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Editorial

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Connecting models, data, and concepts to understand fragmentation's ecosystem-wide effects

Nick M. Haddad, Robert D. Holt, Robert J. Fletcher Jr, Michel Loreau and Jean Clobert

N. M. Haddad (haddad@ncsu.edu), Dept of Applied Ecology, North Carolina State Univ., Raleigh, NC, USA. – R. D. Holt, Dept of Biology, Univ. of Florida, Gainesville, FL, USA. – R. J. Fletcher, Dept of Wildlife Ecology and Conservation, Univ. of Florida, Gainesville, FL, USA. – M. Loreau and J. Clobert, Theoretical and Experimental Ecology Station, CNRS and Paul Sabatier Univ., Moulis, France.

Research on habitat fragmentation over the last 50 years has led to a rich understanding of patterns and processes observed in fragmented landscapes across all levels of ecological systems. Habitat fragmentation has continued apace and new global datasets on the extent and rate of fragmentation have motivated a new generation of experiments, theory, and landscape studies (Haddad et al. 2015). This led us to convene a selected group of theoreticians, experimentalists, observational ecologists, and experts in remote sensing at the Theoretical and Experimental Ecology Station in Moulis, France. This Special Issue has emerged from insights at that meeting. Articles in this Special Issue synthesize theory, coalesce key predictions from an evolutionary to an ecosystem perspective, and test theory with unprecedented long-term datasets collected in fragmentation experiments.

Recent progress in understanding the ecological effects of habitat fragmentation has been inhibited by factors our Special Issue addresses and begins to resolve: a proliferation of conceptual frameworks have often muddled, rather than focused, predictions, and a lack of a synthesis of long-term experimental data has hampered tests of current theories. Here, we draw together for the first time: 1) experiments that are now mature, up to several decades old, permitting evaluations of the effects of fragmentation on different dimensions of biological responses, including never-before documented lengthy time lags in responses; 2) a proliferation of theories that can now be synthesized and evaluated against experimental data, permitting a new round of fresh theory synthesis; and 3) a new understanding of applications of the science of fragmentation to conservation.

This Special Issue focuses largely on the integration of long-term experiments and theory development, in part because these long-term experiments have proved valuable for understanding mechanistically how and why fragmentation impacts ecological systems. Despite this Special Issue's central focus on experiments, we recognize the critical role of observational studies. Observations in particular can be used to examine a variety of landscape contexts, especially at large spatial scales not attainable with experiments. Our Special Issue highlights some of the benefits of observational studies for advancing our understanding of fragmentation, including the use of observational studies to test hypotheses regarding conceptual models of habitat fragmentation (Brudvig et al. 2017), responses in fragmented agricultural landscapes (Carrié et al. 2017), models comparing patch-matrix with mosaic approaches (Leroux et al. 2017), and ecological responses in fragments created by people centuries ago (Reynolds et al. 2017). Our feature articles are followed in this same issue of *Ecography* by a number of others that accomplish objectives not possible in controlled experiments, for example understanding fragmentation's effects over large geographic regions within continents. Indeed, one fruitful potential direction in research will be the integration of experimental landscape studies with analyses conducted at larger spatial scales, where experiments are well-nigh impossible.

Historical perspective

The process of habitat fragmentation has long emphasized reductions in patch area, increase in patch isolation, and increase in the proportion of habitat edge (Haila 2002). These three themes dominated the launch of ecology and conservation efforts in fragmented landscapes. Classic studies of fragmentation were conducted in landscapes fragmented naturally (Hanski et al. 1994) and in landscapes fragmented by people.

For a century, ecologists have recognized the role of habitat edges in structuring populations and communities, most notably beginning with Aldo Leopold: "We do not understand the reason for all of these edge-effects", but they are likely related to "the desirability of *simultaneous access* to more than one environmental type, or the *greater richness* of border vegetation, or both." (Leopold 1933). In the time since Leopold's observation, wildlife biologists have first

recommended increasing the amount of edge habitat to benefit certain wildlife species of interest to hunters (e.g. deer); conservation biologists have then conversely recommended decreasing the amount of edge to protect threatened species (Wilcove 1985); and finally ecologists in recent years have begun to predict more generally a mixture of both positive and negative responses to edges across ecological systems (Ries et al. 2004).

