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PERSPECTIVE

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Addressing the problem of scale that emerges with habitat fragmentation

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Abstract

Fragmentation and scale: Although habitat loss has well-known impacts on biodiversity, the effects of habitat fragmentation remain intensely debated. It is often argued that the effects of habitat fragmentation, or the breaking apart of habitat for a given habitat amount, can be understood only at the scale of entire landscapes composed of multiple habitat patches. Yet, fragmentation also impacts the size, isolation and habitat edge for individual patches within landscapes. Addressing the problem of scale on fragmentation effects is crucial for resolving how fragmentation impacts biodiversity.

Scaling framework: We build upon scaling concepts in ecology to describe a framework that emphasizes three “dimensions” of scale in habitat fragmentation research: the scales of phenomena (or mechanisms), sampling and analysis. Using this framework, we identify ongoing challenges and provide guidance for advancing the science of fragmentation.

Implications: We show that patch- and landscape-scale patterns arising from habitat fragmentation for a given amount of habitat are fundamentally related, leading to interdependencies among expected patterns arising from different scales of phenomena. Aggregation of information when increasing the grain of sampling (e.g., from patch to landscape) creates challenges owing to biases created from the modifiable areal unit problem. Consequently, we recommend that sampling strategies use the finest grain that captures potential underlying mechanisms (e.g., plot or patch). Study designs that can capture phenomena operating at multiple spatial extents offer the most promise for understanding the effects of fragmentation and its underlying mechanisms. By embracing the interrelationships among scales, we expect more rapid advances in our understanding of habitat fragmentation.

KEYWORDS

connectivity, edge, fragmented landscape, habitat loss, MAUP, patch size

1 | HABITAT FRAGMENTATION AND THE PROBLEM OF SCALE

Habitat loss is one of the primary threats to biodiversity across the planet. Although the effects of habitat loss on biodiversity are clear, over the past four decades there has been much debate about the role of habitat fragmentation (Diamond, 1975; Fahrig, 2017; Fletcher, Didham, et al., 2018; Saura, 2021; Simberloff & Abele, 1976). Fragmentation has been conceptualized as both a pattern and a process (e.g., Wiens, 1995), but here we focus on fragmentation when defined as the breaking apart of habitat for a given amount of habitat loss (also known as "fragmentation per se"; Fahrig, 2003). It has long been argued that habitat fragmentation has negative effects on biodiversity, based on evidence of patch-size, edge and isolation effects (for meta-analyses, see Bender et al., 1998; Haddad et al., 2015; Pfeifer et al., 2017). Yet, some recent evidence suggests that the effects of fragmentation per se across entire landscapes might be weak or even positive for biodiversity (De Camargo et al., 2018; Fahrig, 2003, 2017).

At the centre of this debate lies the issue of scale (for key terms regarding scale, see Table 1). On the one hand, it has been argued that only data collected at the grain of entire landscapes are relevant for interpreting habitat fragmentation effects because fragmentation is often considered a landscape-scale phenomenon (Fahrig, 2017; McGarigal & Cushman, 2002). In this way, patch-scale data are not considered to be relevant, because landscape-scale mechanisms might override local mechanisms and because patterns at patch scales can be confounded with variation occurring across landscapes (Fahrig et al., 2019). For instance, patch size and isolation effects, often assumed to be indicative of habitat fragmentation effects, could instead be attributable to variation in the amount of habitat at landscape scales (Fahrig, 2003). On the other hand, it has been argued that even if fragmentation occurs at the landscape scale, its effects can also operate more locally, such as at the patch scale (Chase et al., 2020; Fletcher, Didham, et al., 2018; Haddad et al., 2015). Fragmentation arising across entire landscapes can, for example, result in smaller patches and a greater proportion of edge-affected habitat within patches, leading to effects on biodiversity

TABLE 1 Scale terms and concepts[a] relevant to habitat fragmentation, organized based on the components, dimensions and challenges of scale.

Term	Description
Scale and its components	
Scale	The spatio-temporal domain of study, which can be described by the grain and extent. Applies to patterns, phenomena, sampling or analysis
Grain	The finest level of spatial resolution of data or a process
Extent	The area or region for which inferences are made
Focus	The area at which sampled grains are summarized for analysis, including both responses (e.g., species density in patches) and predictors (e.g., different neighbourhood sizes surrounding plots)
Dimensions of scale	
Scale of phenomenon	The scale at which mechanisms driving fragmentation effects operate. The grain of a phenomenon represents the minimum unit of the phenomenon, whereas the extent is the area or range at which the phenomenon operates
Scale of sampling	The scale of observations. The grain of sampling is the size of the sample unit, whereas the extent pertains to the area of samples, which is a function of grain, number of samples and lag distance between samples
Scale of analysis	The scale at which data are analysed to interpret fragmentation effects. The grain of analysis pertains to the area summarized of response and predictors; also called the focus of response and predictor variables. The extent of analysis is the area/region at which inferences are made, which could be individual landscapes, multiple landscapes and/or an entire region
Fragmentation and scale concepts	
Habitat fragmentation per se	The breaking apart of habitat for a given amount of habitat loss. In this way, fragmentation is described based on a delineated landscape extent
Ecological neighbourhood	The spatial extent around a location wherein an organism or process operates (or has influence) during an appropriate period of time
Scale of effect	The spatial extent around a location at which most variability in response data is explained
Scale challenges and potential biases with fragmentation	
Change of support problem	How changing the support of variables can lead to different conclusions. Modifiable areal unit problem is one type of change of support problem
Interdependence	The covariance of subcomponents of habitat fragmentation, such as relationships with patch size and patch number for a given habitat amount
Modifiable areal unit problem (MAUP)	When spatial aggregation of data based on sampling units that are "modifiable" leads to bias in inference owing to aggregation or zoning (location or shape of units) effects
Scale dependence	When the measured pattern or process varies with scale, such as differences in species richness measured in patches versus within entire landscapes
Spatial misalignment	When response or predictor variables (or both) are measured at different spatial scales, areal units or point locations

[a]All terms and definitions are taken from Didham et al. (2012), Dungan et al. (2002), Fahrig (2003), Gotway and Young (2002), Holland and Yang (2016), Openshaw (1984), Pacifici et al. (2019), Sandel (2015), Scheiner et al. (2000), Turner et al. (1989), Wiens (1989) and Wu (2004).

