

Master of Science Thesis

**Anthropogenic disturbance favors regional generalists
over specialists**

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ABSTRACT

Anthropogenic activities account for changes in communities globally. Anthropogenic disturbances alter the natural disturbance dynamics of ecosystems thus creating environments with novel conditions. These environments are often more favorable to non-native generalist species than to the more niche-confined specialists, hereby leading to the assisted spreading of generalists and to the decline of specialist species. The replacement of a variety of specialists with a few generalists can result in growing similarity among different communities i.e. taxonomic homogenization, which can itself lead to the decrease of biodiversity and to the increase on extinctions. Prime examples of environments affected by anthropogenic activities are drained peatlands. The conditions characteristic of peatlands, have resulted in relatively specialized vegetation in terms of habitat requirements that are no longer completely met after draining. Previous studies support the notion that drainage leads to the homogenization of plant communities between peatlands and to the directional change of specialized peatland species to more generalist forest species. The aim of this thesis was to study the effects of draining on the specialization of peatland vegetation. To test whether the plant species specialized to the pristine conditions are able to adapt to the new conditions of drained peatlands and whether the colonization of more broad-niched generalists increases after drainage, I used vascular plant and bryophyte relative abundance data collected from 118 peatland sites from around Finland. Specialization indexes were used to determine specialization rates for each individual plants species and bryophyte and vascular plant community. These rates were analysed to find out if the occurrence of generalists and specialist plant species of natural communities was affected differently by drainage and if drainage altered the specialist-generalist ratio of a plant community. The results show that the abundances and frequencies of specialist species differed more between pristine and drained peatlands than the ones of generalist species. The occurrence of generalist species was similar in both pristine and drained sites but specialist species had either increased or decreased both in abundance and frequency when comparing pristine sites to drained ones. Closer observations revealed that the decreased specialists were species specialized to specific peatland conditions thus appearing as specialist even on landscape level. The increased specialists were, however, landscape level generalists i.e. forest species that only appeared as specialists on pristine peatlands. Possibly because of the increase of such species in drained sites, the generalist-specialist ratios of plant communities seemed to not significantly differ between pristine and drained sites, even though the number of landscape level specialist species decreased.

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TIIVISTELMÄ

Ihmisen toiminta aiheuttaa muutoksia yhteisöissä maailmanlaajuisesti. Ihmisvaikutteiset, eli antropogeeniset häiriöt muuttavat ekosysteemien luonnollista häiriödynamiikkaa aikaansaaden ominaisuuksiltaan uudenlaisia ympäristöjä. Tällaiset ympäristöt ovat usein suosiollisempia kasvupaikkavaatimuksiltaan generalisteille vieraslajeille kuin vaateliaammille spesialistilajeille. Tämän seurauksena generalistilajit leviävät uusille alueille ja paikallisia spesialistilajeja häviää. Useiden spesialistilajien korvautuminen muutamalla generalistilajilla voi lisätä eri yhteisöjen välistä samankaltaisuutta eli johtaa taksonomiseen homogenisaatioon ja sitä kautta luonnon monimuotoisuuden vähenemiseen ja sukupuuttojen lisääntymiseen. Ojitetut suot toimivat hyvänä esimerkkinä ihmisen vaikutuksesta muuttuneista ympäristöistä. Suokasvillisuus on suhteellisen spesialisoitunutta soiden ominaisille olosuhteille, jotka muuttuvat suon ojituksen seurauksena. Aikaisemmista tutkimuksista ilmenee, että ojitus johtaa kasviyhteisöjen väliseen homogenisaatioon eri soiden välillä ja suokasvilajien korvautumiseen alueellisesti generalisteimmilla metsälajeilla. Tämän tutkielman tarkoituksena oli tutkia ojituksen vaikutuksia suokasviyhteisön spesialisaatioon. Selvittääkseni onko soiden olosuhteisiin spesialisoituneiden kasvilajien mahdollista sopeutua ojitettujen soiden uudenlaisiin olosuhteisiin ja lisääntykö generalistilajien määrä yhteisössä ojituksen jälkeen, käytin 118 suomalaiselta suolta kerättyä aineistoa putkilokasvien ja sammalten suhteellisesta runsaudesta. Määritin jokaiselle lajeille ja putkilokasvi- ja sammalyhteisölle spesialisaatioarvon spesialisaatioindekseillä. Näitä arvoja analysoimalla selvitin vaikuttaako ojitus eri tavalla luonnontilaisten yhteisöjen generalisti- ja spesialistilajien esiintymiseen ja muuttaako ojitus kasviyhteisön spesialistien ja generalistien määrän suhdetta. Tulokset osoittavat, että spesialistien runsaus ja yleisyys vaihtelivat generalisteja enemmän luonnontilaisten ja ojitettujen soiden välillä. Generalistilajien esiintyminen oli samanlaista sekä luonnontilaisilla että ojitetuilla soilla, kun taas spesialistilajien runsaus ja yleisyys joko lisääntyivät tai vähenivät ojitetuilla soilla verrattuna luonnontilaisiin soihin. Spesialistilajit, jotka olivat kärsineet ojituksesta olivat suo-olosuhteisiin spesialisoituneita lajeja, jotka olivat spesialisteja myös alueellisesti tarkasteltuina. Spesialistit, jotka runsastuivat ojituksen seurauksena olivat sen sijaan lajeja, jotka ovat alueellisesti tarkasteltuna generalisteja metsälajeja, jotka olivat luonnontilaisilla soilla paikallisia spesialisteja. Mahdollisesti tällaisten lajien lisääntyminen ojitetuilla soilla aikaansai sen, että kasviyhteisöjen generalisti- ja spesialistilajien määrän suhde ei näyttänyt tilastollisesti merkittävästi eroavan luonnontilaisten ja ojitettujen soiden välillä, vaikka alueellisesti spesialistien lajien määrä väheni.

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1. INTRODUCTION

By definition, natural disturbance is an event that causes changes and disruption, usually producing heterogeneity and patchiness in an ecosystem, community or population (Pickett & White 1985). However, anthropogenic, or human, disturbance can cause effects very different from the ones caused by natural disturbance (Foster et al. 1998). Human generated disturbance differs from natural disturbance both spatially (area) and temporally (frequency and duration), as well as in intensity and predictability (Pavlovic 1994, Harmon et al. 1983). It causes habitat fragmentation in scales rarely induced by natural disturbance and often increases species extinction rates in a way that extinctions become more common than colonisations (Pavlovic 1994). In the case of natural disturbances, species have been exposed and able to respond to the same conditions repeatedly through long periods of time whereas anthropogenic disturbances have originated too recently for adaptations to emerge (McIntyre & Hobbs 1999).

Anthropogenic activities, such as land-use, are responsible for a large proportion of changes occurring in ecosystems and communities (Meyer & Turner II 1994, Vitousek et al. 1997, Foley et al. 2005, Millennium Ecosystem Assessment 2005). The most common ways of land-use (cultivation, modification and maintenance) can have global-scale effects on the environment (Turner II et al. 1994) that can be as intense as the most intense effects of natural disturbances (Turner II et al. 1990). Anthropogenic disturbance can alter the natural dynamics of regions and community structures and cause extinctions (Foster et al. 1997, Larsen et al. 2005).

Many studies show that anthropogenic disturbance assists the spreading of non-native generalist species which are often already adapted to man-made habitats (McKinney & Lockwood 1999, Lockwood & McKinney 2001, Hobbs & Huenneke 1992, Mooney & Hobbs 2000). Human activities that are most effective in spreading non-native species are commerce, travel and most importantly agriculture. Via global commerce and travel the spreading of species is efficient – either accidentally (e.g. through the ballast in ships) or on purpose (e.g. through the cultivation of foreign species) (Williamson 1996). On the contrary anthropogenic disturbance limits the success of native, regional specialists (McKinney & Lockwood 1999, Pavlovic 1994, Hobbs & Huenneke 1992). Specialist species have realized niches that are maintained by their natural disturbances. If a disturbance is novel and differs from the natural dynamics of an area, the whole niche of a species might become eliminated (Pavlovic 1994). It is more likely for a species to both invade and to be transported from anthropogenically disturbed than non-disturbed sites (Williamson 1996). When a particular habitat is altered as a result of anthropogenic disturbance, it is much more common for a generalist to remain in or colonize the area than for a local specialist to adapt to the changes (Devictor et al. 2008).

Generalist species are widespread, usually having broad ecological niches, including high tolerances, rapid dispersal and high reproduction, whereas specialists lack these traits and are capable of living only in very specific habitats that are less disturbed (McKinney & Lockwood 1999, Devictor et al. 2008). When a few species of widespread generalists take the place of a large group of limited “losers”, taxonomic similarity between areas is likely to increase (McKinney & Lockwood 1999). This transformation is also referred to as taxonomic homogenization (Castro & Jaksic 2008). Ultimately, homogenization by anthropogenic disturbance can lead to the decrease and simplification of different ecosystems (McKinney & Lockwood 1999).

The ecological mechanisms underlying taxonomic homogenization of communities essentially result from species invasions and extinctions (Olden & Poff 2003). These

mechanisms consist of the interactions between native and non-native species and their environments. The mechanisms are regulated by, for example, the spatial distributions of species, the level of similarity in species compositions among communities and the taxonomic identities of the species (Olden & Poff 2004).

The decline of specialist species is a global phenomenon (Olden et al. 2004). The main reasons behind the decline are the comprehensive alteration of environments and the assisted dispersal of exotic species – both of which are mainly of anthropogenic origin. The phenomenon is not unforeseen but it has accelerated during recent times (Olden et al. 2004). As mentioned earlier, the replacement of specialists by generalists can lead to the homogenization of communities and thus result in the loss of biodiversity, both through the increased occurrence of the same species and the disappearance of a large number of disturbed species. Along with the biodiversity loss the decrease in the amount of specialist may lead to deteriorated ecosystem productivity and services (Clavel et al. 2011, but see also Vellend et al. 2013). At least in small study plots the decrease of biodiversity has been noticed to alter ecosystem function, for example its productivity. On a larger scale, it has been suggested that an ecosystem's functioning is not dependable on the increases or decreases of global species richness (Vellend et al. 2013). But this is only the case if an ecosystem gets radically altered, for example if a natural field changes into a monoculture through cultivation. In fact, if an ecosystem stays otherwise unchanged, the changes in species richness can have noticeable effects on the ecosystem functions (Vellend et al. 2013).

Peatlands are a case in point example of a habitat with unique characteristics that have led into distinctive vegetation specialized to these conditions (Rydin et al. 1999). Peatlands have been affected by anthropogenic changes in land-use in the peatland-rich Northern Europe, especially in Finland (Armentano & Menges 1986). Large-scale draining of peatlands has significantly altered the habitat's conditions (Venäläinen et al. 1999) to which the highly specialized vegetation cannot adapt. The consequently created novel ecosystems are subject to increased colonization of the more flexible generalist species (Clavel et al. 2011).

Generally, draining leads to heterogeneity within peatland sites (Minkkinen & Laine 2006) but results in homogenisation between sites i.e. causes different types of peatlands to be more similar with each other (Laine et al. 1995). The heterogeneity within a site is caused by for example the ditches themselves that create spatial variation in the site's conditions. Usually the draining leaves behind some wetter patches that can still support the original peatland vegetation, thus causing variation in for example the sites methane emissions and anoxicity level (Minkkinen & Laine 2006). The homogenisation between sites is partly due to the process of the peatlands' hydrochemistry becoming similar after draining. Regardless of the site, when a peatland gets drained the lowering of the water table causes the peat layer to collapse thus leading to the oxidation of the peat decreasing the original differences between sites (Laine et al. 1995).

Another known consequence of draining peatlands is the noticeable directional change in the composition of peatland vegetation. The succession from peatland species to forest species after water drainage is an immediate but lengthy process (Minkkinen & Laine 2006). The first species to suffer from the changes are the wet surface plants whereas the peatland plants preferring drier conditions can even benefit from the situation. The species richness of peatlands usually grows straight after the disturbance when peatland species, forest species and colonizers can all inhabit the area. Over time, when tree growth shades the area and the ground continues to dry out, the site gradually becomes forested and the original species pool gets lost (Laine et al. 1995).

1.1. Communities and the mechanisms underlying them

A community can be defined as a group of organisms living in the same place at the same time interacting with each other (Vellend 2010, Campbell & Reece 2008). The term community can be used to indicate every single living organism in a specific area, or in reference to a more restricted group of individuals (Cox & Moore 2005), for example a guild or a functional group. Because communities can be defined to comprehend any suitable set of organisms (Campbell & Reece 2008), confining a community in space and time is more or less artificial (Cox & Moore 2005). The classification of organisms into communities is, however, very useful in studying patterns in the diversity, the abundance and the composition of species (Vellend 2010).

