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Biodiversity Response to Habitat Loss and Fragmentation

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Introduction

Humans have altered large areas of the Earth surface. By the beginning of the 21st century, 75% of the Earth ice-free land had been modified by humans in some degree (Watson et al., 2016). Approximately two-third of these human-altered areas have been subject to the complete conversion of previously existing native vegetation (Fig. 1). Between 2000 and 2015, global rates of deforestation of native forests ranged between 5,770 and 10,483 million ha/year, leading to a global loss of 124.8 million ha of native forests during this period (Keenan et al., 2015), an area roughly twice the size of France. Such vast conversion has led to a substantial reduction in the areas considered to remain wild, i.e., with negligible human impacts. In 2016, only 23.2% (3.01 billion ha) of the world's terrestrial area meets this definition (Watson et al., 2016), and these wilderness areas are scattered around the globe. While some remain considerably large, such as the Amazon forest or the West Siberian Taiga (Watson et al., 2016), land conversion has led to a vast swath of fragmented native vegetation across most biogeographic realms and phytogeographical domains.

Typically, the loss of native vegetation occurs discontinuously and leads to the breakup of the original land cover into distinct patches, separated by a matrix of land converted to a variety of anthropogenic land-uses (Fahrig, 2003; Ewers and Didham, 2006). These native patches become smaller and more isolated from each other as the loss of native vegetation progresses. As an example of this process, the Brazilian Atlantic Forest, a phytogeographical domain reduced to less than 16.0% of its original extent (from originally around 130 million ha to less than 17 million ha), is divided into more than 240,000 patches (Ribeiro et al., 2009). The three largest patches (>380,000 ha) encompass only 13% of the remaining forest, while more than 42% is divided into patches smaller than 250 ha, which represent 97% of all patches. Less than 10% of this remaining forest is located further than 1 km from a forest edge (down from a historical 90%) and more than 40% is located within 100 m of an edge (Ribeiro et al., 2009; Fig. 2). Such remarkable changes are not limited to forested habitats. Temperate grasslands—considered one of the most altered biomes in the world (Hoekstra et al., 2005)—have declined globally more than 45% in cover, with 37% of remaining grasslands being highly fragmented (Hoekstra et al., 2005). Across the Northern prairies of Canada the maximum native patch size is only about 1000 ha, while the median patch size is merely 0.62 ha (Roch and Jaeger, 2014).

This longstanding, intense, and global process of native vegetation conversion has created a social demand for scientific support for mitigating the effect of habitat loss and fragmentation on biodiversity and ecosystem services (Haila, 2002). Initially, research was greatly influenced by the Island Biogeography Theory (IBT; MacArthur and Wilson, 1967), through the analogy between patches of native vegetation within converted land and islands within the ocean (Haila, 2002; Laurance, 2008; Didham et al., 2012). Beginning in the 1970s, studies firmly tied to this analogy proliferated in the literature (Haila, 2002), focusing on either species richness or presence/absence of particular species as a function of patch area. The IBT is a simple, neutral theory that predicts the equilibrium number of species in an island based on the balance between colonization (inversely related to the distance to the mainland) and extinction (inversely related to population size and thus to the size of the island). As the IBT paradigm emphasized simple patch metrics (area and isolation), the application of IBT to the study of fragmented landscapes often meant a disregard for both landscape heterogeneity and dynamics (beyond probabilistic arrival of colonists across an inhospitable matrix), and of internal patch dynamics (beyond probabilistic extinction rates), as well as species identities, traits, and interactions (Didham et al., 2012). Despite its simplicity and thus poor predictive power, IBT inspired a wave of empirical studies that critically established that not all species perceive converted land as homogeneous or inhospitable, nor respond similar to habitat loss and fragmentation, and that habitat loss and fragmentation involve many other processes, such as edge and matrix effects, species interactions, and ecological cascades (Laurance, 2008). These studies have also highlighted that, beyond patch size and isolation, a spatially explicit account of landscape heterogeneity, structure, and dynamics, and their interaction with species traits is necessary to fully
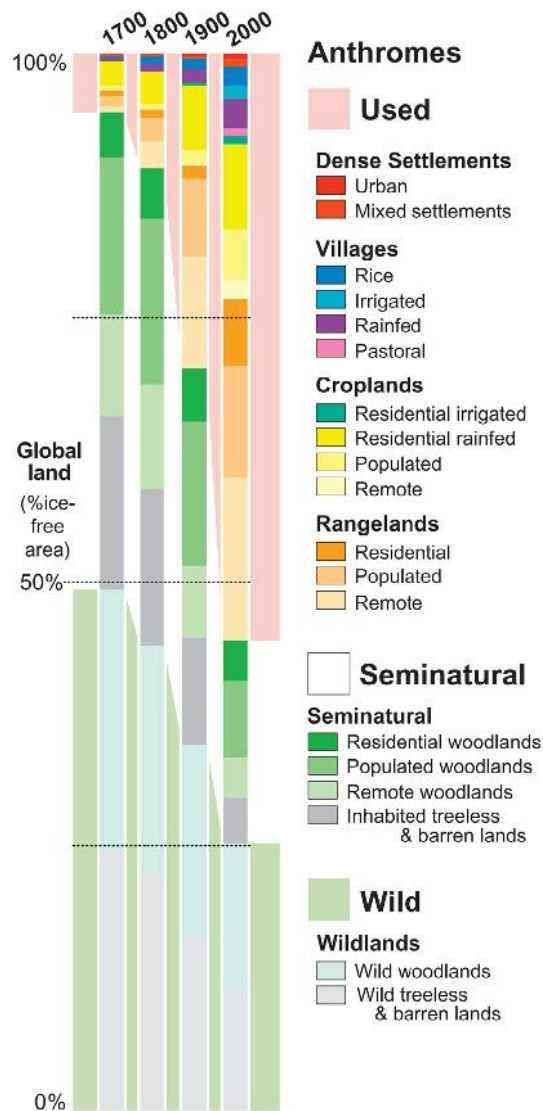
Fig. 1 Global changes in anthromes (anthropogenic biomes), from 1700 to 2000, expressed as a percentage of global ice-free land area. Trends in the combined areas of "used" anthromes are highlighted by red shading and wildlands by green shading; seminatural anthromes left blank. Modified with permission from Ellis, E. C., Goldewijk, K. K., Siebert, S., Lightman, D. and Ramankutty, N. (2010). Anthropogenic transformation of the biomes, 1700 to 2000. Global Ecology and Biogeography 19, 589–606. Copyright 2010, Blackwell Publishing Ltd.

