

1 **Turnover in boreal forest understory following disturbance varies along a fertility gradient**

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### 33 **Abstract**

34 Anthropogenic disturbances greatly alter community composition and diversity. However, it remains largely  
35 unknown which underlying processes - colonizations, local extinctions or abundance changes - drive  
36 compositional changes in response to disturbance, and whether these processes are constrained by  
37 environmental gradients. Here, we investigated the processes underlying temporal turnover of vascular plant  
38 communities in boreal forests in response to silvicultural practices along a soil fertility gradient. Our analyses  
39 were based on long-term data from 1985 to 2006 covering up to 1700 sites across Finland. While average  
40 richness remained static, we found that silvicultural practices induced greatest turnover in the most fertile  
41 habitats. In recently disturbed sites, colonizations and species losses altered dominance structure of the  
42 communities, while the undisturbed old forests were characterized by stable dominant species even when the  
43 majority of species shifted their identity. We conclude that disturbance history and fertility constrain temporal  
44 turnover in boreal forest communities.

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## 51 **Introduction**

52 Anthropogenic pressure on the remaining ecosystems and their biodiversity is accelerating (Sala 2000; Arneeth  
53 *et al.* 2019; Díaz *et al.* 2019). Recent ecological research has highlighted the need to consider community  
54 changes more broadly than as changes in species richness to better understand the causes and consequences of  
55 the observed biodiversity disruption (Chase *et al.* 2018; Hillebrand *et al.* 2018; Blowes *et al.* 2019). Ecological  
56 communities change as species become more or less abundant, go (locally) extinct or colonize new habitats,  
57 and consequently substantial community changes may not be captured by metrics focusing on species richness  
58 alone. To identify what makes an ecosystem susceptible to disturbance, and to predict its consequences, we  
59 therefore need to know which processes underlie community change, and whether environmental gradients  
60 influence their magnitude.

61 To date the key focus of research has been on the spatial dimension of biodiversity change and  
62 hence, the constraints and drivers of temporal turnover remain less known (eg. Magurran *et al.* 2019).  
63 Observational evidence suggests that temporal turnover is higher in the marine than the terrestrial realm  
64 (Blowes *et al.* 2019), and increases along productivity (Virtanen *et al.* 2010; Zhang *et al.* 2018; Maliniemi *et*  
65 *al.* 2019), and temperature gradients (Hillebrand *et al.* 2010). Coherently, it may increase towards the tropics  
66 (Shurin *et al.* 2007). As these environmental gradients influence natural biodiversity change in time, they also  
67 have the potential to regulate the magnitude of disturbance-induced turnover, but this remains poorly studied.  
68 This is probably due to the scarcity of long-term biodiversity data that would allow identifying community  
69 changes before and after disturbance events across varying environmental conditions. Consequently, much of  
70 our understanding on temporal dynamics of community turnover in response to disturbance or environmental  
71 drivers originates from few, mainly experimental, studies (Thrush *et al.* 2008; e.g. Bunn *et al.* 2010; Xu *et al.*  
72 2012; Hodapp *et al.* 2018). For example, using a global multisite experimental network, Hodapp *et al.* (2018)  
73 showed that following fertilizing and grazer removal, temporal turnover rates in grassland were higher in  
74 spatially heterogeneous plant communities. Moreover, a recent meta-analysis demonstrated that community  
75 responses to disturbance (mowing, burning, herbivory) under experimental conditions appear after a time-lag  
76 (Komatsu *et al.* 2019). Collectively, this evidence illustrates that in order to evaluate the vulnerability of

77 communities to disturbances, we need to quantify how colonizations, extinctions and abundance changes vary  
78 both along environmental gradients and over time.

79 Environmental gradients, such as temperature, altitude and fertility have been recognized to  
80 correlate with species richness already since the days of Humboldt and Darwin. These gradients often co-vary,  
81 and their relative importance for species richness is still currently being actively disentangled for different taxa  
82 (e.g. for latitude, see Chown *et al.* 2000; precipitation, e.g. Tedersoo *et al.* 2014; fertility, e.g. Grace *et al.*  
83 2016; elevation, e.g. Peters *et al.* 2016; temperature, e.g. Edgar *et al.* 2017). These large-scale differences in  
84 richness between regions, more or less associated with environmental gradients, may determine the importance  
85 of extinctions, colonizations and abundance changes for community turnover (*cf.* Ricklefs 1987). A community  
86 surrounded by a larger species pool may experience considerable exchange of species identities in response to  
87 disturbance thanks to plentiful assortment of candidate colonizers, while communities surrounded by a small  
88 species pool may mostly experience abundance changes or species losses following disturbance. By fostering  
89 species coexistence, environmental heterogeneity in space and time is expected to increase regional species  
90 pools and thereby enable higher colonizations and temporal turnover after disturbance, which may be one  
91 explanation for the modeled (Adler *et al.* 2005) and observed (Korhonen *et al.* 2010; Collins *et al.* 2018;  
92 Hodapp *et al.* 2018) interdependency between spatial and temporal turnover.

93 Up to 31% of the world's land surface is covered by forests (Keenan *et al.* 2015) and 24% of  
94 this is comprised of boreal forests (UNEP *et al.* 2009). Hence, boreal forests represent the largest biome on  
95 Earth, providing a multitude of ecosystem services (Gauthier *et al.* 2015). Understory harbors up to 80% of  
96 the vascular plant diversity in boreal forests, is tightly connected with insect and fungal diversity both above-  
97 and belowground, and plays an important role in forest ecosystem functioning (Nilsson & Wardle 2005;  
98 Gilliam 2007; Landuyt *et al.* 2019). Forests are increasingly used by humans (Potapov *et al.* 2017) and  
99 therefore, understanding the consequences of frequent silvicultural practices is crucial both for the  
100 development of ecological sustainability, and for protecting the biodiversity of this key ecosystem. However,  
101 identifying changes in biodiversity due to human actions is particularly challenging in forests due to their  
102 naturally changing composition through succession. Although successional theory predicts a decreasing

103 number of species gains and losses from early to late successional communities, we lack knowledge on how  
104 temporal turnover varies over the course of the succession or along environmental gradients (Anderson 2007).