Quantifying changes in nature is always challenging. Therefore, also the changes in species communities are more easily described than measured (Cain et al. 2008). Even though studying changes in community structure is difficult (Solow 1993), it is necessary in order to understand how communities work (Cain et al. 2008). In short, the ultimate processes that influence the mechanisms causing change in a community on any level are colonization and extinction (dispersal, drift and selection) and evolution (speciation) (Vellend 2010). Selection in a community results from the interactions between unequal species, i.e. a change in community composition through selection means that an individual of a species loses to an individual of another species on the account of environmental pressure. A change in an environment can thus change the proportions of different individuals of a species which can via continuing selection pressure lead to local extinctions. In contrast, a change resulting from ecological drift does not need to involve environmental pressure. Drift is the changes in community composition caused by stochastic events that in its purest form happens when individuals are identical. Dispersal, on the other hand, can have various effects on community structure. Being the movement of individuals from one space to another, it can have both increasing and decreasing effects to the total species pool of a community. The dispersal of an individual requires the ability to disperse to another area as well as being located in the range from which the dispersal is possible. Finally, through speciation, the total diversity of species that can form a community through the above-mentioned processes is created. All existing theories and models of community ecology can be associated with a combination of these processes (Vellend 2010).

In the case of many anthropogenic disturbances, the changed conditions should favour species with higher ability to tolerate novel combinations of environmental variables. As a result, the processes behind communities' compositions after anthropogenic disturbances are perhaps highly directed by selection and less by stochastic events (Floren et al. 2001). However, the matter is widely controversial and some support the sentiment that only large-scale and catastrophic disturbances will initiate directionality in the change of community composition (Platt & Connell 2003). Even if the re-colonization of disturbed areas was deterministic in terms of tolerating altered conditions, the source pool for the species that can tolerate the novel conditions can be spatially independent of the disturbance process resulting in some level of stochasticity in the re-organization of the evolving new community (e.g. Vellend 2010).

1.2. Community structure

Changes in communities are most often measured as changes in species composition, species abundances or as a combination of both (Magurran et al. 2010). In addition to compositional measures, structural measures such as species richness, species evenness

(e.g. Shannon index etc.), functional diversity, food webs, or measures of specialization can be used (Solow 1993, Magurran et al. 2010).

The term community structure is used to depict the physical arrangement of species and the resulting effects in a community. It is often detected that in nature the species in a community are not randomly distributed and there are certain patterns and processes that affect the community's structure. The main factors controlling a community's structure are its species richness, the relative abundances of the species and their interactions (Campbell & Reece 2008).

Community structure can be examined in multiple ways. The trophic structure of a community comprises of the feeding relationships between species. Trophic levels represent the feeding categories of organisms and food chains link different levels together in order to show the direction of energy flow in a community (Cain et al. 2008). Food chains can be linked to form food webs that intend to represent the complete feeding structures of communities. Changes in the abundances and composition of one species can change the flow of energy and the species composition on other levels. A trophic structure of a community can be controlled from the top or from the bottom of the system, i.e. it can be limited by either resources or predation (Mittelbach 2012).

An important way of examining community structure is through its species diversity. Species diversity includes the total species richness and the relative abundances of species in a community (Campbell & Reece 2008). Species diversity is often measured as alpha, beta or gamma diversity (Mittelbach 2012) – alpha diversity being the species diversity within a habitat, beta diversity the difference in species composition between habitats and gamma diversity the measure of regional species diversity (Whittaker 1972).

The majority of communities are dominated only by one or a few species and the rest are relatively rare. Although this pattern repeats itself through the different taxonomic groups of communities, the underlying reasons for this kind of community structure are not clear (Magurran 2004). The commonness of certain species in communities could be explained for example through competitive superiority or human interference. Invasive species, commonly spread through anthropogenic activities, are usually good at tolerating and avoiding disturbance and stress factors, for example predation and disease (Campbell & Reece 2008). Invaders are usually generalists of some level, since their habitat requirements are very broad. On the other hand, the specialists of a community can also be the dominant competitive superiors if the environment in question represents their optimal conditions.

When community structure has been viewed more precisely from the perspective of the relationships between specialists and generalists, three notable characteristics have been found. Primarily, generalists tend to have wider distribution and specialists are spatially more restricted. Secondly, in a regional scale the densities of populations of generalist species are traditionally been thought to be higher than the ones of specialist species. Finally, within communities the densities of different generalist species are more varied and the densities of different specialist species more similar (Kitahara & Fujii 1994).

In conclusion, determining which species are specialists and which are generalists is not easy and the division is seldom clear. It is a generic conception that there is a positive correlation between species distribution and abundance i.e. broad-niched species are both wide-ranged and locally abundant (e.g. Brown 1984). However, this does not apply for all occasions. Negative correlations for abundance and distribution have been found especially in cases where the studied habitat differs considerably from the most common habitat of the given study region (e.g. a peatland in the middle of a forest). Species that are specialized to a certain habitat anomalous from its surroundings can be locally abundant

and still not widely distributed (Gaston & Lawton 1990). Thus, generalists are not necessarily the most abundant of species in a community. Conversely, on a small spatial scale, specialist species can be the ones occurring in numbers by having clear competitive advantage over others when their habitat requirements are met. Additionally, it is challenging to define the ultimate reasons for a species being located at a given space because as well as habitat conditions, numerous factors, such as interspecific competition, and the interactions of factors constantly affect all individuals (Cox & Moore 2005).

1.3. Peatlands

Peatlands, as all wetlands, are environments with distinctive characteristics. The distinguishing factor which separates peatlands from other wetlands is the formation of peat. Peat is partially decomposed organic matter that is formed from degrading vegetation in anaerobic conditions. In peatlands, the anaerobic conditions are caused by a high water table that prevents the aeration of the ground. Typical examples of different peatland types are for example fens, pine bogs and wet spruce forests (Rydin et al. 1999).

Sphagnum mosses (*Sphagnum spp.*) are keystone species of most peatland types (Vitt & Wieder 2006). The species of this genus of bryophytes have dead hyaline cells that can store notable amounts of water. The water stored in the cells of both living and dead mosses maintains the high water table of peatlands. The resulting anaerobic conditions slow down the decomposition of organic matter and thus the cycle of peat formation is complete. In addition to slowed-down decomposition, peatlands are relatively poor in nutrients, such as potassium and phosphorous, and have high acidity. Nutrients get stored in the non-decomposing peat and some are lost through leakage to surrounding locations (Rydin et al. 1999). The acidity of peatlands is mostly due to the organic acids produced by Sphagnum mosses (Hemond 1980). For example in bogs the dissolved organic matter can consist almost completely of organic and fulvic acids (McKnight et al. 1985).

Due to their characteristics, peatlands act as carbon sinks of global importance (Clymo et al. 1998, Gorham & Rochefort 2003, Waddington & Price 2001). The slowly decaying peat stores 20 % of the terrestrial carbon of the planet (Gorham 1991). On the other hand, peat soils can emit extensive amounts of carbon dioxide and methane, both considered greenhouse gases, to the atmosphere (Moore & Knowles 1987, Strack 2008). Anthropogenic activities such as harvesting peat for fuel and draining have released significant quantities of peatland-stored carbon to the atmosphere (Kareksela et al. 2015). Draining peatlands by ditching lowers the water table and exposes the previously indecomposable anaerobic peat to oxidation and thus decomposition (Armentano & Menges 1986).

1.4. Peatland vegetation

Plants are a major component of most ecosystems. As primary producers, they form the basis for every other functional group of organisms. This is also applicable to peatlands that are in fact mostly characterized and classified by their vegetation. The groups of plants dominating most peatlands are graminoids (including e.g. grasses and sedges), shrubs and bryophytes (mostly of the genus *Sphagnum*). Especially the *Sphagnum* mosses play an important role in the function of peatland ecosystems: they create the anaerobic, wet and acidic conditions and resist decaying, thus forming the peat itself (Rydin & Jeglum 2006).

Peatland plants have developed multiple adaptations in order to meet the habitat's conditions. The vegetation has to tolerate both flooding and low nutrient availability which is why peatland plants are considered to be stress-tolerators (for stress tolerance see Grime 2001) which means they usually have a low growth rate, are long-lived and invest only a little on reproduction. Common adaptations to peatlands' anoxic conditions for vascular

plants are for instance anchaerymas - empty intercellular spaces for air transportation, growing most of the roots in the aerated top layers of the peat and developing high tussocks in order to avoid the high water table. To cope with the low nutrient availability, vascular peatland plants have developed ways to for example rotate nutrients (e.g. some *Vaccinium* species), form mutualistic relationships with fungi (e.g. ericaceous species) or even get some of their nutrient intake through carnivory (e.g. *Drosera* species). Rootless bryophytes have very different adaptations from vascular plants. *Sphagnum* mosses get their nutrient intake mainly from precipitation and tolerate the low nutrient levels by being able to conserve nutrients and by constantly producing morphological sites that exchange cations from the water into hydrogen ions (Rydin & Jeglum 2006).

Most peatland plant species are specialized to certain conditions within the ecosystem along the gradients of nutrient level and moisture. According to the Euroala et al. (1995) listing of all plant species commonly found in the peatlands of Finland, not one species can be found in all nutrient levels, all peatland types or all moisture levels. Consequently, one could draw a conclusion that peatland vegetation is highly specialized. Yet some of the plants in peatlands are clearly more generalists than others. For example, the bryophyte species *Sphagnum lindbergii* can tolerate all but the most nutrient rich habitats and is found on both wet and slightly drier surfaces, whereas a species from the same genus, *S. auriculatum* is strictly confined to the most nutrient rich and wet areas.

In addition to the habitat specialization of vegetation within peatlands, specialization can be examined between peatlands and other habitat types. A species that can be considered as a generalist in terms of the condition gradients within a peatland can still be highly specialized as a peatland species and is found in no other types of habitats such as forests (e.g. *Vaccinium oxycoccos*). Vice versa, a species whose habitat requirements in peatlands are specific and confined can be found in multiple types of habitats if its requirements are met (e.g. *Vaccinium myrtillus*).

1.5. Peatlands and drainage

Peatland drainage to create more land for forestry and agriculture has nowhere been as comprehensive as in Finland (Venäläinen et al. 1999) where 60 % of the total peatland area has been drained (Paavilainen & Päivänen 1995) mostly during 1960 to 1980. In addition to the global climatic effects, drainage has naturally altered peatlands as environments (Waddington & Price 2001). Changed conditions have led from the partial loss of original fauna and flora and to the decrease of diversity (Laine et al. 1995).

The natural disturbance dynamics of peatlands are relatively slow (Backéus 1972, Gunnarsson et al. 2000). The hummock and hollow structures of peatlands are stable (Rydin et al. 1999) and herbivory is scarce on the low-nutrient vegetation. A large part of the disturbances observed on peatlands, for example water table drawdown and biomass burning, are in fact of anthropogenic origin (Turetsky & St.Louis 2006). Peatland vegetation has been adapted to the conditions of peatland environments, including the relatively high stability of the habitat. Thus, the plant species characteristic to peatlands do not usually adjust well to disturbance. After a human generated disturbance, the atypical conditions that have affected the evolution of peatland vegetation often change in a way that the original plant species are no longer able to remain in the area. Still, even after the disturbance, the conditions remain somewhat distinctive so that often only a few of the more generalist species can colonize or succeed in the altered environment. As a result, peatlands are especially vulnerable to homogenization.

1.6. Research questions

My research questions are: 1) are specialist and generalist species of natural communities affected differently by anthropogenic disturbance and 2) does the specialist-generalist-ratio of a community, i.e. community structure, change due to an anthropogenic disturbance? More specifically I aim to gain insight into the effects of anthropogenic disturbance on peatland vegetation structure in terms of the level of specialization of the peatland plant communities. The focus is also on examining if anthropogenic disturbance has an unequal effect on the survival of specialist and generalist species of natural systems.

The previous studies on the effects of disturbance on the rate of community specialization have concentrated on habitats with disturbance dynamics very different from peatlands (Turetsky & St.Louis 2006). Also, the ecology behind human generated disturbances in general has been very little studied. With climate change being a current issue, there has been growing interest in peatland restoration (Gorham & Rochefort 2003, Kareksela et al. 2015). For the restoration to be fully successful, the effects caused by the quintessential disturbances must be detected. The objective to restore peatlands has created a demand for studying whether broadly dispersed species (generalists) are less prone to the effects of anthropogenic disturbance (draining) than small-range species (specialists) in different peatland types around Finland, and if the ratio of generalists and specialists in a peatland community is changed after the disturbance. The answers to these questions improve our knowledge on the threats associated with the constantly changing nature and on our ability to respond to them. Research on peatland plant community specialization has the potential to detect new information on peatland ecology that can be useful in the restoration and conservation of these environments of current interest.

