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PERSPECTIVE

How does habitat fragmentation affect the biodiversity and ecosystem functioning relationship?

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Abstract
Context The relationship between biodiversity and ecosystem functioning (BEF) has been a central topic in ecology for more than 20 years. While experimental and theoretical studies have produced much knowledge of how biodiversity affects ecosystem functioning, it remains poorly understood how habitat fragmentation affects the BEF relationship.
Objectives To develop a framework that connects habitat fragmentation to the BEF relationship from a landscape perspective.
Methods We reviewed the literature on habitat fragmentation, BEF, and related fields, and developed a framework to analyze how habitat fragmentation affects the BEF relationship through altering biodiversity, environmental conditions, and both, based on the pattern-process-scale perspective in landscape ecology.
Results Our synthesis of the literature suggests that habitat fragmentation can alter BEF relationship through several processes. First, habitat fragmentation causes the non-random loss of species that make major contributions to ecosystem functioning (decreasing sampling effect), and reduces mutualistic interactions (decreasing complementarity effects) regardless of the changes in species richness. Second, environmental conditions within patches and ecological flows among patches vary significantly with the degree of fragmentation, which potentially contributes to and modulates the BEF relationship.
Conclusions Habitat fragmentation can affect the BEF relationship directly by altering community composition, as well as indirectly by changing environmental conditions within and among habitat patches on both local and landscape levels. The BEF relationship obtained from small plots and over short time periods may not fully represent that in real landscapes that are fragmented, dynamic, and continuously influenced by myriad human activities on different scales in time and space.

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Introduction

More than a quarter-century of research has shown that biodiversity plays a vital role in promoting a wide range of ecosystem functions at local scales (Hooper et al. 2012; Tilman et al. 2012). Originally developed in manipulative laboratory and field-based experimental studies, early biodiversity-ecosystem functioning (BEF) experiments generally kept abiotic conditions constant and controlled biodiversity by creating random communities (Brose and Hillebrand 2016). Results from these controlled experiments have been difficult to extrapolate to real landscapes because they: (1) assume species losses and gains are random with respect to life-history traits (Wardle 2016); (2) ignore the influence of changing environmental conditions (Huston 1997; De Laender et al. 2016); (3) utilize sample plots (habitat patches) that are independent from the surrounding landscape (France and Duffy 2006); and (4) underestimate the importance of spatiotemporal scales (Symstad et al. 2003; Chisholm et al. 2013; Brose and Hillebrand 2016). Although BEF studies have become increasingly complex and elaborate in expressing the patterns and processes of real-world biodiversity loss (Table 1), the validity of these theories, especially for dynamic and fragmented landscapes, is yet to be tested empirically in decades to come (Wu 2013a; Isbell et al. 2017).

Fragmented habitats provide important and necessary testing grounds for assessing BEF relationships in the real world. Habitat fragmentation, defined as the breaking-up of habitats into smaller and isolated patches that impede ecological flows across a landscape (Wu 2009), is a global threat to biodiversity. At present, 70% of the world's forest are within 1 km of an edge (Haddad et al. 2015) and the mean patch size of forest fragments in the tropics is smaller than 29 ha and shrinking quickly (Pütz et al. 2014; Brinck et al. 2017). A number of studies have revealed that habitat fragmentation generally results in a loss of biodiversity across a range of taxa (Laurance et al. 2000; Gibson et al. 2013; Haddad et al. 2015; Hanski 2015; but see Fahrig 2017). However, there have been relatively few studies connecting habitat fragmentation to ecosystem functioning (Fig. 1). In recent years, researchers have started to close this knowledge gap (Peh et al. 2014), studying fragmentation's impacts on ecosystem properties, such as carbon storage (Pütz et al. 2014; Chaplin-Kramer et al. 2015), decomposition rates (Wardle and Zackrisson 2005; Crockatt and Bebber 2014), and nutrient cycling (Wardle 1997; Wardle and Zackrisson 2005). All these studies indicate that ecosystem functioning can be affected by habitat fragmentation, and changes in ecosystem functioning may also alter ecosystem services (Mitchell et al. 2013, 2015). Growing evidence suggests that biodiversity loss is as great (if not greater) a threat to ecosystem functioning as that posed by other key drivers of global change (Hooper et al. 2012; Duffy et al. 2017), but few studies have studied how habitat or landscape fragmentation affect the biodiversity and ecosystem functioning relationships.

