PERSPECTIVE

The road to integrate climate change projections with regional land-use–biodiversity models

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Abstract

1. Current approaches to project spatial biodiversity responses to climate change mainly focus on the direct effects of climate on species while regarding land use and land cover as constant or prescribed by global land-use scenarios. However, local land-use decisions are often affected by climate change and biodiversity on top of socioeconomic and policy drivers. To realistically understand and predict climate impacts on biodiversity, it is, therefore, necessary to integrate both direct and indirect effects (via climate-driven land-use change) of climate change on biodiversity.

2. In this perspective paper, we outline how biodiversity models could be better integrated with regional, climate-driven land-use models. We initially provide a short, non-exhaustive review of empirical and modelling approaches to land-use and land-cover change (LU) and biodiversity (BD) change at regional scales, which forms the base for our perspective about improved integration of LU and BD models. We consider a diversity of approaches, with a special emphasis on mechanistic models. We also look at current levels of integration and at model properties, such as scales, inputs and outputs, to further identify integration challenges and opportunities.

3. We find that LU integration in BD models is more frequent than the other way around and has been achieved at different levels: from overlapping predictions to simultaneously coupled simulations (i.e. bidirectional effects). Of the integrated LU-BD socio-ecological models, some studies included climate change effects on LU, but the relative contribution of direct vs. indirect effects of climate change on BD remains a key research challenge.

4. Important research avenues include concerted efforts in harmonizing spatial and temporal resolution, disentangling direct and indirect effects of climate change on biodiversity, explicitly accounting for bidirectional feedbacks, and ultimately feeding socio-ecological systems back into climate predictions. These avenues can be navigated by matching models, plugins for format and resolution conversion, and increasing the land-use forecast horizon with adequate uncertainty. Recent developments of coupled models show that such integration is achievable and can lead to novel insights into climate–land use–biodiversity relations.

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 the main current stressor (Bühne et al., 2021; IPBES, 2019) and climate change effects likely to intensify it in the future (Pereira et al., 2020). One 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 manifold effects on biodiversity (Arneth et al., 2020; Leclère et al., 2020). These effects can feed back into land use and climate, following direct and indirect pathways, such as indirect pathways from climate change into biodiversity change via climate-driven changes in land use (Figure 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; Karger et al., 2020), there has been a large production of modelling approaches with the purpose to explain, understand, predict and explore biodiversity change under climate change (see Glossary for definitions of mechanistic vs. phenomenological approaches). From now on, we refer to these approaches as simply biodiversity models. These models have mostly kept land cover and other global change drivers constant (e.g. Anderson et al., 2013; Sarmento 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 as well as feedbacks into land use and climate (Figure 1) remain relatively underexplored.

Considering that land use is arguably the strongest driver of biodiversity change to date (IPBES, 2019), understanding and predicting the potential effects of climate change on land use is of high importance (Titeux et al., 2017). This has promoted the development of models intended to understand and predict these effects across different scales, from local to global (see reviews Agarwal et al., 2002; Briassoulis, 2020; Camacho et al., 2018; Prestele et al., 2016; Verburg et al., 2004, 2019). Indeed, computational advances promote the increasing development of
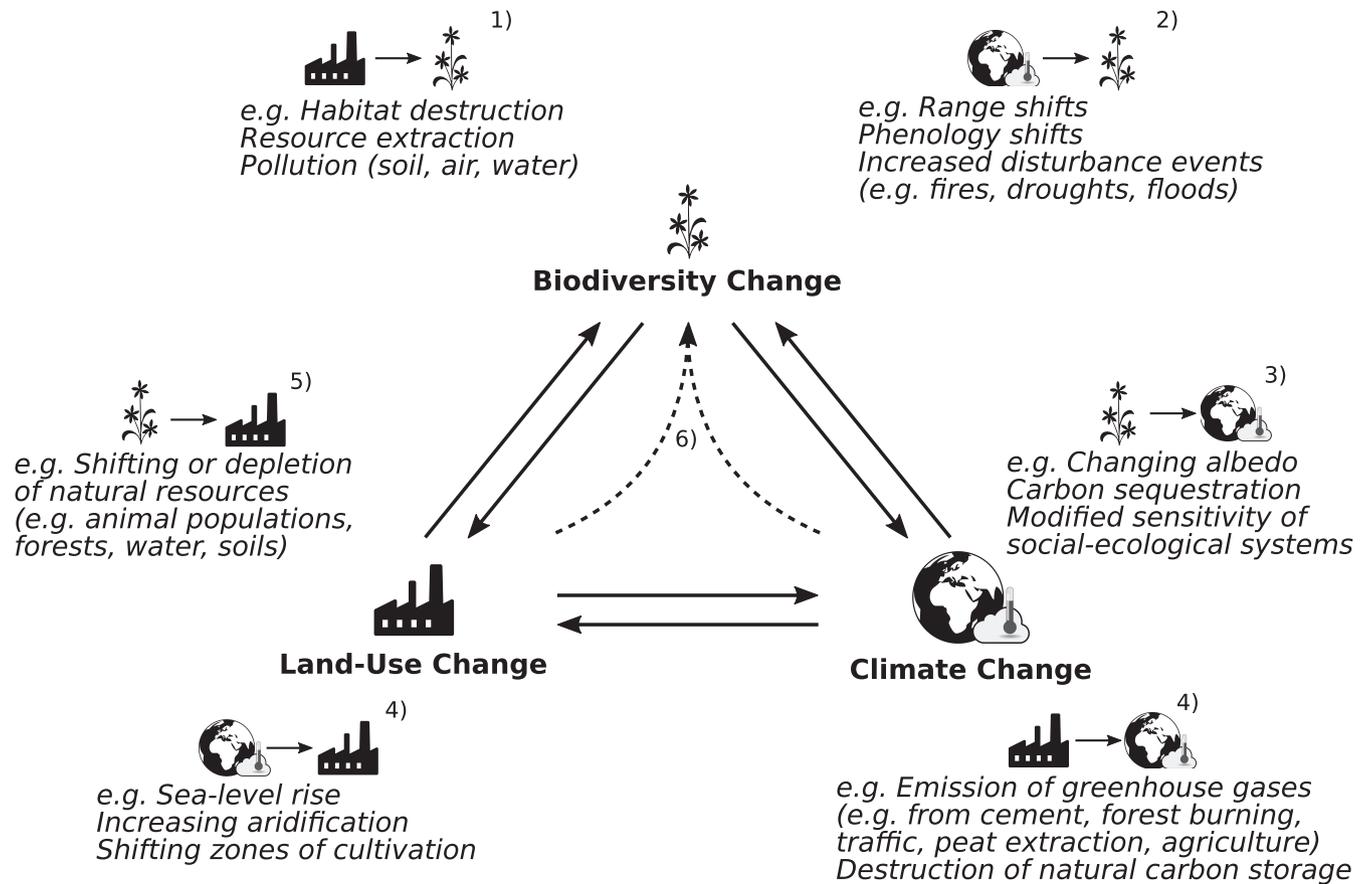
FIGURE 1 Biodiversity change (BDC), land-use change (LUC) and climate change (CC) all interact. In addition to the bidirectional interactions (solid arrows), there are additive and multiplicative effects of LUC and CC on BDC (dashed arrows). Studies on biodiversity response to climate change have largely 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. Numbers in the figure denote references: (1) IPBES (2019); (2) Bühne et al. (2021); (3) Seddon et al. (2020); (4) Dale et al. (2011); (5) Chausson et al. (2020); (6) Oliver and Morecroft (2014).