2. MATERIALS AND METHODS

2.1. Experimental design and data collection

The data used for this research was obtained from the peatland restoration monitoring network by the Parks & Wildlife Finland (a public agency that forms part of the state-run enterprise Metsähallitus) and the University of Jyväskylä. The experimental design applied consists of altogether 118 different peatland study sites widely distributed around Finland (figure 1) and the data collection has been carried out by the Parks & Wildlife Finland in co-operation with the University of Jyväskylä since 2007.

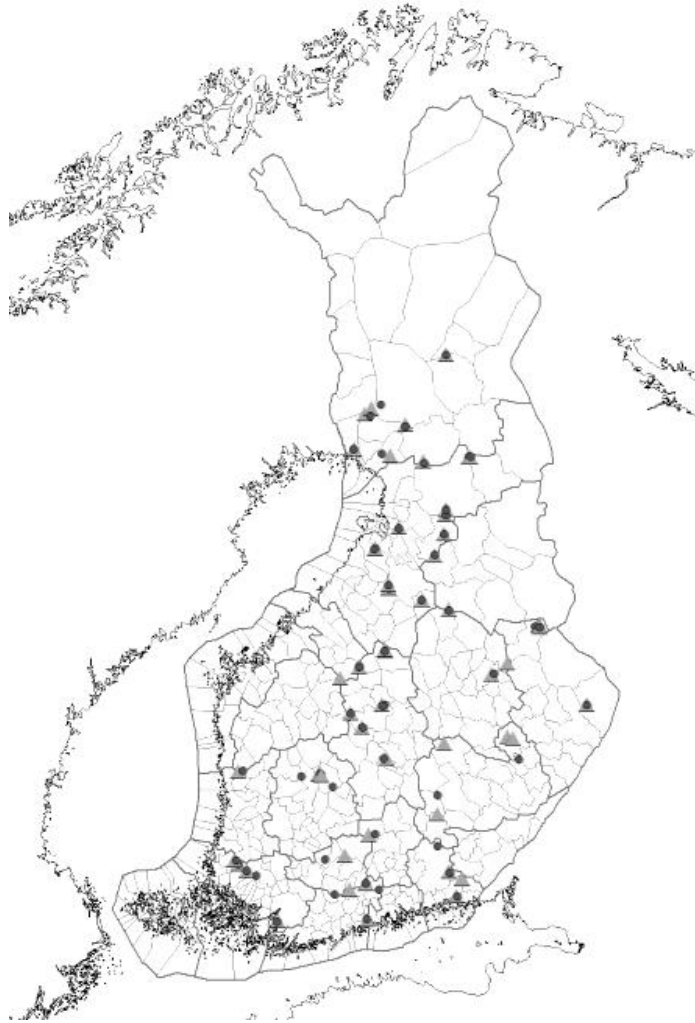


Figure 1. Study site locations. Triangles depict drained sites and circles pristine sites. The symbols overlap since some sites are located on peatlands close to each other or are set on the same peatland but are hydrologically independent of each other. Figure: © Maanmittauslaitos 2010

The 118 study sites are divided into 6 separate groups: unfertile and fertile spruce mires, unfertile and fertile pine mires and unfertile and fertile fens so that each group, or peatland type, is represented by 19 to 21 individual peatland study sites (2 sites had to be removed from the data due to lost bryophyte samples and 1 site had to be moved from unfertile natural fens to fertile natural fens after the identification of sample species) (figure 2). Half of the 118 study sites are pristine and the other half has been drained. The sites have been chosen so that the drained and pristine sites are hydrologically independent of each other i.e. the altered hydrology of the drained sites does not affect the hydrology of the pristine sites. The sites had to also represent typical Finnish peatland types of the defined categories (Vuori 2012). All peatland and treatment types are represented in sites throughout Finland. However, due to the uneven distribution of Finnish peatlands (some peatland types are more abundant in specific areas) there is some spatial correlation between at least the different peatland types.

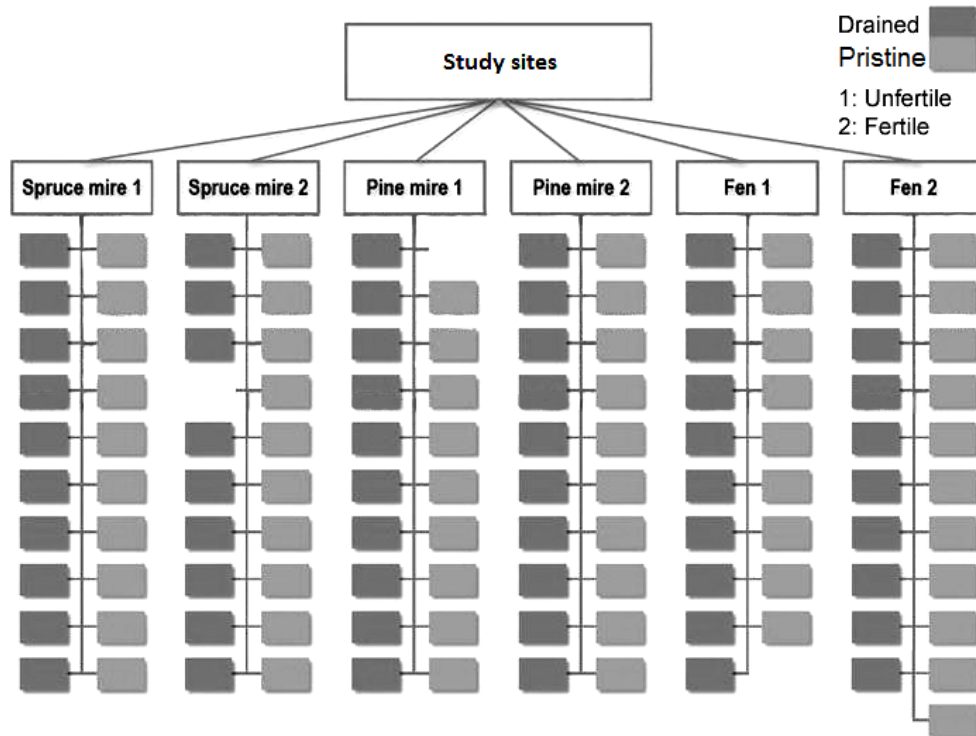


Figure 2. The peatland restoration monitoring sites of Parks & Wildlife Finland. 118 study sites are divided into 6 different peatland types according to their vegetation. Half of the sites have been drained (dark grey boxes) and the other half are pristine (light grey boxes). Figure: © Metsähallitus 2011.

The experimental set up on each of the 118 study sites includes 10 1m² vegetation plots that are situated in two rows 4 m apart from each other forming a grid (figure 3). The starting point of each grid was randomized, conditional to that the whole grid had to fit inside the designated peatland type and that for each vegetation plot the distance from the closest ditch had to be at least 10 m. The relative abundance, i.e. the coverage proportion of each observed species of bryophytes (ground layer) and vascular plants (field layer) in each plot, was determined. The coverage proportions were determined visually with the help of a measurement frame equivalent to the size of the vegetation plots. The proportions were recorded within 1 % accuracy unless a species covered less than a percent in which case the coverage proportion was either 0,2 % or 0,5 %. Contrary to the field layer, in which the vegetation can be in several overlapping layers, the coverage of the ground layer was determined in a way that the total coverage of each plot added up to 100 % therefore including also the coverage of bryophyte-free areas (for example deadwood, bare peat, fixed litter et cetera). The coverage proportion of all the species (mostly bryophytes) that could not be identified in the field was still recorded and a sample was collected for later species identification using a microscope.

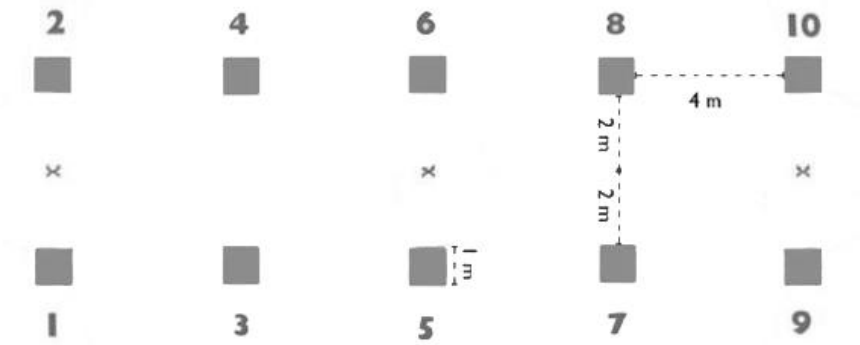


Figure 3. The experimental set up on each individual study site. Each grey square represents a 1 m² vegetation plot. Figure: © Metsähallitus 2011.

2.2. Analyses

All analyses were done separately for vascular plants and bryophytes, since the species of these two groups are likely to have different responses to disturbance due to their differing characteristics. Before analyses the data was modified by combining the species specific coverage proportions recorded from each of the 10 vegetation plots to a one study site specific coverage proportion since site level analysis of the communities was better suited for the study questions.

2.2.1. Specialization indexes

To study species level specialization (question 1) I quantified the degree of specialization for each observed species using a species specialization index (hereafter SSI) following Julliard et al. (2006). The index is based on the coefficient of variance of species' densities across habitats (standard deviation / average) working as a measure of specialization. The use of coefficient of variance of occurrence density to measure specialization is based on the assumption that the variation in species' densities across habitats indicates their level of specialization. Species whose densities do not vary between habitats are considered generalists and species whose densities are at particular habitats higher than elsewhere are considered specialists (Devictor et al. 2008). The values of SSI range up from 0, 0 implying no specialization and the higher values implying higher specialization. Using an index with continuous values as a measure of specialization retains more information on the specialization of individual species than a rough and often artificial dichotomous division into specialist and generalist species and it allows the use of parametric tests.

At community level (question 2), an index was used to quantify the degree of specialization of each vascular plant and bryophyte community. The community specialization index (hereafter CSI) (Devictor et al. 2008) is the average SSI of all species found in a given community calculated as follows:

$$CSI_j = \frac{\sum_{i=1}^n a_{ij}(SSI_i)}{\sum_{i=1}^n a_{ij}}$$

n being the total number of species found, a_{ij} the abundance of species i in site j and SSI_i its specialization index.

The SSI and the CSI both depend considerably on the chosen species pool used in their calculation. A species pool comprises of all the species that are available to colonize an area. When choosing a species pool, the area of interest has to be explicitly defined

since the use of an absolute, global species pool is impossible. The scale of a species pool can be anything from local to widely regional and is an essential factor in interpreting results. In the analyses on the effects of disturbance on specialists and generalists of natural communities, the SSI values of species were calculated from the data collected from pristine state study sites alone. That is to say the species' abundance data collected from the drained sites was not used in determining the specialization of species. This is because if the SSI-values would have been determined also from the abundance data of the drained study sites, the research would no longer depict the effects of drainage on the generalist and specialist species of specifically natural communities. In turn, in the analyses on the change of specialist-generalist ratios of communities, the specialization of the species was determined from the complete data set. By using the species' abundances from both pristine and drained study sites all possible variation was achieved.

2.2.2. Statistical analyses

Statistical analyses were done using IBM SPSS Statistics 22.0. To find out whether specialist and generalist species are affected differently by anthropogenic disturbance, the changes between pristine and disturbed sites in species' total relative abundances (cumulative abundance over all sites) and frequencies (number of sites and peatland types the species was observed in) were compared to species' SSI-values through linear regression. The species whose abundances or frequencies were higher in drained than pristine sites and the species whose abundances or frequencies were lower in drained than pristine sites disturbance were treated separately. This was done because the ranges of positive and negative relative changes in abundance and frequency are different: the relative decrease from pristine to drained site ranges between 0 and 1, whereas the maximum relative increase from pristine to drained site is defined by the total space available for the species. In addition, the method was more practical for viewing possible bimodal effects of the treatment on the species. A simultaneous analysis for the whole data set would not as clearly reveal the possible reverse effects of the drainage on the species that either benefitted or suffered from it. The regression analyses were also carried out without a few obvious outliers visible in the data (figure 4, panels C and D) to ensure that the outliers would not have an effect on the results.

The species whose abundances or frequencies were the same in both treatments were removed from the data since they could not be incorporated either into the regression for the increased species or the regression for the decreased species. The average SSI of the unchanged species was compared to the assumed average SSI to see whether the specialization of the unchanged species was statistically significantly different from the average specialization of all species. However, this comparison was not done for the species whose abundances had stayed the same due to small sample sizes (bryophyte $n = 1$, vascular plant $n = 1$).

