

REVIEW

Grime Review: How Do Species Distribution Models Reflect and Inform Ecological Processes?

Incorporating effects of habitat patches into species distribution models

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Abstract

1. Species distribution models (SDMs) are algorithms designed to infer the distribution of species using environmental and biotic variables and have become an important tool for ecologists and conservation biologists seeking to understand the implications of environmental change.
2. Global datasets of environmental variables at resolutions of a few metres are increasingly available. SDMs fitted using such high-resolution data allow researchers to investigate how local factors affect species occurrences at unprecedented fine spatial scales.
3. As the spatial resolution of SDMs increases, we see a critical need to consider the characteristics of habitat types within or around raster pixels. In particular, we argue that the effects of habitat patches (EHPs, including habitat area, habitat configuration, and habitat diversity), measured focusing on patches or landscapes, have yet to be fully realized in SDMs.
4. We provide guidelines to incorporate EHPs in SDMs. We explain why this development is important, describe approaches to properly conduct such analyses, and discuss pitfalls we foresee in testing EHPs.
5. *Synthesis.* Ensuring that SDMs incorporating EHPs are properly designed will be key to increasing model predictive performance and to understanding which environmental factors influence the distribution of species at fine spatial scales. At a crucial time for nature conservation, we foresee that this will be a key step forward to understanding and protecting biodiversity.

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KEYWORDS

environmental niche models, habitat fragmentation, habitat heterogeneity, habitat loss, habitat suitability models, land use change, landscape ecology, patch area, scale of effect, spatial scale

1 | INTRODUCTION

'How many species are there on Earth?', 'where do they live?', and 'why there?' are some of the simplest, yet most difficult questions to answer in the environmental sciences (Hutchinson, 1959; Mateo et al., 2017; Rahbek et al., 2019). Answers to these questions remain elusive because biodiversity data are sparse across most of Earth and for most species (Hortal et al., 2015). One approach developed to bypass these knowledge shortfalls are species distribution models ('SDMs'; also called ecological niche models, habitat suitability models, or other terms, Guisan et al., 2017), tools designed to understand the distributions of species and to generate predictive maps of such distributions (Elith & Leathwick, 2009; Guisan & Zimmermann, 2000). Most SDMs are mathematical models designed to link environmental conditions, usually represented using categorical or continuous raster data (Lechner et al., 2012; Riva & Nielsen, 2020), with biodiversity data, usually represented by spatial occurrence or abundance records (Figure 1). These links, formalized in niche theory (Hutchinson, 1957), are a staple of biogeography (the 'realized niche', Colwell & Rangel, 2009; Guisan et al., 2017; Soberon & Peterson, 2005) and inspired many SDM approaches (Devarajan et al., 2020; Guillera-Arroita, 2017; Norberg et al., 2019; Waldock et al., 2022).

Application and diffusion of SDMs have been facilitated by the development of new methods (Guillera-Arroita, 2017; Norberg

et al., 2019; Uribe-Rivera et al., 2023) and of guidelines to properly implement such methods (Araújo et al., 2019; Feng et al., 2019; Merow et al., 2014; Zurell et al., 2020), by the need to bypass biodiversity knowledge shortfalls in conservation (Guisan et al., 2013; Kukkala & Moilanen, 2013; Pollock et al., 2017), and by increasingly available data on biodiversity (Besson et al., 2022; Hartig et al., 2023; Pollock et al., 2020) and the environment (Jetz et al., 2019; Wulder et al., 2022). Data availability has recently made important strides: for instance, the Global Biodiversity Information Facility currently hosts ~3 billion openly available records, and a map of global tree canopy height at a 10-m resolution was recently published (Lang et al., 2023).

This availability of large-scale, high-resolution data opens both opportunities and challenges in SDM research. Analyses based on high-resolution data allow a better understanding of the mechanisms determining the distribution of species (Haesen et al., 2023; Randin, Engler, et al., 2009), but they also relate to spatial domains—and thus ecological processes—that have not been traditionally considered in SDMs. Due to physiological constraints (Briscoe et al., 2023; Lenoir et al., 2020), at coarse spatial resolutions (generally >100 km × 100 km) climate is often a major determinant of species distributions (Johnson, 1980; McGill, 2010; Pearson & Dawson, 2003). Conversely, at finer spatial resolutions (generally <10 km × 10 km), the signature of other processes beyond climatic constraints appears more clearly (Johnson, 1980; McGill, 2010;

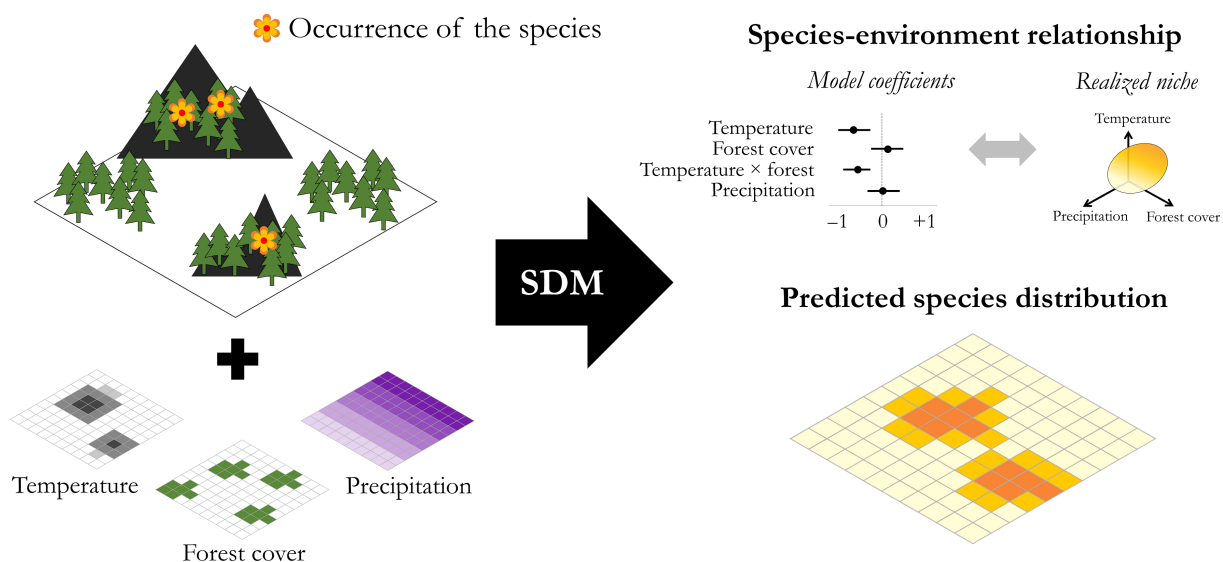


FIGURE 1 Species distribution models (SDMs) are a family of algorithms designed to infer the distributions of species from the association between biodiversity data (top-left) and environmental gradients (bottom-left). In the proposed example, a plant species (yellow flower) inhabits forests at higher elevations. A typical SDM could be used to predict the probability of occurrence of this species (bottom-right) based on temperature, precipitation, and forest cover, as well as the importance of these factors in explaining its distribution, outlining its 'realized niche' (top-right).

Pearson & Dawson, 2003), particularly fine habitat associations. While environmental variables approximating habitat associations are increasingly available to be incorporated in SDMs, changes in land use and land cover remain overlooked when fitting SDMs and when assessing biodiversity scenarios (Mod et al., 2016; Titeux et al., 2016).

In this context, we focus on the importance of land cover patterns—and especially their ‘patchiness’ (Figure 2; Table 1)—for the distribution of species. A long tradition of studies in ecology and conservation demonstrates that patterns in area, configuration, and diversity of habitat patches can influence changes in biodiversity (Fahrig et al., 2022; Laurance, 2009). For instance, the size of habitat patches assessed, the cumulative area of habitat in a landscape, and the diversity of habitats in a landscape can increase the local occurrence and abundance of species (Anderson et al., 2023; Fahrig, 2017; Heegaard et al., 2007; Keinath et al., 2017; Stein et al., 2014). We broadly refer to these diverse effects as ‘effects of habitat patches’ (‘EHPs’), because testing for them in SDMs is intuitive when conceptualizing landscapes as containing discrete patches of habitat (McGarigal & Cushman, 2002; Turner, 1989) (Figure 3).

Tests of the importance of variables representing EHPs in SDMs are rare despite extensive empirical evidence of their relationships with the distribution of species (see below). An overview of the literature found that only a small portion of articles on SDMs mention words related to EHPs in their abstract. Based on a search conducted on 11 November 2023 on the Web of Science platform from the University of Lausanne, the 1000 most-relevant papers to the string ‘species distribution model*’ mention the words ‘patch’, ‘patch area’, ‘patch size’, ‘fragmentation’, or ‘habitat area’ only 71 times (27, 0, 4, 34, and 6 times, respectively). In comparison, the word ‘climate’

appears 1237 times. There is therefore broad potential for addressing knowledge gaps around the importance of EHPs in SDMs. This review is designed to facilitate efforts in this direction.

