



Partitioning the colonization and extinction components of beta diversity across disturbance gradients

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Abstract. Changes in species diversity often result from species losses and gains. The dynamic nature of beta diversity (spatial variation in species composition) that derives from such temporal species turnover, however, has received relatively little attention. Here, we disentangled extinction and colonization components of beta diversity by using the sets of species that went locally extinct and that newly colonized the study sites. We applied this concept of extinction and colonization beta diversity to ground vegetation communities that have been repeatedly surveyed in forests where fire and harvesting were experimentally applied. We first found that fire and harvesting caused no effect on beta diversity 2 yr after the treatments. From this result, we might conclude that they did not alter the ways in which species assemble across space. However, when we analyzed the extinction and colonization beta diversity between pre-treatment and 2 yr after the treatments, both measures were found to be significantly lower in burned sites compared to unburned sites (i.e., the groups of excluded and newly colonized species both showed low beta diversity in the burned sites). These results indicate that the fire excluded similar subsets of species across space, making communities become more heterogeneous, but at the same time induced spatially uniform colonization of new species, causing communities to homogenize. Consequently, the effects of these two processes canceled each other out. The relative importance of extinction and colonization components per se also changed temporally after the treatments. Fire and harvesting showed synergetic negative impacts on extinction beta diversity between pre-treatment and 10 yr after the treatments. Overall, analyses using extinction and colonization beta diversity allowed us to detect nonrandom disassembly and reassembly dynamics in ground vegetation communities. Our results suggest that common practices of analyzing beta diversity at one point in time can mask significant variation driven by disturbance. Acknowledging the extinction–colonization dynamics behind beta diversity is essential for understanding the spatiotemporal organization of biodiversity.

Key words: biotic homogenization; community assembly; dispersal; ecosystem function; extinction debt; fire; forest dynamics; resilience; retention harvest; spatial heterogeneity; succession.

INTRODUCTION

Ecological disturbance initiates community assembly where species dynamically turn over (Caswell and Cohen 1991, Jiang and Patel 2008, Fukami and Nakajima 2011). With recent rises in the severity and frequency of disturbance worldwide (Nyström et al. 2000, Seidl et al. 2017), disturbance-induced reorganizations of species assemblages have become increasingly relevant in ecosystem management and conservation (Mori 2011). Despite substantial efforts, however, links between disturbance and community assembly are not yet generalizable (Jiang and Patel 2008, Myers et al. 2015, Tatsumi et al.

2019). In particular, compared with local and regional species richness (i.e., alpha and gamma diversity, respectively), little is known about how the spatial variation in species composition (i.e., beta diversity) is influenced by the temporal species turnover associated with disturbance (Vellend et al. 2007, Jiang and Patel 2008, Fukami and Nakajima 2011). Disturbance can cause decreases in beta diversity (Vellend et al. 2007), often referred to as biotic homogenization, which can impair ecosystem functionality at large spatial scales (Hautier et al. 2018, Mori et al. 2018). A deeper understanding of the dynamic processes behind beta diversity would provide a critical step towards predicting how the landscape-scale organization of biodiversity and ecosystem functionality might change in response to future disturbance regimes.

Disturbance-induced community assembly should consist of two components: species losses (i.e., local

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extinctions) and gains (i.e., colonizations). While there is a rich body of community ecology research on species losses and gains (Fukami and Nakajima 2011, Legendre 2019, Tatsumi et al. 2019), we are not aware of any study that explicitly divided them into groups with regard to the ways in which they alter beta diversity. As such, we defined six cases that describe how local extinction and colonization drive biotic homogenization and heterogenization (Fig. 1). Case 1 is where disturbance selectively excludes rare species that initially existed in limited numbers of patches. This should make the patches become more compositionally homogeneous (i.e., beta diversity of the remaining species assemblages will decrease) in disturbed sites than undisturbed sites. In case 2, disturbance excludes similar sets of regionally abundant species that existed across large numbers of patches. Similarly, in case 3, disturbance removes regionally abundant species, but only part of them across different local patches. Both cases 2 and 3 are expected to drive post-disturbance increases in beta diversity (i.e., biotic heterogenization). However, they should show contrasting patterns when it comes to beta diversity of the species subsets that went extinct, which we hereafter refer to as “extinction beta diversity” (indicated by orange symbols in Fig. 1). Case 4 is where disturbance induces colonization of new species in such a way that each species colonizes a small number of patches, leading to biotic heterogenization. By contrast, in case 5, similar sets of species colonize multiple patches in disturbed sites. In case 6, species that already existed in some patches prior to disturbance colonize the other patches as well. Cases 5 and 6 should both result in biotic homogenization, but show opposing patterns with regard to beta diversity of the sets of colonized species, which we refer to “colonization beta diversity” (indicated by blue symbols in Fig. 1). Note that beta diversity can reflect two different phenomena (namely, species turnover and nestedness; Baselga 2010), but we do not distinguish between them here for simplicity. The recently developed concept of temporal beta diversity (Legendre 2019) also differs from what we propose here (Fig. 1), fundamentally because while the temporal beta diversity directly compares community composition between two different times, we focus here on the subsets of community members that were lost and gained.

