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The mechanistic basis of changes in community assembly in relation to anthropogenic disturbance and productivity

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Abstract. Anthropogenic disturbance often causes changes in communities. However, the mechanistic basis of these changes remains elusive. As all patterns in community ecology can be understood as a result of four processes (speciation, selection, drift, and dispersal), the effect of disturbance should depend on how disturbance disrupt these processes. We studied the effects of disturbance and productivity on species richness, community composition, and community dispersion (i.e., variation in community composition) in the vegetation of 120 boreal peatlands using null-model approach to determine whether community assembly processes differ between pristine and disturbed sites. Sites represented three peatland ecosystem types, each with two levels of productivity. Half of the sites were disturbed by drainage and half are pristine. Pristine and disturbed sites showed similar species richness. However, their community composition differed indicating a directional selection due to disturbance, whereas dispersion of disturbed and pristine communities did not differ suggesting no change in the relative strength of selection and drift. Our results suggest that understanding the combination of landscape level community changes and local selection pressures is important when restoration of degraded ecosystems is undertaken.

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INTRODUCTION

In the human-dominated world the natural drivers of species diversity, such as productivity and habitat heterogeneity, have been accompanied by anthropogenic disturbance resulting in increased extinction rates at global scale (Barnosky et al. 2011). In addition to losses of biodiversity, anthropogenic disturbance may hamper ecosystem function (Hooper et al. 2012), resulting even in ecosystem collapse (MacDougall et al. 2013). In disturbance studies species richness has been a common measure of diversity (Murphy and Romanuk 2014). However, as species losses may be coupled with immigration, global decrease in species richness does not necessarily result in local decreases in species richness (Sax and Gaines 2003, Vellend et al. 2013). Moreover, species richness provides limited information on processes that cause changes within and between communities (Mendenhall et al. 2012). Ultimately, how disturbance affects species diversity depends on community assembly processes and on whether disturbance disrupts the processes or not.

All patterns in community ecology can be understood as a result of four processes: speciation, selection, drift, and dispersal (Vellend 2010). In addition, community assembly processes have been commonly divided to stochastic (Hubbell 2001, Chase 2010) and deterministic (Tuomisto et al. 2003, Gilbert and Lechowicz 2004) ones. Speciation adds new species to the regional species pool from where they add to local communities either by deterministic or stochastic processes. Our focus here is on ecological time scales and thus we do not consider speciation. By definition, at the community level selection is a deterministic process leading into fitness differences among individuals of different species, and drift is a stochastic process leading into random changes in species relative abundances and following random extinctions. In contrast, although dispersal is often considered to be stochastic limited only by distance (Tuomisto et al. 2003) it is also likely to have a deterministic component (Spiegel and Nathan 2012). Although the relative importance of stochastic (drift, random dispersal) and deterministic processes (selection, selective dispersal) in community assembly process are a subject of debate, it is clear that both of them are important (Ricklefs 1987, Cottenie 2005, Chase and Myers 2011).

Insights on how and by which mechanisms disturbance influences community assembly process can be gained by determining how disturbance influences community dispersion. Community dispersion is variation in community composition among sites, often considered also as beta diversity (Passy and Blanchet 2007, Vellend et al. 2007, Houseman et al. 2008, Murphy and Romanuk 2012). In communities shaped mainly by selection, disturbance may change the direction or magnitude of selection by changing, for instance, local environmental conditions. This may lead to either increased or decreased dispersion, depending on whether the effect of disturbance on local environmental conditions and thus on selection is uniform across the sites. Also, disturbance may result in a change in the relative importance of selection and drift. For instance, disturbance may filter species out of the regional species pool thus increasing the relative importance of selection and decreasing community dispersion [(Chase 2007) but see (Lepori and Malmqvist 2009)]. Disturbance may also limit

dispersal that can result in decreased community dispersion (Vellend et al. 2007). Drift and selection may also interact: small random differences in initial communities may lead to great differences after disturbance (i.e., priority effects [Chase 2007]), and ultimately divergence to multiple states (Houseman et al. 2008).

Productivity-related variables have been found to be major predictors of species richness (Field et al. 2009 but see Adler et al. 2011) and thus it is perhaps not surprising that they have been suggested to interact with disturbance in determining species richness (Huston 1994, Kondoh 2001, Cardinale et al. 2006). Moreover, productivity seems to increase also community dispersion at large scales (He and Zhang 2009). At local scales increased dispersion in highly productive sites has been suggested to be a result of increased relative importance of stochastic processes rather than higher magnitude of among-site habitat heterogeneity, which could in theory increase dispersion in communities shaped by selection (Chase 2010). Thus, both productivity and disturbance may change the relative importance of drift and selection but in opposite directions: productivity increases relative importance of drift, whereas disturbance increases the relative importance of selection (Chase 2007, 2010). Indeed, disturbance and productivity have been shown also empirically to interact in shaping community dispersion (Houseman et al. 2008).

