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Research article

Reviewing and benchmarking ecological modelling practices in the context of land use

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Despite habitat loss and degradation are the primary drivers of biodiversity loss, different conclusions have been drawn about the importance of land-use or land-cover (LULC) change for biodiversity. Differences may be due to the difficulty of framing a coherent model design to assess LULC effects. Recommendations have previously been identified for the design of statistical models and failing to follow them can risk misidentification of drivers, misinterpretation of predictions, overconfidence, high uncertainty, and incorrect management recommendations. We review modelling practices in statistical models assessing biodiversity responses to LULC, and investigated relationships between modelling practices and citations by scientific articles and policy documents. We benchmarked practices across model approaches, political extents, and objectives. From 346 model applications, we found that more than half of the model applications have justified ecologically-relevant predictors, have used 1 km^2 or lower LULC spatial resolution, have used fine LULC thematic resolutions, performed validation or communicated uncertainty. However, we found that the model approach and political extent were strong determinants of the misuse of modelling recommendations. Top–down models followed less frequently three recommendations out of six, compared to other model approaches. Global studies used coarser LULC thematic and spatial resolution than studies at other extents, and thus potentially underestimated the relationships between LULC and biodiversity. Global studies were however more frequently cited by both scientific studies and policy documents. Modelling recommendations are not universally applied, especially because of methodological tradeoff, technical difficulties in their applications and data requirements. However, the multiples risks associated with the misuse of modelling recommendations, particularly in large-scale modelling exercises, raise concerns on model interpretation and policy support from science, regarding the impacts of LULC on biodiversity.

Keywords: conservation policy, ecological modelling, land cover, model validation, modelling uncertainty, review, spatial resolution, thematic resolution

Introduction

Habitat loss and degradation through land-use and land-cover (LULC) change are considered the primary drivers of species extinction, with 62% of species assessed in the IUCN Red List threatened by LULC, more than any other threat (Díaz et al. 2019). Past and ongoing losses of natural habitat extent and integrity are also the primary causes of decline in other biodiversity metrics (Jaureguiberry et al. 2022), such as local species richness, abundance (Newbold et al. 2015, Chaudhary and Mooers 2018, Jung et al. 2019, Schipper et al. 2020), community intactness (Newbold et al. 2016), and several facets such as functional traits, genetic diversity, ecosystem structure and function, and community composition (IPBES 2018). Given these significant impacts on biodiversity locally and globally, LULC remains a core focus of conservation science and practice.

While observational evidence has demonstrated LULC change to be a key driver of biodiversity change, ecological modelling studies have drawn differing conclusions about its relative importance, with some studies giving it relatively lower importance than others (Davison et al. 2021, Di Cecco and Hurlbert 2022). One explanation for this is the difficulty of assessing LULC effects across different spatial extents. At small spatial scale, studies often rely on accurate ecological understanding and local data to quantify relationships between drivers and biodiversity responses (Ferrier and Guisan 2006). These studies are often motivated by scientific and practical questions of local relevance (Spake et al. 2022) rather than macro-ecological patterns and international policies (Lyet et al. 2013). Studies that investigate global biodiversity status and trends typically rely on comparatively large datasets, often combining data collected for different purposes, such as expert-based information, local studies, modelled data, structured surveys and opportunistic observations from citizen science (Alkemade et al. 2009, Newbold et al. 2015, Chaudhary and Mooers 2018, Jung et al. 2019). Thus, the scope and intention of global studies requires making some assumptions about influencing and confounding factors to generalise relationships between biodiversity and environmental predictors.

Ecological models can be categorised into three classes based on the modelling assumptions and the biodiversity measurement they use: top–down, bottom–up or sideways models (Pollock et al. 2020). Top–down models work at a multi-species level to investigate processes structuring communities in macroecological frameworks, to produce community-level metrics such as alpha, beta and gamma diversity, e.g. using species–area relationships or generalised dissimilarity models (Ferrier et al. 2007, Gaston et al. 2007, Chaudhary and Mooers 2018), mean biodiversity abundance and biodiversity intactness, e.g. using dose–response relationships (Newbold et al. 2015, Schipper et al. 2020). Conversely, bottom–up models are species-based and mainly rely on assumptions about the ecological niche of a species, for example in metapopulation or species distribution models (SDMs) (Phillips and Dudik 2008, Bernal-Escobar et al. 2015). While top–down models often lose species-level information, bottom–up models typically neglect community processes (Guisan and Rahbek 2011). Combining these two approaches in what have been defined as 'sideways models' (Pollock et al. 2020) might improve model reliability (but see Dormann et al. 2018, Zurell et al. 2018) by dealing with both species-specific and macroecological constraints (Pollock et al. 2020), for example, using joint species distribution models or spatially-explicit species assemblage modelling (SESAM) (Guisan and Rahbek 2011, Harris et al. 2018, Zurell et al. 2020a). All these approaches are applied for explaining, mapping (predictions at same spatial or temporal scales between inputs and outputs) and transferring (predictions at different spatial or temporal scales between inputs and outputs) the impacts of LULC on biodiversity (Zurell et al. 2020b). However, as every model relies on different algorithms and assumptions, users must be careful to follow recommendations to avoid uninformative or erroneous conclusions (Araújo et al. 2019, Zurell et al. 2020b, Urban et al. 2022).

Recommendations for statistical modelling approaches have been identified in multiple review and methodological papers. We summarised in Fig. 1 six of the most important recommendations relevant for statistical models assessing biodiversity responses to LULC data (Araújo et al. 2019, Zurell et al. 2020b, Jansen et al. 2022, Urban et al. 2022). Failing to follow those recommendations can risk misidentification of drivers from spurious relationships, misinterpretation of predictions, overconfidence in model results, and high uncertainty (Araújo et al. 2019, Zurell et al. 2020b, Jansen et al. 2022, Urban et al. 2022). Thus, it can result in erroneous assessment of the relative importance of LULC impacts on biodiversity and incorrect management recommendations (Zurell et al. 2022).

To avoid identifying spurious relationships and unreliable or overfitted predictions (Urban et al. 2016, Petitpierre et al. 2017, Velazco et al. 2020), ecological models must incorporate 1) ecologically-relevant knowledge when selecting environmental predictors (Fourcade et al. 2018), and should 2) explicitly consider species dispersal and habitat connectivity (e.g. filtering predictions with dispersal distance, considering colonization pathways) when transferring predictions to avoid commission errors (D'Amen et al. 2017, Zurell et al. 2018, Briscoe et al. 2019, Velazco et al. 2020; Fig. 1).

Since LULC impacts on biodiversity are scale-dependent (Bailey et al. 2007, Di Cecco and Hurlbert 2022, Roilo et al. 2022; Supporting information), both the 3) thematic and 4) spatial resolutions of LULC data should be fine enough to capture the effect of LULC at the scale at which the focal species interacts with LULC (Hartley and Kunin 2003, Liang et al. 2013, Remm 2016, Ohashi et al. 2019, Graham et al. 2019; Fig. 1). Because the LULC resolution might affect the estimation of LULC effect size, similar LULC resolutions would be needed to provide comparable results of LULC effects on biodiversity (Graham et al. 2019).

