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Broadening applications of stochastic patch occupancy models over three decades

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Abstract

Aim: Stochastic patch occupancy models (SPOMs) are a type of spatial population simulation. They are arguably well-suited to guide conservation in human-altered landscapes, but their appropriateness for a wide range of species and landscape types has often been questioned. Here, we provide an overview of how SPOM research has expanded over the last three decades and discuss the untapped potential for these models to inform current conservation strategies.

Location: Worldwide.

Methods: We carried out a systematic review of studies that have fitted SPOMs to real species and landscapes. We assessed temporal trends in SPOMs' use in conservation and management studies, their taxonomic and geographic coverage, and the attributes of studied landscapes. We quantitatively and qualitatively evaluated whether the authors' modelling choices reflected the perceived advantages and disadvantages of SPOMs.

Results: The proportion of SPOMs used to answer conservation questions has increased over time. Questions of where, when and how to conserve have all been addressed, sometimes considering additional aspects such as cost-effectiveness and climate change. Taxonomic diversity coverage has increased over time, and SPOMs have been used in landscapes with a higher proportion of suitable habitat. They have, however, been predominantly applied in temperate biomes. Few studies have explored parameter extrapolation in taxonomically and ecologically related species with mixed results.

Main Conclusions: Over the past three decades, authors have exploited the simplicity and flexibility of SPOMs to answer a broad range of questions with practical implications. The use of SPOMs in less fragmented landscapes, and for an increasing range of taxa, suggests that the strictest definitions of their applicability can be challenged. Stochastic patch occupancy models have untapped potential for informing conservation under climate change. Given the urgent need to plan for large numbers of species with limited data for fitting, SPOMs could better fulfil their potential to guide conservation if parameters could be extrapolated to data-deficient landscapes and species.

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KEYWORDS

colonisation, conservation and management, extinction, habitat fragmentation, landscape dynamics, metapopulation modelling, stochastic patch occupancy models

1 | INTRODUCTION

The effectiveness of conservation planning depends greatly on our ability to predict the effects of land use and climate change (Schulte to Bühne et al., 2021). Simulation modelling is a key way of understanding the impacts of these drivers on natural systems and thus has been widely used to inform conservation and management decisions (e.g., Che-Castaldo & Neel, 2016; Larson et al., 2004; Wasserman et al., 2012). Stochastic patch occupancy models (SPOMs) are a type of spatial simulation model, specifically, a type of metapopulation model (Hanski, 1992, 1994). They have been used to understand the effects of habitat fragmentation and loss on the persistence of species, and their potential for influencing conservation strategies was recognised early (Hanski & Gilpin, 1991). Here, we examine how their applications have evolved over the past three decades and discuss their potential for predicting the effects of land use and climate change on a wide range of taxa and landscapes.

A broad definition of a metapopulation can include any 'population of populations' that are distributed patchily across space, but the term was originally applied to systems in which sub-populations experience local extinctions and recolonizations, and that exchange of dispersers ('connectivity') across the hostile 'matrix' between suitable habitat patches maintains the overall viability of the system (Hanski & Gilpin, 1991; Levins, 1969). As one of the earliest types of metapopulation model, SPOMs track the occupancy state (i.e., occupied or unoccupied) of each patch, and use a per-patch probability of colonisation and extinction to simulate what may happen over time. One feature of metapopulations driven by extinction-colonisation dynamics is that not all suitable habitat patches are occupied at any given time, and it is this feature that allows us to estimate the drivers of patch occupancy. In many SPOMs, the area and isolation of the habitat patches control the extinction and colonisation probabilities, although a greater variety of factors can sometimes be included. The size of each sub-population can be implied in a SPOM—for example, in the way that extinction risk scales with patch area—but a SPOM does not explicitly simulate the sub-population demographics. Stochastic patch occupancy models are not to be confused with the similarly named 'occupancy models', used since the early 2000s to statistically infer the past occupancy of under-sampled areas (e.g., MacKenzie et al., 2003); note that the SPOMs we consider here are all informed by field observations of patch occupancy that are assumed to be accurate.

Several key attributes of SPOMs make them particularly relevant for answering conservation questions. First, the basic representation of a landscape formed by suitable habitat patches within an inhospitable matrix corresponds with the increasingly common scenario where many species live in fragmented native habitats within human-disturbed landscapes (Fletcher et al., 2018; Hanski &

Ovaskainen, 2003). Second, conservation managers may not need any more detailed information than the trajectory of patch occupancy under different scenarios, when deciding how to prioritise and manage conservation areas. In other words, the SPOM focusses on the outcome of the highest management interest. Examples of applications include assessing how much metapopulation extinction risk is increased by removing particular patches (Che-Castaldo & Neel, 2016) or by applying certain maintenance or exploitation treatments (e.g., Johansson et al., 2019; Wood et al., 2018). Third, the notion that patch occupancy is dynamic also captures, at least in part, the fact that not all suitable habitat is occupied, and not all occupied habitat is currently suitable. Compared with other ways of projecting species' distributions under climate and land use change (e.g., Species Distribution Models, Velazco et al., 2020), SPOMs stand out because they include a species' dispersal ability and populations' extinction risk, which are both critical aspects for conservation planning (Thrall et al., 2000).