understand the effects of the loss and fragmentation of native vegetation, boosting a vast literature in landscape ecology from the 1990s onward.

However, the insight that the effects of the widespread conversion of native vegetation is a far more complex problem than anticipated, involving a multitude of processes and types of responses, has led some to question the relevance of habitat loss and fragmentation as a central conceptual domain useful for advancing our knowledge (reviewed in Didham et al., 2012). Although conceptual advances certainly still lag behind the accumulated empirical findings in the field (Didham et al., 2012), many consider that the concepts are useful and can help us understand the effects of humans on biodiversity and ecosystems and propose guidelines to more sustainable landscapes (Ewers and Didham, 2007; Hanski, 2011; Didham et al., 2012; Fahrig, 2013).

Definitions and Distinctions

Habitats Versus Native Vegetation Types

While native vegetation is a straightforward term that includes all vegetation originally present in a given area, the meaning of habitat is less intuitive. Habitat is defined as the resources and conditions that allow individuals of a particular species to occupy (i.e., survive and reproduce within) a given area (Hall et al., 1997). Habitat is consequently a species-specific concept, related to the
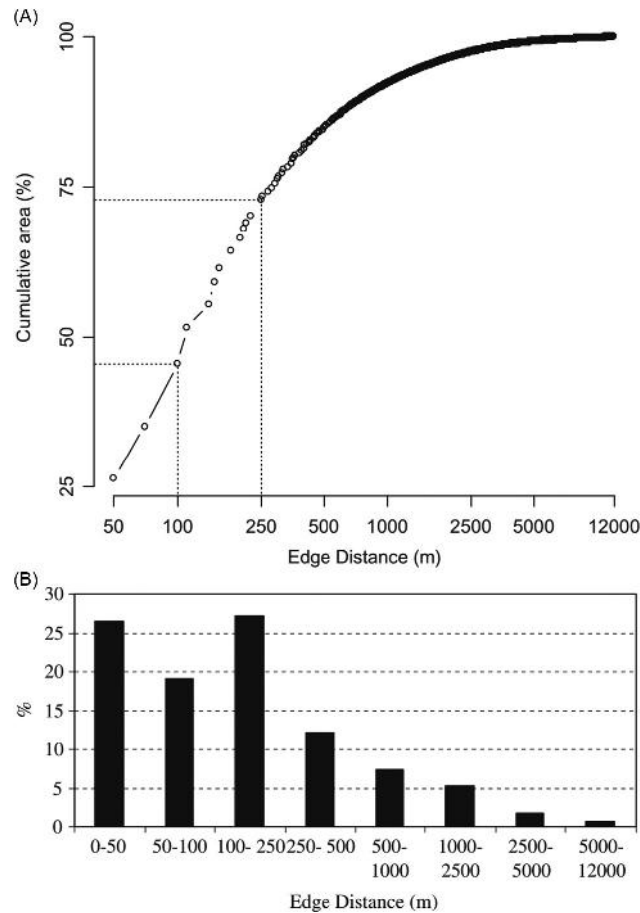
Fig. 2 Cumulative (A) and per class (B) area under edge effect at different depths for the remaining Brazilian Atlantic Forest. Edge depths of 100 and 250 m are highlighted in (A). Reprinted with permission from Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J. and Hirota, M. M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation 142, 1141–1153. Copyright 2009, Elsevier Ltd.

ecological requirements of the species in question. Not all native vegetation is therefore habitat for all native species, and which part of the native vegetation (or converted land-uses) represents habitat varies greatly across species, even within the same taxonomic group (Fig. 3).

Because knowing the ecological requirements of every single species in a community is in itself a huge task, investigating the effects of habitat loss and fragmentation on biodiversity is not trivial. Most commonly, these effects are studied using the human-perceived patterns of distribution of native vegetation as a surrogate for the distribution of available habitat for all species in a community (Fischer and Lindenmayer, 2007). As a consequence, results from empirical studies frequently do not fit the predictions from simple ecological models and vary widely across studies (Watling and Donnelly, 2006; Prugh et al., 2008). This is because the documented changes in native vegetation cover do not necessarily correspond to changes in habitat cover for all species (Ewers and Didham, 2006). For example, several forest species avoid forest edges (Ries et al., 2004). For these species, documented forest loss likely underestimates the loss of habitat, as core areas (without the influence of edges) decrease more rapidly than total forest area as forest conversion progresses. On the other hand, some native species prefer edges or are able to use converted land (Ries et al., 2004). In this case, forest conversion does not necessarily lead to habitat loss and fragmentation.

