models deserves further attention (see Fig. 3). The effects of land-use change on regional and global climate have been assessed focusing on biogeochemical and biogeophysical feedbacks (Pongratz et al., 2010, 2018). Land-use change impacts climate by affecting extreme temperatures (Findell et al., 2017; Wang et al., 2015), precipitation (Woldemichael et al., 2012), evapotranspiration (Krause et al., 2017; Nóbrega et al., 2017), or surface runoffs (Guzha et al., 2018; Krause et al., 2017). For example, afforestation can take up carbon from the atmosphere, while also cool down regional temperature by absorbing radiation and increasing transpiration (Betts, 2011). This effect of vegetation on climate has been studied and exploited across scales, from decreasing urban heat islands to feedbacks between the terrestrial biosphere and the climate. Whereas vegetation models typically do not really account for biodiversity (see Section 3.2), by simulating forest growth and carbon assimilation among other ecosystem-level processes, these models consider important ecosystem functions such as net primary production. Considering that biodiversity has positive relationships with ecosystem function, the so-called biodiversity-ecosystem function (BEF) relationships (see van der Plas, 2019 for a review), we can already assume that maintaining high biodiversity can be central to carbon sequestration and thus also to climate mitigation. In this regard, landscape-level forest models (see Petter et al., 2020 for a comparison), functional-structural forest models (e.g. Petter et al., 2021), or trait-based models in general (see Zakharova et al., 2019 for a review and many of the models in Table 2) better capture biodiversity, as different trait combinations can represent different species. These models have not yet been coupled with land-use and climate models, but we suggest integrating ecosystems' productivity with changes in tree diversity and composition as one promising way to fully integrate biodiversity, land-use, and climate models. A concept showing how to achieve this has recently been proposed (Bendix et al., 2021). That is, biodiversity modelling would link not only to climatic conditions but also to deforestation, afforestation, and agriculture management. This would also represent an improvement over integrated assessment models, which are typically applied to evaluate proposed climate mitigation but still lack explicit biodiversity integration despite attempts of using IAMs for assessing biodiversity loss (e.g. Veerkamp et al., 2020). Ultimately, with fully integrated models including bi-directional effects (Fig. 3), we could explore scenarios considering not only climate mitigation, but also e.g. biodiversity, ecosystem functions, and sustainable development.

4.4 | Directions to modelling developments

Current models can already tackle a series of both land-use and biodiversity processes. However, the full spectrum of climate change effects on land use and land-use effects on biodiversity has not been fully modelled, as revealed by our empirical review. Here, we identify avenues for development in modelling independent of integration across research fields.

For land-use models, there is a need to identify the regional drivers of land-use change to implement well-tailored concepts to simulate human-related changes in the composition of landscapes, ecosystems, and, as argued in previous sections, biodiversity. For climate drivers, further evidence is needed to understand how land users respond to weather extremes in various contexts. For socioeconomic drivers, this means

going beyond simulating agricultural or livestock expansion to integrate production of specific commodities and to address possible responses of decision-makers to biodiversity changes, as they will consider their livelihood demands (Affholder et al., 2013) and/or economic opportunities and risks (Lambin et al., 2001). Via biodiversity-economic value functional relationships (Paul et al., 2020), biodiversity could be integrated in such models as a factor of production. In addition, biodiversity indices could be used to represent the preferences of conservationists (Knoke, Gosling, et al., 2020). For example, changes in the productivity of some land-use types could lead to reallocation of land, which could help understand the relationship among national or regional policies, subnational, or international demand of products and prices. This understanding will help land-use models to go beyond the analysis of historical trends to improve projections, including scenarios that integrate farmers' decisions linked to a globalized world and biodiversity elements as inputs. In addition, common strategies to deal with increasing uncertainty, such as overproduction (Fuss et al., 2015), land-use diversification (Rosa et al., 2019), or the diversion of the available labour to obtain off-farm income (Shannon & Motha, 2015) will influence land-use change processes and associated biodiversity. For instance, off-farm income may reduce crop diversification at the farm level (Ochoa et al., 2019). Accounting for changes in the objectives of farmers or land-use planners is also influential for simulating land allocation (Castro et al., 2018). This may be particularly important if we want to improve land-use practices by considering biodiversity information or other novel decision-criteria such as environmental costs when losing biodiversity, something commonly disregarded in real-world decision-making.

Another characteristic of current land-use models is their limited ability to project far into the future, giving their high demand for data in the fitting process and the above-mentioned socio-economic uncertainties. In this sense, the deficit of integrating uncertainty into land-use models is evident, particularly when historical data are not reliable for quantifying uncertainties. We will then need robust modelling approaches providing acceptable solutions over large uncertainty spaces, which would possibly include future conditions (Gorissen et al., 2015). Extreme events, such as severe floods or droughts, may represent "black swans" (Taleb, 2007) for landowners. "Black swans" are historically seen as often highly improbable, but of utmost economic consequences when occurring.

