



Review

A systematic review reveals changes in where and how we have studied habitat loss and fragmentation over 20 years



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ABSTRACT

Habitat loss and fragmentation are global threats to biodiversity and major research topics in ecology and conservation biology. We conducted a systematic review to assess *where* – the geographic locations and habitat types – and *how* – the study designs, conceptual underpinnings, landscape metrics and biodiversity measures – scientists have studied fragmentation over the last two decades. We sampled papers from 1994 to 2016 and used regression modelling to explore changes in fragmentation research over time. Habitat loss and fragmentation studies are geographically and taxonomically biased. Almost 85% of studies were conducted in America and Europe, with temperate forests and birds the most studied groups. Most studies use a binary conceptual model of landscapes (habitat versus non-habitat) and static measures of biodiversity. However, research on fragmentation is slowly shifting from a focus on coarse patterns to more nuanced representations of biodiversity and landscapes that better represent ecological processes. For example, empirical research based on gradient or continuum models, that offer new insights into landscape complexity and species-specific responses to habitat fragmentation, are increasing in prevalence. We recommend that fragmentation research focuses on developing knowledge on underlying mechanisms and processes of how species respond to landscape changes, and that fragmentation studies be conducted in the full range of habitats currently experiencing high rates of landscape modification. This is crucial if we are to understand relationships between biodiversity and ecosystems and to develop effective management strategies in fragmented landscapes.

1. Introduction

Over the last century, habitat loss and fragmentation have been the main drivers of biodiversity change in terrestrial ecosystems (Laurance et al., 2012; Newbold et al., 2015). A recent synthesis of 35 years of fragmentation experiments across multiple spatial scales revealed that habitat loss and fragmentation has reduced biodiversity by 13 to 75% in five continents, and more than 70% of the world's remaining forests are now in close proximity to modified environments (Haddad et al., 2015). Rapid habitat loss and fragmentation is particularly concerning in biodiversity hotspots such as tropical forests and temperate grasslands, and these trends are likely to continue (Millennium Ecosystem Assessment, 2005; Gardner et al., 2009).

Given its important role in global change, habitat loss and fragmentation continues to be an important research topic in ecology and conservation biology (Tscharntke et al., 2012; Driscoll et al., 2013). The literature on fragmented landscapes is vast and growing: a search of “habitat fragmentation” in Thomson Reuters Web of Science (environmental science ecology research area) from 1980 yielded over 3800

published papers, or more than 10% of total ecology papers available. Rapid progress has been made in habitat loss and fragmentation research in only a few decades, and the results of this work have particularly influenced applied problems such as design of nature reserves, and management of agricultural landscapes, urban areas and forest harvesting (Lindenmayer et al., 2006). However, identifying and quantifying general patterns and processes in this large body of literature remains difficult. The fragmentation literature encompasses many experimental designs and methods (Bennett et al., 2006), choices of landscape measurements (Kool et al., 2013), landscape classifications (Lindenmayer and Fischer, 2007), and ways of representing biodiversity (Ewers and Didham, 2006).

To synthesise habitat loss and fragmentation research, much effort has been applied to the development of the theoretical concepts and landscape models that underpin our understanding of these processes (Fischer and Lindenmayer, 2007; Price et al., 2009; Laurance et al., 2011b; Didham et al., 2012). A simple and influential conceptual model of habitat fragmentation is based on island biogeography theory (MacArthur and Wilson, 1967). This binary view of habitat and non-

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habitat (e.g. Diamond, 1975) led to the development of more complex ways of classifying landscapes such as the patch-corridor-matrix model (Forman and Godron, 1981), the landscape mosaic model (Wiens, 1995), and, more recently, models that recognise habitat gradients and continuums (McIntyre and Hobbs, 1999; Manning et al., 2004; McGarigal and Cushman, 2005; Fischer and Lindenmayer, 2006). A shift from a simple binary model to more complex mosaic and continuum models requires new ways of measuring landscape patterns. We predict that methods to measure landscapes have kept up with the development of these conceptual models. However, which methods have developed and how fast they have developed remains unclear.

Numerous metrics have been developed to measure landscape composition (identity and characteristics of landscape elements), configuration (spatial arrangement of landscape elements), and connectivity (the ease with which organisms move through the landscape) (Hanski, 1994; Hargis et al., 1998; Tischendorf and Fahrig, 2000). A range of tools and software have also been developed to assist this quantification (e.g. “FRAGSTATS” (McGarigal et al., 2002), “Circuitscape” (Shah and McRae, 2008), and “Conefor” (Saura and Torne, 2009)). Landscape metrics have been used to describe habitat loss and fragmentation at a range of different spatial scales from patches to whole landscapes (Bennett et al., 2006). Despite development in experimental design and landscape measures, the use of different approaches has led to very different conclusions regarding the magnitude and direction of fragmentation effects (Fahrig, 2003). There is little consensus regarding which aspects of landscape structure and composition should be studied for describing biodiversity responses to fragmentation (Ewers et al., 2010; Fahrig, 2015; Hanski, 2015). Several narrative reviews have highlighted the range of landscape metrics available (Kool et al., 2013), and alternative ways to study landscape change (Brennan et al., 2002; Bennett et al., 2006; Fahrig et al., 2011), but few studies have quantified how the use of metrics and alternative study designs is changing over time.