high-resolution fine-scale studies up to global extents (e.g. Li et al., 2017; Heck et al., 2018; Hurtt et al., 2020). Whereas local models tend to ignore spatial and higher-level mechanisms, global models often adopt an economic focus and may not account for the diversity of farmer behaviours, decision-making strategies and governance structures across all regions of the globe (Arneth et al., 2014; Rounsevell et al., 2014). This produces less precise estimates of land conversion rates at the regional scales (Bayer et al., 2020). This is however critical for biodiversity change assessments, as most species have rather regional range distributions. 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). Moreover, as people 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, including local tradition and culture. Challenges for modelling land-use change and their

impacts on biodiversity at the regional scale thus lie in plausible climate-integrated, socio-economic models to simulate regional land allocation (de Chazal & Rounsevell, 2009; Newbold, 2018).

Here, we focus on how approaches at regional scales may provide insights to tackle the above-mentioned challenges. We adopt a broad definition of regional scale, from landscape to continental extents, to contemplate a variety of modelling strategies (see Glossary). This retains aspects of local and global studies while limiting our scope to a manageable body of literature. Moreover, climate change is spatially heterogeneous (Bowler et al., 2020), and species, ecosystems, political jurisdiction, management policies, and land users' response and decisions tend to be region specific (e.g. Verburg et al., 2010). Additionally, biodiversity assessments and conservation policies are mostly designed to address adaptation and mitigation options at regional scales (e.g. Carwardine et al., 2019). Therefore, the effects of climate and land use on biodiversity at the regional level can provide direct support for conservation policies at the level in which these are administratively decided.

We argue for an integration of indirect pathways of climate change effects on regional biodiversity via connection between

Glossary

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 functional 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 (e.g. individuals, populations, species, communities), which drive the variability of ecological phenomena (i.e. biodiversity).

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

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, ecological guilds or ecoregions, whereas global land-use models often distinguish several world regions.

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

Land cover: surface characteristics of land (Haines-Young, 2009). This includes natural and human-dominated classes. However, due to existence of a variety of human-dominated land-cover classes (i.e. land-use types) and ubiquitous effects of human activities (including in natural classes), we assumed this as a socioeconomic categorization.

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

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-use types are human-dominated land-cover classes. We assumed this as a socioeconomic categorization.

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

Management: diversity of practices applied to a land area to achieve the intended purpose of the land, for example, 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. They can be also interpreted as bottom-up or first principle models.

Model input: any configuration, parameter value, assumption and data read in during model initialization and iteration.

Model output: values generated by the model and saved for analysis.

Phenomenological models: models in which a variable state is correlated to other variables (e.g. species occurrences to environmental factors), which can be done by machine-learning, econometric and statistical relationships. They can be also interpreted as top-down models.

Regional scales/models: from landscape to continental spatial extents, as long as the study region includes environmental gradients (i.e. tens to thousands km). Regional scales at broad extents can comprise multiple administrative boundaries at which policy decisions are made (e.g. from subnational to national level or even supranational unions). This is an intentionally broad definition to capture a variety of modelling approaches, having elements of both local and global scales at various degrees. 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.

biodiversity and land-use models. To this end, we first provide a short, non-exhaustive review of studies related to climate change effects on regional land use (Section 3), followed by studies related to land use effects on regional biodiversity (Section 4). The review provides insights on aspects not yet modelled, while highlighting the variety of approaches for potential integration avenues and summarizing their properties, purposes and emergent results. These approaches inform our perspective (Section 5) on improved integration of land-use and biodiversity models by matching the resolution and input/output of the various modelling approaches. We focus our perspective on mechanistic approaches to gain explicit appraisal of causal relationships while describing more

responses (e.g. land-use intensity, yields, species abundances and landscape connectivity) than phenomenological approaches (e.g. transition probabilities or suitability estimates). Moreover, mechanistic models are more appropriate for simulating dynamic systems, particularly under non-equilibrium and transient conditions such as climate and land-use change (Cabral et al., 2017; Dormann et al., 2012; Urban et al., 2016). We further 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 (bidirectional) links between climate change, land-use change and biodiversity change models (Figure 1). This perspective will ultimately foster the dialogue between the research communities focusing on predictive land-use and biodiversity research to promote integrated assessments at regional scales.

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 climatic conditions. This is because different plants and animals, including both harvested products and potential pests, have different environmental preferences for optimal productivity. Consequently, environmental change strongly influences productivity and stakeholders' decisions on land use, both of which, in turn, affect regional economies. 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 some current evidence indicating that farmers temporarily and dynamically shift land use after weather shocks—for example, 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 & Bindi, 2002; Ramsey et al., 2021; Salazar-Espinoza et al., 2015).

Climate change will continue to affect agricultural productivity and trigger 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 socioeconomic pathways; O'Neill et al., 2014). As a consequence, changes in these systems are driven by human expectations and decisions, which are 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. Hence, it is crucial to determine the temporal scale at which these systems are satisfactorily predictable in terms of explicitly including the increasing uncertainty with increased temporal extents into the future ('forecasting horizon').