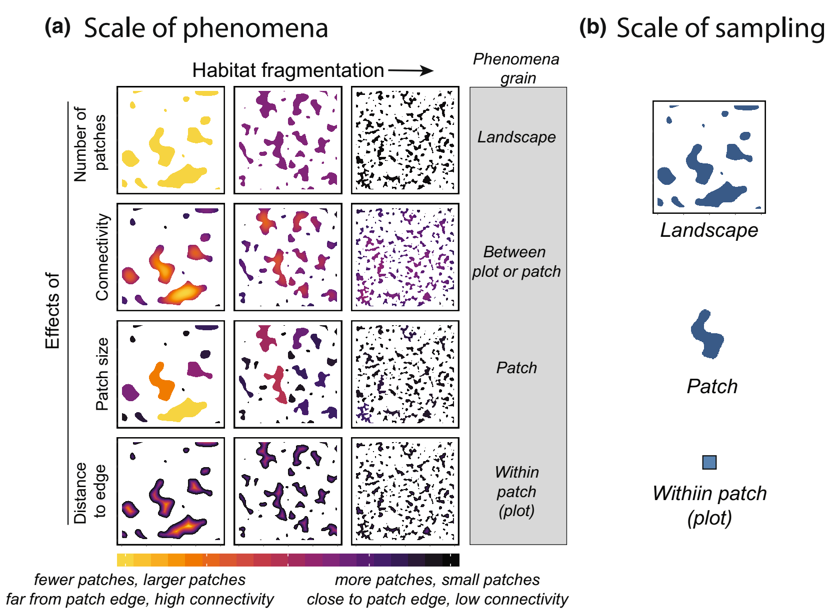
(Figure 1a). Yet, concerns remain regarding whether local effects can be interpreted in the context of entire landscapes (Fahrig et al., 2019). Ultimately, these conflicting views have led to debate regarding what sorts of empirical data provide evidence for understanding habitat fragmentation, what analyses and study designs are required for interpreting fragmentation effects, and more crucially, the importance of habitat fragmentation in conservation.

The problem of scale for interpreting the effects of habitat fragmentation is complicated, because scale is relevant to the mechanisms generating effects, the sampling that investigators use to capture potential patterns and the analyses used to isolate effects. In addition, the term "scale" is often applied loosely (reviewed by Scheiner et al., 2000; Sandel, 2015), but it might be intended to describe either of its primary components: grain and extent (Turner et al., 1989). We organize and evaluate these complexities by extending the three "dimensions" of scale envisioned by Dungan et al. (2002) to the problem of the effects of habitat fragmentation (Figure 1). First, the scale of the phenomenon describes the grain and extent of mechanisms driving the effects of habitat fragmentation. Second, the scale of sampling often varies among studies of fragmentation, where data are collected at the plot/point (i.e., within patch), patch or landscape grains, and sampled extents can vary considerably in relationship to the phenomena of interest. Third, the scale of analysis can vary, in terms of how sampling is summarized to determine the grain of response and predictor variables that attempt to quantify fragmentation patterns; what has also been termed the "focus" (Holland & Yang, 2016; Scheiner et al., 2000). Ultimately, identifying the scales of phenomena driving effects are essential for reliable understanding of fragmentation effects, but research has varied widely in the scales of sampling and analysis used, leading to uncertainty about whether inferences, extrapolation and prediction are reliable for understanding fragmentation effects (Fahrig, 2017; Villard & Metzger, 2014).

Here, we examine the issue of scale in habitat fragmentation research. We first identify the formal interdependence of relationships among spatial patterns in habitat at different scales that arise from habitat fragmentation. We then discuss each "dimension" of scale for fragmentation, focusing on challenges that might arise owing to interrelationships in pattern and process across scales. We end by providing guidance about how scientists can reliably ask questions, design studies and evaluate habitat fragmentation effects in the context of scale.

2 | INTERDEPENDENCE OF FRAGMENTATION PATTERNS WITH SCALE

> The key determinant of whether 'habitat fragmentation' can remain a cohesive framework lies in the concept of 'interdependence'. Didham et al. (2012)



(c) Scale of analysis

	Response variable		Explanatory variable
	Population	Diversity	
Landscape	Abundance	β, γ diversity	Number of patches
Neighborhood	Density	β, γ diversity	Number of patches
Between patch	Dispersal	β diversity	Patch connectivity
Patch	Occupancy	α diversity	Patch size
Within patch	Dispersion	α diversity	Distance to edge

FIGURE 1 The scale dimensions of habitat fragmentation research. By applying scale concepts summarized by Dungan et al. (2002), we argue that there are three general dimensions of scale when addressing habitat fragmentation effects: the scale of the phenomena driving effects, the scale of sampling and the scale of the analysis. Each dimension can be interpreted based on grain and extent. (a) Predictions that emerge from different grains of phenomena vary across landscapes that are increasingly fragmented. Predictions for each phenomenon are largely consistent at the landscape grain, but phenomena vary in expectations within landscapes and patches. For connectivity, we show a metapopulation metric (Supporting Information Equation S2) applied at the pixel sampling grain to account for "habitat availability" (see Supporting Information Section S1). (b) The scales of sampling range from plot to landscape grains and can vary widely in spatial extent (not shown). (c) The scales of analysis can vary based on changes in both the grain of the response variables and the predictor variables, also known as the "focus". Shown are examples based on population and biodiversity metrics.

Although habitat fragmentation is frequently considered a landscape-scale phenomenon, there are changes in spatial pattern that must co-occur within landscapes when fragmentation arises across entire landscapes, leading to what has been termed “interdependence” in habitat fragmentation research (Didham et al., 2012). Many metrics that are presumed to capture fragmentation change with the amount of habitat, such as the number of patches tending to vary in a nonlinear way with habitat loss, complicating interpretation (Fahrig, 2003). Here, we focus on the situation where the amount of habitat (and thus habitat loss) is constant, in order to isolate formal interdependence in fragmentation patterns.

Some of the earliest uses of the term “fragmentation” envisioned that it increased when the number of patches was greater because habitat was more “broken up” (Moore, 1962). Consequently, the number of patches for a given amount of habitat is one key metric that can capture the original intent of the habitat fragmentation concept, and this measure is quantified for entire landscapes (Fahrig, 2017). Yet even in those early studies, the interdependencies of spatial patterns were evident. For instance, Curtis (1956) showed that as the number of patches increased, average patch size declined, and more edge resulted. More generally, the breaking apart of habitat into multiple patches leads to three interdependent patterns that operate within landscapes.

First, as habitat fragmentation increases owing to an increase in the number of patches, the average patch size must decrease for a given amount of remaining habitat in the landscape. This relationship can be observed by noting that the average patch size, $\overline{A}_p$, across a landscape l is:

$$\overline{A}_p = \frac{A_l}{N_p}, \tag{1}$$

where A_l is the total area of habitat in landscape l, and N_p is the number of patches. If we hold the amount of habitat (A_l) constant and increase the number of patches N_p, the average patch size must decrease (Figure 2a). This relationship is linear in log–log space (Supporting Information Figure S1). Consequently, there is a direct relationship between habitat fragmentation for a given habitat amount and expected patch sizes across landscapes.

