

How does the scale of sampling affect conclusions on habitat fragmentation and what can we do about it?

Addressing the problem of scale that emerges with habitat fragmentation

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Where habitat fragmentation occurs, does the scale of sampling and analysis affect the resultant predictions, inferences, and extrapolations? How can researchers best identify and describe affects of habitat fragmentation at the plot, patch, and landscape scales? The authors explore the ways in which differences in scale among phenomena, sampling, and analysis can impact the studies of habitat fragmentation where habitat loss is constant. Additionally, they evaluate different sampling and analysis approaches to address research questions at various scales.

How does patch size relate to scale of phenomena and how does this impact study design?

- The proportion of a patch that is impacted by edge effects increases as patch size decreases because patch radius decreases with patch size, but the size of the edge effect is unchanged.
- Sampling scale impacts the scale of analysis. Large-scale phenomena may be missed with only patch sampling, while fine-scale variation across a landscape may be glossed over by data aggregation. Fragmentation effects may be missed with mismatch between the extent of sampling and of fragmentation phenomena.
- The number of patches across a landscape is inter-related to the patch size. Landscape units should match the scale of the expected phenomena.

What are the main considerations for sampling and analysis to describe phenomena accurately?

- Data should generally be analyzed at the within-patch plot or other fine-grain scale. Choosing the scale of analysis can be guided by the scale of the expected fragmentation mechanism. However, different phenomena may act at different spatial scales.
- Care should be taken to avoid a zoning effect, which can confound data through a spatial mismatch between plot and phenomenon, despite a landscape plot scale match.
- Landscape scale should be small enough to avoid the aggregation effect, whereby phenomena act at finer spatial scales than the sampling plot size.

Are multi-level sampling techniques useful? What care needs to be taken when reporting results?

- Researchers should design studies that aim to evaluate both patch-scale and landscape-scale effects. Investigating at a variety of scales will provide data on biological mechanisms, processes, and patterns resulting from habitat fragmentation.
- Multi-level study designs include fine and broad scale data by nesting patches within landscapes. The authors recommend this approach because researchers can use it to determine multi-scale effects.
- Component (fine-scale, local) and cumulative (pooled, landscape) effects should be clearly reported, as they impact the scope of inference for study findings.

Research Approach/Methods

- In this review and perspective article, the authors use published studies to discuss the challenges of sampling, interpreting, and analyzing phenomena associated with habitat fragmentation that act at different spatial scales.
- They then use a model that changes patch number and size while holding area constant to show how a mismatch in the scale of sampling with the scale of the phenomena it is meant to describe or investigate will lead to incorrect or biased results.
- Finally, they describe the benefits and challenges of three scales of sampling and recommend when each type may be most suitable for use.

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

Images

RANK 1

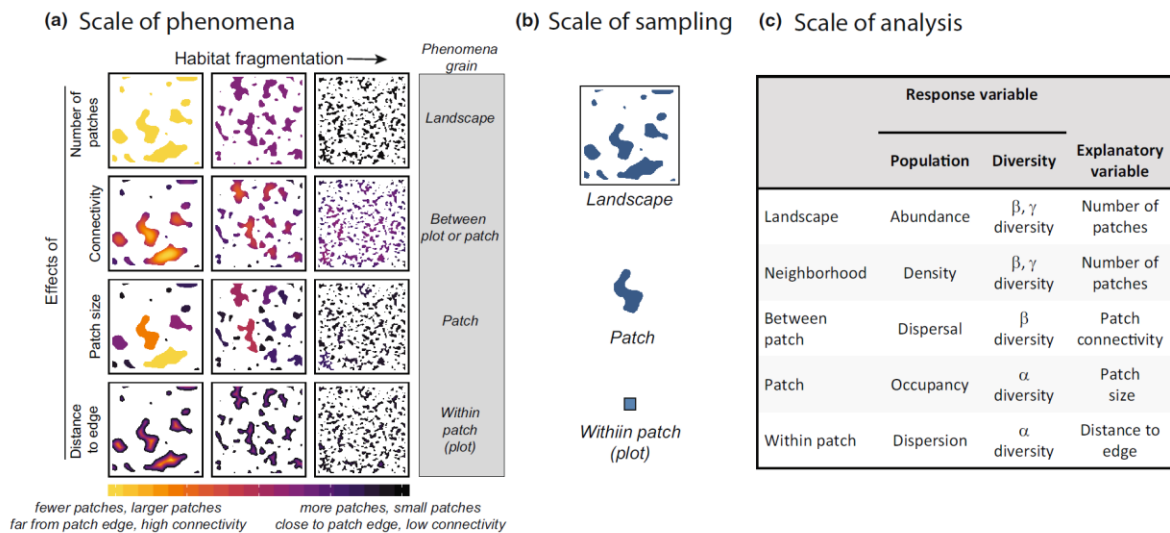
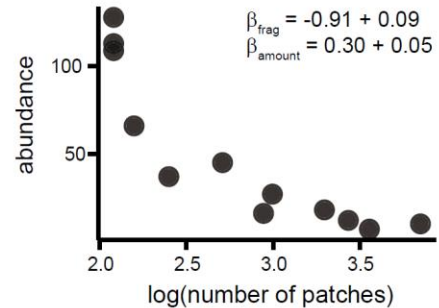
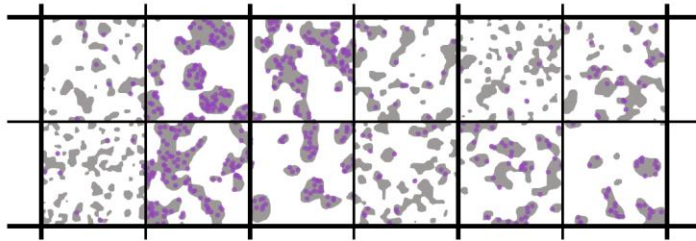