105           In this study, we assess temporal community change of vascular plant understory communities  
106 in response to silvicultural practices along a soil fertility gradient. We measure temporal community change  
107 probed by species gains, losses and abundance changes and test whether these processes of community change  
108 vary along a fertility gradient and in relation to both time since disturbance and disturbance type. Specifically,  
109 we test the following three hypotheses (Fig. 1):

- 110       1. Temporal turnover in forest understory during a decade without silvicultural practices is influenced by  
111       both soil fertility and time since the latest major disturbance.
- 112       2. Species identity shifts drive dominance change in recently disturbed forest stands to a greater extent  
113       than in older forests.
- 114       3. Short-term effect of disturbance on temporal turnover depends on soil fertility, disturbance type and  
115       time since disturbance.

116 We observe high rates of temporal turnover in forest understory communities immediately after a disturbance  
117 event. Turnover of recently disturbed forest sites was greatest in fertile habitats, which are associated with  
118 longer growing seasons and higher local species richness. Rapid community changes were largely driven by  
119 both species colonizations and extinctions in recently disturbed fertile sites. Turnover rates in the oldest forests  
120 were low and independent of fertility.

121

## 122 **Material and methods**

### 123 *Study area and sampling design*

124 Understory vegetation was surveyed on a systematic network of 1700 sites established on mineral-soil in  
125 forested land in 1985–86. These sites are a part of a systematic sampling network of the 8<sup>th</sup> Finnish National  
126 Forest Inventory (NFI, Reinikainen *et al.* 2000). This network consists of clusters, spread 16 x 16 km apart  
127 from each other in Southern Finland and 24 x 32 km in Northern Finland. Each cluster includes four linearly

128 located sampling sites 400 m apart from each other in Southern Finland and three sampling sites 600 m apart  
129 from each other in Northern Finland. All 1700 sites were resurveyed in 1995, and a subset of 443 of them (max  
130 1 site per cluster) were resurveyed in 2006 (Fig. 1). The survey performed on 443 sites in 2006 was part of the  
131 BioSoil project carried out under the Forest Focus scheme, which is a subset of the pan-European UN-ECE  
132 ICP Forests extensive monitoring site network (Level I; Lorenz & Fischer 2013).

133

#### 134 *Vegetation, soil and temperature data*

135 In all surveys, vascular plant species were identified and their percentage cover was visually estimated on the  
136 same four permanent square-shaped sampling plots of 2 m<sup>2</sup> on circular 300 m<sup>2</sup> (1985-1986 and 1995) or 400  
137 m<sup>2</sup> (2006) sites. In the data analysis, species abundances in the four plots were averaged for each site. Presence  
138 of vascular plant species outside sampling plots but inside the 300 m<sup>2</sup> circular site was recorded in 1985-1986  
139 and 1995. We defined ‘local species pool’ as a total number of unique species occurring in a site, encountered  
140 either in or outside of the plots, but within the boundaries of the circular 300 m<sup>2</sup> site.

141 In 2006, 10 or 20 subsamples were systematically collected with a cylinder (d = 60 mm) from  
142 organic layer of 443 sites (400m<sup>2</sup>, Fig. 1). Number of subsamples depended on the organic layer thickness.  
143 Subsamples were pooled to one composite sample per site. Total carbon (C) and nitrogen (N) contents of the  
144 composite samples were determined on a LECO CHN analyzer. This C:N ratio in organic layer was used as a  
145 retrospective indicator of the fertility also in 1985 and 1995, since inter-annual variation in organic layer C:N  
146 is low (0-20% during 16 years, Olsson *et al.* 1996) and silvicultural practices has little or no effect on it  
147 (Johnson & Curtis 2001). To describe the differences in effective temperatures between sites, we calculated  
148 mean temperature sum exceeding +5°C (GGD5) for each site for a ten-year period prior to each survey. Daily  
149 temperature data was obtained from Finnish Meteorological Institute’s interpolation on to a 10 km × 10 km  
150 resolution (Venäläinen *et al.* 2005).

151

#### 152 *Management history of sites*

153 During each survey, the management history of each site was classified by recording management type (nine  
154 categories) and time since the latest management (three categories: 1, 2-5, 6-10 years). We divided the nine  
155 management categories into following three groups: ‘Regeneration cuttings’ which includes all regenerative  
156 cuttings (seed tree cutting, shelterwood cutting, strip clearcutting, clearcutting with a nurse crop, clearcutting),  
157 ‘Commercial thinning’ which includes commercial thinning, selection cutting and removal of reserve trees;  
158 and ‘Pre-commercial tending’ which includes pre-commercial thinning and cleaning of the sapling stand  
159 (descriptions of management types in the Suppl. Table 1). Additionally, management history for preceding  
160 five years was visually estimated with one-year accuracy in 1990 and 1995 yielding annual data on  
161 management history for period 1985-1995. By combining all these recordings, we could determine time and  
162 type of the latest management event for each site for the period 1975-2006 (Fig 1). To estimate the timing of  
163 the latest major disturbance event before 1975, we used stand age as a proxy for a disturbance that removed  
164 most of the canopy. We classified this stand age to following categories: 31-60, 61-80, 81-100, 101-120, 121-  
165 140 and over 140 years.

166

### 167 *Calculating community indices*

168 Observations of two subspecies were merged to species level and observations of group taxa above genus level  
169 were removed from the data. To characterize the change over time in understory communities, we calculated  
170 five temporal community change metrics. First, we calculated change in species richness between two time  
171 steps. Second, we calculated species gains as the number of species that appeared in the later sampling relative  
172 to first sampling. Third, species losses were computed as number of species that disappeared in the later  
173 sampling relative to first sampling. Fourth, to characterize proportion of species that changed identity between  
174 the two sampling events, we calculated richness-based turnover (richness-based species exchange ration,  
175 SERr, sensu Hillebrand *et al.* (2018)) as summed species gains and losses relative to species richness across  
176 both sampling events. This is a complement of Jaccard’s similarity index and based on presence-absence data  
177 (Jaccard 1912). Fifth, to characterize changes in species’ relative abundances over time, we calculated relative  
178 abundance-based turnover (SERa sensu Hillebrand *et al.* (2018)). Abundance-based turnover is thus the most  
179 comprehensive measure of community change of these five metrics. Since it is based on relative abundances,

180 it illustrates shifts in the dominant species and avoids being sensitive to species richness and changes in rare  
181 species (Hillebrand *et al.* 2018). Richness-based turnover was calculated using codyn package (Hallett *et al.*  
182 2019).