2.2 | Modelling regional land-use change

Regional land-use models include a continuum from phenomenological to mechanistic approaches (Table 1; see also the Glossary). Phenomenological models relate a set of explanatory socio-economic or biophysical variables to transitions in local land use without specifying causal relationships, for example via statistical or machine-learning models (e.g. Verburg & Overmars, 2009). Some of these approaches quantify change via model-specific transition matrices of two historical land-use maps (DINAMICA-EGO; Soares-Filho et al., 2013). In other phenomenological top-down approaches, global economic or integrated assessment models are applied to determine the region-level demands (Dyna-CLUE; Verburg & Overmars, 2009). Probability maps of land-use changes can be generated by several phenomenological approaches, including neural networks (Dai et al., 2005; Qiang & Lam, 2015). By contrast, mechanistic models emulate processes in which drivers of change (e.g. sequence of land uses) interact, sometimes based on rules (Rouget et al., 2003; Stéphenne & Lambin, 2001), sometimes based on cellular automata (Clarke, 2008; Diogo et al., 2015; Liu et al., 2017). Agent-based models appear to be best suited to mechanistically integrate the individual stakeholder behaviour, policies and biophysical tags (Murray-Rust, Brown, et al., 2014; Murray-Rust, Robinson, et al., 2014). Such models can include regional trade-offs among socioeconomic input variables as 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 climate models. Moreover, climate change projections are generally global 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 a few regional land-use models that have projected long-term land-use trajectories integrating climate change (e.g. Mendoza-Ponce et al., 2018, 2019). Finally, most of the selected land-use models can deliver outputs that can be relevant inputs for biodiversity models, from the most common output 'land cover' to more refined variables, such as ecosystem service indicators, land-use types with intensification level and areas of fuelwood extraction (see column 'Output variables' in Table 1).

While most land-use models focus on biophysical and socioeconomic drivers, some models have integrated inherent connections to biodiversity. For example, vegetation recovery rates or dynamics can influence the use of fuelwood (Kiruki et al., 2019; Stéphenne & Lambin, 2001) or management strategies (Murray-Rust, Robinson, et al., 2014; Verburg & Overmars, 2009). Other models integrated information on ecosystem

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.

Model	Type	Study Region and Scales	Input variables
CLUE-S (Verburg et al., 2002)	MECHA	GE: Sibuyan island (456 km^2), Klang-Langat watershed (4300 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
Dyna-CLUE (Verburg & Overmars, 2009)	MECHA	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
SALU (Stéphenne & Lambin, 2001)	MECHA	GE: Burkina Faso (274,200 km^2); GR: 2.5×3.75°; TE: 1960–1997	BP: precipitation; Socioeconomic: human population, livestock, cereals imports
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
DINAMICA-EGO (Soares-Filho et al., 2013)	Hybrid	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
SLEUTH (Clarke, 2008)	MECHA	GE: Mainly focused on US cities; GR: variable; TE: variable	Biophysical: slope, hillshade; SE: distance to roads
Aporia (Murray-Rust, Robinson, et al., 2014)	MECHA	GE: Aurau Valley, Switzerland (99 km^2) and Lanan 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)
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
CPV Analysis Model (Dai et al., 2005)	MECHA	GE: Pearl river delta (10,851 km^2); GR: -; TE: 1985–2000	BP: climate, soil water, vegetation, relief; SE: population, technology, policy, profits
Qiang and 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
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
Hietel et al. (2004)	PHENO	GE: Erda, Eibelshausen (11 km^2, 9 km^2); GR: 1:5000; TE: 1945–1998	BP: elevation, slope, aspect, available water, soil texture; SE: land management
Rouget et al. (2003)	Hybrid	GE: Cape Region (129,462 km^2); GR: 1′; TE: 20 years	BP: habitat, alien species, geology, distance to coastline, altitude, slope, roughness, bioclimatic variables; SE: urban area, distance to roads
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

Abbreviations: BD, biodiversity; BP, biophysical; CC, climate change; GE, geographical extent; GR, geographical resolution; LU, land use; MECHA, mechanistic (hybrid models entail major phenomenological and mechanistic submodels); NA, not applicable; PHENO, phenomenological; SE, socioeconomic; TE, temporal extent.

What is modified by CC?	CC effects on LU	BD-related parameter	Output variables
Nothing	NA	None	Land cover (e.g. forest, grassland, urban, coconut and palm oil plantations, rice fields)
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
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, fuelwood extraction
Land allocation	Annual precipitation and temperature	Ecoregions	Extent and location of cultivated areas, forests, grassland and urban covers.
Probability of land use	None	Distribution of mammals	Deforestation area linked to reduced mammal distribution and carbon emissions
Nothing	NA	None	Urban expansion and other LU related to cities
Output yields	Model presentation	Directly via vegetation modelling; indirectly via biophysical and policy tags	Land management practices, ecosystem service indicators, market data with prices
Productivity of the farm	Dairy and forest enterprises will increase	None	LU, farm net revenue, greenhouse gas emissions
Potential change of land-use system	Low CC effects, with LU change driven rather mostly by SE drivers	Vegetation, species diversity	Dominance of land use, patches, fragmentation
Nothing	NA	None	LU maps
Biophysical suitability	Changes in crop yields and productivity	None	LU maps pixelwise

(Continues)

What is modified by CC?	CC effects on LU	BD-related parameter	Output variables
Available water capacity	Change from arable land to grassland with lower water capacity	None	Suitability maps
Nothing	NA	Broad habitat units, alien species threat	Land-cover maps with percentage of transformed area
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

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.

Model	LU approach	Type of the BD model	Study region, scales and group	Input variables
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
LoLiPop (Sarmento Cabral et al., 2013)	No explicit model, reads in habitat loss data	Hybrid, RWS	GE: Cape Region (11,000 km^2); GR: 1′×1′; TE: 10s gen; TR: gen; SG: plants	BP: climate, soil, suitability SE: habitat loss percentage
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
FATE-HD (Boulangeat, Damien, et al., 2014)	No explicit model, reads-in pasture and field data	Hybrid, RWS	GE: Écrins NP (2700 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
Kallimanis et al. (2005)	No explicit model, includes a disturbance submodel	MECHA, HP	GE: 65,536 grid cells: GR: grid cell; TE: 1000s gen; TR: gen; SG: virtual species	BP: habitat SE: disturbance
LandSHIFT (Koch et al., 2019)	Integrative: MECHA	MECHA, RWS	GE: Africa (30.3 Mi km^2); GR: 5′×5′; TE: 2000–2030; TR: yr; SG: vertebrates	BP: forest and vegetation types, abundance per LU type; SE: LU suitability, human population
Dullinger et al. (2020)	Integrative: MECHA	PHENO, RWS	GE: Part of Austrian Alps (1426 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, LU class
Zamora-Gutierrez et al. (2018)	No explicit model, reads in LU data	PHENO, RWS	GE: Mexico (2 Mi km^2); GR: 5′×5′; TE: current-2050; TR: yr; SG: bats	BP: temperature and precipitation variables; SE: LU type, SSP
Bastos et al. (2018)	Integrative: MECHA	MECHA, RWS	GE: Northeast 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
Bonnot et al. (2013)	No explicit model, applies human impacts scenarios	Hybrid, RWS	GE: Central Hardwoods Bird Conservation (0.3 Mi km^2); GR: 30×30 m; TE: 100 yr; TR: yr; SG: birds	BP: grid cell and landscape attributes, habitat suitability, relative productivity; SE: restoration, communication tower strategies
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
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, human population, deforestation rate
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
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