Here, we determine the mechanistic basis of the effect of anthropogenic disturbance and ecosystem productivity on species richness, community composition, and community dispersion (i.e., variation in community composition) in a large scale well replicated comparative field study of 120 study sites across Finland. Our three focal ecosystems are boreal peatlands (spruce mires, pine mires, fens) where we concentrated on bryophyte and vascular plant communities. Each of the ecosystem types were further divided into high productivity and low productivity sites. In our balanced design half of the sites are in a pristine state and the other half have been disturbed by drainage to increase the timber production for forestry. First, we asked if species richness differs between disturbed and pristine sites, and whether the possible changes in species richness are related to the productivity of

the ecosystem. Second, we used a null-model approach to determine whether disturbed and pristine sites are more, less or as dissimilar as can be expected given random distribution of individuals from their species pool. We then used observed deviations from the expected community composition and dispersion to determine whether disturbance causes directional selection to deviate the disturbed sites from the pristine ones and/or whether the relative strength of selection and drift remains constant.

MATERIALS AND METHODS

Study sites and setup

We used bryophyte and vascular plant data from 120 peatlands from National Peatland Restoration Monitoring Network established by Parks & Wildlife Finland and University of Jyväskylä. The data were collected during the years 2007–2010. The sites are located in the southern, central, and northern boreal climatic-phytogeographical zones and represent geographical variation from 66°86′ N to 74°38′ N and 32°24′ E to 36°91′ E (see Appendix S1: Fig. S1). Half of the sites are in a pristine state and the other half have been drained for forestry several decades ago, during 1960s and 1970s. In a few drained sites the ditches have been since cleared to avoid natural overgrowth by bryophytes. The study represents a balanced comparative design where, in addition to the pristine/drained division, the sites are divided among three ecosystem types (spruce mires, pine mires, fens) each of which are further divided according to their productivity (low, high). This division results in 12 groups: (1) pristine low productivity spruce mires (n = 10), (2) drained low productivity spruce mires (n = 10), (3) pristine high productivity spruce mires (n = 9 for bryophyte analyses and n = 10 for vascular plant analyses), (4) drained high productivity spruce mires (n = 9 for bryophyte analyses and 10 for vascular plant analyses), (5) pristine low productivity pine mires (n = 10), (6) drained low productivity pine mires (n = 10), (7) pristine high productivity pine mires (n = 10), (8) drained high productivity pine mires (n = 10), (9) pristine low productivity fens (n = 9), (10) drained low productivity fens (n = 10), (11) pristine high productivity fens (n = 11), and (12) drained high productivity fens (n = 10).

Our study setup represents classical space-for-time substitution (i.e., chronosequence), and in designing these setups care must be taken to allow drawing strong inferences (Johnson and Miyanishi 2008). However, in very large scale long-term well replicated disturbance ecological studies in natural settings such as ours, space-for-time substitution is the best option available: to study the effect of drainage on peatlands as true experiments at this scale would be extremely expensive and ethically questionable. Therefore, in designing the study special attention was paid to replication and the selection of the sites to ensure that the groups reflect natural variation in the selected ecosystem types. The candidate sites were chosen based on extensive search on old pre-drainage aerial photographs combined with inspection of newer aerial photographs, and the final suitability for the study was confirmed by on site field observations. Hydrological independency of the sites was confirmed from topographic data combined with field observations.

Productivity of the sites (low, high) was estimated from the aerial photographs as distinct features of tree and shrub growth. If necessary, the productivity classification was confirmed on site as suggested by Økland et al. (2001) based on the occurrence of certain indicator species (these observations are not from data used in the analyses presented here). In addition to correlating with nutrient availability, productivity in peatlands is strongly associated with pH (Tahvanainen 2004). It must be noted that productivities between ecosystem types are not directly comparable: for instance, productivity in low productivity spruce mires is higher than that in low productivity fens.