183

#### 184 *Statistical modeling*

185 Our first hypothesis was that temporal community change within a decade is affected jointly by time since  
186 disturbance and soil fertility. To test this, we selected sites without any silvicultural management within a  
187 decadal sampling interval (either 1985-1995 or 1995-2006), but with known timing of latest major disturbance  
188 prior to the sampling interval (either clear cutting or other major disturbance, see above). We also required the  
189 selected sites to have data on soil organic layer C:N and local species pool in the site, which resulted in 169  
190 sites for the analysis. For each of these sites, we calculated the above-mentioned five temporal community  
191 change metrics over the sampling intervals (Fig. 1). We fitted generalized linear mixed effect models with  
192 each of these five temporal change metrics as the response variable in turn and time since disturbance, organic  
193 layer C:N ratio and their interaction as the fixed variables. We took location and possible repeated  
194 measurements into account with a nested random factor, which allowed the intercept to vary among bioclimatic  
195 subzones (a factor with five categories) and among sites within bioclimatic subzones. Because time since  
196 disturbance categories '1' and '11-20' years contained only 5 and 6 data points, respectively, they were merged  
197 to neighboring classes, which consequently become '1-5' and '6-20' years.

198 To ensure that organic layer C:N is a relevant environmental factor associated with temporal  
199 turnover, we compared its capacity to explain variation in abundance-based turnover to that of long-term  
200 effective temperature sum (GGD5 over the preceding 10 years) and local species pool at the site. They both  
201 correlated negatively with organic layer C:N ( $r = -0.64$ ,  $p < 0.001$ ; and  $r = -0.65$ ,  $p < 0.001$ , respectively). We  
202 ran three generalized linear mixed effect models, where the fixed factor consisted of interaction between time  
203 since disturbance and one of these three variables in turn ( $N = 169$  in each model) and compared fits of these  
204 models to data by AIC. We calculated explanatory powers of the fixed variables in each of three models  
205 (marginal  $R^2$ , according to Nakagawa & Schielzeth (2013) in piecewiseSEM package (Lefcheck *et al.* 2018)).

206 Since C to N ratio explained more variation in abundance-based turnover than GDD5 or local species pool  
207 (47% vs 39% or 40%, respectively, Suppl. Fig. 1, Suppl. Table 2), we focus on organic layer C:N gradient  
208 hereafter.

209 To test our second hypothesis that species gains and losses are more strongly related to  
210 community turnover immediately after disturbance, as opposed to later successional communities, we modeled  
211 abundance-based turnover (*i.e.* temporal changes in dominance structure) as a response of interaction of  
212 richness-based turnover (*i.e.* sum of proportion of species gains and losses) and time since the latest major  
213 disturbance using generalized linear mixed models. This model allows us to test whether the relationship  
214 between dominance structure and identity shifts (species gains and losses together) is influenced by the time  
215 since disturbance. In this model, the random variable consisted of site nested within block, which was nested  
216 within the bioclimatic subzone. Here we used the same criteria as above, *i.e.* allowed no silvicultural  
217 management within a 10-year sampling interval (either 1985-1995 or 1995-2006), but required known timing  
218 of latest major disturbance prior to the sampling interval. As we did not need C:N data for this analysis, its  
219 availability did not restrict the number of replicates as above, and we could use 533 forest sites for these  
220 analysis.

221 Third, to assess the short-term effects of disturbance on community composition, we selected  
222 sites that were managed between years 1985 and 1995, N = 569. For these sites, we calculated temporal  
223 community change from the pre-management (1985) to post-management (1995) state using the same five  
224 community change metrics as above. For each site, silvicultural management type (three levels: ‘regeneration  
225 cuttings’, ‘commercial thinning or ‘pre-commercial tending’) and time since the last management action (‘time  
226 since disturbance’) were defined with 1-year accuracy for the sampling interval (measured from year 1995,  
227 Fig. 1).

228 We tested the third hypothesis in two parts, because we wanted to use all 569 replicates to test  
229 the effect of time, while C:N data existed for a subset of 142 of these sites. To test whether disturbance type  
230 and time since disturbance influence temporal turnover, we fitted generalized linear mixed effect models to  
231 test the effect of forest management type (categorical, three levels), time since management (continuous, 1-9  
232 years) and their interaction on each of the five community change metrics in turn. We took location into

233 account with a nested random factor, which allowed the intercept to vary among bioclimatic subzones (a factor  
234 with four categories) and among blocks within bioclimatic subzones. In these models we used all 569  
235 replicates. Secondly, to test whether disturbance type and soil fertility influence temporal turnover, we fitted  
236 generalized linear mixed effect models with each of the five community change metrics in turn as a response  
237 variable and the main effects and interaction of management type and organic layer C:N as explanatory  
238 variables. We used the same nested random variable as in the previous models testing the hypothesis three.  
239 Here the availability of C:N data restricted the number of replicates to 142.

240 All models were fitted using package nlme (Pinheiro *et al.* 2020) in R 3.6.1 statistical  
241 environment (R development core team 2019). Model validation plots were used to evaluate the fulfillment of  
242 model assumptions (Zuur *et al.* 2009). In case of one model with unmet assumptions, the response variable  
243 was log-transformed (Suppl. Table 7).

