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Fragmentation affects plant community composition over time

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Habitat fragmentation can lead to major changes in community composition, but little is known about the dynamics of these changes, or how community trajectories are affected by the initial state of habitat maturity. We use four landscape-scale experiments from different biogeographic regions to understand how plant community composition responds to fragmentation over decades. Within each experiment, we consider first whether plant communities in the most-fragmented treatments diverge in composition from plant communities in the least-fragmented treatments. Second, because communities embedded in different fragments may become more similar to one another over time (biotic homogenization), we asked whether beta diversity – compositional variation across space – declines among fragments over time. Third, we assessed whether fragmentation alters the degree to which temporal change in fragmented landscapes is due to ordered species losses and gains (nestedness) versus species replacements (turnover). For each of these three questions, we contrasted patterns of compositional change in mature communities following fragmentation (disassembly; n = 2 experiments) with patterns in newly-developing plant communities in fragments cleared of vegetation (assembly; n = 2 experiments).

In the two studies where communities were disassembling, community composition in the most-fragmented habitats diverged from that in least-fragmented habitats. Beta diversity within a fragmentation treatment did not change over time at any of the four sites. In all four experiments, temporal patterns of compositional change were due mostly to species turnover, although nestedness played a role in the least-fragmented sites in two of the studies. Overall, the impacts on community composition varied among landscape experiments, and divergence may have been affected by the maturity of the plant community. Future comparisons across ecosystems that account for species identities (vs simply richness) will be critical for predicting the effects of fragmentation, managing mature plant communities in remnants, and restoring plant communities where habitat has been lost.

Habitat loss and fragmentation are arguably the greatest threat to global biodiversity (Haddad et al. 2015). Across ecosystems and taxa, landscape fragmentation leads to both immediate and long-term reductions in species richness (Helm et al. 2005, Krauss et al. 2010, Haddad et al. 2015, Lima et al. 2015). It is now becoming clear that community composition is also strongly modified by landscape fragmentation (Harper et al. 2005, Laurance et al. 2006b, Santos et al. 2008), but the effects of fragmentation on temporal and spatial dynamics of community composition are not well understood. In particular, we do not know whether communities in fragments diverge or converge from communities in continuous tracts of habitat, or whether community trajectories in fragmented landscapes are similar across ecosystems. In part this deficit is due to the fact that the most frequently used metric in long term datasets, species richness, obscures compositional shifts (Magurran and Henderson 2010, Dornelas et al. 2014). Importantly, changes in community composition can have cascading effects on ecosystem properties (Tabarelli et al. 2012), highlighting a pressing need for a better understanding of how community composition changes over time in response to habitat fragmentation.

Generalizing results across fragmentation studies is difficult due to confounding factors such as matrix quality (Driscoll et al. 2013) and historical legacies of fragments and the surrounding landscape (Ewers et al. 2013, Longworth et al. 2014, Mesquita et al. 2015) which may vary among

studies. Moreover, compositional trajectories in fragmented landscapes reflect numerous concurrent processes that are challenging to detect and equate across systems including changes to the regional species pool and limited access by potential colonists (MacArthur and Wilson 1967, Zobel 1997, Alexander et al. 2012, Thompson et al. 2017), drift and stochastic forces (Orrock and Watling 2010, Vellend 2010), edge effects (Murcia 1995, Laurance et al. 2006a, Tabarelli et al. 2008, Ewers and Banks-Leite 2013, Magnago et al. 2015, Tuff et al. 2016), and species-specific responses to changes in habitat quality, quantity and configuration (Benitez-Malvido and Martinez-Ramos 2003, Kolb and Diekmann 2005, Damschen et al. 2008, Collins et al. 2009). By replicating more- and less-fragmented habitats at large spatial and long temporal scales, landscape experiments provide a unique and powerful opportunity to compare community change in fragments against reference communities, essentially controlling for all non-fragmentation related changes that happen over time (Debinski and Holt 2000, Haddad et al. 2015). In this study, we ask how fragmentation affects trajectories of compositional change using plant community data from four long-term, large-scale habitat fragmentation experiments – two in the USA, one in Australia, and one in Brazil.

The trajectories of community change over time post-fragmentation remain largely unknown, with at least four possible scenarios (Fig. 1). For illustrative purposes, we assume that initial differences between fragmented and continuous landscapes exist. In an experiment, this could arise by chance. In anthropogenic landscapes, this could result from the non-random creation of fragments across initial environmental gradients (Seabloom et al. 2002, Holt and Debinski 2003, p. 309, Ewers et al. 2017). Because colonization and extinction drive compositional change over time (Jackson and Sax 2010, Soininen 2010, Dornelas et al. 2014) and both processes are mediated by habitat area and isolation (MacArthur and Wilson 1967, Jackson and Sax 2010, Soininen 2010), we might expect community composition in fragments to diverge from communities in continuous habitats (Fig. 1a). Divergence between communities in fragmented and continuous landscapes may be long-lasting, if, for instance, the initial species composition of the community and localized responses to fragmentation set the stage – and in effect constrain – community changes thereafter (e.g. priority effects, Fukami 2004, secondary extinctions, Brodie et al. 2014) (Fig. 1a). This pattern may also emerge if spillover from a spatially homogeneous matrix systematically perturbed fragments away from continuous tracts of comparable habitat. Alternatively, communities in fragmented and continuous landscapes may converge (Fig. 1b) if local effects of fragmentation are eventually overwhelmed by regional dynamics (e.g. climatic shifts or changes to the regional species pool). Divergence may be a transient phase, followed by convergence (Fig. 1c); the reverse may also occur (not pictured). Finally, fragmentation may not lead to a net pattern of either divergence or convergence (Fig. 1d) in continuous vs fragmented communities if compositional change is more strongly influenced by other factors, or if fragmentation simply had no effect on vegetation dynamics.

