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Research article

Resource quantity and heterogeneity drive successional plant diversity in managed and unmanaged boreal forests

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The understory vegetation of boreal forests plays a crucial role in maintaining biodiversity by creating habitats, supplying food resources, and regulating microclimate and soil conditions. This essential layer is frequently affected by disturbances such as forest fires and clear-cutting, which significantly alter understory communities and the ecosystem resource availability and heterogeneity. This study aimed to understand how these disturbances influence the spatial and temporal dynamics of key ecosystem resources, and subsequently the patterns of understory diversity. We analyzed and compared understory vegetation diversity in a rotational management chronosequence and an unmanaged fire chronosequence of Scots pine *Pinus sylvestris* forests across northern Sweden. We assessed the relationship of above- and belowground resource availability and heterogeneity with alpha and beta diversity using generalized additive models and multivariate analyses. We found that belowground resource availability (especially inorganic nitrogen) and aboveground resource heterogeneity (especially variation in forest structural complexity) were most strongly positively correlated with alpha and beta diversity, varying across successional stages. In early stages (0–60 years), high availability of belowground resources and aboveground heterogeneity was associated with high alpha and beta diversity. In mid-stages (100–200 years), reduced belowground resource availability and aboveground heterogeneity was linked to lower diversity. In late stages (> 250 years, which only exists in the unmanaged fire chronosequence), increased aboveground heterogeneity associated with tree mortality was linked to a resurgence in alpha and beta diversity. These results highlight the necessity of maintaining a mosaic of stands with different disturbance regimes and successional stages, particularly early post-fire stands and late successional stands, which are currently much rarer on the landscape, to support biodiversity at the landscape level.

Keywords: Boreal forest, chronosequence, clear-cut, fire, forest structural complexity, understory diversity

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Introduction

Covering an area of 14.7 million km², boreal forests are the most expansive forest ecosystems on Earth (Hart and Chen 2006). While their tree layer is species poor compared to other biomes, they support high biodiversity of other organisms. A single stand can harbor up to 5000 species, predominantly fungi and arthropods, underscoring the complexity and ecological richness of these ecosystems (Kuuluvainen and Siitonen 2013). Boreal understory communities play a central role for this biodiversity because of their strong influence on the diversity of other taxa (Bokhorst et al. 2014, Fanin et al. 2018, Fanin et al. 2019). However, early post-fire and late-successional stands, which often harbor diverse understory communities, are becoming increasingly rare. Understanding how disturbances shape these successional stages is therefore essential for preserving biodiversity at the landscape level.

Boreal forests are frequently subjected to disturbance, notably forest fires and clear-cutting (Bergeron et al. 2002, Seedre et al. 2011). These disturbances significantly shape boreal understory vascular plant, bryophyte, and ground lichen communities, alter the availability and heterogeneity of resources, and promote a mosaic of landscapes with diverse stand ages and species compositions (Nilsson and Wardle 2005, Hart and Chen 2006, Gauthier et al. 2015, Kuuluvainen and Gauthier 2018). While fire has historically been the dominant form of disturbance in boreal forests, it is estimated that nearly two-thirds of the boreal forest worldwide is now under some form of forest management, with clear-cutting being the dominant practice in many regions (Gauthier et al. 2015). However, the drivers of changes in understory community composition following wildfire versus clear-cutting remain poorly investigated, which limits our understanding of the consequences of these different disturbance regimes for boreal forest diversity and ecosystem functioning.

Clear-cuts and fires can have different effects on the availability and heterogeneity of above- and belowground resources (Table 1), and subsequently may cause different changes in understory community composition and diversity. Clear-cutting in boreal forests results in an open canopy, maximizing light penetration. While light availability is greatly increased following clear-cutting, light heterogeneity is low due to the relatively even removal of the canopy, and other management activities that promote the development of a less complex, even-aged stand (Taylor et al. 2013). These changes may lead to a loss of various microhabitats and niches for different species. Forest fires, on the other hand, can partially eliminate the existing understory, and significantly increase light availability on the forest floor (Boyles and Aubrey 2006, Coop et al. 2010). While studies examining light heterogeneity post-fire are sparse, Cansler et al. (2018) and Martin et al. (2022) suggest that forest fires can enhance structural complexity. Variations in forest structural complexity, such as canopy layering and density, influence the understory microclimate and the availability of microhabitats, which may promote understory species diversity due to more variable conditions. These connections highlight the relevance of assessing three-dimensional structural metrics in studies focused on understory diversity (Majasalmi and Rautiainen 2020, Ehbrecht et al. 2021). Clear-cutting and fire can change the availability of belowground resources (Brais et al. 2000, Simard et al. 2001, Pykälä 2004, Hart and Chen 2006, Palviainen et al. 2014, Hume et al. 2016); further, the patchiness of wildfire may result in a more heterogeneous distribution of soil nutrients (Schaetzl et al. 1989).

Disturbance-induced changes in resource availability and heterogeneity significantly influence the composition and diversity of boreal understory communities, but it remains unresolved which factor is more critical (Bartels and Chen 2010). Some studies have suggested understory richness peaks in resource-rich environments, particularly when light and soil nutrients are high (Härdtle et al. 2003, Hart and Chen 2008, Reich et al. 2012, Kumar et al. 2018, Crispo et al. 2021), supporting Wright's resource quantity theory that high availability enables coexistence by supporting more

Table 1. Changes in resource availability and heterogeneity introduced by forest fires and clear-cutting.

Aspect	Forest fires	Clear-cutting	Reference(s)
Aboveground			
Light availability	Increases with significant spatial heterogeneity	Highly increases, but with much less spatial heterogeneity	Boyles and Aubrey (2006), Coop et al. (2010)
Forest structural complexity	Remains constant or increases	Highly decreases	Taylor et al. (2013), Cansler et al. (2018), Martin et al. (2022)
Belowground			
Nutrient release	Ash from burned organic matter releases phosphorus, calcium, magnesium into soil	Biomass removal may decrease immediate nutrient availability	Brais et al. (2000), Simard et al. (2001), Hart and Chen (2006), Palviainen et al. (2014), Hume et al. (2016)
Heterogeneity in nutrient concentrations	High, due to uneven burn patterns and deadwood decomposition	High, due to soil scarification and the patchy exposure of mineral soil	Pykälä (2004)
Stand level			
Physical structure alteration	Creates diverse microhabitats through tip-up mounds and exposed mineral soil	Soil disturbance and scarification create patchy environments with exposed mineral soil	Schaetzl et al. (1989)

individuals and facilitating diverse resource use (Wright 1983). Conversely, Grime (1979) contends that high resource availability can reduce alpha diversity by intensifying competition, while Tilman's resource heterogeneity theory proposes that spatial variation promotes coexistence through niche diversification (Tilman 1982). While these theories were originally developed for dominant vegetation layers, some studies have applied them to understory communities. In one such study, Gundale et al. (2011) showed that both the quantity and heterogeneity of belowground resources (e.g. mineral and organic nutrients; NH_4^+, amino N, and P) declined in late successional stages in unmanaged forests subjected to wildfire, indicating that these properties positively co-vary. These findings emphasize the need for further understanding of how changes in resource availability and heterogeneity impact understory diversity and succession.

