The contribution of theory and experiments to conservation in fragmented landscapes

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The clearing and fragmentation of terrestrial ecosystems is commonly acknowledged as a major cause of the decline of biodiversity. These and other predicted responses to habitat fragmentation are derived from theory, which ecologists have tested with empirical approaches ranging from observations to experimental manipulations. These empirical approaches have also identified areas of theory in need of additional development. For example, experimental studies of fragmentation have provided insights such as the key role played by the matrix surrounding fragments, the importance of edge effects, and the impacts of corridors linking fragments with one another. Much less clear, however, is the extent to which these theoretical and empirical studies – while advancing our conceptual understanding of ecological responses to landscape change – help guide management and conservation practice. We review lessons learned from landscape-scale fragmentation experiments and observational studies, present the results of a survey of fragmentation and conservation experts which probed for links and mismatches between fragmentation studies and conservation practice, and discuss how future studies can contribute to conservation practice. Our survey showed that respondents consider fragmentation theory and empirical studies and their findings important for guiding conservation and management practices. The survey also identified that there are disconnects between what is typically studied by fragmentation ecologists and factors that are central to the practice of biodiversity conservation, notably, community-based human dimensions (e.g. economic, social, health issues), policy and governance, ecosystem services, eco-evolutionary responses of species, and interaction of multiple threats to biodiversity and ecosystem processes. We discuss how these disconnects can present opportunities for experiments to continue to provide valuable recommendations for conservation practice in fragmented landscapes.

Over the last century, the quadrupling of the human population and the accompanying increase in resource consumption have resulted in land-use changes that have transformed biomes (Foley et al. 2011). The resultant loss and fragmentation of habitats is widely regarded as the foremost proximate threat to biodiversity (Haddad et al. 2015). Conservation biology emerged over the last several decades as a 'crisis discipline' to develop scientific tools to conserve biodiversity under such threats (Soulé 1985). The extent of loss and the fragmentation of the remaining habitat stimulated ecologists to develop theory aimed at understanding the impacts of this emerging crisis (MacArthur and Wilson 1967, Levins 1969, Wilson and Willis 1975, Soulé 1985, Hanski 1999a, Hubbell 2001), as well as observational (non-manipulative) and experimental tests of these theories' predictions (Wilcove et al. 1986, Quinn and Harrison 1988, Bierregaard et al. 1992). In addition to generating new knowledge, this research was expected to help guide the conservation and management of rapidly transforming landscapes and has been central to applied ecology especially in the four decades

since ecological theory has become intertwined with conservation in fragmented landscapes (Wilson and Willis 1975, Harris 1984, Harrison and Bruna 1999). But a central question remains: *How do fragmentation theory and empirical tests influence conservation and management practice?*

The potential for mismatches between theory and application has been central to conservation biology since its emergence as a field. MacArthur and Wilson's (1967) island biogeography theory (henceforth IBT) was rapidly adopted as a framework for studying biodiversity in fragmented systems and designing reserves (Fig. 1, Diamond 1975, Wilson and Willis 1975). Yet, an early review of the theory criticized it for dealing with 'characterless species' on 'featureless plains' (Sauer 1969) and debate ensued on the applicability of IBT for conservation (Fig. 1, Diamond 1976, Simberloff and Abele 1976a, Simberloff and Abele 1976b, Terborgh 1976, Whitcomb et al. 1976, Gilbert 1980, Higgs 1981, Simberloff and Abele 1982). Similarly, debates about the size and distribution of habitat remnants, the relative roles of area and isolation, and the application of corridors as
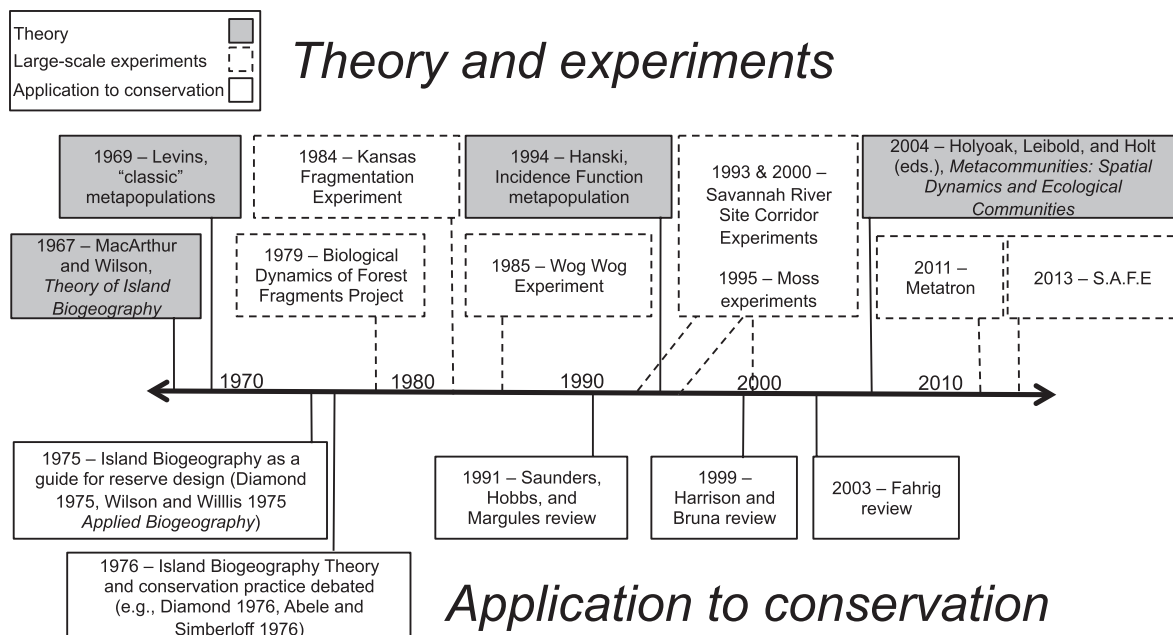
Figure 1. Timeline of key events in fragmentation theory, landscape experiments, and discourse on application for conservation.