Habitat Loss Versus Habitat Fragmentation

Similarly, while the definition and quantification of habitat loss (or habitat amount) is straightforward, habitat fragmentation (or habitat configuration) can be interpreted and measured in different ways. Two landscapes that encompass the same amount of habitat may present different configurations of this remaining habitat (Fahrig, 2003)—for the same amount of remaining habitat, the greater the aggregation of remnants, the lower the fragmentation, and vice-versa. Real landscapes often present very different trajectories overtime resulting in different amounts and configurations of remaining native vegetation (Oliveira de Filho and Metzger, 2006; Lira et al., 2012b; Fig. 4), and both aspects may affect biodiversity (Fahrig, 2003). However, although these two aspects are conceptually distinct, they are not independent (Didham et al., 2012), as the conversion of native vegetation leads
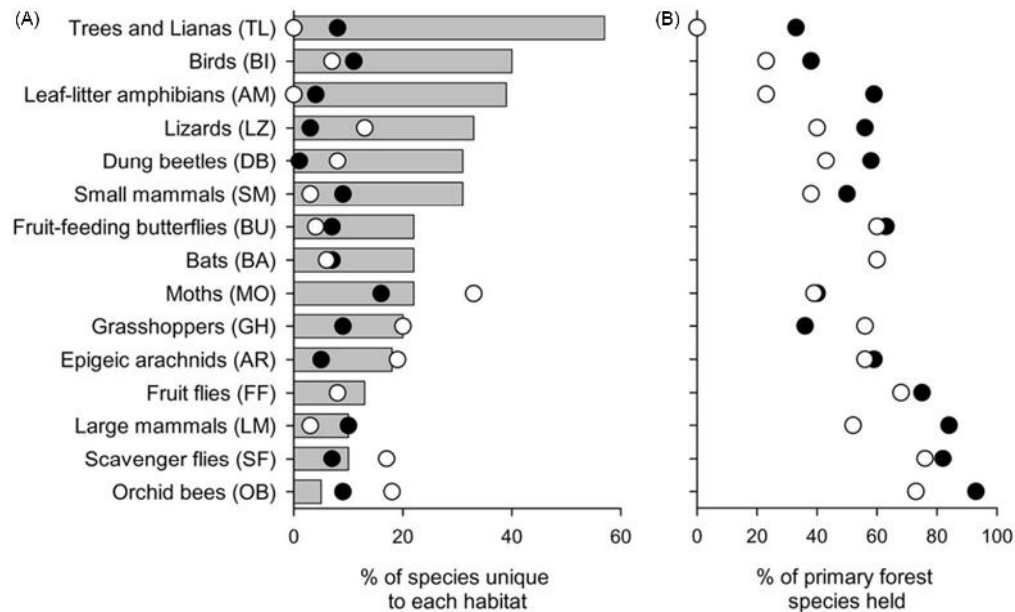
Fig. 3   The percentage of species unique to primary, secondary, and plantation forests (A) and the percentage of species recorded in primary forest that were also recorded in secondary forest and plantations (B) in the Jari forestry project in the north-eastern Brazilian Amazon. Primary, secondary, and plantation forests are represented by *gray bars*, *black circles*, and *white circles*, respectively. Reprinted with permission from Barlow, J., Gardner, T. A., Araujo, I. S., Avila-Pires, T. C., Bonaldo, A. B., Costa, J. E., Esposito, M. C., Ferreira, L. V., Hawes, J., Hernandez, M. M., Hoogmoed, M. S., Leite, R. N., Lo-Man-Hung, N. F., Malcolm, J. R., Martins, M. B., Mestre, L. A. M., Miranda-Santos, R., Nunes-Gutjahr, A. L., Overal, W. L., Parry, L., Peters, S. L., Ribeiro-Junior, M. A., da Silva, M. N. F., Motta, C. D. and Peres, C. A. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proceedings of the National Academy of Sciences of the United States of America 104, 18555–18560. Copyright 2007, The National Academy of Sciences of the USA.

simultaneously to both native vegetation loss and fragmentation, with these two aspects covarying in natural landscapes. In particular, while it is possible to lose habitat without increasing fragmentation, it is not possible to fragment habitat without increasing habitat loss. Consequently, most metrics used to quantify habitat fragmentation are strongly correlated to metrics of habitat amount (Wang et al., 2014). This makes the statistical isolation of their effects difficult in practice (Smith et al., 2009) and has led to biased conclusions, suggesting stronger effects of habitat loss than habitat fragmentation (Didham et al., 2012; Villard and Metzger, 2014).

A more fruitful way may be to view the effects of habitat loss and fragmentation as interdependent, i.e., the effect of habitat loss operates not only directly and separately (i.e., independently) from the effects of habitat fragmentation but also indirectly through the alteration of habitat configuration (Didham et al., 2012; Ruffell et al., 2016). It is also important to consider that the potential for variation in habitat configuration is much greater in a certain, intermediate range of habitat loss, where there is neither too much nor too little habitat left (Villard and Metzger, 2014). This indicates that it is more important to consider the potential indirect effects of habitat loss via habitat fragmentation in landscapes with intermediary amounts of remaining habitat.