The effects of fragment area and isolation emerged as clear themes decades later. In empirical studies, ecologists began to recognize that fragment size changed community structure (Bond 1957). In theoretical studies, Preston (1962) connected species–area relationships on islands to nature reserves, whose fragmentation – reduced size and increased isolation – would inevitably reduce abundances and reduce species richness. He applied this classic concept to conservation, concluding presciently that "The only remedy is to prevent the area from becoming an 'isolate' by keeping open a contiguous corridor with other preserved areas."

Species richness was formally connected to fragment area and isolation in the theory of island biogeography, developed by MacArthur and Wilson (1967), who explicitly stated on p. 4: "The same principles apply, and will apply to an accelerating extent in the future, to formerly continuous natural habitats now being broken up by the encroachment of civilization, a process graphically illustrated by Curtis' maps of the changing woodland of Wisconsin". Figure 1 in their monograph shows Curtis' famed series of maps from 1852 to 1950 of an increasingly fragmented forest in the Cadiz Township, Wisconsin. This theory invoked mechanisms of extinction and isolation that have and continue to guide inquiry into the ecological effects of fragmentation on biodiversity. Although focused on oceanic islands, this theory shifted the discussion in basic research toward spatial ecology in fragmented landscapes, and provided the foundation for central tenets of and debates in ecology and conservation biology (Wilson and Willis 1975).

Whereas island biogeography brought into focus the potential role of fragmentation in structuring ecological communities viewed as a whole, the spatial dynamics of populations has more specifically been guided by metapopulation ecology. The theory was advanced to explain spatial population dynamics in fragmented landscapes, and the critical role of colonization and extinction dynamics (Levins 1969). It wasn't until two decades later that metapopulation ecology became a central theory of spatial ecology when Hanski and Gilpin (1991) championed it and honed a mechanistic focus for understanding metapopulation dynamics. Gyllenberg and Hanski (1992) connected occupancy dynamics to patch area, quality, and degree of isolation, not just from a mainland, but aggregated over an entire ensemble of potential sources for colonists. Hanski's exemplary blend of rigorous theory development with an empirical case study of Glanville Fritillary was applicable as a general approach to data that are often collected by a broad range of ecologists and conservation biologists over a wide range of spatial scales. Although distinct, island biogeography and metapopulation theories share a focus on spatial aspects of populations and communities that can be connected mathematically (Leroux et al. 2017). There was also a personal dimension to this shared interest, as Richard Levins was a close friend of Robert MacArthur, and participated in island field work with him.

From a more mechanistic perspective, evolution in fragmented landscapes, particularly in the trait that is most important in connecting or isolating populations – dispersal – has paradoxically only recently received the intense attention it deserves, both theoretically and empirically (Clobert et al. 2012). Comparison across landscapes has indicated that both increases and decreases in dispersal rates occur in fragmented landscapes (Baguette et al. 2013), likely due to an interplay between fragmentation, species mobility, dominant causes of dispersal, heterogeneity among individuals within species, and processes of habitat matching and local adaptation (Clobert et al. 2009, Cote et al. 2017).

Fragmentation experiments

This Special Issue synthesizes key areas of progress that extend well beyond early concepts and theories. Despite the impressive efforts and collection of results emerging from experiments over time, a thorough synthesis has been lacking since a review almost two decades ago by Debinski and Holt (2000) and subsequent books by Lindenmayer and Fischer (2006) and Collinge (2009). It is now time to take stock of the 'state-of-the-art' of the field, to highlight key messages that have emerged from landscape experiments, to articulate important directions for future research, and even to foster the initiation of new, critical experiments for advancing the field. A first start at such an evaluation was taken in Haddad et al. (2015), and continuing and deepening this evaluation is the purpose of this Special Issue of *Ecography*.

Acceleration of theory and application led to several fragmentation experiments being implemented over the past four decades. Some of these experiments, such as the Biological Dynamics of Forest Fragments Project in Brazil (Laurance et al. 2011), have been operating for many years, while others still are just initiating (e.g. The Stability of Altered Forest Ecosystems in Borneo (Ewers et al. 2011) and the Thousand Island Lake system, a 'quasi-natural' fragmentation experiment in central China (Wilson et al. 2016)). Although the elegance of the initial theory of island biogeography sparked a whole area of ecological research, equating terrestrial fragments with oceanic islands was a starting point that in many ways paralyzed the field (Laurance 2008). Early on, there was some expectation that larger and more connected fragments would always harbor more species. This expectation was despite logic that showed why these theories may not be applicable, as the same theory could be used to predict that many small fragments of contrasting habitats may conserve more species than do large fragments (Simberloff and Abele 1976). Still, it came as a surprise that results were inconsistent and in some cases divergent (Debinski and Holt 2000).