Lastly, SPOM parametrisation is possible with information that is often more accessible than that required for other models (Rabasa et al., 2022). The colonisation and extinction rates needed for SPOMs have often been parametrised from a single snapshot of the occupancy state of a set of patches (based on their area and isolation, although more data may be needed if the SPOM includes additional factors or cannot be assumed to be at equilibrium). Other kinds of population and metapopulation models require detailed demographic data (e.g., fecundity and survival rates) to estimate extinction risk (McCarthy et al., 2001; Ryu et al., 2016). Also, other spatial simulation models require movement data (e.g., Harrison et al., 2011), which can be even more difficult to obtain. Statistical fitting of parameters is desirable, where possible, compared with the alternative of taking parameters from previous studies or expert knowledge, prone to accusations of unreliability (Che-Castaldo & Neel, 2016). It is the simplicity of SPOMs that makes statistical fitting feasible.

Despite these attributes, the appropriateness of applying SPOMs to a wide range of species when these may not function as a 'classic' metapopulation has been widely debated (Che-Castaldo & Neel, 2016; Heard et al., 2012). Several studies have suggested that SPOMs reflect local population dynamics adequately (Crone et al., 2001; Hokit et al., 2001; Pellet et al., 2006), making them a good compromise between capturing sufficient biological detail and being easy to parametrise (Etienne et al., 2004). However, metapopulations in the narrow sense would not arise in cases where inter-patch dispersal is too frequent, such that patches do not support spatially discrete populations; where population turnover is too rare or non-existent, or in cases where the apparent extinction and colonisation events are in fact animals' temporary choices about habitat use (Heard et al., 2012). Also, some authors have challenged the

capacity of SPOMs to predict the dynamics of metapopulations in the real, natural world in general (Baguette, 2004), and especially of those species where metapopulation processes are hard to identify or quantify, including species that are long-lived, or those that have dormant stages, restricted dispersal or local adaptations (Freckleton & Watkinson, 2003; Husband & Spencer, 1996). These concerns have led to suggestions that empirical studies are biased towards small-sized short-lived species, particularly insects, given the ease of quantifying metapopulation processes at the spatial and temporal scale at which they live (van Nouhuys, 2016). Stochastic patch occupancy models also are more challenging to parameterise and interpret when there is a strong decreasing (or increasing) trend in the fraction of occupied patches (Moilanen, 2004). Some of the criticisms of earlier and simpler SPOMs are less applicable to those that include extra factors and/or are parameterised with richer information. Metapopulation models can have sub-population models or individual-based models nested within them and can therefore in principle include any biological process. Here, however, we restrict our attention to SPOMs because of their interesting features mentioned above and aim to shed light on the ways that they can be adapted while maintaining their simplicity.

When any family of models is first developed, it is almost inevitable it will be used in a narrow range of case studies. As time goes by and people can build on experience, we may expect the body of work to become broader in a variety of ways, unless there are theoretical or practical barriers preventing this. Here, we explore whether the applications of SPOMs, especially in the field of conservation biology, have become broader in some of their attributes or have been constrained as mentioned above. Specifically, we used both quantitative scoring and qualitative observations to review the body of studies where SPOMs have been fitted to real species in specific landscapes in order to simulate their dynamics. We first tested whether the application of SPOMs with conservation aims has grown over time (relative to studies aiming for basic biological insight or developing methods). Next, we assessed whether the taxonomic breadth has increased with time or, as suggested by some authors, is inherently restricted to a particular group of species. We also assessed the geographic range of study locations and the types of landscapes (as measured by the total extent and proportion of suitable habitat) for which SPOMs have been used. Finally, and based on the patterns of past SPOM use, we discussed remaining barriers and promising future avenues, in the context of the pressing global need to plan conservation for multiple poorly recorded species, in fragmented landscapes under climate change.

2 | METHODS

2.1 | Review of SPOMs

We performed a systematic search within the Web of Science (WoS; <https://www.webofscience.com>). We carried out a combined search of the terms 'Stochastic patch occupancy model' with other terms

relevant to the SPOM literature (Table 1), retrieving 2757 publications. After reviewing the title, abstract and keywords, we discarded all publications that: (a) were not related to the landscape ecology literature, (b) used other types of landscape models (e.g., individual-based, agent-based, connectivity models) or (c) were not empirical (i.e., were entirely theoretical), reducing the sample to 607 papers. Next, we screened the full text of these papers and added six publications referenced within that were not found through the WoS search. Of these 613 applied articles, we excluded papers in which: (a) virtual species or landscapes were used, (b) landscapes were subject to experimental design, (c) spatial analyses were grid-based (as opposed to patch-based), (d) species detectability data were required and (e) local-population dynamics models were applied (i.e., models that required population-specific data, such as survival and reproductive rates), obtaining a final selection of 82 publications. The publication period considered covered more than 30 years (1991–2023).

2.2 | Data analyses

A list of the data sources is found in Appendix S1—Data Sources. We gathered details that could give us information on the main objectives of the studies, the taxonomic and geographical extent of their application and other features related to SPOMs' supposed advantages and disadvantages. We extracted the publication details, species of interest, study site, patch network features (e.g., total extent, total habitat area, the number of patches, maximum patch size), length of the field study used for parameterisation and the method of assessment of predictive adequacy (see Supporting Information). All analyses were performed in R (R Core Team, 2023; code available in Supporting information).