possible solutions have simmered for four decades, until today (Noss 1987, Simberloff and Cox 1987, Hobbs 1992, Andrén 1994, Fahrig 2003, Fahrig 2013, Haddad et al. 2017). Over this period, theory progressed (Fig. 1) with the concept of metapopulations (Levins 1969, Hanski 1999b) for studying spatially structured populations, which later extended to communities as metacommunities (Leibold et al. 2004, Holyoak et al. 2005), and ecosystem processes as metaecosystems (Loreau et al. 2003). Throughout, empirical tests have been put forward as a means of assessing the application of theory in the real world and providing autecological guidance for managing and conserving fragmented landscapes.

Here we briefly review the main theoretical frameworks guiding the study of biodiversity and ecosystem processes in fragmented landscapes and assess the match between theoretical predictions and empirical results. We then highlight some key implications for conservation and management emerging from studies of fragmented systems, especially experiments. Finally, we present the results of a key informant survey on fragmentation research and landscape conservation and propose mechanisms to bridge disconnects between empirical research and conservation practice.

Theory, the real world, and the emergence of fragmentation experiments

For over three decades following IBT, our understanding of fragmentation's impacts developed mostly in the absence of experimental evidence, that is, results from studies in which the area and spatial arrangement of habitat were experimentally manipulated (Holt and Debinski 2003). The need for manipulative experiments became increasingly apparent as observational tests of IBT revealed the the ways in which confounding variables complicated the direct application of

theory developed and tested with oceanic islands in terrestrial fragmented landscapes (Gilbert 1980, Haila 2002, Margules et al. 1982). Furthermore, while some key features of the IBT were easily extended to terrestrial fragments – namely the spatial effects of area and of distance – several major new issues unique to terrestrial habitat islands emerged (Laurance 2010). The first of these was 'edge effects' – gradients in biotic and abiotic characteristics experienced at the boundaries between fragments and the altered matrix habitat in which they were embedded or from the edges of roads into habitat remnants (Trombulak and Frissell 2000, Laurance et al. 2002, Ries et al. 2004). The second was non-random habitat clearing, which results in fragments being found in areas with steep slopes, poor soils, or other areas undesirable for agriculture (Turner et al. 1996, Holt and Debinski 2003, Vellend et al. 2008, Liu and Slik 2014). Finally, different land-uses resulted in the regeneration of different matrix habitats, which both altered the magnitude of edge effects and influenced the capacity of different species to use or move through the matrix surrounding fragments (Ricketts 2001, Prugh et al. 2008, Brudvig et al. 2017).

