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Toward conciliation in the habitat fragmentation and biodiversity debate

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Landscape-scale conservation planning is urgent given the extent of anthropogenic land-use change and its pervasive impacts on Earth's biodiversity. However, such efforts are hindered by disagreements over the effects of habitat fragmentation on biodiversity that have persisted since the mid-1970s. We contend that nearly 50 years later, these disagreements have become a locked-in debate characterized by polarized, unproductive discourse and a lack of consistent guidance for landscape managers and policy makers. Here, we highlight the need for a unified set of principles regarding conservation in fragmented landscapes, identify potential reasons for disparate conclusions in fragmentation research, and suggest ways for the ecological community to advance research that leads to consensus rather than the perpetuation of disagreement. Explicit efforts to develop and test multiple competing hypotheses, inter-laboratory collaborations, and acknowledgement of multiple interacting effects will be vital for moving the fragmentation debate forward. We argue that we in the ecology community should be responsible for helping to reconcile different views across scales, systems, and methodological approaches to advance conservation planning within a landscape ecology framework.

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The fragmentation debate

Disagreement is fundamental to the scientific process. Rigorous scientific inquiry encourages researchers to be at war with their own ideas, to design studies that challenge their hypotheses, and to ensure that those hypotheses can withstand scrutiny (Popper 1959). More broadly, scientific progress happens in fits and starts with periods of normal, incremental knowledge growth punctuated by moments in which established theories are challenged, tested, and debated (Kuhn 1962). It is during these latter paradigm-shifting moments that the potential for disagreement and division among scientists is highest, but also when the greatest advances in knowledge are likely to occur. When researchers become entrenched in their differing perspectives, however, these debates often become unproductive and locked in (*sensu* Norberg et al. 2022). Recently, Norberg et al. (2022) provided several examples of locked-in debates in the field of

ecology, including disagreements about the relationship between productivity and diversity (Adler et al. 2011; Fridley et al. 2012; Grace et al. 2012; Pan et al. 2012) and local biodiversity dynamics under global change (Cardinale et al. 2018; Gonzalez et al. 2016; Vellend 2017; Vellend et al. 2017). Unfortunately, locked-in debates tend to impede scientific progress by hindering productive discourse and reducing complex ecological processes to polarized arguments. More concerning is that this affords decisionmakers the freedom to single out results that support their agenda or even dismiss scientific findings outright due to a perceived lack of credibility (Norberg et al. 2022). Thus, locked-in debates can be detrimental to scientific progress and conservation efforts.

For half a century, ecologists have wrestled with a locked-in debate regarding the effects of habitat fragmentation per se (conditional on a given amount of habitat; Fig. 1) on biodiversity. Early disparity over the application of island biogeography theory