As forests recover from disturbance, above- and belowground resource availability and heterogeneity are subject to change. Following an initial increase in availability, resources generally decline as tree colonization and growth increases competition for light and soil resources. This shift is accompanied by a gradual nutrient depletion as the forest matures (Hart and Chen 2006). While forest development after disturbance may reduce resource availability, eventual tree mortality may increase heterogeneity not only in light but also in soil nutrients during later stages of succession (Nilsson and Wardle 2005). However, most stands are harvested before reaching these late-successional phases, limiting the opportunity for canopy gaps and natural mortality to foster distinct understory communities.

To investigate the underlying mechanisms that control diversity during post-disturbance forest development, we utilized a study system consisting of two chronosequences: an unmanaged fire chronosequence (F; 4–375 years since fire), which includes unmanaged forests subjected to wildfire, and a rotational management chronosequence (M; 1–109 years since harvest), consisting of forest stands that have been managed through even-aged forestry with each stand having undergone clear-cutting. We tested the following hypotheses:

(1) we hypothesized that disturbances will initially increase both above- and belowground resource availability and belowground resource heterogeneity. However, while we expect forest fires to enhance aboveground heterogeneity due to their patchy nature, we anticipate clear-cutting will reduce it. Resource availability and heterogeneity will generally decrease with time since disturbance. However, very old forest stands (> 200 years) will exhibit increasing aboveground resource availability and heterogeneity due to increased natural tree mortality.

(2) we hypothesize that stand-level understory alpha and beta diversity will track changes in above- and belowground resource quantity and heterogeneity. Specifically, stand-level alpha and beta diversity will be highest during the post-disturbance colonization phase, especially after fire, where both resource quantity and heterogeneity will increase. Further, alpha and beta diversity will decline during stand development. Finally, for the F chronosequence, we predict that alpha and beta diversity will eventually increase again (> 200 years), due to an increase in aboveground resource availability and heterogeneity (Hypothesis 1).

(3) we hypothesize that immediately following disturbance, understory communities in the M chronosequence and F chronosequence will have dissimilar compositions due to the varying disturbance regimes. Forests within the F chronosequence, influenced by the variable severity of wildfires, will display greater variability in understory composition compared to those within the M chronosequence. Over time, we predict communities will converge, regardless of initial disturbance. However, we anticipate that unique communities will develop in very old forests.

In combination, these hypotheses aim to dissect the dynamics of resource availability, heterogeneity, and understory diversity over time, following distinct types of disturbance in boreal forests. This will enhance our understanding of how different disturbance and management regimes influence successional trajectories and their contribution to regional biodiversity.

Material and methods

Our study was conducted in boreal Scots pine (*Pinus sylvestris*) forests in northern Sweden (Fig. 1a). We employed a chronosequence approach (i.e. a space for time substitution), where stands of varying time since disturbance were identified to represent the temporal development of forests (Walker et al. 2010). This method has been widely used in ecological studies to examine forest dynamics over time (Bergeron 2000, Wardle et al. 2005, Stuiver et al. 2015, Mack et al. 2021). A total of 36 stands were selected, evenly divided between two chronosequence types (Fig. 1b), an M chronosequence and an F chronosequence. The stands spanned the entire age range of managed and unmanaged forests typically found in northern Sweden. In the M chronosequence, a range of even-aged forest management practices has been applied, with clear-cutting conducted between 1 and 109 years ago, accompanied by soil scarification, planting, and typically 2–3 thinning operations. In the F chronosequence, stands were subjected to wildfire between 4 and 375 years ago. While there is evidence of historical selective logging in the older unmanaged stands (> 200 years), there has been no active mechanized forest management before or after the most recent fire event. Two of the 18 unmanaged fire stands (F5 and F28) were subjected to prescribed fire instead of wildfire. They were included because there were few wildfire stands in these ages, and because fire-induced tree mortality at these stands fell within the range of the other recent wildfire stands included in the study. Collectively, the fires encompass the entire spectrum of fire severity observed in Swedish forests, ranging from non-stand-replacing ground fires, which primarily affect the soil organic layer, to stand-replacing wildfires that cause the regeneration of an entirely new stand (Eckdahl et al. 2022, 2023, Pérez-Izquierdo et al. 2023).