We stress that incorporating categorical land cover data as predictors in SDMs is not, by itself, sufficient to test for EHPs (Figure 4). When incorporating land cover data as covariates in SDMs, authors usually link biodiversity data with individual raster pixels to either the land cover type in which a pixel containing the species observation is classified, or to the proportion of a land cover type of interest within the pixel (Figure 4, ‘Assumptions of typical SDMs’). While these approaches recognize the importance of habitat associations for SDMs, they might be inadequate because they assume that EHPs do not matter. For instance, they assume that it does not matter whether a pixel of habitat exists separated from other pixels versus within a larger habitat patch, or whether habitat exists continuous versus fragmented within a pixel. Alternatively, one could measure the sizes of the habitat patches containing the pixels where the species observations are made, or the number of patches in which a given habitat area exists inside the pixels; inclusion of these variables in SDMs would allow testing patch size and habitat fragmentation effects (Figure 4, ‘Example of neglected EHPs’). More broadly, a limitation of many SDMs—particularly high-resolution SDMs—is that variables describing the properties of habitat patches within, around, or surrounding individual pixels (Figure 5) are not considered, even though ecologists have demonstrated that such variables often matter in determining the distribution of species.

Here, to resolve this shortcoming, we describe how to test the potential relevance of EHPs to SDMs. Our hope is that authors interested in SDMs will consider whether incorporating variables representing EHPs (i.e., metrics capturing the area, configuration,

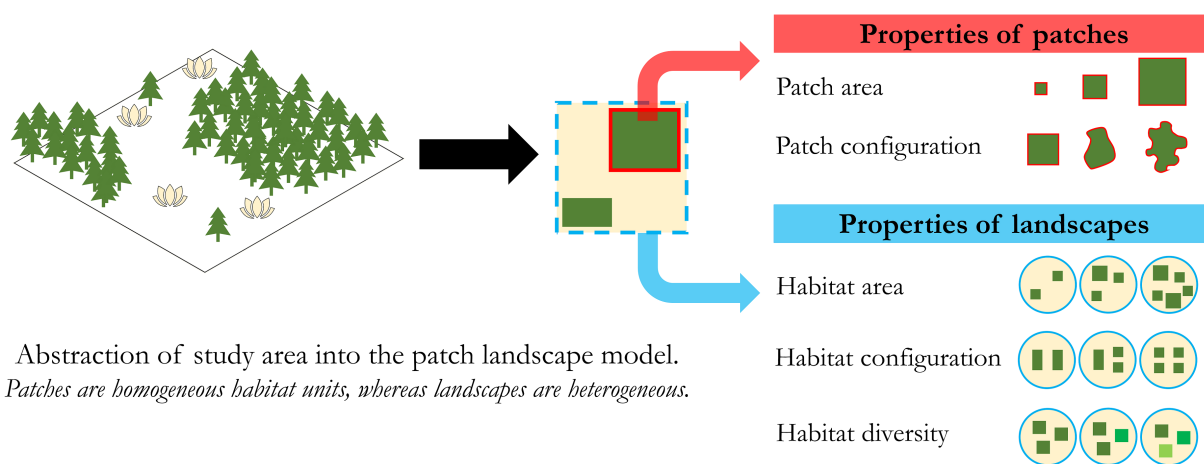


FIGURE 2 A ‘patch’ is an area with relatively homogeneous environmental conditions in comparison to its surroundings. For instance, clusters of trees can be described as forest patches (but not all trees fall within forest patches; left). Measures of habitat patches have played an important role in ecology and conservation, particularly through the discovery of effects of the characteristics of patches (red; top-right) and of landscapes (blue; bottom-right). We refer to such effects as effects of habitat patches (EHPs). Many metrics have been tested when assessing EHPs; we show here three categories of metrics (area, configuration, and diversity) and how they differ depending on the observational units (patches or landscapes) (Table 1). We illustrate these categories showing variation in patch size and edge length (properties of patches), habitat area, number of forest patches—a metric of habitat fragmentation—and thematic diversity (properties of landscapes); see the text for many other examples. Here, green polygons represent forest patches and yellow shading represents a matrix of grassland.

TABLE 1 Metrics developed to assess properties of patches and landscapes related to the effects of habitat patches. Comprehensive reviews of these metrics and of their properties include Turner (1989) and Wang et al. (2014). See also Hesselbarth et al. (2019), and the manual for the software FRAGSTATS at <https://www.fragstats.org/index.php/documentation>.

Observational unit	Type of measurement	Metric	Description	
Patches	Area	Patch size	Area of a patch (in hectares)	
		Core area	Core area of a patch based on specified edge depths (in hectares)	
	Configuration	Edge length	Perimeter of a patch (in metres)	
		Fractal dimension	Equals two times the logarithm of patch perimeter (in metres) divided by the logarithm of patch area (in square metres)	
Landscapes	Area	Habitat area	Sum of the areas of all habitat patches in the landscape (in hectares)	
		Fractal dimension	Equals two divided by the slope of regression line obtained by regressing the logarithm of patch area (in square metres) against the logarithm of patch perimeter (in metres)	
	Configuration	Number of patches	Total number of patches in the landscape	
		Total edge length	Sum of the lengths of all edge segments in the landscape (in metres)	
	Thematic diversity	Land use and land cover heterogeneity measured with the Shannon index		Equals minus the sum, across all habitat types, of the proportional abundance of each habitat type multiplied by that proportion

and diversity of habitat patches; Table 1; Figure 2) might provide insights into their system of interest, and when this is the case, they will properly test whether such variables should be included in their analysis. Specifically, we distinguish four approaches to study EHPs in SDMs based on metric type (metrics of patch vs. landscape characteristics) and assumption on habitat characteristics in relation to grain of analysis (raster pixels assumed to contain homogeneous vs. heterogeneous habitat) (Figure 5). In the Figures and Table 2, we refer to the four approaches as (H1) *homogeneous* habitat within pixels \times metrics of *patch characteristics around the pixel*; (H2) *homogeneous* habitat within pixels \times metrics of *landscape characteristics surrounding the pixel*; (C1) *heterogeneous* habitat within pixels \times metrics of *landscape characteristics within the pixel*; (C2), *heterogeneous* habitat within pixels \times metrics of *landscape characteristics surrounding the pixel*. These different combinations of data and metric types can be used to address different ecological questions, testing for different EHPs (Table 2), with high-resolution data allowing testing for effects of both the characteristics of patches and landscapes containing biodiversity data (Figures 5 and 6). We facilitate these tests by detailing why they matter, by providing an overview of what they require, and by highlighting pitfalls in this process. Box 1 summarizes critical concepts for the rest of the review.

2 | WHAT IS A PATCH OF HABITAT, AND WHAT IS A LANDSCAPE?

Discussing EHPs first requires defining 'patches', 'habitats', and 'landscapes' (Box 1; Figures 2 and 3). A 'patch' is an area that is relatively homogeneous in comparison to its surroundings, and

that can be therefore conceptualized as a discrete environmental unit (Fahrig, 2013; Turner, 1989). A 'habitat' is an environment capable of sustaining populations of a species of interest because it provides the species with the resources needed for its survival and thriving (Kearney, 2006). A 'landscape' is a heterogeneous area, where the ecological question of interest determines the scale of that area and description of that heterogeneity (Arroyo-Rodríguez & Fahrig, 2014; Turner, 1989). Many landscapes host habitat that exists naturally patchy, such as oases in deserts (Tydecks et al., 2023), wetlands surrounded by terrestrial lands (Deane et al., 2017), and lacustrine islands (MacDonald et al., 2018), or that exist patchy due to humans, such as forest remnants within agricultural lands (Decocq et al., 2016) and green areas within cities (La Sorte et al., 2023).

In addition to being respectively homogeneous and heterogeneous in terms of habitat, other aspects separate patches from landscapes. The size of patches typically varies, whereas the size of a landscape remains constant within a given application. Habitat patches are also species-specific entities (e.g., forests can be habitat patches for a woodpecker or a liana species, but not for most grasshopper species) whereas landscapes usually host species associated with different habitat types. Pragmatically, dominant vegetation types are often used to delineate habitat patches within landscapes (Clements, 1916; Pickett & White, 2013; Riva & Nielsen, 2020). Our suggestions apply to any mosaic of discrete habitat patches; we will often refer to habitat patches defined using categorical land cover raster data generated with remote sensing approaches (McGarigal & Cushman, 2002; Riva & Nielsen, 2021; Turner, 1989).