For biodiversity models, the inclusion of evolutionary dynamics at ecological time frames remains understudied (but see Leidinger et al., 2021), even though human activities can trigger evolutionary response. Another direction is to integrate climate-driven behaviour of human agents on the biodiversity. For example, Cabral et al. (2011) assessed the effects of harvesting wild flowers by reducing the number of produced offspring. However, it is unclear how human behaviour may change in the future. Will humans stop harvesting in the wild due to conservation policies, to pressures for decreasing carbon footprint via embargoing overseas flower export, or both? In fact, direct resource exploitation often targets demographic or growth processes in biodiversity assessments, e.g. in fisheries (Melbourne-Thomas, Johnson, Aliño, et al., 2011; Salihoglu et al., 2017), forestry (Albert et al., 2008; Bottalico et al., 2016), sport hunting (Mattsson et al., 2012), or grassland management (Johst et al., 2006; Rolinski et al., 2018; Schröder et al., 2008). In forest management, for instance, forest owners will adapt forest structure and management to enhance the resistance (by establishing mixed forests) and resilience (by enhancing the structural diversity). Planting mixed forests will positively influence species richness (Knoke et al., 2008) and managing forests to increase structural diversity will also increase biodiversity (Schall et al., 2018). However, the biodiversity impact of climate mitigation policies must also be investigated, as typically suggested bioenergy crop expansion can actually be detrimental for biodiversity (Hof et al., 2018).

Another important research direction is to improve harmonization of complex relevant data (often done for occurrence or occupancy, but rarely for demographic rates, dispersal ability traits, and genetic diversity). Data harmonization and standard formats should be also strived across biodiversity models. This means to implement models that consider input and generate output matching current trends in empirical biodiversity assessments to follow the Essential Biodiversity Variables (EBVs) framework (Pereira et al., 2013; Urban et al., 2021). This should promote a better integration across models and data-model integration. Most common model outputs such as species occurrence and abundance (Table 2) are already part of the EBV class 'species populations'. Although this already allows to connect environmental change metrics, standardized biodiver-

sity metrics, and model-data, EBVs are rarely mentioned in biodiversity models. Community composition, another EBV class, is often addressed only through taxonomic diversity (i.e. species richness). However, other community facets typically quantified in empirical assessments such as functional and phylogenetic diversity are far less common (Table 2), although they can be, to some extent, easily derived from merging species occurrence metrics with phylogenetic and trait data from online databases (e.g. PanTHERIA Jones et al., 2009; and PHYLACINE Faurby et al., 2018). The EBV classes such as genetic composition, species traits, and ecosystem functioning are yet rarely reported in biodiversity models. Although modelling of such components may be challenging as it requires additional input data and simulating microevolutionary, niche-based, and metabolic-based processes, recent advances are making the simulation of such EBV classes easier (Leidinger et al., 2021; Zurell et al., 2021).

A few model development trends are common for both land-use and biodiversity models. For example, a hurdle to overcome is linking of terrestrial and aquatic systems (but see Harfoot et al., 2014 for biodiversity models). This is due to fundamental differences in ecological processes and biodiversity and ecosystem functions (Daam et al., 2019). In particular, sediment

and nutrient inputs can be main drivers of aquatic biodiversity (Fernández et al., 2021), which has led to a bias in the selection of land-use types considered in previous studies, with agricultural land being the focus of most analyses. In addition, socio-economic influences on aquatic ecosystems were often ignored or only considered as disturbing factors, with the interactions between aquatic ecosystems and socio-economic effects still largely unassessed by either empirical or modelling studies. Another general necessary development is improving resolution at regional scales. Whereas land-use models can already generate high resolution regional data (Fig. 2b), output from high resolution regional climate models are not yet commonly used in either biodiversity or land-use modelling, including for stakeholder decision-making (Gutowski et al., 2020). This stresses the necessity to synchronize model developments between the biodiversity, land-use, and climate change fields.

5 | CONCLUSIONS

While biodiversity models have become quite sophisticated in predicting biodiversity change due to climate change, efforts must be taken to integrate this development considering climate-driven land-use change. Because land use itself is strongly influenced by climate change, integrating both climate-driven biodiversity and land-use models can tackle the complete appraisal of both direct and indirect effects of climate change on biodiversity. However, disentangling these effects has yet to be addressed by dedicated simulation experimental designs. First attempts to integrate biodiversity and land-use models show that the integration is attainable, although model integration has happened only in studies focused on biodiversity change. In this sense, integrating biodiversity feedbacks into land-use and climate models requires further modelling innovations, but should be feasible. Still, major shortcomings include a better concerted effort in standardizing outputs and resolution, as well as methods to simultaneously optimize multiple outputs (e.g. species number, stakeholder profits, carbon balance, and temperature) in fully integrated, climate-land-use-biodiversity models.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR'S CONTRIBUTIONS

JSC, with contributions of AR, FH, TK, WW, designed the study; JSC, AM, AMP, APS, JK, JO led the writing of sections; JSC wrote the first draft; AK, AMP, APS, AL, DV, JB, JO, SB, SF led the literature search, writing and editing of the tables; DV led the Fig. 1; JSC led Fig. 2, SF led Fig. 3; all authors commented and contributed with the written text, tables and figures.