As studies on fragmentation accumulated, reviews highlighted inconsistencies among the expectations of IBT, empirical observations, and the data needed for conservation (Fig. 1). For instance, Saunders et al. (1991) pointed out that while research on fragmentation had focused on the biogeographic consequences for the biota (and noted that this was of 'little of practical value to managers'), fragmentation also causes large changes in the physical environment such as altered fluxes of solar radiation, wind, water, and nutrients that in turn affect biota. To address this they stressed the importance of considering landscape context and the need for research on the interplay of internal and external factors and isolation (including the role of corridors) and manipulative experiments to guide management. Similarly, Harrison and Bruna (1999) pointed to a mismatch between the

theoretical models applied in fragmented landscapes and the empirical results observed in these systems. They concluded that while theory had emphasized spatial aspects of fragmentation and generated interesting and intricate predictions (e.g. non-linear relationships between remaining habitat and probability of species persistence), empirical studies often documented relatively simple but major degrading effects of fragmentation not attributable to spatial processes: reductions in habitat quality and the strong effects of proximity to fragment edges. They in turn called into question the ability of corridors or the spatial configuration of remaining habitat – on which most theory to date had centered – to compensate for the degrading effects of habitat loss and fragmentation.

As experimental studies of fragmentation sprang up, reviews across experiments became possible. In the most synthetic early review, Debinski and Holt (2000) found inconsistent results that could be positive or negative with respect to responses in species richness and abundance to spatial consequences of fragmentation. This inconsistency was attributed to ecological mechanisms not accounted for in early theory, including edge effects, competitive release in fragments, and spatial and temporal scales of fragments and taxa in the experiments ('species relaxation' in Saunders et al. 1991). Responses to fragmentation also could arise from, for example, differences in responses across species. More consistently supported was the positive role of corridors in dispersal (below).

These conclusions resulted in a push for developing theory that better reflected the biology of fragmented landscapes and their resident species by including, for example, variation in habitat quality (Moilanen and Hanski 1998), matrix permeability (Ovaskainen et al. 2008), and trophic interactions and structure (Holt 1993, 1997, Bascompte and Solé 1998, Holt and Hoopes 2005, Gravel et al. 2011). Of course, with increased theoretical complexity the challenge of parameterizing models with data and meeting model assumptions becomes more difficult.

As accumulating evidence from observational fragmentation studies was often ambiguous and problematic for testing theory, some researchers began tests over longer time scales in ecosystems that were fragmented experimentally. The strengths of these experiments were in the capacity to address confounding factors when testing fragmentation theory. Strengths include controls, replication, randomization, spatial design, and pre-treatment data (Holt and Debinski 2003). Collinge (2009) describes and reviews fragmentation studies at various spatial and temporal scales. While a benefit of small-scale experiments is the relative ease of controlling these variables, extending the results of small-scale experiments to the scales at which landscape conservation and management take place remains a challenge (Turner et al. 1989, Debinski and Holt 2000), especially since different species and processes respond at different scales. Consequently, a number of landscape-scale experiments were established that aimed to rigorously test the application of IBT and provide guidelines for conservation practitioners (Lovejoy and Oren 1981, Margules 1992). An advantage to experiments at these scales is that they exert effects through entire food webs and ecosystems (Fayle et al. 2015), permitting evaluation of responses that extended

well beyond species richness, to fragmented landscapes at scales that often approximate conservation and management activities. Five long-term experiments have lasted two to nearly four decades in duration (Haddad et al. 2015, 2017, Brudvig et al. 2017, Collins et al. 2017, Ewers et al. 2017), namely, the Biological Dynamics of Forest Fragments Project (BDFFP; Brazil), Kansas Fragmentation Experiment (USA), Wog Wog Habitat Fragmentation Experiment (Wog Wog; Australia), Savannah River Site Corridor Experiment (SRS Corridor Experiment; USA), and Moss Fragmentation Experiments (UK, Canada, Fig. 1).

Haddad et al.'s (2015) synthesis from these experiments showed many consistencies with predictions from theory and general expectations. For example, the experiments confirmed degrading effects of fragmentation on dispersal, species richness, species extinctions, species composition, interactions in food-webs, and ecosystem function and provided evidence of corridor efficacy. But these experiments also uncovered some results not expected from theory and gave rise to new or different predictions with important implications for conservation practice. As Lindenmayer and Fischer (2006) wrote about the BDFFP, "This case study highlights how the establishment of major research infrastructure led to many different kinds of studies … that are yielding valuable new insights."