Communities in fragments may not only follow distinct trajectories relative to continuous habitat, but trajectories may also vary among fragments themselves. For instance, communities in separate fragments may diverge (i.e. beta diversity among fragments increases; Fig. 1e). This may be particularly likely if fragments exist in different landscapes where local disturbances, landscape features, and the species pools available for colonization differ (the landscape divergence hypothesis; Laurance et al. 2007). Divergence might also be expected if local dynamics in fragments are strongly stochastic because of small population and community sizes (Orrock and Watling 2010), or if fragmentation promotes priority effects in establishment. Alternatively, communities in different fragments may become compositionally similar over time (i.e. beta diversity among fragments declines) due to the proliferation of widespread, disturbance-tolerant species, or edge specialists (Fig. 1e; 'biotic homogenization'; McKinney and Lockwood 1999, Tabarelli et al. 2012). A similar pattern might be seen if physical changes post-fragmentation make the physical environments of fragments more similar to one another than the same sites were before fragmentation. If the timing of species' responses to fragmentation varies (Whittaker et al. 1989, Damschen et al. 2008, Krauss et al. 2010), differentiation among communities on fragments may be temporary (Fig. 1g), or the staggered timing of compositional change among disparate locations may obscure consistent long-term trends, if trends exist at all (Fig. 1h).

Finally, trajectories of compositional change following fragmentation may depend on the maturity of plant communities. When fragments contain newly established plant communities, the community can be thought of as 'assembling' (Diamond 1975, Keddy 1992, Belyea and Lancaster 1999) through the processes of secondary succession (Connell and Slatyer 1977, Pickett et al. 1987, Whittaker et al. 1989). Alternatively, in the case of mature communities experiencing fragmentation through habitat loss in the surrounding landscape, the subsequent series of species declines and losses may be described as 'community disassembly' (Ostfeld and LoGiudice 2003, Zavaleta et al. 2009). Colonization and extinction occur over time during both assembly and disassembly, driving compositional changes post- fragmentation ('relaxation'; Diamond 1972). However, the number and types of species favored during colonization of assembling communities may differ from the number and types of species most (or least) prone to extinction in disassembling communities (Zavaleta et al. 2009). Consequently, the impact of fragmentation on trajectories of compositional change may differ depending on the initial state of the community.

We explored how fragmentation influences community change using data from four landscape-scale fragmentation experiments (Table 1). Each long-term experiment allowed for comparison between more- and less-fragmented habitats in a replicated way, controlling for many of the confounding factors that change with habitat loss (Haddad et al. 2015). In two experiments, the Biological Dynamics of Forest Fragmentation Project (Brazil; rainforest), and the Wog Wog Fragmentation Experiment (Australia; eucalyptus forest), fragments were created by clearing land around mature forests, thus initiating community disassembly (Table 1). In the other two studies, the Kansas Fragmentation Experiment

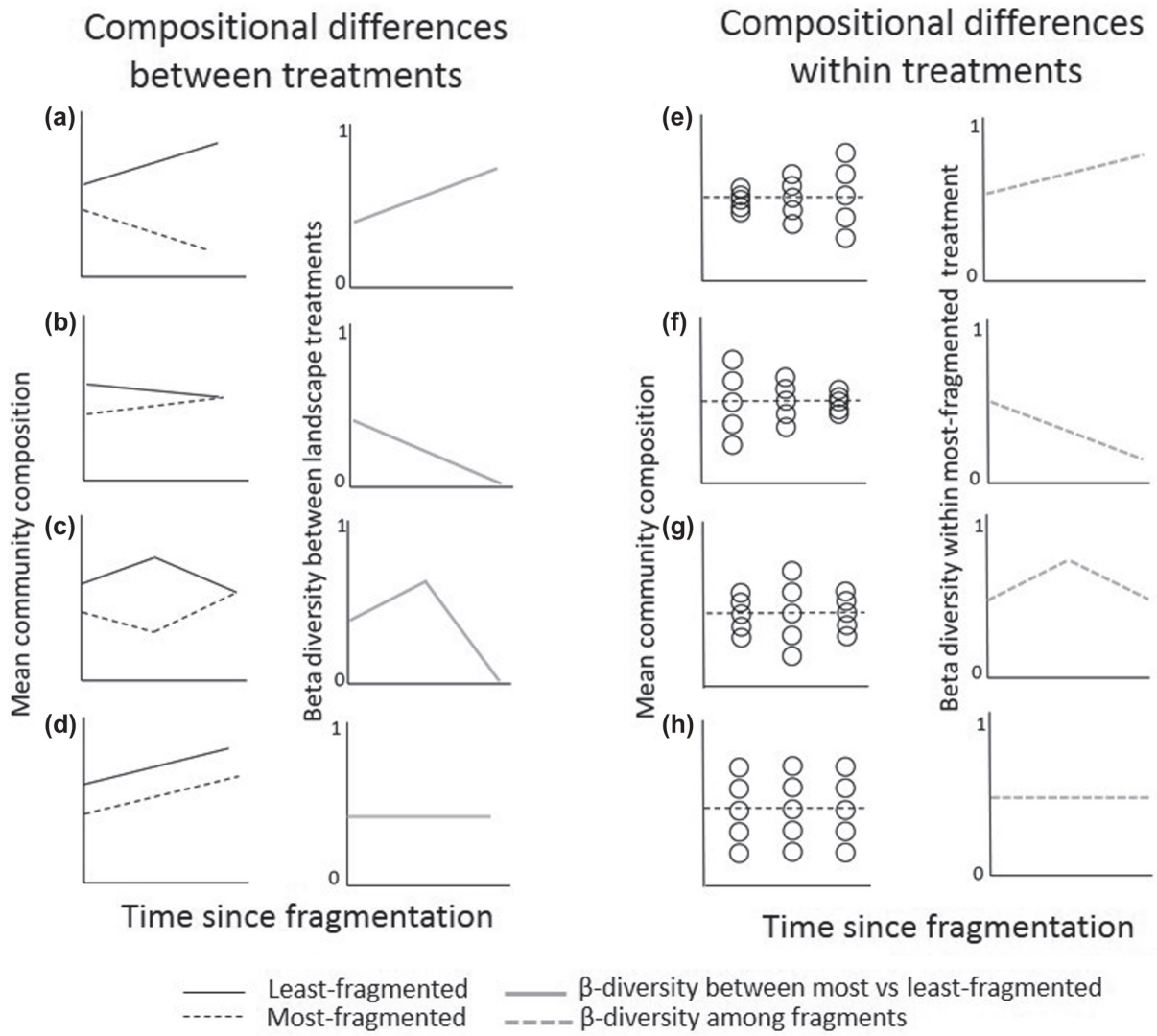
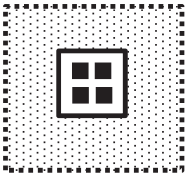
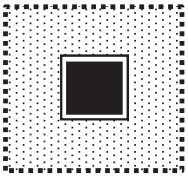
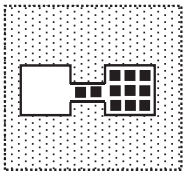
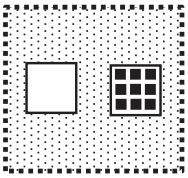
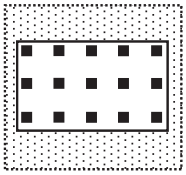
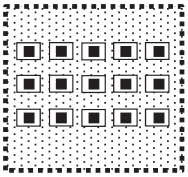