DATA AVAILABILITY STATEMENT

This manuscript does not include any data.

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SUPPLEMENTARY MATERIAL

Supplementary Material S1 - Details on literature search and model classification

Table 1: Examples of regional land-use model implementations, with their respective model type, scales, input variables, climate change impact, outputs, ecosystem/biodiversity parameters and key findings . For details on literature search, inclusion criteria and classification, see Supplementary Material S1. Note that scales often depend on the input, with provided scales reflecting the study system of the particular study or suggested by authors. Abbreviations: PHENO: phenomenological; MECHA: mechanistic; GE: geographical extent, GR: geographical resolution, TE: temporal extent, BP: biophysical, SE: socioeconomic, CC: climate change, LU: land use, BD: biodiversity, NA: not applicable.

Model	Type	Study Region and Scales	Input variables	What is modified by CC?	CC effects on LU	BD-related parameter	Output variables
CLUE-S (Verburg et al., 2002)	PHENO	GE: Sibuyan island, Klang-Langat watershed (456, 4,300 km ²); GR: 150m; TE: 1997-2017, 1989-1999	BP: altitude, slope, aspect, geology, erosion, distance to stream and coast; SE: population density, distances to roads, towns, and ports	Nothing	NA	None	Cover type (e.g. forest, grassland, urban, coconut and palm oil plantations, rice fields)

Dyna-CLUE (Verburg & Overmars, 2009)	PHENO	GE: Europe (27 countries); GR: 1 km ² ; TE: 2000-2030	BP: water deficit, potential evapotranspiration, temperature, water logging occurrence; SE: regional demand of agricultural products	Land allocation and natural succession of abandoned lands	Dry or cold climates lower succession speed	Natural vegetation succession	Abandonment areas linked to regrowth of natural vegetation, agricultural intensification
SALU (Stéphenne & Lambin, 2001)	MECHA	GE: Burkina Faso (274,200 km ²); GR: 2.5 x 3.75°; TE: 1960-1997	BP: precipitation; Socioeconomic: human population, livestock, cereals imports	Yearly changes in land-use allocation	Rainfall determines the productivity. If it decreases, it is compensated by LU expansion.	Vegetation recovery rates for producing fuelwood	Areas of LU expansion and intensification, pastures, fallow and fuelwood extraction
FLUS (Liu et al., 2017)	MECHA	GE: China (9.56 Mi km ²); GR: 1 km ² ; TE: 2010-2050	BP: soil, elevation, temperature, precipitation; SE: population, GDP and technological innovations	Land allocation	Annual precipitation and temperature	Ecological regions	Extent and location of cultivated areas, forests, grassland and urban covers.
DINAMICA-EGO (Soares-Filho et al., 2013)	PHENO	GE: Brazilian amazon (619,946 km ²); GR: 1 km ² ; TE: 2003-2050	BP: soil, vegetation, slope, elevation, distance to rivers; SE: distance to deforested areas, roads, towns, protected areas	Probability of land use	None	Distribution of mammals	Deforestation area linked to reduced mammals distribution and carbon emissions
SLEUTH (Clarke, 2008)	MECHA	GE: Mainly focused on US cities; GR: variable; TE: variable	Biophysical: slope, hillshade; SE: distance to roads	Nothing	NA	None	Urban expansion and other LU related to cities

Aporia (Murray-Rust et al., 2014b)	MECHA	GE: Aurau Valley, Switzerland (99 km ²) and Lanau Catchment (132 km ²); GR: variable (farm); TE:2000-2020	BP: soil, slope, nitrogen; SE: farmers' decisions (e.g. biofuel harvest, food production, traditional practices, diversity of rotation)	Output yields	Model presentation	Directly via vegetation modelling; indirectly via biophysical and policy tags	Land management practices, ecosystem service indicators, market data with prices
Agent-based Rural Land Use New Zealand (Morgan & Daigneault, 2015)	MECHA	GE: Hurunui and Waiau Catchments in New Zealand; GR: variable (farm); TE: 2010-2060	BP: soil, available water; SE: market prizes, productivity current enterprise, social network for imitation and endorsement	Productivity of the farm	Dairy and forest enterprises will increase	None	LU, farm net revenue, greenhouse gas emissions
CPV Analysis Model (Dai et al., 2005)	PHENO	GE: Pearl river delta (10,851 km ²); GR: -; TE: 1985-2000	BP: climate, soil water, vegetation, relief; SE: population, technology, policy, profits	Potential change of land-use system	Main drivers: rapid economic growth, population, infrastructure; low CC effects	Vegetation, species diversity	Dominance of land use, patches, fragmentation
Qiang & Lam (2015)	Hybrid	GE: Lower Mississippi Basin (48,000 km ²); GR: 30m; TE: 1996-2006	BP: elevation, soil, distance to water; SE: distance to roads, human settlements, and pipelines	Nothing	NA	None	LU maps