Drainage for forestry causes an extensive ecosystem level disturbance on peatlands. The major effect of drainage is immediate water level drawdown by 20–60 cm (Laine and Vanha-Majamaa 1992, Haapalehto et al. 2014) cutting off the original flow of minerogenic water from the surrounding water shed. This in turn cuts off the supply of nutrients to the peatland while also resulting in leaching of nutrients from the peat layer to the downstream water courses or to uptake of nutrients by the newly growing trees in the drained peatland. In addition, peat pH decreases

(Laine et al. 1995). The loss of nutrients and decrease in pH are more pronounced in originally productive sites and thus the original differences between sites having different productivities may be diminished (Laine et al. 1995).

A set-up of 10 of 1-m² sample plots was established at each site. The plots were systematically situated in two parallel lines at both sides of the base line, 4 m apart from each other. The base line was situated parallel to ditches (in drained sites), representing typical vegetation to the site in question. The minimum distance to the nearest ditch was set to 10 m. The location of the first plot was randomized given the restrictions above. Abundance as a percent cover for all plant species was recorded from each 1-m² sample plot based on visual estimation at the accuracy of one percent (a cover of 0.5% was used for all species with a cover of 0.9–0.5%, and a cover of 0.2% for species with a cover <0.5%). For each species the mean abundance in 10 plots was used in further analyses, that is, data were pooled to a site-level data. This resulted in a minimum abundance of 0.02% for each species.

Statistical analyses

All analyses were performed separately for bryophytes and vascular plants, and for each ecosystem type to avoid three-way interactions. In species richness analyses we used two-way ANOVA where productivity (low, high), disturbance (pristine, drained) and their interaction were set as independent factors. When the assumption of homogeneity of variances was violated we incorporated variance heterogeneity into the model directly by using linear mixed models (Zuur et al. 2009). The 2-ANOVAs were conducted with IBM SPSS Statistics for Windows (version 20.0; IBM, Armonk, New York, USA).

In analyzing community composition we used null-model approach (Crist et al. 2003, Chase and Myers 2011, Kraft et al. 2011, Myers et al. 2013). Our null model assumes that community composition is not limited by environmental conditions or dispersal but shaped by drift and random unlimited dispersal instead. First, we defined the regional species pool as total number of species and their total abundance observed in a given ecosystem type. Then we calculated observed dissimilarity between each pair of sites within an ecosystem type using incidence-based Sørensen's

dissimilarity index. Next, we simulated expected Sørensen's dissimilarity between each pair of sites by randomly sampling units from the regional species pool while preserving the relative abundance of each species and observed abundance in each site. We considered percent cover of 0.01% as one unit and thus a species with a minimum cover of 0.02% had abundance of two units. From 999 iterations we calculated the standardized effect size (dissimilarity deviation) as the difference between observed dissimilarity and mean expected dissimilarity divided by the standard deviation of the expected values. A deviation of zero indicates that observed dissimilarity does not differ from random sampling: a deviation lower than zero indicates less dissimilar than expected by random chance, and a deviation higher than zero indicates more dissimilar than expected by random chance. If productivity, disturbance or their interaction had an effect on dissimilarity deviation this would indicate the effect of selection and/or limited dispersal.

To test whether productivity, disturbance or their interaction had an effect on observed dissimilarity or on dissimilarity deviation we used two-way permutational multivariate analysis of variance (PERMANOVA) which is a nonparametric test relying on permutations and can be based on any dissimilarity measure (Anderson 2001). The test is sensitive to differences in the dispersion of sites, even though the locations (i.e., mean community composition) do not differ (Anderson 2001). Thus, to infer whether community dispersions differ among the four groups (pristine low productivity, drained low productivity, pristine high productivity, drained high productivity) we used the distance-based test for homogeneity of multivariate dispersions (Anderson 2006). It is essentially a multivariate extension of Levene's test of homogeneity and can be based on any distance or dissimilarity measure. The procedure counts the distance of each site to multivariate centroid of the group, and statistical significance is tested by permutation of residuals (999 permutations) (Anderson 2006). PERMANOVA analyses were done with "adonis" function and multivariate dispersion with "betadisper" function in the "vegan" package (Oksanen et al. 2013) in R (R Development Core Team 2013). Neither PERMANOVA nor distance-based test for homogeneity of multivariate dispersion

allows negative values. A few negative values per group for dissimilarity deviation occurred (Fig. 2c) and thus the values were re-scaled to have a minimum of zero for these analyses.