Second, the proportion of habitat near edges within patches must increase with increasing habitat fragmentation for a given amount of remaining habitat. This pattern arises because as average patch size decreases, the relative proportion of perimeter increases, and core area declines (Didham & Ewers, 2012). For instance, the edge-affected area, A_e, for a circular patch can be quantified as:

$$A_e = dE - \pi d^2, \tag{2}$$

where d is the distance at which edges affect the patch (i.e., the distance of edge influence), and E is the length of edge (Didham & Ewers, 2012). Consequently, the proportion of habitat area impacted by edge within a circular patch is:

$$\frac{A_e}{A_p} = \frac{d(2\pi r) - \pi d^2}{\pi r^2} = \frac{d(2r - d)}{r^2}, \tag{3}$$

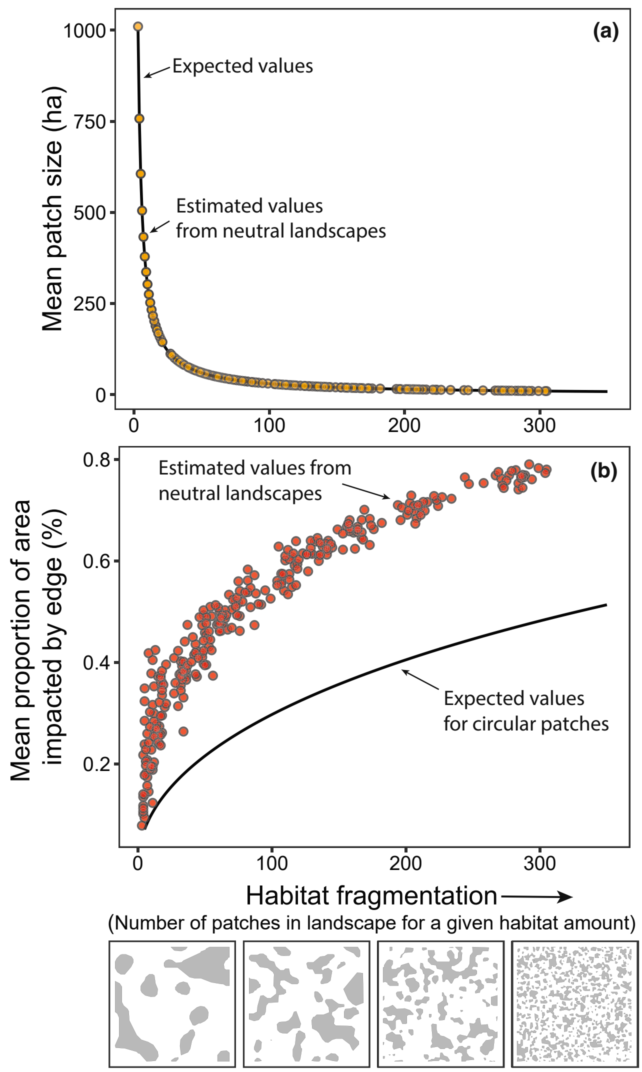


FIGURE 2 Interdependencies between habitat fragmentation (here, the number of patches in a landscape for a given habitat amount), patch size and edge, based on analytical relationships and revealed through neutral landscape models generated from clipped Gaussian random fields, GRF (for more, see the Supporting Information Section S2). Shown are examples taken from 600 landscapes, 10 km × 10 km, with 50 m resolution for a scenario of 70% habitat loss. Other amounts of habitat loss show the same qualitative pattern (see Supporting Information Figure S1). (a) As habitat fragmentation increases for a given amount of habitat, the mean patch size must decrease. The line shows the analytical expression taken from Equation 1, whereas the points show estimated mean patch size taken from GRFs. (b) As habitat fragmentation increases for a given amount of habitat, the mean proportion of area impacted by edge increases (shown is based on area within 50 m of the edge). The line shows the expected value for circular patches taken from Equation 3, whereas the points show estimates from GRFs. The difference between the points and line reflects patch irregularity (shape complexity).

where r is the radius of the patch. As the average patch size declines from habitat fragmentation (Equation 1), the radius r declines but d does not, leading to a greater proportion of edge-affected habitat

TABLE 2 The potential mechanisms of habitat fragmentation effects, their scales of phenomena, relationships with other scales, and potential scaling attributes that can alter expected effects.

Mechanism of fragmentation effects	Rationale	Primary grain of phenomena	Factors that mediate the spatial extent of effect	Relations to mechanisms operating at other scales	References
Edge effects	Changes in abiotic conditions, edge complementarity or geometric constraints	Within patch	Distance of edge influence	Landscape complementarity	Ries et al. (2004)
Patch degradation, extinction	Population size and demographic stochasticity alters extinction risk with patch size	Patch	Minimum patch size/minimum viable area	Between-patch rescue effects, "mega-patches"/"modules"	Hanski (1999); Fletcher, Reichert, et al. (2018); Chase et al. (2020)
Conspecific attraction/ aggregation	Behavioural aggregation imposes geometric constraints such that smaller patches are less frequently occupied	Patch	Range of species aggregation	Within-patch boundary effects	Fletcher (2006)
Dispersal success	Mortality during dispersal in non-habitat is greater than dispersal within habitat	Between patch	Mean dispersal distance, grain of fragmentation	Patch emigration/ immigration rates	Doak et al. (1992)
Changes in competition	Greater refugia from competition between patches than within owing to competition–colonization trade-offs	Between patch	Mean colonization distance	Patch extinction rates	Tilman et al. (1997)
Stabilization of predator–prey interactions	Movement/prey searching is hampered in non-habitat, leading to prey refugia	Between patch	Difference in dispersal distances of predators and prey	Patch extinction rates	Huffaker (1958)
Spreading the risk	Environmental disturbances/ stochasticity is less synchronous across than within patches	Landscape	Range of disturbance autocorrelation	Patch extinction rates	den Boer (1968); Kallimanis et al. (2005)
Geometric fragmentation effects	More, smaller patches are better capture aggregated distributions owing to greater spread of patch locations across landscape	Landscape	Ratio of extent of aggregation to grain of fragmentation	Patch-size effects from conspecific aggregation	May et al. (2019)
Landscape complementation	Access to spatially separated resources increases with number of patches owing to a greater proportion of edge	Landscape	Distances travelled for use of spatially separated resources	Edge complementarity	Dunning et al. (1992)
Habitat diversity	Greater resource variability across patches than within owing to non-stationary or autocorrelated environmental gradients	Landscape	Range of autocorrelation of gradient	Within-patch diversity	Lasky and Keitt (2013)

(Figure 2b). For non-circular patches, Equation 2 can be biased owing to irregularity in patch shape, yet a correction can be applied without loss of generality (Didham & Ewers, 2012).

Third, as the number of patches increases from habitat fragmentation, average isolation of remaining habitat increases. Confusion has nonetheless endured regarding how fragmentation impacts isolation (or conversely, structural connectivity) based on the grain of sampling and the different components of connectivity that might alter expectations (Saura & Rubio, 2010). When a plot or pixel within a patch is the sampling grain, fragmentation increases isolation owing to the breaking apart of habitat, wherein plots tend to be closer to non-habitat (Tischendorf & Fahrig, 2000). Yet when a patch is the sampling grain, an increase in fragmentation can sometimes cause a decrease in the mean nearest distance between patches, a commonly used metric for interpreting isolation (Tischendorf & Fahrig, 2000). Such patterns arise because nearest distances ignore the area within patches as being relevant for connectivity, which can lead to nonsensical conclusions on fragmentation and connectivity (Pascual-Hortal & Saura, 2006). When patch isolation accounts for the connected habitat a patch itself provides, increasing fragmentation causes metrics of structural connectivity to decline (Supporting Information Figure S2).