Diogo et al. (2015)	MECHA	GE: Netherlands (41,543 km ²); GR: 100m; TE: 2007-2012	BP: climate, soil, elevation, hydrology; SE: population growth, diet preferences, access to financing, technology (rotating scheme), political factors, land tenure, fertilizer use	Biophysical suitability	Changes in crop yields and productivity	None	LU maps pixelwise
Hietel et al. (2004)	PHENO	GE: Erda, Eibelshausen (11 km ² , 9 km ²); GR: 1:5,000; TE: 1945-1998	BP: elevation, slope, aspect, available water, soil texture; SE: land management	Available water capacity	Change from arable land to grassland with lower water capacity	None	Suitability maps
Rouget et al. (2003)	Hybrid	GE: Cape Region (129,462 km ²); GR: 1'; TE: 20 yr	BP: habitat, alien species, geology, distance to coastline, altitude, slope, roughness, bioclimatic variables; SE: urban area, distance to roads	Nothing	NA	Broad habitat units, alien species threat	Land-cover maps with percentage of transformed area

CRAFTY-EU (Brown et al., 2019)	MECHA	GE: EU together with Norway, Switzerland and the UK but excluding Croatia; GR: 10'; TE: 2016–2086	SE: five capitals (natural, human, social, manufactured, and financial), timber demand, meat, crops, carbon sequestration, landscape diversity, recreation	Natural capital	Differences in land systems mainly driven by SE scenarios, but also by CC	Ecosystem services, including landscape diversity and recreation value	Transitions between eight land-use types
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Table 2. Examples of biodiversity models which include land use effects, with their respective type, scales, studied taxa, input variables, climate change impact, outputs, ecosystem/biodiversity parameters and key findings . Studies that simultaneously apply LU and BD models are defined as integrative in the LU approach column. Approaches that combine both phenomenological and mechanistic components are termed hybrid. For details on literature search, inclusion criteria, and classification, see Supplementary Material S1. Abbreviations: PHENO: phenomenological, MECHA: mechanistic, gen: generations, yr: year, HS: hypothetical system, RWS: real-world system, GE: geographical extent, GR: geographical resolution, TE: temporal extent; TR: temporal resolution, NP: National Park, BP: biophysical, SE: socioeconomic, BD: biodiversity, LU: land use, SG: study group, CC: climate change, LUC: land-use change, SSP: socioeconomic pathway, NAV: not available.

Model	LU approach	Type of the BD model	Study region, scales and group	Input variables	Output variables	What is modified by LU?	Key findings (LU effects on BD)	CC	CC dr LU
Travis (2003)	No explicit model, includes random habitat loss	MECHA, HP	GE: 2000 grid cells; GR: grid cell; TE: 100s gen; TR: gen; SG: virtual species	BP: habitat type; SE: habitat or not	Occupied grid cells, spatial occupancy	Habitat loss	Thresholds to species survival, with combined CC and LU showing the lowest thresholds	Yes	No

LoLiPop (Sarmiento Cabral et al., 2013)	No explicit model, reads in habitat loss data	Hybrid, RWS	GE: Cape Region (11,000 km ²); GR: 1' x 1'; TE: 10s gen; TR: gen; SG: plants	BP: climate, soil, suitability; SE: habitat loss	Spatial abundance distribu- tion, range size, range filling	Carrying capacity	Lower abun- dances, ranges less affected; highlands act as refugia under CC due to lower LU	Yes	No
RangeShifter (Bocedi et al., 2014)	No explicit model, reads in habitat loss data	MECHA, RWS	GE and GR: variable; TE 100s yr; TR: yr; SG: virtual species	BP: suitability; SE: habitat loss	Spatial abundance distribu- tion, range size	Habitat suitability, movement cost	LU affects abun- dances and con- nectivity between populations	Yes	No
FATE-HD (Boulangeat et al., 2014)	No explicit model, reads-in pasture and field data	Hybrid, RWS	GE: Écrins NP (2,700 km ²); GR: 100 m; GE: 925 km ² ; TE: 100s yr; SG: plants	BP: topo- climatic, climatic, soil variables; SE: grazing and mowing intensity	Spatial abundance distribu- tion, population structure	Habitat area, dispersal, distur- bance (affects abun- dances, seed bank, fecundity)	LU effects can at least partly be simulated through disturbance	Yes	No
Kallimanis et al. (2005)	No explicit model, includes a distur- bance submodel	MECHA, HP	GE: 65,536 grid cells; GR: grid cell; TE: 1000s gen; TR: gen; SG: virtual species	BP: habitat; SE: disturbance	Spatial distribu- tion of occupied grid cells	Grid cell occupancy	Extinction risk higher for low dispersal rates, LU pattern affects population survival	No	No
LandSHIFT Koch et al. (2019)	Integrative: MECHA	MECHA, RWS	GE: Africa (30.3 Mi km ²); GR: 5'x 5'; TE: 2000-2030; TR: yr; SG: vertebrates	BP: forest and vegetation types, abundance per LU type; SE: LU suitability, human population	BD Intactness Index (BII)	Population density, livestock density, crop pro- duction, calories availabil- ity, BII	Land sparing more effective for conserving biodiver- sity (and food production)	No	No

