

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

2 Authors: Kaarlejärvi Elina¹, Salemaa Maija², Tonteri Tiina², Merilä Päivi³ & Laine Anna-Liisa^{1,4}

¹Research Center for Ecological Change, Organismal and Evolutionary Biology Research Programme,
University of Helsinki, Helsinki, Finland

5 ²*Natural Resources Institute, Helsinki (Luke), Finland*

6 ³*Luke, Oulu, Finland*

7 ⁴University of Zürich, 8057 Zürich, Switzerland

8 **E-mail addresses:** elina.kaarlejarvi@helsinki.fi

9 maija.salemaa@luke.fi

10 tiina.tonteri@luke.fi

11 paivi.merila@luke.fi

12 anna-liisa.laine@ieu.uzh.ch

Statement of authorship: The field study was designed and carried out by The Natural Resources Institute Finland. TT and MS participated in organizing the data collection and preparing data for statistical analysis. EK defined the study questions, performed the data analysis and wrote the first draft of the manuscript, and all authors contributed to revisions.

17 Data accessibility statement:

18 Should the manuscript be accepted, the data supporting the results will be archived in Dryad repository and
19 the data DOI will be included at the end of the article.

20 **Running title:** Fertility, disturbance and temporal turnover

Key words: biodiversity change, forestry, nutrient, clearcut, gains, losses, silviculture, richness, succession, productivity

23 **Type of article:** Letters

24 **Number of words in the abstract:** 149

25 **Number of words in the main text:** 4972

26 **Number of words in each text box:** 0

27 **Number of references:** 67

28 **Number of figures, tables, and text boxes:** 6 figures, 0 tables, 0 text boxes

29 **Corresponding author:** Elina Kaarlejärvi, PO Box 65 (Viikinkaari 1), FI-00014 University of Helsinki,
30 FINLAND, tel: +358 50 5560 288, elina.kaarlejarvi@helsinki.fi

31

32

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.

45

46

47

48

49

50

51 **Introduction**

52 Anthropogenic pressure on the remaining ecosystems and their biodiversity is accelerating (Sala 2000; Arneth
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 8th 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 m² on circular 300 m² (1985-1986 and 1995) or 400
137 m² (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 m² 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 m² site.

141 In 2006, 10 or 20 subsamples were systematically collected with a cylinder (d = 60 mm) from
142 organic layer of 443 sites (400m², 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*

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

Calculating community indices

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

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

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

Results

Post-disturbance temporal turnover along a fertility gradient

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

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

403

404 **Acknowledgements**

We thank all field workers, laboratory and data management staff for their valuable work. The study was supported by funding from Jane and Aatos Erkko Foundation to the Research Centre for Ecological Change. The sampling in 2006 was co-funded by BioSoil project carried out under the Forest Focus scheme (Regulation (EC) Nr.2152/2003).

409

410 **References**

- Adler, P.B., White, E.P., Lauenroth, W.K., Kaufman, D.M., Rassweiler, A. & Rusak, J.A. (2005). Evidence for a General Species–Time–Area Relationship. *Ecology*, 86, 2032–2039.
- Anderson, K.J. (2007). Temporal Patterns in Rates of Community Change during Succession. *Am. Nat.*, 169, 780–793.
- Angelstam, P. & Kuuluvainen, T. (2004). Boreal Forest Disturbance Regimes, Successional Dynamics and Landscape Structures: A European Perspective. *Ecol. Bull.*, 117–136.

417 Arneeth, A. *et al.* (2019). Climate Change and Land, an IPCC special report on climate change, desertification,
 418 land degradation, sustainable land management, food security, and greenhouse gas fluxes in
 419 terrestrial ecosystems.

420 Bergeron, Y. & Dubue, M. (1988). Succession in the southern part of the Canadian boreal forest. *Vegetatio*,
 421 79, 51–63.

422 Blowes, S.A., Supp, S.R., Antão, L.H., Bates, A., Bruelheide, H., Chase, J.M., *et al.* (2019). The geography of
 423 biodiversity change in marine and terrestrial assemblages. *Science*, 366, 339–345.