Main Types of Processes Underlying the Effects of Habitat Loss and Fragmentation

Considering the number and complexity of interactions among species as well as among them and the abiotic environment, there are innumerous processes that may underlie the effects of habitat loss and fragmentation on biodiversity. In general, these processes can be grouped into two classes, stochastic and deterministic.

- *Stochastic processes.* When populations become small and isolated from each other due to habitat loss and fragmentation, they become more vulnerable to local extinction due to stochastic processes. Stochastic processes are those that lead to unpredictable (random) changes in population sizes overtime. Considering ecological time scales, two stochastic processes are important to populations in fragmented landscape. Demographic stochasticity (or demographic drift) refers to random fluctuations in population growth rates due to chance events of individual mortality and reproduction (Gilpin and Soulé, 1986). Even assuming that all individuals in a population have the same probability distribution for reproducing or dying, the number of offspring or time of death for a given individual is unpredictable, causing random variation in population size. Environmental stochasticity (including natural catastrophes) refers to variations in the population growth rate due to unpredictable variation in environmental conditions, which have a similar effect on all members of the population (Shaffer, 1981; Gilpin and Soulé, 1986). While stochastic processes are present in all populations independent of population size, they become particularly
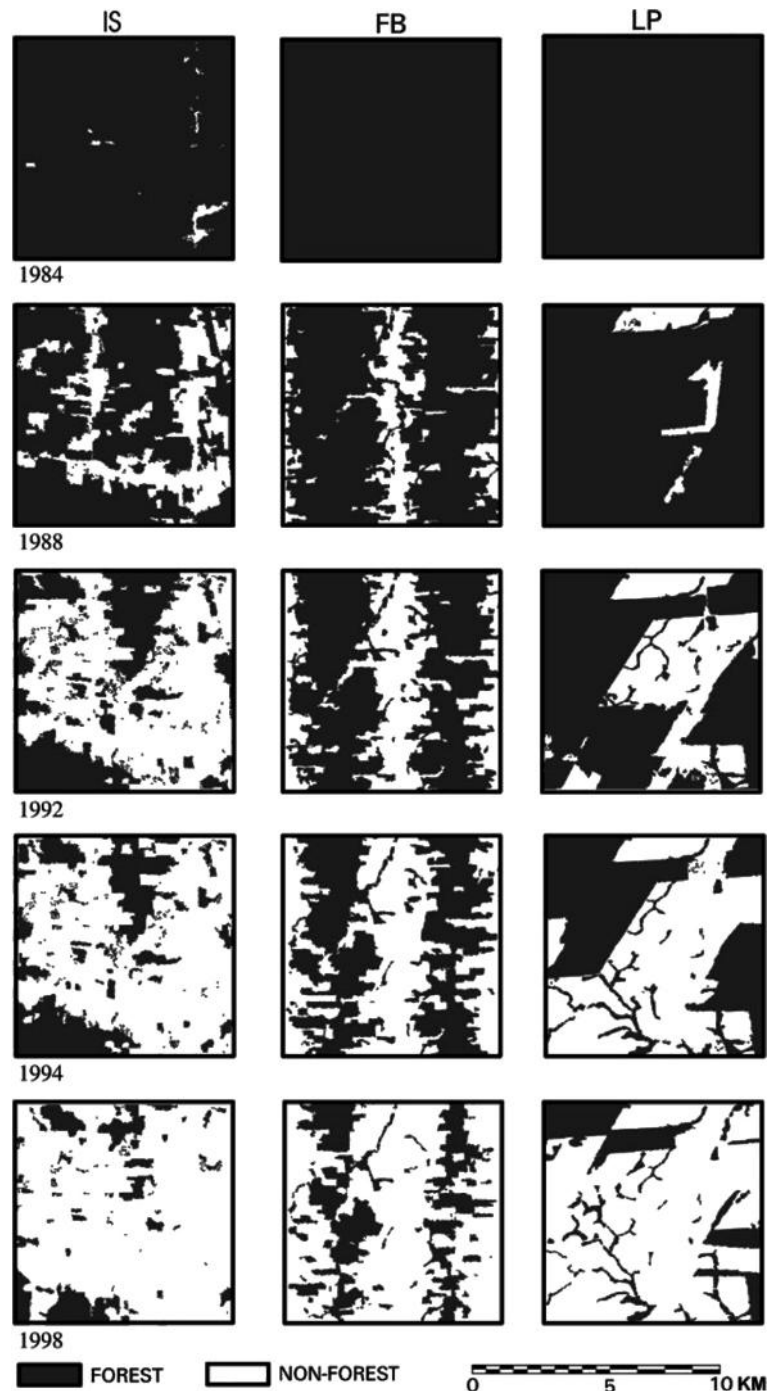
Fig. 4 Temporal sequence of deforestation for three typical patterns of land use in the Amazon: independent settlement (IS), fishbone (FB), large property (LP). Reprinted with permission from Oliveira de Filho, F. J. B. and Metzger, J. P. (2006). Thresholds in landscape structure for three common deforestation patterns in the Brazilian Amazon. Landscape Ecology 21, 1061–1073. Copyright 2006, Springer.

important in small populations (Shaffer, 1981; Gilpin and Soulé, 1986) because of the increased probability that random fluctuations in population size lead to local extinction (i.e., the population size hits zero). In fragmented landscapes, the risk of local extinction due to stochastic processes is exacerbated not only because populations are smaller but also because dispersal of individuals from neighboring populations is diminished or inhibited by increased population isolation. As recruitment by dispersers can buffer local populations against demographic and environmental stochasticity (i.e., the rescue-effect; Brown and Kodric-Brown, 1977), the chance of stochastic extinction is greater in more isolated populations.