Given these interdependencies, what are the implications for interpreting habitat fragmentation effects? We illustrate some key challenges that emerge based on the dimensions of scale in habitat fragmentation research.

3 | THE DIMENSIONS OF SCALE FOR FRAGMENTATION EFFECTS

3.1 | Scales of phenomena

> Without a focus on the mechanisms giving rise to emergent patterns, much of the existing "habitat fragmentation" literature… [is] difficult to generalize.
> Lindenmayer and Fischer (2007)

BOX 1 Scales of phenomena and interdependence of fragmentation effects

The interdependence in spatial patterns of fragmentation can lead to similar expectations for responses generated by mechanisms operating at different grains. To illustrate, we use neutral landscapes (With, 1997) to alter habitat fragmentation and simulate the effects of fragmentation operating at different grains of phenomena using inhomogeneous Poisson point process models. Given that most investigations of habitat fragmentation focus on species distribution, abundance and diversity (Fahrig, 2017), such responses are, at their base unit, point locations of individuals for a given unit of time. Consequently, point processes provide a natural data-generating mechanism for this situation (May et al., 2019; Rybicki et al., 2020). A realization from this model generates random points in geographical space, wherein the probability density function is:

$$f(n, \mathbf{s}_1, \dots, \mathbf{s}_n) = e^{-\int_S \lambda(\mathbf{s})ds} \prod_{i=1}^{n} \lambda(\mathbf{s}_i), \quad \text{(B1)}$$

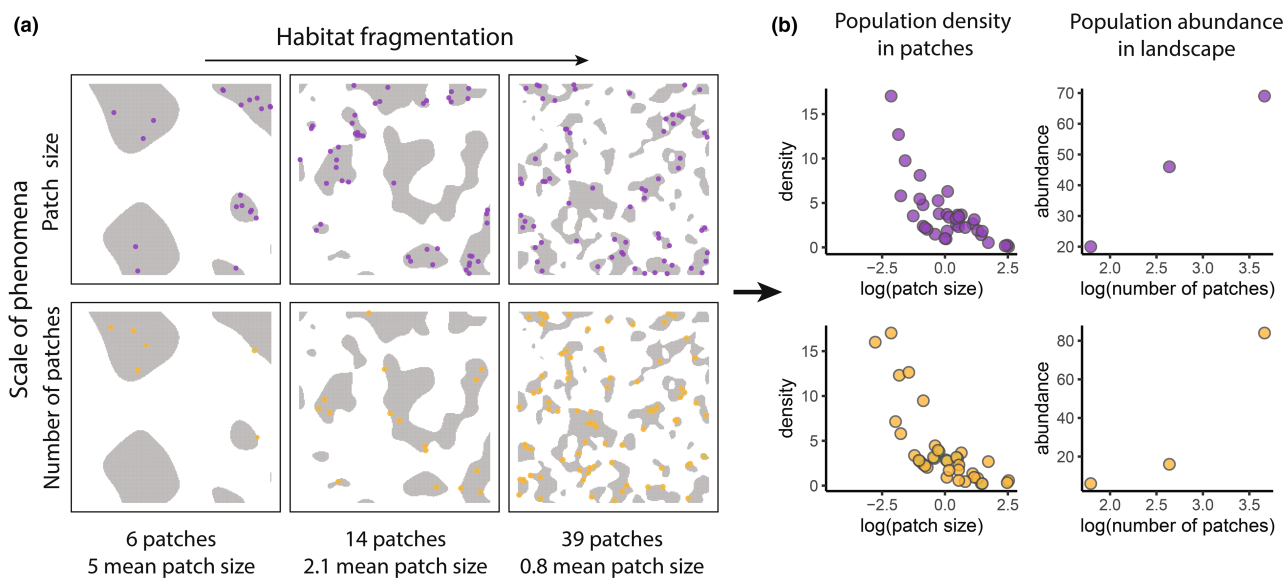
where n is the number of points, $\mathbf{s}_i$ is a vector that contains the coordinates of the ith individual location, and $\lambda(\mathbf{s})$ is the spatially varying intensity function that controls the expected number and location of points within any subunit in the region S (Cressie, 1993). We relate this point process to habitat fragmentation using a multi-level approach by making $\lambda(\mathbf{s})$ a function of the habitat in the landscape:

$$\lambda(s) = \exp\left[\alpha_0 + \mathbf{x}(\mathbf{s})'\boldsymbol{\beta}\right] \quad \text{(B2)}$$

where α_0 is the intercept, and $\boldsymbol{\beta} \equiv (\beta_1, \dots, \beta_n)'$ is a vector of coefficients associated with the n covariates. In this way, we can generate the effects of fragmentation across landscapes, patch size across patches, and edge effects within patches. With this model, we are not attempting to ask whether certain ecological processes (e.g., Table 2) generate habitat fragmentation effects. Instead, we are simply modelling situations where effects do occur at patch or landscape grains, and we do so in a way that can allow for interpreting spatial patterns across scales via realizations of the point process. Here, we contrast effects of patch size and the number of patches in the landscape on species abundance, because these two effects have generated much interest in the fragmentation debate (Fahrig et al., 2019; Fletcher, Didham, et al., 2018). For more details and comparisons, see the Supporting Information Section S3.

We illustrate two scenarios where the total amount of habitat across landscapes is constant. The first assumes that species abundance decreases with patch size (i.e., a negative patch-size effect), whereas the second assumes that abundance increases with the number of patches in the landscape (i.e., a positive effect of habitat fragmentation). Given that the mean patch size declines with the number of patches for a given amount of habitat (Equation 1), even when the patch (e.g., patch-size effect) is the true grain of phenomenon it will generate similar expectations to a model where the landscape (e.g., the effect of the number of patches) is the true grain of phenomenon (Box Figure 1). If both phenomena are operating, observed responses will be either magnified or attenuated, depending on whether the directionality of the phenomena is similar or conflicting (see Supporting Information Figure S3), which can lead to scale dependence in outcomes (Table 1).

BOX 1 Continued



BOX FIGURE 1 The interdependence of scales of phenomena. (a) For three landscapes that vary in the number of patches for a given amount of habitat (30% habitat in 10 km × 10 km landscapes), mean patch size (in square kilometres) declines with an increase in the number of patches. Negative patch-size effects (purple) and positive effects of the number of patches (orange) were simulated with inhomogeneous point processes using Equation B2 (for more, see Supporting Information Section S3). Dots illustrate one realization of these processes. (b) Summaries of population density at the patch scale and population size (abundance) at the landscape scale show similar observed patterns attributable to their fundamental relationships.