There are a variety of possible mechanisms that underlie the six cases (Fig. 1). For example, disturbance can impact rare species more strongly than regionally abundant species by increasing the risks of stochastic extinctions (Pimm et al. 1988; case 1). Alternatively, rare species can be less susceptible to disturbance than regionally abundant species given the potential interspecific tradeoffs between disturbance tolerance and other abilities such as competitive ability (Petraitis et al. 1989; cases 2 and 3). In fact, Myers et al. (2015) found that disturbed sites exhibited higher frequencies of rare species, and thus higher beta diversity, than undisturbed sites. For colonization, theory predicts that beta diversity

should increase if disturbance promotes the spatial variation in population establishment via environmental heterogeneity (Caswell and Cohen 1991), or if disturbance selects for species with low to moderate dispersal abilities that results in constrained dispersal among local patches (Mouquet and Loreau 2003, Chase 2003; case 4). In contrast, colonization can reduce beta diversity if disturbance homogenizes the environment across space under the condition of ample dispersal from the external species pool (Catano et al. 2017; case 5). Furthermore, limited dispersal from the species pool can decrease beta diversity by resulting in dominance of species that already existed before disturbance (Vellend et al. 2007; case 6).

Regional-scale disturbance intensity can strongly determine the consequences of the local extinction and colonization processes for beta diversity (Caswell and Cohen 1991). For example, intense disturbance can make the regional environment more homogeneous, but moderate disturbance can create mosaics of different habitat types, some of which could act as refugial patches or lifeboats (Franklin et al. 1997, Gustafsson et al. 2012, Salo and Kouki 2018, Kouki and Salo 2020). These patches can prevent species from going locally extinct and can thereby increase beta diversity. Furthermore, such patches can serve as sources from which species recolonize the disturbed sites (Banks et al. 2011). However, such disturbance-intensity dependency of beta diversity, mediated by extinction and colonization processes, has received no investigation. With experiments manipulating disturbance intensity, one can test its effects on colonization–extinction dynamics, and how this translates into biotic homogenization or heterogenization. Findings from such tests can help to better cope with future disturbance regimes and provide guidance for regional disturbance-based management.

In this study, we disentangled the roles of the extinction and colonization in shaping beta diversity along disturbance gradients. We did this by separately analyzing the post-disturbance beta diversity and the beta diversity of the subsets of species that went locally extinct and that newly colonized the study sites. We investigated species assemblages of ground vegetation in boreal forests in Finland, where we experimentally applied forest fire and tree harvesting with different intensities in a fully crossed design. Forest fire is the dominant natural disturbance in many boreal and temperate regions. Harvesting was implemented as clearcutting and retention harvesting. Retention harvesting is a silvicultural system in which some portions of the original stand are left unlogged to maintain biodiversity and ecosystem functioning (Gustafsson et al. 2012, Lindenmayer et al. 2012). In our experiment, groups of trees were retained in patches, with the number of patches being manipulated. Fire and harvesting are known to drive disturbance interactions; that is, the downed woody debris produced by harvesting can fuel fire and thereby cause synergetic impacts (Lindenmayer et al. 2009). Our