244

245

## 246 **Results**

### 247 *Post-disturbance temporal turnover along a fertility gradient*

248 To test the first hypothesis, we investigated turnover within a decade in forests stands of varying age, which  
249 experienced no silvicultural management during the sampling decade. We found that time since the last major  
250 disturbance and soil fertility did not influence average species richness during a decade (Figs. 2e & 3e, Suppl.  
251 Tables 3-4). Despite of this virtually static richness, we observed high temporal turnover in communities.  
252 Understory communities in fertile sites (*i.e.* low organic layer C to N ratio) experienced higher turnover  
253 measured by species relative abundances (Fig. 2a), higher proportion of species that shifted identities  
254 (=richness-based turnover, Fig. 2b) and higher number of both species gains and losses (Fig. 2c,d) in  
255 comparison to the communities growing in nutrient-poor sites. More importantly, the effect of soil fertility on  
256 the relative abundance-based turnover and species losses was dependent on time since disturbance (Fig. 2a  
257 marginally significant interaction, Fig. 2d, Suppl. Table 3): The recently (1-20 years ago) disturbed sites  
258 experienced the highest abundance-based turnover and highest species losses in fertile sites, while these

259 changes were considerably lower in nutrient-poor sites (Suppl. Table 4). In over 100-years-old stands, in  
260 contrast, the abundance-based turnover and species losses were low and unaffected by soil fertility (Fig. 2a, d,  
261 Suppl. Table 4). Rate of temporal turnover (slopes) measured by the five community change metrics in the  
262 oldest forest (over 140 years) along the fertility gradient were statistically not different from zero (Suppl. Table  
263 4).

264

#### 265 *Importance of species' identity shifts for post-disturbance temporal turnover*

266 Richness-based turnover, measuring proportion of species that changed their identity relative to total number  
267 of species across both sampling events, was positively related to abundance-based turnover only in sites that  
268 had been disturbed less than 60 years ago (Fig. 4, Suppl. Table 5). In these youngest forest sites, the high  
269 number of species losses and gains led to great changes in the dominance structure of the communities,  
270 meaning that either arriving species gained high abundances, or lost species were originally abundant. In  
271 contrast, if the latest major disturbance event took place more than 60 years ago, abundance-based turnover  
272 remained constantly low (Fig 4, Suppl Table 5), even if up to 75% of the species in the community would  
273 change their identity within a decade.

274

#### 275 *Short-term effects of silvicultural practices on temporal turnover depend on management type*

276 All silvicultural practices triggered substantially greater compositional turnover in forest understory than  
277 observed in the oldest forest stands (Fig. 5). Short-term effects of regeneration cuttings strengthened with time,  
278 while impacts of thinning and tending remained stable during the first decade after management (Fig. 5 Suppl.  
279 table 6). Regeneration cuttings increased species gains on average from four species during the first year to  
280 seven species by the end of the first decade (Fig. 5c, Suppl. table 6). Species losses were the highest  
281 immediately after a regeneration cutting and decreased towards the end of the first decade (Fig. 5d). This  
282 suggests that some of the species that were lost immediately after a regeneration cutting recolonized the site  
283 within next couple of years. Interestingly, species losses after thinning and tending remained constant during  
284 the first decade, meaning that those species that were lost immediately after these management types were not

285 able to recolonize the communities during first decade. Relative abundance-based turnover showed very rapid  
286 increase during the first decade indicating that not only species identities were changing, but also the new  
287 immigrants effectively gained dominance, while the species that dominated the communities before the  
288 management lost their dominant roles (Fig. 5a, Suppl. table 6).

289

#### 290 *Impact of fertility on short-term effects of silvicultural practices on temporal turnover*

291 Soil fertility increased short-term effects of all silvicultural management types on turnover of understory  
292 communities, but had no effect on species richness (Fig. 6, Suppl. Table 7). Immediate community turnover  
293 in fertile sites as a response to any silvicultural management type was clearly higher than natural turnover  
294 during the same period in the oldest forest stands (> 140 years, Fig. 6), but this difference was smaller in  
295 nutrient-poor sites. Fertility increased especially number of species gains as an immediate response to  
296 regeneration cuttings (Fig. 6c, Suppl. table 7).

297

298

## 299 **Discussion**

300 We investigated whether temporal turnover, and its underlying processes, in forest understory communities  
301 depend on time since disturbance, type of disturbance and soil fertility. We found that the fastest changes took  
302 place in most fertile habitats during the first decade after a major disturbance, such as clearcutting. In these  
303 recently disturbed sites, colonizations and species losses altered dominance structure of the communities, while  
304 the undisturbed old forests were characterized by stable dominant species even when the majority of species  
305 shifted their identity. Disturbance history and soil fertility thus constrain temporal turnover in boreal forest  
306 communities by regulating the degree to which species gains and losses translate into changes in dominance  
307 structure.

308

#### 309 *Post-disturbance temporal turnover along a fertility gradient*

310 We found strong support for our first hypothesis that temporal turnover in boreal forest understory is driven  
311 jointly by time since disturbance and fertility. Specifically, species losses and the relative abundance-based  
312 turnover, which is the most comprehensive measure of composition incorporating both abundance and species  
313 identity shifts, increased towards fertile sites in forest stands younger than 20 years, but were insensitive to  
314 fertility in older forests (Fig. 2). Fertility is thus not a driver of community change in the oldest forests as  
315 opposed to more recently disturbed forests. In our dataset, soil fertility correlates with local species richness.  
316 This finding supports the emerging view that spatial heterogeneity (also enabling larger regional species pool  
317 via spatial storage effect (Chesson 2000)) may result in higher temporal turnover (Hodapp *et al.* 2018). Yet,  
318 our results provide two novel aspects on this view. First, our findings reveal that disturbance history, which in  
319 forest systems is mirrored by successional stage, is strongly controlling temporal turnover. Second, we observe  
320 the greatest turnover in recently disturbed forest stands typically characterized by rapidly changing light and  
321 microclimatic conditions as a consequence of fast canopy development. This suggests that also temporal  
322 heterogeneity in the environment may increase community turnover.