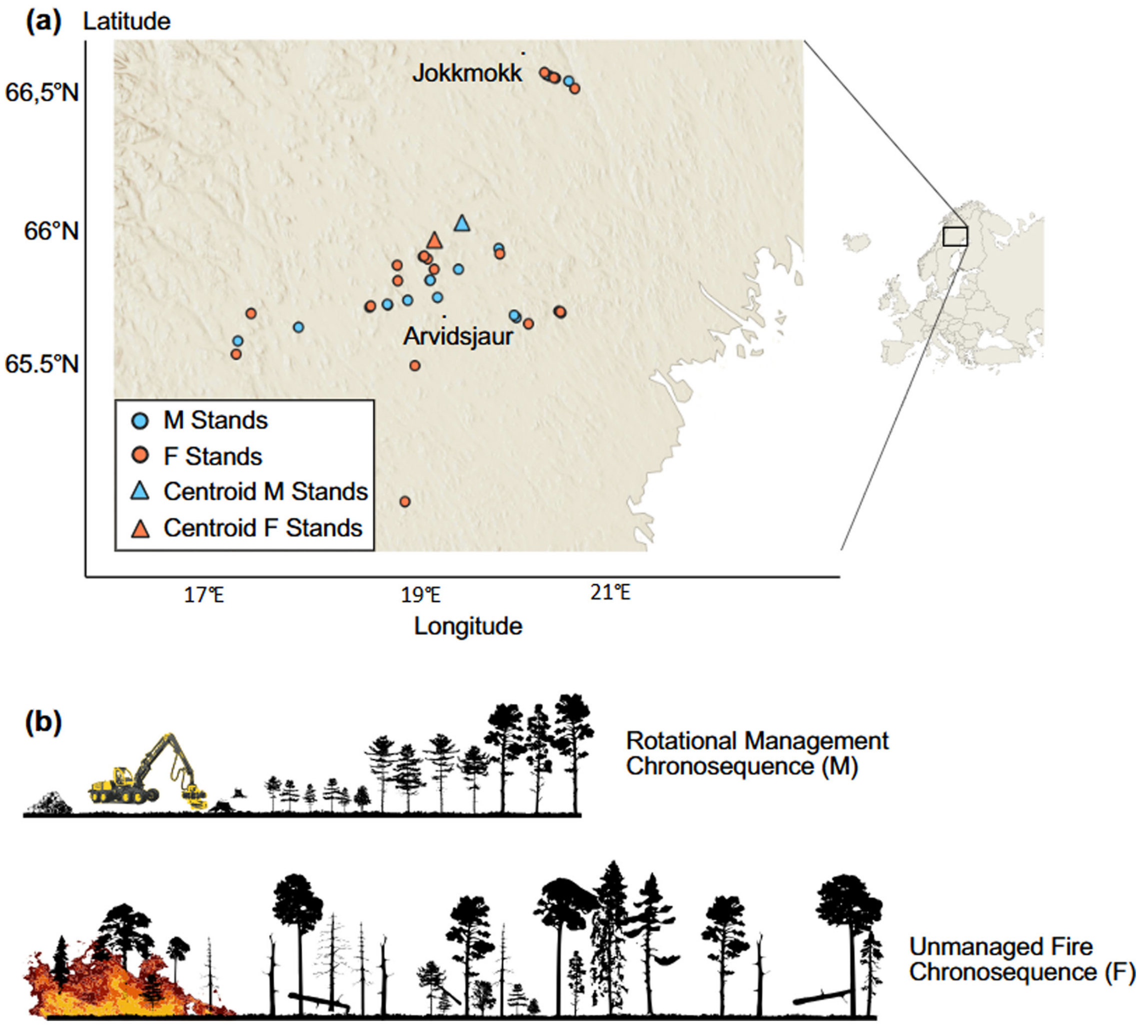


Figure 1. Overview of study sites in boreal pine (*Pinus silvestris*) forests of northern Sweden. (a) distribution of stands in the rotational management chronosequence (M, blue circles) and unmanaged fire chronosequence (F, red circles). Blue and red triangles indicate the geographic centroids of the M and F chronosequences, respectively. Map created using QGIS software (QGIS.org 2024) and the 'Esri Topo' layer (Esri 2024). (b) schematic overview of the two chronosequences. The x-axis represents time since disturbance, illustrating the even-aged stand development in the M chronosequence and the uneven-aged structure with more deadwood in the F chronosequence.

Stand selection

We utilized a forest inventory database provided by Sveaskog AB to identify candidate stands dominated by *Pinus sylvestris* under mesic conditions. Field surveys confirmed mesic conditions through specific understory vegetation and verified historical fire events with visible fire scars and dendrochronological analysis. Stands for both the M and F chronosequences were selected and geographically clustered to ensure comparability and minimal environmental variation. To confirm that our selected sites had no inherent environmental differences between chronosequence types or with time since disturbance, we compared abiotic site factors using principal component analysis (PCA), including geographic longitude, latitude, average summer temperature, summer precipitation, mean daily radiation, texture, and stoniness of the soil. We further assessed tree basal area of different species. Detailed methodologies and additional data are available in the Supporting information.

Vegetation metrics

Fieldwork was conducted from June to September 2023. For the vegetation survey, we installed 20 subplots, each with an area of 0.5 m², in each stand. These subplots were arranged in a 5 × 4 grid, spaced 10 m apart both horizontally and vertically. The grid was oriented with rows running west–east and columns south–north, with the center of the grid aligning with the center of the stand. To estimate the cover of each species in each subplot, we employed the point intersect method (Goodall 1952). We recorded the number of times a species of vascular plants, bryophytes, and ground lichens was intercepted by a metal pin that was downwardly projected 50 times in each subplot (Sundqvist et al. 2011, Gundale et al.

2012). Hence, multiple hits per pin per species were recorded when they occurred, allowing us to accurately account for the three-dimensional configuration of the vegetation.

Aboveground resources

To estimate light availability in the understory, we measured tree leaf area index (LAI) using a solariscope (Behling SOL 300, Wedemark, Germany). LAI represents the total leaf area per unit ground area and has an inverse relationship with light availability. We took vertically upward projected photographs at a height of 2 m in each subplot (Schleppi et al. 2007). Forest structural complexity was quantified using the box dimension (db) derived from fractal analysis of three-dimensional point clouds (Seidel 2018). The point clouds were obtained using a handheld mobile laser scanner (MLS, ZEB Horizon, GeoSLAM Ltd, UK) during leaf-on conditions in July and August 2023. See the Supporting information for further details on the scanning and data processing.

Belowground resources

To capture plant-available nutrients over one vegetation period, we installed one ion-exchange resin capsule (UNIBEST Inc., Kennewick, USA) in each of the 20 vegetation subplots per stand in June 2023. Capsules were inserted at a 45° angle at the interface between the mineral soil and organic surface layers within each subplot (Stuiver et al. 2015). They were collected and cleaned in September 2023, and the adsorbed nutrients were extracted with 1 M KCl. The extracts were analyzed using inductively coupled plasma optical emission spectroscopy (ICP-OES) on a flow injection analysis (FIA) by UNIBEST to determine concentrations of plant available nutrients (e.g. NH_4^+, NO_3^-, Ca_2^+).

For pH measurement, soil samples from the Oa horizon of the organic surface layers were taken directly adjacent to the vegetation subplots. Samples were measured using a 1:5 soil to water ratio, with readings obtained via pH electrode (Mettler Toledo SevenCompact pH meter S210).

Data preparation and analysis

All statistical analyses were conducted using R (www.r-project.org), RStudio (Rstudio Team, 2020), and the 'tidyverse' package (Wickham, 2017).

In this study, we developed four main resource indices to quantify and analyze the dynamics of ecosystem resources: aboveground resource availability (ARA), aboveground resource heterogeneity (ARH), belowground resource availability (BRA), and belowground resource heterogeneity (BRH). Availability indices (ARA and BRA) represent the mean levels of resources in a stand, while heterogeneity indices (ARH and BRH) measure the spatial variability of resources across it. Therefore, resource availability indices were calculated as the average of the mean values of normalized variables, while resource heterogeneity indices were calculated as the average of the coefficients of variation (CV) of the normalized variables. Light availability was defined as '1 – normalized LAI' to account for the inverse relationship. Aboveground resources comprise light availability and forest structural complexity (db). Belowground resources include total inorganic nitrogen (TIN), soil moisture, soil pH, and calcium (Ca^{2+}). All resource measurements were scaled using the min–max method to ensure a common scale from 0 to 1 according to Han et al. (2012). We checked for multicollinearity among the predictors (ARA, ARH, BRA, BRH, chronosequence type, and time since disturbance) using the *vif* function from the 'car' package (Fox and Weisberg 2019). We set a strict VIF threshold of three, beyond which predictors would have been excluded from our analyses.