First, we performed qualitative analyses to identify the feasibility of applying SPOMs to a wide range of landscapes systematically. We identified the commonalities in the authors' definition of habitat patch and the number of years of occupancy data used for model fitting as an indicator of data demand. Then, we assessed the suitability of applying SPOMs to a wide range of species. Specifically, we identified the authors' reasons for assuming that populations described by SPOM function as metapopulations. We assigned studies to one of three categories: (1) those studies where the assumption is not addressed; (2) those where the assumption is asserted based either on previous studies or on particular biological features of the species of interest and/or habitat characteristics; and (3) those who explicitly tested and discussed whether their system functioned as a metapopulation. Additionally, we assessed whether the authors addressed the predictive adequacy of their models and, if so, how they did it. We contrasted three main approaches: (1) not assessed, (2) compared observed vs expected occupancy and (3) quantitative analyses to evaluate landscape variables and/or parameters performance. Lastly, we obtained the conservation status of the species considered according to the IUCN Red List of Threatened Species categories (IUCN, 2022) to identify studies where SPOMs were parameterised with at-risk species.

#1	"Stochastic patch occupancy model" OR SPOM OR IFM OR "Incidence function" OR MANAGE OR Levin AND Patch* OR Fragment* OR Habitat OR Host OR Landscape OR Spatial AND Viability OR Risk OR Sustainab* OR conservation OR management OR future ORExtinct*AND Metapopulation
#2	Metapopulation AND Patch* OR Fragment* OR Habitat OR Host OR Landscape OR Spatial AND Risk OR Sustainab* OR conservation OR management OR future ORExtinct* AND Model* OR Simulat* OR Projecti* OR Forecast* OR predict* OR Stochastic OR "Monte Carlo" OR Probability OR Transition
#3	Coloni* OR Occupancy AND Landscape OR Spatial AND Patch* OR Fragment* OR Habitat OR Host AND Risk OR Sustainab* OR persist* ORExtinct* AND Model* OR Simulat* AND Projecti* OR Forecast* OR predict* AND Stochastic OR "Monte Carlo" OR Probability OR Transition

TABLE 1 Search terms. Terms used in the Web of Science search engine to obtain publications applying stochastic patch occupancy models (SPOMs) in real species and landscapes.

Note: Three searches were combined to retrieve studies that mentioned terms related to either (#1) SPOMs, (#2) metapopulation or (#3) occupancy prediction in their title, abstract or keywords. We used the following settings: 'All years', Indexes 'SCI-EXPANDED, SSCI, A&HCI, CPCI-S, CPCI-SSH, BKCI-S, BKCI-SSH, ESCI, CCR-EXPANDED, IC'; some Web of Science Categories were excluded from the search (see Appendix S1—Excluded categories).

To assess the evolution of empirical applications, we first assessed whether the use of SPOMs to inform conservation and management strategies has changed over time. Based on the description of the study aims, we identified the papers where a SPOM is used to test hypotheses and/or generate scenarios to provide recommendations for conservation and/or management strategies (henceforth 'conservation or management studies') from those studies with either a methodological interest (to describe a new model and/or assess a model's performance) or to gain basic insight into metapopulation dynamics of the species of interest. Then, we performed a logistic regression to assess the relationship between the presence of a 'conservation or management' aim and the year of publication.

We also assessed whether the aforementioned assertions regarding (a) low-data requirement and (b) model simplicity hold for the 'conservation or management' studies. To do so, we used study length (i.e., the number of years taken for collection of occupancy data) as an indicator of data demand. We performed a regression of the study length against the aim of the study (conservation/management or not) to test whether their length differs significantly from those with other aims and assess whether data demand could be a limitation for this type of study. We then assessed the relationship between model complexity and the aim of the study. We categorised the complexity of the models based on their transferability among species and landscapes, from simple to complex as (1) models that are potentially applicable to all metapopulations, these are the spatially realistic Levins model (SRLM), the Incidence Function Model (IFM) and the Propagule Rain Model (PRM); (2) models that base their colonisation and extinction functions on the aforementioned models but include additional parameters, these can still be fitted to other metapopulations (e.g., Ozgul et al., 2006); and (3) models that include parameters that are species- or landscape-specific and would be difficult to apply to other metapopulations, denominated 'Author's' models (e.g., Alados et al., 2009). We identified

whether the environmental impacts assessed in the 'conservation or management' studies were focussed on land-use change, climate change or both and, where relevant, whether the management aspect was addressed (e.g., habitat creation or cost-effectiveness).

We assessed how taxonomic and geographic diversity covered by the studies varied over time. We estimated the Shannon diversity index ('vegan', Oksanen et al., 2022) at the class level, by dividing chronologically ordered observations of unique classes per study into equally sized bins (nine bins, $n = 11$ in each) and performed a regression using the median year within the bin as the independent variable. To assess geographic diversity, we matched the study sites to terrestrial biomes according to the global Terrestrial Ecoregions data set (Dinerstein et al., 2017). The Shannon diversity index was then calculated at the biome level, by dividing chronologically ordered observations (i.e., unique landscapes by study) into equally sized bins (14 bins, $n = 7$); this information was used to perform a linear regression using the median year within the bin as the explanatory variable. Furthermore, we assessed how the spatial extent of study sites (i.e., log-transformed total extent) and the proportion of suitable habitat within study sites (i.e., log-transformed total patch area/total extent) have varied over time. Once the taxonomic and geographic trends were identified, we used binomial GLM to test whether the identified predominance of insect species and temperate biomes depends on whether the study has conservation or management aims.