Output variables	What is modified by LU?	Key findings (LU effects on BD)	CC	CC -driven LUC
Occupied grid cells, spatial occupancy	Habitat loss	Thresholds to species survival, with combined CC and LU showing the lowest thresholds	Yes	No
Spatial abundance distribution, range size, range filling	Carrying capacity	Lower abundances, ranges less affected; highlands act as refugia under CC due to lower LU	Yes	No
Spatial abundance distribution, range size, connectivity	Habitat suitability, movement cost	LU affects abundances and connectivity between populations	Yes	No
Spatial abundance distribution, population structure	Habitat area, dispersal, disturbance (affects abundances, seed bank, fecundity)	LU effects can at least partly be simulated through disturbance	Yes	No
Spatial distribution of occupied grid cells	Grid cell occupancy	Extinction risk higher for low dispersal rates, LU pattern affects population survival	No	No
BD Intactness Index (BII)	Population density, livestock density, crop production, calories availability, BII	Land sparing more effective for conserving biodiversity (and food production)	No	No
Habitat suitability, species richness and LU distribution, LU intensification and homogeneity	Habitat suitability	LU and CC both affect species habitat suitability, LU stronger	Yes	Yes
Habitat suitability	Habitat suitability	Vulnerability of bats to CC and LUC very high	Yes	No
Minimum local biomass index	Landscape composition, local surface temperature	Disruptive effect of LUC in the spatiotemporal distribution of top predators' biomass	No	No
Spatial abundance distribution	Carrying capacity, reproductive rate, survival rate	Habitat conservation must be strategic; source-sink dynamics and dispersal influence population survival	No	No
Potential species distribution, spatial conservation plan	Spatial conservation prioritization	LUC altered spatial location of conservation priority sites	Yes	No
Habitat suitability	Habitat suitability	Most suitable habitat expected to decline due to CC, even if LUC towards more protection	Yes	No
Cover type, bird diversity (richness, specialist richness, total abundance)	Cover type	LU intensification homogenizes landscape, with negative impacts on biodiversity.	No	No
Probability of occurrence; potential richness, potential functional diversity	Habitat suitability	Arable land expansion lowers species richness, even under less intensive cropping	No	No

Continued

TABLE 2 Continued

Model	LU approach	Type of the BD model	Study region, scales and group	Input variables
LAMOS-FATE (Quétier et al., 2007)	No explicit model, applies LUC scenarios and stakeholder assessments	MECHA, RWS	GE: Romanche River headwater (7000 grid cells); GR: grid cell (ca. 42×42 m); TE and TR: Nav; SG: plant functional types	BP: productivity; SE: LU, fertilization, management scenario
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 cover and land-use types
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: freshwater vertebrates	BP: watershed area, water quality; SE: past LU change, economic returns, land cover, conversion costs
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 types, crop type
RangeShifter-CRAFTY (Synes et al., 2019)	Integrative: MECHA	MECHA, HS	GE: 10000 grid cells; GR: grid cell (ca. 500×500 m); TE: 50 yr; TR: yr; SG: pollinators	BP: productivity; SE: land use, demand
Graphab (Foltête et al., 2012)	No explicit model, reads in land cover layers	MECHA, RWS	GE: section of Franche-Comté (252 Mi pixels); GR: 10×10 m; TE and TR: -; SG: tree frog	BP: habitat characterization; SE: land cover/LU resistances
Lautenbach et al. (2017)	No explicit model, applies afforestation scenarios	MECHA, RWS	GE: Mulde Basin (5744 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

Abbreviations: BD, biodiversity; BP, biophysical; CC, climate change; GE, geographical extent; gen, generations; GR, geographical resolution; HS, hypothetical system; LU, land use; LUC, land-use change; MECHA, mechanistic (hybrid models entail major phenomenological and mechanistic submodels); NAv, not available; NP, National Park; PHENO, phenomenological; RWS, real-world system; SE, socioeconomic; SG, study group; SSP, socioeconomic pathway; TE, temporal extent; TR, temporal resolution; yr, year.

threats, such as alien species, to model transformed rates and areas (Rouget et al., 2003). A few examples also consider animal diversity as a driver (Dai et al., 2005; Soares-Filho et al., 2013).

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). While physical actions on land as direct drivers of ecosystem change operate at the local level (e.g. agriculture, forestry or urbanization; Lambin & Meyfroidt, 2010), impacts of land use also scale up to larger spatial extents (Haines-Young, 2009). 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 have developed two main, but not mutually exclusive, 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; Jeliazkov et al., 2016). 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).

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). It has been found that land-use intensification can cause the homogenization of the landscape through intensive land use leading to potentially lower beta-diversity (Gossner et al., 2016; Jeliazkov et al., 2016), to changes in phenology (Barbaro & Halder, 2009; Mimet et al., 2009), and to trait evolution (e.g. selecting for higher dispersal ability; Martin et al., 2017). Finally, some studies show that land-use type

Output variables	What is modified by LU?	Key findings (LU effects on BD)	CC	CC -driven LUC
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
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
Land use type, rarity-weighted species richness, threat to freshwater diversity	Water quality	Urban expansion as major threat in species-rich regions or severe water quality problems	No	No
Habitat suitability	Habitat suitability	Using more LU predictors improved performance. Arable and urban land were mostly negative.	No	No
Spatial abundance distribution, land-use type, crop yield	Carrying capacity	Crop-pollinator system showed greater changes in bidirectionally coupled models	No	No
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
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

seems to mainly drive the functional and taxonomic composition, while land-use intensity may rather drive 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 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 (e.g. the dynamic vegetation models DVMs; see Sakschewski et al., 2015). However, 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 are devoted to understanding 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. These mechanistic models predict abundance distributions, species richness and connectivity, all of which have a higher information value than just habitat or presence probabilities from phenomenological models (Ehrlén & Morris, 2015; see also the output variables in Table 2).