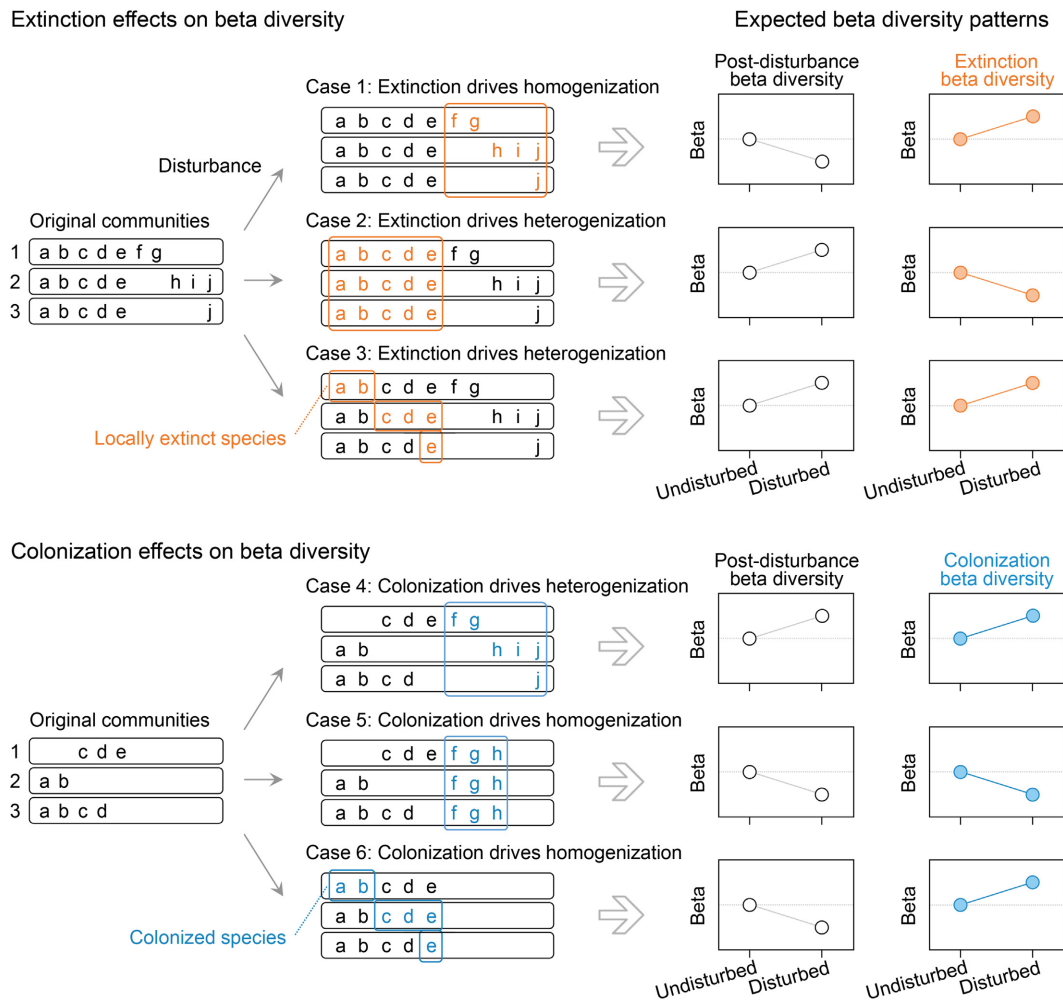


FIG. 1. Schematic representation of the links between disturbance-induced extinction, colonization, and the resultant patterns of beta diversity. Different letters indicate different species. Panels in the right column represent the beta diversity of species subsets that went locally extinct (orange) and colonized the sites (blue). [Color figure can be viewed at wileyonlinelibrary.com]

experiment thus provided an ideal system with which to unravel how the gains and losses of species generate spatiotemporal variation in species diversity across a wide range of disturbance intensities.

METHODS

Experimental design and data collection

We conducted a replicated stand-scale experiment in a boreal forest in eastern Finland (63°10' N, 30°40' E). Before the treatments, the experimental sites consisted of 150-yr-old coniferous stands, which were dominated by Scots pine (*Pinus sylvestris* L.), with sporadic occurrences of Norway spruce (*Picea abies* [L.] Karst.) and two birch species (*Betula pendula* Roth and *Betula pubescens* Ehrh.). The average pre-treatment stand volume (i.e., the total stem volume in each stand) was 288 ±

71.1 m³/ha (mean ± SD). The mean annual temperature is 2°C, and the mean monthly temperature ranges from -12°C in January to 16°C in July. The mean annual precipitation is 500–800 mm, approximately one-half of which falls as snow.

Our experiment featured a 2 × 4 factorial design, with burned and unburned (control) for fire, and four harvesting levels: clear cut (0% retention), small-amount retention (10 m³/ha or 3.5% of preharvest volume), large-amount retention (50 m³/ha or 17.4% of preharvest volume), and no harvest (100% retention; control). In the two retention treatments, the retained trees were aggregated in either three (small-amount retention) or five (large-amount retention) groups of similar size. We selected 24 stands, each ~3–5 ha in size, located within a 20 × 30 km area. Each stand was subjected to one of the eight treatment combinations, with three replicates for each combination. The stands were harvested in the

winter of 2000–2001 and burned in the summer of 2001. See Hyvärinen et al. (2005) and Johnson et al. (2014) for further details of the experimental practices.

Field measurements followed the before-after control-impact (BACI) principle (Green 1979). In 2000, the summer before the treatments, we established 15 2 × 2 m plots in each stand. The plots were placed systematically 20 m apart from each other in the center area of each stand. In each plot, we recorded the presence and absence of all vascular plant, bryophyte, and lichen species, except those on tree trunks (e.g., epiphytes), to represent ground vegetation. For vascular plants, we included grasses, forbs, ferns, clubmosses, shrubs, and trees that were shorter than 1 m in height. We considered the vascular plants, bryophytes, and lichens to collectively represent the ground vegetation (Uotila and Kouki 2005, Johnson et al. 2014), as they often compete for similar resources and constitute a guild. Species were identified in the field or in the laboratory under a microscope. The nomenclature for vascular plants, bryophytes, and lichens followed Karlsson (1998), Hallingbäck et al. (2006), and Santesson et al. (2004), respectively. On average, there were 11.3 ± 3.3 species per plot (mean \pm SD) before the treatments ($n = 360$). The same survey was repeated in 2003 (i.e., 2 yr after treatment) and in 2011 (i.e., 10 yr after). The total sample size was $n = 1080$ (8 treatment combinations \times 3 stands \times 15 plots \times 3 survey years).