The group we convened for this Special Issue recognized three key issues. First, decades-long fragmentation experiments are necessarily whole-ecosystem experiments. Perhaps they were initially designed to test predictions that emerged from early theories focused on population and community dynamics, yet considered over decadal time scales,

there were many consistent, degrading ecosystem effects of habitat fragmentation as well. Second, long-term studies had cumulatively involved a great range of researchers who collectively produced a diversity of results, more than were ever dreamed of when the experiments were created. Finally, there were many results consistent with initial theoretical expectations, but there were also inconsistent results across studies, recognition of which may help catalyze new empirical and theoretical explorations.

By assembling a group of researchers with different approaches to habitat fragmentation, our objectives were to articulate new and more general insights that would steer future research on habitat fragmentation. This would include more sophisticated analyses of community dynamics and emergent ecosystem effects, explicit ties with current ecological theory, and a recognition of the likely importance of rapid evolution in fragmented landscapes.

Beyond simple metrics of biodiversity

Although well supported in theory, that same theory constrained fragmentation's empirical development. Tests of the initial theories were slow to emerge and accumulate. And, by the time synthesis was possible, evidence of fragmentation's effects was mixed (Harrison and Bruna 1999, Debinski and Holt 2000, Fahrig 2003). Theories, and thus empiricists, had simplified too greatly, primarily focusing on two independent variables, patch size and isolation, and two response variables, species richness and population occupancy. We now understand fragmentation's effects in a way that is not as general as first hypothesized, yet is richer. A particularly striking new direction of research is suggested by the fact that the ecosystem-wide effects of fragmentation are strong and persistent.

Landscape context

The habitat matrix has become recognized for its central role in driving fragmentation effects (Sisk et al. 1997, Ricketts 2001), and synthesis of its effects features here (Brudvig et al. 2017). Edge effects have been long-recognized (as noted above), with more recent efforts to make sense of diverse responses across species (Ries et al. 2004). Incorporation of (Ewers et al. 2017) or control of (Haddad et al. 2017) edge effects takes a prominent role in fragmentation research. In addition, there is an increasing emphasis placed on landscape context altering the outcome of fragmentation across large spatial scales, from regions to continents (Prugh et al. 2008, Ruffell et al. 2017).

Effects of fragmentation on species diversity arise in part because of the many idiosyncratic ways species can respond to edges, patch configurations, and matrix quality. Rather than treat all species, not to mention all individuals within a species (Cote et al. 2017, Legrand et al. 2017), as identical in their responses to fragmentation, efforts to understand fragmentation's effects have more realistically analyzed the traits of species (and intraspecific variation in such traits) that respond strongly to fragmentation (Henle et al. 2004, Damschen et al. 2008), and that theme continues here (Brudvig et al. 2017, Carrié et al. 2017, Leroux et al. 2017).

Metacommunities and metaecosystems

Metacommunity (Leibold et al. 2004) and metaecosystem (Loreau et al. 2003b) theories developed as logical extensions of the metapopulation paradigm to understand and predict the properties of spatial networks of interacting species and abiotic factors. These theories have offered new perspectives on the ecological effects of habitat loss and fragmentation, as the dynamical interactions between species, their abiotic environment and space all have profound effects (separately and in combination) on species coexistence, species diversity, and ecosystem functioning. Prior to habitat fragmentation, species would have existed in heterogeneous landscapes, with local communities coupled in complex ways by temporally and spatially varying dispersal of organisms and flows of materials. Fragmentation disrupts this original pattern of movement, and at the same time creates distinct interstitial habitats which can impinge on fragments in many ways. Thompson et al. (2017) explore how removing patches in a network of connected patches can alter the long-term stability of communities and ecosystems in changing environments. In particular, they argue that habitat fragmentation can erode the 'spatial insurance' ecological systems enjoy because of the capacity of many species to track over space the temporally fluctuating conditions to which they are adapted (Loreau et al. 2003a).