Model predictions should be 5) validated to estimate model precision and reliability (Araújo et al. 2005, Jung

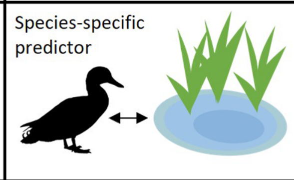
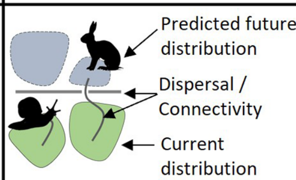
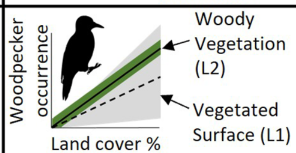
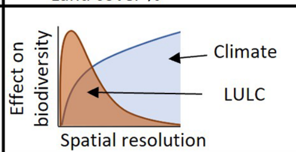
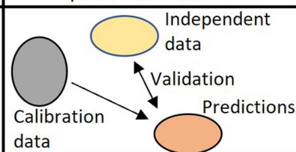
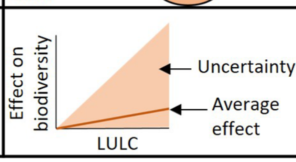
Model element	Recommendation	Illustration	Risk of not following recommendation	References
(1) Ecological knowledge	Environmental predictors are selected using biological justifications		Potentially misleading estimation of the model error; Inaccurate predictions	Fourcade *et al.* 2018 Petitpierre *et al.* 2017
(2) Dispersal / Connectivity	Transferring biodiversity while accounting for species dispersal or habitat connectivity		Overprediction of potential range expansions	Briscoe *et al.* 2019 D'Amen *et al.* 2017 Velazco *et al.* 2020 Zurell 2017
(3) LULC thematic resolution	LULC data are at fine thematic resolution		Effect sizes inaccurate; High uncertainty	Bailey *et al.* 2007 Liang *et al.* 2013 Remm 2016
(4) LULC spatial resolution	LULC data are at adequate spatial resolution		Misidentification of drivers	Di Cecco & Hurlbert 2021 Graham *et al.* 2019
(5) Validation	Predictions are validated with independent data or by cross-validation		Underestimation of the model error; Overconfidence in the predictions	Araújo *et al.* 2005 Roberts *et al.* 2017
(6) Uncertainty	Uncertainty is quantified and communicated		Overconfidence in the predictions; Misinterpretation of the predictions	Jansen *et al.* 2022 Pearson *et al.* 2006 Planque *et al.* 2011 Rocchini *et al.* 2011

Figure 1. Conceptual table with key design elements of statistical models that include land-use and land-cover (LULC), the risks of failing to follow these modelling recommendations, and key references for their importance.

2022; Fig. 1). Using independent data for model validation is among the best practices (Araújo et al. 2005), yet remains rarely conducted. Alternatively, cross-validation approaches are commonly used, and can explicitly account for dependence structures, for instance through spatial cross-validation (Robert et al. 2017, Lee-Yaw et al. 2021).

Lastly, 6) uncertainty is inherent to modelling frameworks – in input data, model design, estimation and prediction (Pearson et al. 2006, Planque et al. 2011, Rocchini et al. 2011; Fig. 1). Quantifying and communicating this uncertainty is necessary to interpret prediction confidence and data deficiency (Mouquet et al. 2015, Clare et al. 2024). Properly communicating model uncertainties facilitates scientific progress as it helps targeting further data collection and technical advancements in data analyses; it also enables more effective conservation policies to be designed, for example by decreasing the risk of misidentifying conservation priorities (Jansen et al. 2022).

Recently, several reviews investigate the extent to which modelling recommendations are followed for specific modelling approaches, such as SDMs (Araújo et al. 2019, Velazco et al. 2020, Lee-Yaw et al. 2021), mechanistic models, metapopulation models, species-area relationship or dissimilarity models (Urban et al. 2022, Zurell et al. 2022). Recent reviews identified taxonomic, geographic and predictor variable biases in studies that modelled biodiversity responses to LULC (Davison et al. 2021, Dullinger et al. 2021). However, despite widespread applications of statistical models using LULC data, the extent to which modelling recommendations are followed has not yet been systematically studied.

Here, we benchmarked modelling practices in statistical models using LULC on biodiversity data, regarding predictor selection, species dispersal and habitat connectivity, thematic and spatial resolution of LULC data, uncertainty and model validation (Fig. 1). Considering that modelling approaches have drawn differing conclusions about LULC relative importance on biodiversity, we question whether modelling approaches also differ in the use of modelling recommendations and in their influence of science and policy. We contrast modelling practices across model approaches (top–down, bottom–up, sideways), political extent (sub-national, national, multi-national, global; and spatial extent) and objectives (explaining, mapping, transferring), and assess potential impacts on informing scientific knowledge and conservation policies using the number of citations in scientific literature and policy documents. Overall, this review provides a benchmark for how LULC impacts on biodiversity have been modelled to date and highlights potential risks for model interpretation and policy design.

Methods

Data collection

We conducted a systematic review of statistical models that made use of LULC data following a PRISMA protocol (Moher et al. 2009; Supporting information), to document modelling practices (Fig. 1). We defined statistical models as model that establishes links between ecological data and external drivers (see below for a definition of model types and search terms). We performed a search query of titles and keywords on Scopus (www.scopus.com) from international scientific journals in English. The query has been done on 1 June 2021, without restriction on the publication year. We expected to capture a consistent pattern of modelling practices and citations by scientific or policy papers from the scientific papers returned by the query. We queried model names commonly used in applied biodiversity conservation and statistical modelling approaches (Pollock et al. 2020), such as single SDM, ensemble SDM, species area relationship, dissimilarity and occupancy models (Supporting information). Dynamic models, such as agent-based or metapopulation models, were included in the query, but not retain in the analysis because of a lack of representativity (Supporting information). We focused on taxonomic terrestrial biodiversity and on studies that used LULC data in a spatially-explicit framework. The search query returned a total of 7532 published studies (Fig. 2, Supporting information).

We first shortlisted the studies by screening the abstracts to select studies that fulfilled the following criteria: 1) made use