The SSI-values of the species that were found only in pristine sites were separately compared to the average SSI (average SSI of all the species found in pristine peatlands) to see whether the SSI of the species that were absent from the drained sites statistically differed from the average SSI, i.e. if they differed in terms of their level of specialization. This was done separately to all measures of change, i.e. the change in abundance, the change in the site frequency and the change in the peatland type frequency. To find out whether the measured direction of change remained the same for a species despite the level on which the change was measured, the number of species that either increased or decreased on one level of analysis was compared to the number of increased and decreased species on other levels. This showed, for example, whether a negative relative change in

abundance of a species indicates that the change has also been negative on the site frequency and peat land frequency levels.

The possible changes in community generalist-specialist ratios resulting from anthropogenic disturbance were analyzed through comparing the CSI-values of communities in pristine and drained sites. The data I used consisted of site level CSI values (altogether 118 sites / communities) and I used the treatment and peatland type as fixed factors. Two-way analysis of variance was used to find out whether the peatland type (fertile/unfertile spruce mire, fertile/unfertile pine mire or fertile/unfertile fen), the treatment (pristine or drained) or an interaction of these two had an effect on the average CSIs. For more detailed information on the possible interactions, peatland type specific univariate tests were also conducted.

3. RESULTS

As mentioned before, the species whose abundances or frequencies were the same in both treatments could not be incorporated into the regression for the increased species or the regression for the decreased species and therefore were removed from the data. For bryophytes, the abundance of 1 species was the same before and after drainage, the frequencies of the number of sites a species occurred in appeared similar in both treatments for 11 species and the frequency of the number of peatland types a species occurred in was same in both treatments for 17 species. For vascular plants, abundance was the same for 1 species, the site frequency for 13 species and the peatland frequency for 32 species. The variation in the number of unchanged species between the different levels of analysis results from the varying precision of the levels. The abundance of a species at a site can vary between 0 and 10000, whereas there were only 118 sites and 6 different peatland types for a species to occur in.

3.1. The effects of drainage on specialist and generalist species

For both vascular plants and bryophytes present at both the pristine and drained peatlands, species' abundances were more often lower in drained peatlands than in natural peatlands. Out of the total 117 vascular plant species, 83 had lower abundance after draining and 34 higher (figure 4, panels B and D). For bryophytes, 48 out of the total 71 species had lower abundance and 23 higher (figure 4, panels A and C). For both vascular plants and bryophytes, the difference in abundance between treatments was dependent on the SSI of a species in the case of the species whose abundances were lower in drained sites (vascular plants: $t = 3,173$, $n = 83$, $P = 0,002$; bryophytes: $t = 3,057$, $n = 48$, $P = 0,004$). The species with a high degree of specialization were generally the ones with largest differences in the abundances between treatments. There was no statistical dependence between the relative change in abundance and SSI for the species whose abundances were higher in drained sites (vascular plants: $t = -1,136$, $n = 34$, $P = 0,264$; bryophytes: $t = -1,190$, $n = 23$, $P = 0,247$). The results remained unchanged even if the two clear outlier species were removed from the data (figure 4, panel A = *Brachythecium salebrosum* and B = *Melampyrum pratense*). The highest possible SSI-value in the case of this data is 2,44949 which is realized when there is only one site or one peatland type that a species occurs in regardless of the species' abundance. In total 55 vascular plant species and 32 bryophyte species had the maximum SSI-value of 2,44949.

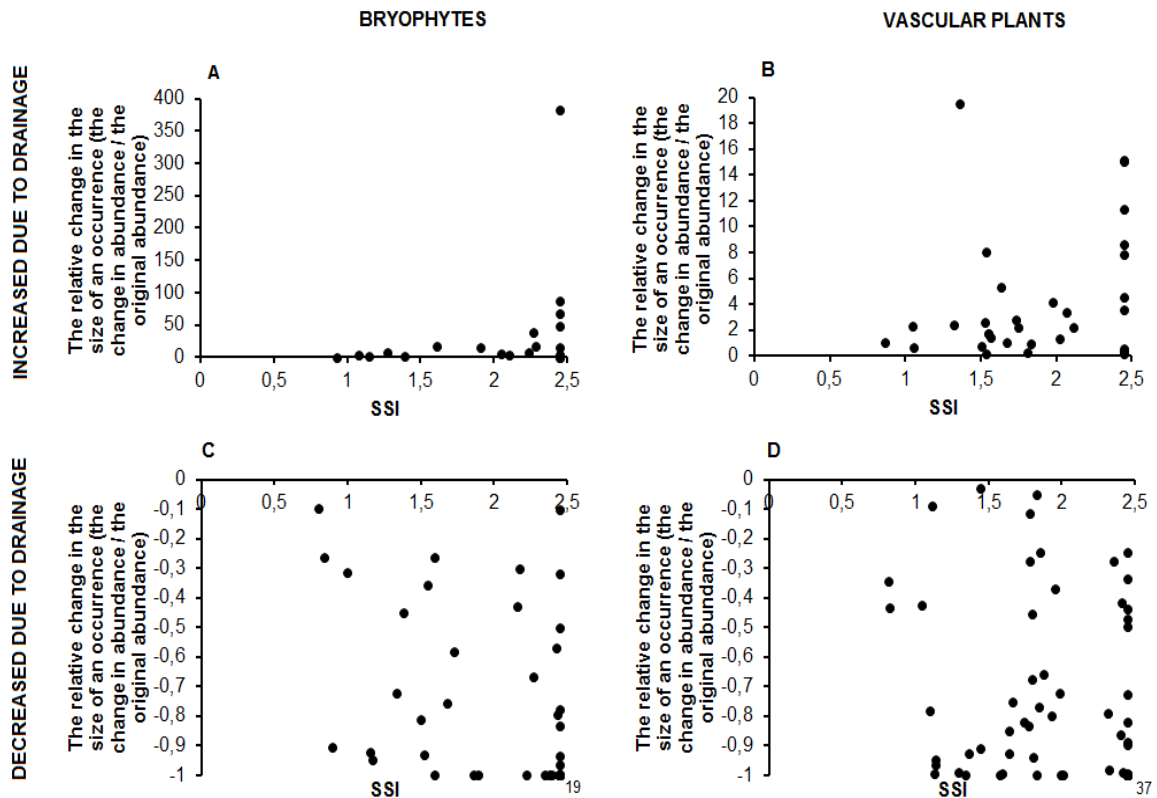


Figure 4. The relationship between the relative change in abundance of a species and its SSI-value. Numbers 19 (panel C) and 37 (panel D) indicate the number of overlapping observation points (when the value of relative change = -1 (i.e. the species disappeared) and the SSI-value = 2,44949). Panels A and B portray the bryophyte and vascular plant species whose abundances were greater in drained than pristine sites (i.e. their abundance increased due to drainage). Conversely, panels C and D portray the bryophyte and vascular plant species whose abundances were greater in pristine than drained sites (i.e. their abundance decreased due to drainage).

Vascular plants and bryophytes were on average more frequent in pristine sites ($n = 59$) and pristine peatland types ($n = 6$) than in drained sites ($n = 59$) and drained peatland types ($n = 6$) (figures 5 and 6). 80 vascular plant species and 39 bryophyte species were more frequent in pristine than drained sites whereas 23 vascular plant species and 20 bryophyte species were more frequent in drained than pristine sites. 64 Vascular plant species and 35 bryophyte species were more frequent in pristine than drained peatland types and 20 vascular plant species and 18 bryophyte species were more frequent in drained than pristine peatland types. The relative difference in the frequency of sites a species was found in between treatments was statistically significantly dependent on the SSI-value of a species in the case of all bryophyte species (bryophytes with higher frequency: $t = -4,666$, $n = 20$, $P < 0,001$; bryophytes with lower frequency: $t = 4,861$, $n = 39$, $P < 0,001$) and vascular plant species whose site frequencies were both lower in drained than in pristine sites ($t = 5,367$, $n = 80$, $P < 0,001$). The only exception was those vascular plant species that were more frequent on drained sites than pristine sites ($t = -1,729$, $n = 23$, $P = 0,098$). The relative difference between treatments in the frequency of different peatland types a species was found in before and after drainage was statistically significantly dependent on the SSI-value of a species in the case of all vascular plant species (vascular plants with higher frequency: $t = -3,302$, $n = 20$, $P = 0,004$; vascular plants with lower frequency: $t = 8,066$, $n = 64$, $P < 0,001$) and bryophyte species that were more frequent in pristine than drained peatland types ($t = 6,953$, $n = 35$, $P < 0,001$). In this case, the only exception was

bryophyte species that were more frequent in drained than pristine peatland types ($t = -1,998$, $n = 18$, $P = 0,062$).

The species whose site specific frequencies were the same in drained and pristine sites had higher than average SSI-values. The difference between the unchanged species' SSIs and the average SSI was statistically significant (vascular plants: $t = 2,859$, $df = 19,998$, $P = 0,010$; bryophytes: $t = 6,030$, $df = 67,197$, $P < 0,001$). The species whose peatland type specific frequencies were the same in drained and pristine sites did not statistically significantly deviate from the average (vascular plants: $t = 1,558$, $df = 58,817$, $P = 0,125$; bryophytes: $t = 0,373$, $df = 23,482$, $P = 0,712$).

In most cases, if a species had increased or decreased on one measure of change (relative change in abundance, site frequency or peatland type frequency) the direction of the change was parallel on the other measure (table 1). For bryophytes, the direction of the change was same with all the measures for 50 cases out of 72 and for vascular plants for 73 cases out of 118 (table 1).

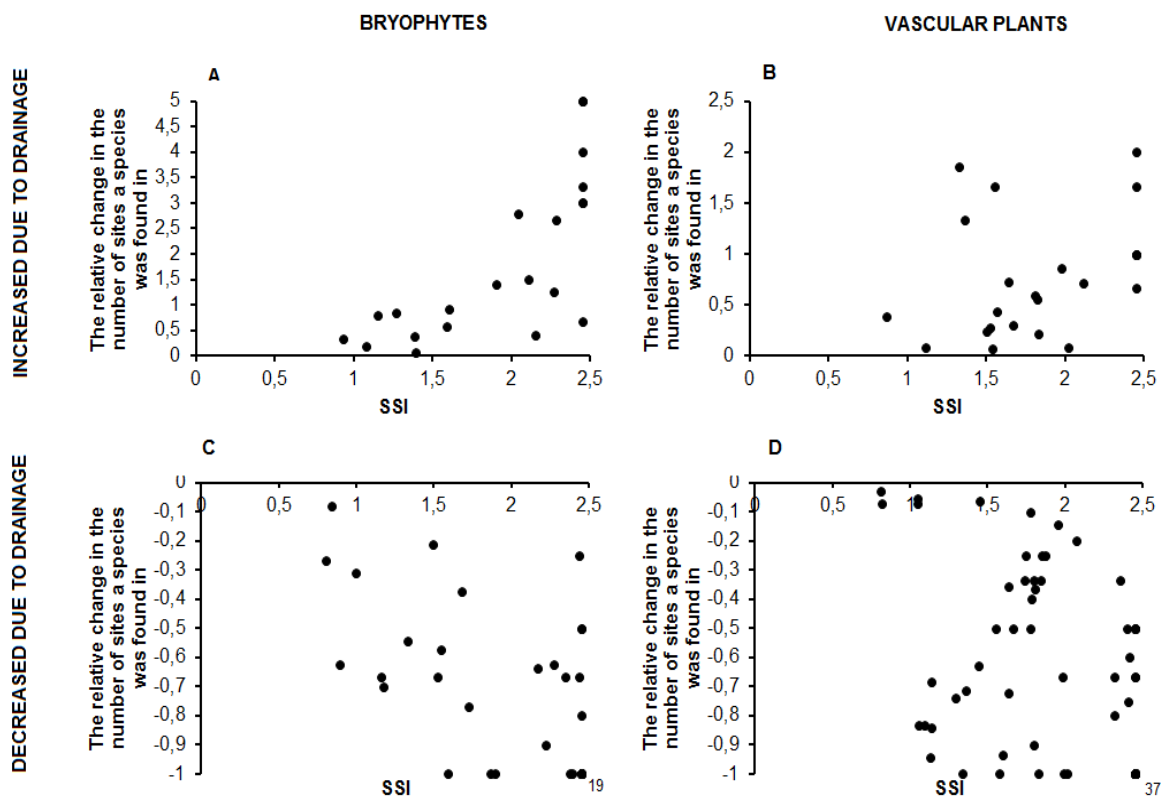


Figure 5. The relationship between the relative change in the number of sites a species was found in and the SSI-value of the species. Numbers 19 (panel C) and 37 (panel D) indicate the number of overlapping observation points (when the value of relative change = -1 (i.e. the species disappeared) and the SSI-value = 2,44949). Panels A and B portray the bryophyte and vascular plant species that were found in more drained than pristine sites (i.e. their site frequency increased due to drainage). Conversely, panels C and D portray the bryophyte and vascular plant species that were found in more pristine than drained sites (i.e. their site frequency decreased due to drainage).