A framework for linking habitat fragmentation with the BEF relationship

Habitat fragmentation, a key research topic in landscape ecology (Wu 2013b), has well established relationships with the abiotic environment and biodiversity, but these impacts vary across spatiotemporal scales (Haddad et al. 2015; Hanski 2015). Therefore, habitat fragmentation could affect BEF relationship through multiple pathways (Fig. 2). For example, habitat fragmentation can cause the non-random loss of species responsible for high ecosystem functioning and reduce complementarity (Wardle 2016). As environmental conditions play important roles in modulating the BEF relationship (Healy et al. 2008), the altered abiotic environments in the fragmented landscapes may influence BEF relationship even when biodiversity doesn't change. In addition, fragmentation effects are both long-term and scale-dependent, which may require decades to become apparent at different spatial scales (Vellend et al. 2006). However, these components in this framework are disconnected, and have been poorly studied (Resasco et al. 2016).

Here, we explore the connection between habitat fragmentation and BEF relationships by examining the existing literature in both the fragmentation and BEF fields. We discuss how and why habitat fragmentation will affect different aspects of BEF relationships, and propose a framework that explicitly

Table 1 Shifting trends in BEF studies

Parameters	From	To
Vegetation types	Grasslands	Forests to diverse vegetation types (see:http://www.treedivnet.ugent.be)
Study locations	Temperate and boreal regions	Expanded to tropical and subtropical regions (Ewers et al. 2011; Clarke et al. 2017)
Study objects	Plants especially grasses	Multiple organisms, including animals and microorganisms (Peh et al. 2014)
Study system	Manipulated experiments	Natural environments to human modified landscapes (Peh et al. 2014; Wu et al. 2015)
Environment conditions	Homogeneous and constant	Heterogeneous and dynamic (Tylianakis et al. 2008; De Laender et al. 2016)
Directions	Species adding or removing experiment	Species loss/increase in natural system (Wardle 2016)
Spatial scales	Local scale, plot based	Landscape to global scales (Liang et al. 2016)
Temporal scales	Short term effect	Long term effect (Fischer et al. 2010)
Mechanisms	Not clear	Complementarity effect, sampling effect, facilitation effect et al. (Loreau and Hector 2001; Cardinale et al. 2007; Wright et al. 2017)
Diversity measures	Species diversity	Functional diversity, phylogenetic diversity, species identity and composition (Flynn et al. 2011)
Ecosystem functioning measures	Single index such as biomass	Multifunctionality (Hector and Bagchi 2007)

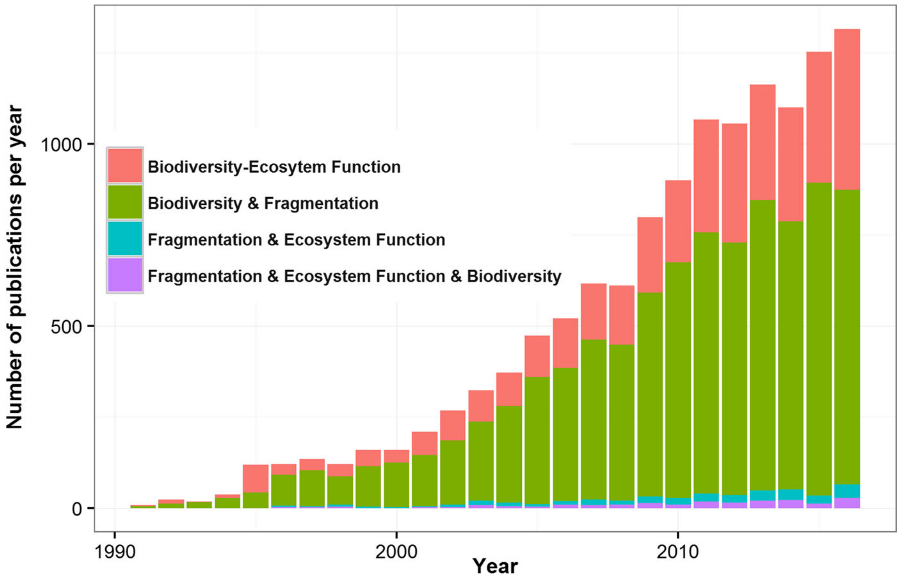

Fig. 1 Studies working on the pair-wise relationships between biodiversity, fragmentation and ecosystem function with key words of "biodiversity" and "ecosystem function" and "fragmentation" respectively since 1990. Publications about habitat fragmentation effect on ecosystem functioning have been much less investigated. Data retrieved from an online search of the Web of Science on 31st May, 2017. In total, there are 3663 (Biodiversity and Ecosystem function), 8792 (Biodiversity and fragmentation), 287 (Ecosystem function and fragmentation), 198 (Ecosystem function and fragmentation and Biodiversity) papers published from 1990 to 2016

connects fragmentation to BEF relationships for future studies.