Statistical analyses

Beta diversity was defined as the extent of compositional dissimilarity within each stand. We used the Raup-Crick index (Raup and Crick 1979) to quantify the dissimilarity among local communities (i.e., plots). There are a number of beta diversity metrics, and the choice of which to use depends on the research question (Anderson et al. 2011). We selected the Raup-Crick index because it controls for random sampling effects based on null models (Chase et al. 2011, Catano et al. 2017). Other beta diversity metrics such as the Whittaker, Jaccard, and Sørensen indices are known to be confounded by sampling effects that derive from variations in alpha and gamma diversity (Anderson et al. 2011). For example, if disturbance increases the mean alpha diversity without altering gamma diversity, the observed beta diversity would necessarily decrease (e.g., $\beta = \gamma/\bar{\alpha}$) (Catano et al. 2017). This decrease in beta diversity would be indistinguishable from a pattern based on random sampling from the species pool and thus would not reflect selective homogenization (Chase et al. 2011, Catano et al. 2017). We therefore used the Raup-Crick index, which quantifies the compositional dissimilarity that is independent of the among-plot variation in alpha and gamma diversity (Vellend et al. 2007, Chase et al. 2011, Catano et al. 2017). We used the mean pairwise dissimilarity among the 15 plots to represent beta diversity in a given stand (~3–5 ha). This spatial

scale roughly matches the average size of forest-management units in Fennoscandian regions (Löfman and Kouki 2003) and was thus deemed relevant for assessing the heterogeneity. The set of 15 plots was defined as the group within which species presence/absence was randomized.

Beta diversity was calculated for (1) species that were present in each survey year, (2) species that went locally extinct from each plot between two survey years (i.e., extinction beta diversity), and (3) sets of species that newly colonized each plot between two survey years (i.e., colonization beta diversity) (Fig. 1). We tested the effects of fire, harvesting, and their interaction on beta diversity using two-way analysis of variance (ANOVA) with beta error distributions and logit-link functions.

Alpha and gamma diversity was defined as the number of species in each plot and stand, respectively. We tested the effects of fire, harvesting, and their interaction on alpha diversity using two-way ANOVA with “stand” as a random effect, and the effects on gamma diversity using two-way ANOVA. The tests were conducted for each survey year. We used Poisson error distributions and log-link functions for both diversity measures.

We defined the numbers of species that went extinct within plots and within stands between two survey years as the extinction alpha and gamma diversity, respectively. We defined the numbers of species that colonized each plot and each stand between two survey years as the colonization alpha and gamma diversity, respectively. The responses of these variables to fire, harvesting, and their interaction were tested using two-way ANOVA with “stand” as the random effect for extinction and colonization alpha diversity, and two-way ANOVA for extinction and colonization gamma diversity. Poisson error distributions and log-link functions were used for both diversity measures.

We quantified temporal species turnover (or temporal community dissimilarity) between two survey years in each plot using the Jaccard and Sørensen indices. The Raup-Crick index was not used here because it cannot quantify the community dissimilarity between two points in time. We used two indices (Jaccard and Sørensen) in order to confirm the robustness of our results. We tested the effects of fire, harvesting, and their interaction on temporal species turnover using two-way ANOVA with beta error distributions and logit-link functions.

We calculated species frequencies (i.e., the number of plots in which each species occurred) and compared their temporal changes among different treatments. All analyses were performed using R 3.5.2 (R Core Team 2018).

RESULTS

Alpha and gamma diversity did not differ significantly among the stands before the treatments (Fig. 2a, d), but changed dynamically after fire and harvesting. Burned

stands had significantly lower alpha and gamma diversity than the unburned stands 2 yr after the treatments (Fig. 2b, e). The fitted models showed that fire decreased the mean alpha diversity to 75% of the controls (i.e., 9.6 species in the burned stands and 12.8 species in the unburned stands, on average; Fig. 2b), and decreased the mean gamma diversity to 67% of the controls (i.e., 24.5 species in the burned stands and 36.5 species in the unburned stands; Fig. 2e). Ten years after the treatments, alpha and gamma diversity were no longer affected by fire, but were significantly higher in the harvested stands (clearcuts and retention stands) than in the unharvested stands (Fig. 2c, f). The mean alpha diversity in the harvested stands was 1.37 to 1.46 times that in the unharvested stands (Fig. 2c), and mean gamma diversity was 1.38 to 1.47 times that in the unharvested stands (Fig. 2f).

Beta diversity showed different patterns depending on the survey years (Fig. 2g–i). Before the treatments, beta diversity differed among the stands subjected to different harvesting intensities (Fig. 2g). Two years after the treatments, this difference became undetectable, and fire also showed no effect on beta diversity (Fig. 2h). Ten years after the treatments, beta diversity showed no significant difference among the harvesting levels, but became significantly lower in the burned stands than in the unburned stands (Fig. 2i).

Extinction beta diversity at the first survey interval (i.e., beta diversity of the sets of species that went locally extinct between pre-treatment and 2 yr after the treatments) was reduced by both fire and harvesting, although their interaction effect was not significant (Fig. 3a). Between 2 and 10 yr after the treatments, only harvesting had a significant effect on extinction beta diversity (Fig. 3b). When compared between pre-treatment and 10 yr after the treatments, extinction beta diversity was reduced by fire, harvesting, and their interaction (Fig. 3c). The decreased extinction beta diversity indicates that fire and harvesting excluded similar suites of species across the plots within each stand (i.e., case 2 in Fig. 1).