3 | RESULTS

3.1 | Common features of SPOM studies

The common features of SPOM studies can give us some insight into minimum standards for data availability and analysis techniques. All 82 studies used a map of patches that were delineated using

prior knowledge of the study species but approaches to developing the map varied. The vast majority of the studies (93%) provided an explicit definition of 'habitat patch'. Of these, 25% of the definitions were based only on the physical environment (e.g., ponds, Vos et al., 2000); 28% were based on vegetation cover (e.g., forest fragments, Schnell et al., 2013); 40% included a particular ecological requirement (e.g., co-occurrence of other species, Biedermann, 2005); and 7% were conditioned by the known occurrence of the species of interest, some including demographics (e.g., adult females, Ozgul et al., 2006). Most SPOMs were parameterized using occupancy data from 3 years or less (42%), some data sets were between 4 and 9 years long (37%) and some used long-term data (≥ 10 years; 20%).

Most studies (60%) justified the fit of their system to a metapopulation structure based on previous studies, particular biological features of the species of interest and/or habitat characteristics, but a substantial minority of studies explicitly tested and discussed this assumption (40%). None failed to address the assumption of metapopulation structure in any way. The vast majority (83%) also addressed the predictive adequacy of their models, either by comparing predicted and observed patch occupancy (19%) or with quantitative analyses to assess the performance of parameters and/or variables (64%). We identified 20 studies where SPOMs were parametrised for at-risk species (i.e., three critically endangered, six endangered, nine vulnerable and seven near-threatened species; see Appendix S2).

3.2 | Adaptations of SPOM structure

Although all the models we reviewed met a fairly strict definition of a stochastic patch occupancy simulation model, they are amenable to many adaptations. Adaptations in model structure can allow more factors to affect the colonisation and extinction probabilities of patches and may ameliorate some of the perceived limitations of SPOMs (or of metapopulation models in general). Half of our study cases used a SPOM potentially applicable to all metapopulations (i.e., the IFM, SRLM or PRM), with the IFM being the most used over all (41%; e.g., George et al., 2013; Rabasa et al., 2022). The modified versions of these models constituted 18% of cases. These studies include the models with added parameters to address specific questions, such as the study by Vos et al. (2000), where extra parameters were added to test the influence of barriers and water conductivity in the landscape dynamics of the tree frog (*Hyla arborea*). Other modifications, used alternative approximations to patch area or inter-patch distance definition; for example, Poos and Jackson (2012) defined a patch network in the seemingly continuous habitat of a river fish, the redbreasted dace (*Clinostomus elongatus*), by replacing patch area with the depth in meters of headwater pools, and the commonly used Euclidian distance between patches with the river distance between pools.

A considerable fraction (31%) used a species- or landscape-specific model. An example is the model proposed by Schnell et al. (2013). They suggest expanding the strict colonisation concept

in SPOMs, that is, the process that describes the movement from one patch to another, to a broader concept that describes patch re-filling, that is, 'self-colonisation', that would allow the application of the SPOMs framework in landscapes with larger and fewer patches. They argue that, in their classic form, models predict that a species in a large contiguous habitat will have a higher extinction risk than one in two small patches since there are no other patches to provide colonists. Thus, they propose a model that eliminates the exclusion of patches from their own colonisation and approaches fragmentation as a process independent of habitat loss. They fit this model to four tropical bird species, where they used taxa- and biome-specific dispersal function, the heavy-tailed log-sech function, known to describe tropical bird movement.

3.3 | Conservation or management studies

Thirty-one studies (38%) used SPOMs to inform conservation or management strategies, and this type of study has increased significantly in prevalence over the years (Figure 1a). The length of data collection for these studies did not vary significantly from that of methodological and basic research studies, suggesting that carrying out this type of study has been possible with short-term data. Equally, we found no evidence that the models used increased in complexity over time for any group of studies (Table 2). The majority (68%) of conservation and management studies assessed the effects of habitat loss or degradation due to regional environmental changes (e.g., land-use change, Johansson et al., 2019; environmental policy implementation, Van Schmidt et al., 2019). However, during the last decade, research has been extended to assess the effects of global environmental change. Some studies (29%) have evaluated the current (e.g., Lawson et al., 2012; Wilson et al., 2010) and potential future effects (Johansson et al., 2020; Mestre et al., 2017) of varying temperature and precipitation patterns on the expansion, reduction or shift of species distributions to provide more robust predictions of extinction risk.