Figure 1. Conceptual models showing ways in which fragmentation may influence trajectories of plant community composition. Plots (a) through (d) depict possible scenarios for divergence or convergence between most- and least-fragmented communities. Lines represents average species composition (the centroid in ordination space) shifting over time since fragmentation. Dashed lines signify mean trajectory for fragmented landscapes; solid lines signify continuous landscapes. For each scenario in the first column, we depict in the adjacent column the pattern we expect to see when comparing beta diversity (Sorensen dissimilarity) between fragmented and continuous vegetation communities following fragmentation: (a) compositional differences between communities in fragments and communities in continuous landscapes increase over time; (b) trajectories converge such that communities in fragments and continuous forest become increasingly similar over time; (c) divergence induced by fragmentation is temporary; (d) communities in fragments and continuous forest follow similar trajectories and dissimilarity does not change over time. Plots (e) through (h) show ways in which beta diversity among fragments may change over time (i.e. within the most-fragmented treatment). Each circle represents a replicate community in: higher beta diversity is depicted by greater spread of circles. Lines represent trajectories for mean community composition. For simplicity, only three points in time are depicted and communities in continuous landscapes are not shown. The last column shows the Sorensen dissimilarity measures of beta diversity that correspond to the compositional response among replicates within the most-fragmented treatment: (e) fragments diverge from one another (differentiation); (f) fragments converge toward similar composition (biotic homogenization); (g) divergence among fragments is temporary; (h) beta diversity among fragments does not change over time.

(USA; old field) and the Savanna River Site Corridor Experiment (USA; long leaf pine savanna), plant communities developed on fragments cleared of vegetation, so changes in fragments reflect community assembly and succession (Table 1). Thus, data from these four experiments provide a unique opportunity to investigate vegetation dynamics in response to fragmentation of mature vegetation versus early-successional plant communities.

For each fragmentation experiment, we asked the following questions: 1) Over time, do plant communities in the most-fragmented habitat diverge from communities in least-fragmented habitat?, 2) Does fragmentation homogenize communities within a fragmentation treatment?, 3) Do mechanisms driving changes in composition over time vary among systems, and with fragmentation? Specifically, to what extent is temporal compositional change due to nestedness

Table 1. A comparison of key attributes for the four experiments used in the study. Illustrations of least- and most-fragmented treatments feature landscape manipulations in each experiment and are not to scale; stippled area = matrix, white = fragment area, black = sub-samples compiled to comprise a single replicate for this study. Detailed site descriptions are included in the Methods and citations therein. Entire site diagrams for each experiment are contained in Supplementary material Appendix 1 Fig. A1–A4.

Experiment	Least-fragmented treatment	Most-fragmented treatment	Dominant process	Initial community state	Matrix description
Wog Wog			Disassembly	Mature	Cleared forest; regrown plantation
Brazil			Disassembly	Mature	Cleared forest; periodically re-cleared
Corridor			Assembly	Early successional	Pine plantation; maintained as plantation
Kansas			Assembly	Early successional	Grassland; maintained by mowing

(dissimilarity due to sites with fewer species containing a subset of species found in sites with more species) vs turnover in time (species replacements that generate differences in composition)? Our study was guided by the overarching hypothesis that fragmentation modifies colonization and local extinction dynamics in ways that alter temporal patterns of compositional change. We predicted that regardless of initial community state (mature versus early-successional), communities in the most-fragmented habitats would, over time, diverge from communities in least-fragmented habitats (Fig. 1a). Based on the weight of previous evidence for biotic homogenization in fragments (Laurance et al. 2006a), we expected beta diversity among fragments to decline (Fig. 1f).

Methods

Field data

Overview

Because our data came from four landscape-scale experiments that manipulated fragmentation in different ways and have different landscape contexts (Table 1), the experiments do not represent replicates, but rather independent tests of our predictions that, taken together, inform our understanding of long-term plant community dynamics in fragmented landscapes. We compared the most- and least-fragmented units in each study (Table 1; full site diagrams: Supplementary material Appendix 1 Fig. A1–A4). For both disassembly experiments (Biological Dynamics of Forest Fragments Project; hereafter: Brazil) and Wog Wog Fragmentation Experiment (hereafter: Wog Wog) we compared the smallest fragments created in the study with the same-sized area embedded in uncleared, continuous forest at each site (Table 1; details below). By contrast, in the two assembly experiments, Kansas Fragmentation Experiment (hereafter: Kansas) and Savanna River Site Corridor Experiment (hereafter: Corridor), the 'least-fragmented' treatments are fragments themselves, but differ in the degree of connectivity relative to the 'most-fragmented' treatment to which they are compared. For Kansas, each replicate in the fragmented treatment includes 15 small patches in a single cluster whose perimeters span the same area as a large patch, which we use as the least-fragmented treatment. Thus, the most-fragmented treatment differs in both patch size and connectivity (Table 1). At the Corridor site, the least-fragmented treatments comprise patches connected to another patch via a habitat corridor, while the most-fragmented are rectangular patches of the same area as the connected fragment plus the corridor, but are unconnected from the center patch (Table 1).