323 Our results demonstrate that high turnover in fertile habitats immediately after disturbance was driven  
324 by high colonization and extinctions rates leading to changes in the community dominance structure. There  
325 are at least two possible and mutually non-exclusive explanations for this pattern. First, the species colonizing  
326 the forest stand immediately after a major disturbance are typically ruderals (as described by Grime's plant  
327 strategy framework (1974)), usually characterized by fast growth, short life cycles, high seed production and  
328 poor shade-tolerance (Zobel 1989; Tonteri *et al.* 2016; Vanha-Majamaa *et al.* 2017). Their existence is by  
329 definition short, giving swiftly space for new colonizers and thereby potentially contributing to rapid temporal  
330 turnover observed in this study. This inference is supported by Collins *et al.* (2018), who found higher temporal  
331 turnover in communities dominated by organisms with short lifespan. Second, faster turnover in young fertile  
332 forest stands can also be driven by larger local (and possibly also regional) species pool, supplying a diverse  
333 array of candidate colonizers with varying environmental preferences. In supporting of this, Heikkinen &  
334 Mäkipää (2010) show that forest plants occupying nutrient-rich end of the soil C:N gradient have narrower  
335 niches, and thus more specialized nutrient requirements than species preferring more nutrient-poor sites.  
336 Moreover, a large species pool is likely to include species that are sufficiently different from the resident

337 species to enable coexistence (Chesson & Huntly 1997; Chesson 2000). High temporal heterogeneity in the  
338 environmental conditions during the first decades after the forest establishment (especially light, as canopy  
339 develops) may lead to shorter coexistence times and higher turnover, as predicted by models by Adler & Drake  
340 (2008), if the first colonizing species do not tolerate changing environmental conditions, as forest canopy  
341 develops.

342 We note that the ultimate drivers of temporal turnover may differ in time. Time since disturbance  
343 serves here as a proxy for a suite of variables that change with time after a disturbance. During the first decades  
344 of stand development, light, microclimatic conditions and soil moisture experienced by the understory plants  
345 change drastically as tree canopy develops from open to fully closed (Kuuluvainen *et al.* 1993; Brown & Parker  
346 1994; Hart & Chen 2006). These environmental changes are here modelled under the umbrella of ‘time since  
347 disturbance’ covering potentially several co-varying abiotic and biotic factors. Future experimental studies are  
348 necessary to disentangle the relative contributions of these co-varying factors on community composition.

349

#### 350 *Importance of species losses and gains for temporal turnover*

351 Contrary to our second hypothesis, we observed high rates of species identity shifts (losses and gains) even in  
352 the oldest forests, but only in the young forests (less than 60 years old) these changes were accompanied by  
353 high rates of change in species abundances (Fig. 4). This finding implies that in the younger stands the  
354 colonizing species rapidly reached high dominance making previously common species less abundant or  
355 locally extinct. The older the forest became, the less the dominance structure changed within the study decade,  
356 even when majority of species changed their identity. This means that the species lost or gained in the oldest  
357 forests were mostly rare and non-dominant, and therefore the dominance structure of the communities  
358 remained stable over a decade despite these rare species blinking in or out. Our results thus suggest that  
359 disturbance opens niche space for all types of colonizers. Immediately after a disturbance some of the  
360 colonizers are able to reach high abundances, while many of the colonizers throughout the succession are so  
361 called transient species, which may be poorly adapted to biotic and abiotic environment and therefore not able  
362 to sustain permanent populations (Taylor *et al.* 2018). Forest is an especially challenging environment for a

363 plant species to thrive due to its continuously changing micro-environmental conditions below developing tree  
364 canopies (Hart & Chen 2006). The stabilization of the dominance structure is a continuous phenomenon during  
365 natural forest succession, as canopy closure increases (Bergeron & Dubue 1988; Rees & Juday 2002;  
366 Angelstam & Kuuluvainen 2004; Hedwall *et al.* 2019), but our results suggest that at least in boreal forests the  
367 age of ca. 60 years may be a milestone, after which dominance structure of understory communities becomes  
368 more stable and is not influenced by species transient species losses or gains.

369

#### 370 *Disturbance and fertility increase both species gains and losses*

371 Our analyses of community changes both after a disturbance and in response to disturbance (Fig. 1) highlight  
372 the importance of species gains and losses for turnover during the first 10-15 years: We observed higher  
373 proportion of species gains than losses driving post-disturbance turnover. In support of this, our results of  
374 short-term effects of disturbance revealed that sites gained more species year after year during the first decade  
375 after a regeneration cutting and more so on fertile than infertile soils. It is not surprising that colonization is  
376 important, as most of the vegetation is typically destroyed because of silvicultural regeneration practices, but  
377 our finding implies that colonizing species are different from those that existed in a site before disturbance.  
378 Species losses also contributed to turnover especially in recently managed sites on fertile soils. However, while  
379 some of the lost species were able to re-colonize the sites within the next couple of years following a  
380 regeneration cutting, this was not the case after other management types. The reason may be that the species  
381 dominating the mature forests before a regeneration cutting are core species (*sensu* Magurran & Henderson  
382 2003), occurring virtually throughout all successional stages (Zobel 1989; Nieppola 1992; Tonteri 1994). In  
383 contrast, the species that disappeared from younger forest stands due to thinning or tending were likely to be  
384 transient species, perhaps living in the edge of their tolerance limits and not able to re-colonize their niche.

385

#### 386 *Conclusions*

387 Our findings based on a unique long-term observational dataset on boreal forest plant communities illustrate  
388 the prominent role of the large-scale soil fertility gradient in controlling temporal turnover in combination with

389 disturbance history. While this evidence supports the recent literature highlighting spatial heterogeneity and  
390 size of the species pool as drivers of temporal turnover (Collins *et al.* 2018; Hodapp *et al.* 2018), it suggests  
391 that a simple measure of soil fertility may serve as a good predictor for temporal turnover at least in boreal  
392 forests. Moreover, our results reveal the processes that lead to high turnover in fertile habitats after disturbance  
393 - colonizations and species losses modify there the dominance structure of the communities. While some  
394 species exchange takes place also in the oldest forests, there it does not translate to changes in dominance  
395 structure. If clearcuttings become more frequent in space, as observed in Finland during the past decades  
396 (Peltola *et al.* 2019), a larger proportion of forest area will belong to recently disturbed category and will be  
397 colonized by new species. This calls attention to functional characteristics of colonizers: if they include  
398 generalists with good competitive abilities, in the long-term high colonization rates may lead to  
399 homogenization of forest plant communities, as observed in Denmark over past 140 years (Finderup Nielsen  
400 *et al.* 2019). Adaptability of ecosystems to future changes is dependent on their biodiversity (Eriksson &  
401 Hillebrand 2019). Consequently, biotic homogenization may lead to a lower adaptive capacity and a decrease  
402 in ecosystem resilience.

