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Disturbance interval modulates the starting point for vegetation succession

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Abstract. Increased frequency and new types of disturbances caused by global change calls for deepened insights into possible alterations of successional pathways. Despite current interest in disturbance interactions there is a striking lack of studies focusing on the implication of decreasing times between disturbances. We surveyed forest-floor vegetation (vascular plants and bryophytes) in a *Pinus sylvestris*-dominated, even-aged production forest landscape, unique because of the presence of stands under a precisely dated disturbance interval gradient, ranging from 0 to 123 yr between clearcutting and a subsequent megafire. Despite a dominance of early-successional species in all burned stands 5 yr after fire, progression of succession was linked to time since the preceding clearcutting disturbance. This was most clearly seen in increased frequency with time since clearcutting of the dominant, late-successional dwarf shrub *Vaccinium myrtillus*, with surviving rhizomes as an important mechanism for postfire recovery. Our results demonstrate the role of legacy species as significant drivers of succession. We conclude that the starting point for succession is modulated by disturbance interval, so that shortened intervals risk reducing development towards late-successional stages. We suggest that a decrease in long successional sequences caused by more frequent disturbances may represent a general pattern, relevant also for other forest types and ecosystems.

Key words: clearcutting; disturbance interaction; disturbance modification; ecological legacy; fire; light; plants; succession; traits; vegetation.

INTRODUCTION

The response of biota to repeated disturbances urgently needs better recognition and a stronger evidence base, particularly in the light of more and stronger disturbances due to global change (Seidl et al. 2020), with large implications for natural resource management (Buma 2015, Leverkus et al. 2018, Turner et al. 2019). Disturbances can produce complex feedbacks with one another through two main pathways. Whereas

interaction chains imply that one disturbance modifies ecological resistance (the ability to withstand disturbance [Nimmo et al. 2015]) to a subsequent disturbance, *interaction modifications* are produced when one disturbance modifies ecological resilience (the capacity to recover following disturbance [Nimmo et al. 2015]) to another disturbance (Foster et al. 2016). Both pathways modulate the ecological response to disturbance (Foster et al. 2016, Burton et al. 2020), and being able to differentiate between them and to understand their underlying mechanisms is paramount to advance disturbance interaction theory (Foster et al. 2016).

The effect of *time between disturbances* is fundamental to interaction chains as well as modifications, but has undergone limited empirical investigation (Kleinman

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et al. 2019). We do know that disturbance interval can be a driver of interaction chains, for example, a recent fire may buffer subsequent fire through reducing fuel loads (Prichard et al. 2017) but we know much less about how disturbance interval may modulate interaction modifications, that is, via changes in resilience. Especially noteworthy is a lack of studies contemplating long disturbance-interval ranges; research targeting the temporal aspect of multiple disturbances commonly includes time intervals up to a few decades only (e.g., Donato et al. [2009], Pidgen and Mallik [2013]). Studies that empirically address the effect of disturbance interval generally do so fortuitously, taking advantage of disturbances that happened to occur, and they therefore lack the capacity for robust statistical inference (e.g., Johnstone 2006).

The rising interest in disturbance interactions and associated theory development has implied increased attention to the concept of *ecological legacies* (biologically derived organisms and structures that persist in an ecosystem or landscape following disturbance [Johnstone et al. 2016]). For forests, residual living and dead trees are main legacies, varying in types and amounts depending on disturbance intensity. Surviving below-ground plant tissues represent other important legacies, with regeneration strategies key to understanding species dynamics (Schimmel and Granström 1996). Legacies may act directly through availability of seed and bud banks on site for recolonization, but also indirectly through the modification of environmental conditions that drive species dynamics, such as availability of light, indispensable for photosynthesis and plant growth (Valdadares et al. 2016).