Does non-random species loss caused by fragmentation affect BEF relationships?

Early studies of the BEF relationship assumed that every species makes a similar contribution to ecosystem functioning (Huston 1997). However, this assumption was soon upset by the discovery of the sampling effect—the fact that species which contribute disproportionally to ecosystem function are more likely to be included in communities with a large number of species (Loreau and Hector 2001). Further, random species loss and gain in the real world is highly unlikely (Wardle 2016), and such non-random species gain and loss will simultaneously affect ecosystems in fragmented landscapes (Wardle et al. 2011; Wardle 2016).

Habitat fragmentation drives a non-random species change with few winners and many losers. It kills large, old and late successional trees, e.g. shade-tolerant species (Hu et al. 2011), which suffer more from edge effects due to the desiccation of canopy trees (Laurance et al. 2000), and promotes the hyper-abundance of alien pioneer species (Tabarelli et al. 2010). Ecosystems thus tend to toward earlier successional stages with a proliferation of fast growing and alien species (Laurance et al. 2006a). These altered community structures will likely exhibit reduced ecosystem functioning. Logically, large trees with higher wood density contribute most to aboveground biomass and are vital to ecosystem functioning (Slik et al. 2013). In contrast, fast growing and alien species tend to cause a rapid decay of forest architecture and carbon storage (Laurance et al. 2006b). As habitat fragmentation causes the non-random loss of important functional traits (Wardle and Zackrisson 2005), it may impair ecosystem functioning through the loss of key functional species and traits (Wardle 2016). Therefore, the non-random species loss caused by habitat fragmentation will likely amplify sampling effects.

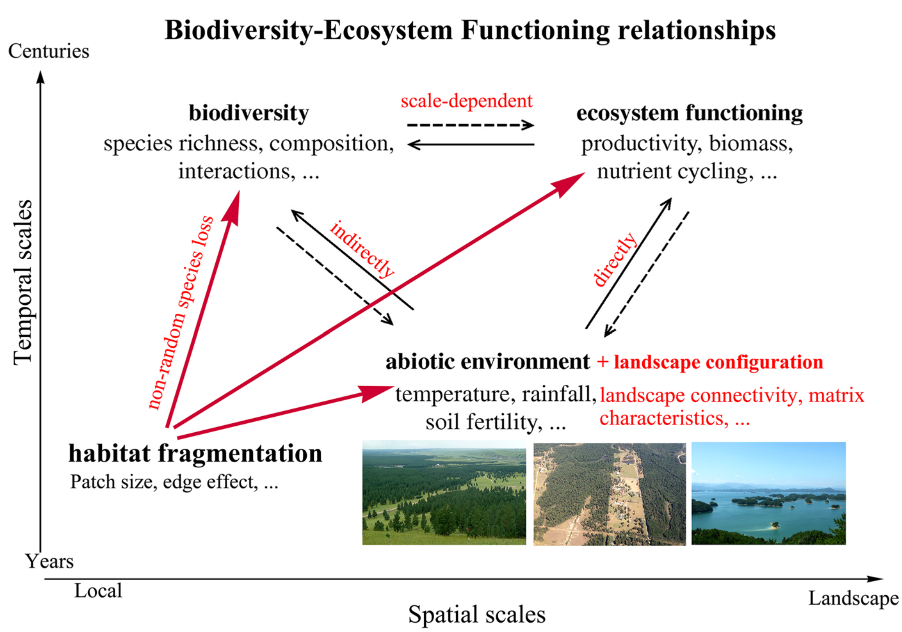

Fig. 2 A framework describing how habitat fragmentation affects ecosystem functioning through changes in abiotic environment, and biodiversity by considering spatial and temporal scales (modified from Loreau 2010). BEF relationships in fragmented landscape are different from small-scale experiments, we should consider (1) non-random species loss caused by habitat fragmentation; (2) direct and indirect effect of changes of abiotic environment on ecosystem functioning after habitat fragmentation; (3) changes of landscape configuration which affect ecological flow among patches (e.g. seed dispersal, pollination); (4) spatial scale-dependent BEF relationships; (5) long term effects of habitat fragmentation on BEF relationships. It is important to build the knowledge of these components in this framework to better understand the BEF relationships in real world with increasing habitat fragmentation