Fig. 1 Landscape (**a**) is composed of 100% habitat (green). Habitat loss can occur without fragmentation (**b**) while the process of fragmentation involves habitat loss that results in multiple smaller patches (**c**). Increasing the number of patches without changing the total amount of habitat in a landscape is referred to as fragmentation per se (**b** to **d** and **c** to **d**)
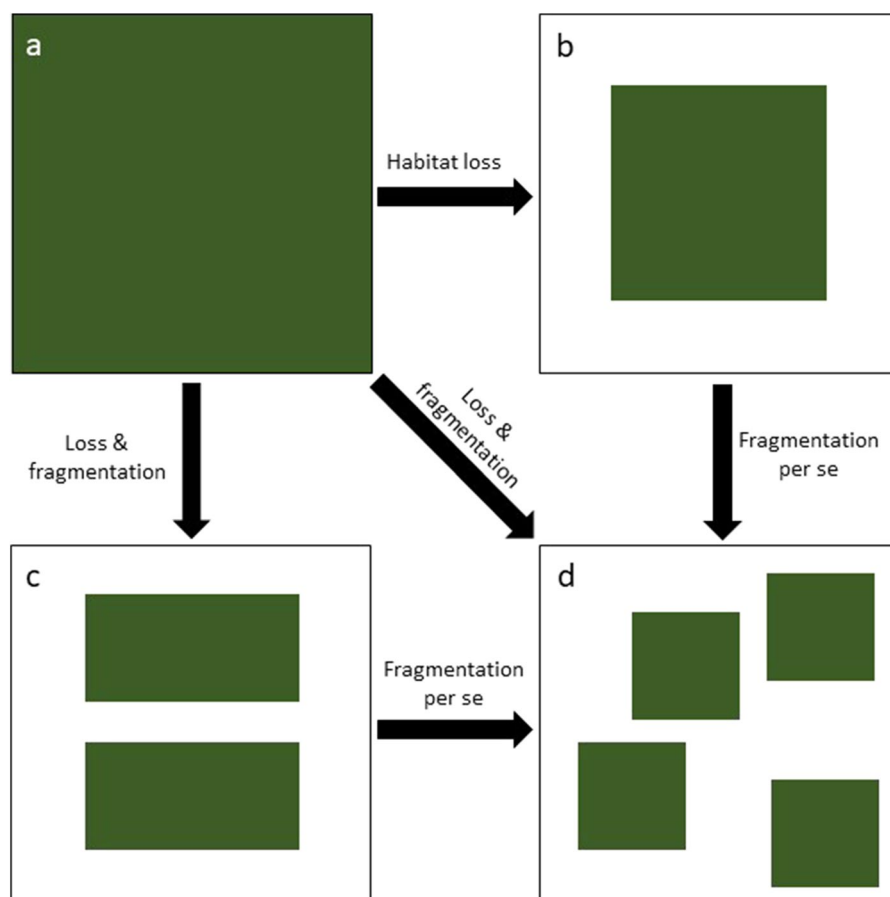
(MacArthur and Wilson 1967) to terrestrial systems fueled the SLOSS controversy in the 1970s and 1980s regarding whether a single large reserve would support greater species richness than several smaller reserves (Terborgh 1974; Diamond 1975; May 1975; Wilson and Willis 1975; Simberloff and Abele 1976; Quammen 1997). This controversy led to a discussion about the effects of fragmentation per se on species distributions (Wilcox and Murphy 1985), which in turn has fractured into numerous interrelated disagreements. These include back-and-forths in the literature regarding the relative effects of habitat loss and fragmentation per se on species distributions and abundances (Betts et al. 2006; Laurance 2008; Fahrig 2003, 2013, 2015; Hanski 2015; Haddad et al. 2017; Watling et al. 2020), the expected effects of habitat amount on species diversity (Fahrig 2013, 2021; Saura 2020, 2021), the general pattern of biodiversity response to fragmentation (Haddad et al. 2015; Fahrig 2017; Fletcher et al. 2018a; Fahrig et al. 2019), and whether habitat patches are relevant units for studying biodiversity in terrestrial systems (McIntyre and Barrett 1992; Lindenmayer and Fischer and 2007; Fahrig 2013; Mendenhall et al. 2014). Most concerning is that while natural systems are being lost and fragmented at an increasing rate globally (Haddad et al. 2015; Taubert et al. 2018), these debates have become more frequent and polarized (Fig. 2).

To appreciate how locked-in and confusing this debate has become, one needs to look no further than two relatively recent reviews by some of the leading thinkers in landscape ecology. Haddad et al. (2015) reviewed 76 studies across five long-running experiments in which habitat fragments were created. They concluded that "… habitat fragmentation reduces biodiversity by 13 to 75% and impairs key ecosystem functions by decreasing biomass and altering nutrient cycles." Shortly thereafter, Fahrig (2017) reviewed 118 studies that measured fragmentation across whole landscapes and concluded that across a range of variables related to biodiversity and ecosystem services, "… the significant responses to habitat fragmentation independent of habitat amount are rare and mostly positive." While there are some important differences in the questions addressed by these researchers and the criteria used for including studies in their reviews, these differences are likely to be lost on many students, land ma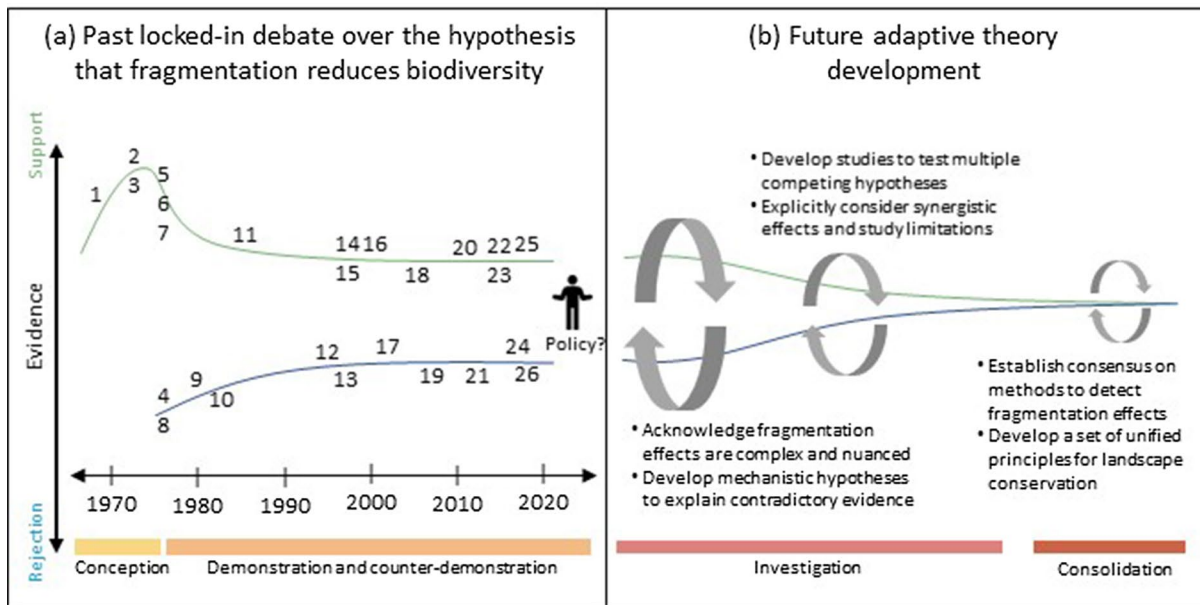nagers, and policymakers. The most salient takeaway from these reviews is that accomplished scientists come to seemingly mutually exclusive, opposite conclusions regarding fragmentation effects on biodiversity and ecosystem processes.