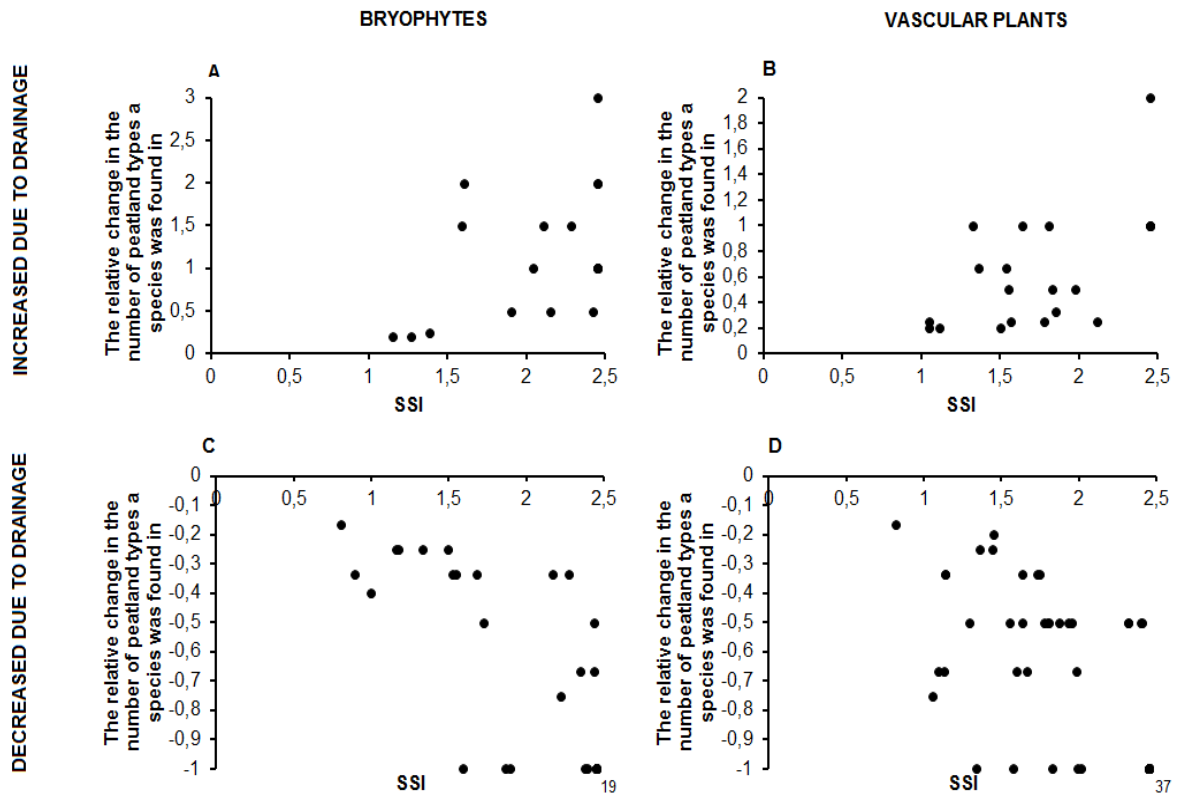


Figure 6. The relationship between the relative change in the number of peatland types a species was found in and the SSI-value of the species. Numbers 19 (panel C) and 37 (panel D) indicate the number of overlapping observation points (when the value of relative change = -1 (i.e. the species disappeared) and the SSI-value = 2,44949). Panels A and B portray the bryophyte and vascular plant species that were found in more drained than pristine peatland types (i.e. their peatland type frequency increased due to drainage). Conversely, panels C and D portray the bryophyte and vascular plant species that were found in more pristine than drained peatland types (i.e. their peatland type frequency decreased due to drainage).

Table 1. The direction of relative change in the different levels of analysis. Plus sign indicating an increase (in abundance or number of sites/peatland types) after drainage, minus sign a decrease after drainage and 0 no change after drainage.

	Total abundance of a species	Number of sites a species was found in	Number of peatland types a species was found in	Number of species
Bryophytes				
	+	+	+	14
	-	-	-	36
	+	+	0	4
	-	-	0	4
	+	0	0	4
	-	0	0	4
	-	+	+	3
	+	0	+	1
	0	0	0	1
	-	0	+	1
Vascular plants				
	+	+	+	13
	-	-	-	60
	+	+	0	6
	-	-	0	10
	+	0	0	5
	-	0	0	4
	-	+	+	3
	+	-	-	3
	+	0	+	1
	-	0	-	1
	-	-	+	3
	+	-	+	1
	+	-	0	4
	-	+	0	2
	+	0	-	1
	0	0	0	1

37 species of vascular plants and 19 species of bryophytes that were found in natural peatlands were completely absent in drained ones. For vascular plants 32 of these 37 species, and for bryophytes 14 out of the 19 species had the maximum value of specialization (SSI = 2,44949). For both groups, the average SSI of species found only in pristine sites (bryophytes = 2,337, vascular plants = 2,355) was higher than the average SSI of all species (bryophytes = 2,053, vascular plants = 2,027). The difference between the average SSIs was statistically significant (bryophytes: $t = -3,321$, $df = 62,446$, $P = 0,002$, vascular plants: $t = -5,255$, $df = 116,437$, $P < 0,001$).

3.2. The effects of drainage on the specialist-generalist ratio of communities

For vascular plants in 4 cases out of 6 and for bryophytes in 5 cases out of 6 the CSI values were higher in drained than pristine communities (figure 7). However, in the case of both vascular plants and bryophytes, the effect of the treatment (drained or pristine) to the communities' CSI-values was not statistically significant (vascular plants: $F = 0,612$, $df =$

1, $P = 0,436$; bryophytes: $F = 0,009$, $df = 1$, $P = 0,927$). Conversely, for both groups the CSI-values of communities were statistically significantly dependent on the peatland type (vascular plants: $F = 32,448$, $df = 5$, $P < 0,001$; bryophytes: $F = 13,75$, $df = 5$, $P < 0,001$). Vascular plants had an interaction between treatment and peatland type ($F = 2,374$, $df = 5$, $P = 0,044$). A peatland type specific comparison indicated that the interaction for vascular plants was statistically significant in the case of fertile fens ($F = 9,212$, $df = 1$, $P = 0,003$). For bryophytes the peatland type specific comparison indicated statistically significant interaction in the case of unfertile fens ($F = 9,212$, $df = 1$, $P = 0,003$), although there was no statistically significant interaction between treatment and peatland type for bryophytes as a whole ($F = 1,68$, $df = 5$, $P = 0,146$). The exceptions in vascular plants were fertile pine mires and fertile fens and in bryophytes unfertile fens. For both groups, the CSI-values of fertile spruce mires were distinctly higher than in other peatland types.

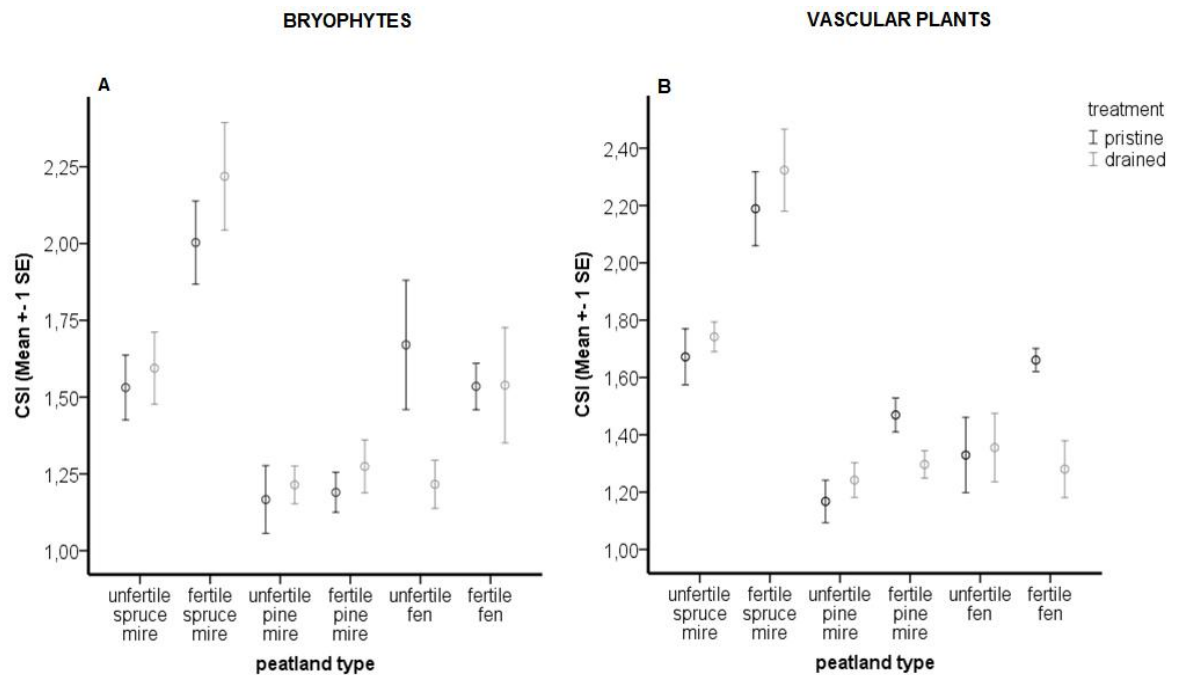


Figure 7. The average CSI-values of different treatments and peatland types.

4. DISCUSSION

4.1. The main results

The results indicate that on natural peatland communities drainage affects species occurring as specialists differently than species occurring as generalists. In the case of both bryophytes and vascular plants and on occurrence frequencies at site and peatland type levels, the general trend is that the changes in the number of a species' occurrences between drained and pristine sites are greater for specialist species than they are for generalist species. Despite the differing responses of specialist and generalist species the specialist-generalist ratios of peatland plant communities did not significantly differ between pristine and drained sites regarding both bryophytes and vascular plants. The community specialization level was not affected by the fertility of the peatland either. Instead, the effect of the peatland type on the specialization level of a community was strong.

4.2. Specialists and generalists react differently to anthropogenic disturbance

The abundances and frequencies of specialist species generally either increased or decreased whereas the abundances and frequencies of generalist species appeared similar in pristine and drained sites. In other words, the generalist species were less affected (either positively or negatively) by environmental change than the specialist species. When measured as change in abundance, the majority of specialist species suffered rather than benefitted from the drainage. Specialist species whose habitat requirements are more specific are likely to either benefit or suffer due to changes in the habitat conditions, in this case caused by drainage. The direction of the effect depends on whether the specialist's habitat requirements are met due to the disturbance, leading to the specialist's increased competitiveness, or whether the previously adequate conditions are changed by drainage in a way that the environment becomes more or less unsuitable. Intuitively it is more probable that a disturbance shifts the habitat's conditions further away from the requirements of a specialist species already present rather than closer to them.

The specialist species whose abundances and frequencies decreased after drainage or were completely absent from drained sites were often species that are commonly found only in peatland habitats (Eurola et al. 1995). For example, *Loeskyppnum badium*, *Rhizomnium pseudopunctatum*, *Rhamnus frangula* and *Carex disperma* are primarily peatland species that were absent from drained sites and had a high level of specialization in pristine peatlands. These species are, in a sense, the true specialists since they are regionally rare and only locally abundant and would appear as specialists also when considering data outside peatland habitats. In other words, the specialists that suffered from the drainage or consequently disappeared completely were most likely heavily dependent on the characteristic conditions of pristine peatlands, such as the high water level. In fact, the specialist species that suffered the most from the drainage were not specialized solely in peatlands regardless of the peatland type and within-peatland conditions but in habitats with specifically high water tables (e.g. *Paludella squarrosa* and *Pedicularis palustris*) and high nutrient levels (e.g. *Helodium blandowii* and *Gymnadenia conopsea*). Both of which commonly change as a peatland gets drained (Laine et al. 1995).