Within each of the four experiments, the same size area was sampled in most- and least- fragmented habitats. For three of the four experiments (Kansas, Corridor, Wog Wog), composition was determined by aggregating sample plots distributed throughout the fragment, or the equivalent area in the least-fragmented habitat; only at the Brazil site were

entire fragments sampled (with the exception of a buffer at the edge; details below) (Table 1). In the two experiments with continuous forest as the least-fragmented treatments (Brazil and Wog Wog), sample plots were located in the interior of the forest, > 350 m from the forest edge. Despite different absolute areas sampled, the proportion of species sampled from the species pool (defined as the total number of species detected in the experimental landscape across the length of the study) in a single sample (alpha diversity) was comparable across all experiments (Supplementary material Appendix 1 Table A1). Data from Kansas, Corridor, and Wog Wog reflect primarily herbaceous species, while Brazil data focus on tree species.

Time since fragmentation was calculated as the number of years elapsed since the fragmentation treatment was applied. For the disassembly studies, negative and zero values for time since fragmentation reflect pre-treatment data. Because not all replicates of a treatment were sampled in a single year in Brazil, we grouped time since fragmentation by increments and used the median time since fragmentation for analyses and graphics.

Site descriptions

The Biological Dynamics of Forest Fragments Project (Brazil; Supplementary material Appendix 1 Fig. A1) is located in central Amazonia, 70 miles north of Manaus, Brazil (28°30′S, 60°W). The full experiment, described in detail in Laurance et al. (2011), was initiated in 1979 and includes repeated surveys of trees > 10 cm diameter-at-breast-height in fragments of three sizes: ca 1 ha, 10 ha and 100 ha. Surveys in comparable plot sizes in continuous forests controls (plots were > 350 m from an edge) nearby serve as the 'least-fragmented' communities (they are actually unfragmented). Matrix areas between patches have been re-cleared and burned on three to four occasions to maintain isolation between the fragments. Here we use data from small fragments (n = 4), each of which comes from a single 1 ha plot surveyed inside a 1.5–1.8 ha fragment, and equivalent areas in nearby continuous forest (n = 4).

The Wog Wog experiment is located in southeastern New South Wales, Australia (37°04′S, 149°28′E). The experiment, which includes six replicates of three fragment sizes (0.25 ha, 0.875 ha and 3.062 ha) in eucalyptus forest (Supplementary material Appendix 1 Fig. A2) was initiated with pre-treatment surveys in 1985 and 1986. In 1987, the surrounding forest was cleared around four replicates of each size, and pine plantations were established in the clearing the following year. By 1996, pines were 5–6 m tall, and by 2010, pines in the matrix were taller than eucalypts in the patches (Farmilo et al. 2013). Plants were monitored annually in two distinct topographical locations (slopes and drainage gullies) between 1987–1998, then again in 2010. We use data for plants < 1m tall occurring on slope plots of the smallest fragments ('more-fragmented'). For the purposes of this study, we aggregated data from four 3 × 3 m plots in each fragment (n = 4 fragments). Vegetation communities in fragments are compared to equal sized survey plots in nearby continuous forest tracts (n = 2; Table 1).

The Kansas Fragmentation Experiment (Kansas) is maintained by the Univ. of Kansas and located in northeastern Kansas, USA (39°3′N, 95°12′W). In 1984 patches of three sizes were demarcated on a single fallow farm field (described in detail in Holt et al. 1995; Supplementary material Appendix 1 Fig. A3). Patches have been maintained by mowing the matrix area several times each growing season while the patches themselves have undergone secondary succession. Each large patch (0.5 ha) spans the same area as contained within a perimeter of a cluster of 15 small patches (fragments). Following Alexander et al. (2012), we consider a single large patch (n = 6) to be continuous habitat ('least-fragmented') relative to a cluster of 15 small patches ('most-fragmented'; n = 4). Two clusters of fragments were eliminated from this study because they contain fewer than 15 fragments, and clusters of medium patches are not considered in this study. Plant data consist of repeated surveys (1985, 1994–2002, 2014) of vegetation < 1 m tall in 1 m^2 plots (30 per large patch or cluster of small patches) that were aggregated at the scale of clusters or single large patches (Table 1, Supplementary material Appendix 1 Fig. A3).

The Savannah River Site Corridor Experiment (Corridor) is a National Environmental Research Park located in South Carolina, USA (33°20′N, 81°40′W). 1-ha fragments were created in 2000 by clearing plantation trees (*Pinus palustris*, *P. taeda*) to create three treatment types: 1) 'connected' patches that are connected to another fragment with a 150 × 25 m corridor, 2) unconnected 'rectangular' patches that are the same area, and 3) unconnected 'winged' patches that are both the same area and the same shape (i.e. similar edge-to-area ratios; Supplementary material Appendix 1 Fig. A4). The full study design is explained in Damschen et al. (2006). Here, we use patches connected by a corridor as the 'least-fragmented' treatment, and rectangular patches to represent the 'most-fragmented' treatment (Table 1), because past work has shown that rectangular patches support the lowest plant species richness, particularly for some plant groups (Damschen et al. 2008). Following clearing, patches have been managed with prescribed fire every 2–3 years, consistent with the historical disturbance regime. We use six blocks that were initiated in the same year (i.e. n = 6 for both most- and least-fragmented treatments). In blocks where a fragment type is replicated, we randomly selected one of the two replicates. Surveys of all plant species < 1 m tall were conducted in thirty-eight 1 m^2 permanent plots from each fragment at four time periods: 2001–2003, 2009, and 2014. Plots within fragments are aggregated to represent species composition for that fragment.

Analyses

We used plant community presence–absence data over multiple years to distinguish between convergence and divergence in 1) temporal trends and 2) final outcomes (community states in the final data collection year) for each experiment. Our choice to use presence–absence data was based on the fact that there were large differences in data collection protocols among study sites (e.g. individual stems vs cover), and that some of our analyses can only be run on presence–absence data (nestedness vs turnover). As Li et al. (2016) have recently emphasized, one can discern different dynamical patterns in communities when using abundance metrics, rather than presence–absence. However, in this paper our emphasis is on compositional change due to local

colonization and extinctions, as reflected in the list of species which comprise local communities.