A large and severe fire hit Sweden in 2014 in a boreal production forest landscape dominated by even-aged *Pinus sylvestris* forest stands ranging from 0 to >120 yr following clearcutting (Gustafsson et al. 2019). The fire area offers unique opportunities to study how vegetation dynamics following a short but intense disturbance (in this case high-severity fire resulting in the death of all trees and shrubs) depend on time since the last severe disturbance (in this case clear-cutting, implying removal of all trees) with a century-long time span. Harvest records such as those used in this study give precise records of the spatial and temporal occurrence of disturbance. Boreal forest-floor succession broadly follows a trajectory of initial dominance of fast-growing pioneer herbs with a later dominance of slow-growing dwarf shrubs and mosses (Engelmark and Hytteborn 1999). Most ground-vegetation plant groups show similar successional patterns after fire and logging disturbance (Uotila and Kouki 2005). Still, forestry measures affect species identities and abundances of ground flora, with dominance of planted conifers as a main factor leading to dense stands with low light levels on the ground, reducing ground vegetation cover (Hedwall et al. 2013).

Our main aim is to increase the understanding of the temporal aspect of disturbance interactions and associated drivers. More specifically, we study how the effect

of time since the preceding clearcutting disturbance influences forest-floor vegetation following the fire. By monitoring plots of equal fire severity we exclude the potential effects of an interaction chain (or effects of disturbance interval on resistance), and thus place our results in the context of the effects on interaction modification (i.e., on resilience). We investigate the role of two types of legacies as potential key drivers of vegetation patterns, first late-successional forest-floor species and secondly dead trees affecting postfire light availability (see Fig. 1 for concept and hypotheses). We predict that plant species composition and cover after the second disturbance, fire, will vary with time since the former disturbance, clearcutting, for two main reasons. First, although early-successional species will dominate post-fire communities irrespective of time since clearcutting, late-successional dwarf shrubs will be more common in stands with a more advanced succession because of their high prefire abundance and their capacity to resprout from rhizomes. Second, light level, decreasing with time since clearcutting through shading from the stems of burned standing trees (increasing in size with time since clearcutting), will affect vegetation composition and reduce vegetation cover. To pinpoint the effect of time since last disturbance, we applied narrow criteria for soil and forest type, and considered distance to fire perimeter as a potentially important dispersal variable.

METHODS

The burned forest landscape that we studied (Västmanland county, south boreal zone) was, before the fire, a production forest landscape with even-aged pine-dominated forests (Scots pine, *Pinus sylvestris*). After the fire (which was the largest for at least 100 yr in Sweden), about half of the area was set aside as a nature reserve, at which point all forestry operations ceased (Hälleskogsbrännan 6,500 ha; map in Appendix S1: Fig. S1). Before the fire, production forests managed through the clear-cutting system covered the area (Gustafsson et al. 2019).

Vegetation was investigated in June and July 2019, 5 yr after the fire, in 10 study plots (50 × 50 cm) in each of 25 stands in an age range of 0–123 yr (reflecting time between clearcutting and fire; see Appendix S1: Figs. S1, S3 for ages). Only stands with high burn severity (<=1 cm humus remaining after the fire, all trees killed) were included. Each study plot was divided into 16 equally sized subplots, in which the subplot-level frequency (0–16) of all species of vascular plants and bryophytes was recorded. The total cover of vascular plants and bryophytes, respectively, was estimated in a percentage scale. At each study plot, a hemispherical photo was taken to estimate canopy openness (i.e., light availability) using image analysis in Gap Light Analyzer (GLA) version 2.0 (radius 1,115–1,120). Species trait values for vascular plants (diaspore mass, specific leaf area [SLA], root buds, and seed longevity) were extracted from the trait