Generally, species that occurred as specialists in pristine peatlands, but were more abundant and frequent in drained peatland sites than in pristine peatland sites are ones that are often considered as forest species rather than actual peatland species (e.g. Eurola et al. 1995). For example *Brachythecium salebrosum*, *Brachythecium oedipodium*, *Gymnocarpium dryopteris* and *Linnaea borealis* are primarily forest species that tolerate only a narrow range of pristine peatland conditions and are much greater in abundance and frequency on drained sites. Peatlands can contain drier microhabitats that resemble the forest floor and are able to support species that could not otherwise succeed in a peatland habitat. If an otherwise peatland intolerable species inhabits one of these microhabitats it will appear as an extreme specialist due to its local abundance in very few locations. Then, after the drainage, when the peatland changes into a drier, generally more forest-like environment, the amount of suitable microhabitats for forest species increases (Laine et al. 1995), resulting in a notably higher frequency of above-mentioned specialists in drained peatlands in comparison to pristine peatlands. Boreal peatlands turn gradually into forests (Lappalainen 1998) so therefore abundant and closely located forest species are able to overtake suitable habitats quickly and efficiently (Laine et al. 1995). Thus, it is likely that the "drainage-benefitting" specialists would appear more generalist when considering wider habitat range, i.e. including forest habitats.

After disturbance the species richness of a community does not necessarily change even if the composition of species was altered (Devictor et al. 2008). In other words, the amount of winners resulting from the disturbance can be the same as the amount of losers.

The difference between the number of bryophyte and vascular plant species in pristine and drained sites was relatively small (72 bryophyte species and 119 vascular plant species on pristine sites and 67 bryophyte species and 92 vascular plant species on drained sites), but the turnover rate of species was high (38 % of bryophyte species and 36 % of vascular plant species were unique to solely pristine or drained sites). Even if the winners and the losers were more or less in balance, the functioning of the ecosystem can change along with the changing community composition. As the replaced species were commonly peatland specialists involved in peat formation and the invaders were common forest species, the ecosystem-level impact of the disturbance can be notable irrespective of the unchanged species richness.

Even though the species richness of both bryophytes and vascular plants was smaller in drained sites, the average abundance of a species increased after drainage in the case of vascular plants and decreased in the case of bryophytes, resulting in a significant change in the biotic structure of the ecosystem. For vascular plants, decreasing species richness and increasing average abundance could indicate that in the drained sites a few species are able to cover large areas either by being superior competitors in the new conditions or purely by filling the newly exposed space resulting from the disappearance of plants unable to tolerate drainage. Vascular plant species whose abundances multiplied after drainage were typically woody shrubs (e.g. *Vaccinium myrtillus*), conifers (e.g. *Picea abies*) and ferns (e.g. *Dryopteris carthusiana*) all of which are abundant and common in forest-like habitats. The total number of bryophyte species found in drained sites was only 5 species smaller than in pristine sites but the average abundance in pristine sites was 1,6 times higher than in drained sites. So even though the species richness was somewhat constant between treatments the abundance of a single species was lower in drained than pristine peatlands. Keeping in mind that the turnover rate of bryophyte species was 38 %, it can be assumed that the species on drained sites were less abundant than the species in pristine peatlands, meaning that drained sites did not have as clear dominant species as pristine sites did. As mentioned before, the abundance of woody shrubs and conifers was higher on drained sites than pristine sites, so drained peatlands have more sources of small dead wood. 4 out of the 14 bryophyte species that were unique to drained sites use dead wood as a primary substrate (Eurola et al. 1995). One explanation to why the species that colonized drained peatlands were locally less abundant than the species on pristine peatlands could be that they are specialized to small, separate micro habitats that are only found here and there.

It is stated that specialist domination in a community is preserved through high levels of interspecific competition in stable environments (Mihuc 1997). Specialist species dependent on the stability and specific conditions suffer directly from the disturbance that alters both factors whereas generalists benefit indirectly from the disturbance through decreased competition (Marvier et al. 2004). It is possible that some of these indirect effects have not yet taken place in the studied peatlands as some peatland specialists might still preserve on the areas where the disturbance has not been as comprehensive as elsewhere. Thus it may be that as time passes the overpowering of generalist species at the drained sites yet increases. In other words, when comparing the pristine and drained plant communities it has to be taken into account that the time scale in which the communities have been forming is very different for the two. The average time since the origin of the drainage of the sites is 50 years so the species composition could still be quite dynamic in its response to the disturbance. How fast the changes in boreal peatlands happen after drainage has not yet been studied comprehensively but for example in peatland restoration the change rate is a crucial, and therefore a closely measured, component. It seems that on average the vegetation of boreal systems recovers in the span of decades (Kareksela et al.

2015, Moreno-Mateos et al. 2012, 2015) but in the case of many rarer species the recolonization can take a lot longer (Haapalehto et al. 2010, Hedberg et al. 2012).

In addition to the time and ability required for a species to disperse to a given area it is also possible that some species still persisting at drained sites will disappear in the future. A population of a species that has gone nearly extinct after undergoing disturbance is likely to experience delayed extinction, or extinction debt over time (Tilman et al. 1994, Hanski & Ovaskainen 2002, Kuussaari et al. 2009). The time frame in which the current pristine peatland communities have been forming without major disturbances is most likely considerably longer, including primary succession that can go on for millennia. On the other hand, 50 years is a relatively long time for the majority of the species composition to form. Especially since the forest species that naturally occur in the surrounding areas of peatlands should not have prominent problems to disperse to the drained sites. Another possible factor affecting the species pool of a drained site even decades after the actual draining procedure is the founder effect: the current community structure can depend heavily on the species present at the site before the drainage or on the very first colonizers after it (Abraham et al. 2009).

4.3. Peatland type determines specialization at community level

The main factor affecting the level of community specialization was the peatland type. Disturbance had no effect on specialization at community level. There are a number of potential reasons for why the treatment did not appear to have a significant effect on plant community specialization even though drainage affected specialist and generalist species differently. As mentioned before, the majority of generalist species were present on both pristine and drained sites but drained sites were lacking peatland specialist species and instead inhabited many species abundant in forests but rare in peatlands. When the number of specialists exclusive to drained sites equals the number of disappeared specialists and the number and the composition of generalists remains somewhat similar between treatments, the specialist-generalist ratio of a community stays stable even if the species in question are replaced. In time the results could still change since again, time is a factor affecting the species pool of a community. Some of the forest species, now interpreted as specialists according to the used specialization index and data from all the 118 sites, may still increase their distribution on drained sites and thus in the future appear as generalists and thereby make the generalist-specialist ratios of drained peatland communities appear different.

A few exceptions stood out from the general trend of community level results (figure 7). First, the effect of peatland type on community specialization was clearest between spruce mires and other peatland types. The initial species richness of spruce mires is higher than it is in any other peatland type and a large proportion of plant species associated with spruce mires are species that are common also in mineral soil forests (Euroola & Huttunen 2006). Accordingly, there are many species that, in the case of different peatland types, occur only in spruce mires and are adapted to forest-like conditions increasing the total specialization of the plant community and keeping it high even as the habitat becomes drier. As spruce mires resemble forests per se and draining peatlands turns them even more forest-like, it is intuitive that, when drained, spruce mires can support multiple forest species that appear as specialists since they are not present elsewhere. The higher species richness and the large number of species common in surrounding forests but seemingly specialists in peatlands present in both drained and pristine spruce mires may create the apparent difference in community specialization between spruce mires and other peatland types.

Secondly, in the case of vascular plants, fertile pine mire and fertile fen communities were more specialized when pristine rather than drained. The acidification of peat through drainage induced oxidation is more intense in fertile than in unfertile pine mires (Laine et al. 1995). As drainage results in less fertile substrate for vascular plants on fertile sites, the differences between fertile and unfertile drained pine mires are smaller than in pristine sites. The effect of nutrient level on the total number of species of different types of vascular plants (=shrubs, trees, sedges, grasses and herbs) was higher on pristine pine mires than in drained pine mires. The difference between the number of different vascular plant species on fertile and unfertile sites was 19 species on drained sites and 30 species on pristine sites. 48 % of the species were shared between drained fertile and unfertile pine mires whereas the same proportion was only 37 % for pristine sites. Larger number of unique species and the effect of drainage to the pH of fertile peat could explain why the level of community specialization of vascular plants was smaller in drained sites. Fertile fens are dominated by low-growth vegetation such as certain sedges (e.g. *Carex limosa* and *Carex pauciflora*) and shrubs (e. g. *Vaccinium oxycoccos* and *Andromeda polifolia*) (Laine & Vasander 2005). They are also biodiversity hotspots with a high number of demanding species specialized to fertile and wet conditions of pristine fens (Mälson 2008). Draining both oxidizes and mineralizes peat which decreases the competitive superiority of fertile fen specialists and yields space for strongly shading, higher growing species. Examples of such species, that were present in drained but not pristine fertile fens, were for example *Picea abies*, *Vaccinium myrtillus* and *Dryopteris carthusiana*. If the majority of the species present in pristine fertile fens require both high water table and high fertility, drainage, altering both abovementioned characteristics, can strongly decrease the species richness and species abundance of the community. It is also possible that even after drainage fertile fens remain still too wet for forest species to colonize the area with the same extent as in for example spruce mires. The extensive disappearance of original plant species together with novel conditions that are at the same time too dry and too wet may account for the decrease in the degree of community specialization from pristine to drained fertile fens.

Finally, the community specialization of bryophytes was higher on pristine than drained sites only in unfertile fens. Unfertile fens have the highest diversity of *Sphagnum* species both proportionally and by the number of different species (Rydin et al. 1999). As in fertile fens, the water table in unfertile fens is only slightly below or even above the peat layer. The majority of the *Sphagnum* species specialized in unfertile fens is also specialized on growing on the wetter pool or lawn levels of the peatland rather than on the drier hummocks (Eurola et al. 1995). Species specialized on wet conditions will be most dramatically affected by the lowered water table resulting from the drainage. The bryophyte species whose abundances decreased most on unfertile fens due to drainage were fen specialists also dependent on a high water table (Eurola et al. 1995), such as *Sphagnum balticum* and *Sphagnum majus*. The bryophytes that on unfertile fens benefitted the most from the drainage, such as *Pleurozium schreberi* and *Polytrichum strictum*, were species also commonly found in other types of peatlands and in drier conditions. The deviation in the community specialization data for bryophytes may result from the specialist species of unfertile fens being especially vulnerable to dryness and, in case of drainage, their rapid replacement by regionally abundant (generalist) species that tolerate or benefit from dry conditions.

4.4. Used measures and sources of uncertainty

Using an index as a measure of specialization has both advantages and disadvantages. Most other ways of measuring the degree of specialization cannot be used equally for all species. For example, using the number of suitable host species as an indicator of

specialization is only practical when the focus is on species that, in fact, have a varying number of host species. However, using an index that is based on the occurrence of a species in different habitats, such as the one used in this particular thesis, is applicable for all occasions (Julliard et al. 2006). Also an index that relies on presence-absence and abundance data is much more objective in determining degrees of specialization than for example using literature or expert knowledge would be.

An index can be used to determine a degree of specialization for each species with the same exact method, therefore enabling the comparison of specialization between species. For example, the level of specialization of the species that were present only on pristine sites could not have been interpreted without using an index. Species and community specialization indexes are also beneficial for being able to quantify specialization on many different levels of niche variation for example as a measure of species abundance or the frequency of a species' occurrence.

In interpreting the results based on indexes it is important to note that an index is limited by the data used for calculating it and therefore cannot as such be applied to other scales without adding more data. For example, in this thesis it was relevant to separate species that appeared as specialists only because the used data was collected solely from peatlands, from the landscape level specialists, both of which can appear equally specialized solely according to the used index.

4.5. Changes in the composition of local communities can be accountable for large-scale biodiversity loss

Previous studies have shown that anthropogenic disturbance advances homogenization between habitats (e.g. Olden et al. 2004). Other studies suggest that the winners of disturbed environments are the habitat generalists (e.g. Marvier et al. 2004), while some results indicate generalist species staying constant regardless of the intensity of the anthropogenic disturbance (Kitahara & Fujii 1994). My results confirm both standpoints, since the majority of the specialist species suffered from the drainage and generalists mostly remained unaffected, thus making the group of generalist as a whole the winner over the specialists. However, the judging of winners and losers is strongly scale dependent, just as is the determination of specialists and generalists. The definition of specialism and generalism depends, indeed, on the used species pool and its extension in space over different types of ecosystems. Here, many of the winning specialists are most likely landscape-level generalists. The fact that the specialization level of the species completely absent from the drained sites was statistically significantly above the average is supported by previous studies showing that the specialization of a species correlates positively with the magnitude of its response to disturbance (Devictor et al. 2008).