Conservation lessons from fragmentation experiments

The study of habitat fragmentation is a relatively young sub-discipline: Burgess and Sharpe (1981) organized the first compendium on the topic in 1981, which was followed by Harris's classic book (1984) and an influential book chapter by Wilcove et al. (1986). The implication is that many of the conclusions now considered pervasive ecological truisms were recent advances that shaped not only ecological understanding of threatened ecosystems, but perhaps the practice of conservation itself. While many of these matched predictions from IBT and other theory (e.g. the relationship between fragment size and species richness), others were completely unexpected and emerged directly from experimental studies. Below, we summarize six key findings from these experiments and how they may have helped shape conservation practice in fragmented landscapes.

The first of these is *the critical conservation value of small fragments.* That species richness was lower in smaller or more isolated habitat fragments was not unexpected (but see Simberloff and Abele 1976a). But many were surprised to find that pollination (Dick 2001), and other interspecific interactions were often quite resilient in small and even highly degraded fragments (Bruna et al. 2005). Although there has been no suggestion that preserving small fragments is sufficient to conserve biodiversity comparable to that in large fragments, they could also play key roles as relict habitats, stepping stones for dispersing species, building blocks for corridors, sources of seeds and pollen for regeneration, and reservoirs of genetic diversity (Aizen and Feinsinger 1994, Turner and Corlett 1996, Freudenberger 2001, Pardini et al. 2005, Mueller et al. 2014, Saura et al. 2014, Lion et al. 2016). Also, small fragments may contain unique subsets

of species, particularly if they contain habitats not present in larger fragments (Simberloff and Abele 1976a), or species that actually achieve higher densities in smaller fragments (e.g. some small mammals in the Kansas Experiment, Diffendorfer et al. 1995). Moreover, reconnecting small fragments by restoration could be an effective way of creating larger fragments and buffering remnant small fragments. Collectively, these conclusions helped practitioners and land managers justify preserving small habitat fragments despite the perception they were ecological sinks unable to sustain viable populations (Turner and Corlett 1996).

The second result was growing observations that *fragmentation influences ecosystem processes*. The community-level consequences of fragmentation were always central to conservation, perhaps because IBT was the conceptual underpinnings of reserve design. However, fragmentation experiments showed that critical ecosystem processes, such as decomposition (Didham 1998), biomass dynamics (Laurance et al. 2011), water loss (Kapos 1989), and natural spread of fire in fire-dependent ecosystems (Brudvig et al. 2012), could all be influenced by habitat clearing and the isolation of habitat fragments, as originally identified by Saunders et al. (1991). While the implications of early results were not immediately apparent for conservation practice, the potential relationships among fragmentation, biodiversity, ecosystems services, and human well-being (Cardinale et al. 2012, Balvanera et al. 2014, Mitchell et al. 2014, 2015, Chaplin-Kramer et al. 2015) has elevated the broad implications of ecosystem responses for land management in fragmented landscapes.

The third result has been that effects of fragment isolation were often mediated not by the size of a fragment or how isolated it was, but by what surrounded it. Put another way, *many fragmentation effects were driven by matrix effects.* Early theoretical approaches to predicting biodiversity in fragments, as well as some early mesocosm experiments, ignored the habitat around fragments or treated it as homogeneous and inhospitable (Fahrig 2013). However, in many of the large-scale experiments it rapidly became obvious that the structure and composition of habitat surrounding fragments influenced ecological processes such as the growth and survivorship of individuals in fragments, the ability of animals to move between fragments, and the degradation of carbon stocks (Laurance et al. 1997, Brudvig et al. 2017). Moreover matrix type was found to be critical in mediating biotic and abiotic edge effects (Murcia 1995, Ries et al. 2004), to which many of the size-dependent effects of fragmentation are attributable. This is a key concern considering the extent of edge effects on forest worldwide (Haddad et al. 2015) and the role of edge effects on, for example, carbon stocks (Chaplin-Kramer et al. 2015). Eventually, the matrix itself became a critical component and focus of conservation when experimental studies demonstrated – albeit unintentionally – the dynamic nature of cleared areas surrounding fragments (Mesquita et al. 2001). These results included an unexpected capacity of cleared land to recover, relationship between regeneration trajectories and the way land is cleared and subsequent land-use, and divergence in different parts of the landscape. These experimental sites also demonstrated the potential conservation value of the matrix itself – if managed well, and with degradation

that was not severe, it could buffer against the degrading effects of fragmentation and it could be valuable habitat not only for species moving between fragments, but also for a diverse community of resident taxa (Mesquita et al. 1999, Davies et al. 2000, Laurance et al. 2011, Mendenhall et al. 2014). Matrix habitats also play an increasingly valuable role in the economics of conservation – in forested ecosystems a regenerating matrix accumulates biomass, and this carbon has emerged as the currency that encourages continued conservation by local, regional, and national and global stakeholders.