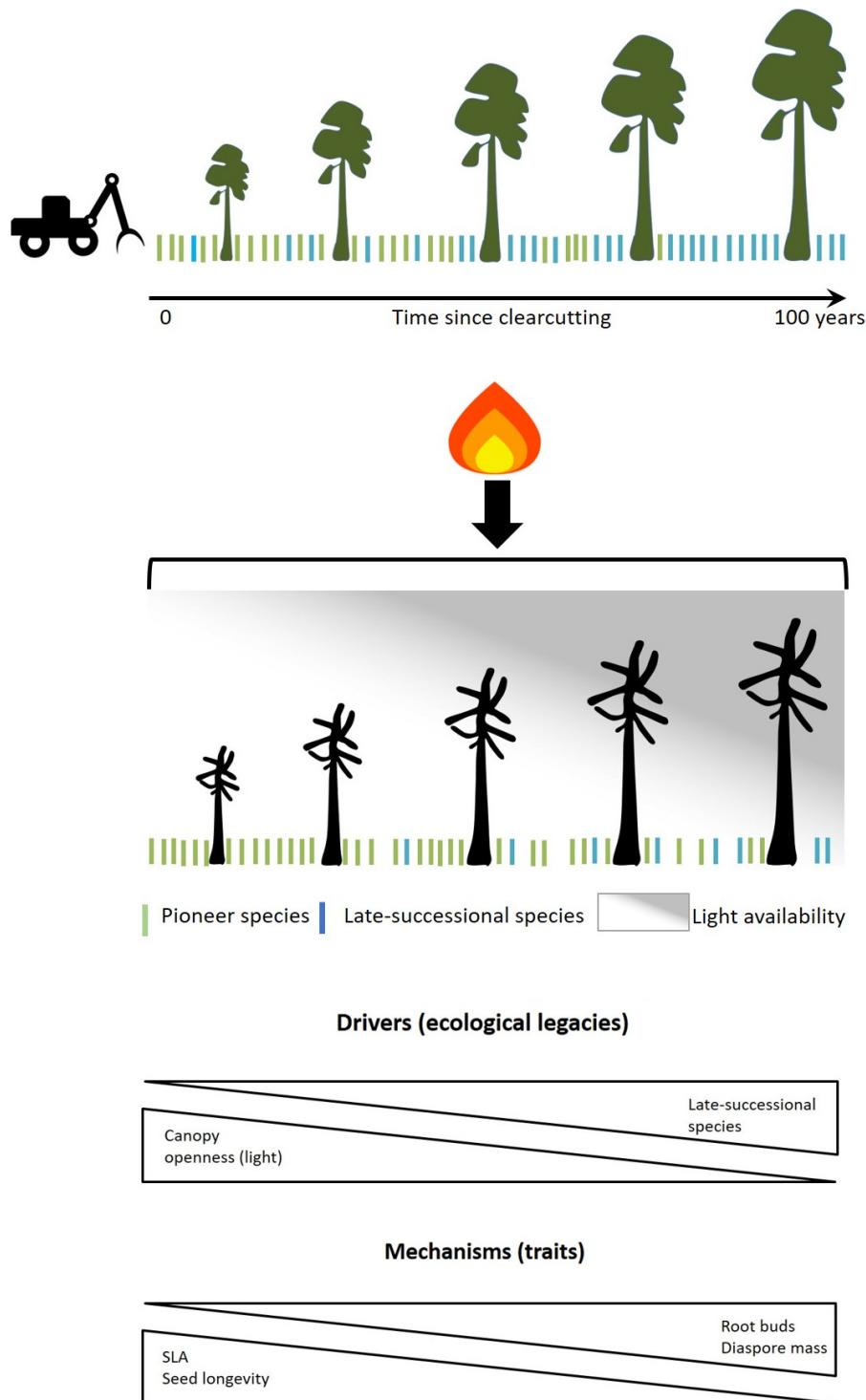


FIG. 1. Illustration of predictions. The expectation is that the time interval between two consecutive disturbances affects forest-floor vegetation. We predict that the vegetation after the second disturbance, fire (lower panel), reflects the time since the preceding disturbance, clearcutting (upper panel), with ecological legacies (late-successional plant species and dead trees affecting postfire light conditions) as primary drivers, and with plant traits as main mechanisms.

databases BIEN (Enquist et al. 2009) and LEDA (Kleyer et al. 2008). Diaspore mass is related to long-distance dispersal ability (lower mass has higher probability to spread longer). Number of root buds indicates capacity for vegetative (postfire) regeneration, and seed longevity relates to potential regeneration from seed bank (re-establishment by germination). Specific leaf area is associated with nutrient acquisition and growth rate in a post-disturbance setting (high SLA means high growth rate). See Appendix S1 for methodological details.