Do plant communities in the most-fragmented habitats diverge from communities in the least-fragmented habitats?

For each experiment separately, we calculated Sorensen dissimilarity for every pairwise combination of most- and least- fragmented communities in each year. Averaging these differences yielded a single point (± SE) representing the mean compositional difference between fragmentation treatments for each year, in each experiment. Although the most appropriate measure of beta diversity is a current topic of debate (Tuomisto 2010, Anderson et al. 2011, Chase et al. 2011, Kraft et al. 2011) recent work comparing metrics across sites that vary in gamma diversity suggests that pairwise multivariate distances are the beta metric most robust to differences in sample size and regional diversity (Bennett and Gilbert 2016).

We determined the effect of time since fragmentation on mean Sorensen dissimilarity in each study with linear models. For Wog Wog, we analyzed the time series in two segments (1–8 years since fragmentation, 9–24 years since fragmentation) due to the marked shift in direction of the trend between years nine and ten. For Kansas, we added a squared term to improve model fit.

To assess composition between the most- and least-fragmented communities in the final time period of each study, we used Permutation Multivariate Analysis of Variance (PERMANOVA from the Vegan package in R).

Does fragmentation homogenize or diversify communities within a landscape treatment?

Following a similar procedure as above, we assessed changes in beta-diversity of communities within each landscape treatment (most- or least-fragmented) by calculating mean Sorensen dissimilarity for every pairwise combination of most-fragmented communities, as well as between each pair of least-fragmented communities. For each study and each fragmentation treatment, we determined the effect of time since fragmentation on mean Sorensen dissimilarity using linear regression. When residuals did not conform to assumptions for least-squares linear modeling, we used rank-based linear modeling from the Rfit package in R (Kloke and McKean 2015). We then quantified beta diversity among replicates within a treatment in the last time period using Permutational Multivariate Dispersion (PERMDISP) tests for homogeneity of variance. We calculated Sorensen dissimilarity between each pair of samples within a fragmentation treatment; we then used PERMDISP to test for significant differences in dispersion between communities in the most- and least-fragmented habitats.

Is compositional change due to nestedness or turnover?

Temporal compositional change can be partitioned into two components: nestedness (dissimilarity due to sites with fewer species containing a nonrandom subset of species found in sites with more species) and turnover (species replacements that generate differences in composition) (Baselga 2010, 2012). We assessed these components across time as the difference in composition between the first year of sampling and every subsequent year. In the context of temporal community change, dissimilarity due to nestedness is typically interpreted as ordered losses (in the case of disassembly) leading to a less-species rich community comprised of subset of the initial community. In the case of assembly, nestedness reflects persistence of initial colonists. Turnover involves the joint effects of species losses and gains over time. To distinguish nestedness and turnover components of temporal change, we used the R Package Betapart (Baselga et al. 2012). Then, for each site, we regressed the values of nestedness and species turnover by time, to calculate the slopes of the regression lines. A positive slope indicates that the nestedness or species turnover component became larger over time, as compositional changes relative to the first year of sampling increase with each subsequent year. We tested whether slopes were on average significantly different from zero in fragmented and continuous sites using one-sample t-tests.

We visually examined compositional changes over time from ordinations produced using Principal Coordinates Analysis (PCoA) because PCoA can be calculated based on the same dissimilarity metrics (Sorensen, in our case) used in PERMANOVA (Supplementary material Appendix 1 Fig. A5–A8). All analyses were conducted in R, version 3.1.1. (R Core Team 2015).

Results

Do plant communities in most-fragmented habitats diverge from communities in the least-fragmented habitats?

Our four experimental landscapes revealed quite different patterns of divergence between most- and least-fragmented treatments. In the two studies where communities were disassembling (Brazil, Wog Wog), composition diverged over time, at least initially, between most- and least- fragmented treatments (Fig. 2). Compared to the other fragmentation experiments, communities in fragments and continuous forest in the Brazil project were most distinct from one another, even at the initial, pre-treatment sampling times (Fig. 2, Supplementary material Appendix 1 Fig. A5). Over time, fragments at the Brazil site gradually diverged from intact forest ($R^2 = 0.77$, $F_{1,3} = 12.13$, $p = 0.03$, Table 2), although the magnitude of change was small. At Wog Wog, we detected a marked divergence during the initial years of the study (Wald Test = 20.87, $p < 0.001$, Table 2), but this trend was temporary (Fig. 2). After ten years, communities in most- and least-fragmented habitats began to converge (Wald Test = 177.75, $p < 0.01$, Table 2), reflecting the time-frame over which the matrix pine plantations reached the height of eucalyptus trees in the fragments. At the two assembling sites (Corridor and Kansas), we detected no strong trend toward divergence or convergence over time (SRS: Wald Test = 0.87, $p = 0.51$; KS: $R^2 = 0.45$, $F_{2,8} = 3.38$, $p = 0.09$, Table 2). In Kansas, most- and least-fragmented communities appear most distinct in the initial and final sampling years (Fig. 2, Table 2). Community composition in most- and least- fragmented habitats in the final time period differed significantly from one another at the Kansas site ($F_{1,8} = 1.96$, $p = 0.013$, PERMANOVA).