Critically, the consequences of this locked-in debate extend far beyond its influences on scientific progress. Although many factors come into play when developing conservation strategies (e.g., location, cost, threatened species), land managers, conservation practitioners, and policymakers tasked with conserving at-risk species and their habitats across the globe are increasingly incorporating the composition and configuration of protected areas into the planning process. Broad-scale initiatives such as the Mesoamerican Biological Corridor (Miller et al. 2001; Independent Evaluation Group 2011), the Yellowstone to Yukon Conservation Initiative (Aenġst 1999), the Northwest Forest Plan (Spies et al. 2019), and the America the Beautiful Challenge (U.S. Depts. of Interior, Agriculture, and Commerce 2021) have all emphasized the need for science-based guidance for improving biodiversity protection through regional planning efforts. Given that decisions regarding resource allocation at large spatial expanses are typically irreversible in the short term, we need to ensure this polarized debate is not undermining effective decision-making.

Our goal here is neither to take sides, nor to criticize the valuable progress that has been made by fragmentation researchers to date, but to provide a framework for moving forward. To do this, we have generated several hypotheses to explain how different scientists can come to discordant conclusions regarding the effects of fragmentation on biodiversity, and we encourage a shift towards exploring these potential mechanisms rather than defending a specific position in the debate. Our hope is that developing an empirically verified understanding of the biological processes and study design factors driving the debate will lead to more unified and management-relevant knowledge of how fragmentation affects species distributions and biodiversity across scales.

Why are we locked in?

The heart of many locked-in scientific debates is a failure to progress from studies focused on testing

Fig. 2 This figure, adapted from Norberg et al. (2022), highlights the four phases of adaptive theory development (conception, demonstration, investigation, and consolidation). The hypothesis that fragmentation reduces biodiversity has been locked in a demonstration and counter-demonstration phase since the mid-1970s, as shown by a non-random sample of 26 published journal articles spanning that time period (panel **a**). Unlocking this debate will require collaboration among researchers with different perspectives to develop a common conceptual framework for habitat fragmentation and to use that framework to develop and test hypotheses to explain disparity in previous findings (panel **b**)

support for a hypothesis or theory (theory demonstration) to those that explore the adequacy and limitations of the theory (theory investigation; Fig. 2; Norberg et al. 2022). In the case of the fragmentation debate, studies focused on theory demonstration do indeed still abound (Evju and Sverdrup-Thygeson 2016; Haddad et al. 2017; Lindgren and Cousins 2017; Watling et al. 2020; With and Payne 2021). However, conflicting findings from such studies cannot fully explain the sustained division given that reviews examining the mechanistic effects of fragmentation on biodiversity have also yielded mixed results (Debinski and Holt 2000; Haddad et al. 2015; Fahrig 2017). For example, Fahrig's (2017) review found no evidence that tropical species are more negatively affected by fragmentation than temperate species, while another global analysis using the BIO-FRAG database (Pfeifer et al. 2014) revealed that species near the equator are 6 times more likely to show negative responses to fragmentation than those at higher latitudes (Betts et al. 2019). In addition, while several studies have identified trait-based predictors of species response to fragmentation, these predictors are inconsistent across studies (Hatfield et al. 2018). Notably, there are several key biological and methodological factors that may cause variability among fragmentation studies and ultimately contribute to such inconsistencies.