Like any abstraction of natural systems, these concepts have limitations (Coops & Wulder, 2019; Fahrig, 2013; Riva & Nielsen, 2020). In some cases, a 'gradient' model that represents

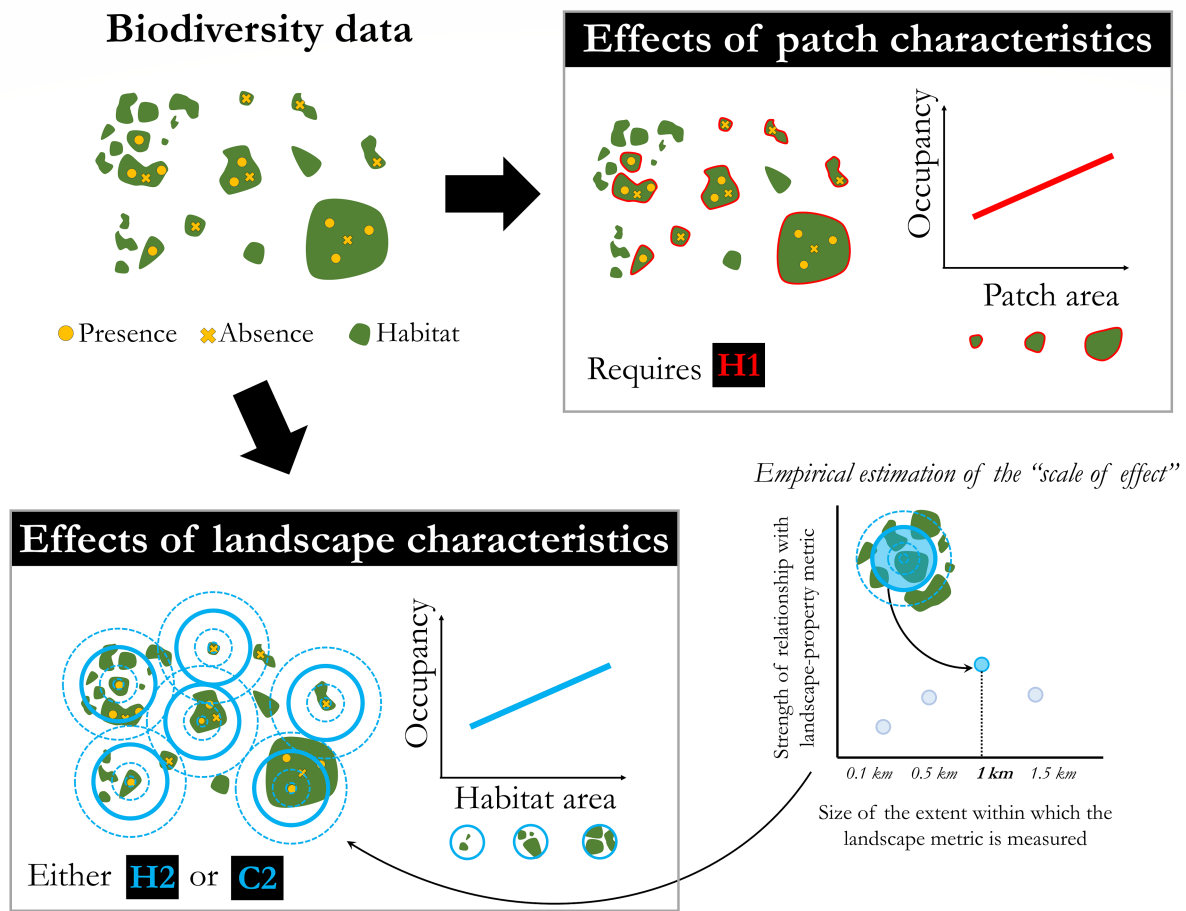


FIGURE 3 Many ecological studies suggest that observations obtained within a patch can respond to properties of that patch (effects of patch characteristics) and that observations obtained within a patchy landscape can respond to properties of that landscape (effects of landscape characteristics). The objective of this review is to facilitate the integration of such effects of habitat patches in species distribution models. Red lines outline patches measured to assess the effects of patch characteristics, whereas blue circles represent landscapes measured to assess the effects of landscape characteristics. The thick, blue circle represents the ‘scale of effect’, that is, the extent at which a metric of a landscape characteristic of interest better predicts the occupancy of this illustrative species. Black squares with letters (i.e., H1, C1, C2) refer to the different approaches described in [Figure 5](#).

continuous variation in a factor of interest over a landscape (e.g., canopy height across a region) (McGarigal & Cushman, 2005), or a ‘hybrid’ model that includes continuous information within discrete patches (e.g., canopy height measured only within forest patches based on a land cover map) (Brudvig et al., 2017), more properly capture the relevant environmental gradient (Coops & Wulder, 2019; Riitters & Vogt, 2023). Even when a categorical landscape model is appropriate, inference can be challenging because patches are often dynamic (Driscoll et al., 2021; Pickett & White, 2013) and their delineation involves arbitrary choices (Fahrig, 2013). Despite these limitations, extensive empirical evidence summarized in the next section strongly supports EHPs ([Figure 3](#)). The habitat patch concept has been instrumental in the development of ecological theory, such as the hierarchical patch model (Newman et al., 2019; Wu & Loucks, 1995) and meta-population theory (Hanski, 1998; Levins, 1969), and it has been used in management and practice (Pickett et al., 2009; Pickett & White, 2013). On-the-ground applications include conservation

principles (Diamond, 1975) and minimum patch area thresholds (Riva & Fahrig, 2023b) in habitat protection policies. Widespread use suggests the value of the patch concept, and thus incorporating variables representing EHPs in SDMs has the potential to reveal useful information about species’ ecological requirements and distributions.

3 | EMPIRICAL SUPPORT FOR EHPs

Much empirical evidence suggests the existence of EHPs ([Figure 3](#)). For instance, positive effects of patch area on biodiversity and the occupancy of species have been found across hundreds of taxa and disparate ecosystems (Keinath et al., 2017; MacArthur & Wilson, 1967; Prugh et al., 2008). Similarly, approximately one-third of studies of fragmentation ‘per se’ revealed significant effects of habitat configuration independent from its area (Fahrig, 2017). Such effects might be relevant for SDMs because associated with

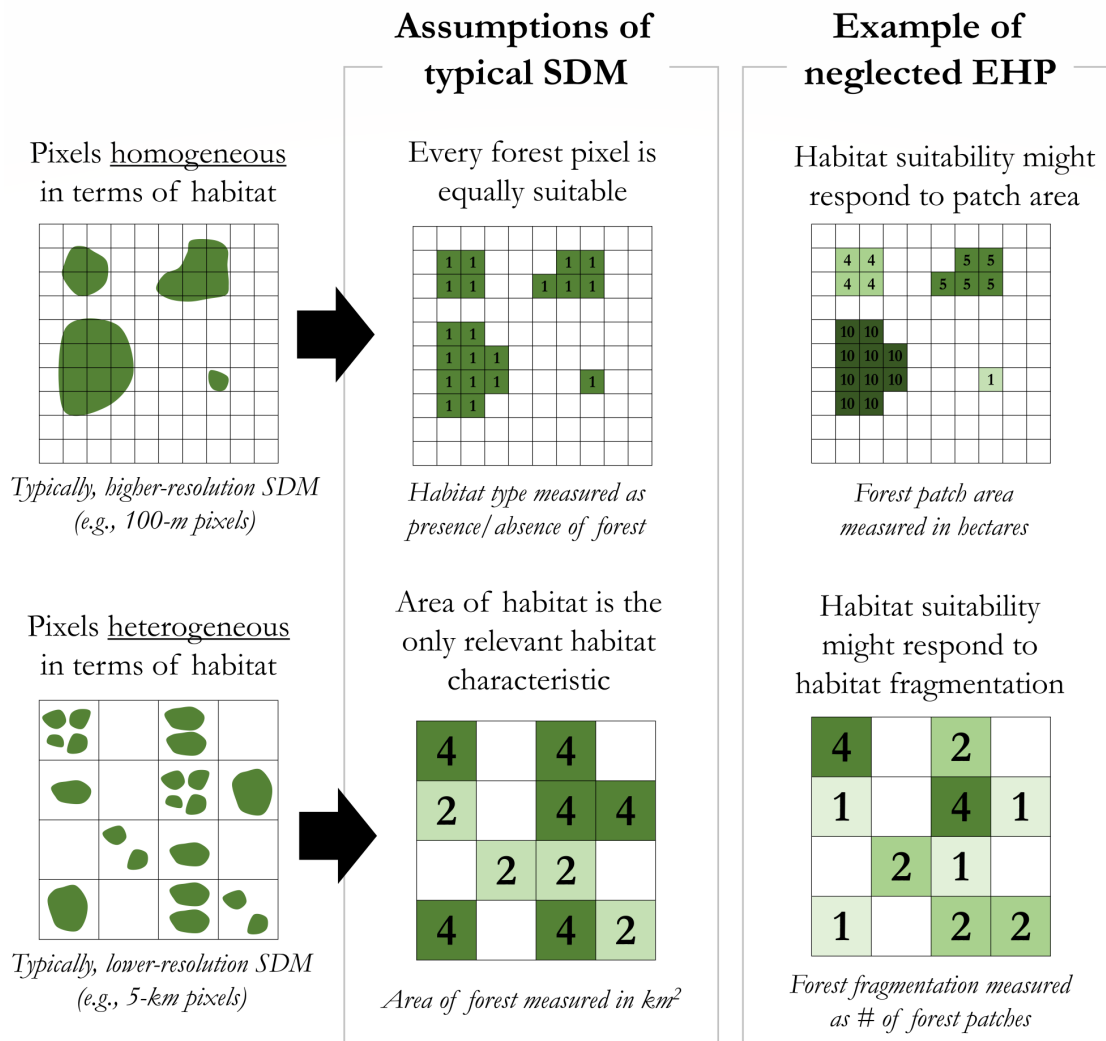


FIGURE 4 Typically, species distribution models (SDMs) do not include variables measured to account for the effects of habitat patches (EHPs). This is illustrated here with two examples in the central column, ‘Assumptions of typical SDMs’. Whether EHPs are relevant can be tested by incorporating in the SDM variables measured to represent properties of patches and/or landscapes hypothesized to influence the species of interest via EHPs. For instance, the suitability of a forest pixel might differ depending on whether that forest pixel is located in a small or in a large forest patch, and the suitability of a pixel might differ depending on whether the habitat that it contains exists continuously or is fragmented into several smaller patches. These two examples are illustrated in the right column, ‘Example of neglected EHPs’.

changes in the distribution of species in pixels existing within larger patches (Figure 5, H1), in pixels containing continuous rather than fragmented habitat (Figure 5, C1), and in pixels surrounded by continuous rather than fragmented habitat (Figure 5, C2).