- *Deterministic processes*. In contrast to stochastic processes, deterministic processes are those that predictably lead to a decline or increase in population size (Gilpin and Soulé, 1986; Fischer and Lindenmayer, 2007). As habitat is lost, fewer resources are available, increasing competition among individuals, decreasing survival and/or reproduction, and leading to a reduction in population size. Two additional deterministic processes affect biodiversity in fragmented landscapes, increasing in importance as habitat loss and fragmentation progress. Habitat degradation (i.e., deterioration of habitat quality) occurs mainly at habitat edges. Edge effects can cause deterministic changes in populations and communities through changes in abiotic conditions (e.g., changes in microclimate or habitat structure), changes in biotic interactions (caused by habitat-induced changes in species abundance, including species invasion, or by habitat-induced changes in the strength or quality of interactions; Murcia, 1995), or increased anthropogenic impacts (e.g., hunting, intrusion of domesticated animals, fire, and logging). Further, isolation of population in habitat patches surrounded by a hostile matrix can lead to deterministic changes in populations and communities by disrupting dispersal and forcing dispersing individuals to spend more time in the matrix and thereby being subjected to increased mortality risk (Fahrig, 2007). The strength and quality of both habitat degradation due to edge effects and disruption of dispersal due to isolation are mediated not only by habitat loss and fragmentation but also by the quality and heterogeneity of the matrix of converted land (Prugh et al., 2008; Prevedello and Vieira, 2010).

Species may become extinct due to either stochastic or deterministic processes, but most commonly by a combination of both. Typically, deterministic processes initially lead to a decrease in population size, which causes increased vulnerability to stochastic extinction. The extinction of one or more species might then cause a series of deterministic consequences for the remaining community, sometimes leading to ecological cascades. The common loss of large bodied top-predators in fragmented landscapes, for instance, has been shown to have far-reaching effects on lower trophic levels, including the increase of prey species that may overexploit resources, changes in ecosystem processes, and secondary extinctions of species (Ripple et al., 2014). Ecological cascades may also be triggered by the invasion of exotic species, which may monopolize resources and thereby cause extinction of native species (Gurevitch and Padilla, 2004).

Identifying the processes underlying observed patterns is much more difficult than describing patterns themselves, and as a consequence in most cases we do not know which processes cause patterns of species response to habitat loss and fragmentation. Early theories and models on the effects of habitat loss and fragmentation, such as the Island Biogeography Theory, focused on stochastic processes (i.e., increased chance of random extinction due to the decrease in population size). However, the relative importance of stochastic and deterministic processes to biodiversity loss following habitat loss and fragmentation is still unknown, and represents a current area of research (e.g., Karp et al., 2012; Püttker et al., 2015).

What Do We Know on the Effects of Habitat Loss and Fragmentation?

Habitat loss and fragmentation have been considered the major threats to biodiversity (Haddad et al., 2015), affecting a larger number of species than biological invasions, overexploitation, or pollution (Baillie et al., 2010; Collen et al., 2012; Corlett, 2016). However, because of the complexity and variability of the processes underlying land-use change across landscapes, the interdependence of habitat loss and fragmentation and other anthropogenic threats, and the variety of habitat requirements, dispersal abilities, and functional traits among species, estimates of the effects of habitat loss and fragmentation are variable across groups of species, types of landscapes, and types of native vegetation (e.g., Murphy and Romanuk, 2014; Newbold et al., 2014).

The impressive number of studies on habitat loss and fragmentation, as well as the great variability in methodological approaches and conceptual frameworks, makes synthesizing and identifying what we know about their effects a difficult task. Below is a tentative list of the most general and consistent patterns that emerge across studies.