Several mechanisms have been proposed to explain fragmentation effects (Table 2). These mechanisms operate over different distances and areas that alter the spatial extent to which these phenomena manifest across landscapes. For instance, the distance of edge influence quantifies the spatial extent at which edge effects play out across landscapes (Ries et al., 2004). When these distances are large (e.g., forest beetle communities in New Zealand; Ewers & Didham, 2008), the effects of edge can be observed across large areas of patches and landscapes, where essentially entire patches are immersed in the effects of edge. When distances are small (e.g., microclimate in Amazonian fragments; Laurance et al., 2002), edge effects are localized, and their influence is likely to vanish as sampling grain increases.

Even when mechanisms are thought to operate at distinct spatial grains (e.g., patch, landscape), they are often related to other mechanisms operating at other grains and extents (Table 2). For example, patch extinction rates assumed to operate at the patch scale are often mentioned as a mechanism for fragmentation effects (Fahrig, 2017), yet patch extinction rates can be sensitive to rescue effects from other patches (Hanski, 1999), a between-patch process. Likewise, effects driven by landscape complementation (i.e., when access to spatially separated, and different, resources provides benefits; Dunning et al., 1992) are inherently linked to within-patch effects of edge complementation (i.e., when areas near edges provide access to spatially separated, and different, resources; Ries et al., 2004).

Different grains of phenomena lead to variation in expectations across landscapes (Figure 1a). Consider a scenario where there are different landscapes across a region, each of which contains variation in the number of patches and their size (Box 1). Phenomena operating at landscape grains (e.g., spreading the risk; Table 2; den Boer, 1968) generate predictions that vary across landscapes, but not across patches within landscapes. Phenomena operating at the grain of patches (e.g., patch extinction) generate predictions that vary across patches, resulting in variation in predictions across landscapes as well. Phenomena observable at within-patch grains (e.g., tree mortality near edges; Laurance et al., 2002) result in predictions that vary within patches, between patches and across landscapes. Yet because of the interdependencies among patch size, edge and the number of patches for a given habitat amount (Figure 2), patterns of responses across landscapes based on mechanisms operating at different grains can be very similar (Box 1; Supporting Information Figures S2 and S3). Consequently, to gain a reliable understanding of habitat fragmentation effects, we need approaches that use scales of sampling and analysis that can capture the interdependence of scale(s) of the expected phenomena.

3.2 | Scales of sampling

> One of the most challenging and fascinating areas … is the synthesis of spatial data collected at different spatial scales. Gotway and Young (2002)

To interpret the effects of habitat fragmentation, different scales of sampling, in terms of both the grain (e.g., plot, patch) and the extent of sampling (e.g., different landscape sizes and regions), have been used. Geographers and statisticians have long emphasized trade-offs in the support of sampling, or changes in the size and shape of sampling units (Gotway & Young, 2002), such as plot, patch and landscape sampling units. Such trade-offs have also been acknowledged repeatedly by ecologists (e.g., Fritsch et al., 2020; Wiens, 1989).

To contextualize potential trade-offs, we contrast different sampling grains in terms of whether they are "arbitrary" or "natural" sampling units. Arbitrary units are those that are potentially modifiable in size or shape, whereas natural units are those that have a distinctive size or shape based on the environment or on the data being collected. Plot-scale sampling grains are beneficial for standardizing sampling effort, because non-standardized effort can lead to patterns driven by effort alone (Coleman et al., 1982). However, the size and shape of plots can be arbitrary, such that responses might be interpreted on spatial units that might or might not be meaningful biologically. Patch-scale sampling is often, but not always, a natural sampling unit, because patch boundaries can provide a process-driven means of delineating sampling frames. Yet sampling effort often varies with patch size, which can lead to inferences that, if not addressed appropriately, are driven by sampling effort alone. Landscape sampling grains are modifiable areal units that can be arbitrary in size, shape or location. When sampling grains are modifiable in area, it can lead to the modifiable areal unit problem (MAUP; Table 1; Openshaw, 1984), which can affect analysis and interpretation of patterns (Figure 3; see Section 3.3 Scales of Analysis).

Changing sampling grains and extents leads to trade-offs in information loss and gain (Wiens, 1989). As the sampling grain increases, information is pooled (e.g., summed or averaged), leading to a loss of fine-scale information and variability (Fritsch et al., 2020; Newman et al., 2019). Given that increasing the size of the sampling unit involves the aggregation of information, the interpretation of fragmentation effects can be affected by aggregation alone (Figure 3). For instance, systems might appear to be more predictable when aggregating data (Levin, 1992), yet the reliability of correlation coefficients, tests of significance and multiple regression can be compromised with data aggregation (e.g., Fotheringham & Wong, 1991; Gotway & Young, 2002). Aggregating data can make it challenging to capture fine-grain phenomena driving fragmentation and related confounding issues, because such effects are typically summarized based on average conditions, ignoring larger moments of variability (Newman et al., 2019). Landscape sampling units result in a lack of information within landscapes to capture fine-scale mechanisms that might drive fragmentation effects (Fritsch et al., 2020; Levin, 1992). Changes in sampling extent can also alter conclusions, particularly when extents do not capture the entire variation of the environment of interest (Sandel, 2015). In fact, Wu (2004) showed that the effects of changing the sampling extent were even less predictable than that of increasing grain size. The decisions on sampling scale have direct consequences for the scales of analysis.

3.3 | Scales of analysis

> In particular, we see that different analyses of fragmentation effects applied to the same data may lead to apparently contradictory results. Rybicki et al. (2020)

Scales of analysis have varied considerably in habitat fragmentation investigations. This variation arises both in terms of how the sampling and predictor variables are summarized for analysis, or the grain of responses and predictor variables, which has also been termed the "focus" of the analysis (Holland & Yang, 2016; Scheiner et al., 2000). Ideally, grains of analysis would correspond to the grains of ecological phenomena (Wu, 2004). However, given that the underlying grains and extents of phenomena are generally unknown before the design of investigations, approaches for analysis that can capture phenomena operating at different scales are needed.

Given that both response and predictor variables can be analysed at different grains that may or may not align with the scales of the underlying phenomena, the potential for scale mismatches needs to be addressed. There are two related issues that broadly fall under what has been termed the change of support problem: (1) spatial misalignment; and (2) MAUP (Gotway & Young, 2002; Pacifici et al., 2019). Spatial misalignment can operate in several ways, in which either response or predictor variables (or both) are measured at different spatial grains or locations. It can be particularly relevant to habitat fragmentation where the response variable is mismatched in space (or time) with the predictor variable. For instance, responses in sampling plots near the boundary of a delineated landscape might be driven by habitat beyond the landscape boundary (for an example, see Figure 4b). MAUP summarizes two problems: the aggregation and zoning effects (Gotway & Young, 2002). In the context of habitat fragmentation, the aggregation effect can occur when sampling within landscapes is pooled to have an overall summary of the response variable for the landscape (e.g., γ-diversity); similar aggregation can occur for predictor variables. The zoning effect can occur when there are differences in the shape or location of the sampling units; such effects can arise when overlaying landscape grids at different locations on a landscape (Figure 3; Wu et al., 2002). In both cases, MAUP can fundamentally change conclusions and lead to biases if not considered carefully (Figure 3; Jelinski & Wu, 1996).

