Making statistics biologically relevant in fragmented landscapes

Robert M. Ewers, Charles J. Marsh and Oliver R. Wearn

Imperial College London, Silwood Park Campus, Ascot SL5 7PY, UK

The biological impacts of habitat fragmentation are routinely assessed using standard statistical modelling techniques that are used across many ecological disciplines. However, to assess the biological relevance of fragmentation impacts, we must consider an extra, spatial dimension to the standard statistical model: the biological importance of a significant and well supported model with large effect sizes crucially depends on the configuration of habitat within the study area. We argue that mapping the outputs from statistical models across a study area generates biologically meaningful estimates of fragmentation impacts. Integrating traditional statistical approaches with geographic information systems will facilitate rigorous comparisons of fragmentation impacts between taxa, studies and ecosystems.

Complexity of habitat fragmentation research

Habitat loss and fragmentation are widely recognised as dominant threats to biodiversity around the world [1–3] and habitat fragmentation has become the single largest topic of research in conservation biology [4,5]. Yet despite intense research effort into fragmentation effects and a vast and diverse literature written on the subject, there is still no comprehensive meta-analysis of fragmentation impacts. This might seem surprising for such a large field of study, but it arises from the composite nature of fragmentation [5–8]: it encompasses, for example, changes in habitat amount, patch size, patch isolation and exposure of patch edges to a novel matrix habitat.

Currently, there is no way of comparing the outcomes of studies that investigate the many different aspects of fragmentation. For example, is the impact of patch size on blue-winged macaws *Primolius maracana* in Brazilian Atlantic Forest [9] greater or less than the impact of isolation on populations of the red-backed vole *Clethrionomys gapperi* in the USA [10]? And how do these impacts compare to that of habitat edges on the beetle *Xylechinus pilosus* in Finland [11]? Although a seemingly incongruent set of studies, these all investigate the impacts of habitat fragmentation on individual species, and for studies of habitat fragmentation to form a coherent literature it is imperative that we find a way of directly comparing studies and results as diverse as these.

Individually, the various components of fragmentation can be subjected to meta-analysis [12–15]. However, a shortcoming of meta-analyses is that they only include a highly selective subset of the various aspects of fragmentation. For example, conducting a meta-analysis on patch size and isolation [13] tells us nothing about how these impacts compare to those of habitat edges on species [14]. In fact, studies of edge effects cannot currently be incorporated into a meta-analysis of area effects, even though it has been shown that edge effects generate many area effects observed in fragmented regions [16–18]. This issue is complicated by the facts that some taxa are negatively affected by habitat fragmentation whereas others benefit [6], and that different taxa can simultaneously respond to more than one component of fragmentation [18].

Combining the data gathered in thousands of fragmentation studies to form a defensible estimate of the impact that habitat fragmentation is having on biodiversity is a daunting task, but we argue that it is an achievable one. To achieve this will require researchers to make the leap from reporting statistical models, *P*-values and effect sizes to assessing the biological relevance of their statistical models. Here, we show how this can be done by amalgamating statistics with geographic information systems (GIS), thereby making integrated assessments of the impacts of habitat loss and fragmentation that directly incorporate real-world patterns of habitat configuration. Quantification of the biological relevance of statistical models will generate metrics that are comparable among species and studies, paving the way to a comprehensive meta-analysis of fragmentation impacts.

Biological relevance of statistics in fragmentation studies

To ask whether existing statistical approaches are appropriate for assessing fragmentation impacts, we must first be clear about what we want to know. In many fragmentation studies the goal is to determine if fragmentation has a significant effect on some ecological parameter. For example, does population density change with patch size? In this situation, standard hypothesis testing is appropriate and will tell the researcher if the patterns in the observed data deviate from a null expectation [19]. However, the value of such a simplistic question is limited and should be challenged. Indeed, in many cases it is self-evident that some effect of fragmentation is inevitable, leaving a null hypothesis as a “straw man” [20]. Simply knowing the statistical significance of the relationship between density and patch size does not help us to gauge the biological importance of that effect [21]. Rather, the magnitude of the effect is far more valuable information [20]. A significant, but small, effect should not influence a management plan in the same

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Corresponding author: Ewers, R.M. (r.ewers@imperial.ac.uk)

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way that a significant, but large, effect should. To quantify the difference between these two options, we can use the statistical effect size, a measure of the practical significance of an observed effect [20,22]. Most simply, this could be visualised as the difference in density between a small and a large patch; a small difference will have little practical significance, whereas a large difference does.