424 Brown, M.J. & Parker, G.G. (1994). Canopy light transmittance in a chronosequence of mixed-species
 425 deciduous forests. *Can. J. For. Res.*, 24, 1694–1703.

426 Bunn, W.A., Jenkins, M.A., Brown, C.B. & Sanders, N.J. (2010). Change within and among forest
 427 communities: the influence of historic disturbance, environmental gradients, and community
 428 attributes. *Ecography*, 33, 425–434.

429 Chase, J.M., McGill, B.J., McGlinn, D.J., May, F., Blowes, S.A., Xiao, X., *et al.* (2018). Embracing scale-
 430 dependence to achieve a deeper understanding of biodiversity and its change across communities.
 431 *Ecol. Lett.*, 21, 1737–1751.

432 Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.

433 Chesson, P. & Huntly, N. (1997). The Roles of Harsh and Fluctuating Conditions in the Dynamics of
 434 Ecological Communities. *Am. Nat.*, 150, 519–553.

435 Chown, S.L., Gaston, K.J., Chown, S.L., Gaston, K.J., Chown, S.L. & Gaston, K.J. (2000). Areas, cradles and
 436 museums: the latitudinal gradient in species richness. *Trends Ecol. Evol.*, 15, 311–315.

437 Collins, S.L., Avolio, M.L., Gries, C., Hallett, L.M., Koerner, S.E., Pierre, K.J.L., *et al.* (2018). Temporal
 438 heterogeneity increases with spatial heterogeneity in ecological communities. *Ecology*, 99, 858–
 439 865.

440 Díaz, S., Settele, J., Brondízio, E., Ngo, H.T., Guèze, M., Agard, J., *et al.* (2019). Summary for policymakers of
 441 the global assessment report on biodiversity and ecosystem services of the Intergovernmental
 442 Science-Policy Platform on Biodiversity and Ecosystem Services, 45.

443 Edgar, G.J., Alexander, T.J., Lefcheck, J.S., Bates, A.E., Kininmonth, S.J., Thomson, R.J., *et al.* (2017).
 444 Abundance and local-scale processes contribute to multi-phyla gradients in global marine diversity.
 445 *Sci. Adv.*, 3, e1700419.

446 Eriksson, B.K. & Hillebrand, H. (2019). Rapid reorganization of global biodiversity. *Science*, 366, 308–309.

447 Finderup Nielsen, T., Sand-Jensen, K., Dornelas, M. & Bruun, H.H. (2019). More is less: net gain in species
 448 richness, but biotic homogenization over 140 years. *Ecol. Lett.*, 22, 1650–1657.

449 Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z. & Schepaschenko, D.G. (2015). Boreal forest
 450 health and global change. *Science*, 349, 819–822.

451 Gilliam, F.S. (2007). The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems.
 452 *BioScience*, 57, 845–858.

453 Grace, J.B., Anderson, T.M., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S., *et al.* (2016). Integrative
 454 modelling reveals mechanisms linking productivity and plant species richness. *Nature*, 529, 390–
 455 393.

456 Grime, J.P. (1974). Vegetation classification by reference to strategies. *Nature*, 250, 26–31.

457 Hallett, L., Avolio, M.L., Carroll, I.T., Jones, S.K., MacDonald, A.A.M., Flynn, D.F.B., *et al.* (2019). *codyn*:
 458 *Community Dynamics Metrics*.

459 Hart, S.A. & Chen, H.Y.H. (2006). Understory Vegetation Dynamics of North American Boreal Forests. *Crit.*
 460 *Rev. Plant Sci.*, 25, 381–397.

461 Hedwall, P.-O., Holmström, E., Lindblad, M. & Felton, A. (2019). Concealed by darkness: How stand density
 462 can override the biodiversity benefits of mixed forests. *Ecosphere*, 10, e02835.

463 Heikkinen, J. & Mäkipää, R. (2010). Testing hypotheses on shape and distribution of ecological response
 464 curves. *Ecol. Model.*, 221, 388–399.