To limit these potential problems regarding scales of analysis, several approaches have been proposed. First, Jelinski and Wu (1996) argued that the grain for analysis should be the finest resolution of the data (i.e., the grain of sampling) to reduce potential effects of MAUP (see also Pacifici et al., 2019). Tuson et al. (2019) emphasized that the grain of sampling should be defined by the process that is expected to drive patterns. Given that fragmentation effects can sometimes be driven by mechanisms operating at the (within-)patch grains (Table 2), we argue that response data should ideally be analysed at a fine grain in most situations, such as plots within patches. Second, "optimal zoning systems" (Openshaw, 1984), where landscape boundaries are varied to

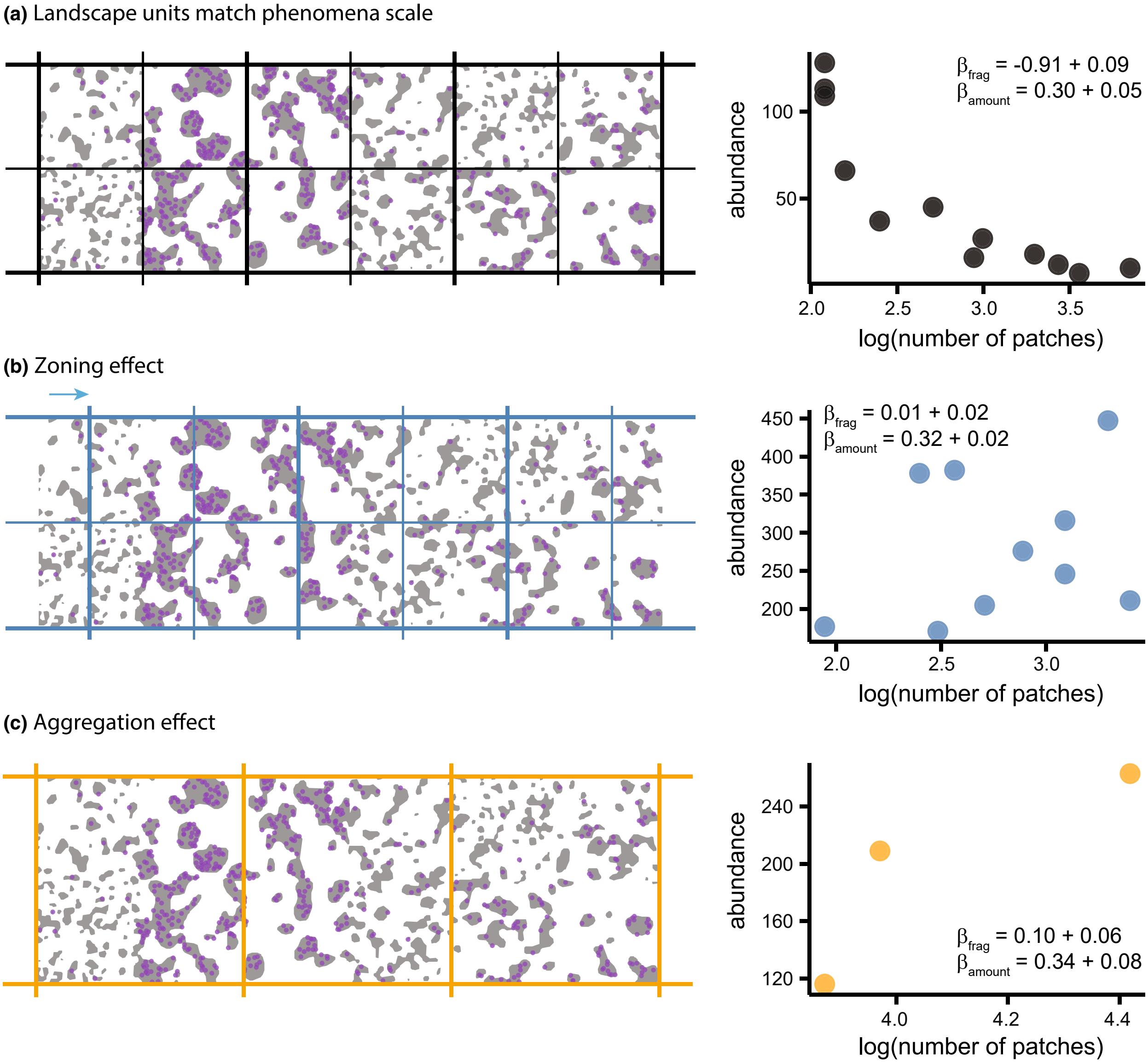


FIGURE 3 The modifiable areal unit problem and effects of habitat fragmentation per se across landscapes. With landscape-scale sampling and analysis, the delineation of the landscape is modifiable, such that the landscape could have been delineated in other ways. (a) A scenario whereby landscape delineation matches the grain and location of the true fragmentation phenomenon. The black grid shows the landscapes considered (10 km × 10 km landscapes, 50 m resolution, *c.* 70% loss), and purple dots are a realization of an inhomogeneous Poisson point process that describes a negative effect of the number of patches in each landscape (see Box 1; Supporting Information Section S4). In this case, the summary of population abundance for each landscape reliably captures the true negative effect of fragmentation. (b) A zoning effect attributable to the location of grids, whereby the chosen landscape grid size matches the grain of the phenomenon, yet grid placement is spatially mismatched (blue arrow). In this case, population abundance for each landscape (blue) does not capture the true effect. (c) An aggregation effect, whereby the chosen landscape grain is larger than the true underlying grain of the phenomenon. In this case, the summary of population abundance for each landscape (orange) also does not capture the true effect. For each panel, we illustrate how inferences might change by fitting a generalized linear model (log link, Poisson error distribution), where we consider both the effects of the number of patches (β_{frag}) and the amount of habitat (β_{amount}) as covariates.

identify the optimal analysis grains (Figure 4b), could be used in similar ways as what has been termed identifying the "scale of effect" in landscape investigations (Figure 4a; Holland & Yang, 2016). Third, hierarchical, geostatistical and point-process models can be "up-scaled" in some situations without biases arising from aggregation effects (Cressie, 1993; Gotway & Young, 2002), but such techniques have not yet been embraced for understanding fragmentation.