Patch-scale vs. landscape-scale study design

A carefully designed study is critical to testing any hypothesis and drawing reliable inferences. Yet what constitutes the best, or even a reasonable approach, to testing fragmentation effects on species or communities remains one of the most divisive issues in fragmentation research. We suggest that study design may be the most important cause of opposing conclusions about fragmentation effects. Some researchers have argued that because fragmentation is a landscape-scale process, and because patch size and isolation can be confounded with habitat amount, effects of fragmentation per se can only be studied by measuring biodiversity responses to fragmentation metrics within whole landscapes (e.g., mean patch size, number of patches, mean interpatch distance; McGarigal and Cushman 2002; Fahrig 2017; Fahrig et al. 2019). On the other hand, the process of fragmentation (which results from habitat loss; Fig. 1) affects

landscapes by altering the size, shape, and isolation of individual patches, which theory predicts should affect species distributions and dispersal rates (MacArthur and Wilson 1967; Levins 1969). For this reason, other researchers have argued that fragmentation effects on biodiversity are best measured as a function of the size, shape, or isolation of individual patches (Thornton et al. 2011; Hanski 2015; Fletcher et al. 2018a, 2023).

Interestingly, there is some evidence that study conclusions can be confounded by the study design. Reviews that rely exclusively on landscape-scale studies designed to measure the effects of fragmentation per se seem more likely to conclude that fragmentation positively affects biodiversity (Fahrig 2003, 2017; Riva and Fahrig 2022). In contrast, reviews relying on patch-scale studies seem more likely to come to the opposite conclusion (Gilbert-Norton et al. 2010; Thornton et al. 2011; Haddad et al. 2015; Chase et al. 2020). We suspect this difference has to do with disparate mechanisms dominating the underlying biodiversity patterns in such studies. When comparing landscapes with similar amounts of habitat, increased fragmentation per se (Fig. 1) will likely result in increased inter- and intra-patch heterogeneity leading to greater diversity within whole landscapes (gamma diversity). Not only does this increase the pool of species in the landscape available to colonize patches, but under this model, fragmentation reduces inter-patch nearest neighbor distances making colonization events potentially more likely, thereby increasing local (alpha) diversity. Therefore, the sum of these processes may have a net positive effect on some biodiversity metrics (see 'Measurements of biodiversity' below). Conversely, the process of fragmentation (which typically stems from habitat loss; Fig. 1) results in patches of habitat that are smaller and more isolated from one another. Populations of species that rely on that habitat are smaller in remnant patches and thus more likely to go extinct, while isolated patches are less likely to be recolonized due to dispersal limitation. Moreover, the quality of individual patches may be reduced for individual species due to altered biophysical properties stemming from edge effects (Ries et al. 2004). Thus, comparisons among patches with different emergent properties stemming from fragmentation may yield negative effects on biodiversity metrics. Further empirical research is needed to
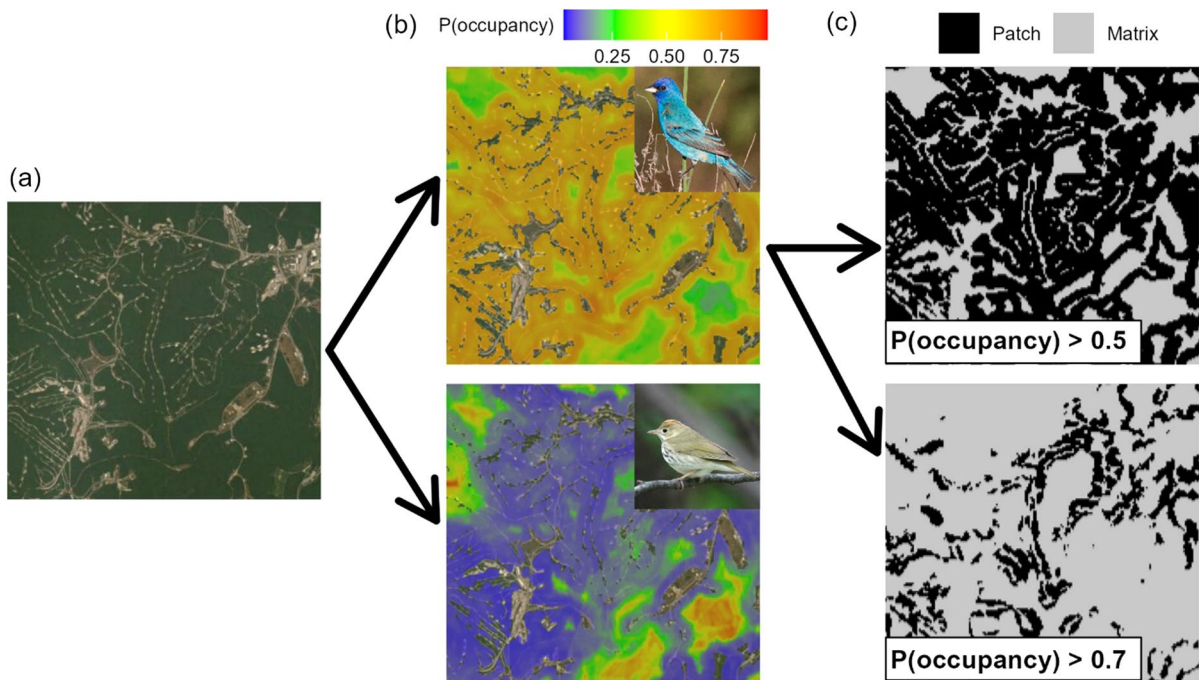
Fig. 3 The process of fragmenting one land cover type can have very different effects on the distribution of habitat for different species. Using species distribution models (SDM) that linked known occurrences with satellite imagery, we (**a**) examined the effects of forest loss and fragmentation from road development on breeding bird distributions in southern Indiana (Valente and Betts 2017; base map from Esri and its licensors, copyright 2023). **b** The forest fragmentation process split Ovenbird (*Seiurus aurocapilla*) habitat into smaller and more isolated units (bottom) but had the opposite effect on Indigo Bunting (*Passerina cyanea*) habitat, creating larger, more contiguous patches (top). **c** To measure habitat amount and fragmentation, these SDMs must be dichotomized by selecting a threshold value in the occupancy probability gradient to distinguish patches from matrix; the choice of this threshold value (0.5 or 0.7) will affect measurements of habitat amount and fragmentation. Unedited Indigo Bunting and Ovenbird images were provided by Dan Pancamo and Mike's Birds, respectively, under a Creative Commons Attribution-ShareAlike 2.0 license (https://creativecommons.org/licenses/by-sa/2.0/legalcode)