465 Hillebrand, H., Blasius, B., Borer, E.T., Chase, J.M., Downing, J.A., Eriksson, B.K., *et al.* (2018). Biodiversity
 466 change is uncoupled from species richness trends: Consequences for conservation and monitoring.
 467 *J. Appl. Ecol.*, 55, 169–184.

468 Hillebrand, H., Soininen, J. & Snoeijs, P. (2010). Warming leads to higher species turnover in a coastal
469 ecosystem. *Glob. Change Biol.*, 16, 1181–1193.

470 Hodapp, D., Borer, E.T., Harpole, W.S., Lind, E.M., Seabloom, E.W., Adler, P.B., *et al.* (2018). Spatial
471 heterogeneity in species composition constrains plant community responses to herbivory and
472 fertilisation. *Ecol. Lett.*, 21, 1364–1371.

473 Jaccard, P. (1912). The Distribution of the Flora in the Alpine Zone.1. *New Phytol.*, 11, 37–50.

474 Johnson, D.W. & Curtis, P.S. (2001). Effects of forest management on soil C and N storage: meta analysis.
475 *For. Ecol. Manag.*, 140, 227–238.

476 Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J.V., Grainger, A. & Lindquist, E. (2015). Dynamics of global
477 forest area: Results from the FAO Global Forest Resources Assessment 2015. *For. Ecol. Manag.*,
478 Changes in Global Forest Resources from 1990 to 2015, 352, 9–20.

479 Komatsu, K.J., Avolio, M.L., Lemoine, N.P., Isbell, F., Grman, E., Houseman, G.R., *et al.* (2019). Global change
480 effects on plant communities are magnified by time and the number of global change factors
481 imposed. *Proc. Natl. Acad. Sci.*, 116, 17867–17873.

482 Korhonen, J.J., Soininen, J. & Hillebrand, H. (2010). A quantitative analysis of temporal turnover in aquatic
483 species assemblages across ecosystems. *Ecology*, 91, 508–517.

484 Kuuluvainen, T., Hokkanen, T.J., Järvinen, E. & Pukkala, T. (1993). Factors related to seedling growth in a
485 boreal Scots pine stand: a spatial analysis of a vegetation–soil system. *Can. J. For. Res.*, 23, 2101–
486 2109.

487 Landuyt, D., Lombaerde, E.D., Perring, M.P., Hertzog, L.R., Ampoorter, E., Maes, S.L., *et al.* (2019). The
488 functional role of temperate forest understorey vegetation in a changing world. *Glob. Change Biol.*,
489 25, 3625–3641.

490 Lefcheck, J., Byrnes, J. & Grace, J. (2018). *piecewiseSEM: Piecewise Structural Equation Modeling*.

491 Lorenz, M. & Fischer, R. (2013). Pan-European Forest Monitoring. In: *Developments in Environmental*
492 *Science*. Elsevier, pp. 19–32.

493 Magurran, A.E., Dornelas, M., Moyes, F. & Henderson, P.A. (2019). Temporal β diversity—A macroecological
494 perspective. *Glob. Ecol. Biogeogr.*, 28, 1949–1960.

495 Magurran, A.E. & Henderson, P.A. (2003). Explaining the excess of rare species in natural species
496 abundance distributions. *Nature*, 422, 714–716.

497 Maliniemi, T., Happonen, K. & Virtanen, R. (2019). Site fertility drives temporal turnover of vegetation at
498 high latitudes. *Ecol. Evol.*

499 Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear
500 mixed-effects models. *Methods Ecol. Evol.*, 4, 133–142.

501 Nieppola, J. (1992). Long-term vegetation changes in stands of *Pinus sylvestris* in southern Finland. *J. Veg.*
502 *Sci.*, 3, 475–484.

503 Nilsson, M.-C. & Wardle, D.A. (2005). Understorey vegetation as a forest ecosystem driver: evidence from
504 the northern Swedish boreal forest. *Front. Ecol. Environ.*, 3, 421–428.