All statistical analyses were performed at the stand level. Time between clearcutting and fire and openness were strongly correlated ($r = -0.7$, Appendix S2: Fig. S1), which makes it difficult to test the independent effect of each variable in a linear model. Thus, we tested whether our response variables were associated with time between clearcutting and fire, openness, and distance to fire perimeter by pairwise correlations. Additionally, complex models with three predictors and interactions/nonlinearity are not feasible given our sample size ($N = 25$). Pearson correlations were used for diversity indices (species richness and Shannon true diversity sensu Jost [2006]) and total plant cover, and we used Spearman rank correlations for testing individual species. To describe the general plant species composition we performed a nonmetric multidimensional scaling (NMDS) analysis on the stand-level mean frequencies of all vascular plants. The NMDS was performed with the R package *vegan* (Oksanen et al. 2013) using the Bray–Curtis dissimilarity index and three dimensions (stress = 0.12). Significant relationships between species composition and explanatory variables were assessed with multivariate ANOVA (function *adonis2* in *vegan*;

Oksanen et al. 2013). We used the stand-level mean frequency (i.e., based on all subplots in a stand), and tested all species occurring in at least eight stands (15 vascular plants and four bryophytes in total; Appendix S2: Table S1).

To test the association between plant traits (diaspore size log-transformed) and the explanatory variables we calculated community-weighted mean trait values (CWM [Sonnier et al. 2010]) for each trait and stand. We then correlated CWM values against our three explanatory variables using Pearson correlation.

RESULTS

A total of 41 vascular plant and six bryophyte species were found in the 25 stands (Appendix S2: Table S1). The most common species were the vascular plants *Chamaenerion angustifolium* (recorded in 78% of the plots), *Populus tremula* (42%), *Vaccinium myrtillus* (25%), and *Betula pendula* (24%), and the bryophytes *Ceratodon purpureus* (79%), *Polytrichum juniperinum* (76%), and *P. commune* (52%).

There was a significant negative correlation between species richness and the time between clearcutting and fire ($P = 0.02$; Table 1). Shannon true diversity also decreased with the time but the support was weak ($P = 0.06$). No correlations between diversity indices and canopy openness were detected ($P > 0.10$), and distance to fire perimeter had no clear relationship to any of the two diversity measures ($P > 0.3$). There was weak support that total cover of vascular plants decreased with time between clearcutting and fire ($P = 0.07$) and canopy openness ($P = 0.09$; Table 1), and no such

TABLE 1. The correlation between (1) species diversity measures, (2) plant cover, (3) individual species (occurring in >8 stands; see Appendix S2: Table S1), and (4) community weighted trait means (CWM), and the explanatory variables: time between clearcutting and fire, canopy openness, and distance to fire perimeter. $N = 25$.