In the pre-fragmentation state, species would have coexisted not just in local communities but at a regional scale in a regional species pool. Given the potential for competitive exclusion, species may nevertheless persist because of the interplay of local and regional processes in providing coexistence mechanisms (Chesson et al. 2005). Many concrete mechanisms of coexistence are known, ranging from classical resource partitioning and habitat partitioning, to storage effects, to competition–colonization dynamics, to food web and host–parasite interactions, among others (Holt 2013).

Habitat fragmentation, in addition to its direct effects on extinction (e.g. because of small-population size effects) and colonization (e.g. rescue effects), is likely to indirectly add to the extinction debt by disrupting essentially all known coexistence mechanisms. For instance, disappearance of a top apex predator that cannot sustain itself in the face of habitat loss and degraded matrix conditions could unleash strong competitive interactions among its prey (Holt 2010, Estes et al. 2011). As another plausible example, altered abiotic conditions in fragments could degrade seed banks, thus vitiating storage effects through which temporally varying environmental conditions might promote species coexistence. As a consequence, the breakdown of coexistence mechanisms may explain observed patterns of temporal trends in community composition in fragments (Collins et al. 2017). Unraveling how habitat fragmentation impacts coexistence mechanisms in webs of interacting species is a largely untouched frontier in fragmentation research, ripe for both theoretical and empirical exploration.

To accomplish these goals, long-term, large-scale, experiments have to be complemented by short-term process-oriented experiments. Processes like habitat selection/matching, dispersal drivers and kernel shapes, and intraspecific and among-species heterogeneity in dispersal responses to fragmentation can all be better investigated

and understood using more controlled and largely replicated experiments that can only be done at smaller scales. In particular, the effect of interspecific interactions, either through competition, predation, or parasitism, on dispersal decisions and habitat selection is largely lacking, and yet of considerable potential importance to understand metacommunity dynamics (Resetarits et al. 2005). More interactions (and explicit integration) among small and large scale approaches to fragmentation effects and mechanisms are needed. Given that patch-level processes can depend greatly upon regional patterns of fragmentation and land use, explicit multi-scale approaches – going from mechanisms at the level of individuals to large-scale explicit landscapes, and beyond – are greatly needed.

Eco-evolutionary dynamics

Fragmentation, whether natural or human induced, will cause evolution of traits favorable to those environments (Merckx et al. 2003). Because there exists more research on eco-evolutionary processes in naturally fragmented landscapes (Legrand et al. 2017), long-term experiments provide an emerging opportunity for tests of fragmentation's eco-evolutionary effects. For example, there is increased recognition that considering heterogeneity in individual dispersal provides the grounding for evolution in dispersal and correlated traits (Table 1 in Cote et al. 2017), whether fragments were created by people or not. Individual personalities, dispersal propensity and habitat preferences have been shown to have some genetic determination, such that genetic changes in species can be driven by population dynamics over short time scales, and such changes can rapidly feed back onto the dynamics of populations, communities, and ecosystems (Fussmann et al. 2007, Schoener 2011). This reciprocal interplay between ecology and evolution can be potentially modulated by any change in the environment – including habitat fragmentation. Because one of the primary effects of fragmentation is the disruption of dispersal, the evolution of dispersal plays a central role in the eco-evolutionary dimension of fragmentation research (Ronce 2007, Clobert et al. 2012, Baguette et al. 2013).

Cote and colleagues (2017) create a framework to put into context the relationship between habitat fragmentation, dispersal dynamics, and trait evolution. Recognizing that there is variation in dispersal among individuals in a population, they argue that this variation may select for diversification of populations (habitat variability across fragments; differences in how phenotypic traits respond to matrix habitat) or simplify population genetics by mixing different phenotypes. In this case, one needs to consider dispersal in terms of 'dispersal syndromes', where there are entire suites of traits that coevolve in concert with dispersal, and also characterize when fragmented landscapes might maintain adaptive genetic variability in such syndromes. Taken together, these observations lead to the conclusion that evolution must be taken into account in dispersal studies generally, and in the context of fragmentation effects, specifically. Given the long-term nature of fragmentation, including human-caused and experimentally-created fragmented landscapes, evolution of dispersal syndromes will surely have occurred (and will be ongoing) in response to fragmentation, and should be measured.

Legrand et al. (2017) go beyond the impacts of fragmentation on dispersal, per se, to examine how shifts in habitat quality and connectivity influence local adaptation and gene flow patterns across fragmented landscapes. Interspecific interactions will markedly change in fragmented landscapes, as will the interplay of evolution and ecology in modulating such interactions. Experimental assessment of such effects is far behind the rich panoply of possible effects revealed by theory. This should be a significant direction of growth in fragmentation studies for years to come.