- *Differential responses to native vegetation loss and fragmentation*. Although the response to the loss and fragmentation of native vegetation varies across species, a consistent pattern commonly emerges from empirical studies. Species that are negatively affected are usually habitat specialists or endemic to the native vegetation type under consideration, while those unaffected or positively affected are widespread, habitat generalist species, or open area specialists that expand their distribution as land conversion proceeds (Pardini et al., 2010; Estavillo et al., 2013; Banks-Leite et al., 2014; Fig. 5). Indeed, species responses to the loss and fragmentation of native vegetation have been shown to depend on habitat requirement traits such as niche-breath (Filippi-Codaccioni et al., 2010). Consequently, the loss and fragmentation of native vegetation contributes to what has been termed biotic homogenization (Solar et al., 2015): an increase in the similarity of biological communities across patches, landscapes, and regions.
- *Importance of landscape context and spatial scale*. The composition and spatial configuration of land cover types in the surrounding landscape greatly influences biodiversity at local scales (e.g., a patch), leading to the general observation that habitat loss and fragmentation should be quantified at larger spatial scales (Andrén, 1994; Fahrig, 2003). However, what spatial scale is most adequate may vary (Jackson and Fahrig, 2015), depending on species' traits (e.g., dispersal ability or diet plasticity), the biological process under consideration (e.g., foraging or dispersal success), the biological response being measured (e.g., fecundity or occurrence), and the regional context (Miguet et al., 2016). This is not to say that patch scale metrics are not important, but rather that their effects may depend on landscape context (e.g., Pardini et al., 2010).
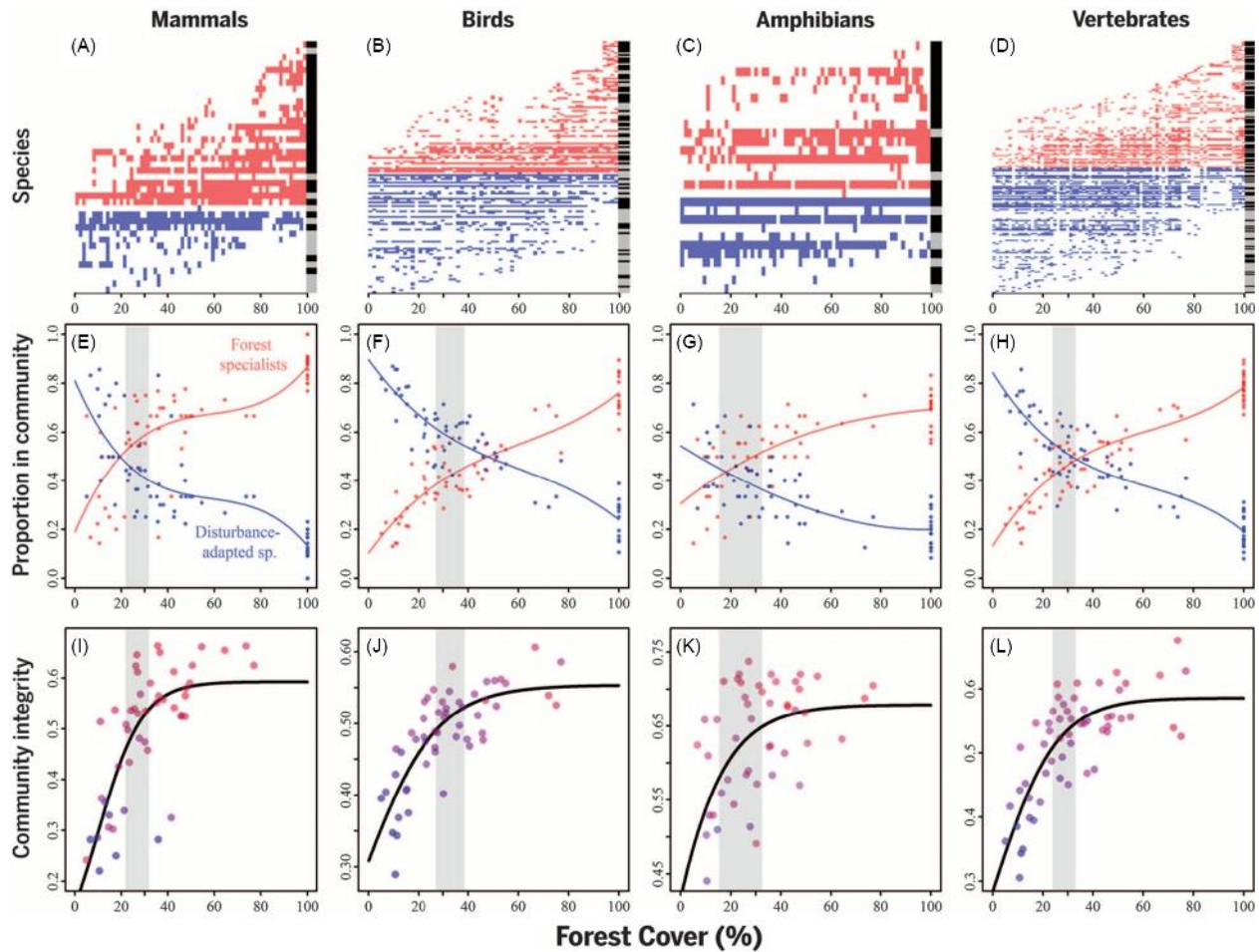
Fig. 5 Responses of vertebrate communities to forest cover in Atlantic Forest landscapes, Brazil. (A–D) Species × site matrix of mammals, birds, amphibians, and vertebrates. Sites (columns) are ordered by forest cover, and species (lines) are ordered by their preference to forest cover. *Red* indicates forest specialists; *blue* indicates disturbance-adapted species. Columns to the right of each panel represent endemism to the Atlantic Forest, with black cells showing endemic species and gray cells showing nonendemics. (E–H) Proportional change of forest specialists and disturbance-adapted species in each community. (I–L) Variation in community integrity (measured as the similarity in community composition between fragmented and continuously forested landscapes). *Shaded areas* in (E)–(L) indicate 95% CIs of threshold estimates obtained from community integrity. In (I)–(L), *points* are colored to represent the proportion of forest specialists and disturbance-adapted species. Reprinted with permission from Banks-Leite, C., Pardini, R., Tambosi, L. R., Pearse, W. D., Bueno, A. A., Bruscagin, R. T., Condez, T. H., Dixo, M., Igari, A. T., Martensen, A. C. and Metzger, J. P. (2014). Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. Science 345, 1041–1045. Copyright 2014, American Association for the Advancement of Science.