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 far been limited (Table 2), 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; Sarmento Cabral et al., 2013). These models address, for example, temporal dynamics

and coexistence of functional groups under land-use management in complex landscapes (Boulangeat, Georges, 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., 2018). The partial effect of land use on biodiversity (i.e. disentangling its effect from climate change) has been considered in a few studies. For instance, Travis (2003) showed that 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 unidirectional and bidirectional effects of crop yields on pollinator populations, demonstrating that the inclusion of bidirectional feedbacks revealed much stronger loss in crop yields. The different strategies for integrating both climate change and land-use effects on biodiversity are discussed in the next sections, as we lay out a roadmap for future research avenues.

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

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

We found four main approaches for the inclusion of land use in biodiversity modelling with increasing levels of integration:

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 a 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. Koch et al., 2019; Santos et al., 2016). 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., 2021; Redhead et al., 2020). This fourth type of approach constitutes the most integrative one. Here, model coupling is defined as both models being simulated simultaneously in a single framework with variables being exchanged among models. This integration remains largely uni-directional, but bidirectional feedbacks can be already found (Synes et al., 2019). Simultaneous socio-ecological dynamics may thus be the key avenue for

upcoming research, as bidirectional models revealed greater influence of land-use change, indicating that uni-directionally coupled models may miss important dynamics (Synes et al., 2019).

Most of the identified studies only account for land-use effects on habitat availability or suitability (e.g. Travis, 2003). This has also been highlighted in recent reviews (e.g. Santos et al., 2021). Land-use effects on demography have been considered by Quétier et al. (2007) through variation of fecundity rates, dispersal ability and mortality (via disturbances) in plant functional groups, while Sarmento 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. Hence, most land-use models have outputs that could be used as input for biodiversity models, in particular land cover (compare Tables 1 and 2). For example, land use and land cover are common outputs of land-use models (e.g. Dai et al., 2005; Diogo et al., 2015; Liu et al., 2017; Morgan & Daigneault, 2015; Rouget et al., 2003; Verburg et al., 2002) which can be readily used as input for biodiversity models (e.g. Bastos et al., 2018; Foltête et al., 2012; Lautenbach et al., 2017; Quétier et al., 2007). More refined results, such as land-use intensity, emerge from some land-use models (e.g. Stéphenne & Lambin, 2001; Verburg & Overmars, 2009) and could be also used as biodiversity model input (Boulangeat, Damien, et al., 2014; Redhead et al., 2020; Santos et al., 2016). Irrespective of how land use affects biodiversity, it has been recently pointed out that land-use change models and the impacts of land use on biodiversity should consider more comprehensively the intensity of land use (Dullinger et al., 2021). However, there are some global studies that integrate land-use intensity and their impacts on biodiversity in their inputs and calculations but not in their projections. For example, Chaudhary and Brooks (2018) projected potential species losses from five broad land use types (managed forests, plantations, pasture, cropland, urban) under three intensity levels (minimal, light and intense use) in terrestrial ecoregions. However, the authors used the global land-use intensity maps from 2000 (van Asselen & Verburg, 2013) without any change through time. Consequently, there is no feedback between land-use change and land intensification and between intensification and biodiversity change. Allan et al. (2015) also included land-use intensity and the impacts on biodiversity and ecosystem functionality, but they do not project the impacts to the future. Hence, there is still missing feedbacks between land-use intensity projections and their impacts on regional biodiversity integrating climate change.

The inclusion of climate change effects has mainly been done through assessment of direct effects on biodiversity (see Struebig et al., 2015; Zamora-Gutierrez et al., 2018). We selected one example of recent 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). However, the incorporation of land use in biodiversity dynamics under climate change has not always modified results (Dullinger et al., 2020: see Table 2, Figure 2a), possibly because climate change-induced effects on land use are not considered.
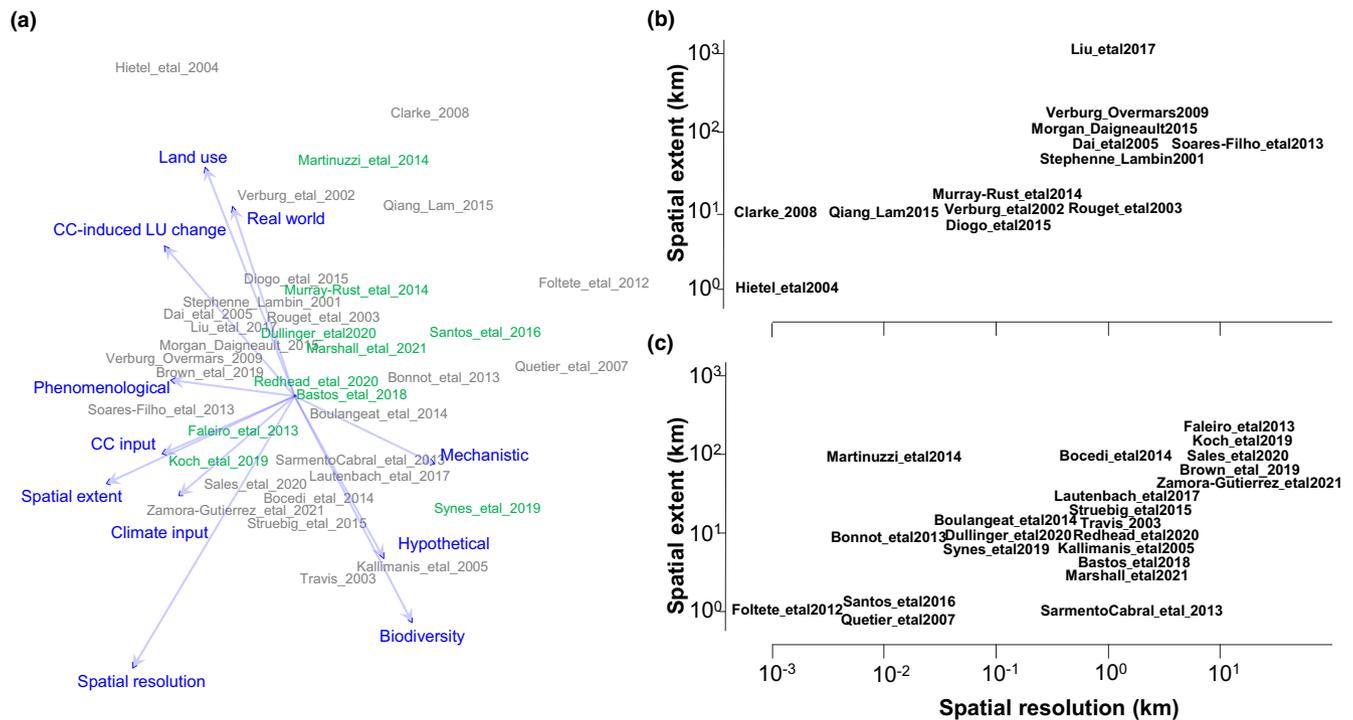
FIGURE 2 Properties of land-use and biodiversity models. (a) Ordination of retrieved models from Tables 1 to 2 with regard to field of research (land use or biodiversity), spatial scale (resolution and extent), study system (hypothetical or real world), method (phenomenological or mechanistic/agent-based), 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 coloured blue, whereas studies are given in grey or green font. Green coloured studies highlight integrative approaches, that is 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) and (c) are in orders of magnitude of km. Several models overlap in 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 in (a) was performed with 'SMACOF' and 'VEGAN' R packages, using Bray–Curtis dissimilarity matrices.