develop a comprehensive understanding of how study design affects conclusions in fragmentation studies.

Fragmentation of habitat vs. land cover

Quantifying the structure of a landscape is a fundamental precursor to measuring fragmentation effects on a species or community. However, while there is a difference between measuring fragmentation of habitat and fragmentation of a land cover type, many studies use land cover to represent habitat in their analyses (e.g., Evju and Sverdrup-Thygeson 2016; Lindgren and Cousins 2017; Valente and Betts 2019; With and Payne 2021). *Habitat* is a species-specific concept that refers to the biotic and abiotic conditions necessary for a given species to occupy an area, which may lead to survival and reproduction (Lindenmayer and Fischer 2007). On the other hand, *land cover* refers

to the physical material on the Earth's surface in an area, such as vegetation communities, water bodies, and artificial structures. A land cover classification (e.g., forest, grassland, or chapparal) can be used as a habitat proxy, but it is unlikely to be a direct analog of habitat for all, or even most, individual species (Halstead et al. 2019).

While fragmentation of a land cover type is likely to affect the distribution of habitat for many species, it will not affect them all equally. For some species, the process of fragmenting a particular land cover type may be comparable to loss and fragmentation of habitat, but for others it could create more habitat aggregated in larger patches (Fig. 3a, b). That is, the fragmentation process makes space for additional species that have niches more aligned with the ecosystems that replace the disturbed land cover type. Fragmentation could also add habitat for species that

respond positively to the altered biophysical properties of the remnant patches stemming from edge effects (Ries et al. 2004; Fletcher et al. 2007). Indeed, this increased heterogeneity could help explain why a collection of small patches of a particular land cover can often support more species than large patches of the same area (Wintle et al. 2019). To be clear, understanding the responses of individual species to fragmentation of both habitat and land cover types is useful from a conservation perspective, but the former is a test of island biogeography and metapopulation theory while the latter is a test of how species with different habitat requirements respond to landscape change. Failure to recognize this subtle, but important, difference could help explain how researchers can find seemingly idiosyncratic responses of species to fragmentation (Betts et al. 2014).