Another important mechanism underlying the BEF relationship is the complementarity effect—the fact that species within specific assemblages may have complementary resource uses and hence improve the function of the system relative to a random assemblage (Cardinale et al. 2002), such as nitrogen niche complementarity between species that live in nitrogen limited areas (Kahmen et al. 2006). The complementarity effect becomes stronger with the increasing complexity of ecosystem processes (Caliman et al. 2013) and in communities with higher niche differentiation biodiversity should have a larger effect on ecosystem function (Zuppinger-Dingley et al. 2014). However, this mechanism can again be modified by habitat fragmentation.

Habitat fragmentation has a negative effect on many positive species interactions (Hagen et al. 2012; Peh et al. 2014), especially for mutualistic interactions (Magrach et al. 2014), leading to decreased complementarity (Smith and Knapp 2003). For example, habitat fragmentation often leads to a biotic homogenization with communities dominated by light-demanding and drought-tolerant species (Lôbo et al. 2011), increased competition and decreased diversification (Bregman et al. 2015). For plant-animal interactions, herbivory and seed dispersal are greatly reduced in fragmented landscapes (Ruiz-Guerra et al. 2010; Knorr and Gottsberger 2012). Such changes in species interactions affect BEF relationship. For example, leaf bacterial diversity is positively linked to plant community productivity and mediates the BEF relationship in plant communities (Laforest-Lapointe et al. 2017), but has been significantly affected by habitat fragmentation (Hagen et al. 2012). Moreover, habitat fragmentation's impact varies across trophic levels, with especially negative effects on large top predators, causing cascading top-down effects on plant species and the trophic complementarity that partially drives the BEF relationship (Terborgh et al. 2001; Poisot et al. 2013).

All these processes will drive ecosystem to an early successional stage and simplify the complexity of ecosystem process (Laurance et al. 2006b; Caliman et al. 2013), reducing ecosystem functioning for any given level of biodiversity relative to randomly assembled communities.

Do fragmentation-mediated changes in environmental conditions affect BEF relationship?

To simplify experiments traditional BEF research has focused on synthetically modified experimental systems in which biodiversity of individual plots varied while all other abiotic variables are controlled (De Laender et al. 2016). However, spatial heterogeneity of environments has strong effects on BEF relationship in natural landscapes (Yuan et al. 2015). First, abiotic factors and biodiversity jointly affect ecosystem functioning (Weigelt et al. 2008; Tilman et al. 2012). For example, a study in tropical tree plantation found that environment explained 35–57% of the total variation of productivity whereas biodiversity explained 20–30% (Healy et al. 2008). Secondly, BEF relationship are modulated by environmental conditions (Hautier et al. 2015; Jucker et al. 2016). For example, increasing temperature can reduce the impact of biodiversity on ecosystem functioning (Steudel et al. 2012) and biodiversity's effect on drought resistance in forest ecosystems is context dependent (Grossiord et al. 2014).

Habitat fragmentation can alter local environmental conditions through edge effects. Edge effects have strong impacts on environmental conditions via changes in temperature, humidity, wind, and solar radiation (Laurance et al. 2002; Latimer and Zuckerberg 2017). For example, wind can influence community structure as much as 300 m from the forest edge (Laurance 2000). These fragmentation-mediated changes in environmental conditions may alter BEF relationships directly, indirectly, or interactively in conjunction with other fragmentation mediated processes (Fig. 2). Fragmentation-mediated environmental changes can cause the significant loss of ecosystem functions, such as the reduction in biomass stored in edge areas relative to forest interiors (Chaplin-Kramer et al. 2015). In particular, larger forest fragments, with higher biodiversity due to island-biogeographic processes, are normally located in relatively stable and resource-rich environments while small fragments, with less of an insurance effect due to their depressed biodiversity levels, experience higher fluctuations in environmental conditions (Gonzalez et al. 2009). Therefore, the extent to which observed BEF relationship in fragmented systems are driven by fragmentation induced changes in environmental heterogeneity or pure biodiversity effects are still unclear (Wardle and Jonsson 2010). This suggests that habitat fragmentation should increase the variability for the BEF relationship. Given the environmental differences within and among forest fragments, it is vital to disentangle the relative contributions of biodiversity and environmental conditions to BEF relationships.