Dullinger et al. (2020)	Integrative: MECHA	PHENO, RWS	GE: Part of Austrian Alps (1,426 km ²); GR: 0.01 km ² ; TE: current-2050; TR: yr; SG: plants	BP: temperature variables, precipitation, solar radiation, bedrock; SE: SSP, land cover type, LU class	Habitat suitability, range size, species richness and LU distribution, LU intensification and homogeneity	Habitat suitability	LU and CC both affect species habitat suitability, LU stronger	Yes	Yes
Zamora-Gutierrez et al. (2021)	No explicit model, reads in LU data	PHENO, RWS	GE: Mexico (2 Mi km ²); GR: 5' x 5'; TE: current-2050; TR: yr; SG: bats	BP: temperature and precipitation variables; SE: LU type, SSP	Habitat suitability	Habitat suitability	Vulnerability of bats to CC and LUC very high	Yes	No
Bastos et al. (2018)	Integrative: MECHA	MECHA, RWS	GE: North-east Portugal (6.6 km ²); GR: 1 km ² ; TE: current-2050; TR: yr; SG: raptors	BP: dispersal corridors, temperature, landscape structure, fire, moisture, NPP; SE: land cover	Minimum local biomass index	Landscape composition, local surface temperature	Disruptive effect of LUC in the spatio-temporal distribution of top predators' biomass	No	No

Bonnot et al. (2013)	No explicit model, applies human impacts scenarios	Hybrid, RWS	GE: Central Hardwoods Bird Conservation (0.3 Mi km ²); GR: 30x30 m; TE: 100 yr; TR: yr; SG: birds	BP: grid cell and landscape attributes, habitat suitability, relative productivity; SE: restoration, communication tower strategies	Spatial abundance distribution	Carrying capacity, reproductive rate, survival rate	Habitat conservation must be strategic; source-sink dynamics and dispersal influence population survival	No	No
Faleiro et al. (2013)	Integrative: PHENO	Hybrid, RWS	GE: Cerrado biome (2 Mi km ²); GR: 0.1°; TE: 2002-2050; TR: yr; SG: non-flying mammals	BP: climate; SE: environmental and infrastructure variables, past LU	Potential species distribution, spatial conservation plan	Spatial conservation prioritization	LUC altered spatial location of conservation priority sites	Yes	No
Struebig et al. (2015)	No explicit model, reads in land-cover data	PHENO, RWS	GE: Borneo (743,330 km ²); GR: 1 km ² ; TE: 1950-2080; TR: 30 yr; SG: orang-utans	BP: climate, ruggedness, distance to water and to karst forest; SE: land-cover class, human population, deforestation rate	Habitat suitability	Habitat suitability	Most suitable habitat expected to decline due to CC, even if LUC towards more protection	Yes	No

Santos et al. (2016)	Integrative: MECHA	PHENO, HS	GE: Northwest Iberia (100 km ²); GR: 1 ha; TE: 1960-2040; TR: 40 yr; SG: birds	BP: patch attributes; SE: soil use, management strategy, human population trend	Cover type, bird diversity (richness, specialist richness, total abundance)	Cover type	LU intensification homogenizes landscape, with negative impacts on biodiversity.	No	No
Redhead et al. (2020)	Integrative: MECHA	PHENO, RWS	GE: Great Britain (209,331 km ²); GR: 1 km ² ; TE and TR: 1 yr; SG: beneficial insects	BP: climate, suitability factors; SE: land cover, protected area, priority, cropping intensity	Probability of occurrence; potential richness, potential functional diversity	Habitat suitability	Arable land expansion lowers species richness, even under less intensive cropping	No	No
LAMOS-FATE (Quétier et al., 2007)	No explicit model, applies LUC scenarios and stakeholder assessments	MECHA, RWS	GE: Romanche River headwater (7,000 grid cells); GR: grid cell (ca. 42x42 m); TE and TR: Nav; SG: plant functional types	BP: productivity; SE: LU, fertilization, management scenario	Abundance of plant functional types, ecosystem services to people	Dispersal, fecundity, disturbance regime (mowing, fertilization, grazing)	Subalpine grasslands is sensitive to land-use change	No	No