	Time between clearcutting and fire	Canopy openness	Distance
Species richness	$r = -0.48, P = 0.015$	$r = 0.32, P = 0.108$	$r = -0.11, P = 0.593$
Shannon true diversity	$r = -0.38, P = 0.061$	$r = 0.31, P = 0.131$	$r = -0.21, P = 0.317$
Total bryophyte cover	$r = 0.15, P = 0.484$	$r = -0.06, P = 0.760$	$r = 0.42, P = 0.036$
Total vascular plant cover	$r = -0.37, P = 0.066$	$r = 0.35, P = 0.089$	$r = -0.24, P = 0.244$
<i>Betula pendula</i>	$\rho = -0.50, P = 0.011$	$\rho = 0.54, P = 0.005$	$\rho = 0.18, P = 0.390$
<i>Calamagrostis arundinacea</i>	$\rho = -0.44, P = 0.026$	$\rho = 0.10, P = 0.623$	$\rho = -0.16, P = 0.433$
<i>Calluna vulgaris</i>	$\rho = -0.54, P = 0.005$	$\rho = 0.52, P = 0.007$	$\rho = 0.12, P = 0.554$
<i>Carex pilulifera</i>	$\rho = -0.37, P = 0.067$	$\rho = -0.03, P = 0.878$	$\rho = 0.06, P = 0.765$
<i>Deschampsia flexuosa</i>	$\rho = -0.52, P = 0.007$	$\rho = 0.37, P = 0.071$	$\rho = 0.03, P = 0.905$
<i>Rubus idaeus</i>	$\rho = -0.37, P = 0.065$	$\rho = 0.31, P = 0.126$	$\rho = -0.27, P = 0.194$
<i>Salix caprea</i>	$\rho = 0.25, P = 0.223$	$\rho = -0.12, P = 0.577$	$\rho = -0.41, P = 0.042$
<i>Vaccinium myrtillus</i>	$\rho = 0.80, P < 0.001$	$\rho = -0.65, P < 0.001$	$\rho = -0.22, P = 0.293$
<i>Pleurozium schreberi</i>	$\rho = 0.44, P = 0.027$	$\rho = -0.43, P = 0.031$	$\rho = 0.41, P = 0.043$
<i>Polytrichum commune</i>	$\rho = 0.41, P = 0.041$	$\rho = -0.51, P = 0.010$	$\rho = 0.28, P = 0.174$
Diaspore mass	$r = 0.40, P = 0.045$	$r = -0.35, P = 0.083$	$r = -0.24, P = 0.246$
Root buds	$r = 0.63, P < 0.001$	$r = -0.30, P = 0.142$	$r = -0.27, P = 0.182$
Seed longevity	$r = -0.65, P < 0.001$	$r = 0.52, P = 0.008$	$r = 0.20, P = 0.337$

Notes: For individual species, we used Spearman rank correlation, and remaining correlations were assessed with Pearson correlation. Only species and traits that have any correlation with a P value < 0.1 are shown. Significant P values (< 0.05) in bold.

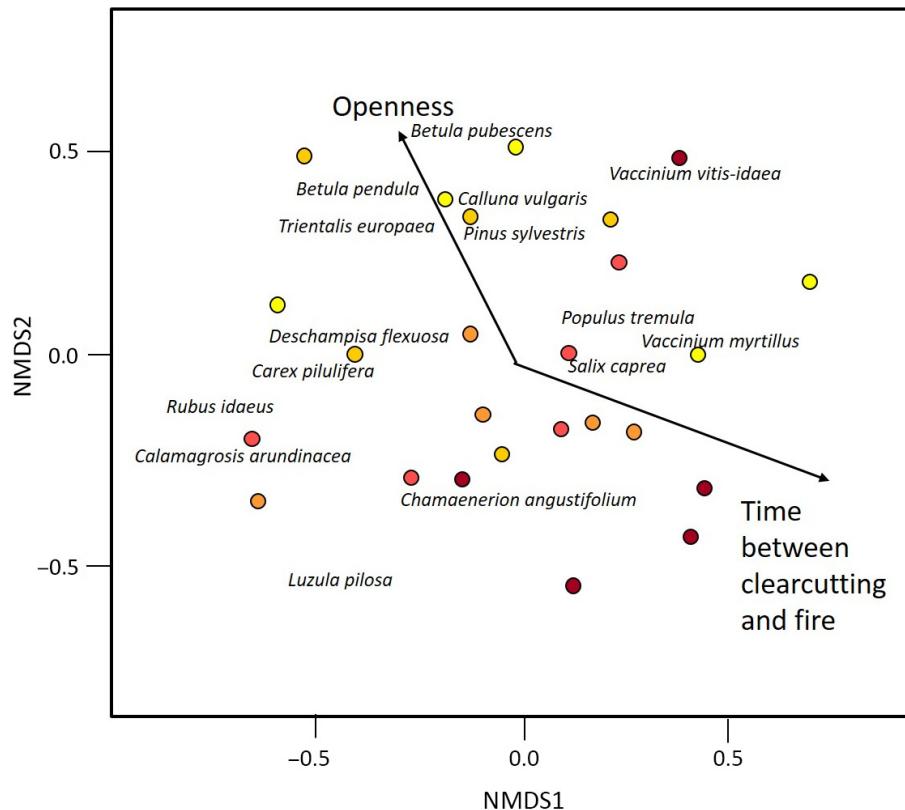


FIG. 2. Nonmetric multidimensional scaling (NMDS) for vascular plants in relation to time between clearcutting and fire, and canopy openness. All species were included but only species present in >5 stands are shown. For illustration, prefire forest ages of stands are separated into age classes (yellow 0–20 yr, ...dark red >80 yr), although the analysis was performed using a continuous age scale. Both time between clearcutting and fire ($F = 5.03$, $R^2 = 0.17$, $P < 0.001$), and canopy openness ($F = 2.38$, $R^2 = 0.08$, $P = 0.016$) significantly explained the species composition according to the multivariate ANOVA. $N = 25$.