Colonization beta diversity at the first survey interval (i.e., beta diversity of the set of species that newly colonized the plots between pre-treatment and 2 yr after the treatments) was decreased by fire and marginally by the interaction between fire and harvesting ($P < 0.10$) (Fig. 3d). Fire and harvesting reduced the colonization beta diversity from 2–10 yr after the treatments (Fig. 3e), as well as between pre-treatment and 10 yr after the treatments (Fig. 3f). The decreased colonization beta diversity indicates that similar sets of species colonized different plots within each stand after the treatments (i.e., case 5 in Fig. 1). Extinction and colonization alpha and gamma diversity were significantly influenced by fire and harvesting (Appendix S1: Fig. S1).

The rates of temporal species turnover were increased significantly by both fire and harvesting (Appendix S1: Fig. S2). The Jaccard (Appendix S1: Fig. S2a, b, c) and

Sørensen indices (Appendix S1: Fig. S2d, e, f) showed the same qualitative pattern. Between pre-treatment and 2 yr after the treatments, the species turnover rates were high in the burned stands (Appendix S1: Fig. S2a, d). From 2 to 10 yr after the treatments, fire continued to be the dominant driver of species turnover, yet the positive effects of harvesting increased with increasing intensity (Appendix S1: Fig. S2b, e).

Between pre-treatment and 2 yr after the treatments, bryophytes indicative of mature forests such as *Dicranum polysetum*, *Dicranum scoparium*, *Hylocomium splendens*, and *Pleuroweisia schliephackei* declined in their frequency in the burned stands, while species typical to post-fire sites such as fireweed *Epilobium angustifolium* and lichens *Polytrichum juniperinum*, *Pohlia nutans*, *Ceratodon purpureu*, and *Funaria hygrometrica* increased (Appendix S1: Fig. S3). Between 2 and 10 yr after the treatments, regionally abundant species such as dwarf shrub *Vaccinium myrtillus* and bryophytes *Hylocomium splendens* and *Funaria hygrometrica* went extinct sporadically in some disturbed stands, while lichens of genus *Cladonia* broadly colonized the disturbed stands (Appendix S1: Fig. S4).

DISCUSSION

Though ample evidence exists for cases in which disturbance increased beta diversity and for cases in which it decreased beta diversity, the dynamic processes that underlie those patterns had not necessarily been articulated. Here, we proposed a conceptual foundation to disentangle the extinction and colonization components of beta diversity. Specifically, we defined six processes by which colonization–extinction dynamics can drive biotic homogenization or heterogenization (Fig. 1). Analyses based on this concept allowed us to detect nonrandom disassembly and reassembly dynamics in plant communities.

The difference in beta diversity was undetectable across an experimental disturbance-intensity gradient 2 yr after the treatments (Fig. 2h). From this result, we might conclude that disturbance caused no impact on how species assemble across space. Nevertheless, when we analyzed the extinction and colonization beta diversity (i.e., beta diversity of the sets of species that went locally extinct and that newly colonized the sites, respectively), we found that both were significantly lower in the disturbed stands than in the undisturbed controls (Fig. 3a, d). These patterns indicate that disturbance excluded similar species subsets across plots, making communities become more heterogeneous (case 2 in Fig. 1), but at the same time induced spatially uniform colonization of new species, causing communities to homogenize (case 5 in Fig. 1). Consequently, the effects of these two processes canceled each other out (Fig. 2h). We further found that beta diversity decreased in the burned stands relative to the unburned stands after 10 yr (Fig. 2i). This pattern was explained by the fact that the spatially uniform colonization continued to make the