However, even an assessment of statistical effect size remains of largely theoretical concern until an additional aspect is considered, that of spatial habitat configuration. For example, a manager might have to decide whether or not a relationship between density and patch size demands specific management actions on the ground. To make a defensible decision, the magnitude (and significance) of the patch size effect must first be assessed, but then the relevance of this effect would have to be quantified by considering the actual prevalence of different patch sizes across the study area in question. In two study areas that have the same total amount of habitat, a reduced density in small patches will have a bigger net impact on population sizes in a study area in which the habitat is finely subdivided into small patches than in a study area in which the habitat is concentrated in one or a few large patches. In both study areas, there might be the same negative effect of fragmentation on the density of a species that is statistically significant and has a strong effect size, but it is the configuration of habitat in the study area that ultimately determines the total impact of fragmentation on population size.

Edge effects provide a further illustration of why statistics alone give little insight into the biological impacts of habitat fragmentation. The strength of an edge effect is a combination of two factors termed extent and magnitude, the distance to which the edge effect penetrates a fragment and the amplitude of the effect, respectively [15,23]. Taken individually, it is possible to compare the extent and magnitude of edge effects among species, ecological phenomena and studies [14,15,24]. However, the extent and magnitude of edge effects are not correlated [23], so it is not at all clear whether an edge effect of large extent and small magnitude has a greater, equal or lesser total impact than an edge effect of small extent and large magnitude. Edge extent and magnitude are important components of the same aspect of habitat fragmentation, but to estimate the total impact of habitat edges on biodiversity we need more information than statistical models alone can provide. Crucially, the total impact will depend on the prevalence of edges and the shape of the fragments within that study area [25–27].

Combining statistics with maps

Habitat maps are a ubiquitous feature of landscape ecology and are routinely presented in published studies as part of the methods. Many fragmentation analyses already use habitat maps within a GIS to obtain the parameters that are used in statistical analyses. However, the same maps are almost entirely ignored when interpreting the results and discussing their implications. Here, we argue that habitat maps should be used at both ends of an analysis; at the beginning to estimate parameters for modelling, and at the end to estimate the biological importance of the modelled effects.

A GIS provides an effective method for representing a given landscape in a variety of ways, emphasising different spatial features as needed. For example, a simple map of a fragmented study area can be represented as a binary map showing areas of habitat and non-habitat. Alternatively, the same habitat cover data can be displayed in a way that highlights fragmentation gradients across the study area (Figure 1a,b), such as the size of a habitat fragment in which sampling is taking place, the isolation or connectivity of that patch to other patches, and the amount of habitat cover surrounding a given sampling point. Researchers commonly extract fragmentation values from the pixels in which they conducted their sampling, and use those pixel values to parameterise statistical models relating a response variable to the various fragmentation gradients in the study area. But we suggest that if a researcher wants to know the biological relevance of such statistical results, they need to take a further step and combine their statistical model with the GIS.

Statistical models generate a formula relating the response variable to the predictors. In the case of fragmentation analyses, the response would be an ecological variable such as the density of a given species, and the predictors would be various metrics of fragmentation such as patch size, distance to an edge and landscape habitat cover. In study areas that contain a complex mosaic of habitats, species responses to fragmentation are often mediated by patch habitat type or by the habitat type of the surrounding matrix [28]. These effects can be incorporated into the statistical model with the inclusion of additional variables (e.g. habitat type or quality [29]) and, if required, using interaction terms to allow fragmentation responses to vary among habitat types (e.g. habitat type × distance to edge). Given that most researchers have maps of each of these predictor variables and that they also generate a statistical formula relating density to these variables, it is a simple matter to overlay the GIS layers and extrapolate density across the landscape by fitting the statistical model to the combination of fragmentation metrics at each pixel (Figure 1c). Using a model formula to predict a value for each pixel in a study area as a function of the values contained in maps is a basic map algebra function included in GIS packages, and enables the researcher to convert multiple GIS layers representing different fragmentation variables into a single map of population density across the study area.

Spatial extrapolation of statistical models is not without precedent in the habitat fragmentation literature [25–27,30–32], although it remains rare. An interesting recent example lies in the application of circuit theory to predict gene flow across fragmented regions [33,34], as well as the use of habitat maps to estimate the viability of metapopulations [35,36]. Most obviously, spatial extrapolation of statistical models is the norm in species distribution modelling [37,38]. In this case, however, the response variable is most commonly the probability of occurrence (although abundance has also been modelled in a number of studies) and the emphasis is usually on abiotic predictors (such as climatic, topographic and edaphic variables) measured at much larger spatial scales than fragmentation-related variables. Nonetheless, some