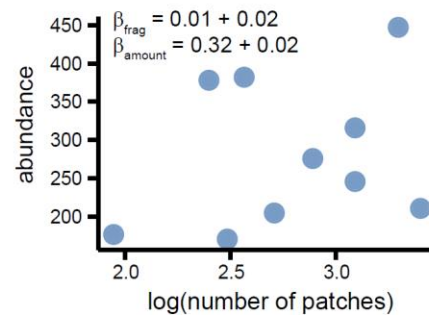
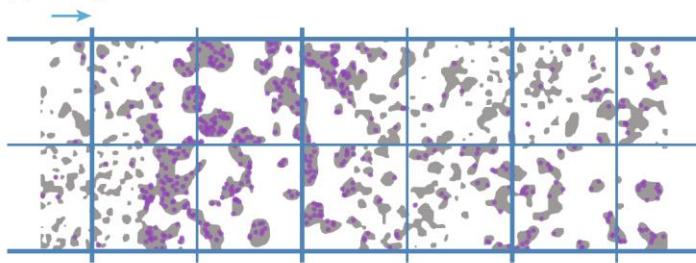
FIGURE 1 in Fletcher et al. 2023. The scale dimensions of habitat fragmentation research. By applying scale concepts summarized by Dungan et al. (2002), we argue that there are three general dimensions of scale when addressing habitat fragmentation effects: the scale of the phenomena driving effects, 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.

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(a) Landscape units match phenomena scale



(b) Zoning effect



(c) Aggregation effect

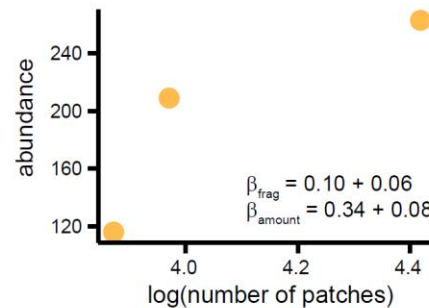
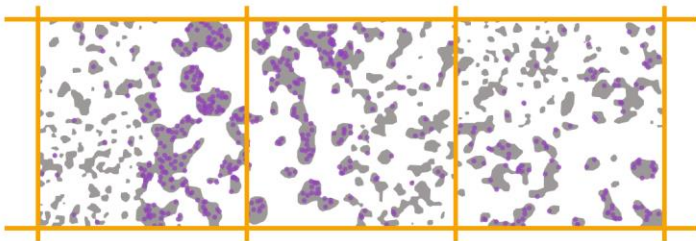


FIGURE 3 in Fletcher et al. 2023. The modifiable areal unit problem and effects of habitat fragmentation per se across landscapes. With landscape-scale sampling and analysis, the delineation of the landscape is modifiable, such that the landscape could have been delineated in other ways. (a) A scenario whereby landscape delineation matches the grain and location of the true fragmentation phenomenon. The black grid shows the landscapes considered ($10 \text{ km} \times 10 \text{ km}$ 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.

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TABLE 1 in Fletcher et al. 2023. Scale terms and concepts^a relevant to habitat fragmentation, organized based on the components, dimensions and challenges of scale.

Term	Description
<i>Scale and its components</i>	
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)
<i>Dimensions of scale</i>	
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
<i>Fragmentation and scale concepts</i>	
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
<i>Scale challenges and potential biases with fragmentation</i>	
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

^aAll 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).