505 Olsson, B.A., Staaf, H., Lundkvist, H., Bengtsson, J. & Kaj, R. (1996). Carbon and nitrogen in coniferous forest
506 soils after clear-felling and harvests of different intensity. *For. Ecol. Manag.*, 82, 19–32.

507 Peltola, A., Ihalainen, A., Mäki-Simola, E., Sauvula-Seppälä, T., Torvelainen, J., Uotila, E., *et al.* (2019).
508 *Suomen metsätilastot - Finnish forest statistics 2019*. Natural Resources Institute Finland.

509 Peters, M.K., Hemp, A., Appelhans, T., Behler, C., Classen, A., Detsch, F., *et al.* (2016). Predictors of
510 elevational biodiversity gradients change from single taxa to the multi-taxa community level. *Nat.*
511 *Commun.*, 7, 1–11.

512 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2020). *nlme: Linear and Nonlinear Mixed*
513 *Effects Models*.

514 Potapov, P., Hansen, M.C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., *et al.* (2017). The last
515 frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. *Sci. Adv.*, 3,
516 e1600821.

517 R development core team. (2019). *R: A language and environment for statistical computing*. R Foundation
518 for Statistical Computing, Vienna, Austria.

519 Rees, D.C. & Juday, G.P. (2002). Plant species diversity on logged versus burned sites in central Alaska. *For.*
520 *Ecol. Manag.*, Forest Ecology in the next Millennium : Putting the long view into Practice, 155, 291–
521 302.

522 Reinikainen, A., Mäkipää, R., Vanha-Majamaa, I. & Hotanen, J.-P. (Eds.). (2000). *Kasvit muuttuvassa*
523 *metsäluonnossa [Summary in English: Changes in the Frequency and Abundance of Forest and Mire*
524 *Plants in Finland Since 1950]*. Kustannusosakeyhtiö Tammi, Jyväskylä.

525 Ricklefs, R.E. (1987). Community diversity: relative roles of local and regional processes. *Science*, 235, 167–
526 171.

527 Sala, O.E. (2000). Global Biodiversity Scenarios for the Year 2100. *Science*, 287, 1770–1774.

528 Shurin, J.B., Arnott, S.E., Hillebrand, H., Longmuir, A., Pinel-Alloul, B., Winder, M., *et al.* (2007). Diversity–
529 stability relationship varies with latitude in zooplankton. *Ecol. Lett.*, 10, 127–134.

530 Taylor, S.J.S., Evans, B.S., White, E.P. & Hurlbert, A.H. (2018). The prevalence and impact of transient
531 species in ecological communities. *Ecology*, 99, 1825–1835.

532 Tedersoo, L., Bahram, M., Pölme, S., Kõljalg, U., Yorou, N.S., Wijesundera, R., *et al.* (2014). Global diversity
533 and geography of soil fungi. *Science*, 346, 1256688.

534 Thrush, S.F., Halliday, J., Hewitt, J.E. & Lohrer, A.M. (2008). The Effects of Habitat Loss, Fragmentation, and
535 Community Homogenization on Resilience in Estuaries. *Ecol. Appl.*, 18, 12–21.

536 Tonteri, T. (1994). Species richness of boreal understorey forest vegetation in relation to site type and
537 successional factors. *Ann. Zool. Fenn.*, 31, 53–60.

538 Tonteri, T., Salemaa, M., Rautio, P., Hallikainen, V., Korpela, L. & Merilä, P. (2016). Forest management
539 regulates temporal change in the cover of boreal plant species. *For. Ecol. Manag.*, 381, 115–124.

540 UNEP, FAO & UNFF (Eds.). (2009). *Vital forest graphics*. UNEP, Nairobi, Kenya.

541 Vanha-Majamaa, I., Shorohova, E., Kushnevskaya, H. & Jalonen, J. (2017). Resilience of understory
542 vegetation after variable retention felling in boreal Norway spruce forests – A ten-year perspective.
543 *For. Ecol. Manag.*, 393, 12–28.

544 Venäläinen, A., Tuomenvirta, H., Pirinen, P. & Drebs, A. (2005). A basic Finnish climate data set 1961–2000-
545 description and illustration. *Finn. Meteorol. Inst. Rep.*, 2005, 27.