Because the data available for an analysis determine which EHPs can be tested in different SDM applications (Figure 5), it is important to consider how previous results in the literature translate to tests of EHPs in SDMs. For instance, while larger patches tend to host more species, one manifestation of the species–area relationship (Matthews et al., 2021), it is not obvious that a raster pixel located in a larger patch should always contain more species than a raster pixel located in a smaller patch, because all raster pixels have the same area. Indeed, turnover among pixels located within patches can determine higher species richness in larger patches, even when

the number of species found within individual pixels does not respond to the size of the patches containing such pixels (Riva, Pierre, et al., 2024). The question then is how patch size moderates species’ responses to the presence of habitat in SDMs. When species have minimum patch area requirements below which they cannot persist (Marquet & Taper, 1998), then habitat pixels existing within patches smaller than these patch area requirements must differ in suitability from pixels existing in larger patches of habitat. Large patches also tend to have larger populations, decreasing extinction risk (Storch et al., 2018), which might increase suitability as estimated by the SDM. Despite these well-known relationships, tests of the importance of EHPs in SDMs have been to date lacking. This might cause us to miss opportunities to increasing the accuracy of SDMs and for understanding the EHPs.

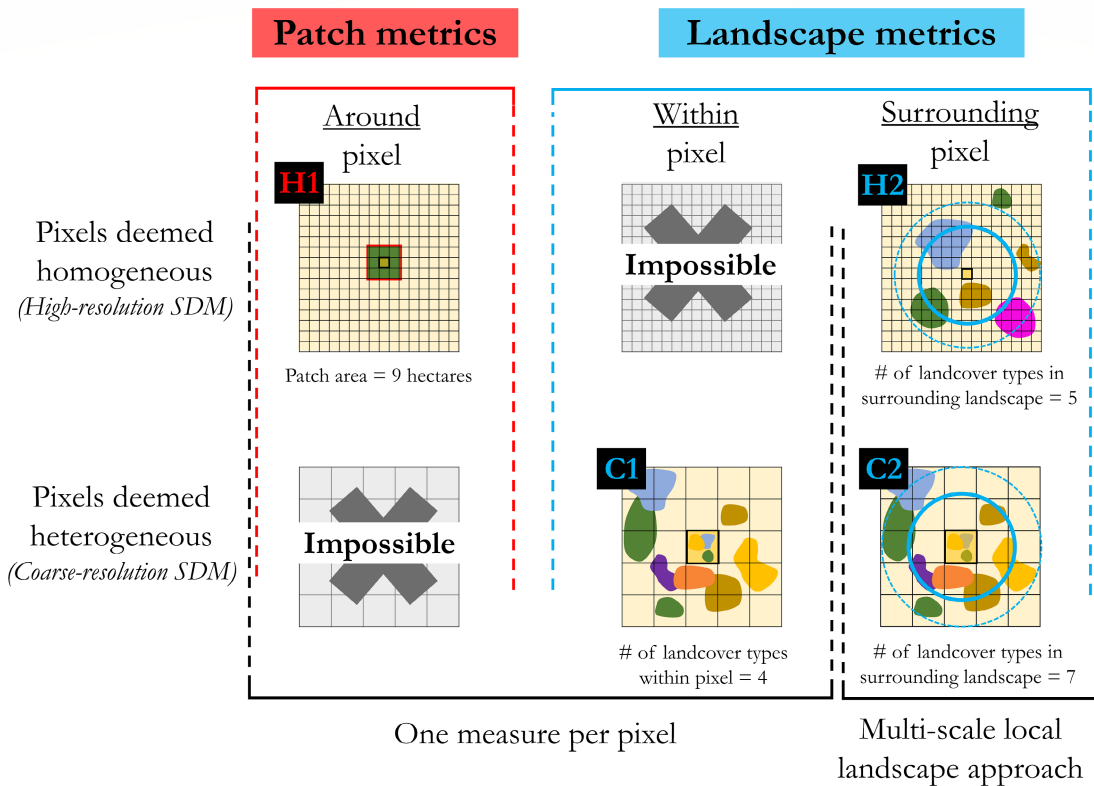


FIGURE 5 The spatial resolution of environmental data available dictates which type of metrics related to effects of habitat patches (EHPs) can be adopted in species distribution model (SDM) applications. Effects of patch characteristics can be measured mostly in high-resolution SDMs (H1), because they require assuming that all pixels are homogeneous in terms of the habitat type that they contain. Conversely, within-pixel habitat properties are more typical of coarse-resolution SDMs (C1), where it is reasonable to assume that pixels contain different habitat types. The multi-scale local landscape approach (see Figure 3) is feasible with both high- and coarse-resolution habitat data (H2, C2).

3.1 | EHPs in patch ecology and landscape ecology

Key for understanding how EHPs might influence SDMs is recognizing connections with extensive work conducted by ecologists. Two general categories of analysis are important for testing EHPs in SDMs: 'patch ecology' and 'landscape ecology' studies (Figure 3).

'Patch ecology studies' link observations obtained within a patch with properties of that patch, such as patch area (Heegaard et al., 2007) or shape (Burchell, 2012) (Figure 3). They identify 'effects of patch characteristics', that is, evidence that observations obtained within a patch respond to properties of that patch. Patch ecology studies have a long tradition that precedes the availability of remote sensing products (Keinath et al., 2017; Prugh et al., 2008). They typically assume a limited role in study extent, landscape moderation of local patterns, or climatic heterogeneity. An important example is studies testing Island Biogeography Theory for the conservation of terrestrial ecosystems (MacArthur & Wilson, 1967), which find that larger and more connected patches tend to host more species (Laurance, 2008; Matthews et al., 2021). Other examples are ecosystem decay, the observation that standardized biodiversity samples from larger patches have higher biodiversity than the same-sized biodiversity samples from smaller patches (Chase

et al., 2020), and minimum patch size effects, when patches smaller than a given area fail to support an ecological phenomenon of interest (Marquet & Taper, 1998).

'Landscape ecology studies' link observations from within a landscape with properties of that landscape, such as habitat amount (Watling et al., 2020) or fragmentation (Fahrig, 2017), and evaluate 'effects of landscape characteristics', that is, evidence that observations obtained within a landscape respond to properties of that landscape (Figure 3). In this view, landscape characteristics are associated with each observational unit. Such units of observation are usually plots or patches in the centre of each landscape (Figure 5), or alternatively, measured at multiple sites across each landscape (Arroyo-Rodríguez & Fahrig, 2014; Jackson & Fahrig, 2015). Landscape ecology studies expanded on patch ecology studies by incorporating landscape moderation of local patterns, or landscape context effects (Tscharnkte et al., 2012), increasing their spatial domain while continuing to assume no effects of climate on the ecological response of interest across the study extent. Examples of landscape ecology studies include assessments of the effects of habitat fragmentation per se (Fahrig, 2017; Fahrig et al., 2022), which suggest limited effects of habitat existing continuous or fragmented after controlling for habitat area,

TABLE 2 Outstanding questions that can be answered by incorporating the effects of habitat patches (EHPs) in species distribution models (SDMs). We assume all SDMs to include the effects of climatic variables and thus focus in this table on the part of the SDM designed to assess EHPs.

Themes of relevance	Outstanding questions	Approaches	Type of data (see Figure 5)
Area-based biodiversity conservation	For how many species are there minimum patch area requirements? And how small are the smallest viable habitat patches for different species?	Evaluate support for SDMs including the area of the habitat patches containing biodiversity data as a covariate. The presence of 'minimum patch area requirements' (patch areas below which species populations collapse) can be tested with approaches designed to identify ecological tipping points in statistical modelling, for example, with 'Threshold' and 'Hinge' features in Maxent. Accounting for habitat area measured in surrounding landscapes while conducting these tests is key to avoid confounding effects of patch size with habitat amount effects	Requires the assumption that pixels contain homogeneous habitat (H1, H1 + H2)
Area-based biodiversity conservation	Does it matter if a certain amount of habitat area exists continuous or fragmented, that is, in a few large patches instead of in several small patches?	Compare models that predict the distribution of species in response to (i) habitat area measured as a landscape property, and (ii) habitat area <i>and</i> habitat fragmentation (i.e., the number of patches in which the habitat exists) measured as landscape properties. If the first model performs as well as the second, then there is no support for habitat fragmentation effects	Can be tested with data assuming habitat homogeneous or heterogeneous within pixels (H1 + H2, C1, C1 + C2)
Management of working landscapes	How do the effects of environmental heterogeneity vary across spatial scales, and how does this change across systems?	Fit SDMs that assess the effects of heterogeneity of land cover classes around or surrounding biodiversity data at different grains of analysis (pixel size) and/or different landscape sizes	Can be tested with data assuming habitat homogeneous or heterogeneous within pixels (H1 + H2, H2, C1, C1 + C2)
Theory development	Do EHPs persist when considering pixels as observational units instead of considering traditional observational units in ecology (e.g., plots or patches)?	Use previously published datasets that contain spatially explicit biodiversity data and demonstrated EHPs with traditional approaches, to test for the same EHPs with SDMs	Can be tested with data assuming habitat homogeneous or heterogeneous within pixels (H1, H1 + H2, C1, C1 + C2)
Theory development	How important are EHPs in comparison to climatic gradients, and how does this vary depending on the grain and extent of a study?	Test for the effect of different characteristics of patches and landscapes (e.g., patch size, habitat amount) at different raster grains and study extents, and evaluate when such effects are relevant for the distribution of species. EHPs should become negligible at coarse spatial grains, but at which spatial domain this change occurs remains unclear	Can be tested with data assuming habitat homogeneous or heterogeneous within pixels (H1, H1 + H2, C1, C1 + C2)
Biodiversity knowledge shortfalls	What is the habitat for a poorly known species?	Evaluate support for SDMs parameterized with the same climatic variables, but different thematic resolutions of land cover classes (e.g., anthropogenic vs. natural land cover; anthropogenic vs. forest vs. grassland; urban vs. agricultural vs. forest vs. grassland, etc.). If one habitat type predicts well the distribution of a species, that habitat type approximates the real habitat of that species	Can be tested with data assuming the habitat homogeneous or heterogeneous within pixels (H1, H1 + H2, C1, C1 + C2)