Reconciling across concepts and mechanisms

The theory of island biogeography spawned an explosion of studies on fragmentation. As the number of empirical tests have grown, new theories have been created to accommodate the range of observed responses that could not be explained by early theories. However, the problem now shifts in the opposite direction: models have increased in number and complexity, and the ability to organize the range of models has been lost.

Viewed in a different way, there is now great potential for new structures to organize the logic behind the proliferation of conceptual models of fragmentation effects. For example, Didham and colleagues (2012) identified two arenas of difference among models. In one arena, the dichotomy between habitat loss and habitat fragmentation can be treated independently, or not (Tischendorf and Fahrig 2000, Moilanen and Hanski 2001). In the other, species respond to fragmentation similarly or differently (Fischer and Lindenmeyer 2006). Didham et al. (2012) asserted that these 'false dichotomies' have inhibited advancement in understanding of fragmentation effects. They advocated a recognition that fragmentation cannot be treated in such black-and-white terms, and that progress will be made through understanding that there is interdependence across both arenas. This Special Issue takes steps toward this goal.

In one attempt to integrate apparently divergent models of species responses to habitat fragmentation that range from interdependent to individualistic, Leroux et al. (2017) review and synthesize competing models based on species–area relationships, metapopulation models, and species distribution models. They observe rightly that these models are typically used independently in studies of fragmentation effects and in conservation planning, whereas they need to be interwoven. They create a common framework for comparison. In a case study, they found that although the species–area relationship was most often supported, support for each model varied across species, and there was value in testing responses across all models.

In another area of conceptual integration, Brudvig et al. (2017) make sense of the range of perspectives that ecologists applied to patch impacts relative to matrix effects in fragmented landscapes. They build their framework from one end, informed by the theory of island biogeography that treats habitat fragments similarly to oceanic islands, to the other, that recognizes variation in landscapes occurring from fragments to matrix. Rather than side with a single camp, they make predictions for the types of species (e.g. predators vs producers, specialists vs generalists) whose

ecologies may best be explained by alternative conceptual models. One value of their approach is the link with analyses of species' responses to environmental gradients (Austin 2002). Manipulations beyond the patch scale have rarely been implemented (but see With and Pavuk 2012) and none over long durations, despite the fact that habitat fragmentation is an issue largely operating at a landscape scale. Such expansive landscape experiments are sorely needed.

Two papers in this Special Issue address the apparent schism between patch and landscape understandings of habitat fragmentation. Yin et al. (2017) create and test models to identify key thresholds in habitat loss with respect to the endemics–area relationship. They show how changes in habitat loss and fragmentation are inter-related. They then show that there is a critical threshold, identified as 40% habitat loss, at which point the endemic–area relationship changes and reduces species occupancy. Drawing on results of two long-term experiments, Haddad et al. (2017) use an island biogeography framework to test the habitat amount hypothesis (Fahrig 2013). This hypothesis posits that the amount of habitat in the landscape, not patch-scale variation, is the primary determinant of species richness. Contrary to the predictions of that hypothesis, Haddad et al. (2017) confirmed that habitat configuration does affect species diversity, with more isolated fragments having fewer species. As the effects of fragmentation cannot be entirely captured by gross measures of habitat loss at coarse spatial scales, new experiments are needed to test thresholds of habitat loss at which the configuration of fragments most affects ecological systems, just as new observational studies are needed that attempt to identify the relevant spatial scales of habitat fragmentation to ecological systems (Smith et al. 2011, Jackson and Fahrig 2014).