Does landscape configuration affect BEF relationship?

Experimental work has often studied communities as independent sample units, assuming there is no ecological flow of material and organisms among patches (Fig. 3). However, an increasing number of studies have found that our ability to understand the maintenance of ecosystem functioning requires a better understanding of landscape configuration (Gonzalez et al. 2009; Thompson et al. 2017) as the mechanisms producing these relationships are different within individual patches and across patch types (Cardinale et al. 2004). For example, ecosystems can be more adaptive and resilient when connected (Wu and Loucks 1995; Staddon et al. 2010). Even neighbor trees can be important for BEF relationships through complementarity effects (Ratcliffe et al. 2015).

Habitat patches are spatially explicit and can be considered as subsets of metacommunities (Staddon et al. 2010; Bogoni et al. 2017). These metacommunities are connected through dispersal processes, such as immigration, pollination and seed dispersal. Thus, habitat patches used for comparison in BEF research are affected by their landscape context, which influences the predictability of ecosystem functioning (Chase and Ryberg 2004; Godbold et al. 2011). For example, a study showed that if grazer species were allowed to move among habitat patches, diversity effects on ecosystem functions will be reduced (France and Duffy 2006). A massive suite of studies has found that habitat fragmentation can change the dispersal process among patches with decreasing habitat connectivity (e.g., increased distance to resources, higher matrix contrast and isolation time) (Potapov et al. 2008; Haddad et al. 2015; Riitters et al. 2016). Such changes are critical for many processes including immigration, seed dispersal and pollination (Hagen et al. 2012). For example, pervasive seed dispersal limitation was found among habitat patches > 100 m from an edge (Germain et al. 2017). However, globally 70% of remaining forest is within 1 km of the forest's edge (Haddad et al. 2015). Low connectivity among patches can stop efficient dispersal that can enhance ecosystem functions (Cook et al. 2005; Watling et al. 2011), leading to biotic homogenization (van der Plas et al. 2016), and finally decreasing landscape level ecosystem functioning (Staddon et al. 2010; Thompson et al. 2017). In

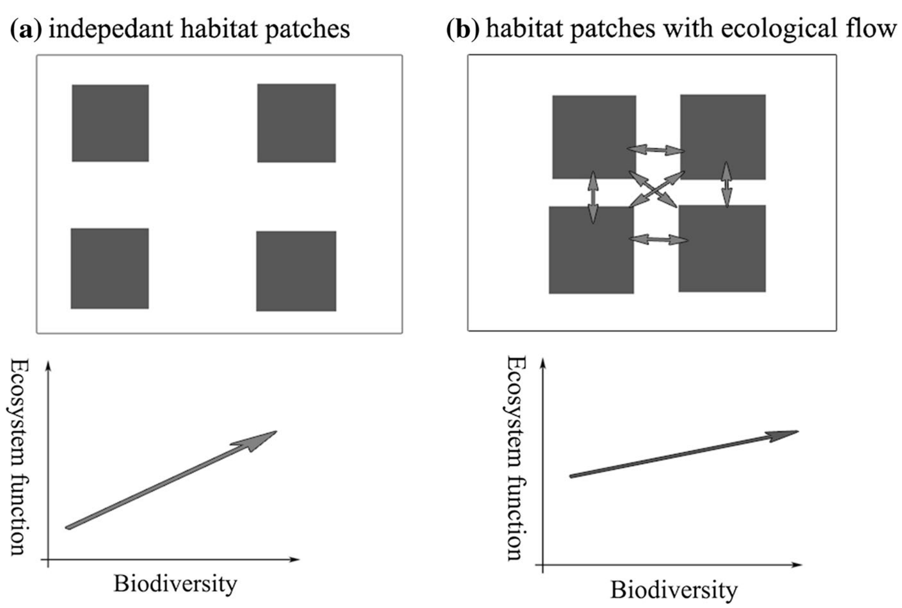

Fig. 3 Traditional BEF studies assumed there is no ecological flow among patches (**a**). However, small patches with less biodiversity in the real world can still benefit from nearby habitat patches through dispersal processes (**b**), influencing the predictability of the BEF relationships, e.g. (France and Duffy 2006)