403

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409

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558

559 **Figure legends**

560 **Figure 1.** Maps of Finland showing the sampling locations in 1985, 1995 and 2006. Data on organic layer  
561 carbon to nitrogen ratio was collected in the colored subsample of 443 sites in 2006. The map for 2006 shows  
562 coarse interpolated organic layer C:N values for whole country based on measured values in black sampling  
563 dots. Schematic illustrations below the time line show how hypotheses 1 and 2 tested post-disturbance turnover  
564 during a 10-year sampling interval relating it to time since disturbance. Hypothesis 3 tested how different  
565 disturbance types during the sampling interval influenced temporal turnover of forest understory communities.

566

567 **Figure 2.** Temporal community change during a decade in boreal forest understory in relation to carbon to  
568 nitrogen (C:N) ratio in organic layer in different time-since-major-disturbance categories. Community change  
569 was measured with five community change metrics: a) relative-abundance based community turnover (SERa,  
570 sensu Hillebrand *et al.* 2017), b) richness-based turnover (the sum of proportions of gained and lost species,  
571 SERr, sensu Hillebrand *et al.* 2017), c) species gains, d) species losses, and e) change in species richness. Grey  
572 dots represent the data from each site (N = 169) and colored lines the linear regression in relation to time since  
573 disturbance. Small inserts show smoothed average response of variable in question to organic layer C:N ratio  
574 ignoring the disturbance history.

575

576 **Figure 3.** Temporal community change in boreal forest understory in relation to time since the latest major  
577 disturbance before the first sampling event. Community change was measured during a decade with five  
578 different community change metrics a) relative-abundance based community turnover, b) richness-based  
579 turnover, c) species gains, d) species losses, and e) change in species richness. In panel b, richness-based  
580 turnover is divided to proportions of species gains (dark grey) and species losses (light grey) relative to total  
581 number of species observed through time. Grey dots show the data from each site (N= 169), colored circles  
582 are means and vertical lines  $\pm$  SE.

583

584 **Figure 4.** Linear regression between relative abundance- vs. richness-based turnover during a decade in  
585 relation to time since the latest major disturbance in the forest stand (N=533).

586

587 **Figure 5.** Effect of silvicultural management on temporal turnover measured by five community change  
588 indices comparing pre- and post-managed communities relative to time since management before the later  
589 sampling: a) abundance-based turnover, b) richness-based turnover, c) species gains d) species losses, and e)  
590 change in species richness. Grey dots describe the original data from each site (N=569), colored lines show  
591 the linear model estimates  $\pm$  SE for different management types. For comparison, the dashed line indicates  
592 average community change during a decade without management in older than 140 years old forests.

593

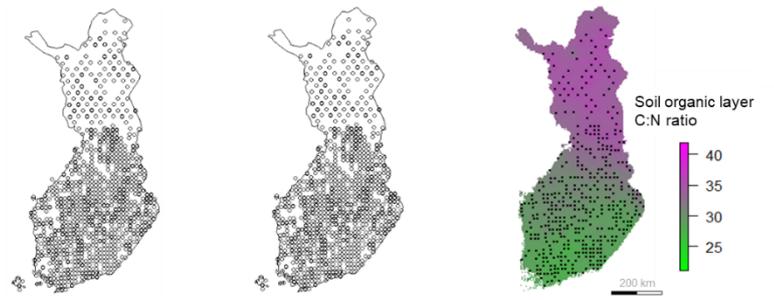
594 **Figure 6.** Effect of silvicultural management during nine years after management on species turnover  
595 measured by five community change indices comparing pre- and post-managed communities relative to  
596 organic layer C to N ratio in different management types: a) abundance-based turnover, b) richness-based  
597 turnover, c) species gains d) species losses, and e) change in species richness. Grey dots describe the data  
598 from each site (N = 142), colored lines show the generalized linear model estimates  $\pm$  SE for different  
599 management types.

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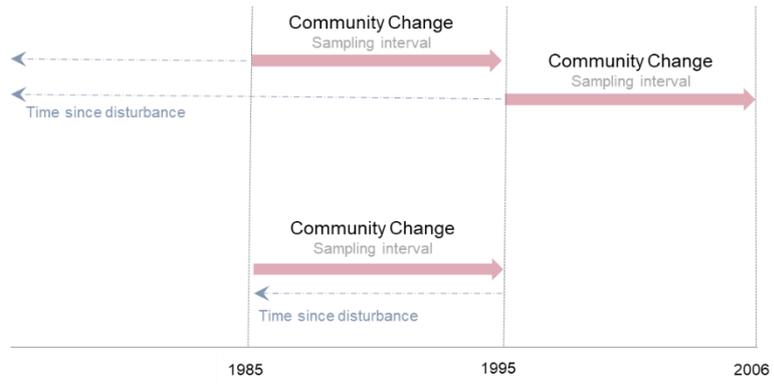
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**HYPOTHESIS 1 & 2**  
 Post-disturbance turnover  
 Disturbance before the sampling interval