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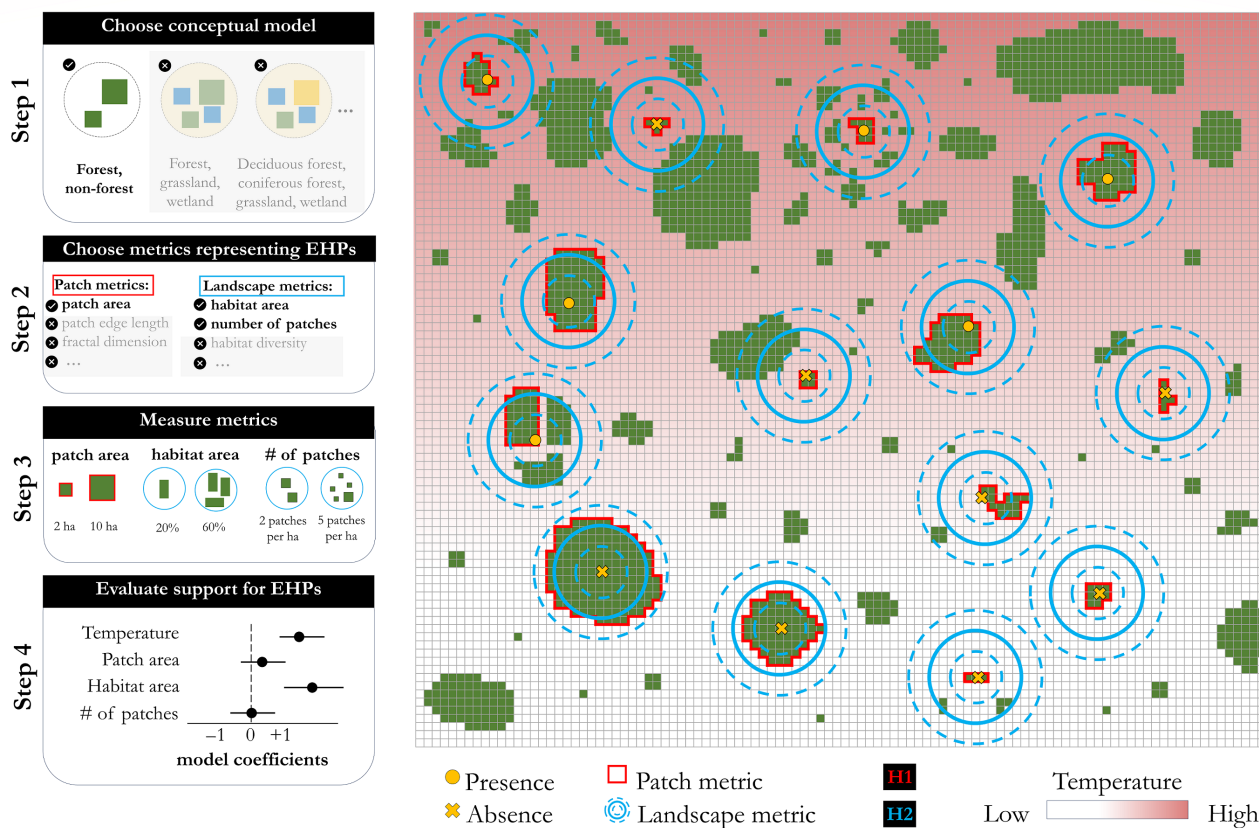


FIGURE 6 Testing the effects of habitat patches (EHPs) in species distribution models requires considering climatic and land cover patterns that potentially affect the distribution of a species. We detail on the left four steps necessary for proper tests of EHPs (see text for details), and on the right, the illustrative case of a forest-dwelling epiphyte, modelled with high-resolution data. This hypothetical species persists only when temperatures are high and at least 20% of the surrounding landscape is occupied by forest. To test EHPs, researchers must select a proper conceptual model (step 1), select metrics of characteristics of patches and/or landscapes (step 2), measure those characteristics (step 3), and test if they are related to the distribution of the species (step 4). On the right side, green areas represent forest patches; golden dots represent sampling sites where the species was present, whereas golden crosses represent sampling sites where the species was absent; red lines represent the patches containing sampling sites, for which patch area was measured; blue circles represent the extents at which landscape habitat area and fragmentation were assessed for each biodiversity sample, with dotted lines showing lower support, and one solid line showing the supported scale of effect (see Figure 3); the pink-to-white shade in the background represents a temperature gradient across the study area.

and tests of the habitat amount hypothesis (Fahrig, 2013), which suggest that species richness at a sampling site might be predicted by surrounding habitat area at least as well as by the combined effects of size and isolation of the patch containing the sampling site (Watling et al., 2020).

In SDMs, the relevance of both EHP types can be tested and could matter in addition to topographic and climatic effects (Figures 1 and 6). Separating the effects of patch versus landscape characteristics is important because the implications of the two are fundamentally different (Arroyo-Rodríguez & Fahrig, 2014; Fahrig, 2023; Riva & Fahrig, 2023a), but can be challenging because of overlaps in concepts and spatial domains (see 'Section 5' below). Studies designed to account for EHPs in SDMs might require consideration of both metrics of patch and landscape characteristics, which is possible only with high-resolution environmental data (Figures 5 and 6), and particular care to avoid confusing the two.

4 | ACCOUNTING FOR EHPs IN SDMs

Accounting for EHPs in SDMs requires first including as covariates in the SDMs some relevant properties of the patches and/or landscapes relevant to the species data analysed, and then testing whether such properties are important to explain the distribution of the species. We summarize this process in four steps, illustrated in Figure 6 with an example based on high-resolution environmental and biodiversity data.

4.1 | Choose a conceptual model representing habitat patches relevant to the study system

Previous knowledge of a system is important when deciding which conceptual model is appropriate to represent the study area (Figure 6, step 1). A binary, 'habitat/non-habitat' conceptual

BOX 1 Key concepts for navigating the review

Scale: General term representing the spatial and/or temporal domains of a study. It is usually composed of two components, grain, and extent.

Extent: The boundaries containing the observations analysed. In SDMs, the spatial extent is the area across which species are modelled and suitability maps created.

Grain: The size of the observational unit considered in the analysis. In SDMs, the spatial grain is the size of the raster pixel (or cell) used to infer environment–species relationships.

Spatial resolution: The accuracy of spatial data used in the analysis. In SDMs, the source data resolution can be finer than grain, for example, an author might summarize land cover data available at a 25 m resolution to a 1 km resolution to match available climatic data.

Habitat: The physical and biotic factors that support the survival and reproduction of a particular species.

Patch: An area that differs substantially from its surroundings for an attribute of interest (e.g., vegetation), and that can therefore be considered as a homogeneous, discrete unit.

Landscape: A heterogeneous area, where the particular ecological question determines the scale of the area (grain and extent) and description of that heterogeneity.

Metapopulation and metacommunity: A set of populations linked by the dispersal of individuals, and a set of communities linked by the dispersal of multiple interacting species. Both can persist in a dynamic balance of extinctions and colonisations in a landscape containing habitat patches.

Landscape moderation: The idea that the properties of a landscape surrounding a sampling site can affect ecological patterns and processes within that sampling site.

Scale of effect: The spatial extent within which the surrounding landscape pattern most strongly affects an ecological response at the centre of that landscape.

Effects of properties of patches: Effects of predictor variables measured as properties of patches. For instance, the probability of a species to be observed in a raster pixel might be higher when that pixel is within a larger than smaller habitat patch. See H1 in [Figure 5](#).

Effects of properties of landscapes: Effects of predictor variables measured as properties of landscapes. For instance, the probability of a species being observed in a raster pixel might be higher when that pixel is surrounded by a landscape containing more habitat or higher heterogeneity of land cover types, or when that pixel contains more habitat or higher heterogeneity of land cover types. See H2, C1, and C2 in [Figure 5](#).