546 Virtanen, R., Luoto, M., Rämä, T., Mikkola, K., Hjort, J., Grytnes, J.-A., *et al.* (2010). Recent vegetation
547 changes at the high-latitude tree line ecotone are controlled by geomorphological disturbance,
548 productivity and diversity. *Glob. Ecol. Biogeogr.*, 19, 810–821.

549 Xu, Z., Wan, S., Ren, H., Han, X., Li, M.-H., Cheng, W., *et al.* (2012). Effects of Water and Nitrogen Addition
550 on Species Turnover in Temperate Grasslands in Northern China. *PLoS ONE*, 7.

551 Zhang, M., Chen, F., Shi, X., Yang, Z. & Kong, F. (2018). Association between temporal and spatial beta
552 diversity in phytoplankton. *Ecography*, 41, 1345–1356.

553 Zobel, M. (1989). Secondary forest succession in Jarvselja, southern Estonia: changes in field layer
554 vegetation. *Ann. Bot. Fenn.*, 26, 171–182.

555 Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009). *Mixed Effects Models and Extensions in*
556 *Ecology with R*. Springer Science & Business Media.

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.

600

601

602

603

604

605

606

607

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

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

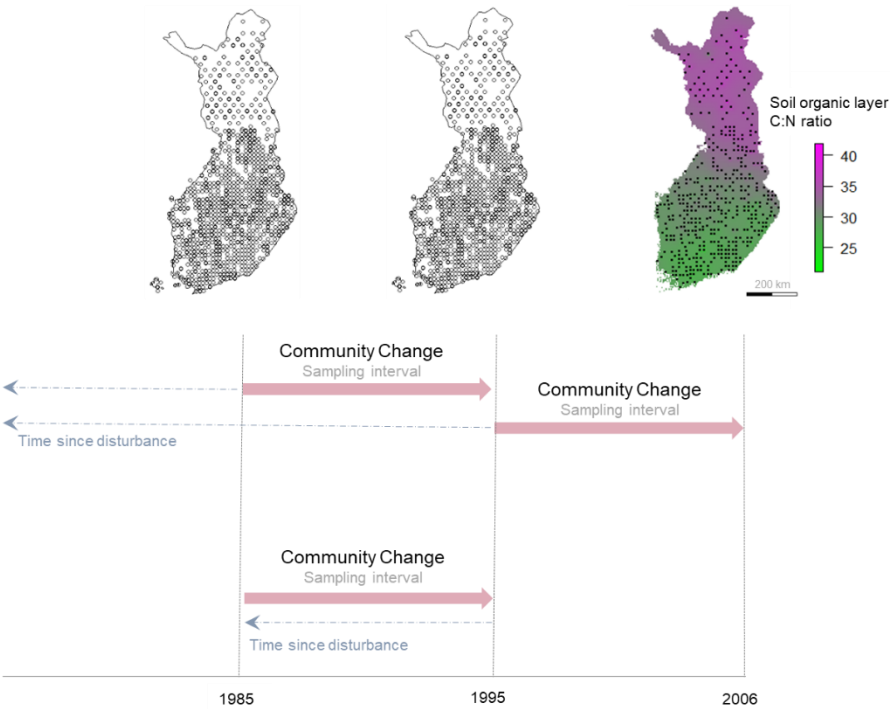
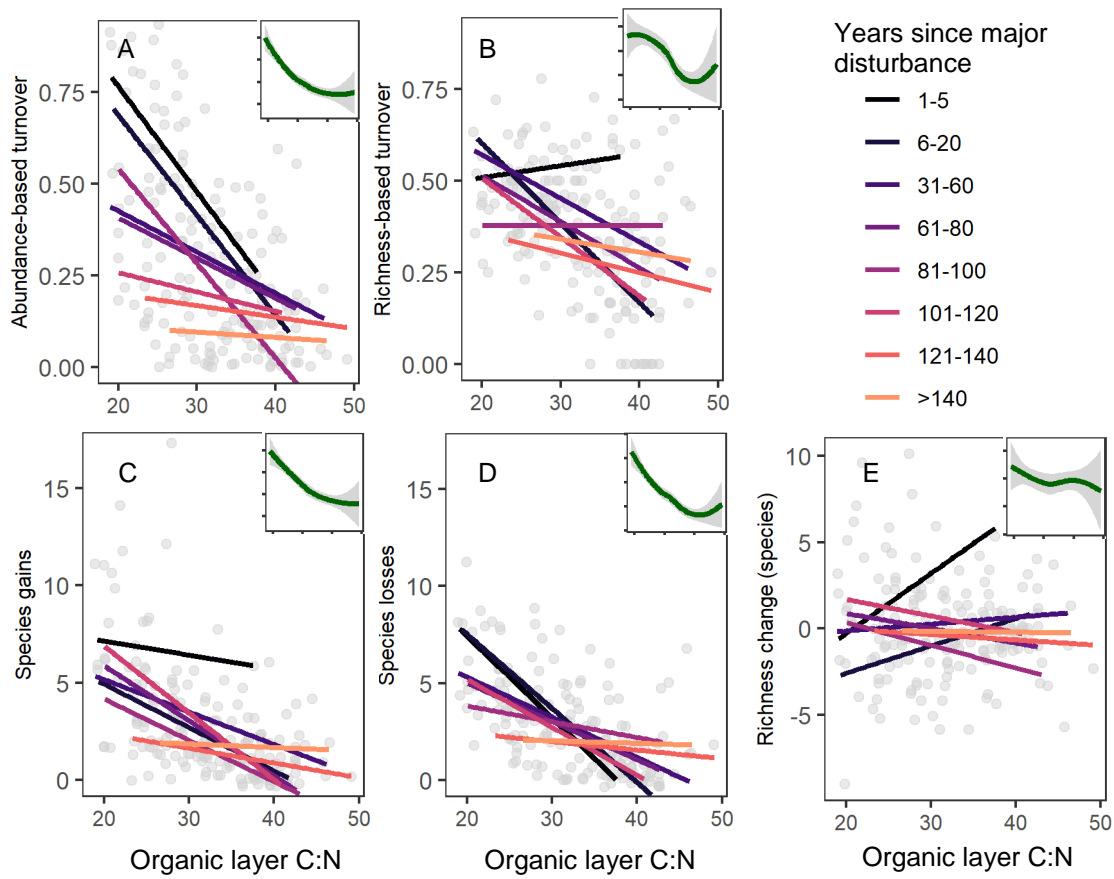
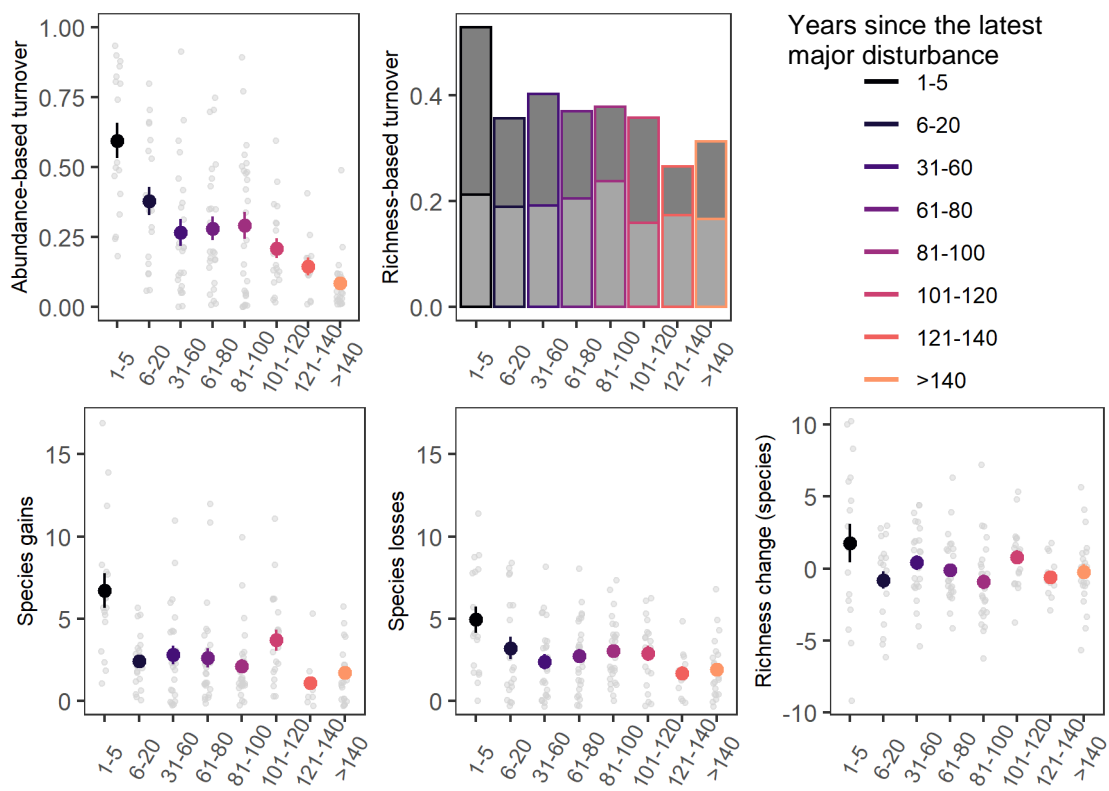