Sales et al. (2020)	No explicit model, applies LUC scenarios	Hybrid, RWS	GE: Tropical South America (17.8 Mi km ²); GR: 10'; TE: 2030-2090; TR: yr; SG: terrestrial vertebrates	BP: climate, vegetation and habitat types; SE: land-use and land-cover types	Potential species distribution, potential alpha and beta richness	Potential species distribution	Climate and land-use change act synergistically, with high turnover rates for ecotonal fauna	Yes	No
Martinuzzi et al. (2014)	Integrative: PHENO	PHENO, RWS	GE: Contiguous USA (30,700 km ²); GR: 1 ha; TE: 2001-2051; TR: 5 yr; SG: fresh-water vertebrates	BP: watershed area, water quality, natural cover; SE: past LU change, economic returns, conversion costs	Land use type rarity-weighted species richness, threat to fresh-water diversity	Water quality	Urban expansion as major threat in species-rich regions or severe water quality problems	No	No
Marshall et al. (2021)	Integrative: MECHA	PHENO, RWS	GE: Belgium (9 Mi km ²); GR: 1 km ² ; TE: 2010-2035; TR: yr; SG: bumblebees	BP: None; SE: land-use class, crop type	Habitat suitability	Habitat suitability	Using more LU predictors improved performance. Arable and urban land were mostly negative.	No	No

RangeShifter-Integrative: CRAFTY (Synes et al., 2019)	MECHA	MECHA, HS	GE: 10000 grid cells; GR: grid cell (ca. 500 x 500 m); TE: 50 yr; TR: yr; SG: pollinators	BP: productivity; SE: land use, demand	Spatial abundance distribution, land-use type, crop yield	Carrying capacity	Crop-pollinator system showed greater changes in bi-directionally coupled models	No	No
Graphab (Foltête et al., 2012)	No explicit model, reads in land cover layers	MECHA, RWS	GE: section of Franche-Comté (252 Mi pixels); GR: 10 x 10 m; TE and TR: -; SG: tree frog	BP: habitat characterization; SE: land cover/LU resistances	Species distribution, landscape connectivity metrics	Resistance values; habitat availability; carrying capacity	LU intensification can reduce connectivity, with negative effects on species abundance and distribution	No	No
Lautenbach et al. (2017)	No explicit model, applies afforestation scenarios	MECHA, RWS	GE: Mulde Basin (5,744 km ²); GR: 1 km ² ; TE: 500 yr; TR: 1 yr; SG: plants	BP: bioclimatic variables, soil texture; SE: protected area, land use, land cover	Species richness, richness of functional groups, carbon storage	Habitat suitability	Non-linear relationships of species richness with afforested area and land use configuration.	No	No

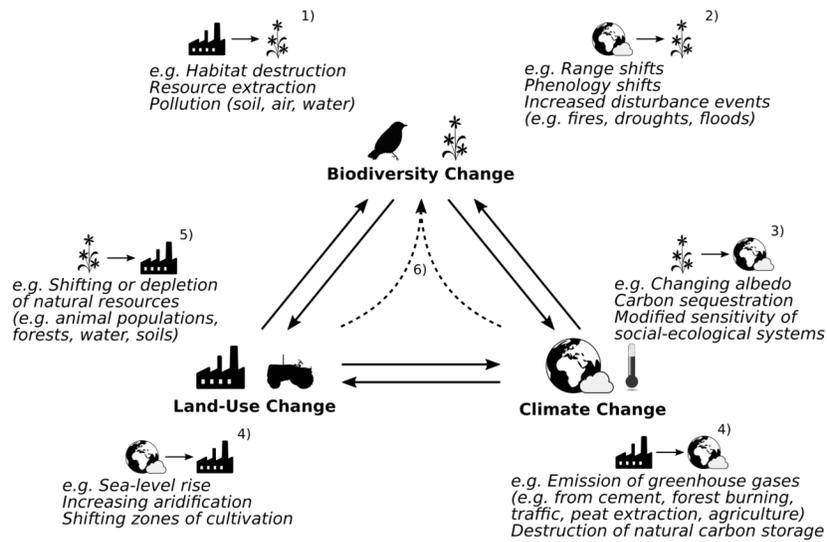


Figure 1. Biodiversity change (BDC), land-use change (LUC), and climate change (CC) all interact. In addition to the bidirectional interactions (solid arrows), there are additive and multiplicative effects of LUC and CC on BDC (dashed arrows). Studies on biodiversity response to climate change have largely focused on the direct link of CC to BDC. Biodiversity assessments considering indirect effects of CC on BDC via CC-driven LUC are largely lacking. References: 1) IPBES (2019); 2) Böhme et al. (2021); 3) Seddon et al. (2020); 4) Dale et al. (2011); 5) Chausson et al. (2020); 6) Oliver & Morecroft (2014).