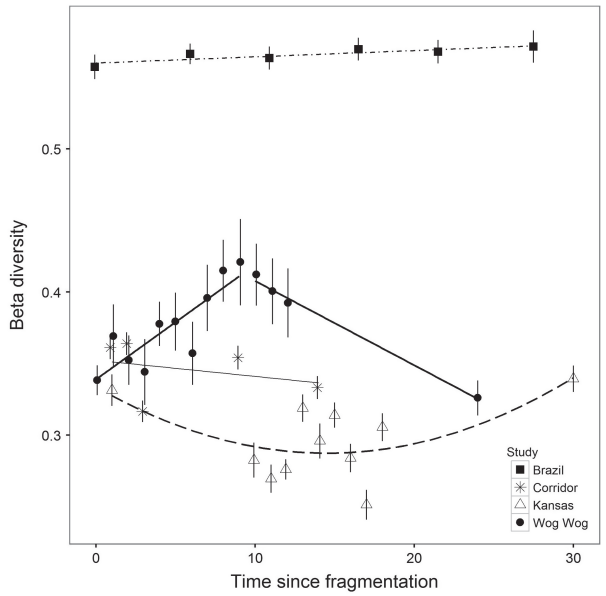


Figure 2. Compositional dissimilarity between plant communities in most- and least-fragmented landscape treatments in each experiment. Each study site is differentiated by symbols and line styles. Each point reflects the mean difference (± SE) in community composition (Sorensen dissimilarity) across pairwise combinations of least- and most- fragmented habitats within a study. Data points associated with time since fragmentation values of −1 or 0 indicate pre-treatment data. See text in Results and Table 2 for regression statistics.

By contrast, community composition in the final year did not differ significantly between fragmented and continuous forests in Brazil ($F_{1,4} = 1.07$, $p = 0.4$, PERMANOVA), Wog Wog ($F_{1,4} = 1.7$, $p = 0.07$, PERMANOVA) or Corridor ($F_{1,10} = 0.904$, $p = 0.64$, PERMANOVA).

Does fragmentation homogenize communities within a landscape treatment?

We found no evidence of homogenization among fragments (Fig. 3). Nor did we detect a temporal trend in community dissimilarity among replicate communities in the least-fragmented forests (Fig. 3). Additionally, in the final year of each study, beta diversity among communities in fragments did not differ significantly from beta diversity among communities in continuous forests (Brazil: $F_{1,4} = 1.33$, $p = 0.31$, Kansas: $F_{1,8} = 2.4$, $p = 0.16$, Corridor: $F_{1,10} = 0.14$, $p = 0.72$, Wog Wog: $F_{1,4} = 4.49$, $p = 0.10$; PERMDISP).

Table 2. Parameter estimates for regression models predicting mean compositional differences between forests in the most- and least-fragmented treatment in each experiment, as a function of time since fragmentation.

Experiment	Estimated slope	Lower 95% CI	Upper 95% CI	p
Brazil	0.0004	0.00009	0.0008	0.03
Wog Wog ($TSF_{0–9}$)	0.008	0.004	0.012	< 0.001
Wog Wog ($TSF_{10–24}$)	–0.006	–0.007	–0.004	< 0.01
Kansas				
TSF	–0.064	–0.013	0.0004	0.062
TSF^2	0.0002	0.00002	0.0004	0.036
Corridor	–0.001	–0.008	0.005	0.42

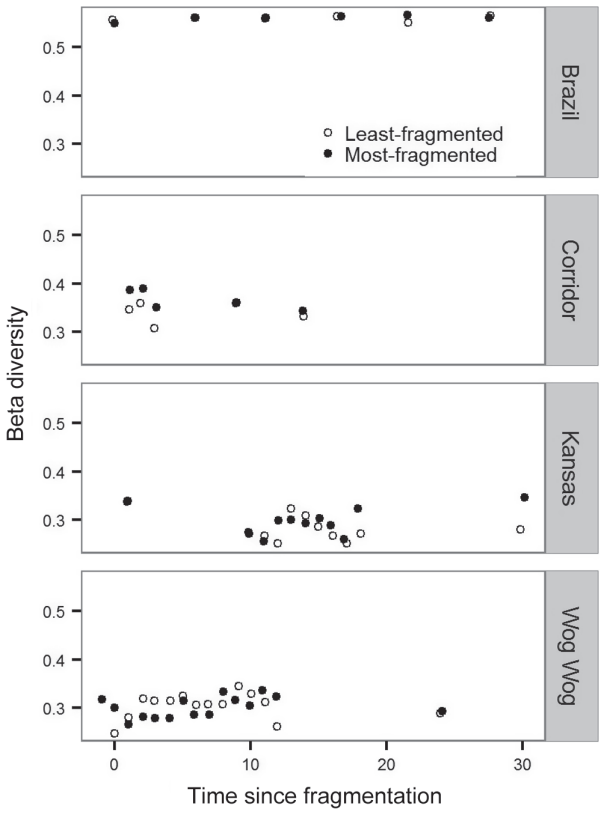


Figure 3. Beta diversity of plant communities among replicate communities within the most-fragmented (solid circles) and least-fragmented (open circles) communities in each study, calculated for each year. Each point reflects the mean difference in community composition (using Sorensen dissimilarity) calculated for every pairwise combination of communities within a treatment, at a single time period. At all sites, beta diversity among fragments did not converge or diverge over time, nor did beta diversity among replicate communities within the least-fragmented treatment.

Is compositional change due to nestedness or turnover?

In most studies, turnover contributed more to compositional change between years than did nestedness (Fig. 4) (Kansas most-fragmented sites: $t = 6.21$, $p = 0.008$, Corridor: most-fragmented sites: $t = 5.71$, $p = 0.002$ and least-fragmented sites: $t = 4.64$, $p = 0.006$, Wog Wog: most-fragmented sites: $t = 3.71$, $p = 0.034$; Brazil: most-fragmented sites: $t = 11.55$, $p = 0.001$ and least-fragmented sites: $t = 11.04$, $p = 0.002$, Fig. 4). The exceptions were the least-fragmented sites in Kansas and Wog Wog, where nestedness played the main role in driving compositional change (Fig. 4, Kansas: $t = 3.21$, $p = 0.023$; Wog Wog: $t = 13.52$, $p = 0.047$).