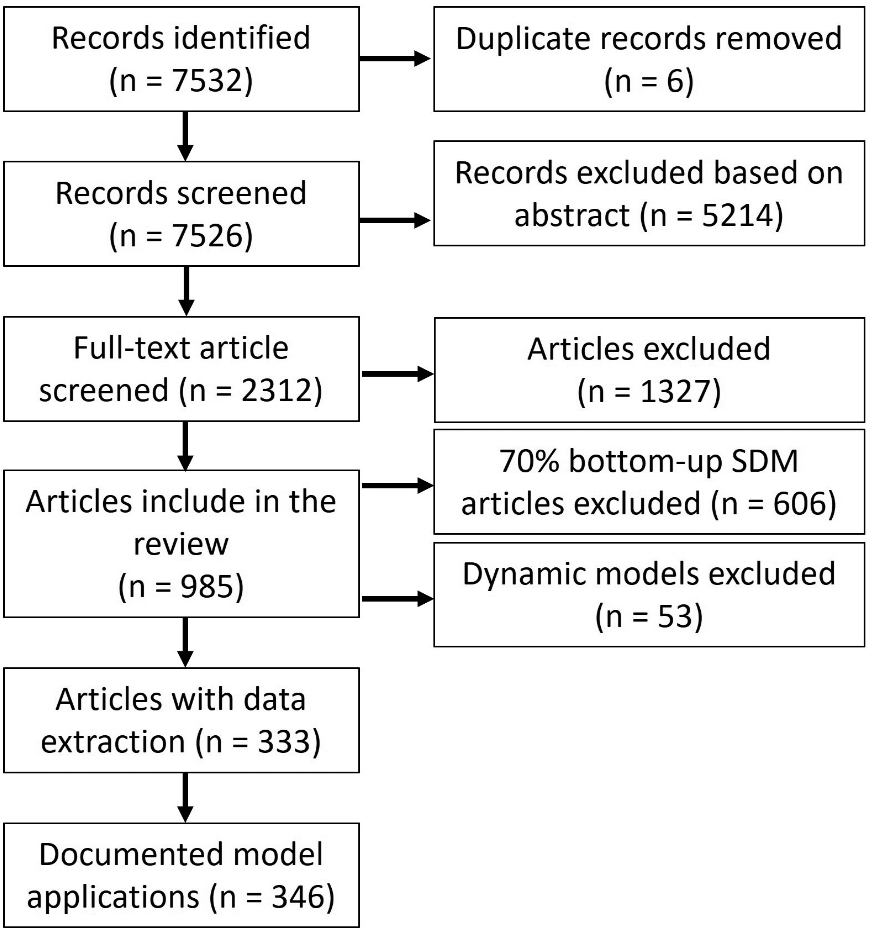


Figure 2. Flowchart of the review process from the scientific articles returned by the query to the data collection on model applications.

of a spatially-explicit modelling framework; 2) focussed on terrestrial biodiversity at the species, community or population level (e.g. species occurrence, abundance, richness); and 3) used a LULC layer as an independent variable in the model.

The abstract screening was performed on CADIMA (www.cadima.info), which allows easy study allocation to several reviewers (Kohl et al. 2018). Studies were selected if the reviewer judged all criteria as fulfilled or uncertain. This abstract screening retained a total of 2312 published studies. Full-text screening was then performed on the studies passing the abstract screening, using the same criteria. This full text screening identified 985 studies relevant to our review. Inter-reviewer reliability of the selection process was assessed by five reviewers evaluating 100 abstracts and 50 full-texts: reliability was moderate for abstract screening (Fleiss Kappa = 0.51, $p < 0.001$) and substantial for full text (Fleiss Kappa = 0.62, $p < 0.001$). Among the diversity of SDMs applications, bottom–up models were very abundant. Thus, to decrease the data collection time, we restricted data collection of bottom–up SDM ('bSDM' hereafter for simplicity, Table 1) on a sub-selection of model applications. To do so, we first classified all SDM applications as sideways (e.g. joint-SDM) or bottom–up (e.g. single-SDM, ensemble-SDM). Second, among the 835 studies identified as using bSDM applications, we randomly selected 225 studies (about 30%) for data collection (Fig. 2). We conducted a sensitivity analysis to ensure the representativity of the sub-sampling (Supporting information). Thus, data collection was finally done on 333 studies, documenting 346 model applications relevant to our review (13 studies applied more than one model).

Data collection aimed at documenting the model approach, political and spatial extent, model objective, modelling practices, and number of citations in scientific articles and policy documents (Table 1). Model approaches were defined as top–down, bottom–up or sideways, after Pollock et al. (2020). Bottom–up models were separated in two categories, bottom–up not SDM for which we included all applications in our analyses and bSDM for which only 30% of the model applications where reviewed in full and analyses. This split was necessary to avoid biasing the conclusions about bottom–up models due to an imbalanced representations of a specific model class. Political extent was defined at administrative units, being sub-national, national, multi-national or global and spatial extent was numerically documented by collecting study's surface areas ($\log(km^2)$). The objective of the model was defined as what the model had been used for: explaining, mapping, transferring (Zurell et al. 2020b; Table 1).

We documented modelling practices with a binary approach (yes/no) as follows: 1) environmental predictors are selected using ecological justification (hereafter, 'ecological knowledge'), 2) transferring future biodiversity changes are done while accounting for either species dispersal or habitat connectivity (hereafter, 'dispersal/connectivity'), 3) LULC data use thematic resolution that distinguished major LULC classes (Bailey et al. 2007, Liang et al. 2013), i.e. being equal to or larger than Level 2 (nine categories) of the Sentinel-2 Global Land Cover classification (Di-Gregorio 2005) (hereafter, 'thematic resolution'), 4) LULC data use a spatial resolution lower equal to 1 km^2 (hereafter, 'spatial resolution'; Supporting information), 5) model predictions are validated by using independent data, spatial cross-validation or cross-validation (hereafter, 'validation'), and 6) uncertainty quantified for either algorithms, scenarios or parameters (hereafter, 'uncertainty').

To our knowledge, universal threshold values of fine LULC spatial and thematic resolutions do not, and should not, exist and can be species-specific or context dependant. The appropriate spatial resolution is specific to the species and landscape under study. The thresholds we used for LULC spatial (1 km^2) and thematic (nine categories) are based on a general assumption that such resolution is small enough to capture a reasonable amount of spatial variability in the biodiversity variables (see also the Supporting information for sensitivity analysis on spatial resolution). We do not consider these thresholds as appropriate in all cases and will depend in particular on the extent of the study area. Also, other modelling practices can affect the estimations of LULC effects on biodiversity, but were not reviewed in our study, such as error propagation, biotic interactions, interaction between predictors, auto-correlation structures and study designs (De Palma et al. 2018).

Table 1. Model characteristics collected between model applications.

Characteristics	Categories	Description
Modelling approach	Top–down	Macroecological models such as species-area relationship, generalized dissimilarity model and dose response model
	Bottom–up SDM (bSDM)	Species-specific models such as single SDM, stacked SDM and ensemble SDM
	Bottom–up not SDM	Species-specific models such as occupancy and N-mixture models
	Sideways	Combination of top–down and bottom–up approaches such as Spatially explicit species assemblage modelling (SESAM), joint SDM and hybrid SDM coupled with assembly rule
Political extent	Global	All continents, except Antarctica
	Multi-national	More than one country
	National	The entirety of one country
	Sub-national	Any extent smaller than national
Objective	Explaining	Assess relationships between species distributions and environmental predictors
	Mapping	Same spatial or temporal scales between inputs and outputs
	Transferring	Different spatial or temporal scales between inputs and outputs

Finally, for each study we collected information on the citations in scientific articles and public policy documents. We recorded the number of citations within scientific articles returned by Scopus (www.scopus.com) (out of the 346 reviewed model applications, 86% of the model applications have been cited more than once, see also the Supporting information). Because studies are rarely cited several times by policy documents, we instead recorded the presence or absence of a citation in policy documents returned by Altmetric (www.altmetric.com) or PlumX (www.plumanalytics.com) (note that Altmetric or Plum Analytic reports were not available for 84 model applications).