Most conservation or management studies (61%) used SPOMs to answer habitat planning questions, such as identifying the best location for habitat protection, creation or restoration, or assessing the minimum size of habitat patch required to maintain the target species (e.g., Alcala et al., 2019; Hodgson, Moilanen, Bourn, et al., 2009; MacPherson & Bright, 2011). Five studies (16%) used SPOMs to inform management approaches that can conserve metapopulations while allowing resource exploitation—grazing (Bergman & Kindvall, 2004; Johansson et al., 2017), forestry (Ranius et al., 2016; Schroeder et al., 2007) and mining (Che-Castaldo & Neel, 2016). Three (14%) evaluated the best time to implement conservation or management plans, that is, optimal time for habitat creation (Southwell et al., 2018), the optimal sequence of management actions, that is, patch enlargement, patch creation and corridor creation (Westphal et al., 2003), and minimum vacancy time before implementing restoration treatments (Wood et al., 2018). Finally, four studies (13%) used SPOMs to

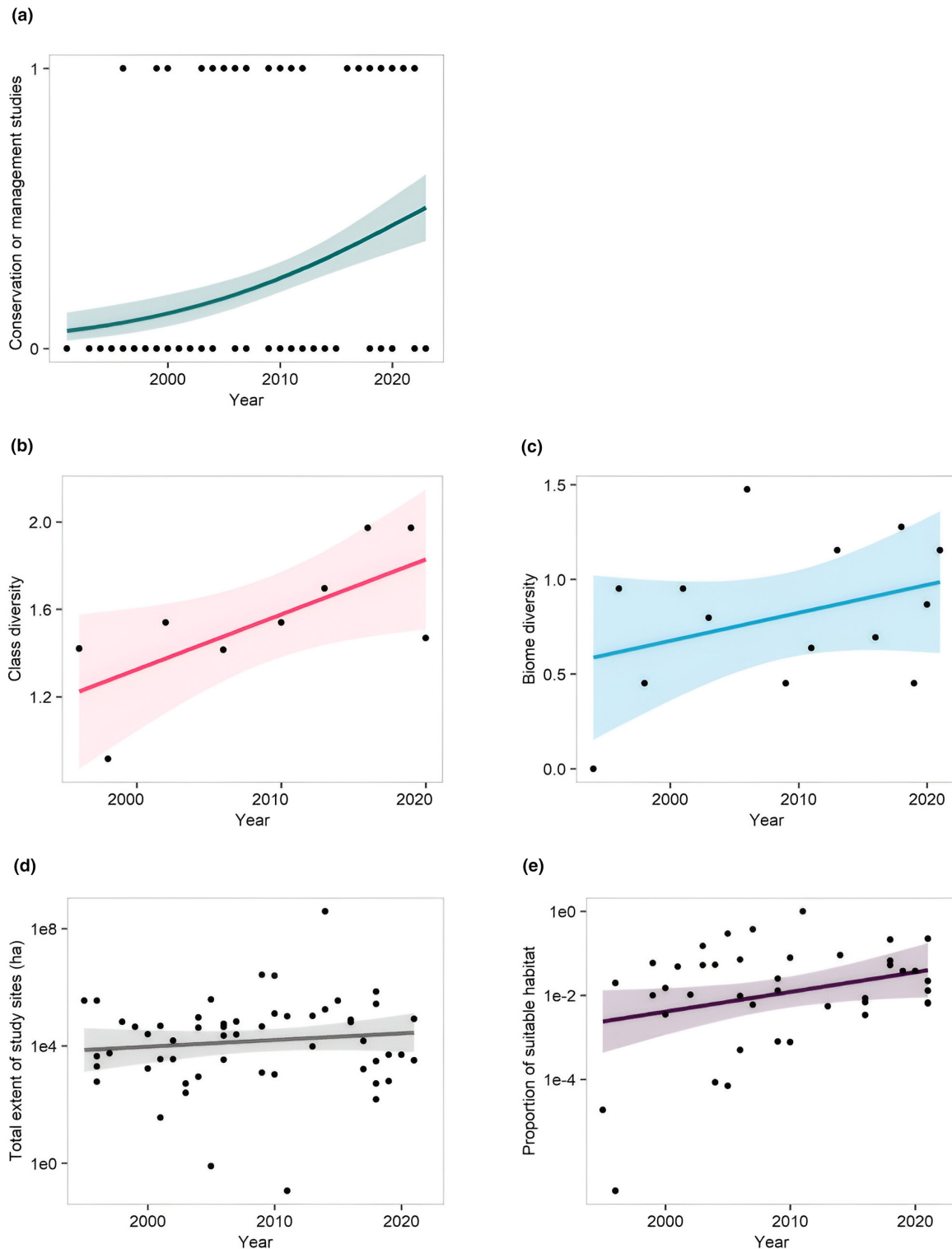


FIGURE 1 Temporal trends of the empirical use of stochastic patch occupancy models. (a) Studies with ‘conservation or management’ aims have increased over time compared to those with basic insight to metapopulation dynamics or methodological interests (glm binomial, estimate=0.075, $p=.012$). (b) Class diversity (Shannon Index) has increased over time (lm, estimate=0.029, $p<.001$). (c) There has not been a significant change in biome diversity (lm, estimate=0.015, $p=.22$). (d) The extent of study sites has varied widely from the beginning of the empirical application of the models up-to-date (lm, estimate=0.017, $p=.42$), but (e) there is a positive trend to use them in landscapes with a higher proportion of suitable habitat (lm, estimate=0.05, $p=.023$). Solid line=generalised linear model (glm) or linear model (lm) regression line, shaded region=95% confidence interval.