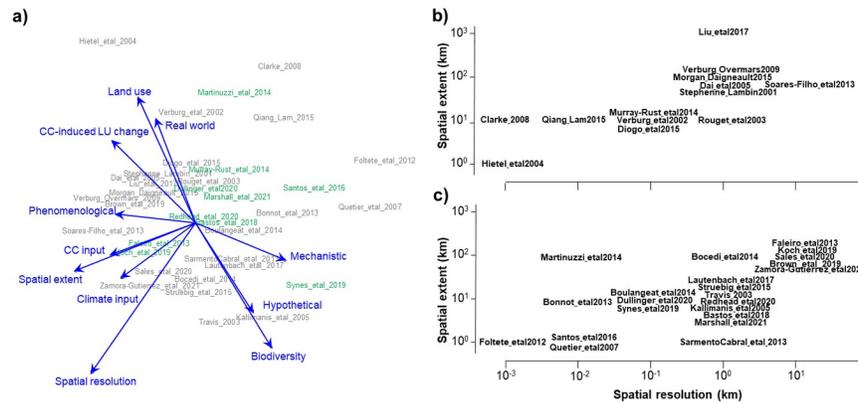


Figure 2. Properties of land-use and biodiversity models . a) Ordination of retrieved models from Tables 1-2 in regard to field of research (land use or biodiversity), spatial scale (resolution and extent), study system (hypothetical or real world), method (phenomenological or mechanistic/Agent-based), as well as whether they use climate, climate change (CC) and CC-induced land-use (LU) change. Except for spatial scales axes (see panels b and c), all these characteristics were classified with yes/no. Ordination axes are colored blue, whereas studies are given in grey or green font. Green colored studies highlight integrative approaches, i.e. simulating both land use and biodiversity. Studies fill the ordination space very well, with ordination arrows pointing to different directions (variation explained by the first two ordination axes <

35%, with five dimensions necessary to reach a stress < 0.05 and stress with 11 dimensions = 0.003). This indicates a high diversity of proposed models and that relevant modelling and experimental aspects (e.g. integrating climate, climate change and climate-change-induced land-use change) are not yet often combined. b-c) Spatial scale properties of land-use (b) and biodiversity (c) models. Note that the scales in b-c) are in orders of magnitude of km, with several models overlap scale properties and could thus be readily integrated. We added jitter in a) and vertical spacing in b) to improve visualization. The principal component analysis was performed with ‘smacof’ and ‘vegan’ R packages, using Bray-Curtis dissimilarity matrices.

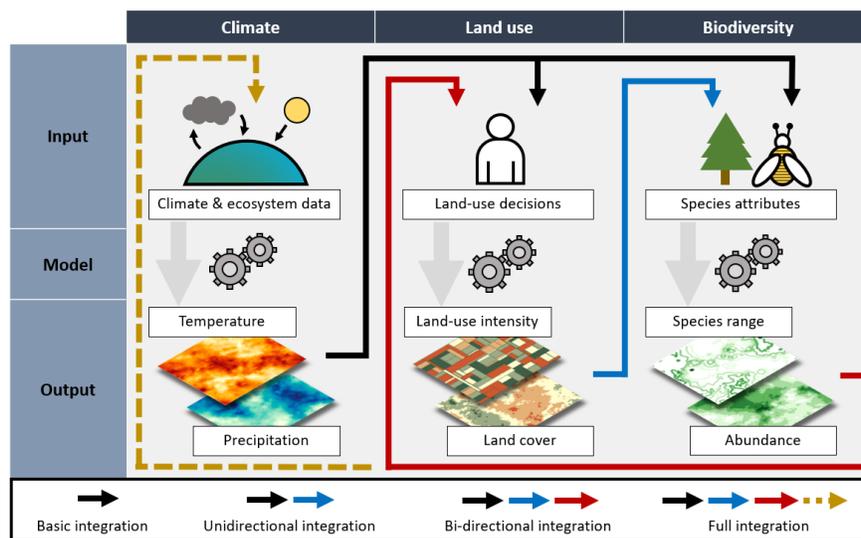


Figure 3. Examples of how climate, biodiversity and land-use models have been integrated. Climate models often provide the basic drivers for both land-use and biodiversity models (black arrow; see Tables 1-2 for climate variables used as input). The blue arrow shows an additional one way coupling (unidirectional) between the output of a land-use model which is used as input for the biodiversity model (e.g. Dullinger et al., 2020) and the red arrow shows an additional integration of the biodiversity model output as additional input for the land-use model. The red and blue arrows together act as a loose bi-directional coupling, therefore creating a feedback loop between the models (e.g. Synes et al., 2019). The yellow dotted arrow displays a possible integration from the biodiversity models, back to the climate model, creating a fully integrated system. To our knowledge, there are yet no regional studies which integrate such a feedback. Note that climate models already integrate land-use model output (not illustrated, but see Pongratz et al., 2018), thus the yellow arrow can be achievable if climate models use the output of both land-use and biodiversity outputs from bi-directionally integrated models.

Supplementary Material S1 - Details on literature search and model classification

This SI accompanies the paper

The road to integrate climate change effects on land-use change in regional biodiversity models

Juliano Sarmiento Cabral, Alma Mendoza-Ponce, André Pinto da Silva, Johannes Oberpriller, Anne Mimet, Julia Kieslinger, Thomas Berger, Jana Blechschmidt, Maximilian Brönnner, Alice Classen, Stefan Fallert, Florian Hartig, Christian Hof, Markus Hoffmann, Thomas Knoke, Andreas Krause, Anne Lewerentz, Perdita Pohle, Uta Raeder, Anja Rammig, Sarah Redlich¹⁰, Sven Rubanschi, Christian Stetter, Wolfgang Weisser, Daniel Vedder, Peter H. Verburg, Damaris Zurell

1| Details on literature search for Table 1

1.1| Literature search and inclusion criteria

We first searched the literature for land-use models using web of science with the search string “land (use OR cover) AND model” and classified them by reading the title and abstract as regional (i.e. maximal spatial extent on a continental extent). Furthermore, we also included models that did not come up in the search, but that we knew existed beforehand. This research was conducted over the scope of one week (02.03.2021-11.03.2021).