Effects of habitat patches (EHPs): The effect of properties of habitat patches, and/or of properties of landscapes, on an ecological response of interest. EHPs are therefore a general category that encompasses both effects of properties of patches and landscapes described above.

model might suffice when focusing on species known to use specific land cover categories, whereas landscape conceptual models accommodating many land cover categories can be used to assess relationships between the occurrence of species and landscape heterogeneity. For instance, some alpine plant species can respond to patch size (Dullinger et al., 2011; Rixen et al., 2022), the amount of natural land cover helps predict the distribution of rare plant species (Rose et al., 2023), the distribution of invasive plants can be positively affected by landscape heterogeneity (O'Reilly-Nugent et al., 2016), and area of forest, but not fragmentation, affects recruitment of tree species (Arasa-Gisbert et al., 2021). Properly defining what are relevant habitat patches for different species is key to unveiling these relationships, and thus requires selecting appropriate conceptual models. Note that, in some cases, EHPs are not necessary because the mere classification of pixels in different land

cover categories ([Figure 4](#), central column in top row) explains the distribution of some species well (Gábor et al., 2022).

How to: The choice of a proper conceptual model should be grounded in knowledge of the system under investigation (i.e., species' natural histories and study area characteristics) and more broadly in ecological reasoning (Popovic et al., 2024; Riva & Nielsen, 2020, 2021). Some resources to assign habitat types to different species are already available and can facilitate assessments of EHPs. These include species–habitat association registries that synthesize expert knowledge, some of which have been compiled by organizations involved in conservation such as the International Union for Conservation of Nature (IUCN) (Cazalis et al., 2022), and some in studies and reports (European Environment Agency, 2024; Kattge et al., 2020; Tobias et al., 2022; van Swaay et al., 2006). Museum specimens along with information on the habitat type in which they

were collected might also be used to infer species–habitat associations (Jones et al., 2024). When prior information is not available, it might be possible to infer species–habitat associations based on preliminary analyses (Table 2).

4.2 | Select relevant metrics to represent EHPs

The next step is selecting characteristics of patches and landscapes that are representative of EHPs of interest (Figure 6, step 2). Because tens of metrics have been developed to characterize both patches and landscapes (Hesselbarth et al., 2019; Turner, 1989; Wang et al., 2014), one should again pick those that are relevant for the system studied based on their understanding of the system itself and on the study hypotheses. For instance, forest epiphytes must live in forests and might respond to forest continuity (Wierzycholska et al., 2020). Therefore, when modelling the distribution of these taxa, one could measure the sizes of the forest patches containing biodiversity sample plots, the total forest area in landscapes surrounding such plots, and the spatial configuration of that forest area in surrounding landscapes. Simultaneously testing for the effects of all three metrics will allow for a better understanding of which of these are important for the distribution of forest epiphytes (Figure 6).

How to: To select relevant metrics, one can either make predictions based on potential mechanisms affecting the system of interest and then measure variables representing EHPs related to such mechanisms, or explore variables that have been shown to be important in most systems. For instance, if changes in microclimates are known to influence a given species, then incorporating in the SDM measures of habitat edges could improve model performance because habitat edges usually differ in microclimate from 'core' habitat (Haesen et al., 2023). On the other hand, habitat area is typically an important factor in explaining the distribution of species, and one might include this variable by default. In fact, because area of habitat is one of the fundamental factors affecting both species occupancy and biodiversity (Fahrig, 2013; Matthews et al., 2021), we suggest that any EHPs related to the properties of a species' habitat should be assessed together with metrics representing total habitat area. If not, the risk is for a metric correlated to habitat area to capture both the ubiquitous effects of habitat area and other relevant properties of patches or landscapes (Wang et al., 2014), generating artefactual results that confound habitat area with such properties. We propose in Table 1 a few influential metrics that represent reasonable starting points for tests of EHPs in SDMs.

4.3 | Measure the selected characteristics of patches and landscapes

Next, authors should measure the properties of patches and landscapes identified as potentially relevant for analysis (Figure 6, step

3). When it is possible to fit high-resolution SDMs, one can measure variables describing both patches and landscapes surrounding every pixel/observation (Figure 5, H1 and H2). Conversely, when only coarse-resolution SDMs are possible, one can typically measure only landscape characteristics (Figure 5, C1 and C2). This is because the assumption of habitat homogeneity within pixels is usually unreasonable with coarse-resolution environmental data. Metrics of patch characteristics (red lines in Figures 2, 3, 5, and 6) are calculated once for a given pixel, with every pixel being contained only in a given patch (Figure 5, H1), whereas metrics of landscape characteristics (blue lines in Figures 2, 3, 5, and 6) can be calculated inside coarse-resolution pixels, and at multiple scales around both high-resolution and coarse-resolution SDMs (Figure 5, H2, C1, C2). When measuring landscape metrics in extents surrounding pixels (Figure 5, H2 and C2), such metrics should be measured at multiple scales, retaining in the final model the 'scale of effect' (Figure 3), that is, the scale that best explains the data (Jackson & Fahrig, 2015; Miguet et al., 2016; Scherrer et al., 2019; Vicente et al., 2014). Measurements of landscape characteristics around each observation with the 'multi-scale local landscape design' (Figure 3) are conducted in larger extents (spatial units), such as buffers, moving windows, or cropped squares, sometimes by incorporating spatial weights that increase the importance of environmental conditions near the biodiversity data locations (Bellamy et al., 2020; Miguet et al., 2017). The choice of the extent to which these metrics are measured can be informed by the ecology of the species assessed (Johnson, 1980), for example, it has been proposed that reasonable scales of effect range between ~4 and 9 times the median dispersal distance of a species (Jackson & Fahrig, 2012). More directions on how to measure properties of patches and landscapes can be found in the literature (Arroyo-Rodríguez & Fahrig, 2014; Bellamy et al., 2013; Freemark et al., 2002; Hesselbarth et al., 2019; Jackson & Fahrig, 2015; Miguet et al., 2016; Spake et al., 2019; Turner, 1989).

How to: Measuring variables related to EHPs requires geospatial data and tools to extract metrics representative of EHPs on such data. Many data sources for global remote sensing products have become available in recent years (e.g., <https://developers.google.com/earth-engine/datasets>, <https://registry.opendata.aws/tag/earth-observation/>, <https://livingatlas.arcgis.com/en/home/>, <https://www.earthenv.org/>, <https://land.copernicus.eu/global/>, <https://www.esa-landcover-cci.org/>), such that the selection of appropriate data is today much more feasible than in the past. Once an appropriate dataset has been selected, several tools are openly available to measure the properties of habitat patches that can be linked to EHPs. These include the package *landscapemetrics* in the R software (Hesselbarth et al., 2019), the *Patch Analyst* extension in the ArcGIS® software, or the *LandSCaPeN* toolbox in Google Earth Engine.

We stress that biodiversity and environmental data should match both spatially and temporally when calculating metrics representing EHPs (Guisan et al., 2017; Guisan & Thuiller, 2005). While all SDMs assume that the environmental covariates included

in the model are representative of the conditions experienced by the species, tests of EHPs require particular attention to timing mismatches because land cover change can occur very rapidly in comparison to climatic change. Authors should also consider potential time lag effects of species responses to changes in habitat (e.g., extinction debt; Figueiredo et al., 2019). Temporal matching of biodiversity data with appropriate land cover data is now possible in most cases thanks to the increasing availability of global, longitudinal remote sensing products. Such products date back to the 1960s and are available at relatively high temporal resolutions (Berner et al., 2023; Munteanu et al., 2024), although older products are inevitably available at coarser grains, limiting applications (Figures 5 and 7).

4.4 | Test support for EHPs in SDMs

Finally, every metric of interest should be included in a model to test whether there is support for the EHPs approximated by such metric (Figure 6, step 4). This requires comparing the importance of EHPs to other environmental variables and evaluating changes in model predictive performance. Support for EHPs can be based on assessments of model coefficients (e.g., statistical significance or posterior credible intervals), model selection criteria such as the Akaike information criterion (Burnham & Anderson, 2002), regularization (Merow et al., 2013), and similar covariate selection approaches. It is also important to assess the magnitude of the effects of EHPs in comparison to other variables, such as climatic and edaphic variables (Buri et al., 2020; Mod et al., 2016). Additionally, one can measure how much EHP variables improve model predictive performance compared with a model without them, or with them but randomized (Buri et al., 2020; Dubuis et al., 2013; Panchard et al., 2023; Randin, Jaccard, et al., 2009).

How to: Any approach designed to assess whether a variable of interest improves our understanding of the distribution of species, and the accuracy of SDM predictions, is suitable to testing whether variables representing EHPs are important in an SDM application. Robust tests of EHPs require awareness that landscape metrics sampled at different spatial extents are correlated (Figures 3 and 5; in C2 or H2), and that patch and landscape metrics can also be correlated (Figures 3 and 5; between H1 and H2). To account for this, we suggest comparing models that retain a basic structure containing the same climatic covariates—selected either a priori, based on knowledge of the species, or empirically, based on preliminary models—and metrics representing contrasting EHPs. Note that SDMs are often based on tens of covariates, and despite great advances in covariate selection, correlation among covariates remains an active challenge both in SDM (Adde et al., 2023) and EHP (Wang et al., 2014) research. No universal solution to this issue exists, but selecting an initial subset of variables of interest based on ecological rationale should still be favoured (Popovic et al., 2024; Riva & Nielsen, 2020, 2021).