- *Thresholds*. Recently, accumulated evidence suggests that the rate of species loss is greatly accentuated below a threshold around 30% of remaining native vegetation in the landscape (Estavillo et al., 2013; Rigueira et al., 2013; Banks-Leite et al., 2014; Lima and Mariano-Neto, 2014; Fig. 5). As most of these studies come from tropical forests in South America and have focused on plants or vertebrates, the universality of this threshold value is open to further investigation, and lower or higher values have been observed for other types of native vegetation or regions. These thresholds are thought to result from key, nonlinear changes in landscape structure as habitat loss progresses, such as the drastic reduction in the size of the largest remnant when total habitat amount decreases below 60% or the drastic increase in the distance among remnants below 30% of remaining habitat (Fahrig, 2003). However, these hypotheses and their underlying mechanisms have not yet been directly tested.
- *The matrix matters*. One aspect of the landscape context that has been considered to be critical to the effects of habitat loss and fragmentation is the composition, heterogeneity, and dynamics of the matrix (Kupfer et al., 2006; Driscoll et al., 2013). In general, consideration of matrix composition leads to improved predictions of species abundance and richness in habitat patches (reviewed in Watling et al., 2011), and matrix types that are more similar to the original vegetation are of better quality to organisms (reviewed in Prevedello and Vieira, 2010), increasing movement rates between habitat patches (reviewed in Eycott et al., 2012). Importantly, recent evidence suggests that even substantially fragmented landscapes can maintain biodiversity, if a small proportion of the matrix is composed of high-quality land cover types (Ruffell et al., 2016).

- *Edge effects matter*. Habitat loss and fragmentation lead to important changes in the quality of the remaining vegetation through edge effects. In tropical forests, for instance, microclimate changes and the impact of wind near the edges with converted land elevate vegetation dynamics (Laurance et al., 1998), drastically decrease tree biomass (Nascimento and Laurance, 2004), and alter vegetation composition by favoring successional species (Laurance et al., 2006). Some have argued that these edge effects trigger a retrogressive succession process that drives all remaining vegetation in highly fragmented tropical forest landscapes toward a persistent, early-successional system (Tabarelli et al., 2008). Edge-induced vegetation changes, together with human-induced disturbances such as logging, make remnants extremely vulnerable to fires (Cochrane and Laurance, 2002; Alencar et al., 2015), leading to widespread forest degradation. Recent estimates for the Amazon suggest that forest degradation by the combined effects of edges, fires, and logging results in carbon (Berenguer et al., 2014) and biodiversity (Barlow et al., 2016) loss that are significant and may be greater than those caused by deforestation.
- *Lagged biodiversity responses*. Biodiversity responses are not necessarily immediate, and different ecological models predict time lags between habitat loss and fragmentation and species extinction (Tilman et al., 1994; Hanski and Ovaskainen, 2002; Mouquet et al., 2011; Halley et al., 2014), creating an extinction debt—a future ecological cost of past and current habitat destruction (Tilman et al., 1994). Likewise, biodiversity responses to habitat restoration aiming at mitigating the effects of habitat loss and fragmentation are also predicted to be delayed, resulting in species credit (Hanski, 2000). Several empirical studies have indeed found evidence of these delayed responses in different biological groups (e.g., Metzger et al., 2009; Halley et al., 2016), which can be very long, especially in long-lived organisms (e.g., Metzger et al., 2009). As a result, both short-term landscape trajectories, which may be very complex (especially in the tropics, e.g., Lira et al., 2012a), and landscape history (Ewers et al., 2013), greatly influence current biodiversity patterns.
- *Interactive threats*. Habitat loss and fragmentation facilitate the spread of other threats, such as fires, invasive species, and hunting, and may interact synergistically with them (Cochrane, 2001; Peres, 2001; Didham et al., 2007; Oliver et al., 2015). Although most studies still focus on the effects of single threats, imperiling our ability to understand and predict biodiversity loss (Brook et al., 2008), the consideration of multiple threats to biodiversity is a growing research area (e.g., Mantyka-Pringle et al., 2012; Stireman et al., 2014).

The Future

The advancements outlined earlier represent significant strides forward in the understanding of how the loss and fragmentation of native vegetation influences biodiversity, allowing the identification of a number of guidelines on how to plan landscapes to maintain biodiversity (e.g., Lindenmayer et al., 2008). Future advances will come from additional research in three main areas.