Our null model expects no dispersal limitation, that is, sites closer to each other have the same probability of sharing species than sites further apart. In the case that sites of different productivity and disturbance status differ in their spatial location, this assumption may cause erroneous conclusions of the importance of productivity and disturbance in our analyses. Thus, we used distance-based redundancy analysis (dbRDA) (Legendre and Anderson 1999) to verify that productivity, disturbance and their interaction do not explain variance after spatial variables have been taken into account. First, we searched the spatial variables which best explained the variation in the data by forward selection ("ordiR2step" function in the "vegan" package) of the available spatial variables which were geographic coordinates of the sites (latitude, longitude) and the spatial eigenfunctions with positive eigenvalues from the Principal Components of Neighbor Matrices (PCNM) (Borcard and Legendre 2002). The effect of the selected spatial variables was then "partialled" out before testing the effect of productivity, disturbance and their interaction on observed dissimilarity and dissimilarity deviation ("capscale" function in the "vegan" package). In the case of dispersion, we would expect that if the groups differ in their spatial dispersion this could cause erroneous conclusions. Thus, we also ran the test of multivariate dispersions using Euclidian distances as a dissimilarity measure to ensure that the groups did not differ in their spatial dispersion.

Results

Species richness of both bryophytes and vascular plants was related to productivity but not to disturbance in almost all peatland ecosystem types (Fig. 1, Appendix S2: Table S1). There were two exceptions: in bryophytes at spruce mires neither productivity nor disturbance had an effect on species richness, and in vascular plants at pine mires there was a significant, albeit a weak, interaction between productivity and disturbance (Fig. 1, Appendix S2: Table S1).

Observed dissimilarity was related to productivity and disturbance but not to their interaction

in all peatland ecosystem types and both species groups (Table 1). As expected, dissimilarity deviations in all the ecosystem types were positive showing that sites within a given ecosystem type had greater dissimilarity than expected by the null model (Fig. 2). In congruence with observed dissimilarity, dissimilarity deviations were also related to both disturbance and productivity but not to their interaction (Table 1). The effect was not an artifact of dispersal limitation or spatially autocorrelated environmental variables because disturbance, productivity and their interaction explained variance after the effect of spatial variables had been taken into account (Appendix S2: Table S2). Results with dissimilarity deviations were highly similar compared to observed dissimilarities, and they differed only for bryophytes in spruce mires where disturbance was a significant factor when observed dissimilarity was analyzed, but not when dissimilarity deviation was analyzed (Table 1).

For a given ecosystem type the four groups (pristine low productivity, drained low productivity, pristine high productivity, drained high productivity) showed no differences in multivariate dispersions, except for vascular plants in spruce mires and in pine mires, and the results were similar between observed dissimilarity and dissimilarity deviation (Fig. 3, Appendix S2: Table S3). In spruce mires pristine high productivity sites had larger dispersion than drained low productivity sites (Fig. 3, Appendix S2: Table S3). In pine mires drained high productivity sites showed greater dispersion compared to pristine low productivity sites. Thus, the results from PERMANOVA of vascular plants in spruce mires and pine mires are partly affected by the different dispersions of these groups. The groups in all of the ecosystem types showed homogeneity of dispersion based on Euclidian distances (Appendix S2: Table S4).