We quantified alpha diversity using the Shannon diversity index, calculated for each stand based on species abundance data using the *diversity* function from the 'vegan' package. Beta diversity was calculated as the average pairwise Bray–Curtis dissimilarity between the 20 subplots within each stand, using the *vegdist* function from the 'vegan' package on species abundance data across subplots. We applied partial correlation analyses to assess the individual contributions of ARA, ARH, BRA, and BRH to alpha and beta diversity. Even when these individual variables exhibited p-values above 0.05, they were retained in the resource indices used in the generalized additive models to maintain ecological relevance and prevent overfitting.

We applied generalized additive models (GAM) to analyze alpha and beta diversity on the stand level using the 'mgcv' package (Wood 2011). Independent variables were time since disturbance, chronosequence type, and the resource indices ARA, ARH, BRA, and BRH. The time since disturbance variable was modeled as a smoothed term with spline functions, using the default $k=10$ basis functions. Chronosequence type was treated as a categorical variable, while ARA, ARH, BRA, and BRH were included as linear predictors. To identify the most parsimonious model, we used the *dredge* function from the 'MuMIn' package, using the maximum likelihood estimation method. To assess model robustness, we utilized the 'caret' package (Kuhn 2008) for 5-fold cross-validation, which allowed for systematic partitioning of the dataset to use each subset for both training and validation. This approach enabled us to evaluate the model's generalizability and predictive accuracy across different data splits. We quantified model performance by calculating the mean squared error (MSE) for each validation subset. The average MSE was then expressed as a percentage of the range of the response variable, providing a relative measure of prediction error. Residual diagnostics were conducted to verify model assumptions, including Q–Q plots for normality, assessing homogeneity of variance through residuals versus fitted values and scale-location plots, identifying outliers in histograms of residuals, and examining influence via observed versus fitted values plots.

Finally, we analyzed how the community composition of each stand contributed to gamma diversity (i.e. regional diversity, defined as the total community composition identified across all stands in our study). We did this by calculating a Bray–Curtis dissimilarity matrix between all 36 stands using abundance data to capture ecological distances. We then performed non-metric multidimensional scaling (NMDS) on the Bray–Curtis dissimilarity matrix values to visualize ecological patterns in two-dimensional space. We subsequently fit the resource indices (ARA, ARH, BRA, BRH) as well as the vectors for time and chronosequence type to the NMDS configuration and assessed their relationships using the *envfit* function from the 'vegan' package.

We applied hierarchical clustering with Ward's method on the stand level, using the Bray–Curtis dissimilarity matrix between stands. We used silhouette analysis and subsequent partial Mantel tests to find the optimal number of clusters. The cluster with the highest mean age was defined as late successional understory composition reference. We then performed indicator species analysis using the *multipatt* function from the 'indicspecies' package (De Cáceres and Legendre 2009) to identify species associated with different clusters of stands.

Results

Stand comparison

PCA of abiotic site factors (Supporting information) demonstrated substantial overlap in the environmental conditions of the two chronosequences. Basal area assessments confirmed a dominance of *Pinus sylvestris*, with *Picea abies* also present in some stands, and an insignificant or entirely absent share of deciduous broadleaf trees.

Resource availability and heterogeneity

Aboveground resource availability (ARA; Fig. 2a) was high initially after disturbance and decreased until 100–200 years in both chronosequences. The F chronosequence showed an increase after 200 years. Aboveground resource heterogeneity (ARH, Fig. 2b) was generally lower in the youngest M chronosequence stands than in the F chronosequence, except immediately after disturbance. Belowground resource availability (BRA, Fig. 2c) was initially high in both chronosequences, followed by a decline. In the F chronosequence, BRA leveled out after ~ 200 years. Belowground resource heterogeneity (BRH, Fig. 2d) started at a low level in both chronosequences and then increased, to a maximum at approximately 80 years in the M chronosequence. In unmanaged fire stands, BRH reached its maximum at approximately 140 years, after which it declined until ca 250 years, and then increased again.

Alpha and beta diversity

Our analysis of alpha diversity, as measured by the Shannon diversity index, revealed distinct trajectories between rotational management and unmanaged fire stands over time (Fig. 3a). In rotational management stands, observed alpha diversity commenced at a relatively high level immediately

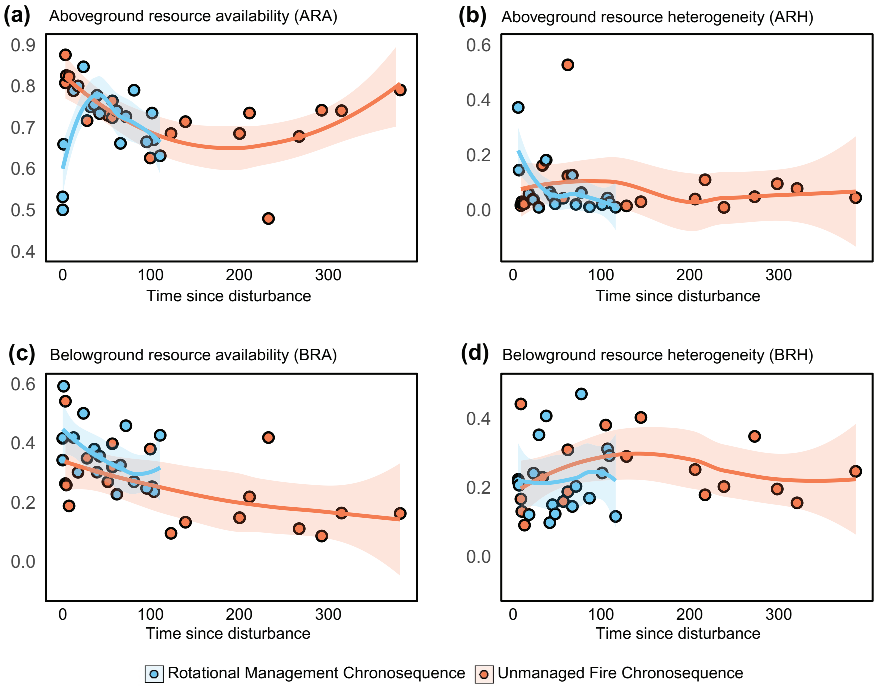
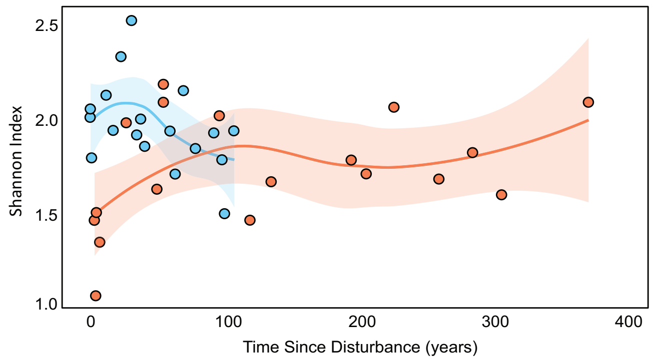