4 | IMPLICATIONS

4.1 | Interpreting effects of habitat fragmentation

Habitat fragmentation for a given amount of habitat loss leads to changes in spatial pattern within and across landscapes that are fundamentally related (Figure 2; Supporting Information

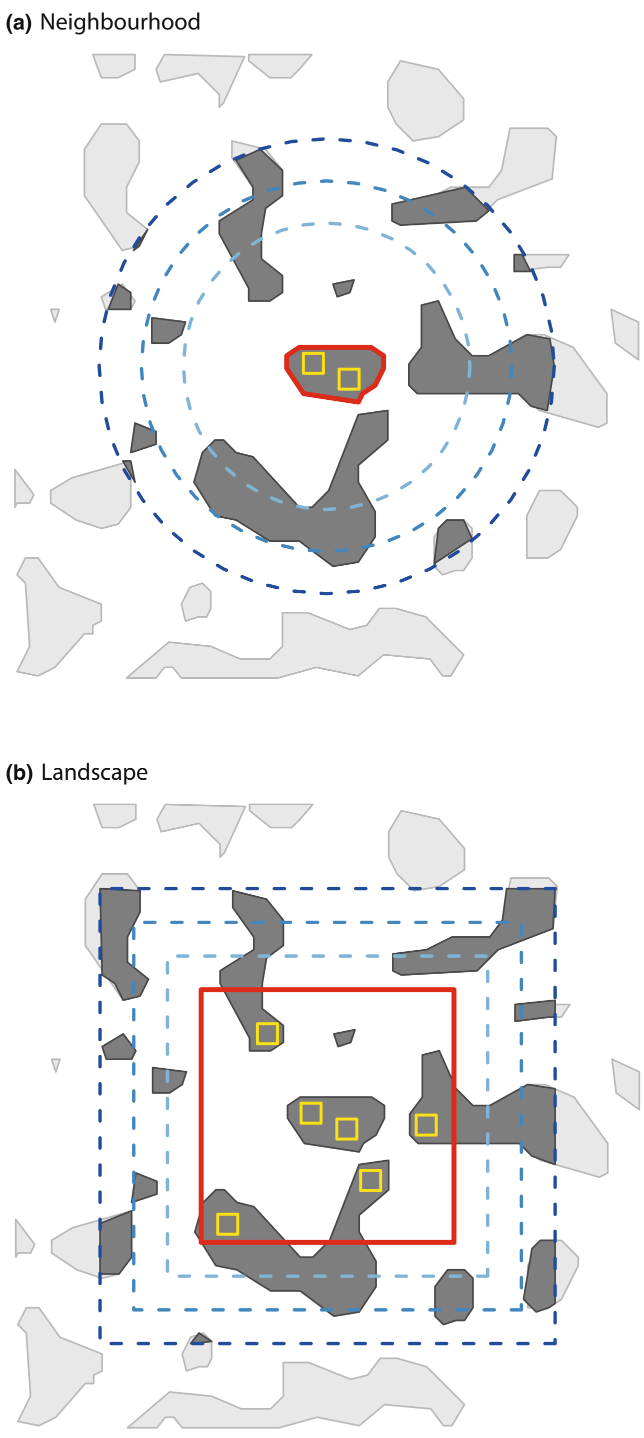


FIGURE 4 Ecological neighbourhoods, entire landscapes and identifying the "scale of effect" for habitat fragmentation. In (a), the ecological neighbourhood concept is assumed, whereby buffers of different sizes (dashed circles) around a focal patch (red) or plots (yellow squares) are compared to identify the neighbourhood size that best explains variation sampled in plots or patches (i.e., the "scale of effect"). In (b), a landscape concept is assumed, whereby buffers of different sizes (dashed) around a focal landscape (red) can be compared to identify the landscape size that best explains variation sampled in plots or patches (yellow squares).

Figures S3 and S4). Embracing these interdependencies is essential to interpret habitat fragmentation effects across landscapes reliably. For a given amount of habitat, fine-grain processes that drive responses to patch size cause variation in species responses across landscapes owing to interdependence of patch size and the number of patches in the landscape (Box 1). Landscape-scale phenomena can generate variation in responses measured among patches as well (Box 1). The fundamental interdependencies shown here demonstrate that patch-scale evidence is highly relevant, although not identical, to interpreting landscape-scale effects (and vice versa).

When would these relationships break down? Differences might arise in four general scenarios that lead to scale-dependent conclusions. First, when multiple processes operate that differ in grain and extent, such processes might either magnify or attenuate observed responses (Supporting Information Figure S3), which could lead to scale-dependent outcomes (Sandel, 2015). In these situations, conclusions can be misleading when landscape designs ignore patch effects and vice versa. Consequently, study designs that can capture effects at both the patch and landscape scales are needed (e.g., Halstead et al., 2019). Second, "geometric" effects of fragmentation (Table 2) could arise across landscapes that might be independent of patch-scale effects. May et al. (2019) illustrated these effects based on species aggregation arising from stochastic processes. Yet similar issues arising from deterministic processes (e.g., conspecific attraction) generate similar patterns across patches and landscapes (Fletcher, 2006). Third, when aggregation of data is mismatched with the underlying grain or location of the ecological phenomena, MAUP can cause relationships to break down (Figure 3). Fourth, nonlinearities in some relationships can lead to scale dependence in outcomes (Sandel, 2015), such as situations when patch-size effects are stronger when patches are small (e.g., Supporting Information Figure S5), leading to different rates of accumulation of individuals or species based on patch-size distributions within landscapes. Taken together, understanding fragmentation requires both patch and landscape perspectives to reveal mechanistic underpinnings and for reliably estimating pattern and process at multiple scales.

The relationships shown here do not imply that patch-size and edge effects are the same as effects from the number of patches for a given habitat amount. Rather, owing to the interdependence in spatial patterns in the same landscapes, they are often related (Fletcher et al. 2023). After controlling for the amount of habitat, fragmentation effects based on the number of patches generate expectations for patterns of patch-size and edge effects and vice versa in the same landscapes (Box 1). However, patch-size and edge effects can also occur irrespective of the number of patches in a landscape. It remains unknown whether the generation of patch-size and edge effects from habitat fragmentation per se are any different biologically compared with effects generated from other types of human-modified landscape changes (e.g., habitat loss alone).

BOX 2 Scale and study designs for interpreting habitat fragmentation effects

We contrast three study designs that could be applied to interpret landscape-scale fragmentation effects: landscape designs, focal-patch/focal-plot designs and multi-level designs. In landscape designs, sampling within landscapes is first pooled to estimate a response variable for the entire landscape (Figure 4b), and the response variable is then modelled as a function of landscape predictor variables (e.g., number of patches). In a focal-plot design, the responses measured in the plot (or the patch for focal-patch designs) are modelled directly as a function of the surrounding landscape neighbourhood (e.g., number of patches within the neighbourhood; Figure 4a). In focal-plot designs, inference on responses at the grain of the entire landscape can be accomplished based on derived estimates from models. In multi-level designs, responses measured in the plot are modelled directly as a function of both the plot and the delineated landscape (e.g., in Figure 4b, plots are the response variable). In this way, habitat fragmentation per se could be interpreted as effects of the landscape surrounding a plot, or inference at the grain of the entire landscape can be considered based on derived estimates or through a secondary analysis of pooled data within landscapes.