trends were supported for total bryophyte cover ($P = 0.48$). Bryophyte cover correlated positively with distance to fire perimeter ($P = 0.04$; Table 1).

Species composition varied along the largely opposite gradients of openness and time between clearcutting and fire, according to the NMDS (Fig. 2). The stand-level community composition of vascular plants was explained by these two variables and distance to perimeter had no effect, based on the multivariate ANOVA. Time between clearcutting and fire explained roughly twice the amount of variation compared to canopy openness. Seven species showed significant correlations with time between clearcutting and fire, including five vascular plants and two bryophytes ($P < 0.04$), with the strongest relation for *V. myrtillus* clearly increasing with time between clearcutting and fire ($P < 0.001$ in Table 1, Appendix S2; Fig. S3). Three vascular plant species and two bryophytes had a significant correlation to openness ($P < 0.03$), and only one vascular plant species and one bryophyte correlated with distance to perimeter ($P < 0.05$; Table 1).

The community weighted traits means (CWM) of three traits had significant correlations with time between clearcutting and fire: positive for diaspore mass

and root buds ($P < 0.05$), and negative for seed longevity ($P = 0.001$; Table 1). The positive relation for root buds remained strong also after excluding the dominant *V. myrtillus* ($r = 0.55$, $P = 0.004$). Canopy openness showed a positive correlation with seed longevity ($P = 0.008$), and distance to fire perimeter did not correlate with any of the CWMs. Specific leaf area did not correlate with any of the three explanatory variables.

DISCUSSION

Our results support the interpretation that plant species remaining as legacies after a disturbance (here: fire) drive vegetation composition, and that the strength of this imprint depends on the time since a previous disturbance (here: clearcutting). Thus, the temporality of multiple disturbances is essential for understanding how one disturbance modifies ecological resilience to another disturbance. A key finding of our study is that postfire succession originates from the legacies of previous successions. Decreasing time between disturbances has the important implication that late-seral stages become more difficult to reach.

The results were largely consistent with our predictions (Fig. 1). First, the composition of vascular plants varied with time between the fire and the preceding clearcutting disturbance (NMDS; Fig. 2, Table 1), most marked for the dwarf shrub *V. myrtillus* and its associated trait of root buds, which were clearly more common in forests clearcut longer ago. The strong signal of this late-successional legacy species is noteworthy because its rhizomes evidently survived also under high fire severity. Second, shading of standing burned trees also affected species composition. Thus, both types of ecological legacies, namely forest-floor species and dead trees, were important drivers of vegetation response to two disturbances occurring at an interval of between 0 and 123 yr. The positive correlation between light and time between clearcutting and fire makes inferences of respective factor difficult. Still the considerably lower explanatory power of light (only about half of the amount of variation explained compared to time between clearcutting and fire) points to a stronger role for time between disturbances. The lack of a positive correlation between cover of vascular plants and light availability in our data was somewhat surprising, because such a relationship is a general phenomenon with much empirical support (e.g., Niinemets 2010). Likely, light variation among stands with different disturbance intervals was too small to have an effect; the youngest forests had only approximately 20% larger canopy openness than the oldest (Appendix S2: Fig. S1). Thorn et al. (2020) also found limited effects on microclimate from standing dead trees.