**HYPOTHESIS 3**  
 Effect of disturbance on turnover  
 Disturbance during the sampling interval

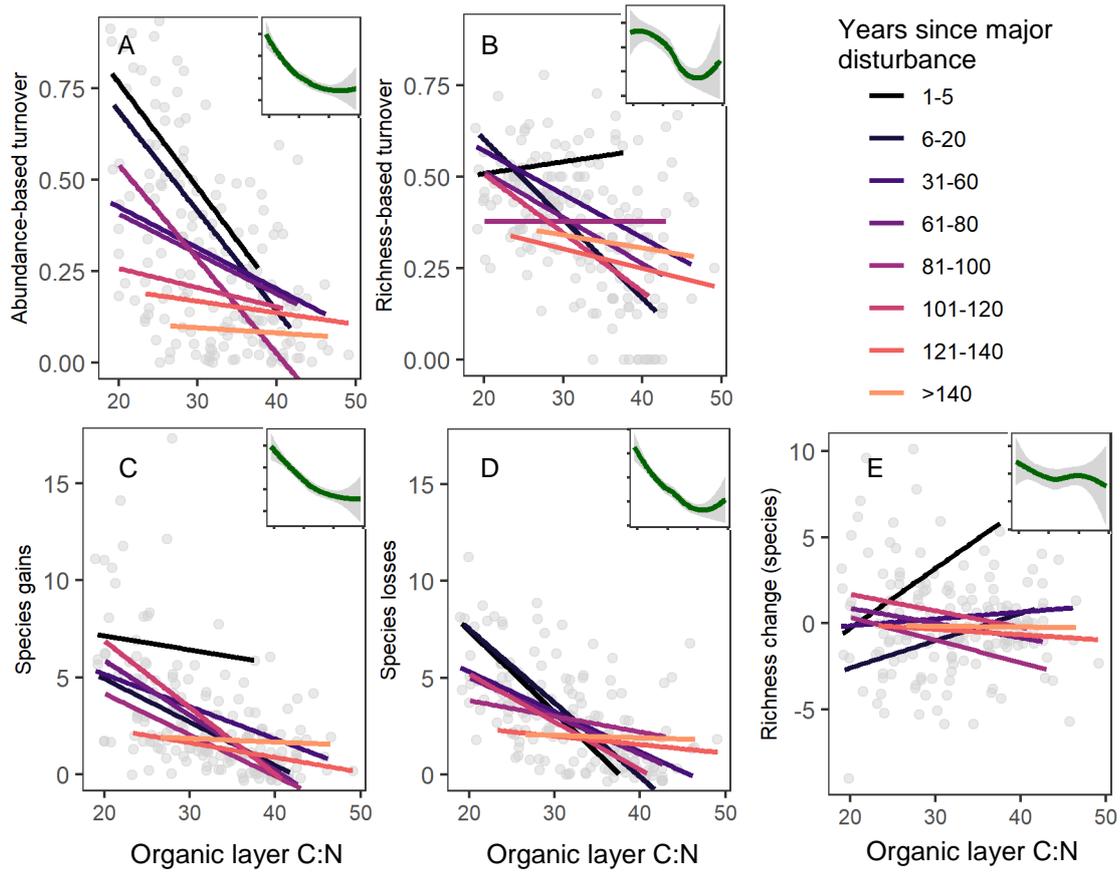


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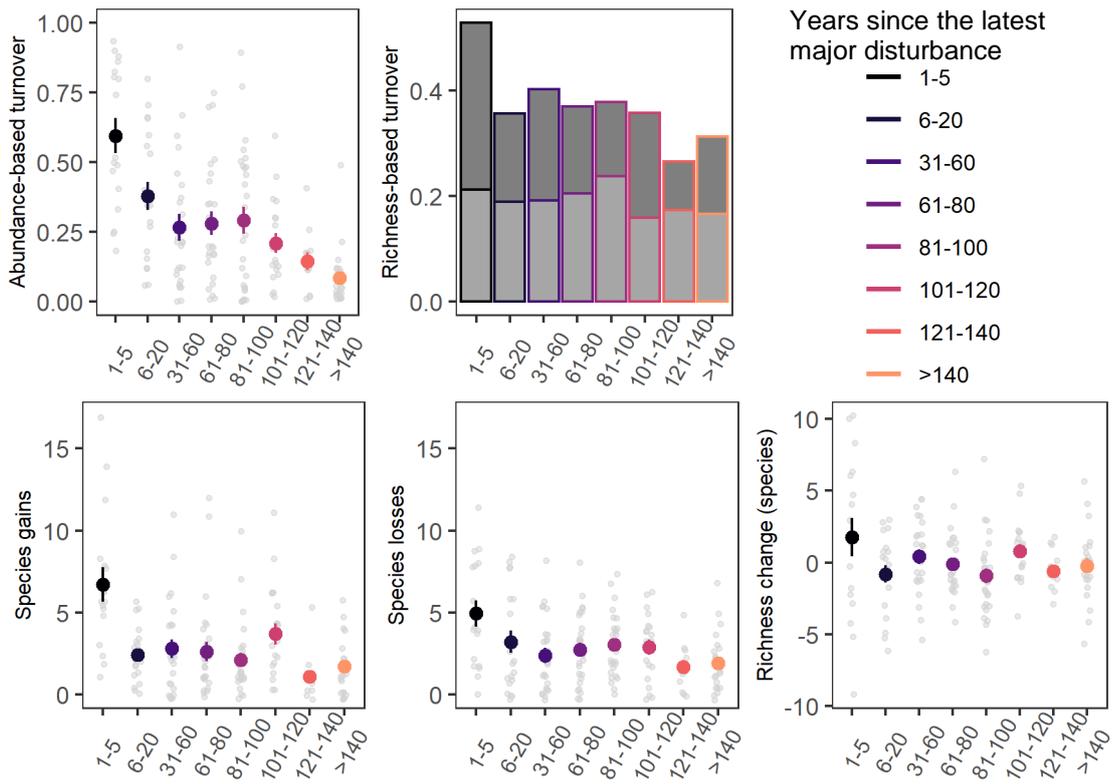
606 **Figure 1.**