contrast, a recent study found that restoration of pollination networks among habitat patches strengthens ecosystem functions (Kaiser-Bunbury et al. 2017). In this way, less isolated landscapes should have weaker BEF relationships with more functioning in species poor patches than expected due to compensation from the surrounding landscapes. Unfortunately, most BEF studies have been conducted from a localized perspective and ignore the influences of the surrounding landscape (Gonzalez et al. 2009). Therefore how variation in landscape configuration influences BEF relationships merits further study.

Does patch size affect BEF relationships?

Empirical studies comparing biodiversity effects on ecosystem functions are generally based on very small sampling units. For example, sampling plots are typically 0.04 ha in forest systems (e.g. Chisholm et al. 2013; Ratcliffe et al. 2015; Liang et al. 2016). However, some studies have found strong scale-dependent relationships between species richness and ecosystem functioning (Chase and Ryberg 2004; France and Duffy 2006). A study based in primary forests found that positive BEF relationships at very small spatial scales (0.04 ha) and became insignificant at increasing spatial scales (0.25, 1 ha) (Chisholm et al. 2013; Fig. 4). Another recent study based on global datasets of old-growth tropical rainforest confirmed this by analyzing diversity-carbon storage relationships (Sullivan et al. 2017). Hence, biodiversity loss in very small habitat patches may undergo severe loss of ecosystem functions but not likely in large patches. For example, in small forest fragments (< 1 ha) where top predators are not present due to limited resources for their survival, the loss of one species can lead to ecosystem collapse (Terborgh et al. 2001). In contrast, large fragments may still maintain similar functions regardless of biodiversity changes. For example, forest fragments greater than 40 ha in Kenya can maintain their multiple ecological functions (Schleuning et al. 2011). This may be especially true for tropical rainforests, where in one case even when large seed dispersers (e.g., elephants) went extinct in forest fragments, some rodent species could replace their roles in seed dispersal and other ecosystem functions (Jansen et al. 2012). Therefore, spatial scales should be considered when scaling the BEF relationship from small fragments to large fragments at broader spatial scales (Loreau et al. 2003; Burley et al. 2016).

However, most of these studies were conducted in large contiguous forests, and underestimated the environmental and ecological differences of habitat patches between intact and fragmented ecosystems. This may lead to the misunderstanding of the BEF relationship in the real world, where the size of habitat patches varies substantially. For example, in tropical

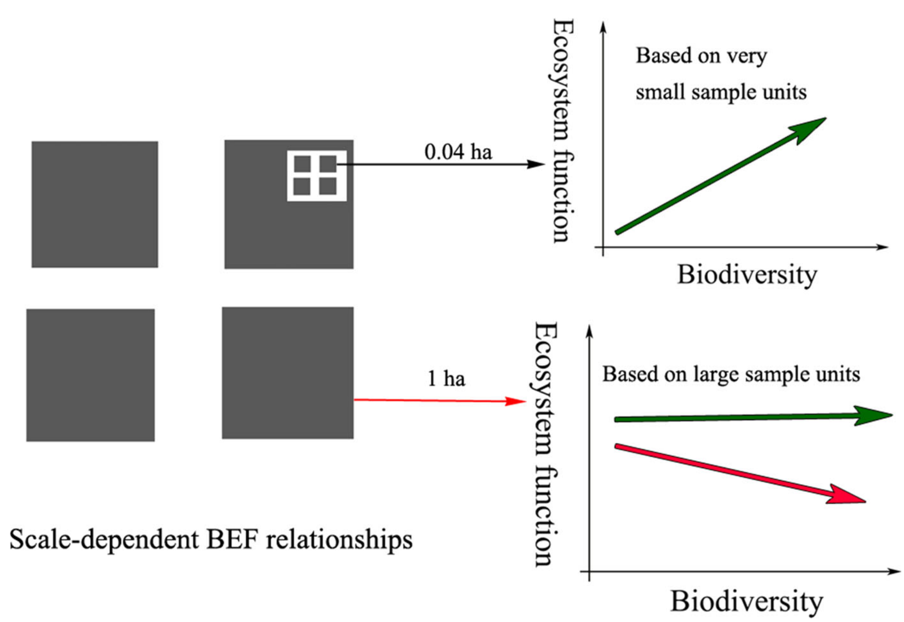

Fig. 4 Significant BEF relationships found in very small sample units may change with increasing fragment size in continuous old-growth forests, making the BEF relationships not significant or negative, e.g. (Chisholm et al. 2013; Sullivan et al. 2017). This makes it a challenge to test BEF relationships in fragmented landscapes with different habitat sizes