5 | CHALLENGES FOR TESTING EHPs IN SDMs

The concepts underlying the approach we propose are widespread in ecology and conservation. Why, then, have EHPs so rarely been considered in SDMs? In addition to two limiting factors that are disappearing—the lack of high-resolution environmental and biodiversity data (Jetz et al., 2019), and separated traditions in patch ecology, landscape ecology, and biogeography (Banks-Leite et al., 2022; Zipkin et al., 2021)—conceptual and technical aspects make incorporation of variables for testing EHPs in SDMs challenging.

5.1 | Confusion around EHPs

Confusion around EHPs plagues the interpretation of results between patch and landscape ecology (Hadley & Betts, 2016; Riva, Koper, et al., 2024). It is paramount that such confusion should not affect tests of EHPs in SDMs. To prevent inappropriate inferences, we describe below five common misunderstandings.

First, the spatial domain of both EHP types depends on the system assessed. One can think of studies focusing on properties of patches with a larger extent than some studies focusing on properties of landscapes (e.g., effects of patch characteristics for tree species, Forsyth & Gilbert, 2021 versus effects of landscape characteristics for mosses, Larsen & Hargreaves, 2020). Metrics of patches and landscapes differ conceptually (Figures 3 and 5), regardless of the spatial dimensions appropriate for different systems.

Second, the response variable (e.g., species occupancy) can be measured in patches for studies focusing on landscape characteristics ('patch-landscape' study design, Arroyo-Rodríguez & Fahrig, 2014). This can be confusing because, in this case, patches are the observational units used to assess the effects of landscape characteristics. While for tests of EHPs in SDMs the observational units are typically pixels (Figures 4–6), we stress that what matters to discriminate different types of EHPs is not the grid resolution, observational units, spatial extent of the study, or the response variable, but rather the *type* of predictor variable measured (Figures 3 and 5). In a study assessing the effects of patch characteristics, the predictor is measured for different patches, whereas in a study assessing the effects of landscape characteristics, the predictor is measured for different landscapes (Figures 2, 3, 5 and 6). Note that studies on the effects of landscape characteristics via SDMs can be conducted at two different spatial scales—the scale of pixels containing biodiversity data (Figure 5, C1; see, e.g., Riva, Barbero, et al., 2023), and the scale of multiple extents surrounding the pixels containing the biodiversity data (Figure 5, H2 and C2; see, e.g., Adde et al., 2023; Scherrer et al., 2019).

Third, some paradigms generate predictions that apply both to patches and landscapes. These include the species–area relationship (Rosenzweig & Ziv, 1999) and metapopulation theory (Hanski, 1998).

For instance, area effects have been tested both when comparing patches of different sizes (Laurance, 2008) and when comparing landscapes differing in their total habitat area (Fahrig, 2017), and metapopulation theory acknowledges that extinction within each of many patches in a landscape is a separate phenomenon from the persistence of the species in the landscape itself (Hanski, 1998; Levins, 1969). When such paradigms are tested, it is key to distinguish predictions that apply to patches from predictions that apply to landscapes (Fahrig, 2023; Galán-Acedo et al., 2024).

Fourth, metrics such as core habitat (Herse et al., 2018) or edge length (Fahrig, 2023) can be measured both when focusing on individual patches and on landscapes (Table 1). Researchers should ensure that the metrics incorporated in their models capture the proper ecological characteristics of the target species and EHP(s), based on their hypotheses and study objectives. Separating the effects of the characteristics of patches from the effects of the characteristics of landscapes is key because extrapolation of the first often fails in predicting the latter (Fahrig, 2023; Galán-Acedo et al., 2024; Riva & Fahrig, 2023a). For instance, the propensity of a species to respond negatively to edges within a patch does not predict how that species will respond to landscapes containing many edges (Fahrig, 2023). Conflating the two types of EHPs implies the risk of failing to understand which environmental gradients affect the distribution of a species, reducing the predictive power of SDMs, and particularly so at local scales.

Last, biodiversity data are often available at grains that differ from the grain of the environmental data used as predictor variables in SDMs, leading to mismatches between the grain at which biodiversity data are sampled, and the grain at which environmental covariates are assumed to explain such data (Estes et al., 2018; Guisan & Thuiller, 2005). In the next section, we address in more detail the importance of grain for testing EHPs in SDMs.

5.1.1 | Grain

Grain is well-known to influence our understanding of ecological patterns and processes (Levin, 1992; Turner, 1989; Wiens, 1989). In SDMs, the spatial resolution of data available for both response and predictor variables determines the finest possible grain at which an analysis can be conducted, and this affects the biological interpretation of results (Moudrý et al., 2023) and model accuracy (Guisan & Zimmermann, 2000). Analyses at grains that approximate the size of the traditionally small sampling plots used in ecology (Estes et al., 2018), such as 25 m × 25 m (Haesen et al., 2023), can capture responses to fine-scale habitat properties that cannot be assessed in a coarser-grained analysis, such as the effects of patch characteristics on pixel suitability (Figure 5, top vs. bottom row). The implications of grain for testing EHPs are therefore clear.

When the grain of analysis is very fine (Figures 5 and 7), and thus habitat in each pixel can be assumed to be homogeneous, it is

more intuitive to test for EHPs because the presence of a species in every pixel might be affected by the properties of the habitat patch *containing* that pixel (Wierzycholska et al., 2020) (Figure 5, H1), and by the properties of the landscape *surrounding* that pixel (Bellamy et al., 2013) (Figure 5, H2). Conversely, when only coarse-resolution data are available (Figures 5 and 7), and thus habitat in each pixels is heterogeneous, one can only calculate landscape property metrics (e.g., habitat amount, configuration, and/or diversity) *within* each pixel (Riva, Barbero, et al., 2023) (Figure 5, C1), or *surrounding* each pixel (Li et al., 2023) (Figure 5, C2), therefore, testing only for effects of landscape characteristics. Although EHPs are more easily assessed with high-resolution data, the appropriateness of a given grain depends on the phenomena of interest in a particular application (Levin, 1992; Wiens, 1989) (Figure 7). Note that species might have independent fine-property requirements that co-occur in the same coarse pixel (e.g., animals with a larval stage needing different land cover types than adults), making some coarse-grain pixels appear artefactually suitable (Bütikofer et al., 2020).

Considerations around grain are also key because the size of habitat patches is heterogeneous in most regions worldwide (Riva et al., 2022; Riva, Koper, et al., 2024). Therefore, in most attempts to understand EHPs via SDMs, some patches will be smaller and some larger than the grain (Figure 7, central inset in top row). This requires assumptions about what are ecologically meaningful patches in each system. It is reasonable to assume that patches smaller than the grain of analysis are negligible with high-resolution data (e.g., considering tree clusters smaller than 10 m × 10 m as 'non-forests'), but less so when grain increases. Another common assumption is that at certain grain sizes, the effect of habitat area reaches an asymptote, and thus all patches bigger than that area can be considered equal in the model (Timmers et al., 2022). Note that both assumptions are implicit when biodiversity data are simply related to the land cover category of the pixel containing it (Figure 4, top row in central inset).

5.1.2 | Extent

Extent also influences our understanding of ecological patterns and processes (Levin, 1992; Turner, 1989; Wiens, 1989), with important implications on testing EHPs (Chevalier et al., 2021; Zipkin et al., 2021). For instance, it has been suggested that biogeographical patterns such as proximity to species' range edges might mediate responses to land cover patterns (Banks-Leite et al., 2022; Valente et al., 2023), making the extent of a study important when testing for EHPs in SDMs. It has also been proposed that deforestation might affect more profoundly species in areas that are historically less prone to disturbance (Betts et al., 2019), which implies that studies conducted regionally cannot detect similar effects. These examples highlight that how species respond to land cover patterns might change as the extent of a study increases. However, small extents