TABLE 2 Analysis of the relationship between conservation or management studies and (a) the study length (years), (b) the model complexity, (c) the condition of the species of interest belonging to the class Insecta (Insect) and (d) the condition of the study area being located in a temperate biome.

Factor	Estimate	SE	Z	p-Value
Study length ^a	-0.144	0.21	-0.685	.493
Model complexity ^b				
2	0.302	0.586	0.516	.606
3	0.349	0.509	0.686	.492
Insect ^c	0.359	0.431	0.832	.405
Temperate biome^c	-1.173	0.443	-2.649	.008

Note: Statistically significant ($p < .05$) relationships are in bold.

^aNegative binomial generalised linear model (glm.nb function, 'MASS', Venables & Ripley, 2002) to account for overdispersed data.

^bMultinomial regression model (multinom function, 'nnet', Venables & Ripley, 2002); model complexity 1 (simplest model) as reference.

^cGeneralised linear model (glm function, R stats, R Core Team, 2023).

inform the most cost-effective strategies for species conservation (Bauer et al., 2010; Polak et al., 2018; Ranius et al., 2016; Southwell et al., 2018). Several studies (22%) considered more than one of these management aspects.

3.4 | Taxonomic coverage

We identified 236 species (Appendix S2), including animals (64 vertebrates, 22 invertebrates), plants (125 flowering plants, five conifers, two ferns), lichens (17) and one fungus, which were targeted by SPOM studies (Figure 2). In one study, it was not possible to identify taxa at the species level; Nieminen (1996) reports fitting SPOMs for 186 species of moths and summarises the model parameters by host plant categories, raising the total number of species to 422.

Insects were the best-represented taxonomic class, constituting 47% of the 472 study cases across the review (i.e., species per study, including Nieminen, 1996), followed by angiosperms (28%) and mammals (10%). Class diversity has increased over time (Figure 1b), although, within the insect class, butterflies and moths are overrepresented (46% of all study cases). A small number of studies included disproportionately many species of plants (140 cases in seven studies) and moths (186 cases in one study, Figure 2). Conservation or management studies have not been more focused on insects than other study types (Table 2).

Four studies explored the potential transferability of SPOM parameters among closely related or ecologically similar species. Wahlberg et al. (1996) found that the parameters of the well-studied metapopulation of the Glanville fritillary butterfly (*Melitaea cinxia*) were useful in predicting the distribution of *Melitaea diamina*, an ecologically similar and endangered congeneric species. In contrast, Lindenmayer et al. (1999) found that the response of one species to habitat fragmentation may not provide a useful guide to the possible response of other closely related taxa when they tested the patch occupancy predicted by the IFM for four closely related arboreal marsupial species. Quintana-Ascencio and Menges (1996) provided evidence of the relationships between some ecological traits and the

Proportion of studies per group ($n = 89$)

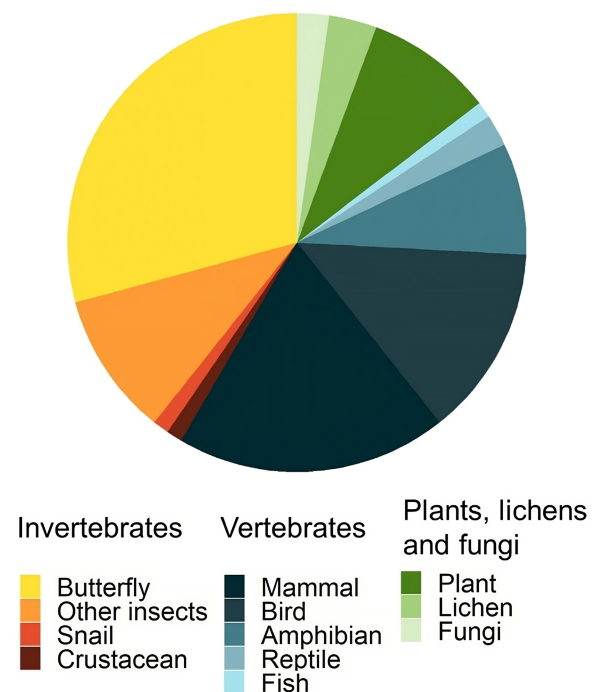


FIGURE 2 Taxonomic coverage. Proportion of studies per taxonomic group, some studies include more than one group, that is, 89 group cases in 82 studies. 'Other insects' category includes studies of the groups: Beetle, Frog hopper, Grasshopper, Wasp and Moth.

extinction risk and colonisation capabilities in unrelated species. They found that specialist species of the Florida rosemary scrub displayed a stronger relationship between species occurrence and patch size and patch isolation, within specialist species, herbs showed greater sensitivity to extinction than woody plants. Finally, Nieminen (1996) found that patterns in the risk of extinction of herbivorous moths are significantly affected by their host plant characteristics rather than by the characteristics of the moths themselves.

3.5 | Geographic coverage

We identified 97 different landscapes for which SPOMs have been developed. Those located in temperate biomes are the most common (65%), followed by Mediterranean (12%) tropical (10%) and boreal (9%) biomes; only 2% occurred in a desertic biome and 1% in mangroves. Although some increase in biome diversity has occurred over the years, it is not statistically significant (Figure 1c). Conservation or management studies have been slightly more prevalent in non-temperate biomes (Table 2).