Statistical analyses and visualisation

We performed three distinctive analyses to investigate prevalence of modelling practices across modelling approaches, extents and objectives (Table 1). First, we used a Sankey diagram to explore how the choice of modelling approach (top–down, bSDM, bottom–up not SDM, sideways) was linked to the political extent (sub-national to global) and the model objectives (explaining, mapping, transferring). Second, we assessed differences in the use of modelling practices (Fig. 1). We used generalised linear models (binomial error distribution) to investigate differences in the use of each practice between model approaches, political extents and objectives. To do so, we fitted one model per modelling practice (coded as use = 1; non-use = 0) and variable of interest (model approaches, political extent, spatial extent and objectives).

Finally, we evaluated which studies were the most cited in scientific articles and policy documents. We used generalised additive models to compare the number of citations by scientific articles (Poisson error distribution) and the presence of citations by policy documents (binomial error distribution) between model approaches, political extents, spatial extent and objectives. Publication year was included as a smooth fixed effect (i.e. basis penalty smoothing; Wood 2015) to ensure a fair comparison between models. The spatial extent was considered with a smooth effect to account for non-linear relationships between study extents and citations. We conducted a sensitivity analysis to ensure that pseudo-replication caused by several model applications within one study did not affect our results. For this, we ran the models for 100 iterations using one model application per article, randomly selecting one model application per article each time, and checked the consistency of the effects.

All analyses were conducted in R ver. 4.1.2 (www.r-project.org), using R packages 'stats' (ver. 4.4.0) and 'mgcv' (Wood 2015), checking model residuals with 'DHARMa' (Hartig 2020), and with visualisation done using 'ggplot2' (Wickham 2011) and 'ggalluvial' (Brunson and Read 2018).

Results

From the 346 statistical model applications using LULC data, bSDM were the most abundant (n = 229), even if only 30% of this model applications have been reviewed (Methods). Bottom–up not SDM approaches were found in 38 model applications, while the remaining models have used top–down (n = 62) and sideways (n = 17) approaches (Fig. 3). Modelling approaches strongly differed between the political extents. Top–down approaches were mostly applied at global extent for explaining or transferring, or at sub-national extent for mapping or transferring (Fig. 3a). Conversely, both bottom–up not SDM and bSDM approaches were used in majority at sub-national extent, for explaining, mapping or transferring (Fig. 3a–b). They have been used less frequently at national and multinational extents for mapping and transferring biodiversity, and not often at global scale. Sideways approaches were rarely used, but applications were mostly done at sub-national and national extents for explaining, mapping or transferring biodiversity (Fig. 3a).

We presented the overall statistics for the model applications with full data collection (bottom–up not SDM, sideways and top–down) followed by the statistics based on the subsampled bSDM applications. Going through the modelling practices among all the reviewed model applications, ecological knowledge was used in 49 and 69% of the models to select the environmental predictors. Dispersal/connectivity was considered in 23 and 39% of the models transferring future biodiversity changes. LULC spatial resolution was lower or equal to 1 km² in 45 and 66% of the models. LULC thematic resolution was lower or equal to the Level 2 of the Sentinel-2 Global Land Cover classification in 54 and 59% of the models. Model validation was performed in 39 and 78% of the models. In addition, in case of validation, model predictions were mostly validated by cross-validation, and rarely validated against independent data or by using spatial cross-validation (Table 2). Uncertainty was communicated to some degree in 67 and 54% of the models. The number of citations by scientific articles was on average 63 and 19 (8 and 3 citations per year on average), ranging from 0 to 1302 and 0 to 157, with only 19 and 13% of the models having been cited by a policy document.

Modelling practices differed among model approaches and extents (Fig. 4; see the Supporting information for full statistics). We found that studies using top–down approaches followed fewer modelling recommendations than the others (Fig. 4a). Top–down modelling studies used ecological knowledge in less than 20% of their applications, and LULC spatial resolution was above 1 km² in less than 40% of their applications. In contrast, bSDM model applications more frequently included ecological knowledge ($\beta \pm SE = 2.01 \pm 0.34$, $p < 0.001$), fine LULC spatial resolution ($\beta = 1.19 \pm 0.30$, $p < 0.001$) and model validation ($\beta = 2.48 \pm 0.34$, $p < 0.001$) than top–down model applications. Similarly, bottom–up not SDM model applications more frequently included ecological knowledge ($\beta = 2.13 \pm 0.47$, $p < 0.001$) than top–down model applications. Predictions have been validated in only 23% of studies top–down approaches (n = 62), while it has been done for 100% of the sideways approaches, both by cross-validation and spatial cross-validation (n = 17; Table 2). The probability to use dispersal/connectivity information,