607



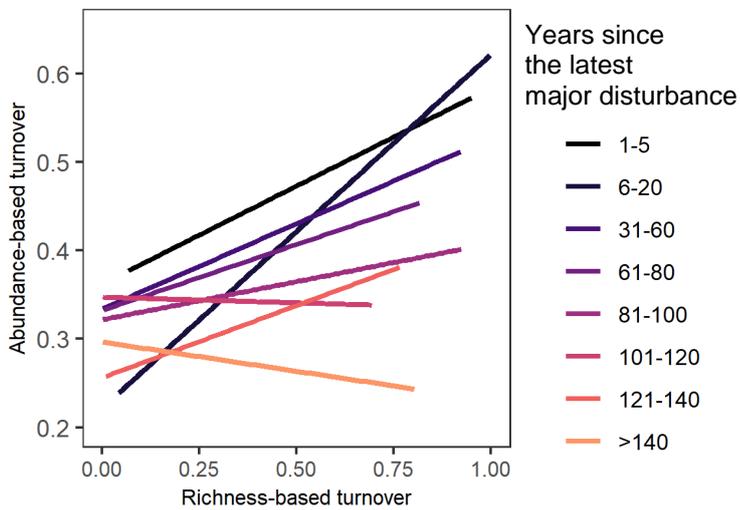
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609 **Figure 2.**



610

611 **Figure 3.**

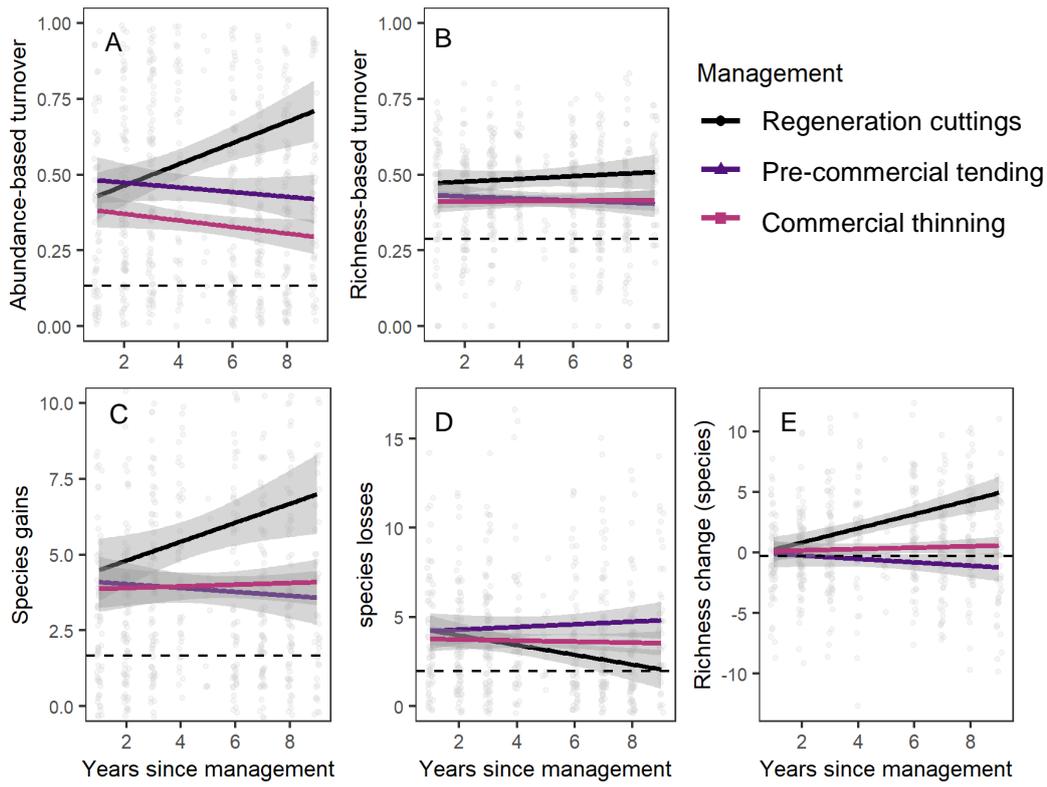


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613 **Figure 4.**

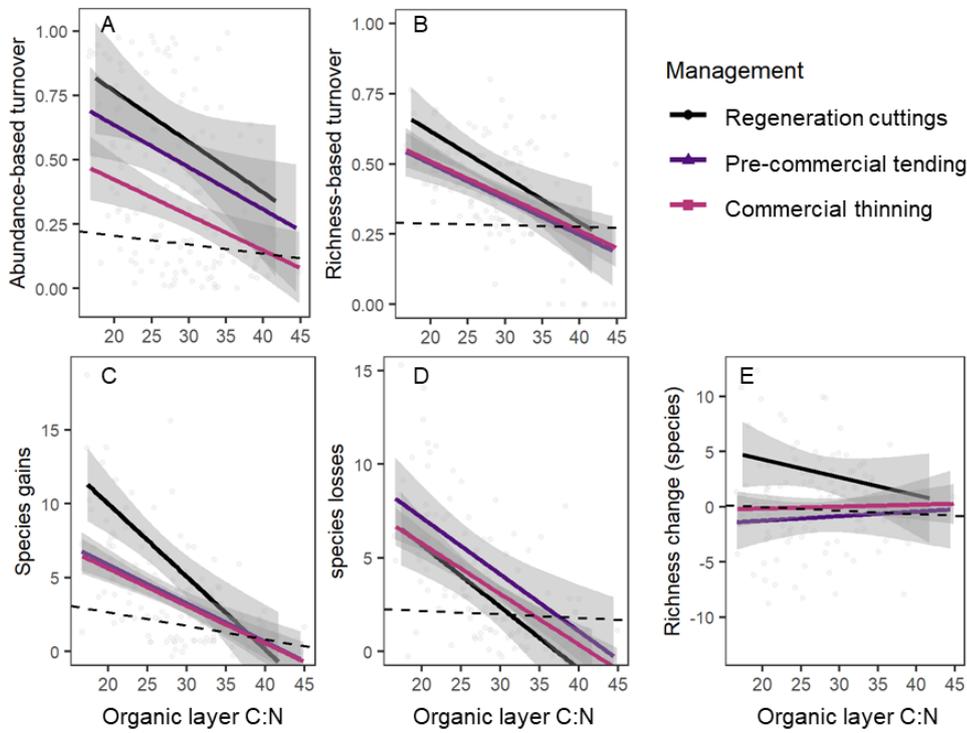
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617 **Figure 5.**



618

619 **Figure 6.**