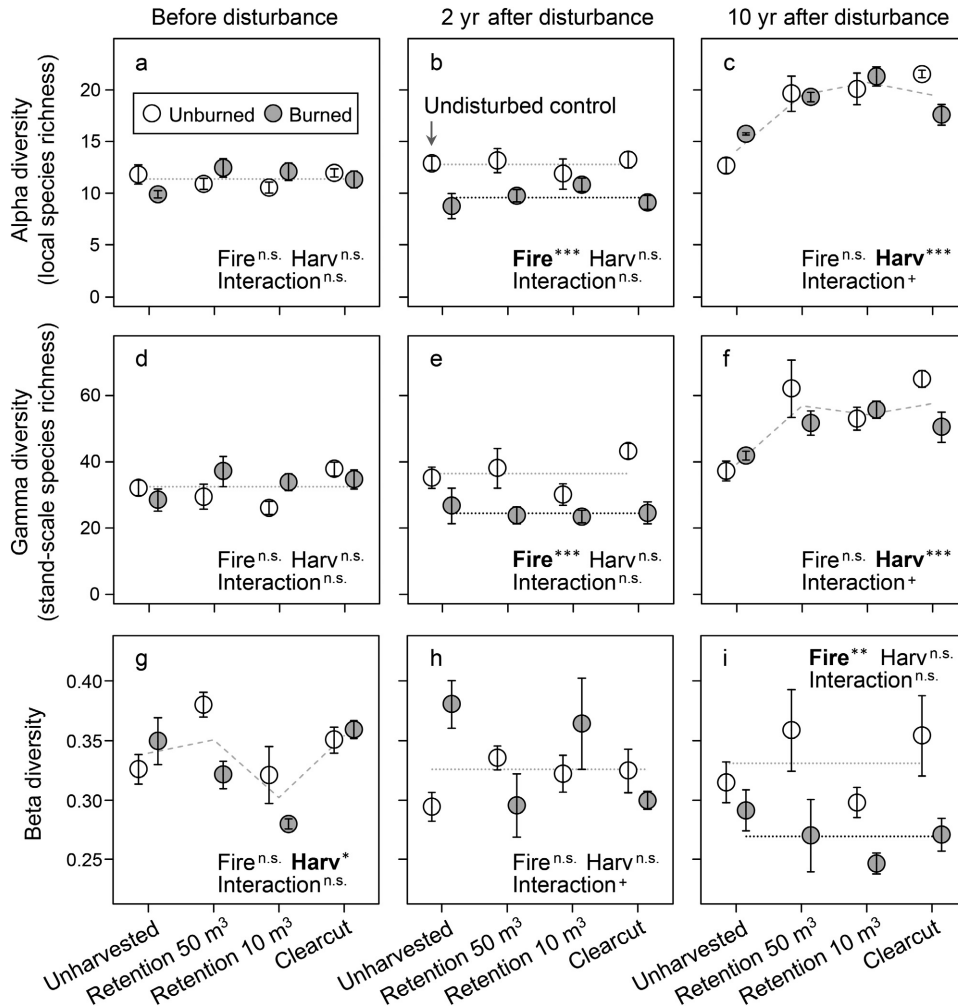


FIG. 2. Effects of fire and harvesting disturbance on (a–c) alpha, (d–f) gamma, and (g–i) beta diversity. “Retention 50 m³” and “10 m³” indicate harvesting treatments in which those volumes of trees per hectare were left unlogged. The results of two-way ANOVA are shown in each panel: Harv, harvesting; Interaction, fire × harvesting. Significance: ****P* < 0.001; ***P* < 0.01; **P* < 0.05; + *P* < 0.10; n.s., *P* ≥ 0.10. Variables are shown in boldface type when their effects were significant (*P* < 0.05). Lines represent the fitted models for significant variables. Black lines and dashed lines indicate significant effects of fire and harvesting, respectively. Values are means ± SE.

communities become more homogeneous over time (case 5 in Fig. 1; Fig. 3e). Overall, our results provide evidence that the beta diversity at our experimental site was determined by nonrandom extinction–colonization dynamics and, moreover, that the relative importance of extinction and colonization components of beta diversity changed with time after disturbance.

Extinction and colonization beta diversity driven by disturbance

Extinction beta diversity was lower (i.e., the excluded sets of species were more similar to each other) in the burned stands than in the unburned stands during the first 2 yr after the treatments (Fig. 3a). This result indicates that the fire disproportionately removed regionally

abundant species that commonly occurred across the stands (case 2 in Fig. 1). In fact, in the burned stands, there were significant declines in frequencies of bryophytes such as *Dicranum polysetum*, *Dicranum scoparium*, *Hylocomium splendens*, and *Pleurozisia schliephackei* (Appendix S1: Fig. S3), which are known as indicator species of mature forests (Hart and Chen 2008, Paquette et al. 2016). While these four species initially occurred, on average, in 85% of the plots (12.7 plots out of 15 plots within each stand), this value dropped to 13% 2 yr after the fire (Appendix S1: Fig. S3).

It is important to note that we quantified beta diversity using the Raup-Crick index, which corrects for random sampling effects (Vellend et al. 2007, Chase et al. 2011). That is, our finding that the fire reduced extinction beta