1.2| Model classification

After thoroughly reading the papers, the model type was classified in phenomenological (e.g. empirical data was used to find statistical correlations) or mechanistic. Mechanistic ones included mathematical descriptions of processes between input and output, but also cellular automata (state of cell at a given time step depends on the state of the cell itself and neighboring cells at the previous time step), agent-based (individuals or collective entities and their decisions connect input and output) and combinations of the previous types. We further compiled the scales (spatial extent and resolution, temporal extent and resolution), input (variables read-in during initialization or simulation), output (reported metrics), whether the study included climate change effects directly on land use, whether the study included biodiversity variables. For input variables, we distinguished between biophysical (e.g. soil, climate) and socioeconomic (e.g. price, land cover type) variables. Further, we noted whether the study included climate change, what variable is modified by climate change, and whether there are climate change effects on land-use change.

2| Details on literature search for Table 2

2.1| Literature search and inclusion criteria

The following is a list of keywords that we entered to web of knowledge’s search engine (webofknowledge.com). Results were not filtered by time, though we did pay extra attention to newer papers, since the field of ecological modelling is still relatively young, and more papers come out each year. We tried multiple different key word combinations, most of which lead to hugely over 1000 results. For these papers, we sorted by newest, and skimmed through the first pages. In the end, our final key words consisted of “(mechanistic OR agent* OR process*) AND model* AND (land AND (*use OR *cover)) AND biodiv* AND region* AND change” which led to a total of 374 papers (final search string listed below). Their abstracts were read to determine if they fitted the scope of this paper, and if so, the paper was read thoroughly and included in this table if fitting. Other papers included in this table were either from other key word combinations as briefly explained above, or were other modelling papers that we knew of independent of this literature research.

This research was conducted over the scope of one week (01.02.2021-08.02.2021). Below we provide a list of search strings and the respective number of hits (Table S1).

Table S1. Key word list (search strings) and their respective results (number of hits).

Search string	Hits
model* AND (landscape* OR use OR *cover) AND climate AND biodiv	5059
model* AND (land*use OR land*cover) AND biodiv*	86
model* AND (landscape AND use OR *cover) AND biodiv	7021
model* AND (land* AND (use OR *cover)) AND biodiv	8187

Search string	Hits
(mechanistic OR agent-based OR population-based OR process-based OR individual-based) AND model* AND (land* AND (use OR *cover)) AND biodiv	287
(mechanistic OR agent* OR population* OR process* OR individual*) AND model* AND (land* AND (use OR *cover)) AND biodiv	4052
(mechanistic OR agent* OR population* OR process* OR individual*) AND model* AND (land* AND (use OR *cover)) AND biodiv AND climate	1248
model* AND (land* AND (use OR *cover)) AND biodiv AND climate	2596
(mechanistic OR agent* OR process*) AND model* AND (land* AND (use OR *cover)) AND biodiv	2019
(mechanistic OR agent* OR process*) AND model* AND (land AND (use OR *cover)) AND biodiv	1549
(mechanistic OR agent* OR process* OR individual*) AND model* AND (land AND (use OR *cover)) AND biodiv AND (human OR anthropogenic)	623
(mechanistic OR agent* OR process* OR individual*) AND model* AND (land AND (use OR *cover)) AND biodiv AND (human impact)	262
model* AND (land AND (use OR *cover)) AND biodiv and search within results for human impact	781
model* AND (land AND (use OR *cover)) AND biodiv AND "human impact"	77
model* AND (land* AND (use OR *cover)) AND biodiv AND region* (mechanistic OR agent* OR process*) model* AND (land AND (use OR *cover)) AND biodiv AND region*	552
model* AND (land* AND (use OR *cover)) AND biodiv AND region* (mechanistic OR agent* OR process*) model* AND (land AND (use OR *cover)) AND biodiv AND region* AND change	374

2.2/ Model classification

Models were classified by land-use approach (if explicitly simulating a land-use model, classified as integrative), type of biodiversity model component (mechanistic, experimental-statistic, or hybrid when combining both; real vs. virtual system), scales (spatial extent and resolution, temporal extent and resolution), study biological group (e.g. taxon or ecological guild), input (variables read-in during initialization or simulation, either empirical or generated by land-use model), output (reported land-use and biodiversity metric), whether the study included climate change effects directly on biodiversity or via climate-induced land-use change. For input variables, we distinguished between biophysical (e.g. soil, climate) and socioeconomic (e.g. price, land cover type) variables. Further, we noted what variable is modified by land use, whether

there is climate change effects whether there is a comparison of land-use change with and without climate change effects, and what land-use effects there are on biodiversity.