Subjectivity in patch delineation

Regardless of whether a researcher measures habitat or a land cover type, they must establish rules regarding patch boundaries before measuring fragmentation. Establishing rules is not necessarily straightforward as it requires drawing hard lines in landscapes often characterized by gradual biogeophysical gradients (Fig. 3c). Where patches are separated by distinct boundaries, they may be functionally connected depending on the species, its dispersal capabilities, and the matrix structure (Taylor et al. 1993; Ricketts 2001), which further contributes to ambiguity regarding where one patch stops and another starts. In many ways, patch boundaries are thus often based on a series of subjective decisions made by the researcher which could affect the values of measured fragmentation metrics and thus the perceived relationship between fragmentation and species or community distribution patterns. While this perception has led some researchers to argue that the patch-matrix model is of limited use in terrestrial systems (McIntyre and Barrett 1992; Fischer and Lindenmayer 2006; Fahrig 2013; Mendenhall et al. 2014), few studies have empirically investigated whether decisions regarding how to define the landscape mosaic affect study conclusions (but see Moilanen 2002).

Fragmentation metrics and measurement scales

After defining patch boundaries, researchers must also choose among the dozens of metrics that can be used to quantify fragmentation (Neel et al. 2004; Wang et al. 2014). To some extent, fragmentation metrics are confounded with study design as landscape-scale studies, by definition, measure characteristics describing the whole landscape (e.g., mean patch size or edge density in a landscape) while patch-scale studies measure characteristics of individual patches (e.g., focal patch size or edge density). Although previous research has compared metrics in their abilities to quantify landscape patterns (e.g., Wang et al. 2014), empirical evidence linking landscape- or patch-scale fragmentation metrics with the mechanistic processes that could lead to a fragmentation response in a species (e.g., dispersal ability, edge effects) are lacking (Li and Wu 2004; but see Fletcher et al. 2018b).

Similarly, researchers must identify a scale at which to quantify selected fragmentation metrics, such as when using a landscape-scale or focal-patch study design (Fletcher et al. 2023). The choice of scale can have strong effects on the value of these metrics (Wu 2004; Wu et al. 2002) and their inferred relationships with biological responses (Holland et al. 2004). For example, Valente et al. (2023) demonstrated that habitat fragmentation had significant positive effects on the distribution of an endangered species when measured at a fine spatial scale, but significant negative effects when measured at a broader spatial scale. Although much has been said about matching spatial scales of measurement with those at which relevant biological processes operate (e.g., Jackson and Fahrig 2012), most ecological studies do not provide biological justification for the scale at which landscapes are defined (Jackson and Fahrig 2014) which could lead to spurious conclusions regarding fragmentation effects.

Context dependency of fragmentation effects

Evidence indicates that fragmentation effects can be highly context dependent which almost certainly contributes added variance. For instance, Betts et al. (2019) demonstrated the role of evolutionary context where species that evolved in regions with frequent

and severe disturbances were less likely to be negatively affected by modern processes causing fragmentation. Ecological contexts also play an important role, as characteristics of the intervening matrix (Prugh et al. 2008; Ricketts 2001) or the amount of habitat remaining in the landscape (Andrén 1994; Herse et al. 2020; Püttker et al. 2020) can moderate fragmentation effects. For example, there is evidence that the effects of fragmentation can be amplified in landscapes with more (Herse et al. 2020; Püttker et al. 2020) or less (Andrén 1994; Betts et al. 2007) habitat. Additionally, intra-species fragmentation effects are known to vary across a species' geographic range (Banks-Leite et al. 2022; Valente et al. 2023), making it difficult to draw unequivocal conclusions from studies conducted at a single location within the range.

Measurements of biodiversity

The United Nations defines biodiversity as the variability of life on Earth, including "diversity within species, between species, and of ecosystems," (Convention on Biological Diversity 2010). In other words, the variety of response variables that can be explored under the banner of "biodiversity" is massive (Haddad et al. 2015; Fahrig 2017). As noted above, responses of individual species to fragmentation can be idiosyncratic and influenced by habitat requirements, life history, or both. Hence, the emergent structure of the biotic community then depends on the cumulative effects of fragmentation on individual species, subsequent inter-specific interactions, as well as interacting effects of local conditions (i.e., habitat quality) and fragmentation. As a result, choices of focal species or species groups (Bender et al. 1998; Valente and Betts 2019) can affect perception of how fragmentation affects biodiversity as can the choice to use taxonomic, phylogenetic, or functional diversity metrics within the resulting community (Devictor et al. 2010). Even within an individual species, fragmentation could have divergent effects on distribution, behavior, fitness, or population genetic structure. For example, fragmentation can simultaneously have positive effects on the distribution of a species but negative effects on its reproductive output (Ries and Fagan 2003). As a result, the choice of which biological process to measure may have strong effects on whether positive or negative effects of fragmentation on biodiversity are detected. Even effects on a metric

as familiar as species richness could vary depending on whether the focus is on local (alpha) richness, regional (gamma) richness, or their ratio (beta richness; Valente et al. 2022).