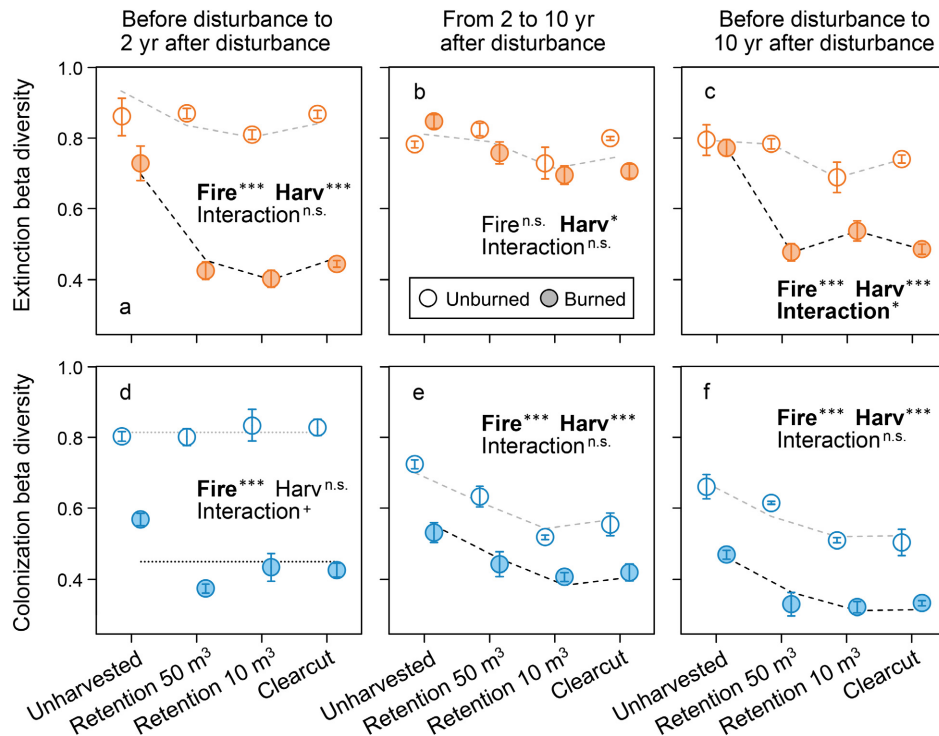


FIG. 3. Effects of fire and harvesting disturbance on beta diversity of (a–c) species that went locally extinct within plots and (d–f) species that newly colonized the plots. “Retention 50 m³” and “10 m³” indicate harvesting treatments in which those volumes of trees per hectare were left unlogged. The results of two-way ANOVA are shown in each panel: Harv, harvesting; Interaction, fire × harvesting. Significance: *** $P < 0.001$; * $P < 0.05$; + $P < 0.10$; n.s., $P \geq 0.10$. Variables are shown in boldface type when their effects were significant ($P < 0.05$). Lines represent the fitted models for significant variables. Black lines and dashed lines indicate significant effects of fire and harvesting, respectively. Values are means \pm SE. [Color figure can be viewed at wileyonlinelibrary.com]

diversity (Fig. 3a) does not result simply from the fact that the regionally abundant species had high local-extinction frequencies due to their widespread occurrence, but rather indicates that the fire selectively excluded them compared to rare species. Tolerance to fire is a cost-intensive plant trait that requires considerable structural and energy investments (Wahid et al. 2007). Having this trait might thus come at the expense of a low rate of local range expansion, resulting in fire causing more severe damage to regionally abundant species than rare species. Furthermore, we found that the effects of fire on extinction beta diversity became undetectable between 2 and 10 yr after the treatments (Fig. 3b). This result further suggests that the direct effects of burning influenced extinction beta diversity more strongly than subsequent environmental alterations, such as a post-fire increase in soil pH (Čugunovs et al. 2017).

Harvesting, on the other hand, continued to reduce extinction beta diversity (i.e., it removed similar suites of species across space) 10 yr after the treatments (Fig. 3a–c). The reductions between 2 and 10 yr after harvesting were partly explained by extinctions of species that had spread across the stands during the first 2 yr (e.g., *Funaria hygrometrica*; Appendix S1: Figs. S3, S4). In addition, the decadal decreases in extinction beta

diversity (Fig. 3b) were associated with prolonged extinctions of initially widespread species such as *H. splendens* and *Vaccinium myrtillus* (Appendix S1: Fig. S4). Previous studies conducted in other regions have also reported that these two species declined in their population sizes until up to two decades after harvesting (Tonteri et al. 2016, Vanha-Majamaa et al. 2017). The time-delayed extinctions and consequent changes in beta diversity, as observed in our harvested stands (Fig. 3b), could be seen as examples of ecosystems incurring extinction debts of beta diversity. Extinction debt refers to expected changes in biodiversity owing to delays in population responses to the environment (Tilman et al. 1994). In our harvested stands, temporal accumulations of light-induced stress may have driven the delayed extinctions of widespread species such as *H. splendens* and *V. myrtillus* (Tonteri et al. 2016; Appendix S1: Figs. S3, S4) and the consequent reductions in extinction beta diversity (Fig. 3b). Our results indicate that spatially replicated, long-term monitoring is necessary to understand the potential long-lasting effects of disturbance on the spatial structure of ecological communities.

When compared between pre-treatment and 10 yr after the treatments, extinction beta diversity was

reduced, especially in stands where fire and harvesting were both applied (Fig. 3c), indicating the signature of disturbance interactions. Such interaction effects were undetectable in the first 2 yr (Fig. 3a) and only became significant after 10 yr (Fig. 3c). These results were attributable to the recoveries of regionally abundant species in the burned unharvested stands. Specifically, in these stands, bryophytes such as *D. polysetum*, *D. scoparium*, *H. splendens*, and *P. schliephackei* initially declined in their frequency during the first 2 yr after fire (Appendix S1: Fig. S3e), but recovered roughly to their original states after 10 yr (Appendix S1: Fig. S4e). Their frequencies thus showed virtually no net change at the decadal scale (Appendix S1: Fig. S5e). In the burned harvested stands, however, the extent of such vegetation recoveries was limited (Appendix S1: Fig. S5f, g, h). Overall, the fact that the burned harvested stands showed decadal extinction patterns distinct from others (Fig. 3c) was largely due to the slow recovery rates of vegetation once removed. This suggests that harvesting reduced the resilience (i.e., the rate at which a system returns to its original state after disturbance; sensu Pimm 1984) of forest vegetation to subsequent fire.