Our data allow assessment of resilience because we held the severity of the second disturbance constant by sampling sites with high burn severity, excluding possible confoundment with disturbance chain effects addressing resistance. To estimate the resilience of forest-floor vegetation, here defined as the deviance of the postfire state (5 yr) from the prefire state, and the role of species legacies in this process, two types of information are needed. First, knowledge on the vegetation in burned forests and unburned forests of similar age following clearcutting is needed. Second, insights on the survival capacity of above- and belowground tissue at severe fire are necessary, that is, how traits relate to fire disturbance. Lacking vegetation data preceding the fire, information from other studies on understory vegetation in unburned north European production forests dominated by *P. sylvestris* can give good guidance. Swedish National Forest Inventory data show that for unburned even-aged forests *C. angustifolium* is a strong indicator of recently harvested stands, grasses are common at intermediate ages, and dwarf shrubs dominate in the oldest forest (Widenfalk and Weslien 2009). In our data, we see that such a postharvest successional pattern may remain even after a subsequent severe fire, with a peak of the dominant grass *Deschampsia flexuosa* at intermediate disturbance interval and the dwarf shrub *V. myrtillus* having >20 times higher plot frequency in the stands clearcut longer ago (Appendix S2, Table S1). We judge that the

resilience of *V. myrtillus* is stronger than that of *D. flexuosa*, because burning experiments show that belowground vegetative tissue of *V. myrtillus* survives fire better than the superficially distributed rhizomes of *D. flexuosa* (Schimmel and Granström 1996). Overall, species forming root buds showed strong affinity to long disturbance interval in our trait analysis (Table 1), a pattern remaining also after excluding the dominant *V. myrtillus*, pointing to a trait-response including several late-successional species. Our trait analysis also supported the hypothesis that seed longevity decreases with time since disturbance, suggesting that seeds of early-successional species are more persistent than seeds of late-successional species, which is a common pattern for many habitats (e.g., Bekker et al. [2000]). Diaspore mass appears to be a key factor, as small seeds generally have greater longevity than large seeds (Thompson 2000). The early-successional dominant herb *C. angustifolium* is an exception to the similarity of pre- and postfire vegetation because it was the most common vascular plant species overall, including stands clearcut longest ago, and thus evidently is favored by fire, as also shown by Johansson et al. (2020) in the same study region. *Chamaenerion angustifolium* most likely dispersed to the area after the fire, because it does not survive fire either as seeds or rhizomes (Schimmel and Granström 1996).

Earlier studies have found that resilience may vary with environmental conditions, for instance, with wet forests being more resilient than dry ones (e.g., Day et al. [2020]), but we are not aware of other studies that include a long time gradient to analyze resilience in relation to disturbance interval. To advance the understanding further, it is essential to explore if effects of disturbance interval are linear or nonlinear, for example, if there are time thresholds with disproportionately more late-successional species.

Our results have clear implications for ecosystem dynamics under global change, with more frequent and severe disturbances (Seidl et al. 2020). Late-successional stages risk decreasing because of repeated natural disturbances pushing back species communities to earlier stages, reinforced by anthropogenic disturbances. This can have negative consequences for biodiversity conservation, as many species of conservation interest are associated with late-successional stages (Paillet et al. 2010), as well as for ecosystem processes. Effects of more frequent disturbances are also seen in other studies, such as Turner et al. (2019), who found fires with shorter intervals to reduce tree recovery and erode resilience. Ecosystem shifts to other forest types, or from forests to nonforest, are also likely (Coop et al. 2020). An example of possible increased anthropogenic–natural disturbance interactions on forests under the clearcutting system in our study region is the increasingly shorter rotation times leading to younger even-aged forests (Roberge et al. 2016). This development, coupled with more severe and frequent fires in the future (Prichard et al. 2017), may aggravate negative ecological impacts.