Discussion

We observed no changes in species richness between the pristine and disturbed sites nicely illustrating that the effects of disturbance do not necessarily show as changes in local species richness (see also Sax and Gaines 2003, Vellend et al. 2013). However, bryophyte and vascular plant communities at disturbed sites were
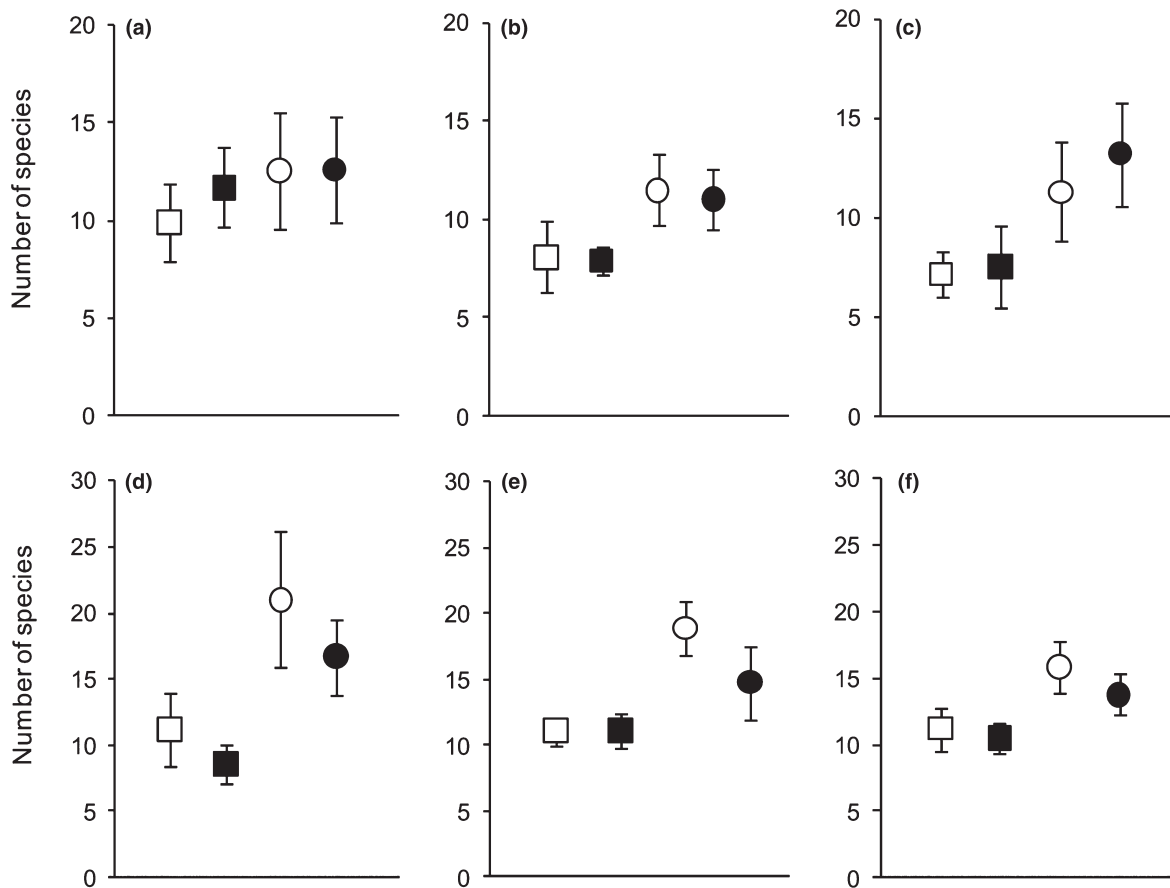
Fig. 1. Species richness (mean and 95% confidence intervals) of bryophytes in (a) spruce mires, (b) pine mires, and (c) fens, and vascular plants in (d) spruce mires, (e) pine mires, and (f) fens within different productivity levels (squares refer to low productivity sites and circles to high productivity sites) and disturbance (open symbols refer to pristine sites and filled symbols to drained sites). Note the differences in the scale of y-axes between (a–c) bryophytes and (d–f) vascular plants.

different from those at pristine sites. Changes in community composition were similar across the three ecosystem types studied, and whether analyzed by observed dissimilarity or by dissimilarity deviation, indicating that the effects were not due to random sampling of individuals from the regional species pool. This indicates that selection, most likely based on changed hydrology, pH and nutrient gradients, strongly shape many different peatland communities after disturbance. The importance of selection is supported also by the fact that vascular plants and bryophytes showed very similar responses: drift and random dispersal cannot explain the congruent patterns of these phylogenetically independent plant groups (Tuomisto et al. 2003).

As dissimilarity deviation was based on the null model of drift accompanied by unlimited dispersal we can not fully dissect between their effects. However, our spatial analysis showed that dispersal limitation and spatially autocorrelated environmental variables did not account for differences in community composition but that the differences were also related to disturbance and productivity. Moreover, the treatment groups were not different on their spatial dispersion. Thus, for dispersal limitation to be able to be the reason for these differences, it should be dependent on productivity and disturbance. Although dispersal clearly can be selective (Spiegel and Nathan 2012) we are unable to come up with any reasonable causality how dispersal could be

Table 1. PERMANOVA analyses on the effect of productivity (low, high), disturbance (pristine, drained) and their interaction on observed dissimilarity and dissimilarity deviation of bryophytes and vascular plants in different ecosystem types (spruce mires, pine mires, fens).