The fourth result is the extent of *evidence for corridor efficacy*. Early concerns about corridors were based on the absence of evidence that corridors work (Hobbs 1992) or concerns about negative effects of corridors (Simberloff and Cox 1987). Over time, a growing number of studies on corridor function for movement grew. A meta-analysis by Gilbert-Norton et al. (2010) confirmed that corridors increase inter-fragment movements in experimental and observational studies, with the SRS Corridor Experiment representing a large proportion of experimental results. This review provided the most compelling evidence to date that corridors often function as intended, and helped to justify the role of large-scale experiments in being informative to real landscapes. Beyond movement alone, this experiment elucidated the role of corridors in the diversity of communities (Damschen et al. 2006), plant–animal interactions (Tewksbury et al. 2002, Orrock et al. 2003, Levey et al. 2005, Brudvig et al. 2015), and potential negative effects of concern (Weldon 2006, Sullivan et al. 2011, Resasco et al. 2014). A literature review revealed that most of the concerns about negative effects of corridors (Simberloff and Cox 1987) were not supported (Haddad et al. 2014). In addition, moss landscape experiments confirmed the role of corridors in the persistence of predators and cascading impacts on prey populations and ecosystem processes of carbon and nitrogen fluxes (Staddon et al. 2010).

The fifth result is the emergence of *a more nuanced view of how individual species respond to fragmentation*. As stated above, IBT's emphasis on species richness was criticized as lacking interactions or species individualities. Fragmentation experiments began to unfold how species responded differently to fragmentation. For example, Cook et al. (2002) found in the Kansas Fragmentation Experiment that making the distinction between species preferring the open, grassy matrix and those preferring the woody fragments resulted in better approximations of species richness predictions of IBT to fragments. The importance of species identity (Laurance et al. 2011, Didham et al. 2012) and species traits as predictors of sensitivity to fragmentation emerged from fragmentation experiments including trophic rank (Didham et al. 1998, Gilbert et al. 1998, Davies et al. 2000, and evidence from a lake-island natural experiment see Terborgh et al. 2001), body size (Lindo et al. 2012), rarity (Davies et al. 2000), dispersal mode (Damschen et al. 2008), and specialization (Didham et al. 1998).

Finally, the sixth result was the *importance of time lags in the effects of fragmentation*. Haddad et al. 2015, showed that the effects of fragmentation on ecosystems (decline in species richness and ecosystem function) were only evident from long-term studies lasting decades. The effects were large. Species

richness declined by 13–75%, and degradation continued for the duration of experiments to date. This confirms theory predicting an extinction debt, or temporal lags in extinction, following fragmentation (Tilman et al. 1994). In the Kansas Experiment, for example, patch size effects on rates of succession were observed only over long time scales (Holt and Debinski 2003), demonstrating how studies of more typical duration (3–5 years) would have reached a completely different conclusion. Recent work suggests that substitutions of space-for-time to assess impacts of disturbances like fragmentation on biodiversity could underestimate impacts (França et al. 2016).

Conservation lessons from observational studies

Because observational studies do not have the same logistical restrictions as experiments (Holt and Debinski 2003), they have the advantage of being able to *assess additive and interactive forces that occur across broad scales and in sum generate impacts of habitat fragmentation.* For example, Cochrane (2001) leveraged the observation of thousands of km² of the eastern Amazon in satellite imagery to determine that 90% of wildfires are associated with forest edges. Moreover, wildfire has been shown to have an effect on Amazonian bird communities that is markedly different from that of fragmentation (Barlow et al. 2006). Thus, the interaction of both disturbances is likely to have a synergistic effect on biodiversity. Habitat fragmentation and logging roads also facilitate access to wildlands by hunters and poachers (Kerley et al. 2002), a key driver that is usually excluded from fragmentation experiments. The combination of these two factors has been suggested to drive midsize and large mammal populations to local extinction (Peres 2001). Similarly, roads accelerate habitat destruction and fragmentation (Barber et al. 2014) and themselves compound the effects of fragmentation (Eigenbrod et al. 2008).