The landscapes assessed in these studies encompassed an enormous range of habitat coverage and patch sizes. The total extent of study areas varied greatly, ranging from 0.0012 to 3,859,375 km² (median = -391.7; IQR = 825 km²; Figure 1d). The number of patches in each patch network ranged from 6 to 9208 (median = 82; mean = 366; IQR = 201), with highly variable total patch area (range = 0.0007–347,375; median = 3.92; IQR = 9.41 km²). On average, 7.05% of the total extent of study sites correspond to suitable habitat patches for the target species (range = 0.002–99.7, median = 1.5, IQR = 4.8%), and there is a trend over time towards studying landscapes with a higher proportion of suitable habitat (Figure 1e).

4 | DISCUSSION

4.1 | Diversity and development

Over three decades ago, Hanski and Gilpin (1991) anticipated that, as the fragmentation of most environments expands, metapopulation research would be increasingly motivated by applied ecology and conservation biology issues. This seems to be the case in the use of SPOMs, where their application to conservation questions has increased over time, reaching 53% of the cases in the last 10 years. Our findings suggest the body of work has diversified and developed in several ways, and some of the models' supposed weaknesses have been challenged. First, we found examples that challenge the assumption that the framework is restricted to small, short-lived species (van Nouhuys, 2016). Studies of insects, especially butterflies, were established early, perhaps due to a combination of a historical accident and ease of study. For context, however, insects comprise around half of all described species, so we do not claim that the SPOM field is taxonomically biased overall. The increase in class-level diversity over the decades broadens the prospects of applying SPOMs to a wider diversity of organisms. We found studies for species where metapopulation processes are hard to identify, such as long-lived species (e.g., *Juniperus* spp., *Pinus* spp., Alados et al., 2009; *Asimina obovata*, *Opuntia humifusa*, Quintana-Ascencio & Menges, 1996), species with dormant stages (e.g., *Chenopodium album*, Omar et al., 2019) or species living in apparently continuous habitats (*Litoria raniformis*, Heard et al., 2012; *Clinostomus elongatus*, Poos & Jackson, 2012). The prevalent application of the less complex models, especially the IFM, throughout the decades together

with the considerable presence of the species- or landscape-specific models, suggests that the increase in taxonomic diversity is a combined result of the dissemination of simple models to other taxonomic groups and the evolution of more nuanced model structures that make more acceptable assumptions.

Similarly, over time, SPOMs have been applied in landscapes with a higher proportion of suitable habitat. Although the proportion of suitable habitat is no indication of spatial configuration, a higher proportion of suitable habitat increases the probability of having large habitat patches or shorter interpatch distances (Villard & Metzger, 2014), which in turn suggests less severely fragmented landscapes in terms of habitat availability and reachability. They have also been applied at an enormous range of spatial extents and patch network sizes. We think that this broad application is appropriate as long as it is based on knowledge of the species modelled, and the spatial scales at which their populations are functionally separated. Earlier views that SPOMs are restricted to highly fragmented landscapes with a large number of patches (e.g., Baguette, 2004; Chapman et al., 2003) reflect too narrow an interpretation of the metapopulation concept. Although not all species whose populations have undergone fragmentation fit a strict definition of a metapopulation, it is acknowledged that keeping a metapopulation perspective brings into consideration critical aspects (i.e., dispersal ability and populations' extinction risk) for species conservation (Grilli et al., 2015; Thrall et al., 2000).

Qualitatively, we have observed how SPOM structures have been diversified to address a wide variety of pressing conservation questions. The relative simplicity of SPOMs and the ability to use off-the-shelf model structures is usually seen as an advantage. Although there is no overall tendency to make models with conservation aims more complex, authors understandably add variables and parameters when they are crucial for their study question. For example, Johansson et al. (2019) weighted the patch area based on the patch condition (i.e., grazed or ungrazed) to assess the impact of grazing on colonisation-extinction dynamics and persistence of the marsh fritillary butterfly (*Euphydryas aurinia*) under four possible management scenarios.

4.2 | Restrictions on applicability

Despite the SPOM field becoming broader, 82 papers represent a small sub-field within ecology and conservation. There could be many reasons why SPOMs have not been fitted and simulated for more species and landscapes, but we will briefly mention three that are noticeable common strands across our reviewed studies. First, statistically fitting a SPOM requires presence and true-absence data from the set of study patches, preferably from two or more time points. Such data are not readily available for many species globally (with presence-only observations, or intensive surveys of a minority of the landscape's sites, being much more common). Second, in the SPOMs we reviewed, background natural history knowledge was needed to define the habitat patch network from the point of

view of the study species, and habitat was never simply equivalent to landcover. The species-specific definition of patches resulted in a wide diversity of scales used for modelling and a custom map for each study. Therefore, it would be difficult to apply a generic approach to defining habitat patches based on land cover categories from readily available maps, increasing the need for ad hoc data collection in the field. Third, authors usually justified the fit of their system to the metapopulation paradigm, and this justification again requires some species- and landscape-specific background knowledge. Having said this, a basic knowledge of a species' background should underpin any ecological model, and SPOMs remain among the simplest spatial simulation models, with a strong history of being statistically fitted to data.