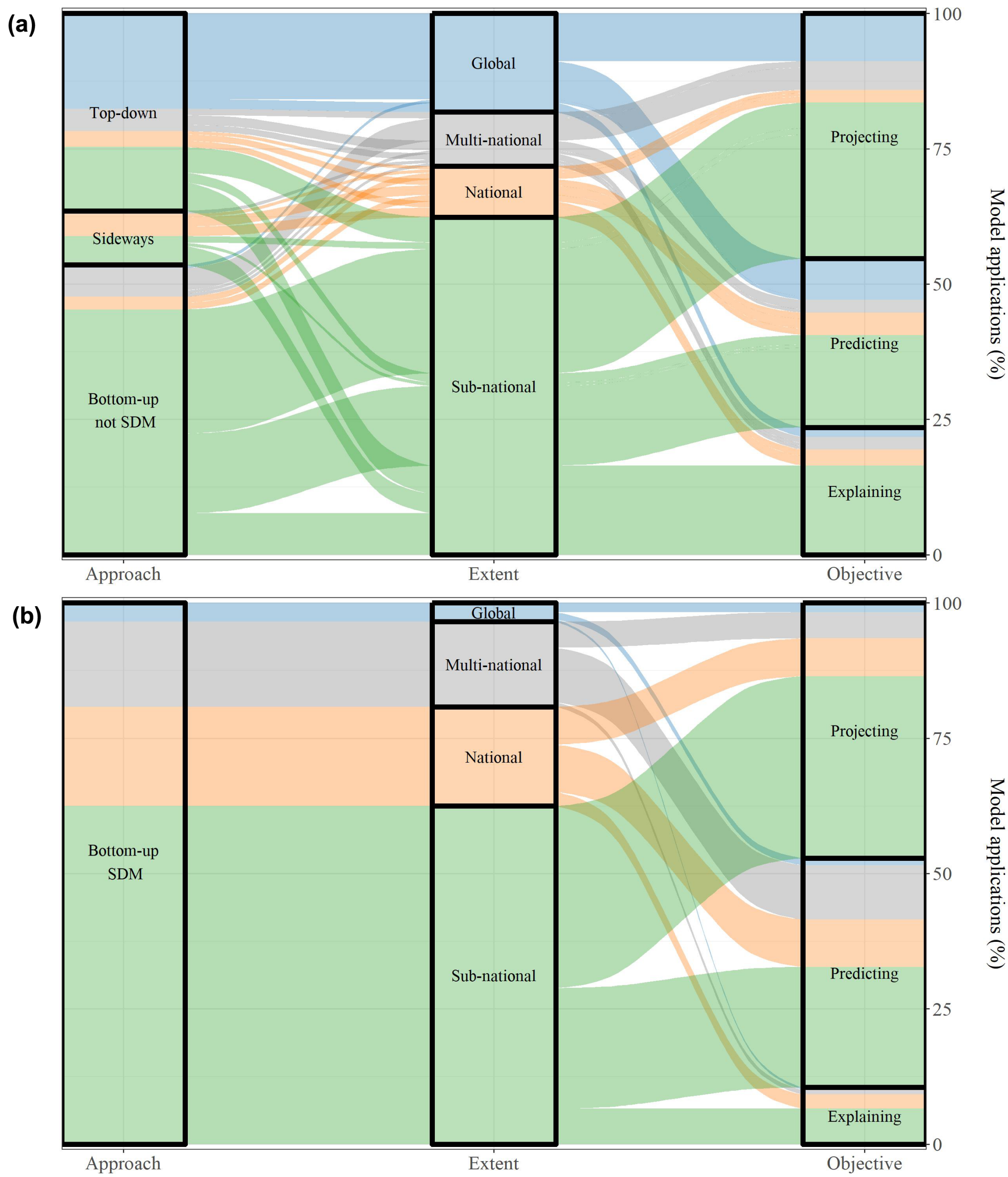


Figure 3. Sankey diagram of the model approach, political extent and objective for (a) top–down, sideways and bottom–up not SDM, and (b), bottom–up SDM (bSDM) model applications. Colours correspond to the political extent of the model applications (dark blue, global; grey, multi-national; orange, national; green, sub-national).

fine LULC thematic or to present uncertainty were not significantly different between model approaches (Fig. 4a).

We observed a clear gradient of modelling practices according to the political (Fig. 4b–c) and spatial extents (Fig. 5a–b). For all model approaches without bSDM, compared to sub-national studies, global studies were less likely to use ecological knowledge ($\beta = -2.30 \pm 0.56$, $p < 0.001$), fine LULC thematic ($\beta = -1.39 \pm 0.48$, $p = 0.019$) and fine LULC spatial resolution ($\beta = -1.32 \pm 0.50$, $p = 0.043$; Fig. 4b). A similar pattern was observed for bSDM model applications, where global compared to sub-national studies were less likely to use ecological knowledge ($\beta = -2.19 \pm 0.84$, $p = 0.045$) and fine LULC spatial resolution ($\beta = -3.15 \pm 1.09$, $p = 0.020$; Fig. 4c). Uncertainty was equally communicated between different extents and used in around 50–80% of model applications ($p > 0.05$; Supporting information). Considering all modelling approaches without bSDM, the spatial extent ($\log(km^2)$) was negatively correlated to the use

Table 2. Percentage of model applications for which predictions were validated by using cross-validation, spatial cross-validation, independent data or were not validated.

Models	Model applications	Cross-validation (%)	Spatial cross-validation (%)	Independent data (%)	Not validated (%)
All	Bottom–up not SDM	26.3	0.0	10.5	63.2
All	bSDM	65.5	1.3	10.9	22.3
All	Sideways	76.5	23.5	0.0	0.0
All	Top–down	19.4	0.0	3.2	77.4
without bSDM	Explaining	29.4	5.9	0.0	64.7
without bSDM	Mapping	31.8	2.3	9.1	56.8
without bSDM	Transferring	28.2	2.6	5.1	64.1
bSDM	Explaining	70.8	8.3	0.0	20.9
bSDM	Mapping	53.7	0.9	18.5	26.9
bSDM	Transferring	77.3	0.0	5.2	17.5
without bSDM	Global	20.0	0.0	6.7	73.3
without bSDM	Multi-national	25.0	0.0	8.3	66.7
without bSDM	National	40.0	20.0	6.7	33.3
without bSDM	Sub-national	33.3	1.7	3.3	61.7
bSDM	Global	62.5	12.5	12.5	12.5
bSDM	Multi-national	66.7	0.0	8.3	25.0
bSDM	National	71.4	0.0	11.9	16.7
bSDM	Sub-national	63.6	1.4	11.2	23.8

of ecological knowledge ($\beta = -0.21 \pm 0.05$, $p < 0.001$), and thematic resolution ($\beta = -0.09 \pm 0.04$, $p = 0.032$; Fig. 5a). Considering only bSDM model applications, the spatial extent was negatively correlated to the use of ecological knowledge ($\beta = -0.13 \pm 0.04$, $p = 0.002$) and LULC spatial resolution ($\beta = -0.15 \pm 0.04$, $p < 0.001$; Fig. 5b). The other modelling practices were not significantly related to the spatial extent (Fig. 5a–b).

Modelling practices were fairly similar between model objectives (Fig. 4d–e, Supporting information), suggesting that conversely to model approach or extent, the objective of the model was not a strong determinant of modelling practices. The only two significant differences were; uncertainty was more reported in model used for explaining than mapping ($\beta = 1.36 \pm 0.52$, $p = 0.033$, modelling approaches without bSDM) and ecological knowledge was more frequent in model used for mapping than models used for transferring ($\beta = 0.90 \pm 0.31$, $p = 0.010$, bSDM).

Across all model approaches, both the citation in scientific articles and the probability to be cited by policy document increased non-linearly with the political extent (Fig. 5c–f; see the Supporting information for full statistics). Global models, and models designed to transfer biodiversity, were cited by scientific articles and policy documents significantly more often than other model applications within bSDM model application or all other approaches (Fig. 6c–e; $p < 0.001$). Top–down approaches were cited on average five times more by scientific articles than either approaches of bottom–up approaches ($p < 0.001$). However, citation by policy documents did not differ between type of model approaches except for sideways models, which were never cited (Fig. 6, Supporting information). Models applied for explaining were cited less often by scientific articles than models used for transferring both for all model approaches without bSDM (Fig. 6g; $\beta = 1.00 \pm 0.03$, $p < 0.001$) and for bSDM (Fig. 6i; $\beta = 0.15 \pm 0.05$, $p = 0.002$). Citation in policy documents was more common for transferring than explaining biodiversity changes in all model approaches without bSDM (Fig. 6h; $\beta = 4.90 \pm 2.02$, $p = 0.02$). These results were robust to the potential pseudo-replication effect when some studies applied more than one model (Supporting information).

Discussion

In this study, we benchmarked modelling practices in statistical models using land-use or land-cover (LULC) on biodiversity data to investigate whether the most influential model applications for science and policy followed modelling recommendations (Fig. 1). We found that large-scale studies tended to use coarser LULC data and ignore modelling recommendations more often than sub-national studies, but received the most attention from scientific studies and policy documents. Sideways models, hybrids between bottom–up and top–down approaches, tend to adopt modelling recommendations more often, but are still under-used in modelling studies and subsequently overlooked by policy documents.