Therefore, explicit comparisons as well as relative quantification of direct vs. indirect effects of climate change require further attention.

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 phenomenological (Dullinger et al., 2020) and mechanistic (Synes et al., 2019) biodiversity models. Agent-based models seem a straightforward way for this integration, as the methodology is used by both the land-use and biodiversity communities (Tables 1 and 2; Figure 2a). We consider the following factors to be key to successful model integration, focusing mostly on mechanistic approaches as these explicitly consider processes and can generate a larger range of outputs (Table 2).

4.1.1 | Spatial resolution and representation

A key direction for improving model integration is the harmonization of spatial scales (in 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 with the respective relevant processes (Figure 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 and representation (Table 1), from polygon-based to raster-based models. Polygon-based models are particularly used when farmers are the agents, resulting in a patchwork or mosaic resolution. This can be problematic as most biodiversity models are raster based. In this regard, besides harmonization, increasing resolution remains another research avenue in both land-use and biodiversity models. Indeed, high resolution seems to improve performance of biodiversity predictions (Marshall et al., 2021). Considering that polygons and raster can be quickly converted back and forth, biodiversity models would require a raster conversion plugin to downscale for higher resolution and 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 and resolution synchronization needs to be done before simulation.

4.1.2 | Temporal resolution and forecasting horizon

Most land-use change studies focus on relatively short temporal forecasting horizons (e.g. 20 years), with few time steps. This reflects the inherent uncertainty in the development of human societies (including behaviour or agents and socioeconomic dynamics), but it also limits the utility of such forecasts for biodiversity modelling, which often use yearly (and sometimes finer) resolution for longer time period (compare temporal extents in Tables 1 and 2). For biodiversity models which have generations as time steps (e.g. Sarmento 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 absolute, generation- and agent-agnostic time steps, such as year or month. Another characteristic of current land-use models is their limited ability to project far into the future, which makes it necessary to consider methods for providing realistic uncertainties for forecasts (e.g. Hartig et al., 2012; Oberpriller et al., 2021). Among possible uncertainties, accounting for extreme events is a priority. Extreme events, such as severe floods or droughts, may represent 'black swans' (Taleb, 2007) for landowners. 'Black swans', or extreme outlier events, are historically seen as often highly improbable, but of utmost economic consequences when occurring.

4.1.3 | Indirect effects of climate change

Although we have not found studies that have tackled indirect effects of climate change using 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
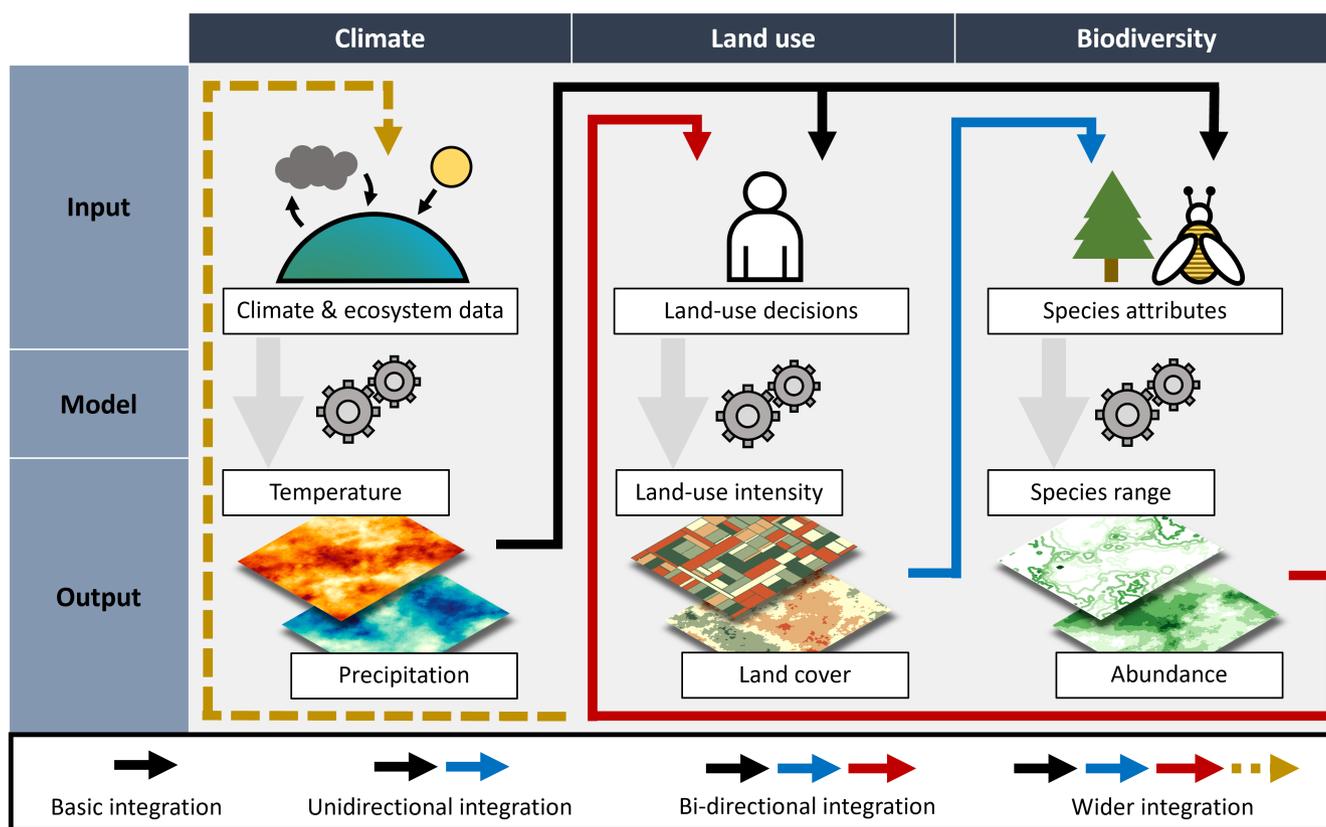
FIGURE 3 Examples of how climate and land-use models have been integrated with biodiversity models. Climate models often provide the basic drivers for both land-use and biodiversity models (black arrow; see Tables 1 and 2 for climate variables used as input). The blue arrow shows an additional one way coupling (uni-directional) 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 bidirectional coupling, therefore creating a feedback loop between the models (e.g. Synes et al., 2019). The yellow dashed arrow displays a possible integration from the biodiversity models, back to the climate model, creating a wider integrated system. To our knowledge, there are yet no regional studies which integrate such feedback. Note that climate models already integrate land-use model output (not illustrated, but see Pongratz et al., 2018); thus, the yellow arrow is achievable if climate models use the output of both land-use and biodiversity outputs from bidirectionally integrated models.