Discussion

Using data from four landscape-scale experiments, we show that fragmentation alters plant community composition,

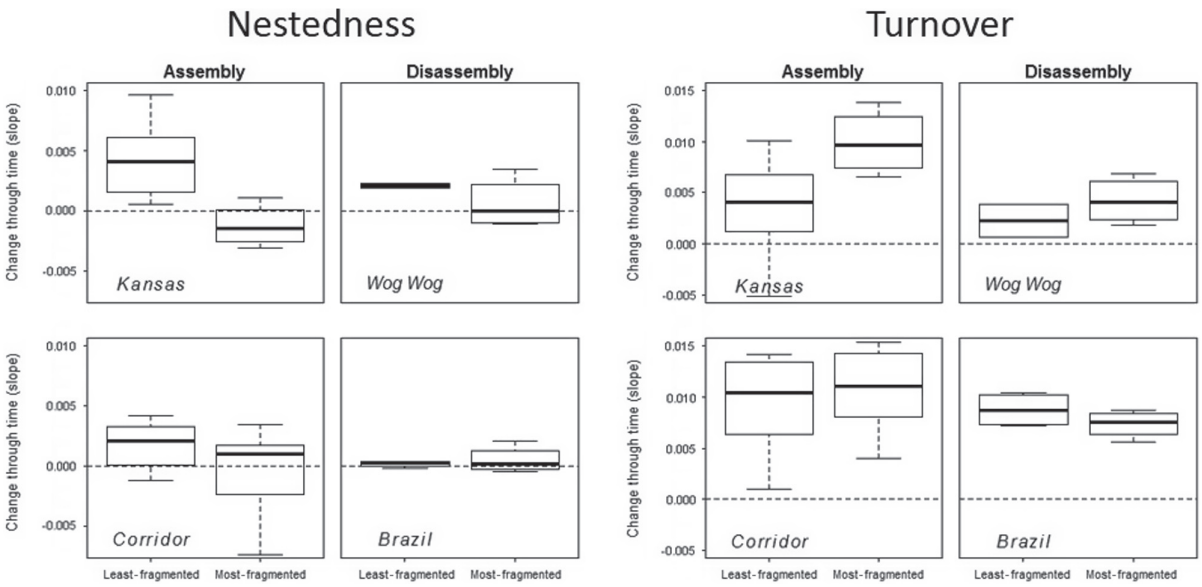


Figure 4. Temporal variation in nestedness and turnover components for compositional change over time. The lines represent the median slope from regressions of nestedness or turnover values against time. Boxes represent the interquartile range, and whiskers indicate the maximum and minimum data values.

but also illustrate variability in how these outcomes play out over time, including in contrasting disassembling versus assembling communities. Although system- and time-scale specific patterns emerged, some generalities that span the landscape experiments of this study warrant closer scrutiny, not just in future experiments, but in studies of anthropogenic landscape fragmentation more broadly. First, fragmentation caused communities to initially diverge from those in continuous areas in our two disassembly experiments (Brazil, Wog Wog), but in neither of the assembling experiments. Second, regardless of starting conditions, we found no evidence that fragmentation causes homogenization or diversification among fragments over time. And finally, species turnover explained the majority of compositional change in these experiments.

Fragmentation effects on convergence and divergence

In the two disassembling systems (Brazil, Wog Wog), community composition in the least-fragmented habitats diverged over time from communities in fragments; at Wog Wog, the divergence was temporary while at the Brazil site the divergence was gradual and sustained (Fig. 2). For the Brazil experiment, these results build on past work (Laurance et al. 2006b, 2007) to illustrate that – in spite of large initial differences in composition among all replicates (Fig. 2, Supplementary material Appendix 1 Fig. A5) and increased rates of mortality and recruitment occurring in both continuous and fragmented treatments (Laurance et al. 2014) – divergence continued over the course of decades. This gradual divergence may result from edge effects, as prior studies in this system have shown that small patches experience higher tree mortality and more frequent establishment of pioneer species from the matrix (Laurance et al. 2006a). Such degeneration of mature forest, or 'retrogressive succession' (Santos et al. 2008), has been observed in other tropical systems and is predicted to have widespread, cascading effects on ecosystem properties (Tabarelli et al. 2012, Ewers et al. 2017). At the Wog Wog site, initial divergence between most- and least- fragmented treatments shifted after a decade (Fig. 2), probably due to the dynamic structure of the matrix habitats in this system (Farmilo et al. 2013, Brudvig et al. 2017). Unlike the Brazil project where the matrix was periodically cleared to maintain fragment isolation (Laurance et al. 2011), the cleared forest that initially formed the matrix at Wog Wog grew into mature pine plantation, eventually exceeding the height of the eucalypt patches (Farmilo et al. 2013). After a decade, perhaps due to increases in connectivity among fragments or the muting of edge effects between structurally-similar forest fragments and plantations, the Wog Wog communities in fragments subsequently began to re-converge with communities in intact forest (Fig. 2).

Conversely, in both assembling systems (Kansas, Corridor), we found no evidence for directional divergence or convergence over time (Fig. 2). Paired with the divergences we observed in Brazil and Wog Wog, our results may suggest that divergence due to fragmentation is more likely during disassembly than assembly. Because early phases of community assembly typically involve species which are good colonizers, similar early-seral communities in most- and least-fragmented treatments may lead to largely congruent dynamics as community processes unfold. However, nestedness did not play a large role in compositional change over time at the Corridor site as we might expect if similar assembly dynamics occurred across treatments, and at the Kansas site, nestedness is stronger in the least-fragmented treatments. Recent evidence suggests that the relative roles of local (e.g. environmental filtering) and regional (e.g. dispersal limitation) processes vary with biogeographic location (Myers et al. 2013); perhaps they also vary between assem-

bling and disassembling fragmented systems. For instance, edge effects can drive niche-based community changes during disassembly (Gilbert et al. 2006, Laurance et al. 2006a), whereas the vagaries of dispersal during assembly may drive idiosyncratic community change in assembling communities (Hubbell 2001, Chase 2003, Fukami 2015).

Alternatively, the time scale at which we see divergence due to fragmentation may differ between assembling and disassembling systems. Indeed, the effects of fragmentation emerge over decades (Fig. 2; Tilman et al. 1994, Cook et al. 2005, Jackson and Sax 2010, Haddad et al. 2015, Alstad et al. 2016). Even 20–30 years after fragmentation, it is possible that communities reflect alternative transient states (Fukami and Nakajima 2011), and that we may eventually observe divergence between fragmentation treatments at sites where we did not detect it. This might be the case in Kansas, where composition was significantly different between most- and least-fragmented treatments in the final year of sampling, despite showing no evidence of diverging trajectories prior to that year. Future monitoring of these studies can address whether divergence is less likely during assembly than disassembly, whether the distinct communities we observed in the most recent sample year at Kansas represent a transient phase, or whether the time-lag before fragmentation effects on composition emerge is greater during the assembly process. In future analyses, consideration of species abundances (Li et al. 2016) and plant functional traits (Damschen et al. 2008, Magnago et al. 2014) may help unravel the mechanisms of community change in fragmented landscapes and provide additional insights into questions of convergence and divergence (Fukami et al. 2005, Suter and Edwards 2013).