Fragmentation research's past and future

Although it has taken decades for fragmentation research to start to catch up to the theory that spawned it, we are now amassing data on the extent of fragmentation's effects across ecological systems (Fletcher et al. 2016). In addition, experiments have now run for durations long enough to gain insight into the long-term outcome of fragmenting landscapes. Haddad et al. (2015) recently reviewed all decades-long fragmentation experiments. Although each individual experiment had reported the changes (or lack thereof) imposed by fragmentation on different aspects of their systems, one response stood out above all: across a variety of plants and animals, fragmentation caused a loss of on average 30% of species. Ecosystem functioning declined similarly. One issue that should receive more attention is the co-dependence of ecosystem functioning and species diversity in fragmentation. Species diversity helps maintain aspects of ecosystem functioning, and in turn, those ecosystem functions affect the conditions of species coexistence. Habitat fragmentation, by impacting species composition in communities, and also determinants of ecosystem functioning, can profoundly impact both directions in this causal feedback. Metacommunity and metaecosystem theory has been used to explore this interconnection, and has generated a number of exciting new predictions on the large-scale relationships between species diversity and either ecosystem functioning (Loreau et al. 2003a, Mouquet and Loreau 2003, Reynolds et al. 2017) or ecosystem stability (Wang and Loreau 2016, Thompson et al. 2017) that are affected by habitat loss and fragmentation. Experimental work in fragmented landscapes, however, is lagging behind theory development. Better integration of theory with experiments specifically designed to test predictions from theory is warranted.

Even more striking in Haddad et al. (2015) was the finding that the decline in species richness and ecosystem functioning continued throughout the 2 + decades of the longest studies; we do not know when fragmentation effects will stabilize, so maybe what has been observed to date is just the tip of the proverbial iceberg. The temporal degradation of communities on fragments has some theory to match these observations. Theoretical predictions of an extinction debt, whereby loss of species can take unexpectedly long times to play out, emerged by adding metacommunity dynamics to more traditional spatial attributes of landscapes (Tilman et al. 1994). Extinction is a long game, and when the game is played out over space, long-term studies are required to detect it. Based on the gain in ecosystem functioning over decades observed in assembling communities with higher species richness, a delayed loss of functioning is predicted for disassembling communities, thus generating ecosystem functioning (Gonzalez et al. 2009) and ecosystem service (Isbell et al. 2015) debts. A sobering lesson from these predictions and results is that the full effects of fragmentation are likely to be overlooked in the typical duration of an ecological study.

Decades-long experiments are now able to look forward and backward at the effects of fragmentation. In an analysis in fragments extending back 1.5–3 decades, Collins et al. (2017) test how fragmentation has altered plant community structure. Their results highlight two characteristics of fragments that affect community composition and provide guidance for future studies. First, change to the matrix (for example via succession) strongly altered community composition. Second, whether community composition within fragments diverged amongst fragments depended on the nature of habitat destruction that created the fragments in the first place.

Looking a century into the future, Ewers et al. (2017) leverage the longest-running experiment, the Biological Dynamics of Forest Fragments project. They similarly found that matrix played a strong role in community composition; however, fragmentation was not predicted to continue to degrade forest over decades. Rather, models based on their 3 + decades of prior data predicted that future composition was strongly dependent on present-day composition. Their modeling framework deserves application across many ecosystems that have experienced anthropogenic degradation. Moreover, as they freely admit, their statistical approach sweeps aside any consideration of how specific taxa respond to environmental attributes, and also does not explicitly account for the reticulate details of interspecific interactions.

Conserving fragmented landscapes

Habitat loss and fragmentation are the main causes of biodiversity loss. The publication of 'Applied Biogeography' (Wilson and Willis 1975) motivated a focus on conservation strategies to reduce the negative effects of fragmentation. With its basis in theory and its clear predictions, it was a major force in the creation of conservation biology. It motivated many of the debates that have shaped the discipline, including for (Diamond 1975) or uncommitted to (Higgs and Usher 1980) large fragments, for (Leopold 1933) or against (Wilcove 1985) the creation of habitat edges, and for (Beier and Noss 1998) or against (Simberloff et al. 1992) the creation of landscape corridors.

For the most part, debate has moved beyond these issues. Rather, it has turned to a more fundamental discussion: relative to the important effects of habitat loss, does fragmentation matter in biodiversity conservation at all? Fahrig (2013) has resurrected challenges that have been leveled since the theory of island biogeography was first published (Simberloff and Abele 1976), placing them in a clear and logical context of species–area relationships. The implications that weave through this Special Issue are that fragmentation must be considered in conservation planning. Whereas experiments that are the focus here occurred in environments with great structural difference between fragments and matrix, arenas for future insights will come from understanding the tradeoffs inherent in land-sharing versus land-sparing (Phalan et al. 2011), and the relationship of variable natural and human-modified (e.g. agriculture) contexts that comprise the ecological systems containing fragments (Mendenhall et al. 2014). Knowledge in these areas will continue to advance via observational studies, in systems that vary in the distribution and intensity of human use, and that expand to scales not possible in experimental research. Computationally-intensive approaches such as individual-based models could be grounded and parameterized at local scales, where experiments are feasible, then extrapolated well beyond the scales of such experiments.