Figure 1.



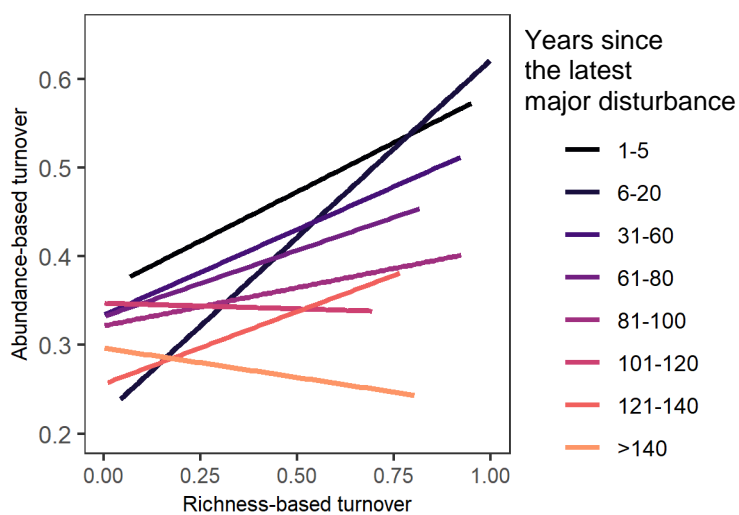
608

609 **Figure 2.**



610

611 **Figure 3.**

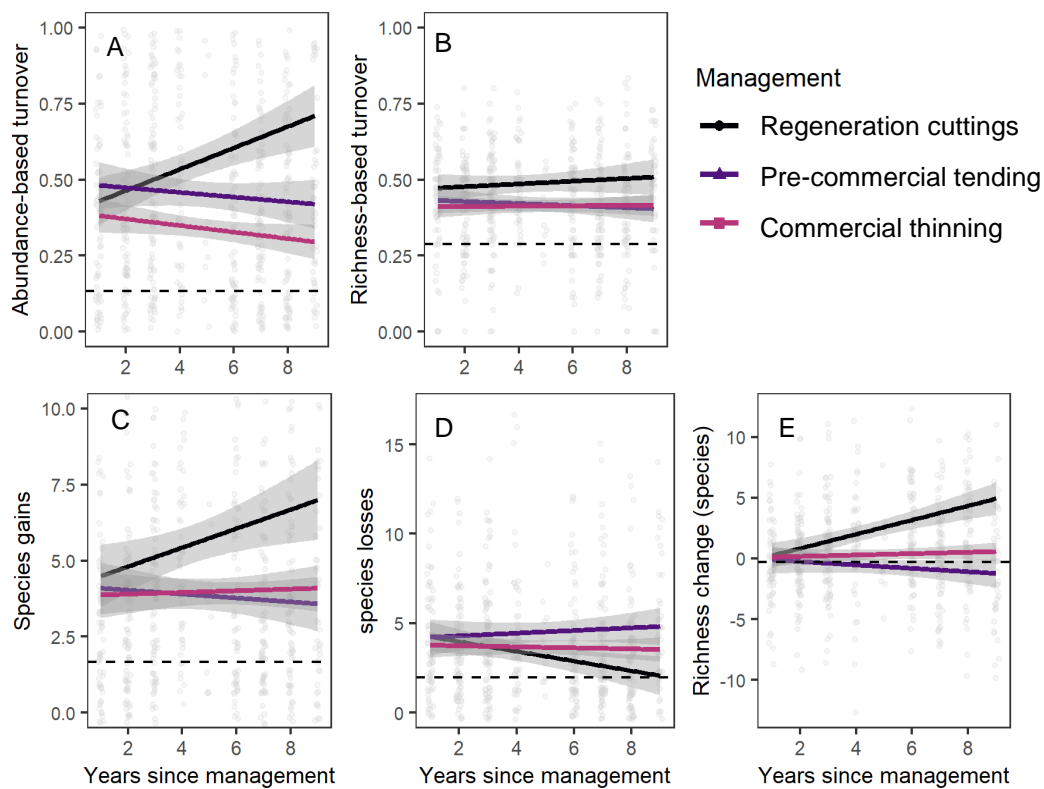