CRAFTY, Murray-Rust, Brown, et al., 2014). 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).

4.1.4 | Bidirectional feedbacks

The simultaneous simulation of land use and biodiversity with process-based models should allow for the inclusion of bidirectional feedback between models (Figure 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 uni-directional effect from land use on biodiversity. To improve bidirectionality, it is, however, important to match inputs and outputs of both land-use and biodiversity models. While standardizing and matching emergent outputs has been touched upon in this section already, for bidirectional model coupling it is important to include biodiversity aspects as input for land-use models. Some models simulating land-use change can already use biodiversity-related input, which could serve as starting point to either direct coupling or to further model development. Examples of current inputs are mostly vegetation or vegetation-related variables (Dai et al., 2005; Stéphenne & Lambin, 2001; Verburg & Overmars, 2009), which could then use the output of vegetation (Sakschewski et al., 2015), forest (e.g. Petter et al., 2021) or plant distribution (e.g. Sarmento Cabral et al., 2013) models. A few other models can use more biodiversity-related input variables, such as species richness to simulate land use change (Dai et al., 2005) or occurrence of invasive plant species to explore loss of natural land cover alongside other human-dominated land-cover types (Rouget et al., 2003). For land-use models to adequately integrate different aspects of biodiversity as input, the models may need further extensions in the decision-making rules (see next section).

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

It seems uncommon for studies of land-use change to consider any facet of biodiversity in land-use decisions (Table 1). This should change, as land users may not solely prioritize profits, but may also consider biodiversity and ecosystem costs, potentially foregoing economically attractive alternatives. In fact, it is unlikely that land users 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 analyse 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 not be profit maximizers, but risk minimizers, going for guaranteed results. They might even have ecological objectives

(Knoke et al., 2014). 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). 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 and regulations underlie the land-use change processes. In this regard, biodiversity is often not included in land-use change models because it is not yet considered a key driver of farmer decision-making or even of human population size, dietary preferences, economy, climate change or technology. Despite this, ecological variables such as species abundances, demographic rates and habitat connectivity may be important for land-use decisions. This can happen either positively to wildlife when wildlife supports traditional practices and attracts further revenue (Nelson, 2012) or negatively when there are no incentives to wildlife tolerance (Kinnaird & O'Brien, 2012). Land-use models can therefore benefit from moving beyond simply including vegetation cover change, to integrating the ability of mechanistic biodiversity models to predict these ecological variables. 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 (Pywell et al., 2015; 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. Hence, biodiversity change can be integrated in land-use models by influencing the decisions of land managers, and by affecting yields, product demand and regional policies. Some integration of this sort has been already achieved, although not in land-use models addressing climate change effects (and thus not featured in Table 1).

Currently, regional land-use change models mainly 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) as 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 the integration of biodiversity as an independent 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; Bocedi et al., 2014, 2021; Sarmento Cabral et al., 2013) that would directly impact the land cover. Another flexible and theoretically coherent 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, for example, cultural practices, subsistence, biodiversity,

leisure or environmental protection. This framework allows for the integration of biodiversity aspects into land-use modelling from a behavioural point of view, which could have positive feedbacks to biodiversity. Indeed, 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 integrating biodiversity model output as land-use model input lie in 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 and scaled. For example, explicitly calibrating a grid cell to $1\,km^2$ to match a given land-use model should be accompanied by adequately scaled values of dispersal ability, carrying capacity, and local population dynamics of the target species, community or functional group. Furthermore, to 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.

4.3 | The wider integration: Challenges to integrating 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 Figure 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) and surface runoffs (Guzha et al., 2018; Krause et al., 2017). For example, afforestation can take up carbon from the atmosphere, while also cooling 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 4.2), by simulating forest growth and carbon assimilation among other ecosystem-level processes, these models

consider important ecosystem functions such as net primary production. Considering the positive relationships between biodiversity and ecosystem functions (see van der Plas, 2019 for a review), we can 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. Hence, integrating ecosystem productivity with changes in tree diversity and composition is one promising way to integrate biodiversity, land-use and climate models. A concept showing how to achieve this has recently been recently proposed, linking climatic conditions with deforestation, afforestation and agriculture management (Bendix et al., 2021). Ultimately, with models integrating bidirectional effects (Figure 3), we could explore scenarios considering not only climate mitigation, but also biodiversity and sustainable development.