Another issue relates to taxonomic and geographical biases in ecology. Ideally, fragmentation research should comprehensively cover a range of geographical regions and taxonomic groups to provide robust data that support effective conservation policies and actions. We predict that, as in conservation biology and ecology more broadly (Trimble and van Aarde, 2012; Burgman et al., 2015), our knowledge of how habitat fragmentation and landscape patterns affect biota is biased towards large faunas in temperate regions. These forms of bias will be particularly problematic if fragmentation affects geographic regions and taxa in different ways (Thornton et al., 2011).

Systematic review is an important tool for evaluating conservation evidence and supporting environmental decision making (Pullin and Knight, 2009). It is also useful for identifying knowledge gaps and methodological inconsistencies across disciplines and to focus research priorities (Pullin and Knight, 2009; Mallett et al., 2012; Haddaway and Pullin, 2014). To date, researchers have systematically reviewed habitat loss and fragmentation studies for specific sections of the literature including experimental manipulations of habitat fragmentation (Debinski and Holt, 2000; McGarigal and Cushman, 2002), the interactions between climate and habitat loss (Mantyka-Pringle et al., 2012), the use of landscape spatial metrics (Uuemaa et al., 2013), dispersal research for landscape planning and restoration (Driscoll et al., 2014), and within particular habitat types (e.g. tropical forests, Deikumah et al., 2014). However, systematic analyses of the broader literature on habitat loss and fragmentation, including a range of ecosystems, study types and measures, are rare and few have examined how the literature has changed over time.

In this paper, we systematically review the development of habitat loss and fragmentation research over more than 20 years to identify where and how research has been undertaken and in what way it has changed over time. Specifically, we asked: 1) What conceptual models have been used in fragmentation studies, and how have the use of these models changed over time? 2) How have biodiversity responses to

landscape modification been measured, and how have these measures changed over time? 3) What landscape metrics have been used to describe habitat loss and fragmentation, and how have their use changed over time? and 4) How are these studies distributed across regions, habitat types and taxa?

2. Methods

To examine trends in habitat loss and fragmentation studies, we undertook a systematic review of the literature. For each paper in our sample we recorded information on the study design, geographic region and taxa considered, and the underlying conceptual model, the biodiversity responses measured, and the landscape metrics used. We then modelled how these attributes have changed over time using logistic regression.

2.1. Systematic literature search

We first conducted a search of all peer-reviewed ecological articles indexed by the Thomson Reuters Web of Science Core Collection (Sci-Expanded) from 1 January 1980 to 31 June 2016 using the keyword “ecology”. We initially searched papers starting from the 1980's because this was when landscape ecology clearly emerged as a unique scientific discipline (Wiens, 2007). We refined the search by type of document (article), research area (environmental science-ecology), and language (English), which resulted in 39,045 articles. We conducted another search using keywords that are related to habitat fragmentation and landscape change: “habitat fragmentation” or “forest fragmentation” or “grassland fragmentation” or “woodland fragmentation” or “savanna fragmentation” or “shrubland fragmentation” or “tundra fragmentation” or “heathland fragmentation” or “xeric shrubland fragmentation” or “scrub fragmentation” or “desert fragmentation” or “mangrove fragmentation” or “river fragmentation” or “landscape fragmentation” or “habitat connectivity” or “landscape connectivity” or “patch connectivity” or “patch isolation” or “habitat isolation”. This search resulted in a subset of 6341 articles from the broader sample. Using both searches, we then calculated the proportion of fragmentation studies within ecological science for each year to examine the prevalence of fragmentation studies in the ecological literature (Supplementary material S1, Fig. A1).

A check of additional search terms including “fragment*”, “isolat*” and “connect*” in Web of Science increased the total number of papers found by approximately 10%. Because adding these new terms added only a relatively small number of additional papers we present the results from our original search in the present paper.

As the number of fragmentation papers increased substantially in the beginning of the 1990's, we decided to limit our systematic review to 6252 papers that were published between 1994 and 2016 (23 years). This guaranteed that we sampled enough papers in each year to develop statistical models of changes in the literature. We randomly selected 20 articles from each of the 23 years (460 in total). We screened the selected articles and excluded articles that did not measure habitat loss and fragmentation or did not examine fragmentation effects on biodiversity. We also excluded articles that did not present empirical or simulated data (including review papers and opinion papers). The remaining 302 focal articles were then reviewed in full for data extraction (Fig. 1). Finally, we calculated the standard error of the sample population for each year to ensure we had a large enough sample size to complete our analysis (following Sokal and Rohlf (1995)). The number of papers analysed each year is presented in Table A2.

2.2. Classification of the literature

We categorised each of the focal articles by a range of attributes including study design (type of study, source of data, unit of inference),

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