Observational studies have also allowed for a better understanding of the *effects of habitat fragmentation on the provision of ecosystem services* like pollination (Aizen and Feinsinger 1994, Kremen et al. 2007, Tylianakis et al. 2008), pest regulation (Mitchell et al. 2014), and spread of infectious diseases (Allan et al. 2003). For example, one study has shown that distance from forest and fragment isolation significantly influenced pest regulation and crop production, but in very different ways (Mitchell et al. 2014). While pest regulation increased closer to forest fragments, crop production was maximized at intermediate distances from fragments. Thus, the ability of the landscape to provide multiple services was dependent on the heterogeneity of the landscape (Mitchell et al. 2014).

A major contribution of observational studies has been on *landscape management and restoration practices.* For instance, Phalan et al. (2011) showed that agriculture of any intensity in Ghana and India can lead to species loss and concluded from these results that land sparing (a land-allocation strategy of setting aside land specifically for biodiversity at the expense of intensive agriculture elsewhere) can be a better strategy to preserve biodiversity than land sharing (a strategy of balancing land use for both biodiversity and agriculture, often at a cost to both; see also Fischer

et al. 2008). More recently, Banks-Leite et al. (2014) showed that 30% is the minimum amount of habitat needed to preserve biodiversity in the Atlantic Forest of Brazil. Using this information, these researchers then estimated the average payment for ecosystem services and restoration costs for the region, and calculated that it would cost US$ 200 million to restore priority areas for conservation (Banks-Leite et al. 2014). Also in Brazil, other large-scale projects have shown that there are no trade-offs between productivity of shaded cocoa and levels of shading (Schroth et al. 2014), findings which have been used to shape local management actions. In the Amazon, researchers have also helped to draft new legislation that defines the age up to which secondary forest can be cut (Fernandes Rocha 2015) using information from their fragmentation studies.

Survey

Given that theory and the empirical work used to test for habitat fragmentation effects has provided some important insights which we put forward as lessons for conservation and that expert knowledge is a valuable resource in conservation science (Martin et al. 2012), we sought to further explore connections between fragmentation studies and conservation practice by surveying experts on conservation and habitat fragmentation. The objective of the survey was to ascertain their views on 1) fragmentation as a threat to biodiversity and ecosystem function and services, 2) the impact of theory and experiments and other sources of knowledge on conservation practice and management, and 3) factors needed to advance conservation practice and management. Most (87%) of the survey participants were identified from the 'find an expert' database of the Society of Conservation Biology, the world's leading and largest professional organization dedicated to conservation, and had 'habitat fragmentation' listed as a professional expertise. The remaining participants were people in scientific leadership positions at conservation organizations (e.g. World Wildlife Fund, Conservation International, The Nature Conservancy) including country offices of international organizations and national organizations based in Africa, Asia, and Latin America. It is important to emphasize this was not a survey of randomly selected respondents from a larger group of scientific and management professionals, but rather a survey of key informants (sensu Bernard 2000); participants in key informant surveys are selected precisely because their background and experience provides unique and important insights, in this case into the relationship of ecological theory and empirical studies on fragmentation for management and conservation in fragmented landscapes. Further details and survey questions are available in the Supplementary material Appendix 1.

We collected a total of 304 responses. A scan of the literature showed that this sample size is comparable to that of other studies that surveyed experts in ecology and conservation, which varied depending on the specificity of the group surveyed (e.g. 141 conservation managers from the UK, Pullin et al. 2004; 244 sea turtle experts, Donlan et al. 2010, 583 conservation scientists worldwide, Rudd 2011; Supplementary material Appendix 1). Survey respondents identified as ~56% academic researchers and ~33%

as conservation practitioners (20% at an NGO, 7% at a government agency, and 6% in the private sector) or ~12% as other (e.g. both academics and conservation practitioners, retired). Responses of conservation practitioners were very similar to those of academics (Supplementary material Appendix 2). Most of the respondents have worked in terrestrial systems (90%) at the regional or landscape scale (68%). The most frequently selected foci of research or conservation efforts (not mutually exclusive), in decreasing order, were populations, communities, ecosystem functions and services, human dimensions, individual organisms, global efforts, and other. Most are employed in the USA, Canada, or Europe (67%) but over half conduct their research or conservations efforts outside of those regions.