Controlling for publication age, global studies received large numbers of citations both in scientific articles and policy documents (Fig. 6), despite the majority having methodological inadequacies regarding ecological knowledge and validation of the predictions (Fig. 5) according to modelling recommendations presented Fig. 1. Both thematic and spatial LULC resolution were often above the thresholds used in our study. This does not mean that thematic and spatial LULC resolutions in global studies were inadequate to capture the effect of LULC. However, it suggests that the relationships between biodiversity variables and LULC might be captured differently at global compare to other political extent. While LULC is one of the leading drivers of past and current declines

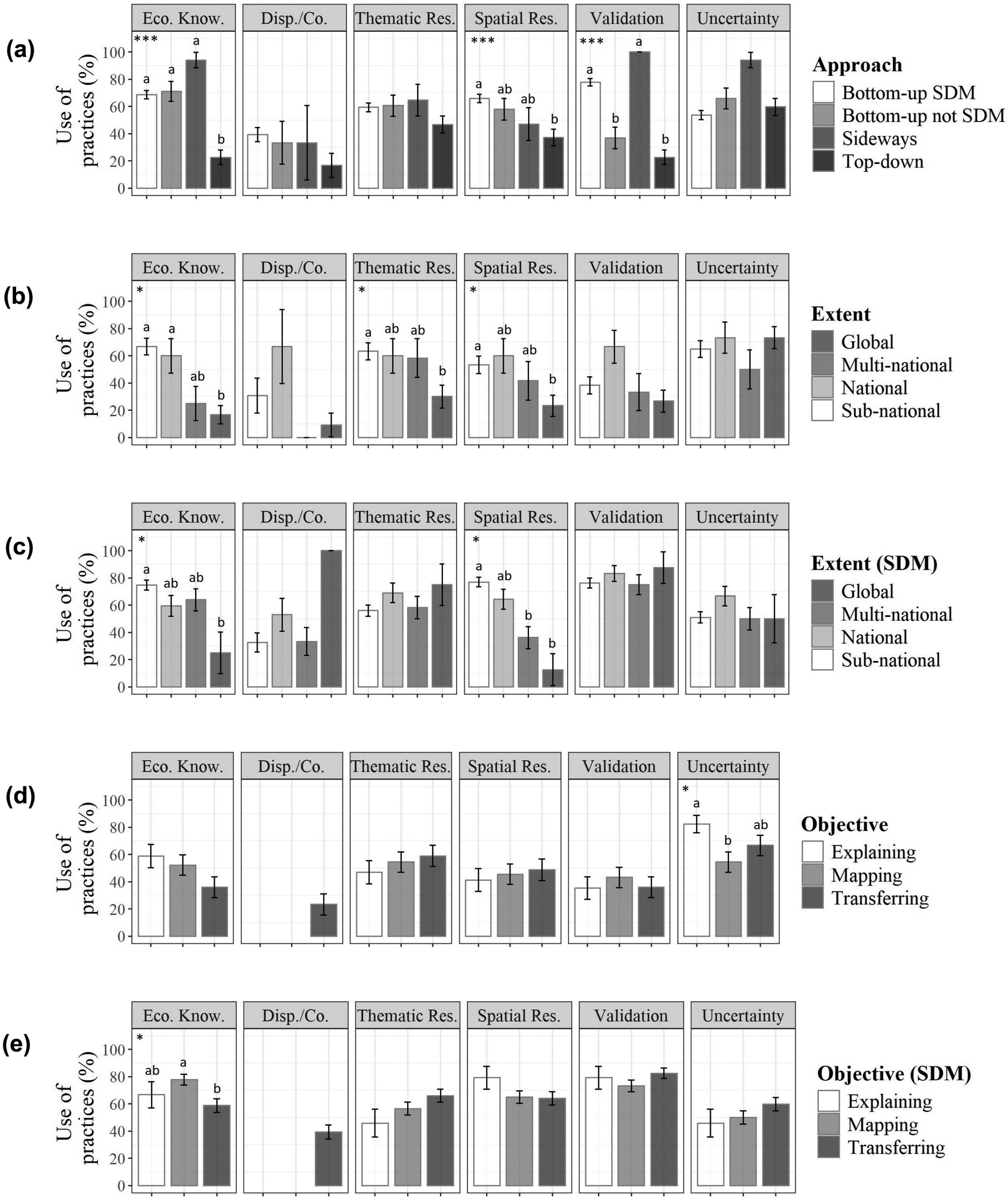


Figure 4. Barplots representing the percentage (± SE) of model applications using the modelling practices per (a) model approach, (b) political extent for models excluding bottom–up SDM, (c) only bottom–up SDM, (d) objective for models excluding bottom–up SDM and (e) objective only for bottom–up SDM, among 346 reviewed model applications. Significant differences are notified by different letters between barplots, with asterisks corresponding to the p-value: $p < 0.05$*, $p < 0.01$**, $p < 0.001$*** (see the Supporting information for full statistics).

in biodiversity, some model projections suggest that the relative role of LULC in driving biodiversity change is diminishing over the 21st century (Bellard et al. 2012). However, is it possible that improper LULC thematic and spatial resolutions of earlier modelling studies have diminished the effect-size of LULC and have impacted this conclusion. We caution that using inadequate resolutions might lead to spurious results underestimating the effect of LULC on biodiversity (Di Cecco and Hurlbert 2022, Roilo et al. 2022).

Between 20 and 50% of the model applications used for transferring future biodiversity changes did not use species dispersal or habitat connectivity (Fig. 5). This risks transferring species distributions in potentially unreachable areas (Cabral et al. 2017), and so potentially misallocating