Figure 2. Trends in aboveground resource availability (ARA, (a)), aboveground resource heterogeneity (ARH, (b)), belowground resource availability (BRA, (c)), and belowground resource heterogeneity (BRH, (d)) over time since disturbance (fire versus clear-cutting) in two boreal forest chronosequences. Blue circles represent the rotational management chronosequence (M); red circles represent the unmanaged fire chronosequence (F). The smoothed lines are fitted using locally weighted scatterplot smoothing (LOESS), with shaded areas representing 95% confidence intervals. The x-axis represents time since disturbance, and the y-axis is scaled to normalized values without units.

(a) Alpha diversity



(b) Beta diversity

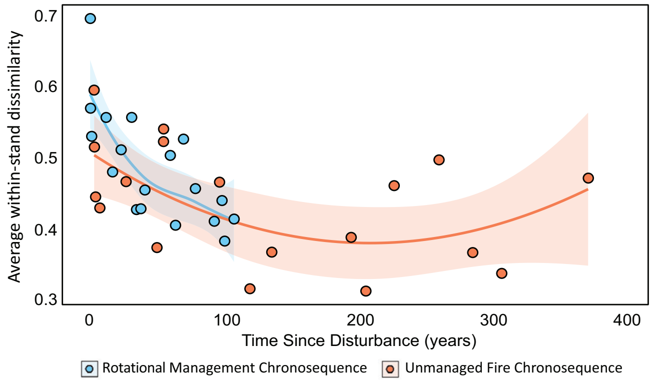


Figure 3. (a) Observed alpha (Shannon Index) and (b) beta diversity (average within-stand dissimilarity) over time since disturbance. Blue circles and blue smoothed line represent the rotational management chronosequence (M); red circles and red smoothed line represent the unmanaged fire chronosequence (F). The smoothed lines are fitted using locally weighted scatterplot smoothing (LOESS) to highlight general trends, with shaded areas representing 95% confidence intervals. The x-axis represents time since disturbance, and the y-axis represents Shannon Index (a) and average within-stand dissimilarity (b).

after disturbance compared to unmanaged fire stands, and peaked shortly after disturbance (~ 20 years). This peak was followed by a gradual decline, with the lowest level of alpha diversity observed towards the end of the chronosequence. In unmanaged fire stands, alpha diversity was lowest immediately after disturbance, after which it stabilized between 120 and 300 years post-disturbance.

In the generalized additive model (Fig. 4a–c), alpha diversity increased with higher belowground resource availability (estimate: 1.219, p-value: < 0.001) and aboveground resource heterogeneity (estimate: 0.843, p-value: 0.006; Fig. 4a). Partial correlation analysis (Supporting information) showed that no individual component of BRA or ARH was significantly related to alpha diversity. However, for BRA, total inorganic nitrogen and Ca^{2+} showed the highest positive relationships with alpha diversity, while for ARH, greater variability in light availability and forest structural complexity increased alpha diversity. Chronosequence type was also associated with alpha diversity (Fig. 4b); unmanaged fire stands had a lower alpha diversity than rotational management stands (estimate: −0.170, p-value: 0.033). When controlling the other variables, the smoothed term of time (Fig. 4c) was significant (p-value: 0.005, effective degrees of freedom: 3.615). Alpha diversity increased with time since disturbance. The model's fit was demonstrated by an R-squared of 0.572, with 65.3% of the deviance explained. The validation of the model by 5-fold cross-validation showed a mean squared error of 4.2%.

Our analysis of observed beta diversity, as measured by average Bray–Curtis dissimilarity (Fig. 3b) revealed that it was higher in rotational management stands than in unmanaged fire stands initially, but declined more quickly to follow the same trajectory after ~ 50 years. Unmanaged fire stands saw a further decrease with time since disturbance with a minimum at ca 200 years, but subsequently increased again towards the end of the chronosequence, almost returning to initial levels.

Our general additive model for beta diversity (Fig. 4d–f) showed that beta diversity increased with higher aboveground resource heterogeneity (estimate: 0.180; p-value: 0.001), as well as higher belowground resource availability (estimate: 0.217; p-value: 0.012; Fig. 4d). Partial correlation analysis (Supporting information) indicated that for the components of BRA, beta diversity was higher at sites with higher pH, and for ARH, it increased with greater variability in light availability and forest structural complexity. Beta diversity did not differ significantly between the two chronosequence types (Fig. 4e). However, the smooth function of time (Fig. 4f) was significant (p-value: 0.018; effective degrees of freedom: 2.164) and showed a reverse hump-shaped correlation with beta diversity. The model's fit was demonstrated by an R-squared of 0.591, with 63.9% of the deviance explained. The validation of the model by 5-fold cross-validation showed a mean squared error of 1%.

Contribution of stands to gamma diversity

The 'envfit' analysis on the NMDS configuration revealed significant influences of the resource indices ARH and BRA as well as time on the NMDS ordination. Notably, the BRA and ARH vectors were associated with younger stands. BRA was also aligned with species that have higher nutrient demands, such as *Carex* species and *Avenella flexuosa* (Fig. 5a), but not with stands dominated by low-nutrient demand species like *Cladonia* species.