Fragmentation effects on homogenization within most- or least-fragmented treatments

We found no evidence that fragmentation acts either to homogenize or to differentiate community composition over time (Fig. 3). In all four studies, there was no temporal trend in community dissimilarity among replicates of either the most- or least-fragmented habitats, nor did we detect different levels of beta diversity in the final year of any study. Even if communities diverge temporarily due to differences in species' dispersal mode or extinction-proneness, we might expect fragments within a single landscape to converge toward similar composition over time (Laurance et al. 2007), particularly when embedded within a single land-use history and matrix type (Ewers et al. 2013), and thus sharing the same species pool of potential community members. Consequently, lack of increasing homogenization is particularly surprising in the Kansas experiment because it is situated in one landscape, a former agricultural field with a single land-use history that now forms one matrix type. It is possible that at Kansas, Wog Wog, and the Corridor sites, compositionally similar communities at the outset limited the potential for much increased homogenization (Fig. 3, Supplementary material Appendix 1 Fig. A6–A8).

Results from the Brazil experiment may not support our homogenization hypothesis for different reasons. The Brazil experiment extends across landscapes with varying land-use histories which produced different successional trajectories in the forest matrix (Mesquita et al. 2001, 2015). Spillover from compositionally distinct matrix environments may explain the lack of convergence we observed among fragments, and relative to other tropical systems where homogenization occurred (Lôbo et al. 2011, Arroyo-Rodríguez et al. 2013). Spatial and temporal changes in the matrix influence community dynamics in fragments, with potential to diversify or homogenize communities (Driscoll et al. 2013, Sfair et al. 2016). It may also be the case that spatial heterogeneity in the matrix may simply counteract homogenizing (or diversifying) processes, leading to no net pattern of convergence or divergence among fragments, as we observed. Nonetheless, our data suggest that despite there being no temporal patterns in beta diversity among fragments, disassembling communities in fragments will ultimately develop compositionally distinct communities from continuous forests.

Nestedness and species replacement

Compositional shifts over time at all four experiments were largely due to species turnover (Fig. 4), and this was particularly true in the most-fragmented treatments. High turnover on fragments are most easily explained by coupling stochastic local extinctions – which we expect to occur on small, isolated patches (MacArthur and Wilson 1967) – with edge-mediated colonization of fragments by pioneer species or species from the matrix (Laurance et al. 2006a, Santos et al. 2008, Ewers et al. 2017). Interestingly, our results suggest that such hyperdynamism (Laurance 2002) may characterize fragments in both disassembling and assembling communities. Moreover, high temporal turnover in the most-fragmented communities may contribute to compositional variation across space, providing another possible explanation for why we did not observe biotic homogenization among communities in different fragments.

Nestedness played a prominent role in compositional change only in the least-fragmented landscapes at Wog Wog and Kansas. In the context of assembly (Kansas), nestedness reflects the persistence of early colonizing species on the least-fragmented patches, highlighting the potential importance of large fragments or continuous habitat for species' persistence during the assembly process. We suspect that the other assembly experiment (Corridor) did not show this pattern due to periodic prescribed burning that occurs across all patch types. Turnover in the least-fragmented sites was higher at the Corridor site than Kansas (Fig. 4), potentially because fires remove biomass of dominant competitors, and frees microsites for new colonists (Zimmermann et al. 2000). In addition, there was no difference in turnover between the most- and least-fragmented sites in the Corridor project, likely due to the fact that repeated burning may also act as a strong filter during assembly (Pausas and Verdú 2008), increasing turnover as fire-adapted species replace early successional species.

While our study does not address nor account for disturbances directly, we recognize that disturbances within fragments such as fire (e.g. prescribed fires at the Corridor site) or their absence (fire suppression at the Kansas site), changes in the regional species pool due to surrounding

land-use changes in the matrix (e.g. Wog Wog and Brazil) or the broader region, and shifts in weather and climate, can individually and collectively impact trajectories of assembly and disassembly. Given that the effects of fragmentation often become stronger over time (Haddad et al. 2015), long-term experiments, such as those included in our study, will continue to be central to testing new predictions that arise from our improved understanding of effects of synergistic and interacting global changes on community composition.

Conclusions

Combining data from four of the largest and longest-running landscape fragmentation experiments in the world allowed us to compare the long-term effects of fragmentation on plant community composition across experiments, including both disassembling and assembling plant communities. We observed fragmentation-induced divergence during the first decade in two disassembling communities located in different hemispheres and ecosystems, and with different regional species pools. However, the notable difference in long-term community trajectories at Wog Wog compared to Brazil (transient vs continuous divergence, respectively) suggests that compositional trajectories may be strongly influenced – possibly even re-directed – by structural changes in the matrix. The fact that we did not observe divergence in assembling experiments may suggest that constraints exist on the assembly process that ultimately reduce the potential to restore composition to even well-connected patches. Finally, turnover comprised the majority of compositional change in all systems, with little evidence for ordered species extinctions or persistence which might facilitate predictions for trajectories in other systems undergoing fragmentation. We caution that our conclusions should be viewed as preliminary, given the small number of fragmentation experiments that have been conducted, the heterogeneity in ecosystems and evolutionary history spanned by these experiments, and the suite of analytical tools we used to evaluate compositional change over space and time. Nonetheless, these results extend existing understanding beyond how fragmentation affects species richness (Haddad et al. 2015) to illustrate the many possible ways that fragmentation influences the composition of ecological communities.

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Supplementary material (Appendix ecog-02607 at <http://www.ecography.org/appendix/ecog-02607>). Appendix 1.

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