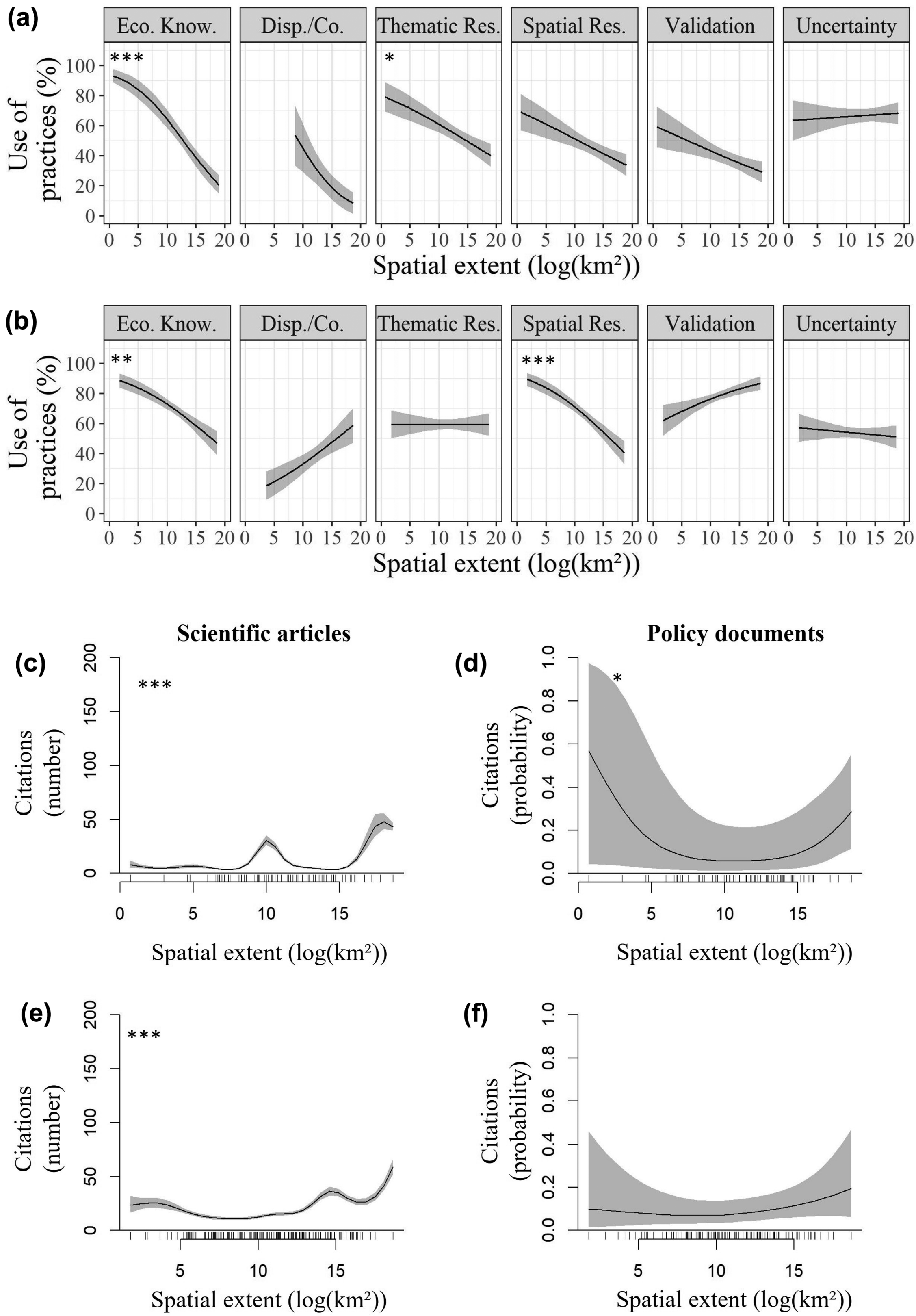


Figure 5. Model predictions (± 95% CI) of the relationship between the spatial extent of the reviewed studies; for top–down, sideway and bottom–up not SDM model applications (a) the use of modelling practices, (c) the number of citations in scientific articles and (d) the probability of citation by policy document; for bSDM model applications (b) the use of modelling practices, (e) the number of citations in scientific articles and (f) the probability of citation by policy document. Significant differences are notified by asterisks corresponding to the p-value ($p < 0.05^{*}$, $p < 0.001^{***}$).

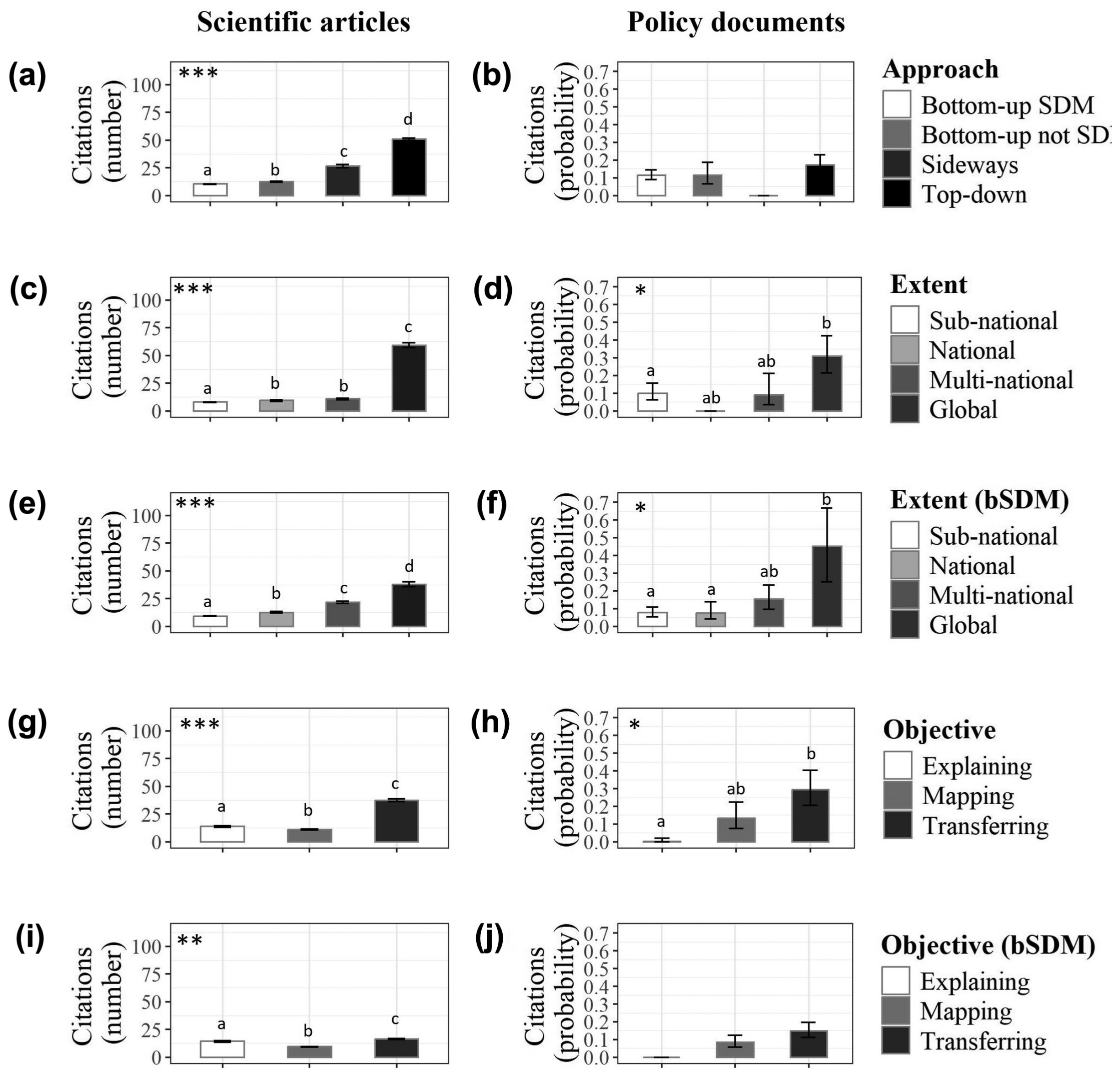


Figure 6. Barplots representing the citations (± SE) in scientific articles (predicted number of citations) and policy documents (predicted probability to be cited) per (a, b) model approach, (c, d) extent for top–down, sideways and bottom–up not SDM, (e, f) extent for bottom–up SDM, (g, h) objective for top–down, sideways and bottom–up not SDM and (i, j) extent for bottom–up SDM (bSDM). Predictions are controlled by the year of publication (methods). Significant differences are notified by different letters between barplots inside a facet, with asterisks corresponding to the p-value: $p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$ (see the Supporting information for details).