Other factors

The list of factors above is not meant to be comprehensive, and other study characteristics might affect a researcher's conclusions regarding the effects of fragmentation on biodiversity. These include, for example, the amount of time since the habitat loss and fragmentation occurred (Vellend et al. 2006; Haddad et al. 2015; but see Fahrig 2020), how the confounding effects of habitat amount are accounted for in estimating the effects of fragmentation per se (Koper et al. 2007), and the variation in quality among remnant habitat patches (Mortelliti et al. 2010). Given such complexity, it is no wonder that researchers who work with different species using different measures and scales of fragmentation in different regions can arrive at contrasting conclusions. Moving forward, fragmentation researchers could explore these disparities so that patterns can be elucidated and communicated to practitioners and policymakers. Identifying the patterns that exist and clearly delineating the situations in which these patterns do and do not hold would benefit effective conservation policy (Fahrig et al. 2022).

How do we unlock?

Norberg et al. (2022) highlighted several instances in which researchers with opposing viewpoints were able to unite and make substantial advancements in their field through collaboration and productive discourse (e.g., Kahneman and Klein 2009). These collaborations can be useful for elucidating the source and extent of disagreement (Scott-Phillips et al. 2014), clarifying the study designs suitable for testing existing hypotheses, generating new testable hypotheses with buy-in from both sides of a debate (Matske et al. 2015), and bringing opposing views closer together (Cowan et al. 2020). Indeed, research indicates that collaborations among individuals with contrasting perspectives generally lead to higher-quality products (Shi et al. 2019). Thus, we hope that a concerted effort by ecologists to come together and

unlock the fragmentation debate will be highly productive for understanding the ecological mechanisms structuring biodiversity and providing consistent, evidence-based recommendations to land managers and conservation biologists around the planet.

Action items for individuals

As a first step in bringing ecologists together, we suggest that the discipline would be enhanced by testing the hypothesized ecological and methodological mechanisms that could underlie inconsistent results described above. It will be important to start with the acknowledgment that our colleagues are competent and acting in good faith, which will fuel open-minded hypothesis development and testing (Loehle 1987). That said, science is conducted by humans who are inherently subject to implicit biases (Betini et al. 2017). Further, the need to acquire grants and publications for career advancement can foment absolute thinking (see Norberg et al. 2022 for details). One way for all scientists to avoid these pitfalls is to push themselves to consider multiple alternative hypotheses or hierarchies of hypotheses when designing studies and then evaluate their relative support based on empirical results (Betini et al. 2017). The multiple working hypotheses approach was originally suggested by Chamberlin (1890) to circumvent becoming emotionally attached to a favorite hypothesis and prematurely dismissing alternative explanations of phenomena (Betts et al. 2021). Indeed, this approach was later championed by Platt (1964) as integral to strong inference and rapid scientific progress.

For example, to understand why results from studies measuring the relationship between fragmentation of a landcover type and species richness vary so widely, we could simultaneously test the hypotheses that this relationship is driven by (i) the scale at which fragmentation is measured (landscape vs. patch) or (ii) the scale at which biodiversity is measured (alpha vs. gamma diversity). We could test these two hypotheses by first selecting landscapes across a gradient of fragmentation per se (keeping habitat amount constant) and then measuring diversity at multiple sites across each landscape to allow calculation of both alpha and gamma richness. Subsequently, we could select one individual patch within each landscape and draw an ecologically relevant buffer around that patch (i.e., a focal-patch design; Fletcher

et al. 2023) and again measure richness in the focal patch (alpha diversity) and in all patches within the buffer (gamma richness). We would then model alpha and gamma richness as a function of landscape-scale fragmentation metrics (e.g., number of patches in the landscape) or patch-scale fragmentation metrics (e.g., focal patch size) while statistically controlling for habitat loss by including remnant habitat area within landscapes or patch buffers as a covariate in our models. Such a study design would also allow evaluating interactions between the two factors (see next paragraph). This exercise of explicitly testing multiple hypotheses can reduce intellectual myopia and the post-hoc tendency to construct compelling narratives around results, including just-so stories (Nuzzo 2015).