- *Advancing theory*. As conceptual advances still lag behind the wave of empirical findings, integrative models are sorely needed to advance both theory and practice and remain a key gap to be filled. These models should integrate the main types of processes (both stochastic and deterministic), consider species interactions, as well as their traits and functions, and be spatially explicit to account for the complexity of real landscapes. This will require the integration of subdisciplines of ecology (e.g., trait, functional, community, landscape, ecosystem, and metacommunity ecology).
- *Testing predictions*. Testing predictions that arise from such integrative models with both experimental and observational data is key to advancing habitat loss and fragmentation research. This depends fundamentally on maintaining and increasing support for large-scale and long-term experimental and observational projects, which have been critical in generating empirical evidence in this area to date. Of the nearly two-dozen experimental projects globally (Debinski and Holt, 2000), five have particularly significant roles in our understanding of habitat loss and fragmentation effects: the Biological Dynamics of Forest Fragments Project (BDFFP; Brazil, 1980-present), the Kansas Fragmentation Experiment (USA), the Wog Wog Habitat Fragmentation Experiment (Wog Wog; Australia), the Savannah River Site Corridor Experiment (USA), and most recently the Stability of Altered Forest Ecosystems (SAFE) Project (Malaysia; Fig. 6; Resasco et al., 2016). These are complemented by a series of important, large-scale observational studies (e.g., Gardner et al., 2008; Gardner et al., 2013; Banks-Leite et al., 2014; Barlow et al., 2016).
- *Supporting practice*. Landscapes are complex social-ecological systems in which humans are both the drivers and the recipients of landscape change (Sayer et al., 2013). Explicit and authentic integration of ecological and human components is critical to guide decision-making and management of sustainably productive landscapes, for several reasons. First, the design and management of multifunctional landscapes that support both agricultural production and biodiversity requires attention to how and where ecosystem services are desired and used by people, not just how they are produced or affected by the conversion of native vegetation or other human activities (Mitchell et al., 2015). Second, while landscapes are fundamentally shaped by the type, extent, and intensity of human agriculture, the relationship between agricultural production and biodiversity outcomes ranges widely along a gradient from zero-sum trade-offs (Power, 2010) to positive synergies (Perfecto et al., 2005). Understanding how and why these different relationships manifest requires the consideration of a complex suite of social, economic, and institutional factors, including governance, equity, empowerment, credit access, supply chains, and social justice (Gardner et al., 2013; Wittman et al., 2016). Similarly, any environmental policy decision that successfully influences biodiversity is likely to have impacts on agricultural production, economic growth, human health, social and economic equality, and political conflict, with differential impacts for different groups of people (Stern, 2005). Third, the development of novel theory in
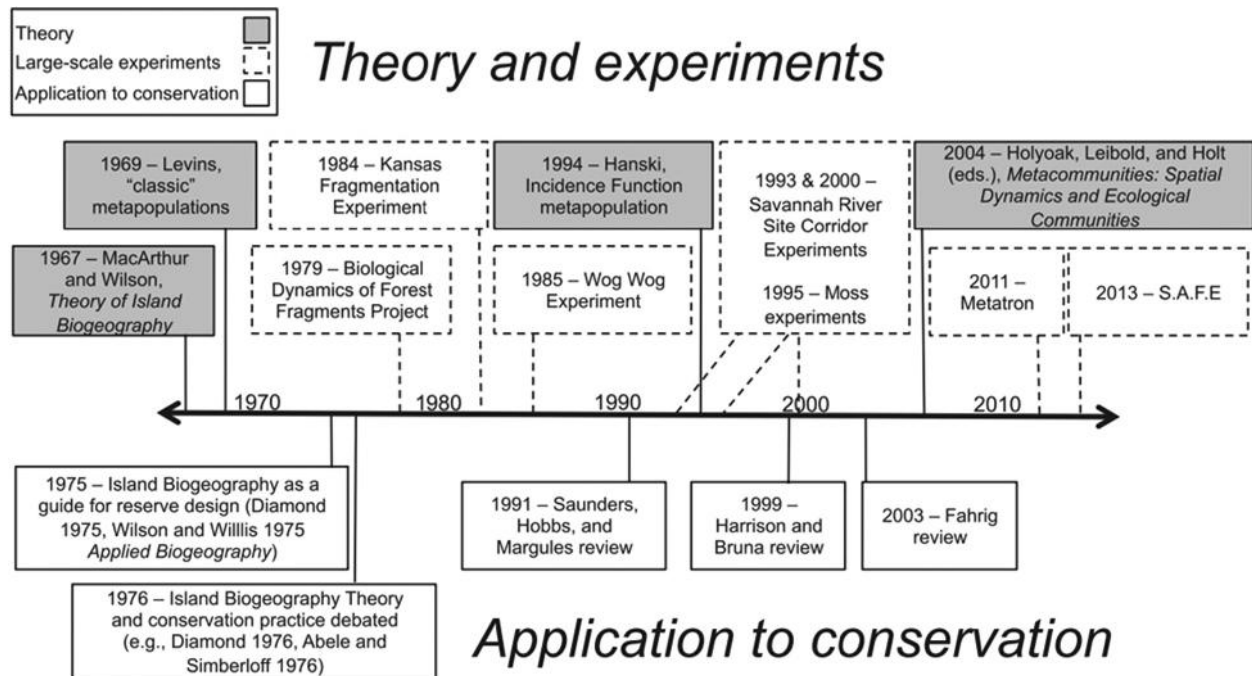
Fig. 6 Timeline of key events related to habitat loss and fragmentation research concerning theory development, large-scale experiments, and discourse on application for conservation. Reprinted with permission from Resasco, J., Bruna, E. M., Haddad, N. M., Banks-Leite, C. and Margules, C. R. (2016). The contribution of theory and experiments to conservation in fragmented landscapes. Ecography 40, 109–118. Copyright 2016, Nordic Society Oikos.

complex systems (e.g., human-modified landscapes) necessitates interdisciplinary approaches, which can lead to conceptual advancements both within and between fields (Lele and Norgaard, 2005). For example, recent integration of urban ecology and urban planning has significantly advanced our understanding of urban ecosystem dynamics (Pickett et al., 2001). Overall, the centrality of these human dimensions to both the drivers and desired outcomes of landscape management implies that real integration of the social and ecological sciences is essential to our understanding of how sustainable landscapes can be designed, implemented, and maintained.

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