Dependent variable	Productivity		Disturbance		Productivity × disturbance	
	F_{df}	P	F_{df}	P	F_{df}	P
Observed dissimilarity						
Bryophytes						
Spruce mires	$4.1_{1,34}$	<0.001	$5.1_{1,34}$	<0.001	$1.0_{1,34}$	0.387
Pine mires	$8.6_{1,36}$	<0.001	$10.1_{1,36}$	<0.001	$0.8_{1,36}$	0.578
Fens	$8.8_{1,36}$	<0.001	$6.5_{1,36}$	<0.001	$1.8_{1,36}$	0.105
Vascular plants						
Spruce mires	$6.6_{1,36}$	<0.001	$2.4_{1,36}$	0.023	$1.7_{1,36}$	0.086
Pine mires	$10.8_{1,36}$	<0.001	$7.3_{1,36}$	<0.001	$0.5_{1,36}$	0.797
Fens	$9.5_{1,36}$	<0.001	$9.6_{1,36}$	<0.001	$1.5_{1,36}$	0.150
Dissimilarity deviation						
Bryophytes						
Spruce mires	$4.7_{1,34}$	<0.001	$1.9_{1,34}$	0.103	$1.9_{1,34}$	0.100
Pine mires	$10.0_{1,36}$	<0.001	$11.4_{1,36}$	<0.001	$0.8_{1,36}$	0.576
Fens	$9.3_{1,36}$	<0.001	$6.0_{1,36}$	<0.001	$2.4_{1,36}$	0.046
Vascular plants						
Spruce mires	$6.0_{1,36}$	<0.001	$2.0_{1,36}$	0.056	$2.3_{1,36}$	0.031
Pine mires	$14.6_{1,36}$	<0.001	$8.3_{1,36}$	<0.001	−0.3	0.985
Fens	$11.2_{1,36}$	<0.001	$10.5_{1,36}$	<0.001	$1.4_{1,36}$	0.273

Note: F values, degrees of freedom (df) and statistical significance (*P*) from permutation analyses.

limited by the productivity or disturbance of the peatland. If dispersal is different depending on the productivity or disturbance status it is most likely that it interacts with selection (Vellend et al. 2014).

High productivity sites encompassed higher species richness, adding to the body of literature providing evidence for the importance of productivity-related variables in determining species richness (Field et al. 2009). There was generally no interaction between disturbance and productivity in determining species richness. This seems to contradict previous studies showing that biological disturbance such as grazing can lead to increased species richness in nutrient high environments, and decreased species richness in nutrient low environments (Proulx and Mazumder 1998). However, our result is in line with a few other studies suggesting that the effect of physical disturbance, as opposed to that of biological disturbance, is not dependent on the productivity level (Kneitel and Chase 2004, Svensson et al. 2010). In addition to biological disturbance being perhaps more selective, the difference may also be due to the way the damage by the disturbance is attributed. If biomass is slowly reduced by grazing it may be easily compensated by increased growth of damaged individuals in high productivity environments (Kondoh 2001), whereas the effect of physical disturbance, such as constant drying, cannot be compensated, irrespective of whether nutrients needed for growth are available or not (Kneitel and Chase 2004, Svensson et al. 2010). In other words, drainage may benefit the growth of species suffering for excess water supply, such as trees and shrubs (the very reason for why drainage for forestry had been performed at the first place) and thus increases their productivity while decreasing the productivity of species adapted to the original wetland conditions.

Besides having lower species richness compared to high productivity sites, low productivity sites had also different community composition. Thus, communities in low productivity sites were not random subsets from those of high productivity sites, in contrast to results of Chase (2010). Generally high productivity sites did not show increased dispersion compared to low productivity sites which contradicts several other studies (Houseman et al. 2008, Chase 2010). Thus, our results illustrate that high productivity does not necessarily promote higher species dissimilarity in concert with higher species richness.
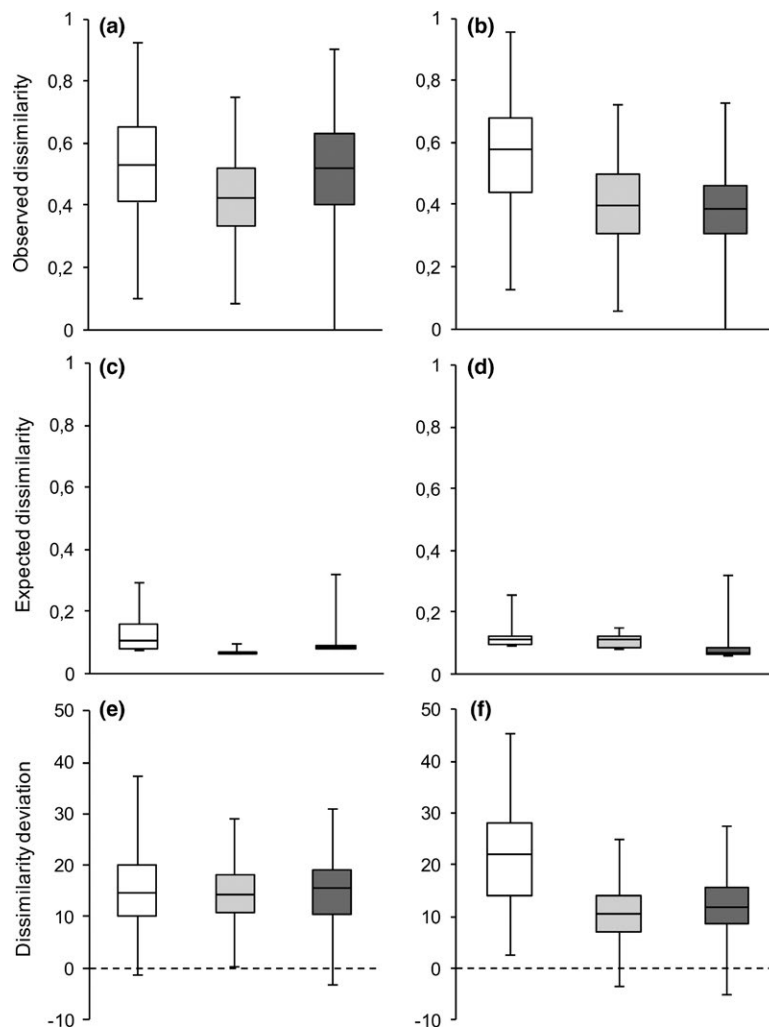
Fig. 2. (a, b) Observed dissimilarity, (c, d) expected dissimilarity, and (e, f) dissimilarity deviation of (a, c, e) bryophytes and (b, d, f) vascular plants within spruce mires (white bars), pine mires (light gray bars), and fens (dark gray bars).