Despite ongoing debate about fragmentation's effects, there is one group whose dedication to reversing fragmentation in conservation has not wavered: conservation practitioners. Perhaps because of the theory, empirical support (though at times limited), and clarity of concept (habitats were once continuous, but now are not), Resasco et al. (2017) found in a survey that practitioners value landscape connectivity and patch area (alongside adjacent human uses and government policy) above a number of criteria in basic ecology and natural history in conservation planning. The advances made in theoretical and empirical studies of fragmentation can be used to fine-tune conservation efforts.

One area of conservation research that has lagged relative to the interests of conservation practitioners is understanding the role of habitat fragmentation in altering ecosystem services. Humans fragment the landscape to gain access to ecosystem services, including agricultural production, recreational areas, wildlife and forest products, and others. But they may then push those fragments past tipping points beyond which services are seriously degraded, as has been found in the longest-running fragmentation experiments (Haddad et al. 2015). Conceptual frameworks have now been established to test the relationship between fragmentation and services in a changing world (Mitchell et al. 2013, 2015). Tests of these relationships are emerging from observational studies of fragments. Mitchell et al. (2014) found that forest fragment isolation and distance from forest fragment edges affected multiple services, including those above (herbivory, productivity) and below (P, N, C) ground. Carrié et al. (2017) provide a detailed cross-ecosystem analysis of how habitat fragmentation affects changes in the response and effect traits in wild bee communities, and thereby indirectly a critical ecosystem service, crop pollination. Understanding the effects of fragmentation on ecosystem services has been limited within the long-term experiments, as they were not created to test these responses. Future experimental and, more plausibly, observational studies should provide more direct tests (Kormann et al. 2016).

In contrast to the dominant focus of this Special Issue on experiments, theory, and conceptual integration, Reynolds et al. (2017) take advantage of a unique setting, namely centuries-old Ethiopian church forests set in a landscape cleared for agriculture, to test for effects of their area and edge on services. They found that larger church forests support higher productivity. This, in turn, increases services such as wood for fuel and construction, food, medicine, and shade. Examples such as this provide some guidance into how fragmentation research can in the future integrate conservation metrics related to biodiversity conservation to metrics related to ecosystem functioning and services. More broadly, this study reminds us of the need to relate analyses of ecological processes that can be assessed at the (relatively modest) scale of landscape experiments to the much broader-scale processes generating patterns over anthropogenic landscapes, including socioeconomic and cultural forces that sculpt those landscapes.

Finally, there is a great need in conservation to better understand the interplay of habitat fragmentation with other major drivers of environmental change (Laurance and Cochrane 2001). Travis (2003) warned that climate change may have synergistic effects with habitat fragmentation, yet experimental work is lacking that tests for synergistic effects of fragmentation with other key issues, such as altered disturbance regimes, invasive species, emerging infectious disease, and climate change.

Conclusions

The body of experimental and theoretical work that has accumulated on the problem of habitat fragmentation has slowly matured over the years, and this Special Issue highlights this growth. Yet, it also provides a springboard to the new frontiers in fragmentation research. These areas include in particular the interplay between evolutionary and metacommunity dynamics with fragments, and this interface should be the subject of inquiry that integrates theory, experiment, and observation with resources at hand. New large-scale, experimental research should be positioned to manipulate the matrix, control fragment configuration and habitat amount simultaneously, and manipulate metacommunities and metaecosystems directly, and existing experiments could be re-evaluated from this perspective. Recently

created experiments foreshadow the types of opportunities that are possible. The Metatron in Moulis, France, retains unprecedented control of fragment size and connectivity, as well as abiotic conditions such as temperature and humidity (Legrand et al. 2012). The Stability of Altered Forest Ecosystems in Borneo created experimental fragments within an active agricultural landscape, permitting tests of ecosystem services (Ewers et al. 2011). New and large experiments are difficult to implement, but numerous opportunities exist to integrate controlled fragmentation into restoration efforts. A new frontier in fragmentation research would be structured around a network of experiments that coordinate across different biomes and spatial scales. Taken together, our Special Issue highlights past achievements in fragmentation research, while at the same time creating a vision towards the richness of advances that are yet to come.

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