4.4 | Directions to modelling developments

Current models can already tackle a range of both land-use and biodiversity processes. However, the various climate change effects on land use and land-use effects on biodiversity have not been widely integrated into predictive studies, as indicated by the review Sections 3 and 4. There are general methodological improvements for any modelling study, such as balancing complexity, scale and mechanistic detail (see Cabral et al., 2017; Evans et al., 2013 for reviews and discussions on this topic for biodiversity models) as well as calibration, validation and parameter optimization (see Hartig et al., 2012). Here we rather identify avenues for more specific development in predictive studies that should be done in parallel with the integration across research fields.

For land-use models, the current trend remains to identify the regional drivers of land-use change to simulate human-related changes in the composition of landscapes, ecosystems, and, as argued in previous sections, biodiversity. It is important to note that regional land-use models already incorporate a series of explanatory input variables, for example, the biophysical and environmental characteristics such as mean temperature, annual precipitation, slope or altitude (see Table 1). These are linked to parameters (e.g. probability of change) as well as to direct or indirect drivers (common crops, population growth and demand). However, land-use models rarely consider the influence of extreme weather events like droughts, which can be regionally restricted and may affect land-use decisions (see Zaveri et al., 2020 for empirical evidence). Probably a key improvement would thus be building large databases on types and rules of decisions taken by the landowners, which can vary within and across regions. This would follow a tendency akin to what is done for biodiversity data, such as functional traits (Kattge et al., 2020) and would ultimately allow improving the relationship between drivers, for example, by integrating components that influence farmers' decision about

land management (e.g. rotation, expansion, intensification). Such elements are more commonly considered in agent-based models (Dislich et al., 2018) than in other mechanistic or phenomenological models, which rather use the population size and the historical rate of change as causes of land-use change (see Table 1). Agent functional types are indeed already featured in the land-use agent-based models (e.g. Murray-Rust, Brown, et al., 2014; Rounsevell et al., 2012). For socio-economic drivers, this means going beyond simulating agricultural or livestock expansion to integrating production of specific commodities and addressing 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). 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 have biodiversity elements as inputs (e.g. regional richness, functional diversity or abundance of a target species emerging from the mechanistic biodiversity models—Table 2). 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.

For biodiversity models, the inclusion of evolutionary dynamics at ecological time frames remains understudied (but see Leidinger et al., 2021; Vedder et al., 2022), even though human activities can trigger evolutionary response (e.g. decrease in reproductive size in fish; Heino et al., 2015). For example, agroforestry may facilitate contact between sister *Zosterops* species, potentially leading to hybridization and evolutionary rescue of endangered endemic species (Vedder et al., 2022). Another direction is to integrate the effects of climate-driven behaviour of human agents on 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 to both? In fact, direct resource exploitation often targets demographic or growth processes in biodiversity assessments, for example, in fisheries (Melbourne-Thomas 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 avenue is to improve harmonization of complex input data (i.e. standardizing or fusing data from different sources and methodologies). Examples of successful harmonization methods can be found for occurrence or occupancy data (e.g. Bowler et al., 2019; Stewart et al., 2016). However, harmonization is less common for other, less available types of biological data, such as demographic rates, dispersal ability traits and genetic diversity. This variety of biological data is essential for validation, calibration and parameter optimization of mechanistic models, as different types of data are useful to constrain different types of integrated processes (e.g. demographic data would be useful to constrain demographic processes; Schurr et al., 2012). As we are experiencing a proliferation and expansion of different types of biological data (e.g. COMPADRE and COMADRE for demographic rates—Salguero-Gómez et al., 2015, 2016; TRY for functional data—Kattge et al., 2020), data harmonization and standard formats should be also strived for across biodiversity models. Moreover, biodiversity assessments and monitoring practices are now strongly converging to follow the Essential Biodiversity Variables (EBVs) framework (Pereira et al., 2013; Urban et al., 2021). This means that implementing models that consider input and generate output matching current trends in biological data is an important research avenue, which should also promote better integration across models. The adherence to the EBV framework might be central for empirical and modelling agendas to converge, as different EBVs match different emergent aspects of mechanistic models, such as abundance, richness and functional diversity outputs. For example, emergent species occurrence and abundance (Table 2) are already part of the EBV class 'species populations', whereas species richness is part of the EBV class 'community composition'. Other community facets typically quantified in biodiversity assessments such as functional and phylogenetic diversity are far less common as model output (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). 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., 2022).

Another generally necessary development is improving resolution at regional scales. Whereas land-use models can already generate high-resolution regional data (Figure 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). Hence, there is an urgent need to synchronize model developments between the biodiversity, land-use and climate change fields.

5 | CONCLUSIONS

Integration of land use into regional biodiversity models is much more common than the other way around. This integration can be summarized in four different approaches, with the most integrative level applying simultaneous model coupling. Consideration of climate change-induced land-use change into biodiversity models is increasing recently, with the appraisal of both direct and indirect climate change effects emerging as a key research avenue. To achieve this, important steps include concerted efforts in standardizing spatial and temporal resolution (including input and output variables), in disentangling direct and indirect effects of climate change on biodiversity, and in explicitly accounting for bidirectional feedbacks. These avenues can be navigated by matching models, plugins for format and resolution conversion, and increases in land-use forecast horizon with adequate consideration of uncertainty. Recent developments of simultaneously applying biodiversity and land-use models to understand socio-ecological systems show that such integration is achievable and can lead to valuable insights that would not emerge without bidirectional model coupling. The climate–land-use–biodiversity model integration will ultimately allow the optimization of multiple outputs, such as species number, stakeholder profits, carbon balance and temperature.

AUTHOR CONTRIBUTIONS

Juliano Sarmento Cabral, with contributions of Anja Rammig, Florian Hartig, Thomas Knoke, Wolfgang Weisser, designed the study; Juliano Sarmento Cabral, Anne Mimet, Alma Mendoza-Ponce, André Pinto da Silva, Julia Kieslinger and Johannes Oberpriller led the writing of sections; Juliano Sarmento Cabral wrote the first draft, with support of Alma Mendoza-Ponce, André Pinto da Silva at final draft and revision; Andreas Krause, Alma Mendoza-Ponce, André Pinto da Silva, Anne Lewerentz, Daniel Vedder, Jana Blechschmidt, Johannes Oberpriller, Sven Rubanschi and Stefan Fallert led the literature search, writing and editing of the tables; Daniel Vedder led Figure 1; Juliano Sarmento Cabral led Figure 2, Stefan Fallert led Figure 3; all authors commented and contributed to the written text, tables and figures at both draft and revision stages.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflict of interest.

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This manuscript does not include any data.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1: Details on literature search and model classification.