Even though the level of specialization did not differ between pristine and drained communities the composition of communities did. Certain measures, such as a specialization indexes, can reveal little to none variation between communities, but even so the changes that are happening can be significant (e.g. Elo et al. 2016). In nature, local species diversity increases equally as often as it decreases (Vellend et al. 2013). When a species goes locally extinct, it will likely be replaced by another species from the surrounding areas which results in no net change in local biodiversity (Thomas 2013) despite the species turnover. Vellend et al. (2013) pointed out, that in maintaining long-term biodiversity locally, a high level of regional biodiversity is required to serve as a "spatial insurance". If the regional species pool that compensates for local extinctions is not diverse, over time homogenization of communities is bound to happen. In summary, while studying changes in communities at a local scale, biodiversity change can be at least

as significant observation as biodiversity loss. Or as in this study, specialist turnover can be taken as a warning signal of specialist decline in longer time scale.

As peatlands are wetland ecosystems whose functioning is heavily dependent on their natural plant communities (e.g. Rydin et al. 1999, Laiho 2006) changes in the plant community structure can have extensive effects on the ecosystem as a whole. The results indicate that the species truly specialized on peatlands suffered most from the drainage. Over a third of the bryophyte species that were completely absent from the drained sites were *Sphagnum* mosses (e.g. *Sphagnum tenellum*, *Sphagnum subnitens* and *Sphagnum cuspidatum*), the keystone species of peatland ecosystems (Vitt & Wieder 2006). On landscape level drainage can lead to homogenization, as the formerly pristine peatlands start to resemble the surrounding forests both through structure and function.

4.6. Conclusions

In conclusion, species and community specialization reflect the amount of variation within and between communities as niche variation affects the degree of interspecific competition and population stability in a community (Bolnick et al. 2003). Thus, quantifying changes in the specialization of species and communities is an effective way of studying changes in the functioning of communities and even ecosystems. Therefore knowledge on species and community specialization furthers the understanding of both ecological and evolutionary questions. The results of this thesis suggest that drainage alters the natural dynamics and community structures of natural peatlands and is accountable for local extinctions. This again supports the argument of anthropogenic activities being responsible for many of the changes occurring in ecosystems today. Similarly to previous studies (e.g. McKinney & Lockwood 1999), these results imply that anthropogenic disturbance assists the spreading of generalist species and hinders the success of specialist species, leading to within-site heterogeneity, between-site homogenization and in the loss of biodiversity. According to my results, the significance of the scale of observation should always be emphasized as the interpretation of the findings can substantially vary, depending on whether the results were viewed e.g. from a habitat or a landscape perspective. As the directional change from peatland species to forest species resulting from drainage is a slow process (Minkinen & Laine 2006), changes in the plant communities of drained peatlands can still be ongoing and future research is needed to examine even longer-term effects that drainage has on the community structure and function of peatlands.

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ATTACHMENT 1

SITE, FREQUENCY, ABUNDANCE AND SSI DATA FOR BRYOPHYTES

Bryophyte species	frequency (pristine sites)	frequency (drained sites)	frequency (pristine peatland types)	frequency (drained peatland types)	total abundance (all pristine sites)	total abundance (all drained sites)	SSI (pristine)	SSI (drained)	SSI (all sites)
<i>Aulacomnium palustre</i>	32	43	6	6	2508	3495	0,932281	0,622663	0,737754
<i>Brachythecium collinum</i>	0	3	0	2	0	327		2,431556	
<i>Brachythecium oedipodium</i>	3	13	1	3	121	6032	2,44949	2,288155	3,186998
<i>Brachythecium reflexum</i>	0	10	0	2	0	1303		2,401004	
<i>Brachythecium rutabulum</i>	1	1	1	1	2	137	2,44949	2,44949	3,410088
<i>Brachythecium salebrosum</i>	1	5	1	2	2	769	2,44949	2,442614	3,44549
<i>Brachythecium starkei</i>	4	9	2	2	58	2322	2,270738	2,410905	3,324933
<i>Brachythecium velutinum</i>	0	1	0	1	0	2		2,44949	
<i>Bryum pseudotriquetrum</i>	1	0	1	0	2	0	2,44949		
<i>Calliergon cordifolium</i>	5	1	1	1	1653	60	2,44949	2,44949	3,333927
<i>Campylium protensum</i>	1	1	1	1	2	2	2,44949	2,44949	2,335497
<i>Campylophyllum sommerfeltii</i>	0	1	0	1	0	2		2,44949	
<i>Cirriphyllum piliferum</i>	0	2	0	1	0	311		2,44949	
<i>Climacium dendroides</i>	1	0	1	0	12	0	2,44949		
<i>Dicranella cerviculata</i>	1	1	1	1	4	2	2,44949	2,44949	2,486326
<i>Dicranum bergeri</i>	3	11	2	5	31	566	2,280474	1,128299	1,727486
<i>Dicranum bonjeanii</i>	1	4	1	2	50	54	2,44949	1,59937	1,967615
<i>Dicranum fuscescens</i>	0	2	0	2	0	36		2,30486	
<i>Dicranum majus</i>	6	15	2	5	971	4611	2,105346	1,326606	1,707271
<i>Dicranum polysetum</i>	10	38	3	6	1379	9883	2,044873	1,433595	1,900449
<i>Dicranum scoparium</i>	12	23	2	6	146	2727	1,606726	1,767134	2,447102
<i>Helodium blandowii</i>	2	0	2	0	16	0	1,890902		
<i>Hylocomium splendens</i>	14	22	2	5	5982	4413	1,59274	1,415652	1,484565
<i>Loeskynum badium</i>	1	0	1	0	4	0	2,44949		
<i>Mnium stellare</i>	1	0	1	0	2	0	2,44949		
<i>Paludella squarrosa</i>	1	0	1	0	2	0	2,44949		
<i>Plagiomnium</i>	0	4	0	2	0	57		1,752507	

<i>curvatulum</i>										
<i>Plagiomnium cuspidatum</i>	2	2	2	2	1112	1000	2,443622	2,423479	2,325199	
<i>Plagiothecium denticulatum</i>	0	6	0	2	0	27		1,769248		
<i>Plagiomnium ellipticum</i>	3	3	1	1	556	36	2,44949	2,44949	3,241093	
<i>Plagiothecium laetum</i>	5	12	2	3	31	527	1,904854	2,161647	2,910672	
<i>Plagiomnium medium</i>	2	0	1	0	12	0	2,44949			
<i>Pleurozium schreberi</i>	28	52	5	6	8104	7452	1,270946	0,962019	1,450293	
<i>Pohlia nutans</i>	15	27	5	6	248	543	1,151298	1,05465	1,167218	
<i>Polytrichum commune</i>	18	25	4	5	9989	5481	1,382182	1,131946	1,350995	
<i>Polytrichum juniperinum</i>	0	1	0	1	0	702		2,44949		
<i>Polytrichum strictum</i>	27	32	5	5	4972	2169	1,076048	1,436919	1,728536	
<i>Polytrichum swartzii</i>	1	0	1	0	10	0	2,44949			
<i>Polytrichastrum formosum</i>	0	1	0	1	0	5		2,44949		
<i>Polytrichastrum longisetum</i>	1	6	1	4	26	78	2,44949	1,926232	2,150082	
<i>Pseudobryum cinclidioides</i>	5	0	3	0	91	0	1,860806			
<i>Ptilium crista-castrensis</i>	2	2	1	2	26	126	2,44949	2,357407	2,781111	
<i>Rhizomnium magnifolium</i>	1	0	1	0	2	0	2,44949			
<i>Rhizomnium pseudopunctatum</i>	2	0	1	0	39	0	2,44949			
<i>Rhizomnium punctatum</i>	2	0	1	0	17	0	2,44949			
<i>Rhodobryum roseum</i>	2	1	1	1	12	2	2,44949	2,44949	2,965479	
<i>Rhytidiadelphus squarrosus</i>	0	1	0	1	0	180		2,44949		
<i>Rhytidiadelphus triquetrus</i>	1	1	1	1	132	90	2,44949	2,44949	2,385126	
<i>Sanionia uncinata</i>	3	5	1	3	13	22	2,44949	1,355984	1,711894	
<i>Sphagnum angustifolium</i>	49	45	6	6	1091	8054	0,839298	0,687466	0,776446	
<i>Sphagnum annulatum</i>	7	0	2	0	31	0	1,590707			
<i>Sphagnum aongstroemii</i>	2	2	2	2	24	205	2,232638	2,378518	3,006377	
<i>Sphagnum balticum</i>	19	15	4	3	3920	7380	1,495976	1,576134	1,891562	
<i>Sphagnum capillifolium</i>	10	14	4	6	8	1050	5995	2,15404	1,315294	1,978921
<i>Sphagnum centrale</i>	9	3	4	3	8	1022	780	1,15607	1,226794	1,709944
<i>Sphagnum compactum</i>	1	4	1	2	4	32	2797	2,44949	2,258677	3,183285
<i>Sphagnum cuspidatum</i>	1	0	1	0	37	0	2,44949			

<i>Sphagnum fallax</i>	32	12	6	4	6374	5946	0,893616	1,342382	1,410478
					2				
<i>Sphagnum fimbriatum</i>	2	0	1	0	780	0	2,44949		
<i>Spagnum flexuosum</i>	11	4	3	2	1243	8705	2,170964	1,549516	1,896114
					1				
<i>Sphagnum fuscum</i>	29	20	5	3	3834	2628	0,993308	1,390731	1,119037
					7	2			
<i>Sphagnum girgensohnii</i>	16	10	3	2	6392	1549	1,67537	1,634889	1,9626
					4	0			
<i>Sphagnum lindbergii</i>	3	1	2	1	1202	2	2,43607	2,44949	3,439986
<i>Sphagnum magellanicum</i>	45	33	6	5	3241	2929	0,802867	0,635325	0,704204
					7	1			
<i>Sphagnum majus</i>	6	2	3	1	9739	6	2,344457	2,44949	3,327302
<i>Sphagnum obtusum</i>	2	0	1	0	255	0	2,44949		
<i>Sphagnum papillosum</i>	24	11	4	3	6426	1784	1,329086	1,372099	1,568586
					0	3			
<i>Sphagnum pulchrum</i>	4	3	3	1	4412	912	2,43485	2,44949	2,821883
<i>Sphagnum quinquetarium</i>	2	0	1	0	2499	0	2,44949		
<i>Sphagnum riparium</i>	10	1	4	1	9351	2	2,222677	2,44949	3,173157
<i>Sphagnum rubellum</i>	13	3	4	2	2039	850	1,726734	2,415074	1,963536
<i>Sphagnum russowii</i>	26	28	6	6	1089	2577	1,391952	1,017716	1,191848
					2	1			
<i>Sphagnum squarrosum</i>	8	3	3	2	317	106	2,270045	2,270738	2,514405
<i>Sphagnum subfulvum</i>	1	1	1	1	432	530	2,44949	2,44949	2,366307
<i>Sphagnum subnitens</i>	0	1	0	1	0	10		2,44949	
<i>Sphagnum subsecundum</i>	6	0	2	0	5830	0	2,378818		
<i>Sphagnum tenellum</i>	8	0	3	0	2153	0	2,38914		
<i>Sphagnum teres</i>	7	3	3	2	2023	1303	1,543686	2,440477	1,822649
<i>Sphagnum warnstorffii</i>	4	4	2	3	3765	1618	2,42207	2,043516	2,514518
<i>Sphagnum wulfianum</i>	0	1	0	1	0	164		2,44949	
<i>Splachnum sphaericum</i>	0	1	0	1	0	2		2,44949	
<i>Straminergon stramineum</i>	20	6	4	3	708	36	1,171214	1,320774	1,776781
<i>Tetraphis pellucida</i>	1	6	1	2	10	44	2,44949	1,572727	1,936596
<i>Warnstorfia exannulata</i>	1	1	1	1	28	445	2,44949	2,44949	3,264973
<i>Warnstorfia fluitans</i>	6	2	3	2	57	4	1,523657	1,549193	2,119752
<i>Warnstorfia sarmentosa</i>	2	1	1	1	18	4	2,44949	2,44949	2,804879