The NMDS analysis, in combination with the cluster analysis (Fig. 5b), revealed that time since disturbance was associated with a reduced variability in NMDS1 and NMDS2. The largest variability along both axes was found among early successional stands (mean age 4–46 years; clusters 1–5), followed by mid-successional stands (mean age 40.1–107.0 years, clusters 6 and 7), and finally older stands (mean age 196 years, cluster 8). Cluster 8 was also associated with the time vector. In early successional stands, *Cladonia* species were significant in groups 2 and 3, contrasting with *Sphagnum* species and *Carex canescens* in group 5, which are found in moister and more nutrient-rich settings. The mid-successional stages

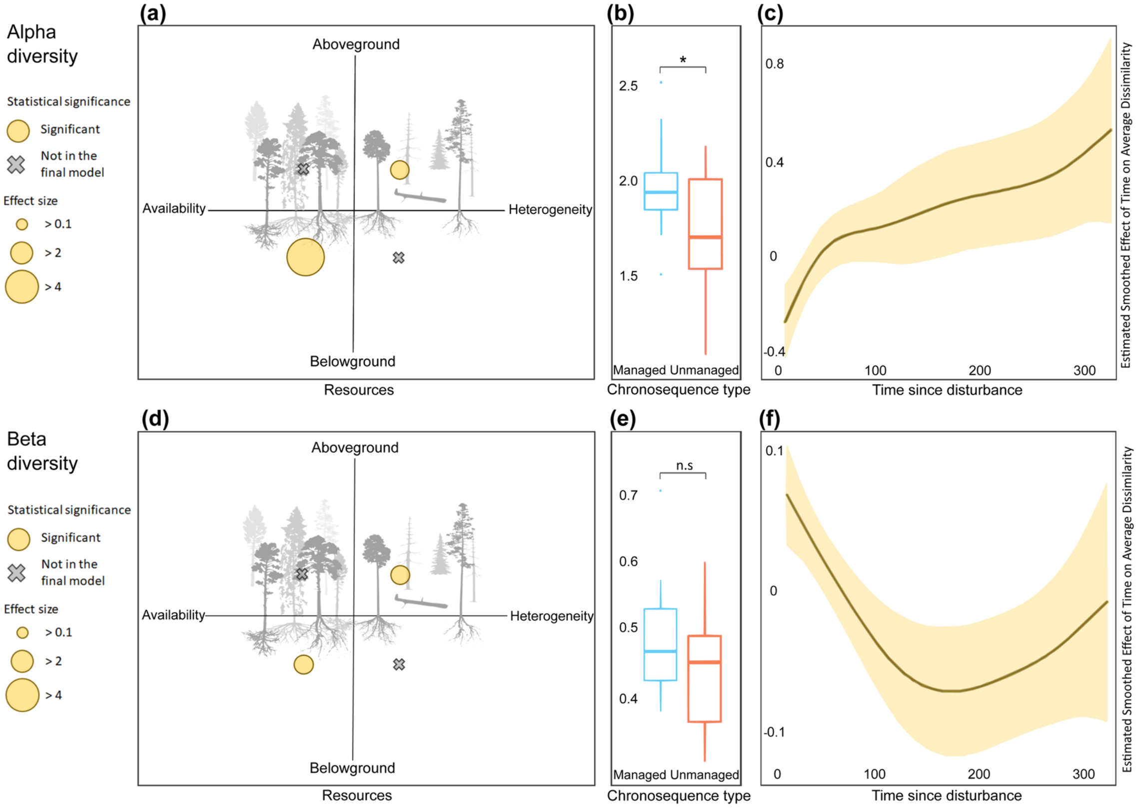


Figure 4. Results from the generalized additive models (GAM) for alpha (Shannon's Index, top row) and beta diversity (within-stand average dissimilarity; bottom row). (a) and (d) show the effect sizes of linear environmental variables: aboveground resource availability (ARA), aboveground resource heterogeneity (ARH), belowground resource availability (BRA), and belowground resource heterogeneity (BRH). The size of each circle indicates the effect size (t-value), and yellow color denotes statistical significance. (b) and (e) Boxplots demonstrate the influence of chronosequence type; the y-axis represents observed alpha and beta diversity, respectively. The rotational management chronosequence (M) is shown in blue and the unmanaged fire chronosequence (F) in red, with significant differences marked by an asterisk (*) and nonsignificant differences as 'n.s.' (not significant). (c) and (f) The estimated smoothed effect of time since disturbance on diversity is shown by a black line, with the yellow ribbon representing the 95% confidence interval. The y-axis represents the effect on alpha and beta diversity, respectively.

of clusters 6 and 7 were marked by the species *Trientalis europaea*, *Avenella flexuosa*, and *Linnea borealis*. In the late-successional stage (cluster 8), the indicator species included *Cladonia*, *Empetrum nigrum*, *Hylocomium splendens*, and *Orthocaulis floerkei*.

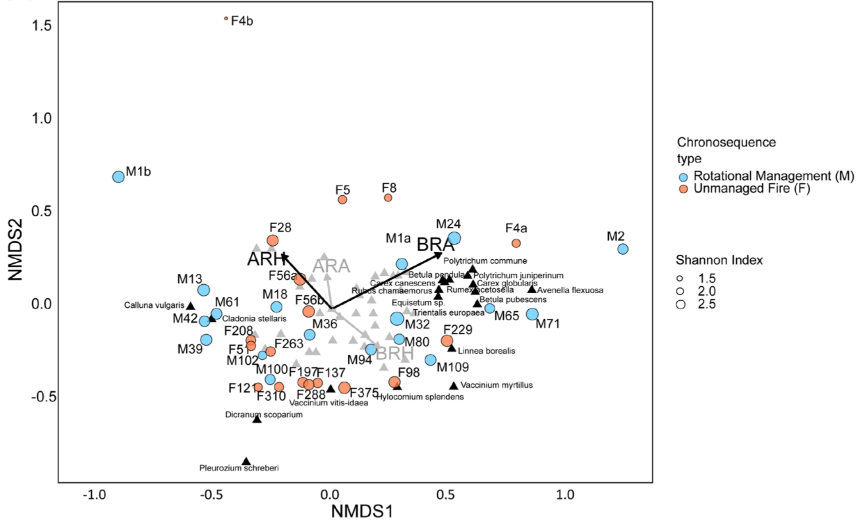
Discussion

Our results show that clear-cutting and wildfire lead to distinct above- and belowground resource dynamics across multiple successional stages, which in turn influence patterns of understory alpha and beta diversity. Early post-disturbance stands (0–60 years) exhibited higher belowground resource availability and structural heterogeneity, supporting greater diversity, whereas mid-successional forests (100–200 years) showed lower resource levels and reduced diversity. In late-successional stands (> 250 years), elevated aboveground heterogeneity associated with natural tree mortality again supported higher diversity. These findings emphasize the importance of maintaining a mosaic of disturbance regimes and successional stages, including the relatively rare early post-fire and very old stands, to sustain boreal forest biodiversity at larger spatial scales. We now discuss our data in reference to each of our hypotheses.

Resource availability and heterogeneity

Our findings partly support our first hypothesis, where we expected resource availability and heterogeneity to be highest immediately after disturbance and to decrease over time, with very old stands showing an increase in aboveground resource availability and heterogeneity. We identified three distinct stages in the successional dynamics of resource availability and heterogeneity post-disturbance (Fig. 2). In both chronosequences, the early stage (0–60 years) is marked by high availability, but low heterogeneity of above- and belowground resources, consistent with Hart and Chen (2006).