regions, the average forest fragment size is 29 ha and ranged from 0.1 to 10^9 ha (Brinck et al. 2017). Certain sampling size (e.g. 0.04 ha) may be not large enough to reflect the BEF relationship across different-sized fragments. In summary, BEF relationship is likely patch size dependent in fragmented landscapes. To address these fundamental issues studies must be completed at multiple, ecologically relevant spatial scales.

How does habitat fragmentation influence long-term BEF relationships?

Time has played an important role in landscape ecology and has been partially integrated into BEF studies. Previous studies have found that BEF relationships are dynamic across successional contexts (Lasky et al. 2014), and effects of biodiversity loss increase through time with decreased functional redundancy and complementarity (Cardinale et al. 2007; Reich et al. 2012). Unfortunately, most BEF experiments are short-term studies in controlled systems (Symstad et al. 2003; Bai et al. 2004), whereas the drivers of BEF relationships are at least partially dependent on the temporal scale of measurement.

The observed effects of fragmentation on BEF relationships can be affected by the choice of temporal scale. On one hand, habitat fragmentation has a time delayed effect on biodiversity loss (Helm et al. 2006), where some tree species can still survive in forest fragments but there is no seedling recruitment in the understory (Cordeiro et al. 2009). Such long-term effects may persist for more than a century (Vellend et al. 2006). Therefore, it is expected that such "extinction debt" should be paired with a time delayed "functioning debt" (Gonzalez et al. 2009), making BEF relationships fragmentation stage-dependent (Isbell et al. 2015). On the other hand, habitat fragmentation drives ecosystems to an early successional stage with more radiation and light availability (Laurance et al. 2006b, 2011), and such environmental changes will slow down the succession rates of the fragmented landscapes (Helsen et al. 2013; Goosem et al. 2016). However, ecosystem functioning and biodiversity recover or loss at different rates in disturbed systems (Gonzalez and Chaneton 2002; Martin et al. 2013), resulting in succession stage-dependent BEF relationships (Lasky et al. 2014). How BEF relationships will change with habitat fragmentation through time still needs further exploration.

Discussion and conclusions

In this paper we have analyzed the potential effects of habitat fragmentation on BEF relationships from a landscape ecological perspective. We also propose a framework that explicitly connects habitat fragmentation to BEF relationships through fragmentation-mediated changes in abiotic environments and biodiversity. Specifically, we ask how and why habitat fragmentation affects the BEF relationships, and how BEF relationships in the fragmented landscapes are influenced by the choice of spatial and temporal scale.

Based on the review of the literature, we draw the following conclusions: (1) Habitat fragmentation may cause the non-random loss of species that make high contributions to ecosystem functioning (decreased sampling effect) and reduce mutualistic interactions (decreased complementarity and facilitation effects) (2) Habitat fragmentation is a major determinant of environmental conditions at both local and landscape levels, which contributes to and modulates BEF relationships; (3) Ecological flows (e.g., seed dispersal, pollination, etc.) among habitat patches are critical for the maintenance of ecosystem functioning, but the impact of landscape context on BEF relationships has rarely been studied; (4) The choice of spatial scale matters when quantifying BEF relationships, but BEF studies are biased toward to large continuous systems rather than habitat fragments with different sizes; (5) Assessing BEF relationships in fragmented natural and human-dominated landscapes requires long-term multiscale studies, representing a new research frontier yet to be studied. Our study creates a theoretical framework that connects habitat fragmentation to BEF relationships by integrating community ecology and biogeography. To understand BEF relationships in an increasingly fragmented landscape, a clear understanding of its mechanisms is essential. Now is the time to study this complex relationship through long term experiments and high resolution datasets (Wu et al. 2003; Haddad et al. 2015; Wilson et al. 2016).

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