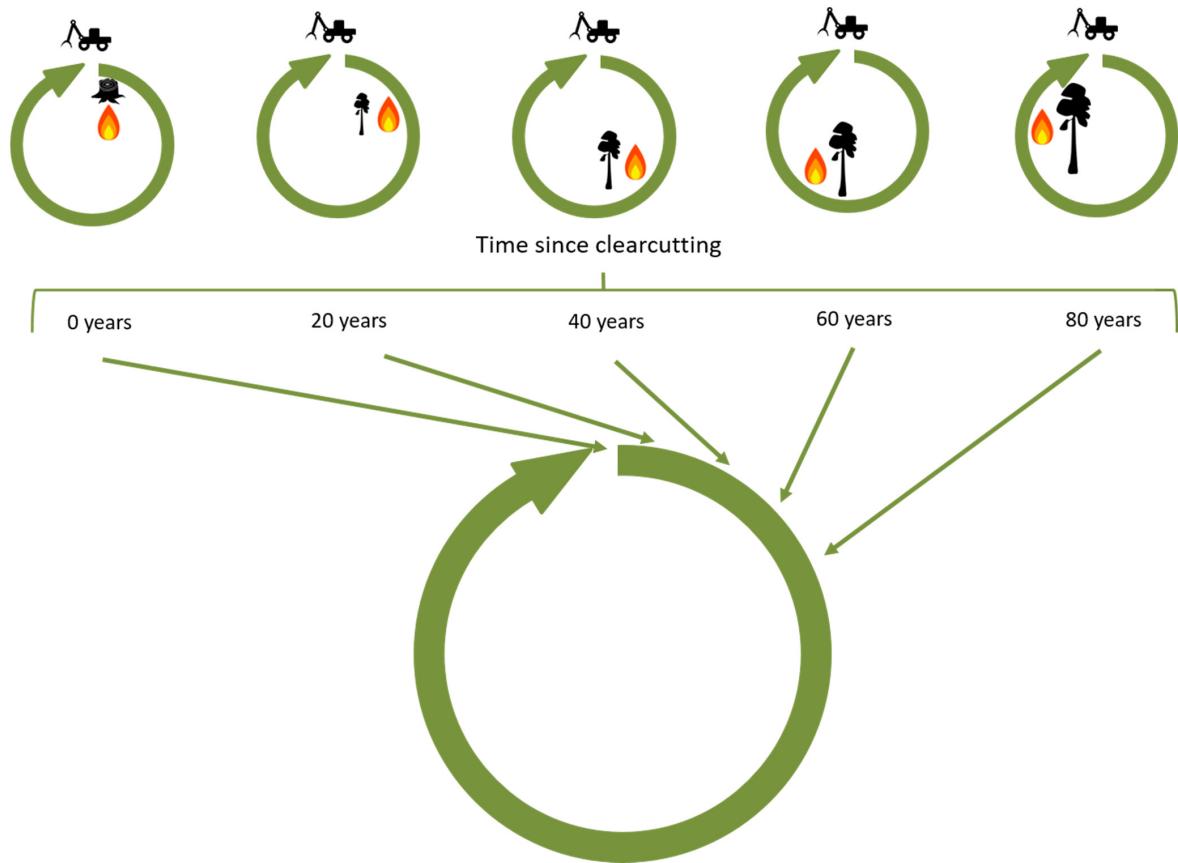


FIG. 3. Schematic representation of the key finding in the study, that time since a previous disturbance modulates the position in succession following a second disturbance. Longer times since a preceding disturbance (in this case clearcutting) promote a more advanced successional stage following a second disturbance (in this case fire). More specifically, for our study system, forest-floor vegetation of old even-aged production forests had developed further in succession than young forests, due to dwarf-shrub legacy species. An important implication of our results is that increased disturbance frequency in the future will shorten successional sequences and hereby reduce late-successional stages. We suggest that increased dominance of early-seral stages is probably a general pattern, applicable to other forest types and ecosystems.

In conclusion, our study improves understanding of the pathways on how disturbances interact to modify resilience, and contributes to a necessary improved evidence base for disturbance management. The results strongly point to a fundamental role of disturbance interval affecting the starting point of succession, conceptually illustrated in Fig. 3. Because successional age is significantly linked to trait-space distribution of forest forest-floor plant species (Kumordzi et al. 2015), we propose that the time effect revealed in this study could represent a general pattern also for other forest types, and likely also valid for other types of ecosystems and disturbances.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3439/supinfo>

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Data (Gustafsson et al. 2021) are available from The Swedish National Data Service: <https://doi.org/10.5878/gxm0-cp19>.