It is also important to consider among the set of alternative hypotheses explanations that involve two or more potentially interacting factors rather than only those that limit inference to mutually exclusive univariate hypotheses (Hilborn and Stearns 1982). Inclusion of multifactor explanations reduces the likelihood of eliminating potential synergistic causes of a pattern or factors that only act in a subset of scenarios and is vital to recognizing compatibility among multiple competing hypotheses (Hilborn and Stearns 1982; McIntire and Fajardo 2009). For example, physiological stressors, competition, and bioclimatic suitability experienced by a species vary in space and these factors can interact with landscape disturbances to cause heterogeneity in effects of fragmentation across the species' range (Banks-Leite et al. 2022; Valente et al. 2023). As another example, Fahrig et al. (2022) proposed (and suggested methods for testing) the "SLOSS cube hypothesis," which posits that the effects of fragmentation per se on gamma diversity can be predicted from the intersection of three factors: between-patch movement, across-habitat heterogeneity, and the effects of spreading-of-risk on landscape-scale population persistence.

Finally, we also suggest researchers consider biological null models that address patterns and processes expected in the absence of mechanisms being tested. Indeed, some models for the neutral geometric effects of fragmentation on biodiversity have recently been developed (e.g., May et al. 2019; Deane et al. 2022). These null models allow researchers to test whether hypothesized mechanisms are necessary and sufficient to explain observed patterns (Pearson and

Gardner 1997). Understanding what processes or situations might allow the patterns expected under the null model to occur can also lead to more biologically realistic alternative hypotheses (Nuzzo 2015).

Community-level action items

We propose that the way to resolve scientific disagreement on the human front is to facilitate constructive conversation between opposing sides of the debate, allowing all perspectives to be heard and understood. We therefore envision a collaborative effort among ecologists with the main goals being to: (1) develop a set of consensus principles to serve as best practices for landscape management and biodiversity conservation; and (2) identify hypotheses that may help explain the continued lack of consensus regarding fragmentation effects on biodiversity (building on our incipient effort here) and use these hypotheses to steer future research into when, where, why, and how fragmentation affects biodiversity (e.g., Fahrig et al. 2022).

One potential way to achieve both goals is to use the Delphi method, a technique developed to help groups of experts (hereafter "participants") achieve consensus on complex problems (see Mukherjee et al. 2015 for review). In a Delphi study, communication between participants is highly structured, anonymous, and indirect. First, participants respond to a survey, after which a facilitator summarizes the responses and shares the summary with the group; the summary can also include explanations for any dissenting responses. Then, participants take the survey again, providing an opportunity to revise answers based on group feedback. The process continues until consensus (or an alternate goal) is reached. Although use of the Delphi method remains relatively rare in ecology (Mukherjee et al. 2015), this approach has nevertheless proven useful in numerous conservation applications, including evaluating the conservation value of different forest types (Geneletti 2007), estimating species-specific connectivity (Scolozzi and Geneletti 2012), summarizing the effects of forest management on biodiversity (Filyushkina et al. 2018), and assigning IUCN Red List status (McBride et al. 2012).

Another logical step may be to organize a series of symposia at international scientific meetings, such as that of the International Association for Landscape Ecology or the International Congress for Conservation Biology. The goal of these symposia would be to highlight and discuss different perspectives, or to develop a working group that generates a set of consistent principles to communicate to policy makers and land managers. This approach has precedence in conservation biology (Lindenmayer et al. 2007). Indeed, straightforward efforts to reach out to colleagues with opposing positions to develop collaborative projects examining the root causes of conflicting findings will likely lead to a much stronger understanding of how landscape configuration structures biological communities and will represent an important step towards a more productive scientific discourse.

Conclusions

Nearly 50 years after the initial application of island biogeography theory to terrestrial conservation planning, we appear to be no closer to a discipline-wide consensus regarding the effects of fragmentation on biodiversity or the role of landscape configuration in designing effective reserve networks (Fig. 2). We as scientists are responsible for this debate and should hold ourselves accountable for helping to settle it and ultimately provide clear, scientifically defensible, and timely messaging to managers and policymakers. Critically evaluating management and policy recommendations indicated by multiple competing hypotheses may enable recognition of the degree of commonality in their practical implications and consolidate points of agreement regarding conservation strategy (Sutherland et al. 2019). With a renewed spirit of collaboration, curiosity, and humility, we hope that ecologists can begin to unlock the fragmentation debate and provide sound, unified advice to policymakers and practitioners who desperately need it.

Declarations

Competing interests The authors have not disclosed any competing interests.

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