Respondents ranked habitat loss and fragmentation as the primary threats to biodiversity and ecosystem function and services, both worldwide and in their focal systems, with these threats being ranked ahead of other major threats such as climate change, infrastructure, exploitation, invasive species, and pollution (Fig. 2). On a scale of 1 (not important/not useful) to 5 (critical), responses showed that to make conservation and management decisions, system-specific data (4.1) and tests of theory with observational data (4.0) were *very important*, and ecological theory (3.6), experimental tests of theory (3.4), and expert opinion (3.5) were between *important* (3) and *very important* (4; Fig. 2). Respondents on average agreed that experimental tests of habitat fragmentation were *very useful* for testing ecological theory (3.8), broadening general ecological understanding (3.8), providing general guidelines for conservation and/or management that transcend specific location (3.8), and providing recommendations for conservation and/or

management in the same region (4.0, Fig. 2). For factors of importance for implementing successful conservation plans in fragmented landscapes, respondents believed that the following were on average *important* to *critical* (3.5–4.5), ranked in descending order of importance: connectivity, human uses of land and resources, policy and governance, landscape context, patch isolation, area effects, matrix effects, population ecology, edge effects, community ecology, ecosystem function and services, species richness and diversity, abiotic effects, and natural history (Fig. 2). It is interesting that among these are both factors that are typically emphasized in fragmentation studies (e.g. connectivity, population and community ecology) and factors that are not typical typically emphasized in fragmentation studies (e.g. human uses of land and resources, policy and governance). Factors missing from fragmentation studies that respondents identified as needed to advance conservation and management in order of frequency of selection were: community-based human dimensions, policy and governance, ecosystem function and services, community ecology, population ecology, natural history, other factors (free answer), and biodiversity surveys and taxonomic research. Free answer responses included interactions of multiple threats, genetics, eco-evolutionary dynamics, interaction networks, long-term monitoring, focus on habitats other than forests (e.g. grasslands), decision science (involving multiple stakeholders), and behavioral ecology.

Taken together, these results lead us to four conclusions: 1) respondents believe that habitat loss and fragmentation are chief threats to biodiversity and ecosystem processes and that 2) fragmentation theory, experiments, and observational studies are relevant for conservation practice and
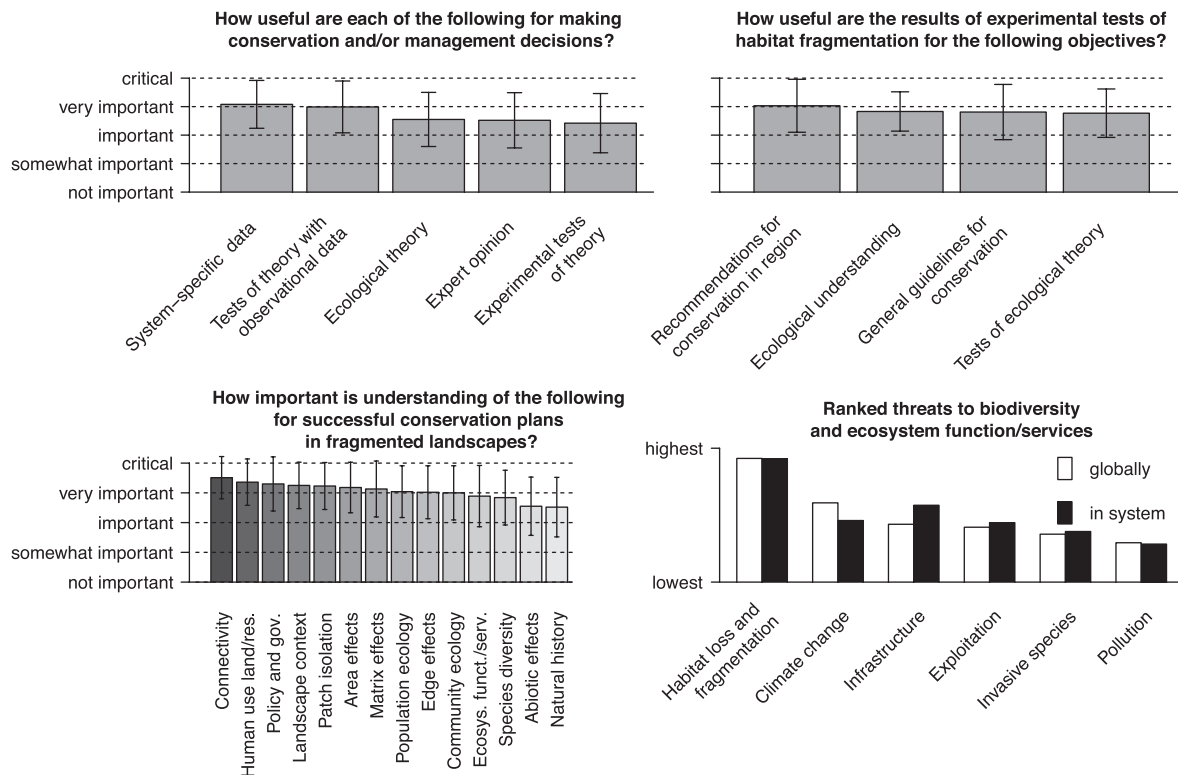