612

613 **Figure 4.**

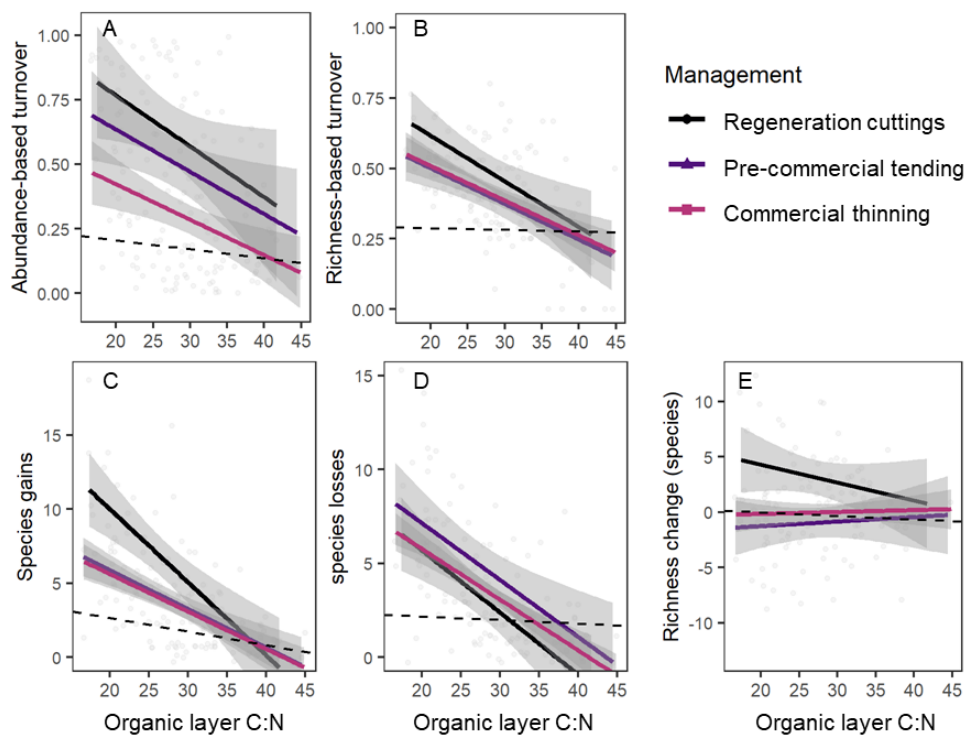
614

615



616

617 **Figure 5.**



618

619 **Figure 6.**