Each of these designs can be described based on the three dimensions of scale, and each has benefits and limitations (Box Table 1). Overall, the primary benefit of landscape designs is that the grain of the response variable is the landscape, which provides a transparent means to ask questions regarding the cumulative effects of fragmentation across localities in a landscape. Yet there are challenges in addressing several scaling problems, including problems associated with MAUP (Figure 3). In contrast, focal-plot and multi-level designs are better positioned for addressing scaling issues and confounding as a function of scale, yet inference at the landscape grain is based on derived estimates.

BOX TABLE 1 Study designs implemented for interpreting the effects of habitat fragmentation, their dimensions of scale, and their benefits and limitations with regard to scaling issues.

	Study design		
Characteristic	Landscape	Focal plot	Multi-level
Grain of sampling	Landscape	Plot (or patch)	Plot
Grain of phenomenon best captured	Landscape	Multi-scale	Multi-scale
Grain of analysis	Landscape	Multi-scale	Multi-scale
Analysis strategy[a]	Pool sampling first, then model	Model first, then pool to derive estimate	Model first, then pool to derive estimate or pool first, then model
Benefits	Response variable at the grain of landscape Assessment of cumulative effects of fragmentation	Allows for multi-scale inference on phenomena Control for local confounding Reduces problems of aggregation and zoning effects of MAUP Reduces problem of spatial misalignment of predictor variables	Allows for multi-scale inference on phenomena Control for local confounding Reduces problem of aggregation effect of MAUP Assessment of cumulative effects of fragmentation possible
Challenges	Loss of information for interpreting multi-scale phenomena Potential bias from aggregation and zoning effects of MAUP Appropriate delineation of landscape extent	Landscape-grain inference only from derived estimates Spatial dependence in response variable	Potential bias from zoning effects of MAUP Appropriate delineation of landscape extent Spatial dependence in response variable

[a]Analysis strategy describes how data are considered for interpreting fragmentation effects, where focal-plot and multi-level designs provide inference for analysis response grains at the plot/patch, but can be used to calculate derived estimates for the landscape with nested sampling.

4.2 | Guidance for study design

Reliable inference based on different study designs aimed at interpreting habitat fragmentation effects involves trade-offs (Box 2). Field experiments provide a rigorous means to isolate effects at different scales and to control for potential bias (Haddad et al., 2015), but in practice landscape-scale experiments are rare. Instead, much of the evidence of habitat fragmentation effects has come from non-experimental studies that vary widely in study design.

For non-experimental investigations, delineation of a landscape is a key first step because it provides the lens for enumerating loss and fragmentation. This step can be based on the concept of the ecological neighbourhood (Addicott et al., 1987) or by delineating a landscape based on other general criteria, such as considering watersheds as landscapes or overlaying grids across regions (Figure 3). The ecological neighbourhood concept leads naturally to considering "focal patch" designs for interpreting habitat fragmentation effects (Brennan et al., 2002) (Box 2; Figure 4a). Both landscape and focal-patch designs have been applied to understand habitat fragmentation effects (e.g., Betts et al., 2019; Puttker et al., 2020; Trzcinski et al., 1999). In focal-patch designs, the landscape extent can be optimized to best explain responses based on model-fit criteria (Figure 4a; Holland & Yang, 2016), and some scaling challenges can be addressed (Box Table 1). Yet in many landscape investigations, the ability to delineate the landscape is often constrained (De Camargo et al., 2018), although the focus of the predictor variables could potentially be optimized with similar approaches (e.g., using model-fitting criteria) to those for estimating scale of effect (Figure 4b; Holland & Yang, 2016). Multi-level designs delineate landscapes in a similar way to landscape designs, but sampling is nested within landscapes, which allows for estimating effects arising at multiple scales (e.g., Fletcher et al. 2023) . Finally, we note that some studies have not delineated landscapes but aggregate data in different combinations within a region to interpret how species richness might be related to the number of patches for a given amount of aggregated habitat (e.g., Riva & Fahrig, in press). Such studies provide important insight into potential scale dependence arising from data aggregation and MAUP but do not provide inference for real landscapes.

Regardless of how landscapes are delineated, we recommend that sampling occurs at the plot or patch grain whenever possible, such that multi-scale effects can be determined. Some landscape studies are constrained by sampling protocols whereby information is pooled across the entire landscape during data collection (e.g., De Camargo et al., 2018). However, such pooling limits inferences on habitat fragmentation effects, because mechanisms operating within landscapes can alter outcomes across entire landscapes and vice versa (Supporting Information Figures S3 and S4). By sampling at the plot (or patch) grain, researchers have the ability to control for sampling and environmental effects operating within landscapes, address some scaling issues and deliver richer insight into the extents of phenomena generating effects (Box Table 1). We encourage the identification of optimal neighbourhood and/or landscape grains (Figure 4) and reporting of effects operating both within and across landscapes both to interpret the potential reasons for fragmentation effects and to provide insight regarding the power of designs to identify landscape-scale effects.

4.3 | Scale and questions for habitat fragmentation research

The effects of habitat fragmentation can be determined based on different grains of sampling and analysis. This will enable ecologists to answer different questions about effects of habitat fragmentation. First, effects of habitat fragmentation can be caused by phenomena operating within landscapes (Table 2), such that responses observed at a patch grain might be impacted by fragmentation at the landscape scale. In this way, the number of patches in a landscape for a given amount of habitat might lead to local variation in species abundance, diversity, etc., that is measured across plots or patches (e.g., Puttker et al., 2020; Saura, 2021). Such effects naturally lead to questions regarding the degree to which landscape fragmentation explains more or less variation than local effects, such as habitat structure within patches or other patch characteristics (Thornton et al., 2011) and whether patch-scale effects can predict effects across entire landscapes (Fletcher et al. 2023). Second, cumulative effects can arise when pooling sample units within a landscape (i.e., the response grain is the entire landscape). Such effects lead to questions that can be similar in scope to the single-large versus several-small (SLOSS) debate (Simberloff & Abele, 1976). Both effects arise from habitat fragmentation per se, but their implications for ecology and conservation might differ. We encourage clear reporting of these different types of fragmentation effects (and the dimensions of scale considered) and suggest the former effect be considered a component effect of habitat fragmentation per se, whereas the latter be considered a cumulative effect (also termed "local" and "landscape-wide" effects; Tscharntke et al., 2012). Explicitly acknowledging component and cumulative effects of habitat fragmentation is necessary for understanding the scope of inference for investigations.

4.4 | Moving forward

Habitat fragmentation effects are diverse, and their mechanisms can span a wide range of spatial and temporal scales. Advancing our understanding of habitat fragmentation requires scale to be embraced, which can be clarified by the dimensions of scale for fragmentation we describe here. These dimensions emphasize the interdependence among scales and highlight the need for study designs that can capture both patch and landscape phenomena.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article because no datasets were generated or analysed during the present study.

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BIOSKETCH

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SUPPORTING INFORMATION

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

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