(a) Chronosequence type and Shannon Index



(b) Clusters and within-stand average dissimilarity

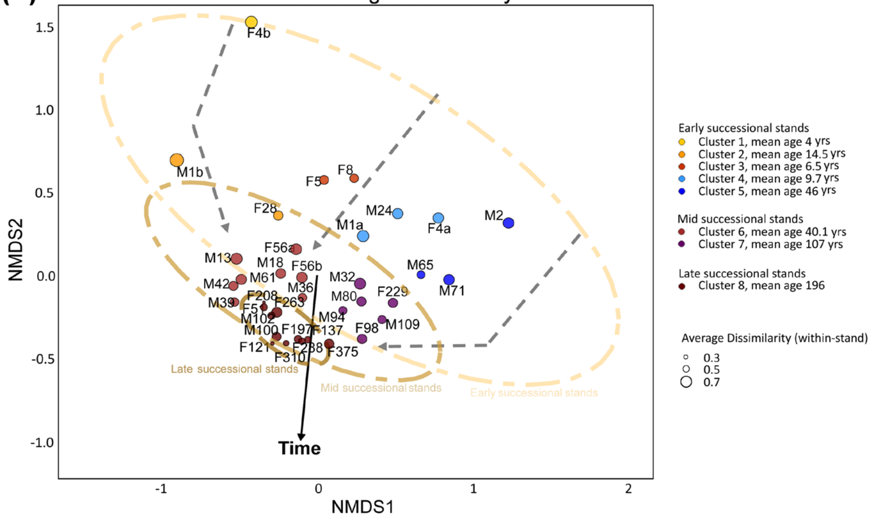


Figure 5. Non-metric multidimensional scaling (NMDS) ordination of the 36 sites based on their community composition, using the average Bray–Curtis dissimilarity index. (a) sites represented as points; size reflects alpha diversity (Shannon diversity index). Blue circles indicate stands of the rotational management chronosequence (M), red circles of the unmanaged fire chronosequence (F). The figure in the stand name represents time since disturbance in years. Understory species are shown as triangles, with significant ones in black and non-significant in gray, according to envfit analysis. Environmental vectors ARA, ARH, BRA, and BRH are shown as arrows, with significant ones in black and non-significant ones in grey. (b) the same sites, with the point size reflecting beta diversity (average within-site dissimilarity). The color of the points corresponds to clusters 1–8, derived from cluster analysis. The arrow represents the significant effect of time, as identified by envfit analysis. Ellipses denote successional stages, with yellow for young, light brown for mid-, and brown for late successional stages. Dashed arrows schematically trace the typical path of stands through succession, starting spread out and converging in the late successional stage.

The mid-stage (100–200 years) presents a pattern where above- and belowground resources are lowest, but belowground resource heterogeneity unexpectedly increased, contrasting with our initial hypothesis. The late stage (> 250 years) is characterized by a further decline in belowground resource availability, but an increase in aboveground availability and heterogeneity, which is likely due to increased tree mortality (Supporting information). The steady decline in belowground resource availability aligns with Gundale et al. (2011), who observed the lowest nutrient heterogeneity in late-successional forests.

Alpha diversity

Our alpha diversity data partially supported our second hypothesis, where we expected that diversity would be high after disturbance, decrease during the mid-stages of succession, and increase again in late succession. Our data showed that alpha diversity (Fig. 3a) increased after disturbance, peaking at approximately 20 years post-clear-cutting and 100 years post-wildfire, where it decreased to a minimum (100–200 years) before slightly increasing again in late stages (> 250 years). Belowground resource availability was a key driver for alpha diversity (Fig. 4a), notably TIN, Ca^{2+}, and soil moisture, in line with previous reports of key drivers of plant diversity (Beatty 1984, Hart and Chen 2006, Barbier et al. 2008, Wu et al. 2021). However, aboveground resource availability was not significantly correlated with alpha diversity, which contrasts with several studies (Bartels and Chen 2010, Kumar et al. 2018, Dormann et al. 2020, Crispo et al. 2021). Instead, and in line with findings by Reich et al. (2012) and the resource heterogeneity theory by Tilman (1982), aboveground resource heterogeneity (notably light variability) emerged as an important driver of alpha diversity following disturbance. Hence, these findings suggest that highly localized variability in light conditions support a broader diversity of micro-sites, and therefore biodiversity. The positive relationship between alpha diversity and belowground resource availability provides further support for the resource quantity theory (Wright 1983), and suggests that increased nutrient availability enhances habitat suitability for more species to co-exist. Thus, our results show that both aboveground resource heterogeneity and belowground resource availability are simultaneously important for driving changes in understory alpha diversity following disturbance in these forests. However, it remains to be explored whether these patterns are consistent within the wider boreal zone or across more diverse biomes, where additional environmental variables or larger species pools might alter community assembly processes.

We found that chronosequence type also significantly affected alpha diversity, with unmanaged fire stands showing a slightly lower mean than rotational management stands (Fig. 4b). This difference is likely due to several factors. First, unmanaged fire stands had a lower average nutrient availability due to very low nutrient status of the very old stands. Further, recently burned stands experience highly variable wildfire severity, meaning that fire-induced nutrient increases are not universal or uniform (Stark and Hart 1999, Knicker 2007, Ibanez et al. 2022). Second, soil scarification and sunlight exposure after clear-cut may stimulate higher nutrient availability. Third, a higher survival rate of trees in fires compared to clear-cuts (Supporting information) can lead to increased competition for resources, potentially limiting understory diversity. Therefore, the higher belowground resource availability in rotational management stands likely contributes to their greater alpha diversity compared to post-wildfire conditions (Chipman and Johnson 2002, Bartels and Chen 2010, Crispo et al. 2021).

When time since disturbance was isolated in our model (Fig. 4c), with resource availability, heterogeneity, and chronosequence type held constant, it exhibited a positive relationship with alpha diversity. The rapid early increase is presumably driven by colonization of newly available habitats post-disturbance (Connell and Slatyer 1977, Sousa 1984, Turner et al. 1998). The steady increase suggests that the arrival of new colonizers outweighs the loss of early colonizers (Huston 1979). Our model results did not show signs of alpha diversity saturating over time.