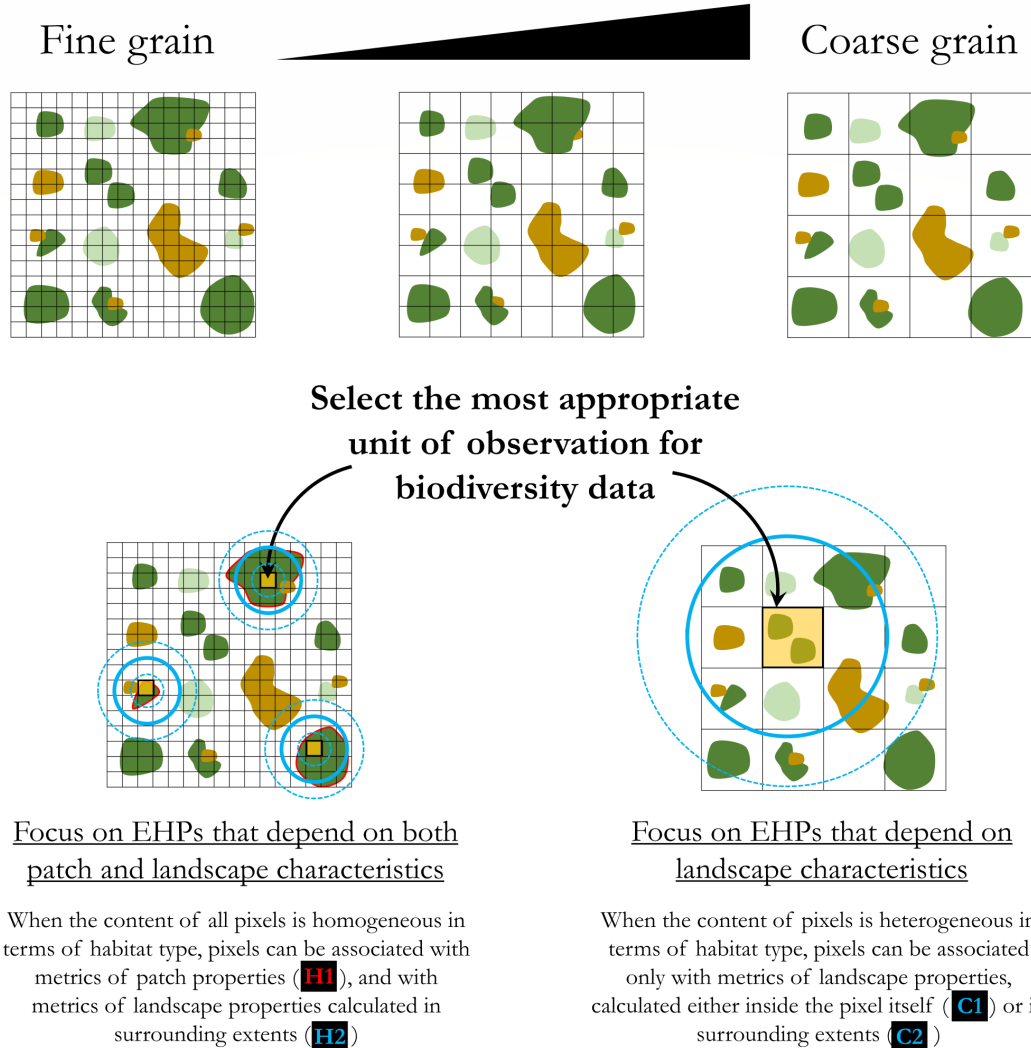


FIGURE 7 Selecting a proper grain of analysis is key to assess the effects of habitat patches (EHPs). Here, the same region is shown at three different grains (top row), and the proper grain for an analysis depends on the objective of a specific study. When every raster pixel can be assumed to be homogeneous, one can associate them with metrics capturing both the characteristics of the patch containing the pixel, and of the landscape containing the pixel. Conversely, when pixels are better conceptualized as heterogeneous spatial units, biodiversity data cannot be related to individual patches, but only to metrics of landscape characteristics, measured either inside the pixel or in the extents surrounding it.

risk 'truncating' the climatic niche of species (Chevalier et al., 2021, 2022): when selecting restricted extents, models designed to predict changes in distribution with climatic conditions might underestimate the potential future distribution of species because the data used to calibrate the SDM do not capture the full range of environmental conditions within which the species can exist. These trade-offs should be critically evaluated to ensure proper tests of EHPs via SDMs.

5.1.3 | Habitat

Even the simple habitat concept used here—different land cover types that compose a mosaic of discrete habitat patches across landscapes—presents some challenges in the context of identifying

EHPs. For instance, for species for which the habitat association is well understood, it is possible to find biodiversity data outside of the known habitat (e.g., forest-dwelling species recorded outside forests) because of (i) errors in the spatial coordinates of the record (Graham et al., 2008), (ii) errors in the classification of the habitat map (Lechner et al., 2012), or (iii) the species was actually observed outside of its habitat, for example, during dispersal or in a sink (Dunning et al., 1992). It is unclear how such data should be treated when researchers are interested in assessing the effects of patch characteristics (Figure 5, H1), because these records are not associated with habitat. It is impossible to determine based on the data alone which of the three reasons above underlie the mismatch between a species and its habitat, calling for caution when analysing such observations. Conversely, when assessing the effects of landscape characteristics (Figure 5, H2, C1, C2), observations recorded

outside of species' habitats can be more easily analysed, because it is less likely that a species will be found far away from its habitat when considering larger spatial domains.

Additionally, for many species, it is still unclear what exactly constitutes habitat (Hortal et al., 2015). Testing for EHPs in SDMs could provide valuable insights in this direction (see approach described in Table 2) but implies computational challenges. Recent advances with covariate selection procedures are promising in this direction because they can rapidly process thousands of potential covariates, reducing them into a set of uncorrelated predictors appropriate for SDM fitting (Adde et al., 2023). However, similar covariate selection approaches would need to be adjusted to the 'scale of effect' paradigm, that is, would need to allow comparisons among models with the same covariates measured at different extents while also reducing a priori the number of candidate environmental conditions. Using artificial intelligence approaches might also provide solutions when facing many predictors (Brun et al., 2024). Similarly, not all tools developed for SDMs allow incorporating dependencies in the model that might be necessary, for example, when several observations are located inside a single patch.

5.1.4 | Data

Because EHPs are well supported in the empirical literature, there is no doubt that the incorporation of variables representative of EHPs in SDMs will improve predictions and inference—at least in some cases. However, the question is *how often* such effects will be relevant depending on the different scopes of SDM analyses (Figure 7). While previous meta-analyses and syntheses suggest that many species might be affected by EHPs, it is unknown whether such effects are negligible when the goal is predicting the distribution of species (i) at different grains than typical studies in ecology, and (ii) across large extents, as it is typically done with SDMs. Furthermore, as the complexity of the model structure increases (Merow et al., 2014), larger datasets are needed to evaluate whether EHPs matter in space and time. For most species on Earth, therefore, assessing EHPs is currently unfeasible because we lack sufficient data (Hortal et al., 2015). When data are sparse and the extent is large, it is reasonable to expect that climatic variables will capture most of the variation in the distribution of a species, and thus EHPs might appear to be negligible. Still, entering a future of increasing availability of biodiversity data (Besson et al., 2022; Hartig et al., 2023; Pollock et al., 2020), these limitations will be progressively reduced. We therefore believe that EHPs will play a key role for high-resolution SDMs and other biodiversity models. We propose a few outstanding research questions to stimulate advancements in this avenue of research (Table 2).

In addition to the need for large datasets, the type of biodiversity data used in SDMs—typically biased in space (Bowler et al., 2022; Chauvier et al., 2021)—has important implications for tests of EHPs. The information content of 'big' unstructured data can be limited

even when considering large datasets (Boyd et al., 2023), and when sampling biases are correlated with landscape characteristics, it is possible to confuse biases in the data with EHPs. For instance, landscapes with smaller patches, less habitat, or more fragmented habitat are likely to be sampled more intensely because these land cover patterns are typically associated with anthropogenic landscapes, and thus more easily accessible to scientists (Bowler et al., 2022). This might result in positive, artefactual associations between the distribution of a species and lower habitat amounts and/or higher habitat fragmentation. Care should be taken to avoid misleading inferences by accounting for biases, either via statistical models (Chauvier et al., 2021) or by implementing proper sampling designs (Pasher et al., 2013).

6 | CONCLUSIONS

At its core, this review aims to bridge the divide between research based on SDMs and an extensive body of evidence suggesting that species respond to properties of habitat patches. We therefore suggest that incorporating variables representing EHPs in SDMs has the potential to enhance our understanding of species distributions, particularly when considering an increasing availability of high-resolution data. While a few SDM studies already incorporated variables representing EHPs as predictors, the practice has been to date sporadic and disorganized. We call for efforts to understand when incorporating EHPs in SDMs can be useful, and suggest that following the four steps outlined in Figure 6 will aid in organizing and expanding ongoing work.

Resolving knowledge gaps around EHPs is important and timely because researchers are using high-resolution SDMs increasingly often in biodiversity conservation applications (Guisan et al., 2013; Pollock et al., 2020). Such analyses inform management actions and policies that refer to spatial domains where EHPs are important for many species. SDMs that neglect EHPs risk therefore compromising the success of on-the-ground biodiversity conservation (Guisan et al., 2013; Velazco et al., 2020). Correct tests of EHPs in SDMs will also help in designing effective policies and actions that target patterns in habitat amount, configuration, and diversity, answering key questions such as 'for how many species are patches smaller than a certain area too small to be viable?', or 'when is there too little habitat left for the persistence of species in a landscape?' (Table 2). These have been key research questions in ecology and conservation for decades, and analyses based on SDMs that incorporate EHPs have the potential to provide novel, useful insights.

More broadly, our review adds to recent efforts towards connecting historically disconnected disciplines such as landscape ecology, biogeography, and macroecology (Banks-Leite et al., 2022; Chaplin-Kramer et al., 2022; Zipkin et al., 2021). We share the enthusiasm of other authors who suggested integrating information across spatial scales will be key in ecology and conservation, but also acknowledge the inherent difficulties of this task (McGill, 2019;

Newman et al., 2019; Riva, Graco-Roza, et al., 2023). In this context, we believe that proper tests of EHPs with SDMs will aid in resolving some of the long-standing, unsolved questions that persist around biodiversity change across spatial scales.

AUTHOR CONTRIBUTIONS

Federico Riva wrote the first draft. All authors reviewed and provided important insights to the review.

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CONFLICT OF INTEREST STATEMENT

No conflict of interest to declare.

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