Colonization beta diversity was low in stands disturbed by fire and/or harvesting (Fig. 3d, e, f). This suggests that similar suites of species uniformly covered the stands after the treatments (case 5 in Fig. 1). Specifically, in the first 2 yr, the burned stands were broadly colonized by bryophytes such as *Polytrichum juniperinum*, *Pohlia nutans*, *Ceratodon purpureu*, and *F. hygrometrica*, as well as fireweed *Epilobium angustifolium* (Appendix S1: Fig. S3), which are all typical of early post-fire succession communities (Slack 1990, Hart and Chen 2008, Paquette et al. 2016). From 2 to 10 yr after the treatments, there were widespread occurrences of multiple lichen species (*Cladonia* spp.; Appendix S1: Fig. S4). This result coincides with previous findings that colonizations of lichens do not become prominent until several years after disturbance (Newmaster and Bell 2002, Uotila and Kouki 2005, Vanha-Majamaa et al. 2017).

In the first 2 yr after the treatments, similar suites of species colonized the sites especially in stands where fire and harvesting were applied in concert ($P < 0.10$; Fig. 3d). In our experimental sites, fire intensities (measured as the post-fire humus depth and height of charred bark) were significantly higher in the harvested stands than in the unharvested stands (Hyvärinen et al. 2005). Thus, the low colonization beta diversity in the burned and harvested stands (Fig. 3d) suggests that large fires, fueled by the downed woody debris, have homogenized the environment and made spaces available for new species to colonize across the stands. Furthermore, we found that the large-amount retention stands had higher colonization beta diversity 10 yr after the treatments than the small-amount retention stands and clearcuts (Fig. 3e). This pattern suggests that the retention patches served as refugia (Franklin et al. 1997,

Gustafsson et al. 2012), which allowed species with poor dispersal abilities, that otherwise could have hardly reached the post-disturbance areas, to recolonize them sporadically. In future studies, it would be worthwhile exploring whether such “chance colonization” will amplify biotic heterogenization over time (Chase 2003, Fukami and Nakajima 2011).

General and future applications

The concept of extinction and colonization beta diversity (Fig. 1) can be applied to any taxonomic group and only requires community survey data (site \times species matrices) collected at two time points. It is applicable not only in the context of ecosystem disturbance, but also of any environmental changes that can drive spatiotemporal species turnover (e.g., climate change, biological invasions, habitat fragmentation, or ecosystem restoration). For example, extinction and colonization beta diversity could be utilized in a restoration project that aim to reverse biotic homogenization, i.e., it can be used to identify whether a given recovery of beta diversity is due to local species extinctions (case 2 or 3 in Fig. 1) or colonization of new species (case 4), the latter of which may often be more expected.

Extinction and colonization beta diversity can also be highly relevant for understanding ecosystem functionality. Recent studies using snapshot data have shown that spatial dissimilarity in species composition can affect regional-scale ecosystem functioning as strongly as, if not more strongly than, local species richness (Hautier et al. 2018, Mori et al. 2018). By linking extinction and colonization beta diversity with temporal changes in ecosystem functionality, one could discern which species should be removed or added to enhance ecosystem functioning. Moreover, extinction and colonization beta diversity could help us quantify the spatial variation in the capability of communities to withstand extinction (i.e., resistance) and recover via colonization (i.e., resilience; sensu Pimm 1984) during and after environmental perturbations. A natural extension of our framework (Fig. 1) would be to incorporate species abundances and functional traits, which are often strongly linked with ecosystem resistance, resilience, and functioning.

Conclusions

In this study, we defined six processes through which species extinction and colonization shape beta diversity. Analyses based on repeated community measurements revealed that relying only on snapshot data can sometimes mislead us to superficial perceptions that disturbance has not caused any detectable variation. Our results indicated that accounting for colonization–extinction dynamics could help us test and expand some current ideas in community ecology. Specifically, extinction beta diversity allowed us to detect nonrandom

extinctions, where a higher proportion of regionally abundant species compared to rare species was removed. We also found time-delayed changes in spatial community variation, which can be seen as case examples of extinction debt in the form of beta diversity. In burned harvested stands, recoveries of vegetation once removed were relatively slow, suggesting that fire and harvesting synergistically reduced the resilience of forest vegetation. Colonization beta diversity indicated that retained habitats could indeed serve as refugia from which species recolonize disturbed areas, providing evidence for the conservation benefits of retention patches at the community level. Overall, our results show that the concepts of extinction and colonization beta diversity form a useful link between community assembly studies, which have often been spatially framed, and ecological disturbance and dynamics studies, which have focused primarily on temporal changes. Dynamic appraisals of beta diversity will help us to better understand the spatiotemporal organization of biodiversity and its consequences for ecosystem functioning.

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