Disturbed communities were clearly different from pristine ones whether measured as observed dissimilarity or dissimilarity deviation suggesting that disturbance induced directional selection on communities. Moreover, disturbed sites were generally not converged or diverged among each other in comparison to pristine sites, whether measured by observed dissimilarity or dissimilarity deviation. These two results together indicate that species losses or species gains or both are selective. This is because if both species losses and gains had been random, species richness at drained sites would not have differed from pristine sites (like

we observed) but community dispersion of drained sites would have differed from pristine sites. The fact that dispersions of pristine and disturbed sites did not differ suggests that disturbance did not change the relative importance of drift and selection. However, this conclusion lays on the assumption that habitat heterogeneity was similar within pristine and drained sites. We cannot verify this assumption as we did not measure environmental variables. Within sites drained peatlands may actually be more heterogenic than pristine peatlands, as ditch creates an artificial gradient from moist to dry. However, this may not be transferred to an increased
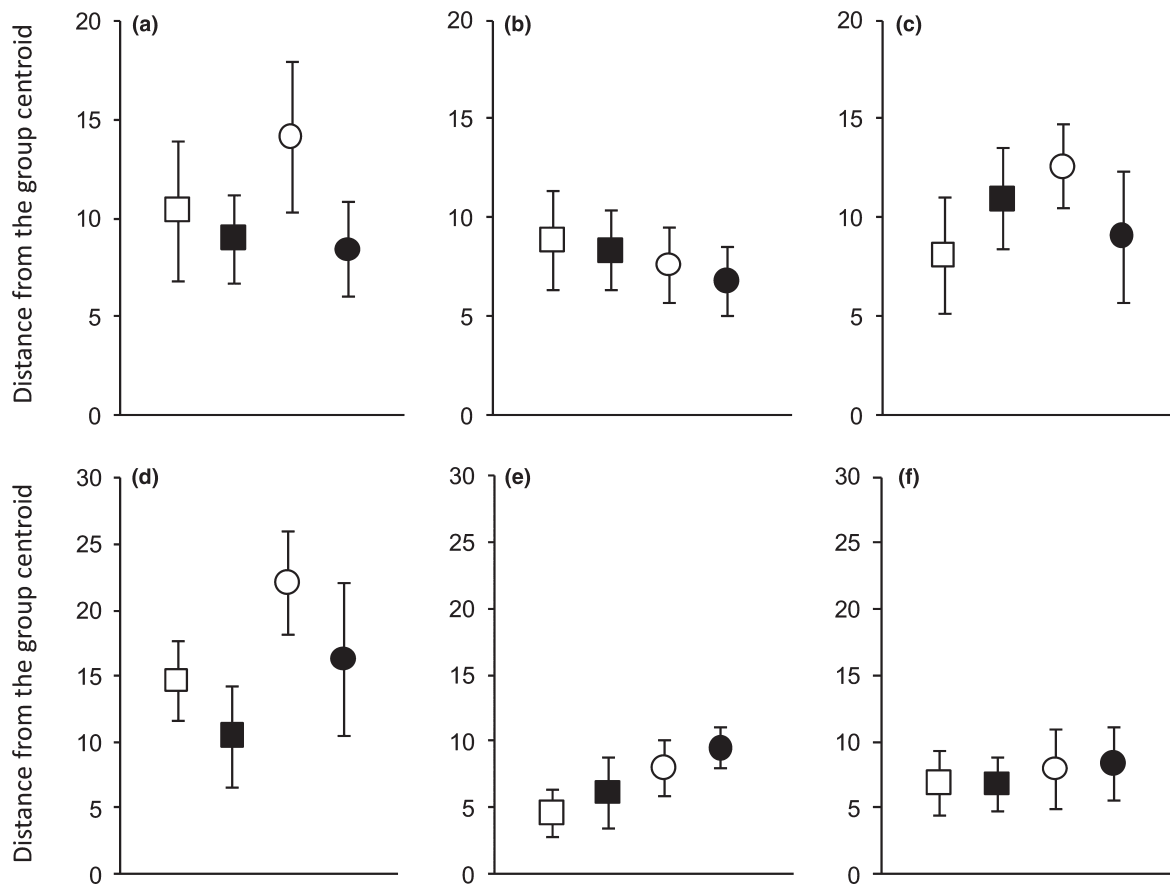
Fig. 3. Distance from the group centroid (mean and respective 95% confidence intervals) of bryophytes in (a) spruce mires, (b) pine mires, and (c) fens, and vascular plants in (d) spruce mires, (e) pine mires, and (f) fens within different productivity levels and disturbance (symbols as in Fig. 1). The units are arbitrary units describing distance in multidimensional space (see *Materials and Methods* section for further information). Differences between groups are statistically significant in panels D ($P < 0.01$) and E ($P < 0.05$). Note the differences in the scale of *y*-axes between (a–c) bryophytes and (d–f) vascular plants.