conservation efforts and funding. This issue is prevalent in top–down approaches (Cabral et al. 2017). For instance, the species–area relationship (SAR) is a common top–down approach suffering important limitations when coming to dispersal and connectivity (Fattorini et al. 2021), in which the dependence between species richness and area is modulated by a unique constant value accounting for dispersal abilities and habitat connectivity. Methodological improvements have been proposed, such as the countryside SAR (Martins and Pereira 2017) and the triphasic SAR (Chisholm et al. 2018), integrating to the analytical calculation either the relationships between species and habitats or clearing patterns of habitat fragmentation related to species dispersal and speciation rate, respectively. Producing a diverging cluster of SAR from a range of plausible dispersal and scale dependent values can also be valuable for risk assessment and decision making (Hovestadt and Poethke 2005, Drakare et al. 2006). In bottom–up models, although single or ensemble SDMs are often not flexible enough to account for species dispersal or habitat connectivity, one option would be to couple the SDM with a separate dispersal model (Visconti et al. 2016, Zurell et al. 2016, Seaborn et al. 2020), or constrain SDM predictions based on species' maximal dispersal capacities (Engler and Guissan 2009), geographic barriers (Lessmann et al. 2016) or to implement cost distance filters (Gherghel et al. 2020) (reviewed by Zurell 2017, Velazco et al. 2020).

Statistical models aim at explaining, mapping or transferring biodiversity patterns, yet we found that most modelling approaches have not systematically considered prior ecological knowledge (e.g. key parameters or known relationships between covariates and biodiversity measures), particularly in top–down and global models (Fig. 5). Macroecological frameworks addressing multi-species changes in occurrence or distribution face the difficulty of choosing predictors that are relevant to all modelled species, often ignoring species-specific relevance and trusting in the estimating algorithm to determine correct links. Similarly, models using species richness or beta diversity as input and outputs (Biber et al. 2020), can hardly consider individual species requirements, habitat preferences or affinities.

However, sideways models can return species richness or beta diversity as macroecological outputs based on species-specific settings (Pollock et al. 2020). For example, joint-SDMs such as the hierarchical modelling of species communities framework described in Ovaskainen et al. (2017) can be used in a spatially-explicit design to model spatio-temporal changes of multiple species distributions, considering functional traits and phylogeny to assess species co-occurrence patterns. Hybrid models like SESAM (Guisan and Rahbek 2011) can provide unified frameworks using a top–down approach to constrain bottom–up outputs considering biological processes like species dispersal or habitat connectivity. However, sideways approaches have their own limitations, sometimes resulting in lower performance than other approaches (Zurell et al. 2018). For instance, joint-SDMs may assume a correlative nature of species interaction patterns from residual correlation matrix, with the risk of assessing abiotic and not biotic interactions (Poggiato et al. 2021). Thus, these models might not be modelling species interactions because of the unintended impacts of shared unmeasured environmental variation. Further developments and investigations and would be needed (Pollock et al. 2020). In our study, sideways approaches were rarely used, but their methodological flexibility to incorporate modelling recommendations mean that they represent a potential improvement to both bottom–up and top–down approaches and should be considered more often to model biodiversity response to LULC.

Independent data have been rarely used to validate model predictions (Table 2), despite being the gold standard in model validation (Newbold et al. 2010, Jung et al. 2017, Jung 2022). Model performance can be wrongly assessed, i.e., having an artificially low predictive error, when data used for calibration and validation share dependence structures (Roberts et al. 2017, Lee-Yaw et al. 2021). The number and diversity of ecological datasets have increased globally (e.g. thousands of records available from the GBIF), making it substantially easier to obtain systematically independent data than previously (Araújo et al. 2005). This is particularly the case for taxa like birds, mammals, plants and charismatic insect groups. For example, bird occurrences in Europe are documented over the Pan-European Common Bird Monitoring Scheme, eBird, iNaturalist, Euro Bird Portal, Important Bird Areas, EU Birds Directive Article 12 reports, and several national to continental atlases. Ongoing initiatives to improve the visibility and the accessibility of ecological data (e.g. GEO BON, GBIF), including systematic open access of data used in publications, should facilitate future progress to validate predictions with independent data.

While our review highlights important concerns on global and top–down models using LULC, global perspectives are nonetheless necessary, especially to develop international conservation policy and regularly raise awareness of biodiversity issues (Jetz et al. 2019, Santini et al. 2021, Chaplin-Kramer et al. 2022). Macroecological studies are often criticised for their lack of applicability at local scale, but they still contribute significantly to a better understanding of the ecological processes unreachable by local studies (Santini et al. 2021).

Considering the speed of the technical progresses in modelling (Sillero et al. 2023), and the absence of evidence for increased uptake of modelling recommendations over time (Araújo et al. 2019), embedding recommendations within ecological research might also necessitate knowledge transfer and capacity building to researchers. As shown in this review, modelling practices minimizing the risks of overconfidence, overprediction, effect size inaccuracy or high uncertainty can be used in all reviewed categories of model approaches, political extent, and objectives (Fig. 4). Thus, the lack of systematic use of modelling recommendations might depend more on the study design and methodological choices than in the feasibility of following recommendations in a given study, irrespective of their aims, thematic, geographic and taxonomic scope. User-friendly methodological frameworks can promote the use of modelling recommendations (Zurell et al. 2022) such as the successful development of Maxent (Phillips and Dudik 2008, Elith et al. 2011) and BIOMOD (Thuiller et al. 2003, 2009) to cross-validate predictions as standard and to return model uncertainties from an ensemble of algorithms, respectively. Further software development should be designed to improve the use of modelling recommendations (e.g. from no validation toward cross-validation, spatial block cross-validation and independent validation) and simplify their adoption to software users. For example, methodological developments can include options to consider species dispersal and habitat connectivity when forecasting species distribution change (Urban et al. 2022, Jung 2023). In addition to user-friendly implementations of modelling recommendations in standard methodological workflows, capacity building is needed to transfer modelling knowledge to ecologists. University teaching, workshops and online training offer several ways to improve awareness on statistical modelling.

Improving the availability and the use of LULC data at high spatial and thematic resolution is required, but it can be challenged by practical issues. For instance, getting LULC data at fine thematic and spatial resolution might require funding or collaborations with data owners. Downscaling LULC data risks inflation of thematic uncertainty and requires attention to LULC quality prior to biodiversity model conception. In addition, running models and cross-validating predictions at very fine spatial resolution at global extent can be computationally intensive, requiring access to a high-performance-computer or limiting model complexity. Global multi-species models ideally require ecological knowledge for thousands of species across their entire distribution range implying that extra competences from naturalists or integration of data from broad-scale databases such as the habitat and ecology information collected by the IUCN are necessary (Santini et al. 2021, www.iucnredlist.org). Collaborations between statisticians, LULC modelers, ecologists and naturalists can help overcome modelling challenges to improve both biodiversity model quality and transfer to conservation policies (Leclère et al. 2020). Similarly, there is also a need to further advance statistical models to being able to integrate better ecological knowledge on species biology and testing their use across scales (Urban et al. 2022).

We urge ecological modelers to better integrate local ecological knowledge and fine LULC data resolution to minimize ontological differences between empirical observations and model predictions and improve the quality of statistical model for scientific and practical applications.

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Data availability statement

Data are available from the Zenodo repository: https://doi.org/10.5281/zenodo.15489650 (Gaget et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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