Figure 2. Responses to selected survey questions. Text is abbreviated for display clarity. Bars represent mean scores (± 1 SD error bars).

management. 3) Respondents think that general lessons that have emerged from large-scale fragmentation experiments above are important, but 4) there are some disconnects between typical foci of ecological studies on fragmentation and conservation priorities.

Theory, experiments and the conservation of fragmented landscapes – future directions

The development of theory and the testing of predictions from that theory with both experiments and observational data has increased understanding of fragmented landscapes and provided results that could be useful for management applications. Studies to date have also revealed avenues of research that would warrant more critical investigation. As noted at the beginning of this paper, most impacts on habitat fragments originate in the surrounding landscape (Saunders et al. 1991). So landscape scale management will be needed to support the biodiversity and ecosystem processes retained within fragments. Landscapes are complex social–ecological systems in which trade-offs are constantly being made (Sayer et al. 2013). Many of these trade-offs are not easy to resolve as they are influenced by social, economic and political concerns (Cronon 2000). Decisions are often made on the basis of anecdotal information. One way that science can support the process of decision-making is by providing empirical evidence in the form of experimental results that test predictions from theory and observations. Future experiments might better inform landscape scale decision-making by including human dimensions. The Stability of Altered Forest Ecosystems (SAFE) Project in lowland tropical forests of Borneo (Sabah, Malaysia), is designed to embed experimental fragments in a matrix with a gradient of land-use intensity and associated interactions (Ewers et al. 2011). Studies like this can test not only human impacts on ecosystems but also the extent to which ecosystem services are retained in fragmented human-dominated landscapes. Experiments can also better inform landscape scale decision-making by including the interactions between multiple stressors (e.g. fragmentation and climate change). For example, the Metatron experiment in the Midi-Pyrénées region of France (Legrand et al. 2012) and moss experiments in the sub-Arctic of Canada (Lindo et al. 2012) allow for manipulation of abiotic variables associated with climate change in addition to connectivity.

The personal experience of two of the authors (Margules, Bruna) reflects something frequently taught in our conservation biology classes – that conservation practitioners cannot afford to wait for experimental results; that conservation is too urgent to wait on science. Perhaps through collaboration between academic scientists and managers or conservation practitioners, future experiments could be designed using real conservation activities and generate knowledge co-production (Nel et al. 2016). This would have the added benefit of ensuring that results would inform management on the ground. Varying management practices experimentally in collaboration with agri-businesses (e.g. oil palm or rubber plantations), could present opportunities for experimentally studying fragmentation with greater applicability. It would be logistically difficult to conduct the same experiments under different policy prescriptions or governance arrangements, with the caveat that all of the experiments mentioned above have been established in the face of enormous logistical difficulties. It would be illuminating to test, for example, differences between local level management of fragmented landscapes and management directed from a central authority.

Given the importance of time in mediating the effects of fragmentation, long-term monitoring has proven critical. Over decades, fragmentation imposes ongoing degradation of ecosystems. Is there a time when degradation stabilizes, or when ecosystem responses are reversed, halting or ameliorating the ongoing effects of fragmentation? In addition to collecting data, archiving and organizing data to be able to synthesize across sites is crucial. The BIOFRAG database, for example, is a database for biodiversity responses to fragmentation (Pfeifer et al. 2014). It would also be beneficial to coordinate systematic data collection with consistent methodology.

In conclusion, a sound understanding of the dynamics of fragmented landscapes requires the integration of insights from observations, experimental manipulations, and theory (Holt and Debinski 2003). Thus, long-term field experiments in fragmented landscapes will continue to be needed to improve our understanding of how ecosystems, habitat fragments, and people interact with one another, to provide evidence on which to base management decisions, and to give rise to new theories and observations that in turn will need to be tested with experiments.

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