heterogeneity among peatland ecosystem types where peatlands have actually shown to homogenize (Laine et al. 1995). If habitat heterogeneity among drained peatlands had diminished then our result would have indicated that the relative importance of drift had actually increased in drained peatlands. On the other hand, if habitat heterogeneity among drained sites had increased this would have indicated a shift toward increased relative importance of selection.

Although disturbed sites were neither converged nor diverged among each other compared to pristine sites, it must be borne in mind that they are not islands but rather they are situated in the forest-dominated landscape. As species richness of pristine and disturbed sites did not differ but community composition did, on average there has been an equal number of extinctions and colonizations. Pristine sites were characterized by species tolerating the wet and partly anoxic conditions, for example, *Sphagnum fallax*, *Sphagnum riparium*, and *Carex* species, whereas from drained sites these species were absent. Instead, common forest bryophytes, such as *Pleurozium schereberi* and *Dicranum polysetum*, were present. This spread of the forest species to peatlands may lead to an overall homogenization of the communities at the landscape scale (Laine et al. 1995, McCune and Vellend 2013). Thus, although biotic homogenization has originally

been seen as a result of colonization of exotic species (McKinney and Lockwood 1999) the impoverishment of the distinct features of ecosystem types may well also be due to expansion of native species from the nearby habitats (McCune and Vellend 2013).

Ambitious international targets have recently been set for restoring peatlands and other degraded ecosystems to halt the loss of biodiversity and ecosystem services (Convention on Biological Diversity 2010). In addition to yielding knowledge of the key drivers of community dynamics, understanding the processes underlying the changes in community assembly after disturbance are likely to help to predict whether communities will return to their predisturbance state after restoration efforts (Suding et al. 2004, Murphy and Romanuk 2012). For example, decreased dispersion after disturbance have been considered to indicate strong selection which may inhibit recolonization of the original species (Murphy and Romanuk 2012). On the other hand, as we have argued, increased dispersion may also indicate stochastic responses to disturbance. Our result of no difference in dispersions of pristine and drained sites indicates that restoration of boreal peatlands may be rather straightforward in terms of community dispersion recovery: it indeed may be sufficient if we can restore the original hydrological regime. However, whether the rarest species are still available in the landscape to recolonize the peatlands will most likely influence the composition of the recovering communities.

In conclusion, our results from 120 peatlands of three different ecosystem types showed that species richness and community similarity did not differ between pristine and disturbed sites. Instead, peatland communities in disturbed sites showed changes not attributed to drift but to selection, most likely based on altered hydrology, pH, and nutrient gradients. Moreover, the changes due to disturbance were toward forest communities which could lead to landscape level homogenization. Effective ways to combine knowledge of the landscape level changes among disturbed areas and the understanding of the mechanisms affecting communities locally are important for reaching the ambitious global targets of restoring the degraded ecosystems.

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