Beta diversity

We found that within-stand beta diversity (Fig. 3b) was highest immediately after disturbance, reached a minimum in the mid-stage of succession (100–200 years), and increased again in the later stages (> 250 years). This pattern was best explained by the combination of belowground resource availability and aboveground resource heterogeneity (Fig. 4d), notably by variation in forest structural complexity. These findings are consistent with our second hypothesis, as well as both the resource quantity theory (Wright 1983) and the resource heterogeneity theory (Tilman 1982). Our findings indicate that stands with high within-stand beta diversity tend to support a higher alpha diversity at the stand level, with two potential mechanisms at play. First, high variability in forest structural complexity seems to create a variety of microhabitats that facilitate within-stand species turnover. Second, the influence of belowground resource quantity on beta diversity may act indirectly. For example, higher soil resource availability may enhance the potential for a greater diversity of species to establish. However, the specific species composition in each micro-patch is likely influenced by which species colonize first (i.e. priority effects). These priority effects could result in patches with identical resources developing distinct species compositions, potentially driving significant within-stand species turnover over time (Davis et al. 2000, Fukami et al. 2005).

In contrast to alpha diversity, chronosequence type did not show a significant correlation with beta diversity (Fig. 4e). Our findings are therefore consistent with Reich et al. (2001), who reported similar species diversity in forest stands of comparable age and type, regardless of whether they originated from logging or wildfire. Additionally, Paillet et al. (2010), in a comprehensive meta-analysis across European forests, found that while species composition differed significantly between rotational management and unmanaged fire stands (discussed further in the section below), the differences in alpha and beta diversity were only marginally significant.

While controlling all other variables (resource availability and heterogeneity), the modeled effect of time since disturbance (Fig. 4f) showed a reverse hump-shaped relationship with beta diversity. We attribute the initial peak of beta diversity to the disruption of vegetation by disturbances such as clear-cutting combined with soil scarification in rotational management stands, and the patchy nature of fires in unmanaged fire stands (Lavoie and Mack 2012). The lowest beta diversity we observed in the mid-successional stage coincides with the lowest levels of belowground resource availability and aboveground resource heterogeneity. During this phase, the forest canopy is closed, leading to both high competition for resources and fewer ecological niches (Hart and Chen 2006). Further, the increase of beta diversity in the late stages of succession is accompanied by a resurgence in aboveground resource heterogeneity. This suggests that small-scale disturbances, caused by tree mortality (Supporting information), are key in driving beta diversity in late successional forests (Beatty 1984, Schaetzl et al. 1989, Goldblum 1997).

Contribution to gamma diversity

We predicted that post-clear-cut and post-fire understory communities would show distinct compositions, with a greater variability immediately after disturbance, and converge over time. Contrary to our third hypothesis, our analysis did not reveal distinct communities for the different disturbance types (Fig. 5b). Instead, the understory species compositions overlapped significantly across both types of disturbance throughout all successional stages. Furthermore, the data did not reveal a greater variability of post-fire compositions than post-clear-cut. However, our results showed broad variability in the community composition of younger stands in general, indicating an important contribution of young post-disturbance stands to gamma diversity (Fig. 5b). Consistent with our third hypothesis, older stands were more closely clustered than young stands, demonstrating convergence and uniqueness in understory communities over time. Despite not showing distinct communities immediately after disturbance, our findings demonstrate how the different disturbance regimes indirectly influence gamma diversity (i.e. regional diversity). This is primarily due to an increase in alpha and beta diversity in late successional unmanaged fire stands, and enhanced species turnover across stands at different successional stages. Since managed forests generally have a rotation period of approximately 100 years or less in this region, our findings suggest that longer disturbance interval periods (e.g. such as longer harvest intervals), would lead to enhanced diversity on a landscape scale by promoting unique late-successional communities, regardless of whether the initial disturbance was due to clear-cutting or wildfire.

Considering the regional diversity of boreal forests, all stages of succession appear to make an important contribution, but early post-fire stands and late successional stands are particularly rare (Kuuluvainen and Gauthier 2018), which limits their overall contribution to landscape-scale diversity. Specifically, in Sweden, of the remaining 1.673 million hectares of boreal forest predating the year 1880 (Roberge 2023), 1.4% are being clear-cut each year. If the current rate of cutting remained constant, all unprotected older forests would be clear-cut by approximately 2073 (Ahlström et al. 2022). Moreover, the formation of young post-fire stands occurs over a relatively small area, with only approximately 1656 hectares of Swedish boreal forest affected by fire annually (Sjöström and Granström 2020). This underscores the ecological importance of these types of forests to promote biodiversity and ecosystem functioning in the Nordic region (Kuuluvainen and Gauthier 2018).

Conclusion

Our study across northern Swedish boreal forests has several implications. First, we found that stand-level alpha and beta diversity are driven by high belowground resource availability immediately after disturbance; while high aboveground resource heterogeneity becomes important in late stages of succession. This indicates that mechanistic theories focused on resource availability (Wright 1983) and heterogeneity (Tilman 1982) both appear to be correct in particular contexts, and are important for explaining the understory dynamics through time. Second, our results demonstrate that time since disturbance has a stronger effect on vegetation alpha and beta diversity than the type of disturbance itself. This indicates that human impacts on within-stand diversity not only depend on the intensity and type of disturbance, but also the intervals between disturbances. Thus, these data are relevant for understanding the consequences of shortened disturbance intervals on stand level diversity. Finally, our study also revealed how different successional stages and disturbance types contribute to regional diversity (gamma diversity). Here, unique communities emerge immediately after both wildfire and clear-cut disturbance, and then converge in mid-succession. Finally, very late successional stands, which only occur as unmanaged forests, also develop unique communities that differ from early or mid-successional stages. This underscores the importance of time as a fundamental factor that controls regional vegetation diversity. Further, because the landscape is strongly dominated by managed forests, and young post-fire and late-successional forests are relatively rare, our data suggest that each of these forest types provides a disproportionate contribution to enhancing regional vegetation diversity, and deserves more focused conservation attention.

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Author contributions

Vincent Buness: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (equal); Visualization (lead); Writing - original draft (lead). **Maja K. Sundqvist**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing - review and editing (lead). **Syed Tuhin Ali**: Conceptualization (equal); Data curation (equal); Methodology (equal); Writing - review and editing (equal). **Peter Annighöfer**: Conceptualization (equal); Methodology (equal); Supervision (equal); Writing - review and editing (equal). **Carlos Miguel Aragon**: Data curation (equal); Writing - review and editing (equal). **Isabelle Lanzrein**: Conceptualization (equal); Data curation (equal); Methodology (equal); Writing - review and editing (equal). **Daniel B. Metcalfe**: Funding acquisition (equal); Writing - review and editing (equal). **Marie-Charlotte Nilsson**: Funding acquisition (equal); Methodology (equal); Writing - review and editing (equal). **Michael J. Gundale**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Supervision (lead); Writing - review and editing (lead).

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2547d7x1f (Buness et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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