ATTACHMENT 2

SITE, FREQUENCY, ABUNDANCE AND SSI DATA FOR VASCULAR PLANTS

Vascular plant species	frequency (pristine sites)	frequency (drained sites)	frequency (pristine peatland types)	frequency (drained peatland types)	total abundance (all pristine sites)	total abundance (all drained sites)	SSI (pristine)	SSI (drained)	SSI (all sites)
<i>Agrostis canina</i>	1	0	1	0	10	0	2,44949		
<i>Agrostis capillaris</i>	1	0	1	0	2	0	2,44949		
<i>Alnus incana</i>	2	2	2	1	110	22	1,930555	2,44949	2,285855
<i>Andromeda polifolia</i>	42	39	6	5	15988	9065	0,82123	1,130419	0,94166
<i>Anemone nemorosa</i>	2	1	2	1	17	2	1,773077	2,44949	2,311834
<i>Angelica sylvestris</i>	1	0	1	0	14	0	2,44949		
<i>Athyrium filix-femina</i>	4	1	2	1	640	375	2,408327	2,44949	2,398718
<i>Betula nana</i>	36	34	4	5	10246	33602	1,048324	0,898452	1,138021
<i>Betula pendula</i>	0	1	0	1	0	10		2,44949	
<i>Betula pubescens</i>	7	20	3	6	224	757	1,325156	1,129222	1,359231
<i>Calamagrostis canescens</i>	3	2	2	2	324	235	2,352517	2,230133	2,23871
<i>Calamagrostis epigejos</i>	1	0	1	0	20	0	2,44949		
<i>Calamagrostis purpurea</i>	6	3	3	1	1261	314	1,665992	2,44949	2,006923
<i>Calamagrostis stricta</i>	1	0	1	0	17	0	2,44949		
<i>Calluna vulgaris</i>	7	12	4	5	2557	8264	2,113485	1,876105	2,119284
<i>Caltha palustris</i>	1	0	1	0	50	0	2,44949		
<i>Carex aquatilis</i>	2	0	2	0	340	0	1,827148		
<i>Carex canescens</i>	3	6	0	0	582	294	2,44949	1,672017	2,392687
<i>Carex cespitosa</i>	2	2	1	3	641	859	2,4495	2,44949	2,36491
<i>Carex chordorrhiza</i>	14	9	1	1	2922	439	1,636427	1,968497	2,080303
<i>Carex dioica</i>	5	1	4	2	100	2	2,317863	2,44949	3,224603
<i>Carex disperma</i>	1	0	2	1	355	0	2,44949		
<i>Carex echinata</i>	6	0	1	0	652	0	1,338527		
<i>Carex globularis</i>	12	13	4	0	1184	2749	2,022612	0,846646	1,216373
<i>Carex lasiocarpa</i>	23	6	4	4	16073	139	1,295893	1,580685	2,013016
<i>Carex limosa</i>	15	1	4	2	939	5	1,595006	2,44949	2,375074
<i>Carex loliaceae</i>	1	1	3	1	87	2	2,44949	2,44949	3,380069

<i>Carex magellanica</i>	7	6	4	2	421	265	1,95505	1,585321	1,826371
<i>Carex nigra</i>	3	1	3	1	72	20	1,986063	2,44949	2,258107
<i>Carex pauciflora</i>	27	10	4	3	3507	321	1,439917	1,424282	1,996882
<i>Carex rhynchophysa</i>	1	0	1	0	170	0	2,44949		
<i>Carex rostrata</i>	18	5	3	2	5261	379	1,636979	1,570092	2,242183
<i>Carex vaginata</i>	3	1	2	1	198	42	2,317798	2,44949	2,726172
<i>Carex vesicaria</i>	1	0	1	0	170	0	2,44949		
<i>Chamaedaphne calyculata</i>	16	15	5	4	4714	4567	1,445405	1,490174	1,399271
<i>Cirsium helenoides</i>	2	0	1	0	357	0	2,44949		
<i>Cirsium palustre</i>	1	0	1	0	20	0	2,44949		
<i>Cornus suecica</i>	1	0	1	0	30	0	2,44949		
<i>Dactylorhiza maculata</i>	6	1	3	1	46	10	1,095717	2,44949	1,50721
<i>Deschampsia cespitosa</i>	3	2	2	2	86	20	1,844321	1,777631	2,186864
<i>Deschampsia flexuosa</i>	3	8	2	3	74	206	1,552409	2,247036	2,372706
<i>Drosera longifolia</i>	3	2	2	2	155	28	1,738132	2,246085	2,175528
<i>Drosera rotundifolia</i>	35	10	4	3	2215	161	1,361132	2,215611	1,951431
<i>Dryopteris carthusiana</i>	7	13	2	3	1275	5731	1,977013	2,292873	2,665379
<i>Dryopteris expansa</i>	1	2	1	1	630	992	2,44949	2,44949	2,404282
<i>Empetrum hermaphroditum</i>	2	1	2	1	1303	179	2,397979	2,44949	2,978035
<i>Empetrum nigrum</i>	29	36	5	6	6983	12533	1,504053	0,844251	1,072107
<i>Epilobium angustifolium</i>	0	1	0	1	0	20	2,44949		
<i>Epilobium palustre</i>	2	0	1	0	9	0	2,44949		
<i>Equisetum arvense</i>	3	1	1	1	126	13	2,44949	2,44949	3,127355
<i>Equisetum fluviatile</i>	19	3	3	2	840	30	1,136481	2,082306	1,773008
<i>Equisetum palustre</i>	5	2	2	2	3366	32	2,41659	1,990478	3,3896
<i>Equisetum pratense</i>	1	0	1	0	136	0	2,44949		
<i>Equisetum sylvaticum</i>	11	7	4	2	6385	373	1,804925	2,435325	2,474694
<i>Eriophorum angustifolium</i>	12	9	3	4	541	409	1,848567	1,587902	1,680075
<i>Eriophorum gracile</i>	1	0	1	0	10	0	2,44949		
<i>Eriophorum vaginatum</i>	37	40	5	6	27185	24717	1,113616	0,802789	0,950543

<i>Filipendula ulmaria</i>	3	1	1	1	980	110	2,44949	2,44949	3,102329
<i>Galium palustre</i>	1	0	1	0	42	0	2,44949		
<i>Galium uliginosum</i>	1	0	1	0	4	0	2,44949		
<i>Geranium sylvaticum</i>	1	0	1	0	72	0	2,44949		
<i>Geum rivale</i>	1	1	1	1	110	30	2,44949	2,44949	2,755329
<i>Goodyera repens</i>	1	3	1	1	29	162	2,44949	2,44949	2,894299
<i>Gymnocarpium dryopteris</i>	5	5	1	1	222	2142	2,44949	2,44949	3,126051
<i>Gymnadenia conopsea</i>	1	0	1	0	2	0	2,44949		
<i>Juncus filiformis</i>	1	0	1	0	50	0	2,44949		
<i>Juniperus communis</i>	2	2	1	2	7	62	2,44949	1,655723	2,205071
<i>Linnaea borealis</i>	10	8	2	2	166	708	2,071486	2,090148	2,432059
<i>Listera cordata</i>	2	1	2	1	4	11	1,552409	2,44949	2,563854
<i>Luzula pilosa</i>	3	5	1	2	73	95	2,44949	2,285474	2,261081
<i>Lycopodium annotinum</i>	5	3	2	2	66	54	1,784181	2,218209	1,886209
<i>Lysimachia thyrsoflora</i>	3	0	1	0	822	0	2,44949		
<i>Lysimachia vulgaris</i>	1	0	1	0	97	0	2,44949		
<i>Maianthemum bifolium</i>	10	13	2	2	1498	2526	1,670253	1,974735	1,909263
<i>Melampyrum pratense</i>	3	7	3	5	17	349	1,362365	1,22424	1,833189
<i>Melampyrum sylvaticum</i>	6	1	4	1	65	67	1,052281	2,44949	1,778382
<i>Melica nutans</i>	1	0	1	0	20	0	2,44949		
<i>Menyanthes trifoliata</i>	19	6	3	2	16656	874	1,136542	2,44277	1,742192
<i>Molinia caerulea</i>	4	3	3	2	373	1214	1,749018	2,196172	2,420647
<i>Moneses uniflora</i>	2	0	1	0	6	0	2,44949		
<i>Orthilia secunda</i>	10	1	2	1	418	222	1,798666	2,44949	1,978788
<i>Oxalis acetosella</i>	3	8	1	2	1301	5961	2,44949	2,336814	2,734859
<i>Paris quadrifolia</i>	2	1	1	1	28	35	2,44949	2,44949	2,352733
<i>Parnassia palustris</i>	1	0	1	0	5	0	2,44949		
<i>Pedicularis palustris</i>	1	0	1	0	15	0	2,44949		
<i>Phegopteris connectilis</i>	1	2	1	1	135	90	2,44949	2,44949	2,390892
<i>Phragmites australis</i>	1	1	1	1	10	10	2,44949	2,44949	2,335497
<i>Picea abies</i>	15	26	3	6	464	2621	1,637405	1,030212	1,427442
<i>Pinguicula</i>	0	1	0	1	0	2	2,44949		

<i>vulgaris</i>									
<i>Pinus</i>	26	36	5	5	874	1778	0,866293	1,02466	1,065174
<i>sylvestris</i>									
<i>Poa</i>	0	1	0	1	0	4		2,44949	
<i>nemoralis</i>									
<i>Poa remota</i>	0	1	0	1	0	2		2,44949	
<i>Poa trivialis</i>	0	1	0	1	0	350		2,44949	
<i>Potentilla</i>	1	0	1	0	2	0	2,44949		
<i>erecta</i>									
<i>Potentilla</i>	9	6	3	3	1970	641	1,794111	1,546996	1,989504
<i>palustris</i>									
<i>Pyrola minor</i>	1	1	1	1	55	10	2,44949	2,44949	2,931163
<i>Pyrola</i>	1	1	1	1	55	29	2,44949	2,44949	2,466097
<i>rotundifolia</i>									
<i>Ranunculus</i>	1	0	1	0	150	0	2,44949		
<i>acris</i>									
<i>Ranunculus</i>	1	0	1	0	69	0	2,44949		
<i>repens</i>									
<i>Rhamnus</i>	3	0	1	0	58	0	2,44949		
<i>frangula</i>									
<i>Rhododendro</i>	14	17	4	6	5162	9901	1,828646	1,653688	1,723454
<i>n tomentosum</i>									
<i>Rhynchospora</i>	2	1	1	1	985	5	2,44949	2,44949	3,446951
<i>alba</i>									
<i>Rubus</i>	3	3	1	1	141	1749	2,44949	2,44949	3,192565
<i>arcticus</i>									
<i>Rubus</i>	35	34	6	6	15795	10332	0,812574	0,998214	0,879886
<i>chamaemorus</i>									
<i>Rubus idaeus</i>	0	2	0	1	0	516		2,44949	
<i>Rubus</i>	4	3	2	1	503	166	1,870612	2,44949	2,125145
<i>saxatilis</i>									
<i>Salix aurita</i>	1	2	1	2	880	495	2,44949	1,703774	2,288647
<i>Salix cinerea</i>	1	0	1	0	140	0	2,44949		
<i>Salix</i>	2	1	1	1	20	322	2,44949	2,44949	3,227829
<i>lapponica</i>									
<i>Salix</i>	5	5	3	2	277	1065	1,731207	1,619535	1,90534
<i>myrtilloides</i>									
<i>Salix</i>	2	0	2	0	25	0	1,992474		
<i>phylicifolia</i>									
<i>Scheuchzeria</i>	18	1	3	1	1808	12	1,129098	2,44949	1,830296
<i>palustris</i>									
<i>Scirpus</i>	0	0	0	0	0	0			
<i>sylvaticus</i>									
<i>Scutellaria</i>	1	0	1	0	4	0	2,44949		
<i>galericulata</i>									
<i>Selaginella</i>	0	1	0	1	0	4		2,44949	
<i>selaginoides</i>									
<i>Solidago</i>	3	3	1	1	45	34	2,44949	2,44949	2,362509
<i>virgaurea</i>									
<i>Sorbus</i>	9	14	2	2	330	309	1,823951	1,560982	1,62315
<i>aucuparia</i>									
<i>Stellaria</i>	0	1	0	1	0	17		2,44949	
<i>longifolia</i>									
<i>Stellaria</i>	0	1	0	1	0	4		2,44949	
<i>palustris</i>									
<i>Trichophorum</i>	2	0	2	0	9	0	1,577894		
<i>alpinum</i>									
<i>Trichophorum</i>	8	8	3	3	883	8025	1,538819	1,634976	2,16543

<i>cespitosum</i>									
<i>Trientalis europaea</i>	14	15	3	5	654	675	1,53509	2,105181	1,778334
<i>Vaccinium microcarpum</i>	20	18	4	5	1044	755	1,776584	1,571672	1,67909
<i>Vaccinium myrtillus</i>	20	32	3	6	18235	21870	1,81011	1,862739	1,765948
<i>Vaccinium oxycoccos</i>	42	39	5	6	11186	6444	1,045696	0,808793	1,015773
<i>Vaccinium uliginosum</i>	25	32	6	6	4653	16620	1,524284	1,07518	1,353746
<i>Vaccinium vitis-idaea</i>	23	33	4	5	6931	16214	1,568951	1,035412	1,236667
<i>Valeriana sambucifolia</i>	1	1	1	1	22	355	2,44949	2,44949	3,249816
<i>Viola epipsila</i>	2	1	1	1	327	380	2,44949	2,44949	2,343358
<i>Viola palustris</i>	4	0	2	0	367	0	2,010582		