In the context of conservation planning, statistical Species Distribution Models (SDMs, also known as Ecological Niche Models) have been widely used (Feng et al., 2019; Velazco et al., 2020) to make ecological inferences with virtually no background knowledge. Compared with SDMs, SPOMs still appear as data- and knowledge-demanding yet SDMs cannot adequately capture the interaction between habitat loss and climate change. Many SDMs simply do not include habitat/land cover variables, although it is becoming more common (Milanesi et al., 2020), and they typically ignore the dispersal capability of the species. This can lead to overprediction of distribution and consequently to misleading conservation decisions, for instance, giving high priority rank values to sites where species do not occur due to dispersal constraints (Velazco et al., 2020). Stochastic patch occupancy models are one way to at least partly overcome these limitations, and so they may be a good next step towards planning conservation in a world where it is unsafe to assume species will survive where they are currently found (Pecl et al., 2017).

4.3 | Prospects for future use to support conservation strategies

Globally, there is a need to forecast the loss of biodiversity under alternative climate change and land-use scenarios to guide strategies that are likely to slow and reverse this loss (CBD, 2022). Based on the studies that use SPOM-based projections to address these pressing issues, we reflect on how researchers and practitioners could expand the SPOM applications, as well as the research opportunities that could escalate the usefulness of these models. The cases we found lead us to think there is potential to expand the research on one particular effect, species range shift. Many of the SPOMs that estimated and projected species' range expansion relied on long-term data of one relatively well-known species, the silver-spotted skipper butterfly *Hesperia comma* (Bennie et al., 2013, 10 years; Lawson et al., 2012, 9 years; Wilson et al., 2010, 18 years). However, the approach used by Mestre et al. (2017) to estimate the future range shift of the Cabrera vole (*Microtus cabreræ*) in the Iberian Peninsula also shows potential to be applied to other species and landscapes. This method combines

SPOM and Ecological Niche Models (ENM, Peterson et al., 2011), using shorter occupancy (3 years) and presence-only data to incorporate both species' dispersal ability and environmental affinity to produce more accurate projections of range shift under different scenarios of climate and land use change. This method adds to the multiple approaches needed to understand the several levels at which climate change impacts biodiversity, complementing other approaches that address effects below and above the species level (e.g., physiological changes at the organism level or composition changes at the community level, Bellard et al., 2012; Parmesan, 2006).

Although Mestre et al. (2017) demonstrate a promising way forward, they still apply their model to a single species. Is it possible that SPOMs fitted to hundreds or thousands of species could be used for forecasting and planning similarly to SDMs? If any simulation model has the potential to expand its remit into this area, arguably a SPOM would be the frontrunner candidate. Yet, our literature searches did not reveal any significant steps towards this kind of application, and the three barriers listed above probably contribute to this. There is limited evidence to support viable methods for capturing the needs of multiple lesser-known species, without having to model each one explicitly. The use of an umbrella species to infer the dispersal abilities and habitat patch size requirements of several species living in the same ecosystems has been suggested (Baguette et al., 2013; Mortelliti et al., 2009), but the benefits of conserving a particular umbrella species for other species remains to be assessed (Driscoll et al., 2014). Similarly, SPOM parameters might be predictable from (geographically distant) species with similar traits, and/or via taxonomic relatedness, as suggested by the successfully predicted distribution of *Melitaea diamina* based on the parameters of *Melitaea cinxia* (observed = 0.37 vs. predicted = 0.40 ± 0.04 fraction of occupied patches; Wahlberg et al., 1996). Still, caution is needed since the knowledge of the response of one species to disturbance may not necessarily provide a useful guide to the possible response of other closely related taxa, as observed by Lindenmayer et al. (1999). They found that the predicted probability of occupancy of the mountain brushtail possum (*Trichosurus caninus*) was not related to the actual patch occupancy, contrasting with the significant relationship found for the sister species, the brushtail possum (*Trichosurus vulpecula*). Further research would be needed both to develop multi-species models and to synthesise their outputs into robust spatial conservation plans.

5 | CONCLUSION

The current body of empirical studies confirms that SPOMs have been increasingly used to answer a wide range of conservation and management questions. The growing diversity of taxa studied, the wide range of landscapes covered and the rising variety of approaches used to address different conservation aspects indicate the potential of SPOMs to inform conservation strategies.

Although authors often use an off-the-shelf model structure, they still make important species- and landscape-specific choices, not least regarding the definition of habitat patches and the appropriate spatial scale of the model. We thus lack precedents for automating the application of SPOMs to large numbers of lesser-studied species, analogous to the broad application of ecological niche models (ENMs/SDMs). However, our results indicate the potential of SPOMs to be used in a wide variety of systems and we expect that the use of SPOMs in conservation will continue to grow. There is particular potential for SPOMs to be used to plan conservation under climate change and a need for future research exploring the use of taxonomic or ecological traits for parameter extrapolation.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.


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DATA AVAILABILITY STATEMENT

Data supporting this study are included in the article Appendices and Supporting Information (<https://doi.org/10.5061/dryad.pzgm5bcst>).

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Author contributions: CGA carried out the data collection and performed statistical analyses. JAH conceived the idea and supervised the project. CGA, EEC and JAH contributed to the hypothesis formulation. EEC, NP and JAH guided the objectives and discussion. All authors discussed the results and contributed to the final manuscript.

SUPPORTING INFORMATION

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

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